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ADVANCES IN AGRONOMY

VOLUME IV

ADVANCES IN

AGRONOMY

Prepared under the Auspices of the
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VOLUME IV

Edited by A. G. NORMAN
University of Michigan, Ann Arbor, Michigan

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Preface

Although the duties of an editor often call for him to take decisions that may seem to be arbitrary, most editors are susceptible to criticism, and are not beyond reading the reviews of their publication that may appear in other journals. This editor is no exception. The reviewers have in general been generous; some indeed have provided usable ideas. One recent review, however, included the statement that this series, "like most other review journals . . . tends to sit uneasily on the edge of two stools." The reviewer went on to explain that one type of review consists of a complete and fully documented account of a specialized topic. The other type, the function and appeal of which are quite different, "are really essays on the present state of knowledge on a particular subject," and "are of the greatest interest to the non-specialist."

The only exception that might be taken to these comments is the use of the adverb "uneasily," and the limitation of the number of stools to two. Agronomists have diverse interests, they sit on many stools, and some face in different directions. It is the policy of this series to include various types of articles of a review or progress report nature, the test for inclusion being whether they are likely to be of interest and assistance to a substantial group of the profession. Some papers may go beyond what is normally considered agronomy; indeed two such are to be found in this volume. Some will be more "specialized" than others, but it must be recognized that the definition of what constitutes a specialized article may well depend on the personal interests of the reader. The editor's position in this matter, therefore, is not uneasy but deliberate.

In this, Volume IV, the paper by Professor Trumble is in continuation of the policy announced in Volume III, to include from time to time reviews of agronomic developments and trends in particular countries or areas. Trumble's article contrives at the same time to bring out the principles upon which the improvement of Australian pastures has been based, and is, therefore, more than a narrative essay. Similar papers will appear in later volumes.

Once again the editor feels it incumbent on him to acknowledge the counsel and assistance received from the Advisory Board, and to point out that it is only through the ready support and co-operation of contributors that these volumes are possible.

A. G. NORMAN

Ann Arbor, Michigan,
September, 1952.

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Grassland Agronomy in Australia

H. C. TRUMBLE

Waite Agricultural Research Institute, University of Adelaide, South Australia

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I. Introduction

1. *The Environment*

a. Geographical Features. The continent of Australia occupies an area of three million square miles within the latitudes of 10° and 44°S. It thus approximates the United States in size, but a major portion is located between 15° and 35° connoting an extremely high degree of aridity. Conditions of climate comparable to those of the central portion are found in northern Mexico, the North Africa Sahara, Saudi-Arabia, southern Persia, Pakistan, and northwestern India. Australia may be classed as 40 per cent arid, 32 per cent semi-arid, 15 per cent temperate, and 13 per cent subtropical to tropical. New Guinea, which slightly exceeds in area one-tenth of Australia, lies between the equator and 11°S; it is characterized by conditions that are essentially tropical.

Hills (1949) describes the land surface as largely of low or moderate relief. The highest mountain is 7328 ft.; only a few peaks exceed 5000 ft., and most of the country is characterized by low altitude plateau or plain. Highlands occur along the eastern margin from Tasmania to northern Queensland. Erosion, associated with dissection by intermittent streams, has etched a variety of rocks from all geological ages. The highlands owe their form to warping and block faulting, while differential elevation of peneplain has produced a variety of plateaux. The residual ridges and mountains are frequently of hard rock masses. Tertiary earth movements have yielded volcanic extrusions in eastern Australia, while soft strata, frequently of limestone, are common near the southern coastline. Extensive artesian basins hold underground water that has assured livestock industries under conditions of low and infrequent rainfall. Sandplains and lateritic cappings frequently occur in the south and west. Schists, gneisses, and granites are common in the ranges. Streams flow toward the center at frequent intervals, ending in large salt "lakes" such as Lake Eyre, which is approximately 40 ft. below sea level, but is almost invariably dry.

b. Factors of Climate and Soil. Sporadic rainfall and frequency of drought naturally characterize a broad land mass of low topography located in an arid belt of high atmospheric pressures. Monsoonal rains

occur in northern Australia during the summer months, and Antarctic low pressure systems produce rain over much of the south in the winter season. The elevated eastern portion tends to receive all the year-round rainfall, because overlapping of the summer and winter low pressure systems is augmented by moisture-laden air from the Pacific, which brings some rain at all seasons. Precipitation is thus of four major types: (a) summer rainfall of the coastal north, (b) winter rainfall of the coastal south, (c) all the year rainfall with some snow of the coastal east, including most of Tasmania, (d) occasional sporadic rainfall of the inland. Leeper (1949) emphasizes (a) the arid center, (b) extensive areas with moisture available for one to five successive months, (c) a restricted neocoastal region with moisture available for five to nine months, and (d) elevated land that is moist for more than nine months of an average year. As the rainfall increases above 20 in., on a third of the continent, both dependability and the length of the wet period increase.

Maximum temperatures frequently exceed 100°F. in the summer months, especially toward the center. Apart from northern and eastern Australia, hot conditions are usually accompanied by low relative humidity. Snow is rare except in the southeastern highlands. Minimum temperatures of 32°F. or slightly less occur in the winter months of June to August, but autumn and spring frosts are generally confined to land above 1000-ft. elevation, which is also liable to occasional summer frosts. Growth is entirely inhibited by low temperatures over the three winter months on only a restricted area.

The soils are mostly associated with aridity, or leaching where seasonal rainfall is heavy. Low geochemical content of the original rocks is reflected in a limited nutrient status; shallow profiles follow incomplete weathering where rainfall is infrequent. Organic matter and available nitrogen content are only rarely high.

c. Native Vegetation. The vegetation is dominated by arid influences, but soil deficiencies also govern the types of flora that have evolved. Rainfall increases from the arid center toward the east, north, and northwest, southeast, and southwest. Most of the western coast, like the center, is arid; practically the entire east coast on the other hand is humid. As the rainfall improves, desert gives away to scrub in the south and grassland in the north, with woodland and forest occupying the wettest regions. The formations are classified by Wood (1949) into sclerophyllous grassland and desert steppe, sclerophyllous grass steppe, shrub steppe, and various types of scrub; savannah, mallee scrub, savannah woodland, and mallee heath; monsoon forest and dry sclerophyll

forest; rain forest, wet sclerophyll forest, alpine woodland, and high moor.

The indigenous pastures have been described by Christian and Donald (1949) and their location at the same time mapped. Most native perennial grasses form small tussocks, characteristically separated by bare soil; rhizomatous species are rare. The most common families in the south are Aveneae (*Danthonia*), Agrostideae (*Stipa, Sporobolus, Agrostis*), Festuceae (*Eragrostis*). Native pastures of the north are, on the other hand, characterized by Andropogoneae (*Bothriochloa, Dicanthium, Heteropogon, Chrysopogon, Iseilema, Themeda*), Paniceae (*Panicum, Brachiaria*), Chlorideae (*Chloris*), Hordeae (*Astrebla*). Chenopodiaceae (*Atriplex, Kochia, Bassia*) are dominant in shrub steppe. Legumes, apart from *Acacia* species which occur as trees, are rare to absent in Australian native pastures. There are no native clovers or clover-like plants apart from *Trigonella suavissima,* which may occur on flooded country.

Some early comments of famous botanists and explorers are of interest. On the light coastal soils Sir Joseph Banks found the grass "tall enough but thin set," with trees far apart. Captain Cook described the woods as interspersed "with some of the finest meadows in the world." Darwin noted a thin brown pasture "which appears wretched but excellent for sheep grazing." Early settlers were often misled by transient "bright green grass" which on much country soon changed to a thin dry stubble. In northern Australia the grass was "tall and rank."

2. Historical Aspects of Settlement

a. Coastal Pockets. Settlement proceeded largely from pockets of natural fertility located at intervals along the eastern and southern coast. Here rivers with their adjoining flats of alluvium ensured the successful early settlement of an otherwise inhospitable country. Crops and herbage plants from western Europe, together with sheep, cattle, and horses, were able to multiply within such favored areas, but the coastal soils were of low productivity on the whole; the extension of settlement farther inland emphasized problems of decreased moisture as regions of moderate to good fertility were discovered. At first a major problem was to gain self-sufficiency in food; but the entry of Australia into the world wool market about 1820 focused attention on the improvement of merino sheep. Vast areas of native pasture invited wool production for which the climate was also suitable; and the capacity of wool to be transported and stored over long periods without deterioration in the absence of refrigeration enabled a rising world demand for wool to be met. Attractive returns from wool between 1820 and 1850

resulted in a flow of capital for development; the discovery of gold in 1851, however, stimulated migration most. A certain mental vigor leading to resourcefulness arose from the migration, largely but not exclusively from Britain, of fairly hardy and adventurous settlers whose survival depended upon a degree of inventiveness.

b. Use of Indigenous Pastures. A wide range of grasses and edible shrubs provided a natural basis for a livestock industry. Ruminant grazing began in 1788; stock numbers expanded most rapidly between 1850 and 1890. Totals of 106 million sheep and 12 million cattle were attained in 1891 and 1894 respectively. After 1940, sheep exceeded 120 million for a time, falling to 96 million, 1946-47, and rising again to 113 million in 1950. Cattle have exceeded 13 million since before 1940, rising to above 14 million in 1949-50. In general about eight times as many sheep as cattle have been maintained, and the totals thus provide comparable grazing equivalents. For a start livestock were supported by native pastures in the form of the tufted perennial grasses associated with woodland savannah, grass plains of the "prairie" type, and low edible shrubs. Davidson (1938) showed that the growth of the sheep population in South Australia followed the Verhulst-Pearl logistic curve, indicating that the animal population that the native pastures could carry was determined by their reserves of food and the regrowth of the plants eaten. The livestock in Australia exceeded this value toward the end of the nineteenth century, and the carrying capacity of pastures throughout Australia subsequently declined greatly.

Settlement by pastoralists had been opportunist and exploitative, frequently leading to denudation through overstocking. The first quarter of the present century brought a realization of the consequences; but constructive pasture improvement has only become a factor of national importance within the past two or three decades. Over much of northern Australia, livestock are still supported by native grasslands; but the pastures of southern and eastern Australia are tending largely to become replaced by introduced species. The native grasses evolved under conditions of low or moderate soil fertility, periodic drought, and occasional light browsing by marsupials, whose numbers were restricted and whose migrations were favored by rarity of permanent waters. Under this treatment, tall, poorly branched grasses and bushes flourished. The introduction of ruminants and permanent fences imposed a type of close, persistent grazing to which native herbage plants had not previously been subjected. They tended to disappear as a result of close persistent grazing and the competition of more aggressive herbage species from Europe, Africa, and western Asia; their replacement by more productive pastures has been hastened by modern trends of development.

Marked seasonal incidence of growth is a common feature of both native and improved pastures, and this is especially evident in regions with a conspicuous winter or summer incidence of the rainfall.

c. The Impact of Drought. Wheat growing, dairying, and meat production all expanded actively from 1880 to 1930. Wool production reached a peak about 1893, when virtual saturation of the natural pastoral resources with livestock occurred in southern Australia. Factors of drought incidence and natural soil fertility governed the distribution and form of production which developed; thus dairying grew in close proximity to the eastern and southeastern coasts where available moisture for most of the year coincided with limited areas of fertile soil; wheat growing was practiced more and more beyond the coastal ranges on naturally fertile soils with a high incidence of seasonal drought. The use of bare fallow added to the supply of available soil moisture and led to specialized cropping; but livestock have become increasingly associated with wheat production. Wool growing has extended into regions receiving as little as 7 in. of mean annual rainfall in the southern portion of the continent, where high temperatures are only infrequently accompanied by high atmospheric humidities; beef production on the other hand is a feature of the northern region, where tropical conditions of sporadic rainfall and the capacity of cattle to range over long distances have favored this form of industry.

Frequency of drought has been one objective of recent work in agricultural climatology. A drought period is defined as one in which the moisture content of the surface soil (0-4 in.) does not exceed the wilting point. The relationship of monthly rainfall to free water surface evaporation from a standard 36-in. tank with guard ring has been employed by Trumble (1937, 1945, 1948) to determine drought incidence and its frequency.

d. Factors of Transport. The production of food and other materials required for the support of a relatively small local population did not figure so prominently as wool production in the general development of the Australian economy. Although climate, soils, and indigenous pastures determined this in large measure, no other commodity for which the environment was appropriate could have lent itself to particular conditions of transport and export demand as they concerned Australia and western Europe. The high value of wool per unit of weight, or compressed volume, and its durability and keeping qualities under all kinds of conditions rendered it appropriate for long-term storage and transport over considerable distances. The export of meat and dairy products only became a possibility with the development of refrigeration. Within Australia, meat is frequently transported long distances on the

hoof and this, of course, prejudices the quality of the beasts finally brought to slaughter. To a lesser extent, living animals are transported by rail. High quality beef is produced on improved and sometimes irrigated pastures close to the cities. The export of beef, mutton, lamb, and dairy products is closely limited by availability of refrigerated shipping space. A growing population in Australia and an increasing emphasis on high quality home-grown foods is likely to stimulate the production of meat and dairy products in contrast to wool in the future.

3. Early Constructive Improvement

a. Livestock. The pattern of livestock distribution in Australia was described and illustrated by Kelley (1949). Although all progenitors of the present day animals were imported, there was little, if any, planning. Food for the new settlements was first supplied from overseas, and the urgency of local food needs tended to discourage discriminate selection. Private agencies were largely responsible for livestock improvement through local selection and cross-breeding. Merino sheep were brought from Spain to South Africa and then to Australia in 1797. A decade later, a single bale of wool was carried to London from their descendants. It was not until fifty years later that the strains of sheep which now produce the bulk of Australia's mediumfine wool clip originated. The finest quality wool has resulted from rigorous selection of the early merinos as maintained in the regions of New England and Canberra-Yass in New South Wales, the western district of Victoria, and in Tasmania. Toward the center and in the drier districts of Australia the wool tends to be stronger or coarser in character but of higher production per sheep. British breeds of sheep, used for meat production, and cattle of both beef and dairy types have been frequently imported from England to augment local studs. Far more attention was devoted to livestock improvement than to pasture improvement in Australia until about twenty years ago.

b. Plant Introduction. The introduction and naturalization of improved herbage species has been reviewed by Davies (1951). Numerous species that are now important were introduced intentionally or accidentally before the turn of the century, but their use was restricted by absence of strain selection, and lack of knowledge concerning their ecological requirements or the role of soil improvement through the use of artificial fertilizers. Among the earliest introductions were herbage plants commonly used in western Europe, including perennial ryegrass (*Lolium perenne*) and Italian ryegrass (*L. multiflorum*), cocksfoot or orchard grass (*Dactylis glomerata*), white clover (*Trifolium repens*), red clover (*T. pratense*) and lucerne or alfalfa (*Medicago sativa*).

Lucerne was favorably reported upon in 1806 and had become the most extensively grown forage crop by the end of the nineteenth century (Fig. 1).

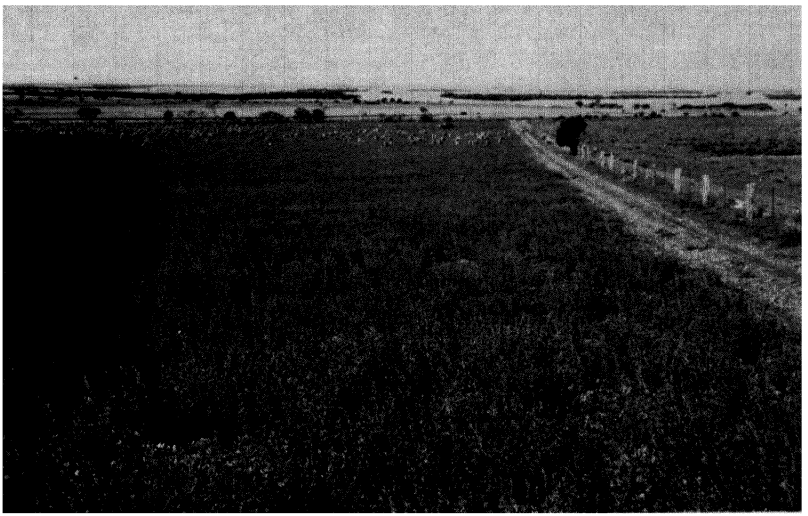


FIG. 1. Lucerne at 1½ lb. per acre established with a cover crop of wheat on fallow. Annual rainfall=13 in.; South Australian Mallee.

Paspalum or Dallas grass (*Paspalum dilatatum*) was introduced from South America by von Mueller in 1881 and became valuable as a constituent of pastures used for dairying, especially on the northeast coast of New South Wales. Prairie or rescue grass (*Bromus unioloides*) also proved an important pioneer species in eastern Australia. *Phalaris tuberosa,* introduced into Queensland from New York where it had been obtained from Italy about 1884, was distributed by Harding, investigated in detail later by Trumble (1933), and has now become one of the important grasses of southern and eastern Australia (Fig. 2). Rhodes grass (*Chloris Gayana*) and Kikuyu grass (*Pennisetum clandestinum*) have also become widely used in Australia following their deliberate introduction, Rhodes grass by Browne, a New South Wales grazier, about the turn of the century from South Africa, and Kikuyu by Breakwell (1923) from the Belgian Congo in 1919. Perennial veldt grass (*Ehrharta calycina*) has been investigated by Rossiter (1947a); it apparently developed in Western Australia before 1900, from incognizant introduction.

Subterranean clover (*Trifolium subterraneum*) is the most important

economic plant of Australia. It occurs in several outstanding agronomic forms, but there is no record of how any of these entered or developed from insignificant weeds in southern and western Europe to the status of first class herbage legumes, now actively commercialized in Australia and exported to several other countries. Hill (1936) has described the dis-



FIG. 2. *Phalaris tuberosa* with subterranean clover. Annual rainfall=24 in., Waite Institute.

covery and eventual advocacy of the original Mt. Barker strain by Howard. Various species of *Medicago,* including barrel medic (*M. tribuloides*), have also arisen from accidental and unintentional introduction, and this applies similarly to cluster clover (*Trifolium glomeratum*) and woolly clover (*Trifolium tomentosum*). Strawberry clover (*T. fragiferum*) is a perennial herbage legume of increasing importance; some strains of this species have developed naturally, but the Palestine variety was introduced.

Modern pasture improvement in Australia is based upon the use of introduced and selected herbage plants, and the most important of these are legumes which have entered Australia by accident, many years before their discovery and subsequent economic use.

c. Phosphate Application. The significance of herbage legumes was

little recognized until soluble phosphate came to be employed on land where they had become established. The use of superphosphate in conjunction with wheat growing first emphasized the widespread need of Australian soils for available phosphate. Experiments in South Australia toward the end of the nineteenth century demonstrated its value for wheat production, and the cultivated area treated with phosphate expanded rapidly. The spontaneous development of naturalized legumes in the stubbles of the wheat crops increased livestock maintenance and soil productivity, thus emphasizing the long-term value of superphosphate in the minds of Australian farmers. Tests of phosphate on grassland were conducted in South Australia and Victoria from 1902 to 1907, but it was not until the end of World War I in 1918 that interest in pasture improvement led to an active expansion in the use of superphosphate for this purpose. The combination of superphosphate and subterranean clover has rendered unproductive soil highly productive. Land that formerly carried a sheep to two acres can now support three or four sheep per acre. Commercial clover seed production has yielded high financial returns. The nitrogen enrichment of soils, formerly considered worthless, by the use of clover species has led to the successful establishment and maintenance of associated permanent grasses.

1. Technical Reconnaissance

a. Botanical. The work of early botanists laid a foundation for the subsequent development of agrostology and grassland agronomy. Inquiries by E. Breakwell in New South Wales provided a landmark of increasing interest in pasture improvement throughout Australia. Breakwell's "Grasses and Fodder Plants of New South Wales" (1923) brought together information derived from the experiences and observations of farmers and pastoralists, augmenting that arising from official tests. Breakwell's work as Agrostologist of the New South Wales Department of Agriculture was a first attempt to lift from botanical treatises and the visual observations of farming practices a popular classification and inventory of the forage plants with which practical farmers came in contact.

b. Agricultural. Agricultural practice in many parts of Australia has built a fund of experience, supplemented at times by tests and demonstrations conducted by State Departments of Agriculture, which has led to a philosophy of grassland improvement based upon the observations of progressive farmers and technical advisers. Paramount among these, especially in South Australia, were the undoubted value of superphosphate, applied (a) to sowings of subterranean clover or lucerne and (b) to noncultivated land, the natural pastures of which

had become populated with volunteer clovers, including subterranean clover, which had been carried by livestock in wool, hides, or droppings. The term "topdressing" has become synonymous with improvement of available phosphate status through dressings of superphosphate averaging for the most part 20 lb. P_2O_5 per acre. This is contained in half a bag (93 lb.) of Australian superphosphate. Recent investigations indicate that the three nutrients, phosphorus, calcium, and sulfur, must be considered independently as constituents of superphosphate.

The seeding of subterranean clover, barrel medic, Wimmera ryegrass and lucerne with cover crops has become widespread, largely for economic reasons. The practice of sowing legumes has been favored by the tendency of sustained cereal cropping to reduce the nitrogen status of the soil. This lessens the competitive effects of the crop, and the available nitrogen supply has frequently become so low that only legumes can actively produce. The ultimate result is nitrogen enrichment, increase of grazing value, and improved yields of future crops.

The observations and interest of progressive farmers have done much to stimulate agronomic research in Australia, and increasing mechanization has widened the application of increasing scientific understanding as in other countries. The foundations for the researches in grassland agronomy of the past two decades were thus a synthesis of early botanical investigation, practical experience, and commercial encouragement. Scientific research, aided in many cases by stimulus from overseas, has now built substantially on this foundation.

II. The Approach to Modern Grassland Improvement

1. *Environmental Analysis*

a. Climatic Factors. The annual precipitation has served as the main index of moisture available for purposes of pasture development. In the south 12 in. is regarded as a minimum for lucerne and Wimmera ryegrass, 18 in. for early strains of subterranean clover and *Phalaris tuberosa,* 20 to 24 in. for later strains of subterranean clover, strawberry clover, and perennial ryegrass. In the north much higher rainfall is associated with the seeding of improved pastures. The seasonal incidence, reliability, and effectiveness of rains as governed by the rate of evaporation are all decisive factors, while the amount of runoff, which depends on slope, cover, and general penetrability of the surface soil, and the capacity of the soil profile to hold reserves of moisture need further to be considered.

Investigations by Prescott (1931, 1934) on soil formation, by David-

son (1934) concerning insect ecology, and by Trumble (1937) in grassland ecology have led to a better understanding of agricultural climatology in Australia generally. Wet and dry bulb temperatures enable both relative humidity and temperature to be determined. With these values, the saturation deficiency of the air can be read directly from appropriate tables, and the loss of water from a standard evaporimeter tank estimated with accuracy.

Studies of evaporation from soil indicated that the top 4 in. lost a fifth to one-half the moisture evaporated from a standardized water surface over the time between wetting by rain and drying to the wilting point. The ratio was highest at a low rate of water loss as in winter, and lowest when the rate of evaporation was high, as in summer. For the critical months at the commencement and termination of the effective rainfall season the evaporation from an exposed soil surface was one-third that from a standard evaporimeter, and this ratio has been employed by Trumble (1948) for assessing drought frequency. Prescott (1949) has employed the ratio $\frac{P}{E^m}$ as a climatic index of the leaching factor in soils, and different values of this ratio indicate varying degrees of soil moisture status.

Climatic data for a single season are appropriately treated on the basis of sequential calendar months to form a unit. Monthly rainfall, mean air temperature, relative humidity, and standard evaporation, together with the mean length of day for each month have been employed by Trumble (1949b, 1950a, b) to form integrated climatic patterns which give a useful picture of the climate over a particular year. The frequency of occurrence of particular quantitative forms to which the behavior of pastures, as shown by appropriate field experiments, may be related provides an inventory of climatic combinations which determine the capacity for grassland production from year to year.

b. Soil Factors. The investigations of Prescott (1944), Taylor (1949), Stephens (1949), and their colleagues, embracing surveys over more than twenty years, have revealed that Australian soils are extremely diverse in both genesis and morphology. Geochemical poverty accounts in part for a general lack of phosphate and certain trace elements, hence of available nitrogen; successive cycles of weathering associated with particular conditions of climate have, moreover, led to immobilization of some constituents. Much land is characterized by what Stephens (1949) has classed as "virtually fossil soils and their later derivatives." Podsolization and solonization of calcareous or siliceous material account for phosphate and trace element deficiency in some areas.

As conditions become less arid from the center toward the eastern coast, brown light soils, gray and brown heavy soils successively occur within the semi-arid belt. Red brown earths and black earths follow within the subhumid belt, and finally podsolized soils become fairly general in the humid coastal fringe. Skeletal soils occur extensively in northern Australia and to a lesser extent in the south. According to Taylor (1949) tablelands and ranges of low productivity, desert sandhills, loams, sandplains, and stony deserts account for 56.5 per cent; brown soils (light), gray and brown soils (heavy), solonized brown soils, and sandhills of the "mallee," and solonetz soils account for 21.0 per cent; red loams, red brown earths, terra rossas and black earths 8.3 per cent; and podsols, residual podsols, and lateritic sandplain 12.4 per cent of the total land area.

The major characteristic of Australian soils is their generally low order of natural fertility, to which the indigenous flora and fauna are well adapted. The P_2O_5 content of the podsolized and solonized soils ranges from less than 0.01 per cent to 0.10 per cent, the K_2O content from less than 0.01 per cent to 1.25 per cent, and the N content from 0.01 per cent to 0.25 per cent. Corresponding values for red brown earths range up to 0.10 per cent, 1.60 per cent, and 0.20 per cent for red loams to 0.40 per cent, 0.40 per cent, and 0.70 per cent and for black earths to 0.55 per cent, 0.70 per cent, and 0.50 per cent, respectively. Soluble salts, largely sodium chloride and sulfate, may exceed 0.2 per cent in the south through submergence in the Tertiary and the accession of cyclic salt in winds from the sea in Pleistocene and recent periods.

c. Biotic Factors. The Australian native grasses tended to be tall, sparsely branched, tussock, noncreeping, and incapable of active regrowth after ruminant grazing. They were, on the whole, drought and fire resistant, adapted to low or moderate soil fertility, and capable of active regeneration from seed under restricted competition. Under persistent grazing with sheep, perennial grasses and bushes became eliminated over extensive areas. Ratcliffe (1936) estimated that at least 80 per cent of the perennial bush in South Australia had been lost during pastoral occupation. *Danthonia* spp. have survived grazing by sheep better than other native grasses. With the sheep came *Erodium* spp., *Medicago* spp., *Bromus, Hordeum, Vulpia* and other gramineous species, the seeds of which readily adhere to wool. These plants have doubtless evolved under the influence of the sheep and accompanied it through western Asia and Mediterranean countries to the Americas, South Africa, Australia, and New Zealand. The introduced species have steadily replaced the native grasses as these have been eliminated, and there is now a trend toward technical synthesis of new pastures.

2. *The Contribution of Stapledon*

a. Grazing Influences. The publications of Stapledon and his colleagues became available from about 1921 onwards and these emphasized defoliation as an essential condition of pastures. It was pointed out that the mower or hand shears could be employed to simulate grazing and provide yields of herbage from swards, and this helped to eliminate the mistaken view then held in Australia that grass was a crop. There was more to pasture, however, than mere defoliation. The condition of grazing included trampling, selective choice, and the return of livestock droppings. The need of pastures to withstand close grazing was emphasized from the outset of the grassland investigations which began at the Waite Institute in 1925, and the pronounced changes induced in native pastures by ruminant grazing gave it added weight. In early experiments frequent mowing, cutting for hay, and grazing were employed to compare their effects on the same pasture. These tended to confirm the thesis of Stapledon (1927) that the grazing animal determined the sward. In practically all the Australian experiments grazing of an appropriate type has benefited pasture considerably, leading to improved composition and productivity. This has applied even to shrub pastures under an average annual rainfall of 7 to 8 in. Occasional mowing may also prove advantageous to pastures, in addition to increasing animal production.

b. Ecotypes. Stapledon (1928) further demonstrated that an endless variety of strains or ecotypes existed within each species of herbage plant. The thesis and its application followed logically from Vavilov's "Law of Homologous Series in Variation" and Turesson's original work with ecotypes. Stapledon's work on the ecotypes of cocksfoot was a classic investigation of strain analysis in a pasture grass according to ecological considerations. Frequently variants of a herbage species occurred as physiological products of environment. Continued growing for seed tended to isolate types with a high proportion of seed but of little value for permanent pasture. On the other hand, long-term persistent stocking tended to encourage low-growing, dense, leafy, and persistent forms. Thus suitable pasture types were frequently to be found in old grazings or where conditions made for a high degree of variability. Modern plant breeding has, of course, built a good deal further on these premises, giving particular attention to combining ability and hybrid vigor. Stapledon, however, succeeded in establishing one criterion at least which is still and always will be vital, namely, physiological adaptability as the result of long-term environmental selection from exceedingly heterogeneous material.

c. The Philosophy of the Whole. Again, Stapledon (1938) was an active proponent of integration in contradistinction to scientific specialization. He has spoken with gratitude of one "who seemed intuitively to understand the ways of nature and always saw the intricate pattern as one majestic whole." Stapledon, himself, spoke freely of the pasture complex and the animal complex, which are intimately linked by common integrating factors of causation. A knowledge of these has only become possible through the progress of modern ecological thought, which dates from about 1912. Clements, Tansley, and Cockayne were conspicuous among the early plant ecologists, but it was Stapledon who revealed in its true light the intimate and essential association of the pasture with the grazing animal.

Grazing is now regarded in Australia as an essential part of the environment of all pastures, which even in their simplest form must be regarded as associations. These are usually mixtures of plant forms, representing widely different families; and the forms may be distinct species or varieties of species. Competition between species and varieties is an essential feature, and associations become modified by changes in the pressure of specific environmental factors, which exercise differential effects on the individual plant forms and greatly influence the trend of competition. Finally, the evaluation of the pasture is best expressed in terms of its capacity for nutrition and the synthesis of animal products.

Grassland agronomy implies a consideration of pastures in their full environmental setting as well as restricted studies of the separated parts, the interrelations of which are frequently all important, and can assure the completeness of synthesis that characterizes nature. It is perhaps a little ironical that although Stapledon tended to distrust statistics, possibly because the tool rather than the prize at first occupied most attention, R. A. Fisher's "Analysis of Variance" has supplied the very means by which the interactions common to all processes of integration can be assessed with scientific precision.

d. The Personal Equation. Although methods of science are the foundation of modern agronomy and objectivity is necessary for a proper scientific attitude, it is impossible to disregard the personal equation in work on grassland improvement. Stapledon visited Australia and New Zealand in 1926, and the author was fortunate to be associated with him and his colleagues at Aberystwyth in 1928. The Welsh Plant Breeding Station was already coming to be recognized as a world center in grassland improvement, and the atmosphere of the Station then was dominated by Stapledon's personality. Visitors from overseas were escorted by Stapledon to trials established in different parts of the Welsh countryside. All who met him have received tremendous stimulus which

prompted new activities on their return to their own countries. J. G. Davies, who worked with Stapledon prior to 1928 joined the staff of the Waite Institute in that year and later became Australian Agrostologist. William Davies began work with E. Bruce Levy on herbage strain improvement in New Zealand the following year and subsequently visited Australia in 1931 to 1932. Davies (1933) reported on Australian grasslands as a result of this visit. Cardon, Aamodt, H. L. Ahlgren, Chapline, and others of the United States gave active support to the views developed at Aberystwyth, and a tremendous impetus was given to grassland investigation in America from about 1937 onward. The establishment of the Imperial (later Commonwealth) Bureau of Herbage Plants (later Pastures and Field Crops) at Aberystwyth was a factor of the greatest importance; the work of R. O. Whyte enabled grassland workers of the British Commonwealth and the United States to come closer together, and the results of their investigations to become readily accessible. The contacts that arose made for a camaraderie and a common language concerning grass that has characterized grassland agronomy throughout the world. Too much stress cannot be placed upon the personal factors involved, and Stapledon contributed toward this more than his extensive writings can possibly indicate. His ultimate achievements, shared in part by William Davies, included grassland survey, the plow-up policy, and the temporary ley. These, while applying primarily to the critical prewar and wartime condition of England, exercised an influence on thought and practice elsewhere.

3. The Technique of Pasture Investigation

a. The Attitude of Agronomy. The term agronomy was not employed in Australia until 1925, but it has now come to be generally adopted. Agrostology, employed earlier, connotes a more restricted application to grassland problems than agronomy, which covers a wider field of plant-soil relationships. A review was made by Trumble (1943) to define scope and attitude in Australian agronomy. The term was apparently derived from the Greek *agros*—field, *nomos*—management, which implies, in addition, principle, custom, or law on which the management of a field is based. *Nomós* indicates a pasture or district, and *agronomos* means an overseer of public lands. The term *nome* is an ancient one implying the direction, law, or management of an administrative unit.

Agronomy in Australia covers the relationships of field crops and pastures to climate, soil, and management. Emphasis is toward the plant as an integrated expression of environmental influences, and the

quantitative testing of ecological or physiological hypotheses by direct experiment gives the agronomist considerable scope. Practical problems, to which economic considerations are attached, are usually involved, but fundamental rather than *ad hoc* investigation is desirable. The agronomist seeks to establish new facts as well as to apply scientific knowledge to practical problems, and original creative thought is as important in agronomy as in other sciences. Agronomy is, however, broad in scope and may serve as a meeting place for more specialized sciences. Much of its ambit is coordinative. Although assisted by field observation and depending much upon constructive interpretation, it is required at all times to be accurately quantitative, and like any other branch of science is based on tested verifiable knowledge.

Agronomists may need to augment field investigations by researches in the laboratory or glasshouse; they learn not to generalize from the results of tests conducted under artificial conditions of environment, but to rely finally on the results of their own field experience. The agronomist, invariably appeals to the method of plot testing, and a feature of modern agronomy is the competent planning of replicated field experiments which are accurately executed and sensibly interpreted. A sound working knowledge of statistics and of ecological and physiological principles is indispensable in the successive stages of planning, analysis and interpretation. The scope of agronomy in Australia has been deliberately confined to the plant side, and it has not been extended to include work in soil science as it has in some other countries. Moreover, genetics and to some extent plant breeding, plant physiology, and some aspects of ecology and climatology have progressed in fields other than agronomy. Rather has the agronomist sought the cooperation of specialized workers in these specific fields, his major work being based on field observation and experiment, together with the integration of plant behavior with environmental changes. Most contributions have been in the field of grassland improvement, which presupposes a knowledge of climatic and soil factors based on survey and analysis, the building of suitable stocks of plant material, and the investigation of field responses by direct experiment, which may be supported by farm surveys.

b. Grassland Surveys. Ecological orientation and detailed scientific investigation of specific factors were stimulated at the Waite Institute from 1930 onward, and cooperation between the Australian Council for Scientific and Industrial Research (C.S.I.R.) and the University of Adelaide was actively fostered by Richardson (1930, 1932). Much of this work was directed to soil deficiencies and eventually led to active programs concerning the relation of phosphate and trace elements to grassland improvement. The research programs of C.S.I.R. (C.S.I.R.O. since

1949) were subsequently enlarged to cover a wide range of Australian problems, and the federal body has made increasingly important contributions to Australian grassland improvement, e.g., Riceman, Donald, and Piper (1938), Riceman, Donald and Evans (1940), Riceman and Anderson (1943), Anderson (1942, 1946, 1948), Riceman (1945, 1948a,b, 1949, 1950), Anderson and Spencer (1950), Anderson and Neal-Smith (1951), Davies (1951).

Detailed ecological surveys were not attempted until 1945 when a comprehensive survey was made by Tiver and Crocker (1951) of the pastures of lower southeastern South Australia, covering an area of 5800 square miles. The region has considerable potentialities for future grazing, and the survey, conducted over four years, resulted in the definition of the major pasture types and their relationsips to factors of climate, soil, and management. The Levy point quadrant technique, described by Levy and Madden (1933), was used throughout the survey after the reliability and objectivity of the technique was established by Crocker and Tiver (1948). Appropriate modification of Levy's original methods were made. The field was taken as the unit, or if the field was too large, a transect several chains in width was frequently selected. Where definable soil and treatment differences occurred within the one field, separate analyses were made of each. The past histories of all areas examined were obtained as accurately as possible, and because of the short developmental period, these were usually good. The changes resulting from treatment, on a series of defined soil types, were accurately assessed, and the survey provided a sound basis for future pasture improvement in the region.

c. Field Plot Trials. The field plot trial is the chief source of new information. Davies (1931) investigated the experimental error of the yield from small plots of natural pasture at Adelaide and found the optimum size of plot under the conditions examined to be 450 square links in area and 5 by 90 links in dimensions. The standard error of such a plot was 13.75 per cent of the mean yield. The unit of measurement in all trials by the Waite Institute has been one link = 7.92 in.; one square link = 0.00001 acre. A long narrow plot was more efficient in reducing the standard error on natural pastures than a square or nearly square plot of equal area. Investigations of sown pastures, in which border effects become more important, have been based largely on replicated nearly square plots of approximately 0.01 to 0.005 acre. These have been found satisfactory for experiments involving comparisons of species, strains, mixtures, or fertilizer treatments. Trumble and Donald (1938), in work concerning the development of seeded pasture on podsolized sand, employed plots 20 by 25 links (1/200 acre) with ten

treatments replicated ten times on the basis of a Latin square in the original design, resulting in standard error values from 3.74 per cent to 6.86 per cent over a period of three years of sampling. Sufficient replications in the first year enabled differential second and third year treatments to be imposed, which proved a considerable advantage.

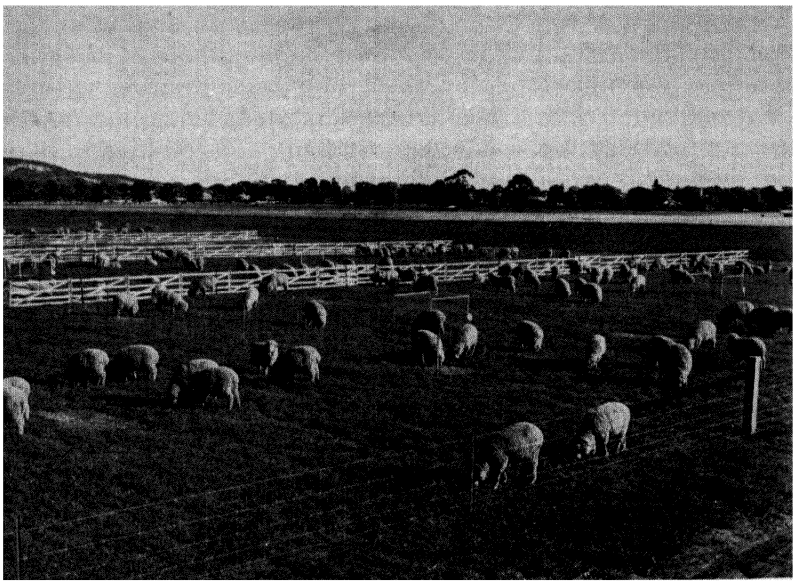


FIG. 3. View of productivity trial under grazing.

The determination of botanical composition, yield of herbage, its grazing value, and chemical composition were briefly reviewed for Australian conditions by Davies and Trumble (1934). Methods of sampling, botanical analysis, estimation, and the use of the camera are included in a general account of the methods adopted at the Waite Institute. Figure 3 shows a typical grazing experiment. Where major findings from small field plots have required substantiation under conditions of practical grazing, it has become necessary to employ a small number of treatments and plots varying in size from an acre to 160 acres according to carrying capacity. An absolute minimum of six sheep per treatment has characterized these trials. As a general rule a minimum of four replications has been employed, and the experiments have been kept as simple as possible; randomized blocks have become standard except in rare cases. Occasionally where extremely large areas or long transects

have been used, such replication has been found to be unnecessary, or impossible of practical adoption. The technique of pasture experimentation, including the determination of yield under grazing, as practiced in Australia, has been discussed by Donald (1941).

d. Pot Culture Trials. Investigations in pot cultures have been necessary to elucidate with precision factors which cannot be controlled under field conditions. Some critics pay little regard to results from pot cultures because of an artificial environment, but if conditions are standardized and related to parallel field experiments, such criticism is redundant. The advantages of pot culture methods include comparisons of different soils under standard conditions, the control of soil moisture, plant nutrient supply, and other soil factors. Examples of investigations regarding chemical composition are available in the work of Richardson, Trumble, and Shapter (1931, 1932), Trumble, Strong, and Shapter (1937), and Shapter (1935).

The need to explore soil fertility problems in a broad regional sense led to tests with extremely small pot cultures from 1942 onward. A high degree of freedom from contamination, together with the degree of control and applicability attained, enabled a useful picture of the probable widespread incidence of complex deficiencies to be secured fairly rapidly (Ferres and Trumble, 1943).

Pot cultures have proved especially useful in work with molybdenum (Anderson and Thomas, 1946; Anderson and Oertel, 1946; Trumble and Ferres, 1946). This element is difficult to investigate in field experiments owing to the readiness with which molybdates wash down a slope, or with which molybdenum trioxide is carried by moving air. Extremely small quantities of the order of 1/16 oz. to 1 oz. per acre are effective, and contamination of untreated plots readily occurs unless exceptional precautions are taken. The use of pot cultures eliminates this difficulty and has frequently provided precise evidence of deficiency in the field. The pot culture technique was used extensively by Richardson and Trumble (1928, 1937) to investigate the water requirements of herbage plants.

e. Herbage Strain Production. Until 1929, little attention was paid to the question of strain in herbage plants; the search for new species dominated enquiry. Variation in subterranean clover was first recorded by Adams, Carne, and Gardner (1927) in Western Australia. Following Stapledon's visit to Australia, the Dwalganup, Muresk, Mt. Barker, and Wenigup strains were grown at Aberystwyth in 1928. Tests of single plants begun at the Waite Institute in 1929 established the capacity of the two early-maturing strains, Dwalganup and Muresk, to mature seed and regenerate annually where the rainfall season was too short for the

later standard Mt. Barker commercial type to succeed. The Wenigup variety was later than Mt. Barker. Investigations by Harrison (1932) resulted in the discovery of many new varieties of subterranean clover in Victoria. All variants of this clover have occurred spontaneously and have proved to be fully homozygous; the flowers are cleistogamous and hence automatically self-fertilized. It is not known whether these strains have entered as separate introductions or have arisen as mutations in Australia, but the former hypothesis is more likely. Donald and Smith (1937) investigated their behavior under South Australian conditions. Bacchus Marsh subterranean clover from Victoria was shown by Smith (1942) to be well adapted to extensive areas of South Australia where the Mt. Barker strain did not succeed, and this strain has almost entirely replaced the earlier Dwalganup strain which was widely sown in the decade following 1930. Two other early-flowering types, Seaton and Clare, have occurred spontaneously in South Australia, but neither approaches the Bacchus Marsh strain in productivity. Barrel medic (*Medicago tribuloides*) was commercialized for soils above pH 7 after investigation by Trumble (1939b). Although much variation occurs, the Noarlunga type selected originally for commercialization, has remained superior to others. Palestine strawberry clover (*Trifolium fragiferum*), described by Donald and Trumble (1941) was introduced via southern Rhodesia by Trumble in 1929; it has proved superior to other strains in South Australia, especially for winter production (Fig. 4). Selection of the



FIG. 4. Variation in strawberry clover. From left, original commercial, Palestine, and two naturally occurring strains.

above strains for practical use has followed extensive field testing at a variety of centers, first as single plants, then in pure swards, and finally in mixtures. Among grasses, *Phalaris tuberosa* has been extensively investigated by Trumble (1933), Trumble and Cashmore (1934), Trumble (1935), and the Gb81 strain was produced at the Waite Institute by hybridization following progeny testing. This proved superior to other

types in density of sward formation, drought resistance, seed production, and recovery after close grazing. Most new seedings in South Australia have been made with this strain. Seed certification of important strains has come to be adopted by the State Departments of Agriculture, but there is still scope for improvement in the services made available.

III. Environmental Control

1. Climatic Attributes

a. Rainfall. The rainfall pattern of a particular region is readily gained from a study of monthly precipitation over periods approximating to fifty years, as recorded at a sufficient number of representative centers. The total amount for the year can be regarded as merely a provisional index. Herbage plants in most environments can maintain growth for a month or more on moisture available in the soil from previous rains, and the calendar month is an appropriate unit of time by which provisionally to assess the seasonal distribution of rainfall throughout a single year. Two-way tables based upon monthly values for long enough periods of years reveal after statistical examination the frequency with which rainfall in selected amounts for any month is likely to occur. Examination of the tables indicates the degree of frequency with which each month tends to be wet or dry; and treatment can be employed in a variety of ways to assess the seasonal incidence of the rainfall over the years. It is essential to consider the rainfall pattern in conjunction with the capacity for plant growth as controlled by temperature and light, and this leads to a consideration of integrated climatic patterns, as described in Sec. V,2a. An example of treatment, in terms of monthly rainfall, to provide a picture of the rainfall pattern of a country not previously investigated, is given by Trumble (1950b) in the Report of the FAO Mission for Nicaragua.

b. Evaporation. Monthly evaporation was employed in conjunction with monthly rainfall by Trumble (1937) to determine the effectiveness of rains falling at different times of the year, and the length of the effective rainfall season. It was found that provided a suitably standardized evaporimeter was utilized and maintained as a scientific instrument, evaporation from a free water surface was closely related to saturation deficiency, as derived from temperature and relative humidity, for any given month; moreover, the evaporation for each month varied little from year to year in comparison with rainfall which at Adelaide varied widely. Over an initial period of eleven years, 1925-1935, the percentage variability as indicated by the standard error was as follows:

	Annual	*Monthly*
Rainfall	2.8%	9.8–33.2%
Evaporation	1.9%	1.8– 5.5%

Days taken for an inch of water to be evaporated varied from 4.2 in midsummer to 16.8 in midwinter. In general, the time taken for this quantity of water to be lost by evaporation from bare soil was three to four times the above intervals.

Water is lost from a pasture mainly by transpiration, and so long as a cover of pasture is maintained, evaporation from the soil is reduced to a minimum. Values for standard free water surface evaporation have been used in Australia rather than potential evapo-transpiration because the latter combines two quite separate processes which are characterized by few compensatory effects. Soil evaporation and transpiration are both closely related to free water evaporation as a common controlling factor, but the first decreases with the cover, whereas the second increases with the amount of transpiring leaf surface. Both are affected, but in different ways, by management.

c. Drought Frequency. A drought year in Australia is one characterized by sufficient persistence of soil desiccation at critical periods of the year to preclude any possibility of normal or near normal production. In southern Australia, under conditions of winter rainfall, a drought year has been defined by Trumble (1948) as one in which the season of continuously effective rainfall is less than five calendar months.

The three winter months, June, July, and August, are characterized in the south by relatively low mean air temperatures (48°–53°F.) and short days (9½–11 hr.), which do not inhibit growth but restrict it decisively. Effective rainfall in April-May, May-September, or September-October, extends the period over which moisture is available to bring two relatively favorable months within this period, making possible sufficient growth to render supplementary feeding unnecessary. Provided the pastures are green for this minimum period, lambs can usually be raised and weaned prior to the drying of the feed. For wool or meat production the pasture is nutritionally effective when dry, so long as it is not deficient in protein and essential minerals.

Over the agricultural and pastoral areas of South Australia, the percentage drought frequency varies from nil to 95 per cent. The centers of highest rainfall, in which pasture development is progressing most actively, are associated with values of below 10 per cent. The most productive wheat-growing areas have values of 20 to 30 per cent, and seeded pastures are economically feasible to about the 30 per cent limit. Marginal wheat-growing areas show drought frequency values of 60 to 70

per cent. Tables have been prepared by Trumble (1948) for South Australia which indicate for 204 centers the mean effective rainfall season in months, the probability of effective rainfall for each month, the frequency of seasons characterized by drought, and the mean air temperatures for the coldest month. The tables show the drought risks associated with seeding in any month and the wet weather risks at times when harvests might be made.

d. Temperature. The mean monthly value in shade has been taken as the most convenient single measure of air temperature in Australia. Maps prepared by Leeper (1949) show that January isotherms range from 90°F. in the northwest, where the rainfall is lighter than elsewhere in the north, to 55°F. in the highlands of Tasmania; the July isotherms range from 75°F. along the northern coast to 45°F. in the Tasmanian and southeastern continental highlands.

Maximum temperatures above 100°F. are common in the summer and occur occasionally throughout the continent except in the southeastern highlands. Physical discomfort is frequently minimized by associated low vapor pressures. The mean wet bulb temperature exceeds 70°F. for six months only within the coastal strip north of the Tropic of Capricorn and for ten months at the extreme northern tips of the continent.

Winters are warm in the north, with mean July temperatures exceeding 60°F. above the Tropic; in the south they range from 45° to 50°F. over the elevated country and 50° to 55°F. at lower elevations, especially toward the southwest. Snow is recorded only above 2000 ft. and then for a short period of the year within limited areas. Minima of less than 32°F. occur mainly south of the 25°S parallel, in the period June-August. Earlier or later frosts are mostly confined to land above 1000 ft. in southeastern Australia. Frosts outside the winter months are rare in western Australia. The monthly temperature and moisture status at centers in the southern portion of the continent have been employed by Trumble (1939a) for agroclimatic classification.

Changes in atmospheric temperature influence both the rate of photosynthesis and the rate of respiration; moreover changes in soil temperature govern permeability and root respiration, both of which affect nutrient uptake. Prescott (1948) has shown that for pasture between the temperatures of 46° and 80°F. the yield may be expected to increase, in general conformity with the Van't Hoff law, 2.3 to 3.7 times for each rise of 18°F. in atmospheric temperature, provided soil moisture is not limiting. There has been little or no investigation in Australia to determine the differential effects of temperature on herbage plants in the

presence or absence of light as conducted in the United States by Went (1943) in studies of thermoperiodicity.

e. Duration of Light. The length of the daily photoperiod not only affects vegetative and reproductive development and hence survival, but also exercises nutritional effects upon herbage plants. At Adelaide (35°S), the mean daily photoperiod varies from 9.7 hours in June to 14.3 hours in December. Varieties of herbage plants from high latitudes of North America or northwestern Europe frequently fail to flower and set seed. Examples are particular samples of *Phalaris arundinacea, Avena elatior, Agropyron tenerum, Bromus inermis, Dactylis glomerata, Phleum pratense, Lolium perenne,* and cereals from northern European sources. On the other hand, ecotypes from southern Europe or the southern United States tend to behave normally. Grasses such as Kikuyu (*Pennisetum clandestinum*), from elevated equatorial habitats, produce flowers and form seed with readiness at Adelaide. Annuals which grow abundantly in southern Australia run to stem and seed rapidly with comparatively little vegetative growth in high latitudes of the Northern Hemisphere. The limits of yearly day length amplitude in Australia are 11.5 to 12.7 hours in the extreme north and 8.9 to 15.5 hours in the extreme south. Ferres (1949) has shown that the uptake of zinc by subterranean clover is substantially increased by lengthening the photoperiod from 10 to 12 hours at mean air temperatures of about 60°F. On the other hand, a similar effect is obtained with red clover by reducing the photoperiod from 14 to 12 hours. Owing to the simultaneous operation of changes in light duration, temperature, and moisture status, it is necessary to employ integrated climatic patterns, as described in Sec. V,2, in order to appreciate the combined effects of the climatic factors concerned on herbage production.

2. *Soils and Their Fertility*

a. Relation of Soils to Climate. The soils of Australia have been related to vegetation and climate by Prescott (1931), and it has been shown that leaching, the capillary movements of soil water, seasonal temperature effects, and wind have characterized soil formation in Australia. Crocker (1946) has related the major soil types of South Australia to Post-Miocene climatic and geological history. Over extensive areas, solonized, podsolized, terra rossa, and rendzina types of soils are considered to have been formed in the Pleistocene and recent ages, with consequent fossil morphology. The distribution within the profile of water-soluble salts, calcium and magnesium carbonates, oxide of iron, and manganese and clay determined in part the physical characteristics and nutritional properties of the soils as they now occur. The accession

of cyclic salt and the control of leaching by the intensity of the daily rainfall are also important factors. Mobility and availability of certain constituents are affected both by hydrogen-ion concentration and the oxidation-reduction potential. The use by Prescott (1931, 1949) of saturation deficiency and evaporation in conjunction with precipitation has facilitated understanding of the derivation and current properties of Australian soils.

b. pH, Nitrogen, and Organic Matter. Prescott (1931) established a marked general correlation between the hydrogen-ion concentration of the soil and the rainfall. Leaching effects are most marked where high rainfall is associated with a low rate of evaporation for specific periods of the year. The nitrogen content of the soil has also been shown to relate closely to the intensity of rainfall. The association of deficient parent material with leaching, surface runoff, and in some cases laterization under previous conditions of climate has established a condition of acute and widespread nitrogen deficiency over the greater portion of Australia which receives sufficient rainfall to ensure modern pasture development. This has emphasized the use of herbage legumes in conjunction with fertilizer dressings of available phosphate, together with trace element additions according to the soil type and its past history. The use of these combinations makes possible fairly rapid soil enrichment in both nitrogen and organic matter.

Some deficient soils are relatively high in organic matter derived from the native sclerophyll vegetation prior to development, but this material is high in lignin and low in nitrogen and the trace elements lacking in the soil to which the original vegetation was adapted. This organic matter has little if any nutritional value. On the other hand, breakdown products of lignin under conditions of deficiency may prove adverse to the point of toxicity so far as the rhizobia of herbage legumes is concerned. Leaching, or oxidation from repeated plowing, may eventually eliminate this factor. The type of legume grown is closely dependent upon pH. Subterranean clover is adapted to soils that are acid to neutral; annual species of *Medicago* on the other hand are adapted to soils that are neutral to highly alkaline.

c. Soil Fertility. The status of phosphorus is generally low. In the south neither crop production nor pasture improvement is undertaken without the application of superphosphate. Copper is extremely low in calcareous and siliceous sands and laterized soils on which the most widespread cases of deficiency occur. Many of these soils are also deficient in zinc. Solonized sands of high silica content are particularly low in phosphate, copper, and zinc. Molybdenum deficiency has been associ-

ated, for the most part, with a sloping topography and much older rocks or laterite high in total iron and aluminum.

It has been shown by Piper (1942, 1947) that extremely low concentrations of copper, zinc, and molybdenum will satisfy the needs of herbage plants provided these concentrations are maintained. Plants secure sufficient copper if the element remains available at 0.1 p.p.m., and concentrations as low as 0.001 p.p.m. are capable of increasing growth. Availability tends to rise with pH but this element is less susceptible to changes of pH than zinc and is much less susceptible than manganese or molybdenum. Zinc can also satisfy the needs of the plants at extremely low concentrations provided absorption is continuous and utilization by the plant effective. Availability decreases as the pH of the soil rises from 5.6 to 7.5. Molybdenum, on the other hand, becomes increasingly available as the pH rises. In the absence of applied molybdenum, Piper and Beckwith (1949) have shown an increase in molybdenum content from 0.2 p.p.m. at pH 4.8 to 6.5 p.p.m. at pH 8.3 in the dry material of *Medicago denticulata*. Where molybdates were applied, the concentration was 5 p.p.m. at pH 4.8 and 56 p.p.m. at pH 8.3. Symbiotic nitrogen fixation appears to be able to supply in full the nitrogen requirements of subterranean clover and associated grasses to the limits allowed by climate in South Australia provided the supply of available nutrients and their balance are satisfactory and restrictive influences are not limiting.

d. Soil Building under Pastures. The need to build soil fertility is apparent both on soils that are naturally unproductive and on cultivated lands that have rapidly declined in productivity and have reached a critically low level of nitrogen and organic matter. Cornish (1949) has shown by regression analysis, eliminating the effects of rainfall, that in spite of improved crop varieties and technical improvements in farming, yields of wheat over extensive areas have fallen substantially and are continuing downward. Fertility depletion has been inevitable under the methods of exploitative farming practiced in wheat-growing areas. More or less continuous cropping with cereals with occasional substitution by volunteer weeds or fallow has been characteristic. Frequent cultivation of the soil has broken down aggregates, destroying organic matter, rendering the soil liable to loss of structure and vulnerable to erosion. The investigations of recent years have shown that if appropriate legumes are utilized and soil deficiencies other than that of nitrogen are overcome, striking gains in available nitrogen can be secured under grazing, with economic derivation of livestock products during the soil-building process. The legumes of greatest value in southern Australia are subterranean clover, lucerne, annual *Medicago* species and field peas. As an

example, seeded pastures for ten years following cropping at the Waite Institute resulted in values of 58.85 p.p.m. of nitrate nitrogen following incubation compared with 5.75 p.p.m. on land that had continued under cropping for the same period (Woodroffe, 1949).

3. Factors of Management

a. Pasture Establishment. The farm machinery available in Australia, apart from importations, has been largely that designed for cereal production, and this limitation is further intensified by lack of research in agricultural engineering. Most inventions have been the products of individuals associated with farming. Active schools of agricultural engineering in conjunction with the university faculties of agricultural science, as fostered in the United States, are badly needed. In the meanwhile, Australia has persisted with comparatively minor modifications of standard wheat-growing machinery, and this has sometimes reduced the success of pasture establishment.

Subterranean clover and lucerne are usually seeded with a cereal cover crop which may be harvested for grain or hay or grazed *in situ*. Perennial grasses and legumes are, for the most part, sown on land either freshly cleared from scrub or established on fallow following a period of cropping. Extremely low seeds rates of the order of ½ to 3 lb. of each constituent have proved successful over a wide range of conditions. The mixtures most frequently employed consist of one to two legumes associated with one to two grasses. The "Majestic" stump-jump plow with 26 to 30 in. disks, which are pushed upward out of the soil against the tension of extremely strong springs when the disks meet an obstruction, has proved a vital factor in the development of poor scrublands in South Australia. Two plowings to a depth of 8 to 10 ins. are normally employed between the phases of burning and seeding. Land has been effectively seeded for pasture within two months of being under undisturbed scrub.

b. The Use of Fertilizers. Practically all phosphate has been added as superphosphate. From the inception of trace element application in South Australia, fertilizer companies have been prepared to mix manganese sulfate, which is used mainly for cereals, copper sulfate, zinc sulfate, and molybdenum trioxide with superphosphate at the factory. The quantities used have been based on amount per bag of superphosphate weighing 187 lb., ranging from 7 to 28 lb. manganese sulfate 3½ to 14 lb. copper sulfate, 3½ to 14 lb. zinc sulfate and 1 to 2 oz. molybdenum trioxide. Common quantities per acre in recent years have been 7 lb. copper sulfate, 7 lb. zinc sulfate, and 1 oz. of molybdenum trioxide (Fig. 5). The amount per acre of the trace element mixture has, on

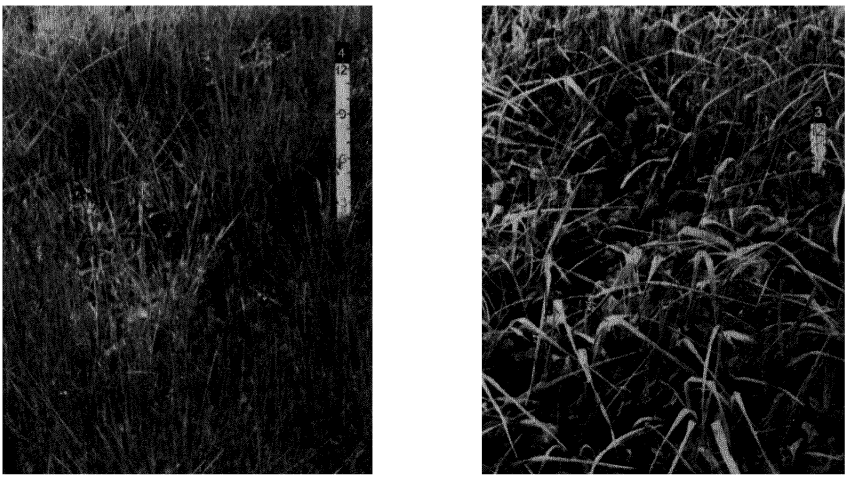


FIG. 5. Left, pasture on molybdenum-deficient soil. Right, top-dressed with molybdenum (Anderson, 1942).

the whole, varied from 1 to 2 cwt. per acre, for the initial seeding, followed by reduced rates after two or three years. Annual topdressings of superphosphate appear to be necessary, but for at least several years, one initial application of the trace elements is sufficient. Costs of applying the fertilizer are greatly reduced following the seeding year by the use of a broadcasting spinner, a South Australian invention, attached to and driven by a motor truck which also carries the fertilizer required. Some effects of superphosphate are now considered to be attributable in part to its content of sulfur (Anderson and Spencer 1950).

c. Intensity of Grazing. There has been a tendency to undergraze rather than overgraze freshly sown pastures. Experience indicates that provided establishment is vigorous, some grazing in the first year is an advantage, largely in controlling strongly competitive elements such as sown or volunteer annual grasses and quick-growing weeds that are eaten by livestock. Moreover, once the root system has penetrated sufficiently, and the seedling has tillered or branched, the young plant's reserves are sufficient for recovery; as defoliation reduces transpiration, loss of soil moisture is retarded, with subsequent advantages. If subterranean clover has been seeded with a cereal, stock may be withheld for some years, and the clover raked for seed, which at yields of 200 to 400 lb. per acre, has given high financial returns.

A livestock carrying capacity of at least 1½ sheep per acre, equivalent to a beast per 5 acres, is regarded as the minimum capacity of the pas-

ture to support livestock in order to render modern pasture improvement economically successful.

d. Frequency of Grazing. Investigations of irrigated pastures at Wood's Point on the Murray River in South Australia by Richardson and Gallus (1932) and Trumble and Davies (1934) resulted in the establishment of pastures capable of maintaining an average of fifteen sheep for fattening per acre per annum. This fell to six sheep for a short period in midwinter and rose to more than twenty sheep per acre in spring and early summer (Fig. 6). The carrying capacity of the best

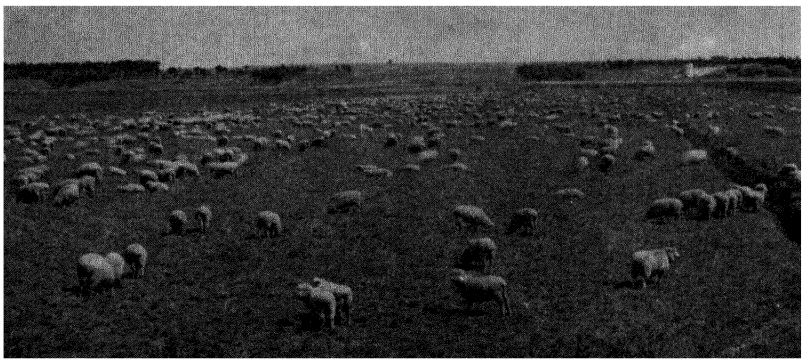


FIG. 6. Heavy stocking with sheep on irrigated pastures of perennial ryegrass, cocksfoot, and white clover.

pasturage could be assessed at two head of cattle fattening or 1½ milch cows per acre. The question of grazing management arose early and stock were rotated on a cycle of three weeks in accordance with the findings of Woodman (1928, 1929) in England that frequent defoliation resulted in extremely high concentrations of nutrients. This proved a disadvantage, neither the carrying capacity nor the condition of the stock proving as satisfactory as when the pasture was grazed at longer intervals of four to six weeks. Beruldsen and Morgan (1946) reached similar conclusions in Victoria. As the growth rate of the pasture is much higher in the spring and summer than in winter, it becomes necessary to develop methods whereby less drastic grazing can be applied during the periods of lowest production. One aim has been to graze at longer intervals in autumn and winter, with supplementary feeding, and to maintain later a higher rate of stocking on a reduced area, supplemented by the use of the mower; during the periods of most active growth. Roe and Allen (1945) found continuous grazing of a Mitchell

grass pasture as satisfactory as winter and summer rotation. Investigations by Davies (1946), Moore, Barrie, and Kipps (1946) at Canberra, and at the Waite Institute (1950), showed that rotational grazing in no case was advantageous, and that a commonsense system involving manipulation of livestock numbers supplemented by the use of the mower is preferable to a rigid rotational pattern. Under irrigation, of course, conformation to a schedule is usually necessary.

e. The Role of Fodder Conservation. Investigations at the Waite Institute (1950) conducted over the period 1940-45 showed that cutting sown pastures for hay yielded comparable or slightly higher yields of forage under continuous grazing than under rotational grazing. Live weight per head of sheep responded only slightly to feeding back, but the capacity of hay, representing surplus production from the pasture, to maintain additional livestock was considerable in some seasons, especially those characterized by drought. Over a succession of favorable years, cutting the surplus spring growth of pastures proved uneconomic, but the financial gains in one very unfavorable season more than outweighed the cumulative losses from the practice over the four previous seasons. The values of cutting and feeding back was greater in the case of sheep employed in part for meat production than in the case of merinos used entirely for wool production. The results of experiments on pasture management involving conservation of some pasture for hay can be summarized to indicate that the management of livestock on pastures should be along commonsense lines, without the imposition of rigidly set schedules, because the seasons cannot be predicted. The aim should be to maintain a sufficiently good cover but to prevent excess growth. The use of the mower is essential when production greatly exceeds consumption by livestock and to provide conserved fodder as insurance against the inevitable years of reduced productivity. The use of labor-saving machinery for fodder conservation is likely to prove of tremendous value in Australia as it has in the United States.

f. Management of Shrub Pastures. Shrub pastures dominated by *Atriplex, Kochia* spp., although greatly depleted by former exploitation, are still important sources of wool production in arid southern Australia. Investigations were commenced in 1940 by Woodroffe (1941, 1951) on pastures of bluebush (*Kochia sedifolia*) in the northwest of South Australia to examine the effects of differential stocking practices on such pastures (Fig. 7). The seasons over this period have yielded rather better than the long-term average of just under 8 in., and the effects of the various grazing treatments may be different in a cycle of unfavorable years. Nevertheless, it appears that pastures of this type actually benefit from grazing; the pruning effects lead to economies in

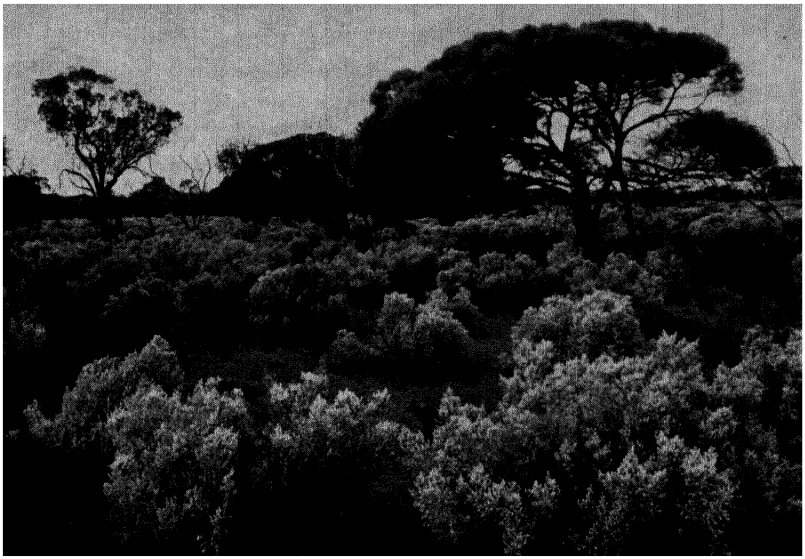


FIG. 7. Bluebush *(Kochia sedifolia)* with myall *(Acacia Sowdenii)* undamaged by heavy stocking. Annual rainfall=7.8 in.

water lost by transpiration. Particularly high rates of stocking, compared with recognized practical standards, have been imposed without deterioration under fairly close subdivision, and it seems evident that a major reason for past damage has been insufficient subdivision of the holdings and failure to provide sufficient watering points.

IV. Specific Lines of Agronomic Investigation

1. Water Requirements of Pastures

a. Available Water Supply and Its Uptake. The amounts of water received and lost by pastures have been considered on the basis of the time intervals over which moisture is available near the soil surface in conjunction with the capacity of the root zone to store available moisture. The pasture mixtures that have come to be developed tend to be based on legumes and grasses which are capable of exploiting both the surface horizons and the deeper layers of the subsoil. Deep-rooted herbage species such as lucerne and phalaris are valuable where long periods of surface soil desiccation occur, but moisture is still held in quantity at lower depths. The rate of movement of soil water is controlled by the size and continuity of the air spaces within the soil, the suction gradient,

and the viscosity of the water (Russell, 1950). The downward flow of water through sands is thus considerably more rapid than through loams and clays, although it is dependent on the structure of the latter. Deep sands have the advantage of being usually free from excess water; they are capable of storing available moisture at considerable depths and also retain minimal amounts at the wilting point. Moreover, there is no time in the rainfall season when mechanical operations of seeding are prevented by too wet a surface condition of the soil. Annual *Trifolium* and *Medicago* species exploit the soil to a relatively shallow depth and are thus dependent on continuity of available moisture near the surface while conditions of temperature and light are favorable.

b. Evaporation and Transpiration. The evaporation of water from bare soil depends upon the amount of water available at the surface and the evaporation rate from free water. The loss from saturated level soil is comparable with that from water but, as the surface dries, less water becomes available for evaporation—the surfaces of the particles hold less water and suction forces provide increasing resistance. Cover, whether it is of dead or growing material, impedes evaporation through shading and reduction of surface air movement.

Most workers on transpiration, for instance Briggs and Shantz (1913), Richardson (1923), Maximov (1929), Richardson and Trumble (1937), have found a close dependence of transpiration on atmospheric factors.

Briggs and Shantz obtained correlation coefficients of 0.82 to 0.89 between transpiration and solar radiation and 0.75 to 0.86 between transpiration, air temperature, and wet bulb depression. Richardson and Trumble obtained values of 0.91 to 0.95 for correlation between evaporation and the transpiration of saltbush, ryegrass, subterranean clover, and wheat. Wrenger (1934) found increases of from 12 per cent to 150 per cent of the transpiration rate in still air due to the influence of wind. Plants transpiring actively prior to treatment lost more initially but subsequently transpired less than in still air.

Annual determinations of the transpiration ratio * of ryegrass and subterranean clover at the Waite Institute have indicated wide shifts due to season. Values for ryegrass varied from 284 to 497 and for subterranean clover from 478 to 653. Differences in temperature and light during the period of active growth, combined with differences in atmospheric relative humidity, account for major seasonal fluctuations.

c. Transpiration Ratio According to Species. Rather more than two hundred determinations of the transpiration ratio of eighty-five

* Ratio of water transpired to dry weight of plant.

species were made at the Waite Institute over the period 1925-39. A standard variety of barley was employed in all tests for purposes of comparison.

The transpiration ratio of summer growing grasses, representing *Astrebla, Cynodon, Eragrostis, Iseilema, Panicum, Paspalum, Sorghum, Spinifex* and *Sporobolus,* ranged from 201 to 508 averaging 328 or two-thirds that of barley grown under comparable conditions. Winter annual grasses, including *Hordeum* and *Lolium,* together with *Erodium,* ranged from 203 to 629 with a mean of 379. Eight *Atriplex* species averaged 459. Annual species of *Medicago,* which grow actively in winter and mature early, gave values of 200 to 412 with an average of 282, but were 15 per cent higher than barley grown under comparable conditions. Perennial winter grasses, *Danthonia, Ehrharta, Oryzopsis,* and *Stipa,* ranged from 248 to 666 with an average of 480 and were higher than barley. The standard midseason strain of Mt. Barker subterranean clover grew with an average transpiration ratio of 493 and was 46 per cent to 50 per cent higher than barley under comparable conditions. Earlier-maturing strains of subterranean clover had water requirements comparable with those of annual *Medicago* species. Cultivated biennial and winter grasses, including *Dactylis, Holcus, Lolium,* and *Phalaris,* varied from 437 to 619 with a mean of 531 and were 56 per cent to 87 per cent higher than barley under the same conditions. Red, white, and strawberry clover varied from 500 to 601 with a mean of 566, and lucerne from 555 to 966 with a mean of 743, 40 per cent higher than barley.

Richardson and Trumble (1937) showed that the transpiration ratio of herbage plants tends to rise as the growth stage advances. Most herbage plants mature in southern Australia with increasing rates of evaporation, and transpiration tends to rise without corresponding increases in the rate of dry matter production. Symon (1950) found that transpiration per unit leaf area in barrel medic rose steadily as maturity advanced, becoming steep toward completion of growth. The relative growth rate declined throughout when the moisture content was maintained, becoming steady in the later stages when it was reduced.

Soil factors which reduce the relative growth rate will on the whole tend to enlarge the transpiration ratio. This applies to deficiencies of soil nutrients and in particular to nitrogen; it applies also to unfavorable structure or tilth restricting soil aeration. Reduction of soil moisture on the other hand, by lowering the transpiration rate to a greater extent than the relative growth rate, invariably reduces the transpiration ratio.

d. The Influence of Defoliation. Defoliation, as in grazing, reduces transpiration either in proportion to the reduction of total dry matter

or to a greater degree. The yield of ryegrass was reduced 83 per cent, transpiration 89 per cent, and the transpiration ratio 33 per cent, without loss of protein in experiments by Richardson and Trumble (1937) (Fig. 8). Similarly, the protein production of phalaris was trebled and the amount of water transpired reduced 60 per cent as a result of appro-

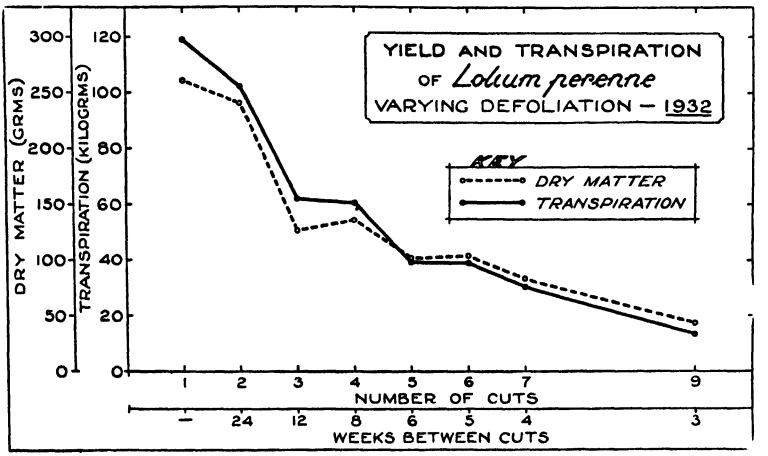


FIG. 8. Reduction of yield and transpiration of perennial ryegrass *(Lolium perenne)* with increasing frequency of defoliation.

priate defoliation. The control of pastures by grazing or cutting can restrict considerably the amount of water lost by transpiration. The root system tends to be reduced by defoliation; cutting phalaris at five-week intervals reduced the weight of the roots to one-fifth of that not defoliated. The quantity of nutrients available to livestock tends greatly to be increased by defoliation; maximum quantities of nitrogen were gained under ten-week defoliation in the case of phalaris and five-week defoliation in the case of ryegrass. Nitrogen absorbed per liter of water transpired by phalaris rose from 62 mg. in grass cut once to 468 mg. in grass cut five times at five-week intervals. Nitrogen absorbed by ryegrass rose from 154 mg. per liter in one cut to 1383 mg. per liter in nine cuts at three-week intervals. The amount of nitrogen gained by the herbage per unit of water lost by transpiration was thus seven and a half times in phalaris and nine times in ryegrass (Fig. 9) that of a single cut, as a result of the above frequencies of defoliation.

The effect of cutting on the economy of water usage depends on the capacity of the plant to produce new herbage soon after defoliation, and on the succeeding evaporation rate. In twelve comparisons with ryegrass

and phalaris, increased defoliation in no case increased the transpiration ratio significantly. This value either remained unaltered or was reduced 9 per cent to 32 per cent, and in all cases the percentage of nitrogen was, moreover, increased. Pastures heavily defoliated in the spring months at Adelaide have invariably responded more actively than those un-

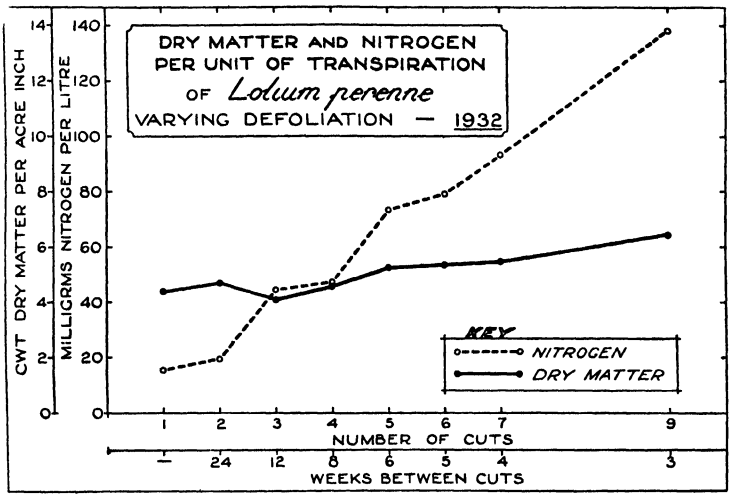


FIG. 9. Increase of nitrogen yielded per unit of water transpired by *Lolium perenne* with increasing defoliation.

grazed or little defoliated. In such cases, the total yield of pasture for the year has been greater and the quantity of protein gained considerably more than where the pastures had received little or no grazing up to the period of most active growth. The influence of defoliation is closely dependent on the nitrogen available for renewed growth of the pasture as this governs the subsequent growth rate. The effect of nitrogen on reducing the transpiration ratio has been shown by Ballard (1933) to be purely an effect on growth, the transpiration rate itself being unaffected.

e. Reduction of Soil Moisture Content. Persistent reduction of the soil moisture content to the wilting point has lowered the transpiration ratio of all herbage species tested on a variety of soil types by from 15 per cent to 44 per cent. Although restriction of the water supply tends invariably to lessen growth, the rate of transpiration is lowered further. Increased osmotic pressure probably accounts in part for this. Reduction of the soil moisture content increases the concentration of soluble salts in the plant and may also raise the content of pentosan colloids

of high hydration capacity as shown by Wood (1934). Reduced soil moisture content under conditions of fairly low evaporation have resulted in extremely low values for the transpiration ratio. The following are examples: *Atriplex semibaccata* 164, *A. vesicaria* 174, *Medicago tribuloides* 176, *Ehrharta calycina* 180, *Trifolium subterraneum* 255. Examination of the moisture content at successive depths of the profile throughout the root zone by Cashmore (1934) has shown that perennial ryegrass reduces the soil moisture content to the wilting point to a depth of 42 in., after effective winter rains have ceased. Phalaris, with a much deeper root system, was found to reduce soil moisture to the wilting point to a depth of 78 in. Phalaris and lucerne may eventually exhaust the soil water available within the root zone, but are able to endure wilting for considerable periods. The relative rates of transpiration and production in the field conform to those indicated by determinations under open glasshouse conditions, provided significant differences in temperature and the evaporation rate are taken into consideration.

f. Yield in Terms of Available Moisture. Determinations under glasshouse and field conditions of water usage at the Waite Institute have indicated that the range of production per acre inch of water transpired by a pasture is from 2 to 12 cwt. Lucerne and irrigated pasture under South Australian conditions are likely to produce from 2½ to 4 cwt. dry matter per acre inch of water transpired. Richardson (1923) obtained 2.75 to 2.88 cwt. dry lucerne per acre inch of water under field conditions in Victoria; the mean transpiration ratio of lucerne under glasshouse conditions at Adelaide indicates 2.73 cwt. Seeded pasture and natural pasture grown under conditions comparable to those of the Waite Institute are likely to average 4 to 5 cwt. per acre inch transpired. Oats may produce slightly more, approaching 6 cwt. Under favorable conditions seeded pasture has produced 7.33 cwt. per acre inch of available moisture at Adelaide. Data submitted by Watkins and Lewy-van Severen (1951) show that Napier grass (*Pennisetum purpureum*) grown under tropical conditions is capable of producing 10 to 12 cwt. per acre inch of moisture available, which is probably close to the maximum possible. This forage yielded 35 tons of dry herbage per acre in a single year in El Salvador, and the figures quoted emphasize the extremely large quantities of nitrogen and other essential nutrients required under conditions of active growth.

2. *Factors Affecting the Mineral Content of Pastures*

a. Species. Numerous determinations have been made of the mineral composition of different herbage species, but many of these are scarcely comparable owing to wide differences in the stage of growth at which

samples have been collected or in the conditions of soil and climate under which the plants have been grown. Comparisons of different herbage species in regard to chemical composition require to be based on growth under identical conditions of soil and climate and harvest of samples at the same stage of growth. The results of such comparisons have been published by Richardson, Trumble, and Shapter (1931), and by Shapter (1935). These investigations indicated the uniformly high protein and calcium content of herbage legumes, the high protein and mineral content of certain miscellaneous herbs or forbs such as *Erodium,* and the capacity of most grasses to reflect the nutrient content of the medium in which they grow, according to the availability of the particular nutrients in the region of soil profile explored by the roots, and the total amount of growth made by the grass. Native Australian grasses of the genus *Danthonia,* and shrubs of the genera *Atriplex, Kochia,* on which much wool was produced in the earlier phases of settlement, are characterized by a fairly high protein and mineral content, which is assisted by their limited total production per acre. These plants are well adapted to the modest soil resources which characterized the Australian wool-growing areas in their original condition. Wool production makes small demands upon the supply of soil nutrients, especially if meat production is not simultaneously involved. The introduction of higher yielding herbage species, such as those now employed for pasture improvement, involves considerable improvement of the status of available plant nutrients in the soil.

b. Stage of Growth, Defoliation, Management. Stage of growth largely determines the protein and mineral content of herbage plants. The processes of nitrogen absorption, photosynthesis, and transpiration do not proceed at similar rates throughout the growth period; phosphorus, nitrogen, and potash in particular are absorbed most actively in the earlier stages of growth, while carbon assimilation and transpiration reach a maximum much later. As a consequence of the differential rates involved, the protein, phosphorus, and potassium content of most herbage plants tends to decrease rapidly as maturity advances. This is especially marked in the case of grasses. Herbage legumes show less acute drifts and it can be generally said that in mixed pastures the grasses attain their maximum nutritive value prior to the appearance of inflorescences, whereas legumes have their highest feeding value at or after this stage. Subterranean clover is still of higher nutritive value after seeds have formed than many grasses prior to flowering.

The influence of growth stage and frequency of cutting on the composition of *Phalaris tuberosa* was investigated in detail by Richardson, Trumble, and Shapter (1932). It was shown that the protein content

fell from 33 per cent at an early tillering stage to 3.4 per cent at the conclusion of growth in the case of ungrazed herbage. The percentage of crude fiber and nitrogen-free extractives increased continuously from tillering to the conclusion of growth. The ratio of protein to carbonaceous constituents was 1 to 1.6 at an early tillering stage and rapidly widened as growth proceeded, reaching a value of 1 to 26 in the final stage. The phosphate and potash content of the herbage was exceedingly high at early stages and fell steadily to a minimum at the end of the growing season. In this work a loss of 27.8 per cent of the total intake of potash was sustained from all portions of the plant, including the herbage and the root system, during the final phases of growth. This occurred as a migration of potash from the plant to the soil due to passive diffusion from the root system at a stage when physiological activity was declining. The influence of defoliation was also investigated and has been commented upon in Sec. IV,1d in connection with the influence of defoliation on transpiration, and in Sec. III,3 in relation to herbage management.

c. Soil Factors. That the mineral composition of mixed herbage tends to reflect the available nitrogen supply in the soil was originally held by Lawes and Gilbert (1900). There is now much evidence to indicate that the nutritive value of a mixed pasture is in large measure dependent on the available supply of essential nutrients in the soil as determined by initial soil fertility and the application of artificial fertilizers. The evidence accumulated in southern Australia shows that the composition of individual species grown on different soils varies according to the available supply or deficiency of nutrients in each soil type. In the northern portions of Australia, as in tropical and subtropical regions generally, the natural pastures tend to be acutely deficient in protein. This is in part due to limited available nitrogen in most soils, in comparison with active carbon assimilation at high temperatures. Protein deficiency in the north is accentuated by the relative absence of legumes in the natural herbage. The problems involved are of considerable importance in northern Australia as they are in other tropical and subtropical regions throughout the world.

Adverting to the south, the application of soluble phosphate does not materially affect the phosphorus content of plants grown on soils high in available phosphate, but on phosphate-deficient soils dressings of superphosphate increase the phosphate content of introduced herbage to a value comparable with that grown on phosphate-rich soil. The major effect of phosphate on mixed pastures is to increase the content of protein and calcium in addition to that of phosphate due to enrichment of the pasture in herbage legumes. Trace element deficiencies are usually

controlled by the addition of deficient elements to the fertilizer. This results in a high enough content of these elements in the pastures to overcome animal deficiencies.

d. Climatic Factors. The nutrition of herbage plants is substantially modified by climatic changes. The influences of temperature and light on photosynthesis, their direct effects on growth rates, and in the case of temperature, on respiration, lead inevitably to shifts in the percentages of the carbohydrate and nitrogenous fractions as shown by Nightingale (1927). Trumble (1949b) has pointed out that these changes may also be associated with modifications in the symptoms of trace element deficiencies or in the uptake of particular nutrients such as phosphorus and zinc.

Decreases of soil moisture content have been found to decrease the percentage of phosphate but to increase the percentage of total nitrogen in ryegrass as shown by Richardson, Trumble, and Shapter (1931). Richardson (1933) emphasized the differences in the chemical composition of plants grown in tropical and temperate regions. Under tropical and subtropical conditions, the high rate of photosynthesis may be expected to produce herbage of low protein and mineral content more rapidly than is the case at higher latitudes. The rate of carbon assimilation is much reduced by the comparatively low temperatures which govern the vegetative growth characteristic of temperate regions. The summer months of high latitudes are attended by exceptionally long days, which compensate in part for the lower temperatures and light intensities experienced; but the very much higher temperatures of the tropics are decisive in producing higher growth rates.

3. Herbage Plant Improvement

a. Plant Introduction. The value of plant introduction to Australia has already been indicated in Sec. I,3b and Sec. II,3e. Davies (1951) has pointed out that many of the grasses and legumes now employed in Australian pastures were introduced to Australia prior to 1900 although only a very small fraction of their present day distribution had by then been attained. Nevertheless, importation of new species and strains in the past two or three decades has led to valuable results. The introduction of nonseeding kikuyu grass from the Belgian Congo by Breakwell (1923) and seed-producing forms by Trumble from Kenya in 1940 (Parker, 1941) has provided raw material of an active sward-forming species which associates well with most herbage legumes and can be used with considerable advantage for permanent pasture in many parts of Australia where sufficient moisture is available over the greater portion of the year. This species is proving highly productive in irrigated pas-

tures devoted to grazing by sheep; it colonizes the borders of dams, channels and waterways generally, maintaining these free from weeds, providing additional grazing, and giving strength to banks. Investigations by Trumble and Davies (1934) demonstrated the value of New Zealand strains of perennial ryegrass, cocksfoot, white clover, and of Montgomery red clover, grown in New Zealand, for irrigated pastures in South Australia. Morgan (1949), reviewing the development of irrigated pastures in Victoria where much greater areas have been established under irrigation than elsewhere in Australia, indicates that the New Zealand strains have been extensively employed, in addition to naturally adapted Victorian strains. New Zealand hybrid H_1 ryegrass is characterized by high vigor under Australian conditions and is tending to replace Italian ryegrass.

Palestine strawberry clover, introduced in 1929, proved to be an extremely vigorous strain of *Trifolium fragiferum*. This was commercialized ten years later and has been sown over increasingly large areas in the southeast of South Australia. Its particular advantage over other strains of this species lies in the activity of its winter production and generally higher yield. *Medicago solerolii*, *M. hispida sardoa*, *Trifolium Balansae*, and seed-producing *Ehrharta villosa* are recent introductions of promise. *Paspalum scrobiculatum* introduced by the Australian Division of Plant Industry, C.S.I.R.O., has been shown by Paltridge (1942) to be a valuable improved pasture species in the better rainfall areas of the southeast of Queensland when properly grown and managed. Other species introduced by C.S.I.R.O. and the Waite Institute in recent years and now under test appear likely to play an important part in future pasture improvement. Active overseas exploration for new herbage plant material was not begun until 1951, although persistently advocated by the author since 1928.

b. Use of Locally Adapted Strains. Despite the undoubted value of introduced strains, confidence in selected variants of herbage plant material that have survived in different parts of Australia over long periods has been fully justified. Such material has provided the basis for strain improvement in subterranean clover (Bacchus Marsh, Tallarook, Yarloop), and barrel medic (Noarlunga), Victorian and New South Wales forms of perennial ryegrass, cocksfoot, white clover, and prairie grass (*Bromus unioloides*), the last named investigated by Donald (1939). The white Dutch type of white clover, commonly seeded until about twenty years ago, has been replaced by New Zealand white and the Victorian "Dingee" type, which resembles ladino in growth form. These are now widely used for irrigated pastures in southern Australia. Lucerne shows regional variation according to climate and management; environmental

selection has operated over a period of a century in some cases. Australian lucernes are well able to withstand grazing by sheep. Some types have been grown for many years under conditions of extremely low rainfall, and regeneration from seed under grazing has been observed. Rhizomatous types are under investigation; these are based upon derivatives of natural hybrids which in some cases have been established in South Australia for a century. Most progress in the actual breeding of improved grasses has been obtained with the Gb81 type of *Phalaris tuberosa* developed at the Waite Institute. This has come into general commercial use as an improved drought-resistant, actively tillering, permanent form of phalaris which is more productive under conditions of hard grazing than most commercial types. It is also lower in stature and higher in seed production than standard commercial forms of the grass. Interspecific hybrids between *Phalaris tuberosa* and *P. arundinacea* have been produced at Aberystwyth by T. J. Jenkin, at Adelaide by the author, and at Davis, Cal. by R. M. Love. Sterility is evident in some of the material, but there is obviously scope for the development of extremely valuable new forms.

4. Soil Deficiencies

a. Phosphate. A detailed field investigation of changes in phosphate and nitrogen status and their effects on the development of seeded pasture from an originally unproductive condition was conducted by Trumble and Donald (1938). An examination was made of the effects of varying dressings of phosphate upon an unproductive podsolized sand with 0.006 per cent P_2O_5, loss on ignition 1.47 per cent, pH 6.4, and yielding only 10 lb. nitrogen and 1.4 lb. P_2O_5 per acre in sown but unfertilized herbage. This land was characterized by stunted *Eucalyptus* forest and heathlike shrubs. After clearing and seeding to a pasture of subterranean clover and *Phalaris tuberosa*, application of 2 cwt. superphosphate per acre per annum for three years, containing a total application of 150 lb. P_2O_5, was found sufficient to develop extremely productive pasture. In the absence of applied phosphate, the yield was 6.2 cwt. dry herbage per acre, after clearing and seeding down. Application of 2 cwt. superphosphate per acre per annum for three years produced a pasture which averaged 48.5 cwt. dry herbage per acre over three seasons (Fig. 10). The yield rose from 33.2 cwt. in the first season to 56.6 cwt. in the third. The average protein production was 796 lb. supporting five sheep per acre, compared with 81 lb. protein and a sheep to 2 acres on unfertilized land. The production through the use of clover, associated grasses and phosphate was thus ten times the original and was attained at comparatively low cost. The relationship of dry clover

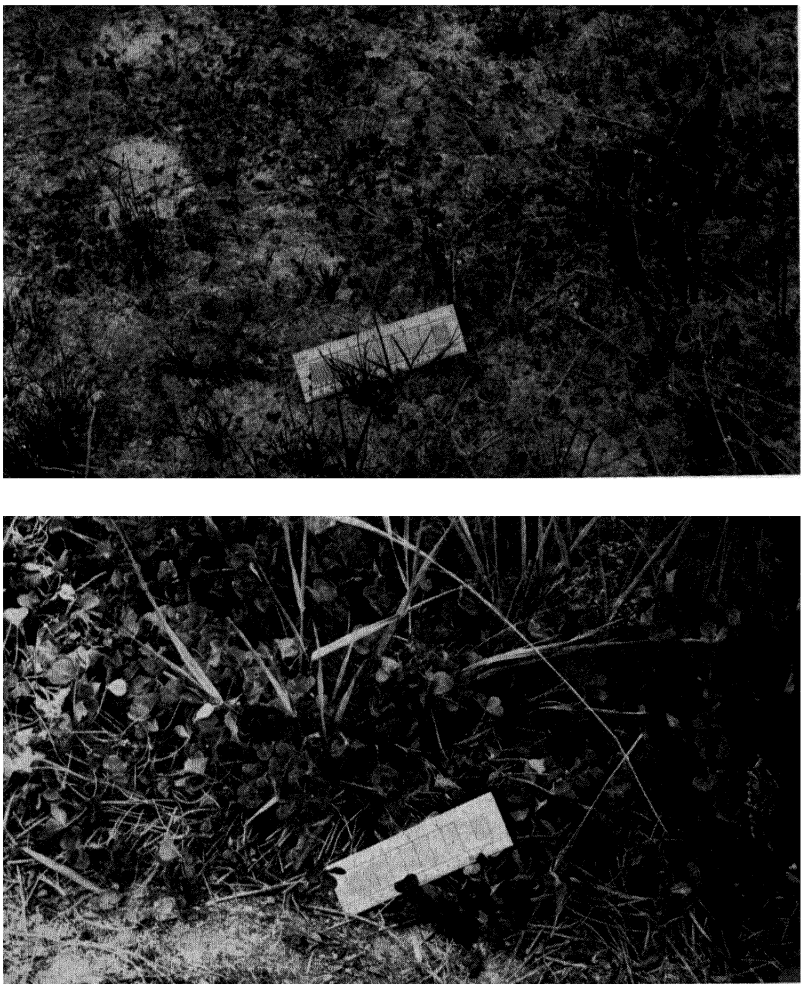


FIG. 10. *Upper,* podsolized sand seven months after seeding to subterranean clover, without phosphate. *Below,* with 2 cwt. superphosphate (47 lb. P_2O_5) per acre at seeding.

production to phosphate dressings followed the logarithmic Mitscherlich type in each of the three seasons; phosphate recovery was directly proportional to the effective phosphate dressing up to a maximum of 4 cwt. superphosphate per acre in any one season (Fig. 11). The percentage of nitrogen in the herbage rose with increasing phosphate application and the perennial associated grasses developed actively in the third year

despite the initial low phosphate and nitrogen content of the soil. Analysis by partial correlation and multiple regression indicated that in the early part of the season nitrogen accumulated previously was highly significant in determining the development of associated grass. Later in the season residual phosphate assumed an important role in determining further development. In addition to the effects on production, the count of soil bacteria was increased tenfold and the general

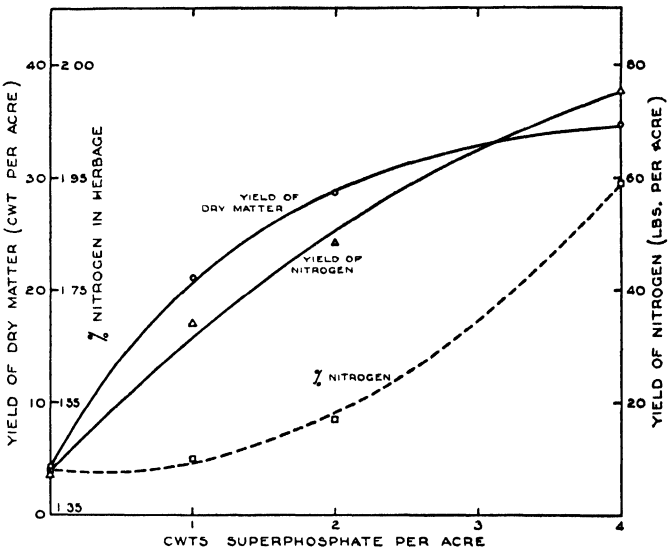


FIG. 11. Differential increase in nitrogen fixed compared with total yield of subterranean clover pasture under increasing phosphate application.

level of soil fertility as indicated by nitrogen level and organic content greatly increased. Riceman (1948a, 1949) has produced evidence of differential response by herbage plants, e.g., Bacchus Marsh subterranean clover, lucerne, phalaris, to varying phosphate applications; lucerne in particular requires substantial quantities. Williams (1948) concluded that the effects of phosphorus treatment on the protein content of young grass were due primarily to variation in nucleoprotein content.

b. Copper. Riceman, Donald, and Piper (1938) and Riceman, Donald, and Evans (1940) revealed the need of calcareous sands, and Riceman (1948a) the need of siliceous sands in South Australia for applications of copper to ensure pasture development. Variation in the response of different herbage species to applications of this element was shown in these experiments and in investigations by Trumble and Ferres

(1946). Lucerne and subterranean clover were both found to respond actively to applications of copper on copper-deficient soil. Lucerne, which persists through the perenniality of its root system, fails to survive on acutely copper-deficient soil in the absence of applied copper. The seed production of subterranean clover, on the other hand, under conditions of copper deficiency, is restricted sufficiently to prejudice survival. Applications of copper sulfate to copper-deficient soil thus have a marked effect in ensuring the persistence and subsequent productivity of these two legumes. As future productivity of the pasture depends upon their nitrogen fixation, the application of copper has important economic effects on the level of pasture production obtained. Deficiency of copper in South Australian soils was established by the investigations of Marston and his colleagues (1938). Striking effects of copper on wool production and animal health have resulted from both direct administration to the animal and application to the pasture. The quantity of superphosphate containing copper annually applied to South Australian pastures is approximately 15,000 tons, and in all probability, upward of a million acres have now been dressed with copper in southern Australia. Copper deficiency has also been recorded in Western Australia by Teakle and Stewart (1939), Teakle (1942), Rossiter (1951a); it occurs extensively on sands, frequently associated with lateritic gravels.

c. Zinc. Investigations by Riceman and Anderson (1943) revealed that deficiency of zinc accompanied copper deficiency on the calcareous soils of Robe, in the southeast of South Australia, on which the original work of copper deficiency was conducted. Whereas lucerne and subterranean clover were particularly responsive to copper, barrel medic and, to a lesser extent, subterranean clover on this soil, responded to zinc, and it was established that to attain a satisfactory pasture of sown grasses and legumes, dressings of both copper and zinc were needed. Subsequent investigations by Riceman (1948a) on deep siliceous sands in the upper southeast of South Australia demonstrated the need for phosphate, copper, and zinc over an extensive region. Subterranean clover, lucerne, and phalaris, the three important constituents of the herbage mixtures now being used, differed considerably in their response to the various fertilizer treatments. The addition of zinc brought about a marked increase in the size of individual plants of subterranean clover and in the yield of this species per acre. The addition of both zinc and copper led to a considerable increase in seed production and rate of multiplication, ensuring persistence and continued production of the clover. The addition of zinc did not enhance the yield of lucerne. The yield of phalaris, which finally becomes the dominant constituent of the pastures, depended largely upon the gain by the soil in available

nitrogen; it became productive only after several years of legume dominance. The use of superphosphate at the rate of 1 to 2 cwt. per acre, the addition of copper sulfate, 3 to 7 lb. per acre, and zinc sulfate, 7 to 14 lb. per acre, together with seedings of subterranean clover, lucerne, and *Phalaris tuberosa*, should make possible the economic development of at least a million acres of heathland in southern Australia with a reasonably good rainfall but formerly regarded as "desert" in view of its extremely low natural productivity. Rossiter (1951a,b) has recorded fairly extensive zinc deficiency in Western Australia where multiple deficiencies of phosphate, copper, zinc, and potash are evident.



FIG. 12. Response of subterranean clover pasture to molybdenum.

d. Molybdenum. Molybdenum is concerned primarily in symbiotic nitrogen fixation, and direct effects on the host legume (Fig. 12), unlike those of copper and zinc, are slight by comparison. Jensen (1948) has calculated that 10 to 25 p.p.m. of molybdenum in the nodule are required for maximum nitrogen fixation. The rate of fixation decreases with concentrations below 10 p.p.m. The plant appears to have a wide tolerance of molybdenum concentration. Adverse effects on grazing animals become evident with total plant concentrations above approximately 10 p.p.m., associated with suboptimal copper. Investigations of laterized, podsolized soils related to Archaean crystalline rocks, with sloping topography and high winter rainfall, led to the establishment by Anderson (1942, 1946) of molybdenum deficiency in these soils. Anderson and Thomas (1946) showed that molybdenum was essential for symbiotic nitrogen fixation; in the presence of sufficient molybdenum, phosphate also directly increased nitrogen fixation (Fig. 13). Anderson and Oertel (1946) found that applications of lime stimulated symbiotic nitrogen

fixation by increasing the availability of molybdenum to the legume. These findings were of unusual interest in explaining the improvement of clover production following the burning of logs or stumps. Traditionally these effects had been attributed to potash. The South Australian investigations showed that responses to 5 tons of woodash per acre were due entirely to the presence of approximately 1 oz. of available molybdenum in the ash. Responses to molybdenum have now been obtained over a wide range of soils in southern and eastern Australia by

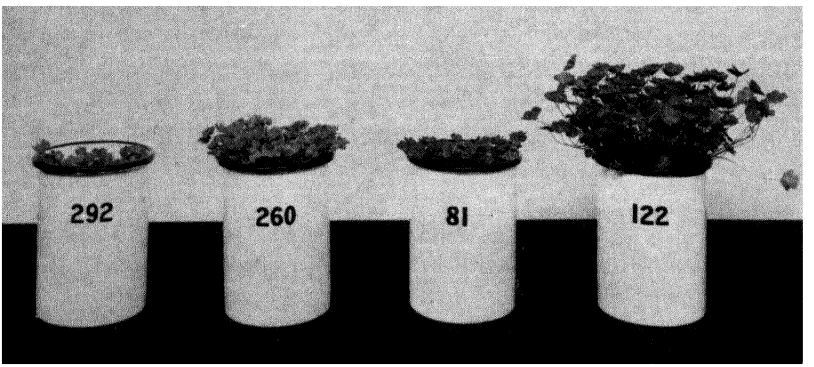


FIG. 13. Interaction of molybdenum with phosphate on lateritic podsol deficient in both elements. 292 = nil. 260 = +P. 81 = +Mo. 122 = P+Mo. (Anderson, 1946).

Trumble and Ferres (1946), Anderson (1948), Rossiter (1951). The element is most frequently deficient on leached soils of pH below 7 with sloping topography to which subterranean clover is well adapted.

e. Potassium. Potassium deficiency has been known in Victoria for many years under conditions associated with exhaustive cropping and especially persistent cutting for hay. Responses to potash fertilizers on subterranean clover pastures have been reported for example by Twentyman (1938), Newman (1948), and Hexter (1948), but practical application of the experimental findings has been restricted by the high cost of the amounts of potassium fertilizer required per acre and the necessity for frequent dressings. Trumble and Ferres (1946) recorded potassium deficiency in a series of surface soils collected from different parts of South Australia, and positive interactions of potassium with molybdenum were frequent with Mt. Barker subterranean clover in these tests. Field tests in South Australia have however not yielded a single case in which potassium application could be economically justified, and it is assumed that subsoil exploration by the roots of associated grasses

assures at least for a time, and especially under grazing, an adequate potassium supply. Rossiter (1947b, 1951a,b) has obtained marked responses to potassium by Dwalganup subterranean clover in Western Australia, in pot culture and field experiments. Significant interactions were observed with potassium and copper.

f. Sulfur. Sulfur deficiency has been obscured in Australia for many years by the presence of calcium sulfate in all superphosphate dressings. Sulfur deficiency has been suspected in New South Wales since about 1929, and this deficiency has now been recorded on the basalts and granites of the southern tablelands of New South Wales by Anderson and Spencer (1950). It has also been found, according to Davies (1951) in several other parts of Australia, including Western Australia and southern Queensland. In some cases, including both New South Wales and South Australia, a dual deficiency of sulfur and molybdenum has been established.

g. Multiple Deficiencies. All deficiencies so far established in Australia are associated with phosphate deficiency, and responses to one or more trace elements cannot be anticipated unless phosphate ceases to be limiting. Because nitrogen is almost invariably lacking in the soils which respond to phosphate and trace elements, symbiotic nitrogen fixation is a first goal and effective legume nutrition becomes essential. Apart from a lack of phosphate in available form, and one or more nutrients other than nitrogen, the presence of (a) toxic derivatives of lignin in deficient wet heathlands and (b) high concentrations of soluble salts, may inhibit nitrogen fixation, first through an effect on rhizobia and secondly through an effect on the host legume. The nutritional aspects involved have been dealt with by Anderson (1949). The most frequent examples of multiple deficiency, apart from that of nitrogen in South Australian soils are: (a) phosphorus, copper, zinc; (b) phosphorus, copper, molybdenum; (c) phosphorus, copper, zinc, molybdenum; (d) phosphorus, copper, zinc, manganese. Other cases have occurred in which phosphate, copper, zinc, molybdenum, and potash have proved to be deficient, and again combined deficiencies of molybdenum and sulfur are now known to occur. Potash deficiency appears frequently to be overcome in practice through exploration of deeper soil horizon containing abundant available potash where the surface horizon may be potash deficient. All legumes that have been tested have been found to respond actively to molybdenum on molybdenum-deficient soils. Barrel medic, subterranean clover, and strawberry clover are especially responsive to zinc where the soil status of zinc is low; lucerne and subterranean clover are among the most responsive legumes to copper. Significant interactions occur between individual elements. Manganese is most frequently concerned in

egative interactions, especially as pH falls. Excess manganese has een found by Kipps (1947) to reduce lucerne production on an acid oil, although the growth of subterranean clover on the same soil was ot similarly affected.

5. *Associated Growth*

a. Compatibility in Herbage Swards. The question of compatibility etween species and strains is an important consideration in designing eeds mixtures. A first principle of modern pasture establishment is he association of grass with legume in any pasture that is to remain own for more than one or two seasons. Subterranean clover and lucerne astures in Australia in the past have usually been sown as pure stands ith a cereal cover crop, but these have become invaded in due course y *Hordeum, Vulpia, Bromus, Cryptostemma,* and other annuals. The alue of phalaris in southern Australia is greatly enhanced by its apacity to associate with herbage legumes, and this applies also to kikuyu rass. On the other hand, *Lolium* and *Ehrharta* which form dense ulti-tillered clumps tend to depress to a greater extent such legumes s may be associated with them The competitive effects of *Lolium* are ell illustrated by the investigations of Cashmore (1934) and Trumble, trong, and Shapter (1937). These species when sown in pastures are requently established at extremely low seeds rates. Four-species pas- ures based on phalaris, ryegrass, clover, and lucerne have given good esults in South Australian field experiments, affording a 2 by 2 com- ination of grass and legume, surface soil and subsoil exploiting in each ase. Root distribution of the constituents and the nitrogen status of he soil are major considerations, as emphasized by Trumble (1949b). he type of combination may be employed wherever the supply of mois- ure held by the profile is sufficiently liberal.

b. Competition in Herbage Swards. Competition to which herbage egumes are exposed is naturally slight in soils that are low in available itrogen, and the dominance of grass or legume in a pasture is frequently function of the available nitrogen content of the soil. As the nitrogen tatus improves, grasses and other non-legumes tend to become dominant, nd their capacity to reduce the intensity of light available to the egumes results in legume depression and eventual suppression, as shown y Blackman (1938) and Blackman and Templeman (1938). Reduction f the grass by grazing or mowing usually results in a significant im- rovement of the legume complement, despite a moderately high nitrogen tatus. Numerous field experiments have now confirmed the fact that epeated mowing or continuous grazing, as compared with deferred otational grazing, greatly increases the amount of herbage legume in

a pasture. The presence of weeds in pastures frequently follows overgrazing or depletion of the soil nutrient supply. This arises from increased soil moisture through reduced competition from grasses, which transpire, shade, and respire less under such treatment. Weeds are usually though not invariably plants of low nutrient content and therefore of low feeding value; they are thus able to survive and dominate unproductive pasture through the development of shade volume, based largely on high fiber or high water content. Permanent control of weeds in such cases must depend largely on the improvement of soil fertility through the elimination of soil deficiencies, the establishment of productive pasture, and its maintenance by sound management.

c. Excretion of Nitrogen from Legumes. It was shown by Trumble, Strong, and Shapter (1937) that grasses do not derive nitrogen from herbage legumes grown in association with them under the conditions of South Australia except during the senescent phase of the legume when the root nodules are actively breaking down and nitrogen is made available from the roots as a consequence of root decomposition. Under certain conditions, where photosynthesis in a legume is reduced by unfavorable conditions of light as shown by Strong and Trumble (1939), nitrogen may be actively excreted from the root system to the legumes during its active growth. A temporarily high rate of transpiration may reduce the water content of the legume, and further increase the amino-nitrogen concentration, thus also favoring excretion, but the necessary conditions are probably so rare in practice under Australian conditions that the phenomenon may be disregarded as being mainly of academic interest. The main gains of nitrogen by associated grasses are in the return of urea from ingested leguminous material, together with the breakdown of legume protein in roots and surface residues.

d. Control of Botanical Composition by Management. It is evident from a wide range of practical experience, in addition to the principles outlined in this paper, that the botanical composition of a pasture can be closely governed by management. If the practical aim is to develop a pasture containing say two-thirds grass and one-third legume, on a dry weight basis, such a condition can be attained by selection of legumes appropriate to the climatic and soil environment, fertilizer treatment that field experimentation indicates, the addition of long-term grasses, and finally by grazing management, together with, if necessary, occasional mowing. It may be argued, and with good reason, that a pasture containing two-thirds grass and one-third legume is by no means desirable if the nitrogen status is already high. Purely gramineous pastures can be immediately more productive under such conditions than mixtures of the same grass with a legume. If, on the other hand, the nitrogen

status is low, stands of pure legumes are likely to produce more protein per acre than mixed associations. If the legume is to be mown for forage there is every justification for growing it as a pure stand as, e.g., lucerne, red clover, ladino white clover, subterranean clover; but if the mixture is to be used for long-term grazing, it is as well to plan from the outset according to initial nitrogen status and the ultimate purpose in view, developing synthetically according to a definite plan of management, rather than permitting changes to occur fortuitously.

6. Irrigated Pastures

Observations of the principles that have governed the development of irrigated pastures in Australia have already been made. The principal areas devoted to irrigated pastures in Australia are in proximity to the River Murray and its tributaries in Victoria and New South Wales. Similar areas are located near the mouth of the Murray in South Australia and at Collie and Harvey in Western Australia. These are indicated on a map accompanying a brief review of Australian pastures by Christian and Donald (1949) and Trumble (1949a).

Lucerne and mixtures of perennial ryegrass, cocksfoot, and white clover have provided the main basis for the development of irrigated areas in the south. On the other hand, Wimmera ryegrass and subterranean clover frequently received supplementary irrigation to extend the natural winter rainfall season. This is commonly employed in New South Wales to aid fat lamb raising during the winter and spring months. Irrigated pastures have extended greatly in Victoria, where the early work of Bartels (1928) did much to encourage approved irrigation practices. Commencing with 5 acres established at the State Research Farm, Werribee, in 1914, the total was stated by Morgan (1949) to have reached a third of a million acres by 1947.

The available nitrogen content of the soil has often been low to moderate in the early stages of these developments, and herbage legumes such as lucerne, white clover, and strawberry clover have therefore received particular emphasis. High yields of perennial ryegrass, cocksfoot, white clover with some phalaris, prairie grass, and red clover were recorded at Wood's Point in South Australia by Richardson and Gallus (1932) and Trumble and Davies (1934). The establishment of lucerne for long periods prior to sowing down to pasture is considered to be largely responsible for the level of production attained, namely 10.9 tons of dry matter per acre, supporting twenty-six sheep per acre for two months, and an average of fifteen sheep per acre or better for the full year.

Many of the areas that have been seeded to pasture under irrigation have been characterized by moderate to high salt content which has

tended, in time, to be completely removed by successive irrigations. Morgan (1947) states that over a period of twenty years the acreage of visibly salt-affected land in Victoria has been decreased through the institution of the border check system of irrigation with suitable grading, the sowing of improved pastures, and sound management in regard to manuring and grazing. Grading is regarded as especially important to make possible uniform application of water for leaching purposes. Morgan (1947) found in one case, a decrease from a salt concentration of 0.41 per cent at 0 to 6 in. and 1.01 per cent at 12 to 24 in. to 0.05 per cent at 0 to 6 in. and 0.19 per cent at 12 to 24 in. over a period of seven years. Moderate irrigations were employed on a basis of twelve to nineteen applications totaling approximately 2.44 acre ft.; and the yield of the pasture at the same time increased substantially. Recent investigations by the Waite Institute (1950) have demonstrated that a high initial content of total soluble salts is a major factor to be considered in the reclamation of heavy clay flats adjoining the River Murray. Concentrations in this case may vary from 0.5 per cent to above 4.0 per cent. Rhodes grass and lucerne, both capable of high salt tolerance, have proved successful pioneer species; both persist at concentrations of 0.5 to 1.0 per cent total soluble salts provided irrigations are sufficiently frequent and surface cover, which can be rapidly provided by the Rhodes grass, is maintained. Surface ridging and the frequent use of some excess water to flush the surface, tend to accelerate the removal of surface salt. As the surface concentration is reduced, perennial ryegrass, barrel medic, subterranean clover, and white clover become important constituents of the pastures. Kikuyu grass has also proved to be a useful species as development proceeds. Applications of copper, zinc, and molybdenum, over and above the basal dressings of 2 cwt. superphosphate per acre per annum, improved the mean yields of both the pasture mixtures and lucerne by 40 per cent to 60 per cent in the above tests.

V. Integration

Although specialized subfields related to if not forming part of agronomy have developed in Australia as in the United States, the scientific investigation of field problems has proceeded for sufficient time to make possible the integration of specific lines of approach, leading to a certain degree of completeness. An attempt has been made therefore to present in this contribution as full an account of interacting principles as space permits. Because climate overshadows all other factors in Australia, relationships of climatic factors to those of soil, species, strain, and management have in particular been emphasized.

1. *The Edaphoclimatic Environment*

a. Value and Limitations of the Soil Survey. The soil survey has proved a prerequisite to effectiveness in Australian agronomy. Its value lies in the definition of soil boundaries and the separation of categories based upon physical and geochemical factors. Its limitations largely concern an unavoidable failure to assess nutrient properties owing to the dependence of these upon the plant and the climate in which it is grown. Grassland covers a much wider range of topography and soil type than any single field crop because the latter depends upon relatively narrow limits in regard to soil properties, including usually a fairly high degree of soil fertility.

Pastures on the other hand are frequently employed to utilize soils unsuitable for cropping and to create soil fertility. Most field investigations prior to 1929 were conducted with complete disregard to soil type and the applicability to other areas of the field experimental data derived. It is now customary to choose experimental sites as representing a particular soil type, the distribution of which has been revealed by a competent soil survey. The physical characteristics of the profile, field capacity, pH, and content of soluble salts are most important. Nutrient status is best determined by field experimentation supported by glasshouse investigation.

b. Relevant Climatic Measures. The climatic environment with which any given soil type is associated must be known. This is a complex of sequential changes in temperature, light, and moisture status, but usually one or two factors are especially restrictive and call for particular examination. Moisture is by far the most important single factor affecting production in Australia, and studies of moisture status have characterized investigations of both soil formation and pasture production. The degree of leaching closely determines the character of the soil profile and its capacity for plant nutrition. As precipitation and the rate of evaporation together determine the leaching factor, it is not surprising that ratios of precipitation to evaporation are prominent in the derivation of agroclimatic measures under Australian conditions. Prescott (1949) has shown as a result of examination of Australian soil boundaries, the records of drain gauges, the use of water by field vegetation, and measurements of transpiration that the most efficient single climatic index of leaching in soils is P/E^m, where P represents precipitation, E is evaporation from a free water surface, and ^{m} is a constant varying from 0.67 to 0.80 with a probable mean of 0.73. A value of 0.6 for the index corresponds with the margins of Australian deserts; at 1.1, soil drainage is nil and at 1.3 to 1.5 precipitation tends to balance transpiration. At

1.7 pedocals separate from pedalfers. Determinations of soil moisture content in the field by Butler (1950) using electrical resistance gypsum blocks indicate that values of this index may be satisfactorily related to soil moisture status in the field, but that the value of the index may require modification according to the conditions. Despite the overwhelming importance of moisture in Australia, the conditions of temperature and light while moisture is available closely govern plant behavior, and the edaphoclimatic environment can only be given some degree of expression when measures of these factors are related to an appropriate soil index or indices.

c. The Ecological Place of the Field Experiment. The field experiment is coming to be regarded as a sample unit of the particular environment that is being investigated. It is now recognized that an experiment conducted in a single year will represent only the conditions of climate and soil which pertain in that particular year. Climatic analysis, based on discernment of the practical agricultural consequences involved, can establish the probable frequency of a particular class of season in a long-term series.

Field experiments require thus to be designed not only to cover the major soil types that characterize a given region but the major kinds of climatic combinations that are likely to occur with significant frequency over a long period of years. An example is given of a joint rotation and fertilizer experiment at the Waite Institute (1950) in which pasture followed four different crops, each after wheat, over a period of years involving several cycles of rotation. The experimental design consisted of sixteen blocks enabling each course of four rotations to occur every year. Each block was divided into 27 plots on a 3 by 3 by 3 factorial design. Such an experiment enabled differences between rotations in terms of yield of wheat on fallow and the yield of pasture following the four different crops to be assessed and, moreover, the interactions of the responses with both season and cycle of rotation to be measured. An effective climatic measure or picture of each season enables the variations of treatment effects with season to be interpreted.

Australian experiments have tended to emphasize the incorporation of pastures for varying periods in crop rotations to regain soil structure and nitrogen in overcropped lands. Hodgson (1939) has emphasized the new outlook gained by farmers now that the pioneering stage has gone, and lucerne, subterranean clover, and Wimmera ryegrass have been employed for temporary pastures in rotation with wheat in New South Wales. The grazing of sown top-dressed pastures for five years or more followed by cropping for an approximately equal period is recommended. Woodroffe (1949), dealing with the results of South Australian experi-

ments, emphasizes the value of peas, followed by short-term pastures, on the one hand, and perennial pastures maintained for up to ten years, on the other, in improving soil organic matter and nitrate content. Forster (1950), reviewing the results of field investigations presented at the British Commonwealth Specialist Agricultural Conference, Adelaide, 1949, has emphasized the decline of organic matter in Australian wheat-growing soils and further stressed the effect of clover pastures in improving soil fertility, particularly at the Rutherglen Experimental Farm, Victoria. A much cultivated field gave 31 per cent aggregation, whereas one under subterranean clover for eight years and then cropped gave 53 per cent. There is now in Australia a marked swing toward the establishment of long-term leys between intensive periods of cropping. This has resulted in a reduction of wheat acreage in recent years, and this has also been favored by high world prices for wool.

2. *Integrated Climatic Patterns*

a. The Factors Involved. The concurrent expression of indices of temperature, light, and moisture over given intervals of time has rarely been attempted. Trumble (1949) presented diagrammatically an analysis of twenty-four seasons at the Waite Institute in terms of effective rainfall, air temperature, and the light duration for each month per season. The yields of pasture were dependent upon the type of climatic pattern, and a study of the patterns concerned enabled variations in production from season to season to be understood. The factors employed were (a) mean monthly duration of daylight, plotted horizontally for the twelve successive months, (b) corresponding mean monthly air temperatures in shade in excess of 45°F. plotted vertically to form a rectangular block for each month, (c) superimposition of available moisture in units of 0.25 in. and according to the approximate relation of temperature to growth. Such a method of attempting concurrent expression of light, temperature, and moisture values over given intervals of time is doubtless open to refinement, but there are advantages in presenting such patterns at first in as simple terms as possible. The mean of the patterns constructed for Adelaide differs in significant features from each one of the twenty-four individual seasons and is thus fictitious. Initial comparisons of contrasting environments, however, can be appropriately made on the basis of means, although the final goal should be in terms of individual seasons. Trumble (1950a) has employed the method to indicate probable nutrient requirements of pasture in widely contrasting environments such as those of tropical, temperate, and high latitude climates. Trumble (1950b) has also in this way described the four major climatic types of Nicaragua and compared them with conditions at ex-

perimental stations in adjoining Central American countries, and the southeastern United States, at which agronomic data of possible application to Nicaragua are available. These studies emphasize the high potential for growth in the tropics and the consequent emphatic need for soil improvement.

b. Short- and Long-Term Variability. Variation in the shorter term includes that between day and night, from day to day, over successive phases of the same season, and from season to season within the range covered by a short-term experiment of two or more years. Few grassland experiments have been conducted for more than a limited number of seasons, and the exceptions have usually been affected by upward or downward fertility trends, or a treatment such as cutting for hay which has departed from accepted grazing practice. Investigation by Trumble and Cornish (1936) of production for ten seasons of a natural pasture showed that coincidence of early seasonal rains with favorable conditions of temperature and light governed in large measure the total

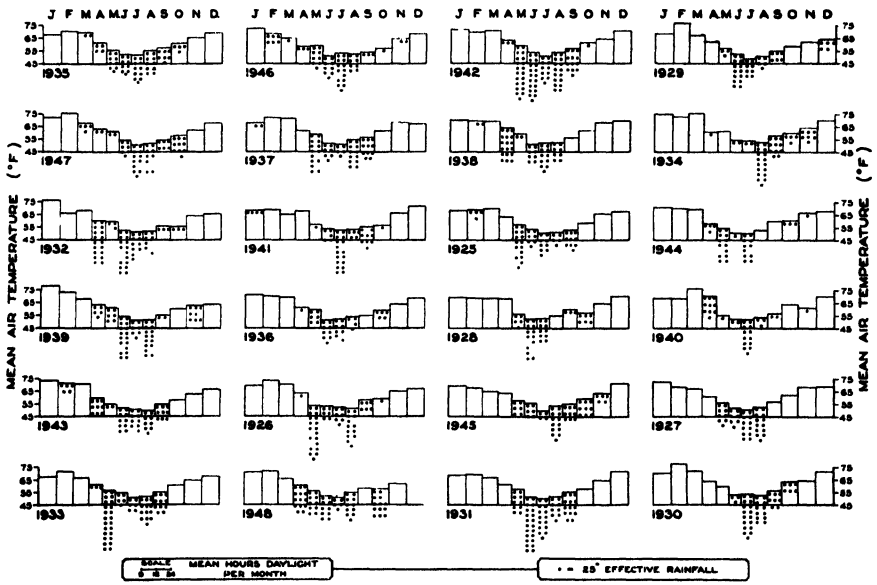


FIG. 14. Integrated climatic patterns showing nature of individual seasons at the Waite Institute, 1925-48. The patterns are in order of seasonal production, as closely as can fairly be judged. Seasons 1935 and 1947 with effective rainfall commencing in March and continuing for eight months were outstandingly high in production. Seasons 1944, 1940, 1927, 1930 gave considerably lower yields than all others. Late spring drought (1944), low rainfall in autumn and spring (1940), short season (1927), short season commencing very late (1930).

yield for the season. This led to emphasis on the length of the effective rainfall season by Trumble (1937) and investigations of its variability in the longer term by Wark (1941).

The amount of moisture required for transpiration will depend upon both temperature and the duration of light. Mean monthly values for these appear adequate, and only temperature will vary from year to year in any month. The differences of temperature which follow changes in latitude or altitude are frequently so great as to multiply the rate of production several times. Integrated climatic patterns from widely separated latitudes suggest that nutrients are required to be absorbed from the soil at considerably higher rates in the tropics than in temperate regions to produce comparable concentrations within the growing plant. Copper, for example, needs to be absorbed in the tropics at a rate fifteen times that characteristic of temperate conditions; and a total production of 30 tons of dry material per acre per annum, which is readily attained at low altitudes near the equator, requires nitrogen equivalent to 3½ tons of sulfate of ammonia, and phosphate equivalent to 1 ton of

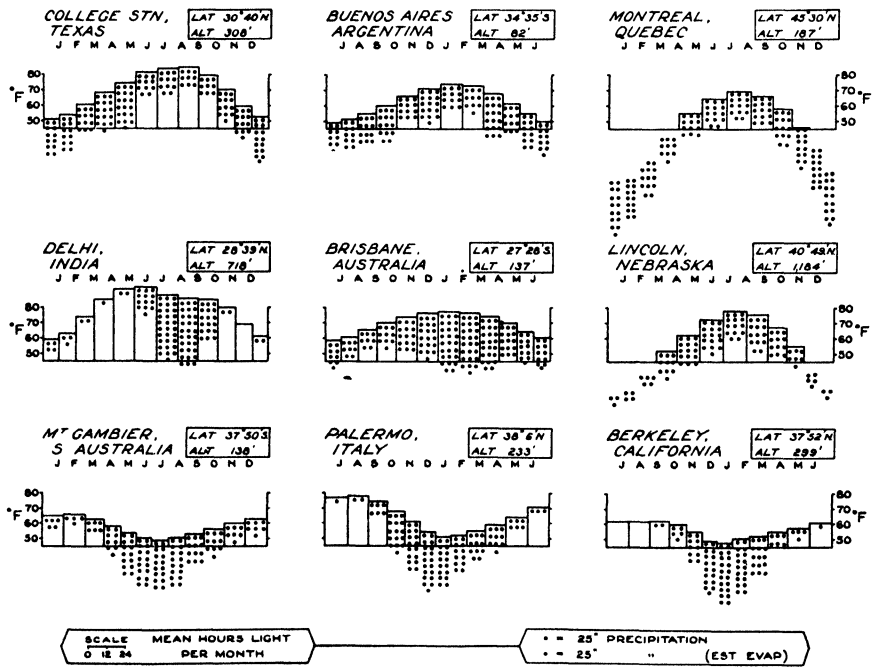


FIG. 15. Comparison of climatic patterns for two Australian centers (Mt. Gambier winter rainfall, southern Australia; Brisbane summer maximum, sub-tropical, north-eastern Australia), with patterns for other centers in middle latitudes.

superphosphate to provide the minimal requirements of nitrogen and phosphorus for satisfactory animal nutrition through herbage alone. Such global differences far outweigh variations from season to season at one center and could with justification receive greater attention. Increasing distance from the equator leads to reduced growth rates and increasing protein concentration, but the marked increase of daily light duration in midsummer compensates in part for lowered temperature.

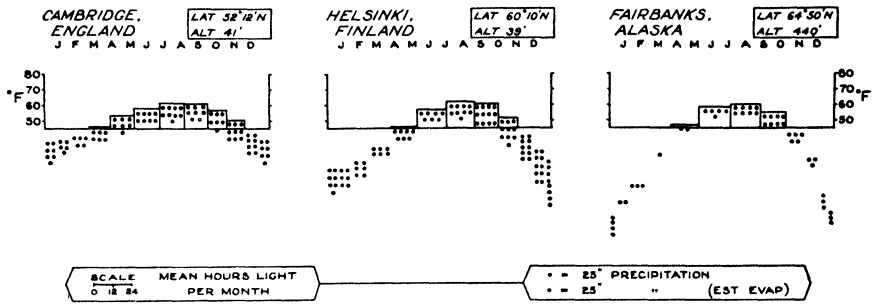


FIG. 16. Climatic patterns for three centers at high latitudes.

c. Estimation of Possible Production. Trumble (1950a) has employed a summation index of potential production. This is based on transpirational needs in units of one acre inch and is assessed by fitting the number of acre inches of moisture available for transpiration to the light-temperature pattern (Fig. 14). The ratio of transpiration to growth varies with the plant and the environment and should be considered in relation to data on the response of particular plants to the chief ecological factors of causation. On the basis of the experiments on transpiration conducted at Adelaide and the earlier work of Briggs and Shantz (1913), transpiration ratios of 300 and 500 have been tentatively adopted at mean air temperatures respectively above and below 65°F. In the patterns so far employed, four dots depict an inch of precipitation gained by the soil in the absence of surface runoff, and a single dot equivalent to 0.25 in. occupies 25°F. mean daily light-hours per month decreasing to 12°F. mean daily light-hours per month at temperatures above 65°F. Examination of these patterns has indicated a dry herbage potential of 1.8 to 8.0 tons (2240 lb. per ton) per acre per annum within areas of South Australia where the mean wet period exceeds seven months and the total rainfall is considered sufficiently high for sown pasture production. The potential production in the tropics is probably in the order of 35 tons per acre per annum, a value already obtained by Watkins and Lewy-van Severen (1951).

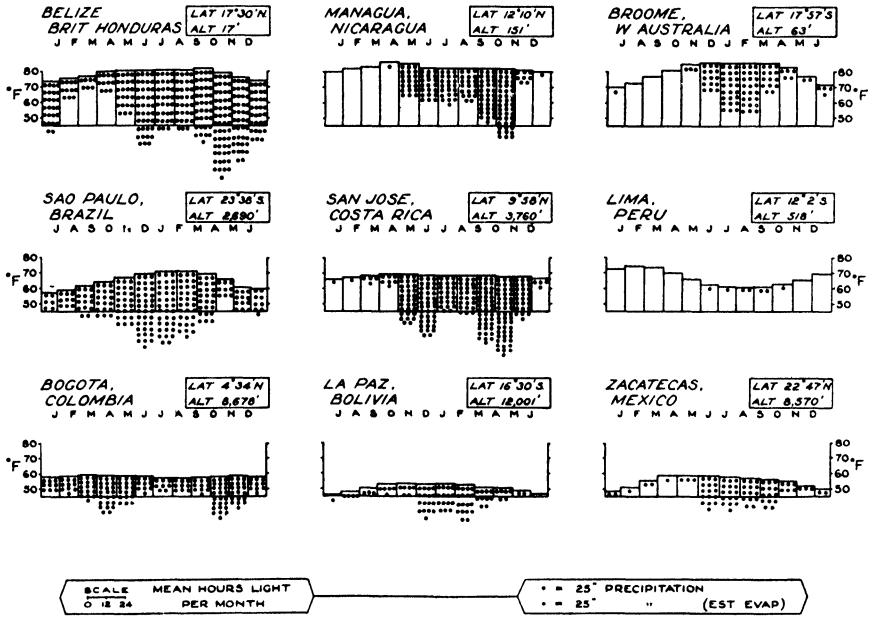


FIG. 17. Climatic patterns for nine centers at varying altitudes within the tropics.

While there are dangers in oversimplification and the use of generalized estimates, the principles involved invite ecological examination on a world basis, and where suitable records of both production and the climatic factors governing yield and composition are available, a fuller biological interpretation of regional and seasonal effects should be possible.

3. *The Realization of Potential Production*

a. Fitting Herbage Plants to the Environmental Pattern. Although many successes have attended past trials of new species, there have probably been countless failures for every single success, involving a good deal of wasted effort under trial-and-error methods. Nowadays new species and strains can be selected for test more efficiently on the basis of the fairly effective climatic and edaphic comparisons that can be made, and better comparisons are possible than have been the rule. Despite this, the agronomist still requires to conduct numerous field tests and engage upon comprehensive breeding programs; but the better he is equipped with a knowledge of the ecological factors that govern the conditions to which the tests are to apply, the more expeditiously will new herbage plants be fitted to these conditions. The results of a single

year's test of a new species or strain should be judged in terms of the environmental pattern of that particular season, for the performance of the plant material grown is a consequence of both environmental resources and genetic efficiency, and it is the latter that it is important to gain.

b. Scientific Investigation and Field Practice. The scientific investigations required to realize the maximum production possible take numerous forms, but a first logical step is analysis of environment to define those factors that overwhelmingly limit growth, and this stresses a discriminate survey of practical experience as well as of scientific factors. The key to increased production in Australia has so often been found in the combination of an appropriate herbage legume with appropriate fertilizer treatment that this aspect has come to be one of the first examined. Sources of existing and possible new herbage material are so extensive that few edaphoclimatic situations exist which cannot be met outside the arid to semi-arid regions. The field investigations required seem most effective in simple randomized blocks, with separate tests numerous enough to uncover all possible factors and all possible combinations of factors that might matter. Work that is essentially academic can quickly lose agricultural significance, and perhaps the deeper lines of scientific investigation are best detached in practice from field experimentation but linked for the purpose of answering specific questions that have frequently arisen as a result of interested enquiry. Many new principles, once they are fully uncovered, can be related in simple and effective economic terms to the farmer or grazier, whose association with agronomic enquiry has certainly so far proved an advantage in Australia, and such enquiry can lose much of its value if not persistently associated with farming practice itself. Success in this regard appears to have been one of the most stimulating results of grassland agronomy as carried out so far in both the United States and Australia.

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Type of Soil Colloid and the Mineral Nutrition of Plants

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I. Introduction

As has been pointed out by Beeson in his excellent review (Beeson, 1946), the relation between soils and the mineral composition of crops encompasses a host of interrelated factors. Perhaps we are presumptuous in attempting to consider one of these factors, the type of soil colloid, as though it can stand alone. However, a considerable amount of work has shown that plant cation nutrition is definitely related to type of clay, in that the ionic environment of plant roots in soils depends to a large extent on the amounts and proportions of the various colloidal acids, bases, and salts present.

In contrast to the earlier view that clay minerals could be divided into a few discrete groups, it is now well known that large numbers of transitional forms exist in soil (Jackson *et al.*, 1948). Nevertheless, for the purpose of this review, we will consider that soil colloids can be divided into the five groups—expanding lattice minerals, kaolin minerals, hydrous mica minerals, hydrous oxides, and colloidal organic matter.

The phenomelogical aspects of ion absorption from solution have been amply demonstrated by Hoagland *et al.* (1928), Collander (1941), Beckenbach *et al.* (1938), Beeson *et al.* (1944), and others (see Hoagland, 1944). Such aspects of the absorption process as selective accumulation are out-

side the scope of this review. Others, such as the effect of ion supply and of competition between various cations, are pertinent.

It is well established that there is a rough proportionality between the concentration of a given cation in a plant and that of the nutrient solution in which it was grown. Beeson *et al.* (1944), through the use of elegant statistical techniques, have shown that around 80 per cent of the variation in Ca, Mg, and K contents of tomato plants grown in nutrient solutions could be ascribed to variations in the supply of these and other ions. Not only was content of a given ion found to be correlated with its own supply, but also in some cases positive or negative correlations with the supply of a second ion was indicated. Thus, Ca content increased regularly with Ca supply at a given level of K, but decreased when K supply increased and Ca supply was held constant.

The latter observation is an example of so-called ion antagonism or ion competition, which has been noted by many investigators. Hoagland *et al.* (1928) found from studies with Nitella that an increase in the relative concentration of one metal cation in a culture solution resulted in decreased uptake of the other metal cations present. That this principle is applicable to many situations has been shown by Lundegårdh (1949), Chapman and Brown (1943), Hunter (1943), Hoagland (1944), Mattson (1948), and Leonard *et al.* (1948). In general, Na and particularly K are very effective competitors, and if present in large proportions they greatly decrease the Ca and Mg contents of plants. Competition between Ca and Mg is usually somewhat less marked, as is the depressing effect of Ca and Mg on K content. Collander (1941) noted great competition between pairs of chemically similar ions such as K and Rb, Ca and Sr. Beeson *et al.* (1944) have observed instances in which such ion competition was of minor importance. Pierre and Bower (1943), considering the effect of Ca on the absorption of K, conclude that Ca may increase K absorption when K is high and the ratio Ca : K is low (the Viets effect, Viets, 1944) or when Na is high as compared with K, but that Ca reduces K absorption when Ca is present in high concentration.

The effect of hydrogen ion concentration (pH) on ion absorption from nutrient solution has been studied thoroughly by Arnon *et al.* (1942) and by Arnon and Johnson (1942). They found Ca absorption by tomato, lettuce, and Bermuda grass to be relatively constant between pH 5 and 9, but to be significantly lower between pH 4 and 5. In this lower pH range, an increase in the Ca concentration of the culture solution overcame the deleterious effects of low pH on Ca absorption and on the growth of tomato and lettuce. Magnesium and K absorption also tended to be less in the pH range 4–5 than in the range 5–9, but the differences were not so large as those observed with Ca. De Turk (1941)

reported much more substantial changes in Ca absorption by red clover with changes in pH. Increasing pH from 5 to 7 resulted in a twenty-fold increase in Ca absoption from a solution containing 150 p.p.m. Ca.

Arnon *et al.* (1942) observed that plants actually lost metal cations to culture solutions at pH 3. Recently Jacobson *et al.* (1950) have observed appreciable losses of K from excised barley roots to HCl solutions below pH 4.5. Loss of K was very large at pH 3, but loss could be decreased and even changed to accumulation by addition of high concentrations of KCl to the HCl solution. They interpret this as evidence for a reversible chemical reaction involving the exchange of K and H in roots.

While the relationships between ion concentrations and ratios in culture solutions and in plants are by no means completely defined, the general concepts presented above will serve as reference points in the consideration of ion absorption from soils and clays.

In the study of ion absorption by plants from soils and clays we are concerned not only with the effect of ion concentrations and ratios (possibly activities and activity ratios) on the plant. We must consider as well the problem of defining and measuring the effective ion concentrations in the soil. The idea of a static soil solution from which plants obtain their mineral elements has long been discarded. Regardless of the mechanism envisioned to be operative in the transfer of metal cations from the soil to the roots of plants, we must look upon the exchangeable ions as being the immediate source of cationic plant nutrients in most soils.

To illustrate the problem we will quote some recent observations of Mattson (1948). Mattson grew barley plants in three systems, nutrient solutions, kaolinite, and bentonite-sand mixtures. K and Ca were added

TABLE I

Composition of Three-Week Old Barley Plants Grown in Nutrient Solutions, in Kaolinite, and Bentonite-Sand Mixtures

Substrate Concentration *		Plant Content, mc. per 100 g.					
		Solution		Kaolinite		Bentonite	
K	Ca	K	Ca	K	Ca	K	Ca
1.0	9.0	201.9	48.7	141.0	46.5	139.3	28.2
2.5	7.5	210.8	42.4	195.5	32.4	189.0	17.1
5.0	5.0	222.9	28.3	190.2	20.8	206.8	9.7
7.5	2.5	231.2	22.2	200.0	16.3	204.7	5.4
9.0	1.0	234.4	12.8	208.1	10.5	210.4	3.8

* Milliequivalents per liter of cultural solution, or milliequivalents per pot (300 g)

as chlorides to the solutions, and as exchangeable ions to the clay systems. N, P, Mg, and Fe were constant. Table I shows the quantities of K and Ca supplied and the amounts of these ions in the plants grown on each substrate. Note that K and Ca delivery from the nutrient solutions and from the clays differs, and that there are large differences, particularly with respect to Ca delivery, between the two clays. Each clay had a distinctive influence on the effective concentrations of Ca and K. As Marshall (1944b) has pointed out, in order to define the ionic environment of plant roots in soils, we must consider not the total concentrations but the effective concentrations of the various ionic species present. Two general lines of experimental attack have been followed in attempts to delineate the role of the soil or of colloidal clay in influencing the effective ion concentrations. The one embodies the study of ion exchange reactions, the other the measurement of single-ion activities.

II. Approaches to the Study of the Ionic Environment of Plant Roots in Soil

1. Ion Exchange

The general nature of the ion exchange process has been thoroughly treated elsewhere (Davis, 1945; Kelley, 1948; Gieseking, 1949; Krishnamoorthy and Overstreet, 1949, 1950a, 1950b). We shall discuss only those aspects which have bearing on the present problem, i.e., those which deal with the adsorption and release of cations as related to type of clay.

Jenny (1932) and Gieseking and Jenny (1936) made an extensive study of the exchange-adsorption of various ions by Putnam clay (beidellite). The order of the common cations for ease of entry was Li<Na<K<Mg<Ca<H. Jenny (1932) also observed that relative to the metal cations hydrogen was adsorbed less strongly by bentonite than by Putnam clay. Jarusov (1937) measured the "mobility" (exchangeability for K^+) of various metal cations adsorbed on several soils. He concluded that the exchangeability of a particular ion was related not only to its degree of saturation and the nature of the other exchangeable ions, but also depended on the nature of the exchange complex. Thus he found the exchangeability of Ca to be much greater in a laterite than in a chernozem, and the exchangeability of both H and Ca to be greater in a chernozem from which organic matter had been removed than in the natural soil.

A comprehensive study of ion exchange with several minerals and with organic soil colloids was reported by Schachtschabel (1940). He

found relative ion affinities, measured by adding 1 symmetry concentration of alkali or alkali earth chlorides to NH_4 clay, to be:

Montmorillonite	Li<Na<K<H<Mg<Ca
Kaolinite	Li<Na<H<K<Mg=Ca
Ground muscovite	Li<Na<Mg<Ca<K<H

Such series as are listed above are found to vary somewhat with the concentration of the salt solution and with the ion initially adsorbed on the clay (Jenny, 1932; Schachtschabel, 1940; Vanselow, 1932), but differences between types of clay are evident, regardless of such effects.

Schachtschabel was especially impressed with the differences in the selective adsorption of NH_4 and Ca by montmorillonite, kaolinite, and organic colloids on the one hand and by ground micas on the other. After leaching with a mixture of equimolar solutions of NH_4 and Ca acetates he found the ratio Ca absorbed: NH_4 adsorbed to be 11.3 and 10.3 for two samples of organic matter, 1.71 for montmorillonite, 1.42 for kaolinite, and 0.066 for ground muscovite. Hendricks and Alexander (1940), however, did not observe such large differences between montmorillonite and three micaceous minerals, sericite, glauconite, and illite. They did find, in agreement with Schachtschabel, that H is more strongly adsorbed by micaceous minerals than by montmorillonite.

The data considered above show that there are large differences in the exchange properties of the several colloidal materials studied. They have served as a foundation for subsequent work on the relative affinities of the various common cations for the several types of clay.

Mehlich (1941) presented titration curves of various H clays. The pH-degree of base saturation relationships for the different types of clay are quite characteristic. Similar observations have been made by Mitra *et al.* (1943), Muckherjee *et al.* (1943), and others. Such observations may be interpreted as reflecting different relative affinities of the various clays for H and for the alkali earth cations employed in the titration. Thus, montmorillonite may be inferred to have a relatively high affinity for Ca or Ba and kaolinite for H, whereas beidellite, halloysite, and illite are intermediate. Mehlich (1941) observed that while humic acid has a titration curve much like that of montmorillonite, the pH-base saturation relationships of a muck soil are similar to those of halloysite and kaolinite.

Elgabaly *et al.* (1943) observed that addition of 1 symmetry HCl released more Zn from Zn-saturated kaolinite than from bentonite. Similarly, more K was replaced from K-kaolinite than from bentonite. Extraction of homoionic clays with CO_2 saturated H_2O (essentially replacement with H_2CO_3) resulted again in greater release of Zn from

kaolinite than from bentonite, and of K from Aiken clay (kaolinitic) than from Yolo clay (montmorillonitic).

Mehlich and Colwell (1943) measured the release by 1 symmetry HCl of Ca and Mg from several soils with identical degrees of Ca and Mg saturation. Release was greatest from organic and kaolinitic soils and decreased as the proportion of montmorillonite in the soils increased. The ratio Ca released: Mg released was higher for kaolinitic and muck soils than for montmorillonitic soils, though this may reflect a solution of nonexchangeable Mg from the latter rather than a difference in the relative affinities of the several colloids for Ca and Mg.

Allaway (1945) found that addition of HCl equivalent to exchangeable Ca at various degrees of Ca saturation resulted in widely different amounts of Ca release from several clays. The order of decreasing release was: peat>kaolinite>Wyoming bentonite>illite>Mississippi bentonite.

Differences between clays were marked, as is shown in Fig. 1. Allaway also reported results of replacement of Ca from various clays by $BaCl_2$. Differences between types of clay were small in this case, indi-

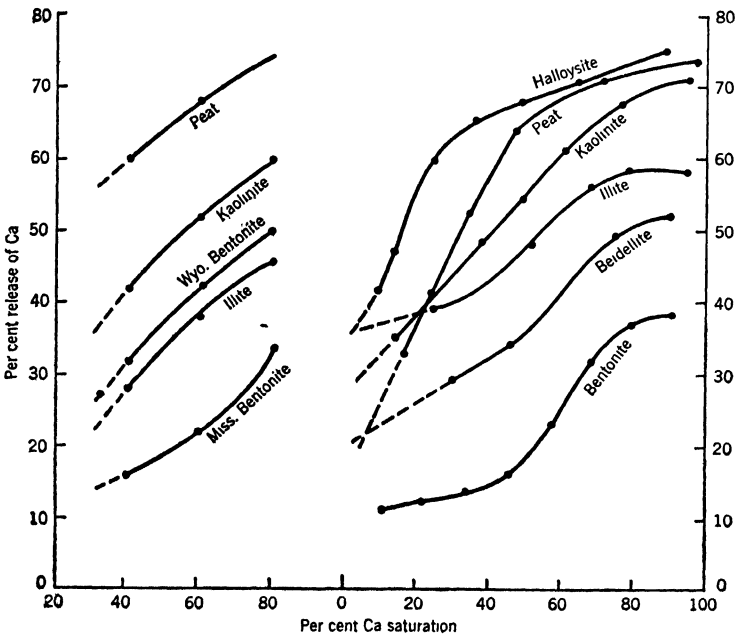


FIG. 1. Per cent Ca replaced by an equivalent amount of HCl as affected by type of colloid and percentage Ca saturation. (Data on left taken from Allaway, 1945; data on right taken from Mehlich, 1946.)

cating perhaps that it is the affinity for H in which the several clays differ most.

Mehlich (1946) studied the release of Ca from various clays when HCl equivalent to the exchangeable Ca was added. His findings are qualitatively similar to those of Allaway (1945). The order of release at all degrees of Ca saturation (Fig. 1) was: halloysite>peat>kaolinite>illite>beidellite>montmorillonite. This order was unchanged when HCl was added in small but constant amounts to the various clays, rather than in amounts equivalent to the exchangeable Ca.

With reference to the clays used by Mehlich (1946), we have more recently found from electron micrographs that the "kaolinite" referred to in Fig. 1 is actually halloysite. This finding in no way changes the significance of the results. In relation to H, Ca is much more strongly adsorbed by expanding lattice clays than by kaolinitic clays and organic colloids.

Recently Krishnamoorthy and Overstreet (1949, 1950a, 1950b) have propounded a theory which seems to describe satisfactorily ion exchange equilibria in a variety of clays and other exchange materials. Experimentally they found (1950a) that the exchange constant for a given ion pair varies considerably from one exchange material to another. For K-Ca exchange, as an example, their data gives exchange constants of 0.057 for bentonite, 0.091 for Yolo clay (montmorillonitic), 0.098 for Hanford clay (micaceous), and 0 340 for Aiken clay (kaolinitic). For ion exchange involving H, Krishnamoorthy and Overstreet (1950b) found the active mass of adsorbed H to vary in a manner suggestive of "surface ionization." Thus, the effectiveness of H in replacing metal cations from various clays would be characteristically affected by the degree of base saturation.

The studies cited above include the most ambitious attempts to delineate the role of type of clay in cation exchange. It is still pertinent to mention a few observations which support the general thesis that type of colloid plays a major role in clay-electrolyte interactions.

Vanselow (1932) compared equilibrium constants for Ca-NH_4 exchange with bentonite and with an oxidized Hawaiian soil and concluded that there must be at least two kinds of soil clays, one with a relatively greater affinity for Ca than for NH_4. Bentonite, as compared with the Hawaiian clay, held Ca very strongly against ion exchange [compare with Krishnamoorthy and Overstreet (1950a) data for bentonite and Aiken clay]. Harward (unpublished data), working in the authors' laboratory, has found Ca-K exchange equilibrium constants to be very similar for halloysite and kaolinite. Montmorillonite, on the other hand, gives Ca-K

constants which indicate greater relative affinity for Ca than is the case with the kaolinitic clays.

An interesting approach to the problem of relative ion affinities and type of clay has been made by Mattson and his students (Mattson, 1948; Elgabaly and Wiklander, 1949). They believe that differences between the affinities of mono- and divalent ions for different clays depend upon the exchange capacity of the clay. They base this belief on a hypothetical Donnan distribution of ions between an "inside solution," that portion of the clay-water-electrolyte system occupied by the ionic double layers, and an "outside solution" consisting of intermicellar liquid. If one sets up Donnan equilibrium expressions to describe the distribution of mono- and divalent ions between the "inside" and "outside" solutions, one reaches the conclusion that for a given ion ratio in the "outside solution," the greater the sum of the ion activities in the "inside solution" the larger will be the ratio of divalent ion: monovalent ion "inside," and the greater will be the proportion of the divalent ion in the exchangeable ions. Mattson (1948) cites as an example of this an exchangeable Ca: NH_4 ratio of 8.4 for bentonite (exchange capacity 90 me. per 100 g.) as compared with a ratio of 3.3 for kaolinite (exchange capacity 3.5 me. per 100 g.), both clays being in equilibrium with a solution 0.005 *N* with respect to both Ca and NH_4. Mattson concludes, "if two soils having different cation exchange capacities (due to different acidoid content or strength), contain the same proportion of a monovalent and a divalent ion, then the soil with the higher exchange capacity should yield its monovalent ions more readily and its divalent ions less readily than the soil having the lower exchange capacity."

Although the Donnan equilibrium has been used by Mattson and his co-workers to explain many ion exchange phenomena in soils, Davis' (1942) stand that we are dealing with unmeasurable quantities when we speak of ion activities, particularly in the "inside solution," should be reemphasized. Any conclusions drawn from Mattson's theory seem to be qualitative, at best.

A second point made by Wiklander (1946) concerns the position of H in the lyotropic series for exchange-adsorption. The point is that H apparently varies in its ability to replace metal cations, depending on whether the ion exchanger in question behaves as a weak or a strong acid. This has been pointed out before (Jenny, 1932; Allaway, 1945; Mehlich, 1946). Marshall and Krinbill (1942) give the order of increasing strength of clay acids as: montmorillonite>beidellite>illite>kaolinite. Their affinity for H would then be in the opposite order. As pointed out by Krishnamoorthy and Overstreet (1950b); however, affinity for H depends more on degree of base saturation than does affinity

for metal cations. Thus, the series quoted above might be modified by degree of base saturation.

From the above cited work we are certainly justified in saying that there are major differences in the relative exchangeability of various ion pairs when adsorbed on different types of clay. The differences are especially pronounced for ions of different valence, i.e., Ca and K, for pairs of which H is one member. The extremes are represented by kaolinite on the one hand and the expanding lattice clays on the other. Quite understandably, there is considerable overlapping between the exchange properties of the expanding lattice clays on the beidellite end of the series and the so-called hydrous mica minerals. The lack of quantitative agreement between the results of different experimenters may be attributed in part to differences in experimental techniques and in part to the fact that they used different specimens as typical of a particular mineral.

The conclusions reached from consideration of the experiments cited above are not in agreement with those of Melsted and Bray (1947), who seem to believe that ion exchange in all clays may be described by considering concentrations and relative affinities of ions, the relative affinities being characteristics of the ions alone, and not affected by type of clay.

2. Ion Activity

Marshall and his associates (Marshall, 1939, 1942, 1944a, 1944b, 1948a, 1948b, 1950; Marshall and Bergman, 1941, 1942a, 1942b; Marshall and Ayers, 1946, 1948; Marshall and Eime, 1948; Marshall and Barber, 1949; McLean and Marshall, 1948; McLean, 1949), using clay membrane electrodes, have made a number of measurements of single-ion activities in clay suspensions. To date they have been able to handle systems containing a maximum of two metal cations in addition to the omnipresent hydrogen ion. Recently, Peech and Scott (1950) and Schuffelen and co-workers (Schuffelen and Loosjes, 1942; Schuffelen, 1944, 1948; Schuffelen and Barendregt, 1946), have constructed cells in which the alleged Donnan potential between a clay or soil suspension and its equilibrium dialyzate could be measured. From the measured potential and the analytically determined concentrations of cations in the liquid phase they have been able to calculate single-ion activities identical with those measured by Marshall. This latter scheme seems more flexible and more adaptable to heteroionic systems, though it lacks the attractive simplicity of the membrane electrode method.

Some far-reaching inferences have been drawn between measured ion activities and the cationic nutrition of plants (Marshall, 1944, 1948b,

1950; McLean, 1949; Schuffelen, 1948). Marshall (1948b), for example, states, "The differences . . . between the kaolinite and montmorillonite groups of clays on the one hand and between monovalent and divalent cations on the other, are destined to be of especial importance in soil science, plant nutrition, and plant ecology. . . . the uptake of cationic nutrients from the soil is a function of the activities of the ions with which the growing root is in contact. . . ."

Most of the measurements of single-ion activities in clay suspensions have been made by Marshall and his students. The results which are pertinent to the present subject are summarized briefly below.

Considering first the ion activities in homoionic clay suspensions, at constant cation concentration, the activities of the alkali metal cations decrease in the order: kaolinite>montmorillonite>beidellite>illite (Marshall, 1950). Differences between the activities of the alkaline earth cations are more pronounced, and decrease in the order: kaolinite>illite >mortmorillonite>beidellite (Marshall and Ayers, 1948; Marshall and Eime, 1948). The above generalizations refer only to clays at the equivalence point. The changes in cation activity when H clays are progressively neutralized are distinctive for each clay mineral (Marshall, 1950).

With regard to the difference in activity of various ions associated with a given clay mineral, the order at the equivalent point is Na>K> NH_4 for kaolinite and montmorillonite, K>NH_4>Na for illite. For the divalent ions above 70 per cent saturation, Ca montmorillonite, kaolinite, beidellite, and illite ionize more extensively than do the corresponding Mg clays. Below 70 per cent saturation Ca is more ionized from montmorillonite and kaolinite, while the reverse is true for beidellite. Illite in this range shows almost equal ionization of the two cations (Marshall, 1950).

McLean (1949) and Marshall and Barber (1949) have studied bi-ionic clays containing various ion combinations. With montmorillonite, substitution of Ca for H greatly increases K activity. Conversely, substitution of K for H decreases Ca activity, particularly at low levels of Ca saturation. With kaolinite, K activity is also greater when Ca rather than H is the complementary ion. In contrast with montmorillonite, however, the activity of Ca is considerably increased when K is substituted for H. In its Ca-H-K relationships, halloysite is found to be quite similar to kaolinite.

Beidellite and illite are similar in their behavior with regard to ion activities in biionic systems. Ca as compared with H, increases the activity of K. At high degrees of Ca saturation, Ca activity is greater

in Ca-K clay than in Ca-H clay, whereas the reverse is true at lower degree of saturation.

Qualitative correspondence between the behavior of Ca-H-K systems and Mg-H-K systems has been noted (Marshall, 1950). The activity of potassium in K-Mg clay, however, is not so high as that in K-Ca clay with the same ion ratios (McLean and Marshall, 1948; McLean, 1949).

Marshall and Barber (1949) have summarized K-Ca activity ratios as related to exchangeable ion ratios for a number of clays. For a given ratio of exchangeable ions, montmorillonites have high A_K/A_{Ca} ratios, kaolinite has low ratios, and illites, beidellite, and halloysite are intermediate. It is pertinent, perhaps, to note that the differences observed by Marshall and Barber between two samples of montmorillonite and between two samples of illite are large as compared with the differences between mineral species. Perhaps it is unsafe to generalize on the basis of the few data we have at hand.

It is only fair to point out that from strict thermodynamic principles it can be argued that measurements made with cells as are used by Marshall, Peech, and Schuffelen have no significance (Guggenheim, 1929). This has recently been emphasized by Low (1951) for the case of soils and by Jenny *et al.* (1950) for colloidal systems in general. The test of the usefulness of single-ion activity measurements in clays and soils in making predictions concerning rates of cation absorption by and mineral composition of rooted green plants has not yet been made.

III. Growth and Cation Contents of Plants Grown on Natural and Synthetic Soils

1. General Considerations

The ability of plants to utilize soil exchangeable cations is no longer questioned. This was first established by Nostitz (1925) and was soon confirmed by Joffe and McLean (1927), Gedroiz (1930), and Jenny and Cowan (1933). A great deal of subsequent work was concerned with the effect of the concentration and distribution of exchangeable cations on the growth and mineral composition of plants. Growth of plants in response to liming and fertilization of different soil types was studied as well, and certain broad differences between soil types became apparent. Thus, Alway and Nygard (1927) found alfalfa to make optimum growth on peat soils with pH as low as 4.5, whereas a pH at least as high as 5.7 was required for similar growth on mineral soils. Austin (1930) found the soil type more influential in determining the composition of soybeans growing thereon than the application of moderate

amounts of fertilizer. Some ten years ago Vandecaveye (1940) summarized the current status of knowledge concerning plant composition-type of soil interactions as follows: "It is evident that the chemical composition of grasses, small grains, and legumes is influenced to a significant extent by certain broad soil properties, but it is obvious also that the specific soil factors which are responsible for changes in the composition of these crops need further investigation." Since 1940 considerable attention has been devoted to the problem of identifying and studying the soil factors to which Vandecaveye refers.

After the discovery that, in addition to organic exchange colloids, the clay minerals of the montmorillonite, kaolinite, and hydrous mica groups occurred in large amounts in soils, it was a logical consequence that these minerals would be studied in relation to inorganic plant nutrition. Of course, type of colloid is but one of the variables entering into soil-plant nutrition relationships. Intimately associated with type of colloid effects are the effects of degree of base saturation, competition of ions for adsorption and release, and cation exchange capacity. In addition, since this paper is concerned mainly with certain soil factors which affect in one way or another the availability of ions to plants, we cannot avoid occasional excursions into the realm of the plant physiologists. The interactions between different plant species and different soil exchange materials are a very important part of the type of colloid effect.

2. *Degree of Base Saturation*

Degree of base saturation was defined by Hissink (1922) as $100S/T$, where S is the sum of the exchangeable metal cations and T is the cation exchange capacity. The most generally accepted definition of the latter, due to Bradfield and Allison (1933), is the sum of the bases held in exchangeable form by a soil which has reached equilibrium with a surplus of $CaCO_3$ at the partial pressure of CO_2 existing in the atmosphere and at a temperature of 25° C. The difference between T and S is generally designated as exchangeable H, though considerable evidence exists (Paver and Marshall, 1934; Muckerjee *et al.*, 1947) that exchangeable Al comprises a large part of the ions on base-unsaturated clay.

Base-saturated soils have pH values in the range 8–8.5. According to Radu (1940), kaolinitic clays require a higher pH for complete base saturation than do montmorillonites. With decreasing degree of base saturation this difference in pH persists, and for a given per cent saturation, montmorillonitic clays invariably have a lower pH than do kaolinitic clays. The consequences of the differences in the pH-per cent base saturation relationships in the growth and cation content of plants are

far reaching. Before considering these relationships more fully an examination of the soil-plant root system is in order.

In discussing inorganic plant nutrition as related to ion uptake from soils it is desirable to consider soil and plant together as a system. As early as 1928 Kostychew (quoted by Scheffer, 1946, p. 117) suggested that in the process of ion absorption two colloidal systems, the soil and the plant root, are involved. Scheffer concludes that it is reasonable to assume that ion uptake will depend in large measure on the properties of the two colloidal systems involved and on the interactions between them. Recently Williams and Coleman (1950) and Drake *et al.* (1951) have shown experimentally that plant roots actually have cation exchange capacities of considerable magnitude.

These findings coincide to some extent with the views of Lundegårdh (1949, p. 327), who assumes the first step in the absorption of cations by plant roots to be exchange adsorption of the ions concerned on the surface of the root protoplasm. Such an exchange presumably would involve substrate metal cations and metabolically produced H ions. Lundegårdh obtained evidence that the process thought to be exchange adsorption of metal cations by roots follows the mass action law. Recently Schuffelen and Loosjes (1942) have successfully described the course of ion absorption by excised barley roots by means of an equation based on an adsorption hypothesis.

To explain some observations with regard to K absorption by, and outgo from, excised barley roots, Jacobson *et al.* (1950) have postulated the reaction:

$$HR + K^+ \leftrightharpoons KR + H^+$$

in which HR is a product of root metabolism and serves as a K-binding compound in the absorption of K. Of particular significance is their finding that the above reaction is reversible, that is, K is lost from the roots in acid media.

In view of the above current ideas concerning the process of ion absorption by plant roots, it is apparent that the effective concentration of H ions in the substrate is perhaps as important as the effective concentration of the metal cations whose uptake is being considered.

In addition to H^+ derived from root compounds such as those postulated by Lundegårdh (1949) and Jacobson *et al.* (1950), large amounts of metabolically produced CO_2 enter the soil. This CO_2, when dissolved in the soil solution, furnishes further H ions. For root metabolic activity to continue, this CO_2 and its engendered acidity must be removed. In culture solutions this is accomplished by aeration, together with the use of salts which buffer the solution against great fluctuations

in acidity. In soils, the colloids serve as buffers through the exchange adsorption of root-produced H ions.

The amount of H^+ produced by the roots of various plant species varies greatly. Vageler (quoted by Scheffer, 1946, p. 124) has estimated the range to be between 3.6 lb. of H^+ per acre produced by small grains and 22 lb. per acre produced by cotton. In most instances root-produced CO_2, on the basis of chemical equivalents, exceeds many fold the amount of metal cations absorbed by the plants. This root factor was taken into consideration by Truog (1918) in the classification of plant species according to their "feeding power." Newton (1923) and Mehlich and Reed (1948a) considered the relationship between CO_2 produced by roots and the amounts and proportions of various metal cations taken up by different plant species. They concluded that species the roots of which produce large amounts of CO_2 are high in total metal cations and contain a high proportion of divalent cations, as compared with species the roots of which produce smaller amounts of CO_2.

Mattson (1948) and Drake *et al.* (1951) have observed that in general the same plant species which evolve large amounts of CO_2 and which contain high proportions of divalent cations also have roots of high cation exchange capacity. This is shown in Table II. The general correspondence between CO_2 production and root exchange capacity, as

TABLE II

Some Properties of Roots of Various Plant Species

Plant	Energy for Utilizing Ions from Minerals *	CO_2 Respiration † mg./g. in 24 hrs.	Cation Exchange Capacity ‡ me./100 g.
Wheat	Small	74.6	9.0
Barley	Very small	70.5	12.3
Rye	Fairly high	110.8	15.1
Oats	Small	118.9	22.8
Corn	Fairly high	125.5	26.0
Buckwheat	Very high	128.0	——
Potatoes	High	82.3	38.1
Sugar beets	High	130.6	——
Field peas	Very high	106.3	49.6
Red clover	High	146.8	47.5
Alfalfa	Very high	160.5	48.0
Mustard	High	234.4	——

* After Remy; reported by Scheffer (1946), p. 134.
† After Stoklasa, reported by Scheffer (1946), p. 134.
‡ After Drake *et al.* (1951).

well as the general agreement of both with the cation absorption properties of the various species, is apparent. Not so apparent, however, is which factor, CO_2 production or root exchange capacity, is of more significance in affecting the amounts and proportions of metal cations absorbed by plants.

Undoubtedly the fate of root-produced H^+ is intimately related to ion absorption. Overstreet and Jenny (1939), for example, measured rates of accumulation of Na by excised barley roots from equal concentrations of NaCl, Na_2CO_3, and Na clay. At the lower levels of Na, uptake increased in the order given. At higher levels of Na, approximately the same uptake from each source was observed. Considering the exchange of root H^+ for substrate Na^+, the substrate end products are completely ionized HCl, partially ionized H_2CO_3, and partially ionized H clay. From what has been said earlier about the mechanism of ion absorption by plant roots, it seems that the greater uptake of Na from $NaHCO_3$ and Na clay than from NaCl may have been due to the partial immobilization of H^+ in the former systems, that is, the less completely ionized the acid formed in the substrate, the greater the uptake of metal cations. This factor is of greatest significance in dilute systems, in which the proportion of acid formed to salt present is fairly large. As shown by the similar rates of uptake observed by Overstreet and Jenny (1939) from the three sources at high levels of Na, it is of little importance when substrate salt concentrations are high. The idea of substrate H^+ decelerating rates of ion absorption seems valid, in view of the previously quoted work of Arnon *et al.* (1942) and Jacobson *et al.* (1950).

The various types of soil colloids appear to vary widely in their apparent acid strength. Marshall (1944) has given the order of H ionization from clay minerals as kaolinite<illite<montmorillonite. Organic soil colloids probably belong near kaolinite in this series (Allaway, 1945; Mehlich, 1946).

The apparent differences in acid strength noted above are reflected by very different pH values for the several colloidal materials at a given per cent base saturation. As an example, Mehlich (1941) found the pH at 25 per cent Ca saturation to be 5.3 for kaolinite, 3.8 for montmorillonite, 3.9 for illite, and 4.8 for a muck soil. It is not surprising, then, that crops are known to grow successfully at lower degrees of saturation on kaolinitic than on montmorillonitic soils. While not discounting the possible toxic effects of Al and Mn (Schmehl *et al.*, 1950) on plants grown in acid soils, it seems that high effective concentrations of H^+ may have a serious depressing effect on the rate of uptake of metal cations from soils. Jarusov (1938) found the exchangeability of H to

increase with increase in H saturation (fall in base saturation). The yield of mustard also decreased as exchangeable H rose.

A point related to this subject concerns the failure of $CaSO_4$ to improve plant growth on acid soils where Ca may be presumed to be a limiting factor (Fried and Peech, 1946; Lineberry and Burkhart, 1951; Welch and Nelson, 1950). Since addition of this salt serves to replace H ions from the acid clay, its use may make worse rather than better the ratio of the effective concentrations of metal cations to that of H^+. An exception to the generalization that $CaSO_4$ additions to acid soils do not increase Ca uptake is found in work with Ca absorption by peanut fruit. In this case $CaSO_4$ additions are extremely efficacious in increasing the Ca content of the fruit (Mehlich and Reed, 1946; Reed and Cummings, 1948). Application of gypsum to peanuts is standard agricultural practice. A possible explanation for this divergence from the ordinary lies in the low metabolic activity and H^+ production of peanut pegs as compared with plant roots.

In view of the previous considerations and in light of the fact that montmorillonitic clays behave as stronger acids than do kaolinitic clays, it seems that the former will be less efficient in lowering the effective concentration of root-produced H^+ and thus will require a higher degree of base saturation for optimum cation availability and plant growth than will the latter. In addition, Marshall (1948) measures the active fractions of exchangeable alkali and alkaline earth cations to be smaller in montmorillonitic than in kaolinitic systems, particularly at low degrees of base saturation. It is not surprising, then, that all evidence bearing on the subject of cation availability from various types of soils and clays is in essential agreement in showing the necessity for a higher degree of base saturation with montmorillonitic materials than with kaolinites. Mehlich and Colwell (1943, 1946), Allaway (1945), and Chu and Turk (1949) have all obtained evidence which agrees in this respect. Mehlich and Colwell and Allaway obtained results for Ca uptake by plants from various clay systems which closely paralleled the chemical release data shown earlier in Fig. 1. That is, Ca uptake by plants, as well as growth, increased rapidly as the degree of Ca saturation of kaolinitic materials increased to about 40 per cent, but showed only small increases with higher percentages of Ca. With montmorillonites, on the other hand, growth and Ca content of the plants did not reach maximum values until about 80 per cent Ca saturation.

It has generally been found that organic colloids are more like kaolinitic clays than like montmorillonites with respect to degree of Ca saturation necessary for optimum plant growth. This similarity to kaolinite has already been mentioned with respect to pH-per cent saturation relation-

ships and with respect to the release of metal cations by H^+. However, it is not possible to generalize concerning the relative availability of Ca from kaolinitic and organic soil colloids. Allaway (1945) found more Ca in soybeans grown on peat than in those grown on kaolinite with the same per cent Ca saturation and the same level of total Ca. Mehlich and Colwell (1943) also found soybeans to contain slightly more Ca when grown on peat than when grown on a kaolinitic soil when the cation exchange capacity was very low (2 me. per 100 g.), but found the reverse to be true when the cation exchange capacity was 4 me. per 100 g.

Mehlich and Reed (1946), working with peanuts, found consistently higher fruit quality and a higher Ca content of the shells when the fruiting medium was kaolinitic than when it was organic. Peanut plants, however, contained more Ca when grown in organic rather than in kaolinitic media. Water-soluble Ca was found to be higher in the kaolinitic systems, and the authors suggested, in line with the effect of gypsum on peanut fruiting, that Ca absorption by peanut fruit is proportional to solution concentration of Ca.

Mehlich (1952) has suggested that the presence in soils of hydrous oxides of Fe and Al may modify Ca availability-per cent base saturation relationships for the various clays.

The evidence we have thus far considered deals largely with the influence of degree of base saturation on Ca availability to plants. In general, Ca absorption and plant growth increases as the degree of Ca saturation rises. The degree of Ca saturation necessary for optimum growth varies with plant species, but it is generally higher for montmorillonitic than for kaolinitic clays. This is in essential agreement with the chemical release data and ion activity data cited earlier. According to Chu and Turk (1949), soils containing hydrous mica clays may require even higher degrees of Ca saturation than montmorillonite. Chemical studies generally have indicated, however, that in this respect illite should be intermediate between montmorillonite and kaolinite.

Data of several investigators have shown that the availability of Mg and K also increases with degree of base saturation, the soil ratio of Ca : K and Ca : Mg remaining constant as degree of saturation is increased. Thus Chu and Turk (1949) found the K and Mg content of oats and rye grown on bentonite-sand mixtures to increase several-fold as degree of base saturation rose from 20 to 80 per cent. Raising K and Mg levels of the substrate by increasing the exchange capacity (adding more clay at the same degree of saturation) resulted in much smaller increases in the contents of these cations in the plant. It seems, then, that with regard to cation availability from montmorillonitic clays, at least, degree of base saturation is an exceedingly important factor.

In the case of oats and rye grown on kaolinite-sand mixtures, Chu and Turk (1949) observed no such striking increases in Mg and K contents with increase in degree of base saturation. As Mehlich and Colwell (1943) have previously stated, cation availability from montmorillonitic clays seems dependent on degree of base saturation, whereas in the case of kaolinitic clays, though per cent base saturation may still be important, cation availability is more nearly proportional to the total amounts of the ions present.

Epstein and Stout (1951) have related the uptake by tomato plants of certain bentonite-adsorbed micronutrient cations (Fe, Mn, Zn, Cn) to their degrees of saturation. At low percentages of saturation (<0.1 per cent), the amounts of these elements absorbed by plants were found to be nearly proportional to the degree of saturation of the ion in question. It appears, then, that per cent saturation is important when dealing with the availability of the so-called minor elements, as well as that of Ca, Mg, and K.

The plant experiments cited thus far have been concerned almost entirely with cation absorption from partially base-saturated systems. The effect of type of colloid has been striking. When dealing with completely base-saturated systems, the effect of type of colloid on the uptake of cations by plants seems less pronounced and rather inconsistent. Mattson (1948) and Mattson *et al.* (1949), working with completely base-saturated clays in which Ca and K were varied reciprocally from 10 to 90 per cent saturation of each ion, found pea and barley plants to contain consistently more Ca when grown on kaolinitic clay than when grown on montmorillonitic clay. This is in agreement with most findings. In a subsequent report from the same laboratory (Elgabaly and Wiklander, 1949), however, a somewhat similar experiment in which excised barley roots were used as cation accumulators showed more Ca to be taken up from Ca-Na montmorillonite than from Ca-Na kaolinite. Elgabaly *et al.* (1943) found greater absorption of K and Zn by excised barley roots from montmorillonitic clays, though the amounts of these ions released by HCl or H_2CO_3 were in the reverse order. The reasons for these divergent findings are not apparent at present.

3. Associated Metal Cations

Although it is generally found that increasing the degree of saturation of a given ion increases its availability to plants, still a large number of studies have shown the availability of one ion to be greatly affected by the associated ions on the exchange complex. Thus, Horner (1936) found that while the Ca uptake by soybean plants increased

regularly with degree of Ca saturation in Ca-H, Ca-K, Ca-Ba, and Ca-Mg systems, the uptake of Ca was constant when strongly adsorbed methylene blue was the reciprocal ion. Also, Wadleigh (1949), citing the work of Ratner, stated that in a Ca-Na system in the soil Ca availability to plants was reduced.

The celebrated complementary ion principle was evolved by Jenny and Ayers (1939) to account for such findings. According to this, the exchangeability, and presumably the availability, of an exchangeable ion is greater the more strongly adsorbed are the other exchangeable ions, the so-called complementary ions. Thus, a given exchangeable cation, K for example, would be considered more available when the complementary ion is strongly adsorbed Ca, than when it is weakly adsorbed Na. Figure 2, taken from the work of Jenny and Ayers (1939), illustrates the effect of the complementary ions Na, NH_4, and Ca on the release of exchangeable K. Jenny and Ayers found good agreement between the results of chemical release studies such as those summarized in Fig. 2 and the uptake of K by excised barley roots.

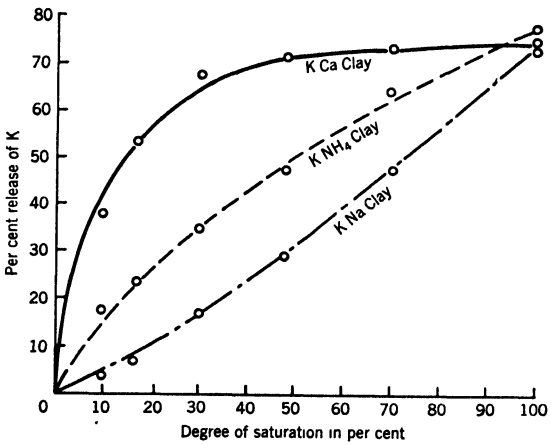


FIG 2. Effect of complementary ions on the release of K by HCl in amounts equivalent to K on the colloid. (Taken from Jenny and Ayers, 1939.)

Thus, far more K was absorbed from Ca-K clay than from Na-K clay. Results of parallel studies by Jarusov (1938) lead to the same conclusions with regard to the effect of associated exchangeable ions on the availability of a given ion species.

In considering the complementary ion effect on plant composition, one must remember that the complementary ion principle as enunciated by Jenny and Ayers (1939) applies to the release of exchangeable

cations from soil colloids. The effect of one ion in either accelerating or retarding the actual root absorption of another ion is a second and independent phenomenon.

In view of the previously discussed different relative affinities of the various types of soil colloids for the important metal cations, the complementary ion principle would lead us to expect different patterns of ion availability from the several clays as the complementary ions are varied. A more or less classic example of this is the question of changes in K availability when an acid soil is limed, resulting in the replacement of H by Ca. Jenny and Ayers (1939) found K to be more available to excised barley roots from K-Ca montmorillonite than from K-H montmorillonite. Bray (1942), on the other hand, concluded from release studies with various Illinois soils, probably containing illite-beidellite-organic exchange materials, that substitution of Ca for H on the exchange complex would decrease K availability. The point is (Mehlich, 1946) that probably both Jenny and Ayers, and Bray are right under certain circumstances. The affinities of the exchange materials they used for H and Ca are very different. Reference to Fig. 1 shows that both Allaway (1945) and Mehlich (1946) found certain bentonites to have a greater apparent affinity for Ca than for H, whereas the reverse was true for illites and for organic colloids. From this, one would expect K availability to increase when certain montmorillonitic soils are limed, whereas K availability might decrease when illitic, organic, or kaolinitic soils are limed, provided, of course, that the degree of total base saturation is sufficiently high to avoid per cent base saturation effects such as those discussed earlier. These considerations seem to call for some modification of Peech and Bradfield's (1943) stand that K availability is decreased by liming an acid soil containing neutral salts, while substitution of exchangeable Ca for exchangeable H in a more or less salt-free soil results in increased K availability.

Marshall and Barber (1949) and McLean (1949) found substitution of Ca for H to increase K activity in systems containing kaolinite, illite, and halloysite, as well as in those containing montmorillonite. These findings are somewhat at variance with the results of the chemical release studies quoted above, in that they infer that K availability should be increased by liming, regardless of type of clay.

The above considerations do not take into account such factors as K fixation by certain clays. This problem has been discussed recently by Gieseking (1949). We will merely point out that K fixation of considerable magnitude occurs in montmorillonitic-illitic soils, whereas fixation of appreciable amounts of K by kaolinitic or organic soils apparently does not occur. Bower (1950) has recently presented evidence to show

that NH_4 fixation by 2:1 clay minerals also takes place. Fixed NH_4 was found to be oxidized only slowly to NO_3 and to be very slowly available to plants.

The results of both ion exchange studies and ion activity measurements have pointed to great differences in the relative probable availabilities of mono- and divalent ions from different types of soil colloids. Such differences have also been reflected in the composition of plants grown on the various types of colloidal materials.

Most attention has been focused on the K and Ca contents of plants. Mehlich (1946) has shown that of plants grown on kaolinitic and montmorillonitic soils with identical cation exchange capacities and percentages of saturation with Ca and K, those grown on the former are relatively higher in Ca and lower in K than those grown on the latter. Similar results have been obtained by Chu and Turk (1949), Elgabaly and Wiklander (1949), and Mattson (1948) (see Table I). From the work of Chu and Turk, it would appear that illite behaves much as montmorillonite with regard to relative Ca and K availability; Mehlich (1946) has found organic colloids to be more like kaolinite.

Since the several types of soil colloidal materials appear to differ with respect to relative affinities for K and Ca, one would expect from the complementary ion principle that increasing degree of K saturation would reduce Ca availability more with certain types of clay than with others. For example, Marshall (1950) finds that addition of exchangeable K reduces Ca activity markedly in the case of montmorillonite, whereas in the case of kaolinite Ca activity is actually increased when K is substituted for exchangeable H. Unfortunately, few data by which we can judge whether Ca availability also becomes smaller for montmorillonite and larger for kaolinite with increase in exchangeable K are at hand. Many data, of which those discussed by Wadleigh (1949) are typical, have shown that high levels of exchangeable K decrease Ca availability. No type-of-colloid effect, however, is apparent. Chu and Turk (1949) found that the amount of Ca taken up by oat and rye plants from both bentonite and kaolinite decreased in about the same manner with increases in exchangeable K at a constant level of Ca. The present authors believe, however, notwithstanding the lack of evidence in its favor, that kaolinitic soils can be saturated to a larger degree with K than can montmorillonitic soils before Ca availability is seriously repressed.

Several papers have dealt with the effect of complementary Mg on Ca availability to plants. Vlamis (1949), for example, found the Ca content of lettuce and barley to decrease sharply when the degree of Ca saturation of Ca-Mg soils fell below 20 per cent. Giddens and Toth

(1951) also observed Ca availabilty to be decreased by large amounts of exchangeable Mg, but observed no effect due to type of soil colloid. Chu and Turk (1949) and Mehlich and Reed (1948) reported similar reductions in Ca contents of plants when soil levels of exchangeable Mg were increased. In general, however, the effect of Mg as a complementary ion on the availability of Ca is less pronounced than that of either Na or K.

The Na ion behaves in a rather erratic manner with regard to its effect on plant contents of other metal cations. In general, from ion exchange and ion activity considerations, one would expect Na as a complementary ion to have a large depressing effect on the availabilities of other exchangeable ions. Apparently, however, the well-known differences between plant species with regard to the absorption of Na (Collander, 1941) largely overshadow the complementary ion effect. Baird and Mehlich (1950), for example, found that Na as a complementary ion had a very large effect on the Ca content of Swiss chard, whereas its effect on the Ca content of cotton was very small. Na was absorbed to a small extent by cotton, but was found to be present in Swiss chard in amounts as high as 207 me. per 100 g. dry weight. Similarly, Lehr (1951) found that additions of $NaNO_3$ to soils decreased Ca taken up by turnips and lupines (species which absorb large amounts of Na), whereas its effect on the Ca contents of rye grass and oats (less Na absorbed) was much smaller. On the other hand, Itallie (1935) found that addition of Na_2SO_4 to soils consistently reduced the Ca and Mg contents of various plant species, without regard to the Na contents of the plants.

No type-of-colloid effect has thus far been observed in the interactions between soil Na and cation uptake by plants. As was deduced for K, Na should depress Ca and Mg availability more in montmorillonitic than in kaolinitic soils.

4. Cation Exchange Capacity

In general, soils are potentially more productive when the cation exchange capacity is high than when it is low. This is well illustrated by the work of Bear and Prince (1945) with alfalfa grown on twenty New Jersey soils. In view of the previous considerations with regard to degree of base saturation and plant growth, it is apparent that this generalization is true only when the cation exchange complex is well charged with bases, particularly Ca and Mg. Mehlich and Colwell (1943) and Mehlich and Reed (1948) found yields of soybeans, oats, and turnips to be greater on high than on low exchange capacity soils when per cent base saturation was constant for all exchange capacity levels.

This was true regardless of type of colloid, of which kaolinite, montmorillonite, and organic were studied. Chu and Turk (1949), however, observed no large increases in yield of oats and rye as cation exchange capacity increased at constant degree of base saturation.

The effect of soil cation exchange capacity on the cation contents of plants is well illustrated by the data presented in Fig. 3. The data are

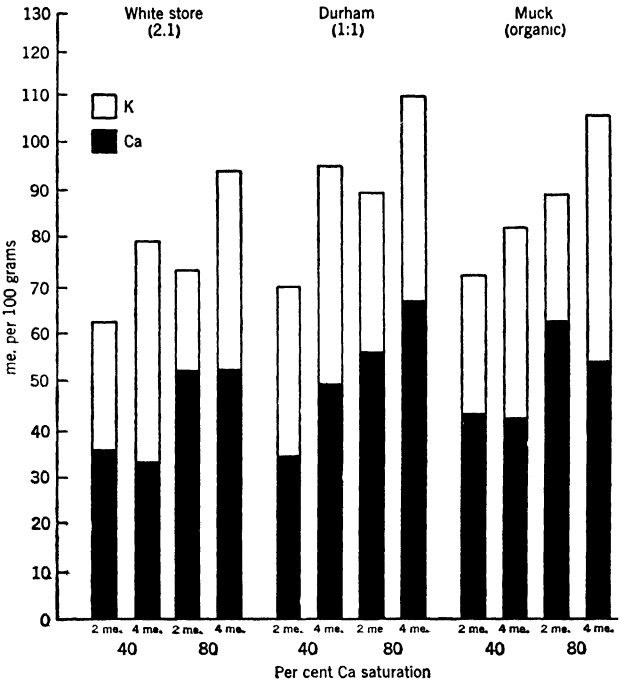


FIG. 3. Ca and K in soybean tops in relation to type of colloid and percentage Ca saturation at 2 and 4 me. cation exchange capacity. (Taken from Mehlich and Colwell, 1943.)

taken from Mehlich and Colwell (1943) and include the contents of Ca, Mg, and K in soybeans grown on montmorillonitic, kaolinitic, and organic soils, each at cation exchange capacities of 2 and 4 me. per 100 g. Ca saturations were 40 and 80 per cent, Mg saturation was 10 per cent, and K saturation was 5 per cent.

In plants grown on the montmorillonitic soil, neither Ca or Mg content was influenced by cation exchange capacity, although Ca in the plants was much higher at the 80 per cent than the 40 per cent saturation level at both exchange capacities. In the case of the kaolinitic soil, Ca

in the plants increased greatly with increased cation exchange capacity. The potassium contents of plants grown on the higher exchange capacity soils, both kaolinitic and montmorillonitic, were considerably above those of the low exchange capacity series.

Mehlich and Reed (1948) studied the cation composition of plants grown on organic colloid-sand mixtures. Cation exchange capacity was varied from 5.2 to 20.8 me. per 100 g. The results with three plant species showed little influence of exchange capacity on the total cation content of the plants. Again it was observed that an increase in cation exchange capacity, at constant per cent base saturation resulted in increased K contents of the plants. On the other hand, when cation exchange capacity was increased and the degree of Ca and Mg saturation and K level were held constant, the Ca and Mg in the plants increased, while K in the plants decreased.

Although the above observations concerning the influence of cation exchange capacity on the relative amounts of K and Ca taken up by plants may at first sight seem analogous to the considerations by Mattson (see Sec. II, 1, p. 74) a distinction must be made between this situation and the one Mattson has treated. In the above cited experiments cation exchange capacity was varied by adding more or less clay to a given amount of sand. The concentration of the "micellar solution," the hypothetical solution containing the exchangeable ions, would be essentially constant in all such sand dilutions of a given clay. Thus the greater availability of K relative to that of Ca when exchange capacity is so increased cannot be ascribed to differences in the concentration of the micellar solution.

In presenting an explanation for this observation, we refer to the idea of Marshall (1944b). He has suggested that in considering the release of K and Ca from any clay, the smaller the percentage of the total exchangeable ions released, the greater will be the proportion of K in the displaced ions. This has been confirmed in many ion exchange studies. Brown and Albrecht (1951), for example, found relatively more Ca than K to be transferred across a collodion membrane from a soil to a H-clay suspension when the proportion of H clay : soil was large than when it was small. It follows, then, that if plants grown on two soils of different exchange capacity remove approximately the same total amounts of ions from each, the proportion of K removed from the higher exchange capacity soil will be great and that of Ca will be small.

It is tempting to extend this reasoning in an attempt to explain, in part, the differences in K and Ca contents of different plant species grown on the same soil with identical levels of soil cations. Reference to Table II shows that plants such as alfalfa and red clover, which con-

tain large percentages of Ca, are high producers of CO_2, whereas cereals such as wheat and barley, which generally contain small amounts of Ca as compared with K, are low producers of CO_2. It seems possible that the release of soil cations accomplished by this root-produced CO_2, large in the former case as compared with the latter, may be such that relatively great amounts of Ca are made available to alfalfa and red clover roots, while less Ca and more K are released in the vicinity of cereal roots.

5. *The Ecological Array of Plants*

An interesting application to the question of the effect of Ca-K ratio and P on the ecological array of plants has been proposed by Albrecht (1940). He assumes that since N is ultimately derived from the atmosphere, the major portion of soil fertility or plant nutrient supply is represented by Ca, P, and K. In view of the variations in these three elements in relation to the degree of soil development, a relationship between these effects and the ecological array of plants may be anticipated. In experiments with colloid cultures he showed that N and P, as well as the Ca-K ratio in the plant, increased with widening Ca-K ratio in the culture medium. These data indicate that the plant quality, at least in terms of N or protein, is improved with increases in the Ca-K ratio. Albrecht then invites the reader to examine the theory in the light of possibly wider experiences. Attention should be called in this connection to the paper by Parker and Truog (1919), which showed the existence of a direct relationship between N and Ca in various plant species. The K content of these plant species fluctuated rather widely although a trend within certain groups of plant species for the K to increase with increasing Ca, is indicated. In an investigation by Horner (1936) with soybeans, the percentage N decreased but the total N increased (due to increased vegetative growth) with increasing Ca-K ratios. Similar results are obtained when the complementary ion is H, Mg, or Ba. With methylene blue as the complementary ion the degree of Ca saturation had no effect on the N content. Data by Marshall (1944c) with four pasture species show the N percentages in the crop to be negligibly influenced by Ca-K ratios. This applies whether the per cent Ca saturation is moderate or whether it is high.

These data indicate that although Ca-K ratios have some effect on the quality of plants, other factors, such as per cent Ca saturation, need to be considered. In an experiment with type of colloid and varying degree of Ca saturation Mehlich and Colwell (1943) found the N content in soybeans to be influenced by both of these factors. Figure 4 reproduces part of their data and shows increasing N content with increasing degree

of Ca saturation for the 1:1, 2:1 and organic colloids. For any given degree of Ca saturation the N content increased in the above order of colloid types. The P supplied was in all cases 5 mg. P_2O_5/100 g. soil. In a supplementary experiment 10 and 20 mg. P_2O_5 were added to the 1:1 type soil. The addition of extra P greatly increased the N content

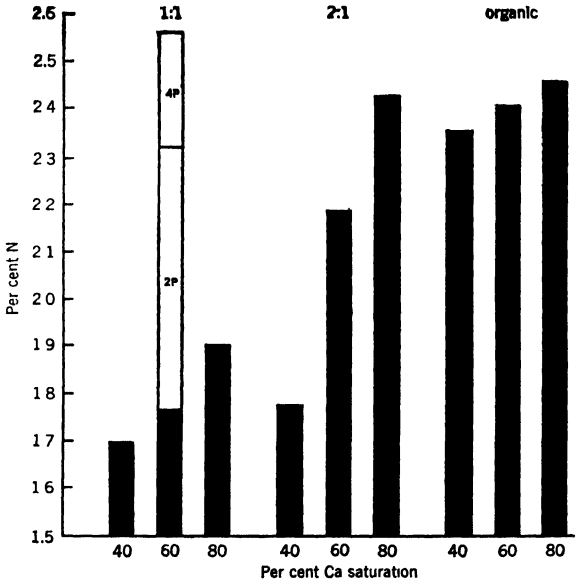


FIG. 4. Per cent N in soybean tops in relation to type of colloid and degree of Ca saturation. (The rate of P_2O_5 was 5 mg. per 100 g. soil. At the 60 per cent Ca saturation level of the 1:1 type 2P and 4P is equivalent to 10 and 20 mg. P_2O_5, respectively. Data taken from Mehlich and Colwell, 1943.)

of the plants, as shown in Fig. 1. It appears, therefore, that other factors in addition to the Ca-K ratio, such as degree of base saturation and supply of P and N greatly influence the quality of plants. To the extent also to which Ca may influence the organic acid content of the plant, plant quality may be affected (Schroeder and Albrecht, 1942; Wittwer *et al.*, 1947).

The mineral content of any plant species may vary so greatly with treatment or nutrient level of soil as to render meaningless classification of plant species in terms of their "average" quality. An example of this is illustrated by some data of Bender and Eisenmenger (1941) in Table III. They grew various plant species on an unlimed soil (pH 4.4) and a limed soil (pH 7.3). The differences in Ca content between species, which initially caused them to be classified either as calciphilic

or calciphobic, were smaller than those produced by liming. Fertilization with K was constant, yet the K content shows no relationship either to feeding power for K [which according to Drake and Scarseth (1940) is low for oats and high for wheat], or to the exchange capacity of roots, [which according to Drake *et al.* (1951) is lower for wheat than for

TABLE III

Cation Content of Plants Grown on an Acid (pH 4.4) and a Basic (pH 7.3) Soil (From Bender and Eisenmenger, 1941)

Plants	Ca		Mg		K	
	A*	B**	A	B	A	B
	%	%	%	%	%	%
Barley (Calciphile)	0.23	0.82	.12	.17	2.18	2.04
Wheat (Intermediate)	0.27	0.50	.15	.18	2.50	1.96
Oats (Calciphobe)	0.21	0.78	.16	.20	2.66	1.56
Sweet clover (Calciphile)	1.27	1.97	.41	.25	2.81	2.49
Cowpeas (Intermediate)	0.66	1.88	.24	.38	3.36	3.32
Peanuts (Calciphobe)	0.77	2.51	.40	.42	2.48	2.74
Kentucky bluegrass (Calciphile)	0.36	1.00	.20	.22	2.56	2.64
Timothy (Intermediate)	0.25	0.96	.13	.21	2.02	2.44
Redtop (Calciphobe)	0.28	1.09	.27	.23	1.79	2.43

* A, acid soil, ** B, basic soil.

oats]. Hou and Merkle (1950), also found the K content of "calcifugous" plants to have as wide a range as "calcicolous" plants. As a further example, the data of Blaser and Brady (1950) on the K content of different plant species grown in different New York soils may be cited. They found the K content of alfalfa to range from 1.0 to 3.71 per cent; for Ladino clover from 0.42 to 4.17; and for timothy from 1.5 to 3.71 per cent, depending on treatment. Equally wide ranges in K content of alfalfa were obtained by Hunter *et al.* (1943). Physiological factors influencing the metabolic activity of roots, which in turn influences the proportion of cations taken up, need to be taken into account as well (Hoagland, 1944; Pepkowitz and Shive, 1944; Cooper *et al.*, 1948).

V. Agronomic Applications

Recognition of the type of colloid as one of the factors influencing the availability of ions and hence crop yield and quality would be expected to have an important bearing on lime and fertilizer practices. In gen-

eral, in soils predominately of the 1:1 type, Ca availability is higher than in soils of the 2:1 type. Since, in addition, the former have lower cation exchange capacities than the latter, smaller amounts of lime are needed to bring the soils to a given degree of Ca saturation (Jones and Hoover, 1950). Furthermore, the lower availability of Ca in soils containing the 2:1 types of clay mineral requires that these soils be limed to a higher degree of Ca saturation. Under New Jersey conditions of agriculture, Bear *et al.* (1945) and Bear and Toth (1948) stipulated that in an "ideal soil" the exchange complex should be made up of 65 per cent Ca, 10 per cent Mg, 20 per cent H, and 5 per cent K. These quantities, calculated on the basis of 1 me. per 100 g. soil, correspond to 260, 24, and 39 lb. of Ca, Mg, and K per acre, respectively. With each milliequivalent increase in cation exchange capacity these amounts would increase accordingly. The Ca-Mg and Ca-K ratios in this system are 6.5 and 13, respectively. The Ca-Mg ratios suggested as "ideal" correspond very closely to those calculated as being optimum for several plant species by Mehlich and Reed (1948b). These ratios were found to lie between 4 and 6. Since, in addition, the proportionate amounts of Ca to Mg taken up by plants were observed to be relatively little influenced by cation exchange capacity (Mehlich, 1946; and Mehlich and Reed, 1948a) the proportions of Ca and Mg suggested by Bear *et al.* may well be the "ideal" condition to strive for. The exchange complex would then be saturated to the extent of 75 per cent. This should be a satisfactory condition for most agricultural crops grown in soils containing colloids of the organic-2:1 mineral lattice type associations. With increasing amounts of organic colloid the percentage Ca saturation necessary for optimum plant growth may be lower (Welch and Nelson, 1950). With decreasing organic colloid, and with crops having unusually high Mg requirement, such as Swiss chard (Baird and Mehlich, 1950), a somewhat higher degree of base saturation and narrower Ca-Mg ratio will be required. In soils containing primarily the organic-1:1 mineral lattice type colloid associations good availability of Ca and Mg should be assured at 40 to 60 per cent base saturation with Ca-Mg ratios of 4 to 6.

The "ideal" of 5 per cent K suggested by Bear *et al.* corresponding to a Ca-K ratio of 13 may require appreciable modification. In contrast to the lower order of interaction between Ca and Mg, the interaction between Ca and K is great and is influenced by type of colloid, cation exchange capacity and plant species. In view of the greater release or availability of Ca from the 1:1 than from the 2:1 type of colloid, a given percentage saturation of K will suppress the availability of Ca in the 2:1 type more than in the 1:1 type. In consequence of the cation equiva-

lent constancy in plants (Itallie, 1938; Bear and Prince, 1945; Lucas and Scarseth, 1947; Wallace *et al.*, 1948) the suppression of Ca will result in a corresponding greater uptake of K. The relative availability of K also increases with increasing cation exchange capacity. Since the cation exchange capacity of the 2:1 clay minerals is greater than that of the 1:1 type it follows that a constant percentage K saturation in the soil will result more readily in "luxury consumption" of K with soils of the former than the latter colloid type. The relatively high availability of K of organic colloids, together with the high cation exchange capacity of this type of colloid will be expected to have the same effect as that of the 2:1 type.

In addition to the soil effects referred to, great variability in the optimum Ca-K ratios in soil required by different plant species are to be taken into account. These ratios, as observed by Mehlich and Reed (1948b), range, for example, from 18 to 36 for oats and timothy and from 18 to 29 for alfalfa and red clover, whereas the "ideal" soil requires a Ca-K ratio of 13.

Using data from the North Carolina Experiment Station, Winters (1945) calculated the K requirement for a 90 per cent yield of soybeans to be 50 and 155 lb. per acre when the cation exchange capacities of the soils were less than 4 and greater than 6 me. per 100 g., respectively. He also found that 90 lb. of exchangeable K produced 70 per cent and 50 per cent yields of cotton for the low exchange capacity soils (about 3 me.) in Georgia, as compared to the higher exchange capacity soils (5 to 12 me.) in Tennessee, respectively. For a yield of 90 per cent the corresponding figures were 160 and 180 lb of K. In a similar comparison with corn, the K levels were 155 and 180 lb. for soils at Tennessee and Illinois, respectively. The highest amount of K, 220 lb. was needed for Irish potatoes. For yields greater than 70 per cent somewhat higher amounts of K are indicated.

Since, as indicated above, the exchangeable K content at 5 per cent saturation corresponds to 39 lb. per 1 me. cation exchange capacity, the amount of 310 lb. or 0.4 me. (which appears to be in fair excess for optimum plant requirements) would be obtained with 8 me. cation exchange capacity. On the basis of the foregoing consideration, it seems, then, safe to conclude that the 5 per cent K level would be "ideal" up to 8 me., whereas the per cent K may safely decrease with increasing cation exchange capacity above this value.

The problem of the availability of K is complicated by the fact that certain members of the 2:1 lattice type, notably vermiculite, fix large quantities of K in nonexchangeable form. In contrast, certain members of the 2:1 lattice family and primary minerals contain large quantities

of nonexchangeable K which becomes convertible into exchangeable and plant available forms.

Studies of the effects of type of colloid on the plant availability of cations can obviously not be fully interpreted from measurements of their exchangeable cation content. Supplementary measurements, involving partial release of cations and particularly the determination and calculation of "fII" values should be considered useful (Bray, 1942; Mehlich, 1946, 1952). Further consideration of the plant factor as influencing the proportionate amounts of cations taken up may likewise aid in the interpretation of the interaction involved (Mehlich, 1946; Mehlich and Reed, 1948b).

A major influence of type of colloid can be expected also in connection with the availability of phosphorus and fertilizer practices with phosphatic fertilizers. In general, the availability of P diminishes with the organic, 2:1, 1:1 and sesquioxide colloids. In view of the associations of large amounts of such oxides as gibbsite, goethite, and hematite with clay minerals, notably those of the 1:1 lattice family, the problem of P availability occupies a major portion of soil research activity (for further details and literature review, the reader is referred to Dean, 1949). Theoretically it may be assumed that the greater the anion exchange capacity in relation to the cation exchange capacity the lower will be the availability of phosphorus for any given percentage P saturation. If this concept should prove to be correct the determination of the cation exchange capacity-anion exchange capacity ratio should prove to be useful supplementary information to the measurement of "available" phosphorus.

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The Physiological Basis of Variation in Yield

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I. Introduction

The kind of knowledge that can be put to practical use in crop husbandry consists essentially of relationships established between crop yield and variation in the environment, especially variation that can be brought about by changing cultural procedures, or in internal factors of the crop plant that can be modified by plant breeding. Such knowledge has been derived partly from the accumulated experience of farmers, but it has been greatly extended and made more precise by scientific field experimentation. These empirical relationships describe the connection between the end points of a long chain of interdependent processes in the environment and the plant, and, broadly speaking, the object of agronomic research is to obtain information on all the links in the chain. To accomplish this, research is necessary, firstly, on the environment itself, to identify and investigate the processes controlling the intensity of

environmental factors that affect plant growth, and secondly, on the growth reactions of the plant that determine yield. On the whole, more attention and effort has been devoted to the study of the first aspect of the yield-environment relationship than to the second.

The problem of accounting for variation of yield in terms of growth and development of the crop plant is obviously very complex, for ultimately it involves the effect of external factors on all the physiological processes of the plant, the interrelation between different processes, and their dependence on internal factors determined by the genetical constitution of the plant. Plant physiological research has produced much information on many of these processes, but it is difficult to apply the results to interpret the behavior of field crops, for the way in which different processes interact to determine growth is little understood. This has been emphasized by Brooks (1948), who pointed out that "the producer of crops is concerned with the integration of all the factors which determine plant growth and development, and it is basic knowledge of this integration which is at present deficient." The plant material used in laboratory studies may consist of detached organs or tissues, and the measurements may be made over short periods of time and in conditions that may fall outside the range normally encountered in the field. The academic physiologist has no special interest in crop plants, but choses species that are experimentally convenient. For all these reasons, the application of the results of physiological research to field problems may involve wide extrapolation and lead to incorrect conclusions. Though, theoretically, it should be possible to predict how crop yield will vary with environment from a synthesis of known effects of variation in environmental factors on individual processes in separate organs of the plant, this would demand a far more extensive and detailed knowledge of plant physiology than exists at present, and perhaps than is ever likely to exist. To discover the physiological basis of variation in crop yield it is therefore necessary to supplement laboratory studies by direct observations on crops growing in field conditions, measuring the simultaneous changes with time throughout the growth period in as many growth attributes as possible, and selecting especially those attributes that are susceptible of a simple physiological interpretation.

Physiological techniques appropriate for laboratory studies are, in general, not suitable for investigations on crops growing in field conditions. One reason for this is that such techniques may themselves change the environment; for example, although it is possible with elaborate apparatus to measure directly the gas exchange of plants growing on a field plot (Thomas and Hill, 1949), this involves enclosing the plants in an airtight chamber or glasshouse, inside which the factors of illumina-

tion, temperature, atmospheric CO_2 concentration, and water supply must differ in intensity in greater or less degree from those outside. A more serious difficulty is that the high variability in the plant population of a field crop necessitates the repetition of each observation on a large number of samples, if accurate estimates of the population means are to be obtained. Consequently only simple measurements, easily and quickly made, are practicable for field studies. Steps can be taken to reduce the labor of sampling by ensuring greater uniformity in the plant population of an experimental plot than is common in practice, for example, by accurate spacing of the plants, but there is a danger that such procedures may produce results inapplicable to normally variable crops.

II. Techniques of Growth Analysis

One of the first attempts to analyze yield in terms of antecedent growth was made by Balls and Holton (1915) and Balls (1917) on the cotton crop in Egypt. They measured the daily growth in height of the main stem, the daily rate of flowering, i.e., the number of flowers opening each day, and the weekly rate of production of ripe bolls throughout the later part of the growing period. The flowering and bolling curves were used to interpret variations in yield produced by differences in spacing and sowing date, water supply, especially the rise of the water table, climatic factors, and boll-worm attack. The height measurements were used chiefly to account for short-period fluctuations in flowering; Balls maintained that these fluctuations, at least in the early part of the flowering period, were correlated with fluctuations in the rate of stem extension occurring about one month earlier, implying that climatic conditions at any time "predetermined" the rate of flowering a month later.

A few years later, Engledow and his colleagues at Cambridge began an investigation of yield in cereals, designed to improve the technique of plant breeding by basing selection from the progeny of hybrids on measured characters of the plant instead of eye judgment. In the first of a series of papers in the *Journal of Agricultural Science*, Engledow and Wadham (1923) outlined the object of their work as follows: "for solving the yield problem by raising new hybrid forms . . . the procedure should be to find out the plant characters which control yield per acre and by a synthetic system of hybridizations to accumulate into one plant-form the optimum combination of yield-controlling factors. It may be that the best existing forms already embody the optimum combinations for a succession of seasons, and thus that owing to the vagaries of the climate no further improvements can be wrought by raising new forms. Only by resolving the cumbersome but economic 'attribute' of

yield into biological characters can these doubts be probed. The procedure for this seems to be a determination of the relation of all acceptable 'plant characters' to yield and of their inter-relations. To carry out the full project for increasing yield by plant breeding, such determinations would have to be followed by investigations of the mode of inheritance of the characters which proved to be related to 'yield' in order that hybridization might proceed on definite constructive lines."

The experimental procedure followed was to make a census of the growing crop, recording at intervals the number of plants per unit area, number of tillers per plant, shoot height, and, at harvest, number of ears per plant, number of grains per ear and weight per grain—the "plant characters" assumed to be related to yield. In some cases, more detailed studies were made, recording the growth of each of the successive tillers and their individual contributions to yield. Many similar investigations were subsequently made in Britain, Australia, and New Zealand (e.g., Forster and Vasey, 1931; Frankel, 1935; Stephens, 1942; the last paper includes a review of the literature), and in nearly all field experimentation on cereals it became the fashion to supplement yield data by so-called developmental studies. In Britain a scheme for making similar observations on wheat at a number of centers was carried on for several years before World War II (Yates, 1936); this had a different aim, namely, to provide data for forecasting yield from measurements of growth made at successive stages prior to harvest.

The experimental techniques of Balls and Engledow consisted in the measurement of morphological characters, or enumeration of organs; the results therefore give a quantitative description of the morphological changes that take place during the growth of the crop, but throw little light directly on the underlying physiological causes, though they may suggest physiological explanations. This was fully realized by Engledow and Wadham (1923) for they remark: "To plant physiology we must look for the final solution of the 'yield problem,' but meantime for plant-breeding the only practicable course is to seek an advance by investigation of the statistical characters which are more amenable to observation than those in terms of which physiology has to proceed."

These census studies did not succeed in defining easily measured yield-controlling characters that the cereal breeder can use as a basis for selection. The reason is that the different yield attributes are not independent expressions of growth. Some of them are inversely correlated; circumstances that increase one tend to decrease another. Consequently, selection for one attribute, for example, ear number per plant, may involve counterselection for another, such as number of grains per ear or grain size, with little or no improvement in yield, but only a change in

its morphological constitution. The chief outcome of the work was to focus attention on plant density as a factor affecting cereal yield. Engledow and his colleagues found that the yield of foot-lengths of drill row within a cereal crop was positively correlated with plant number, and concluded that irregularities in seeding were an important cause of loss of yield. Smith (1937) pointed out, however, that the observed correlation is a result of competition; foot-lengths of drill row with high plant density must on the average be adjacent to less densely planted areas, and therefore suffer less from competition, than foot-lengths with low plant density. If a uniform distribution of plants were established at the higher plant densities found in a normally variable crop, competition would be more severe, and the yield of the crop would not necessarily be increased. Other aspects of this type of analysis of yield, applied to the wheat crop, are discussed by Russell and Watson (1940).

The yield of a field crop is the weight per unit area of the harvested produce or of some specific part of it, and it is therefore more logical to base an analysis of yield on the weight changes that occur during growth than on changes in morphological characters. The first step in developing a procedure for analyzing growth in terms of dry weight change was made by Blackman (1919). He pointed out that increase in dry weight can be regarded as a process of continuous compound interest, the increment produced in any interval adding to the "capital" for growth in subsequent periods. The rate of interest, or relative growth rate,

$$R = \frac{1}{W} \cdot \frac{dW}{dt}$$

where W is the dry weight of the plant at any time, represents the efficiency of the plant as a producer of new material. This Blackman called the efficiency index. The dry matter yield of a plant can then be considered as dependent on (1) the initial capital, i.e., the seed weight, (2) relative growth rate, and (3) the length of the growth period, and variations in yield can be analyzed in terms of these three quantities. However, the dry weight of a plant is not all productive capital, for a considerable part of it consists of skeletal material not active in growth. As dry matter increase is attributable to photosynthesis, apart from the small contribution of mineral nutrient uptake from the soil, a better measure of the productive capital or "growing material" of the plant is leaf size. The rate of increase of dry weight per unit leaf area, $(1/L) \cdot (dW/dt)$ where L is the total leaf area of the plant, is obviously a measure of the excess of the rate of photosynthesis over the rate of dry matter loss by respiration. Gregory (1917) was the first to suggest the use of this function in the analysis of growth and called it net assimila-

tion rate (NAR). Briggs, Kidd, and West (1920) preferred the term unit leaf rate (symbol E). It is clear that the relative growth rate (RGR) is the product of NAR and the ratio of leaf area to total dry weight; this ratio (L/W, leaf area ratio) may be regarded as an index of the amount of "growing material" per unit dry weight of the plant. A possible method of analysis of change in dry weight, therefore, consists in the calculation of RGR, and the further analysis of RGR in terms of NAR and leaf area ratio.

Both RGR and leaf area ratio are complex functions, difficult to interpret, and a form of analysis is possible which does not involve their use. This depends on the fact that the product of NAR and total leaf area gives the *absolute* growth rate in dry weight (dW/dt), and the total dry matter accumulation in any time interval is the integral of this product. Consequently, the progress of dry matter accumulation and its end point yield at harvest can be completely described in terms of the two attributes, NAR and leaf area. The first of them, NAR, is capable of relatively simple physiological interpretation, but the second is the resultant of many physiological processes, and a deeper analysis of yield would involve an examination of the internal and external factors that determine leaf area.

One other attribute that has been used in the analysis of leaf area changes should be mentioned, namely, the relative leaf growth rate $(1/L)\cdot(dL/dt)$. This is useful for comparisons of growth in leaf area at different times in the growth period and for correlation of leaf growth rate with external factors, for it provides a means of eliminating the effect of varying plant size at different stages of growth. However, it is not easy to interpret changes in relative leaf growth rate in physiological terms, as the relation between the growth of new leaves and existing leaves is obviously very indirect, depending on the provision of material by photosynthesis, on cell division in meristems, and on cell extension in leaf initials.

It is convenient to have a name for the technique of investigating growth and yield by the use of the growth functions described above, and among British plant physiologists the term "growth analysis" is commonly used in this special sense.

It is not practicable to make a continuous record of the changes with time in total dry weight and leaf area; instead, they are measured by taking samples from a population of similarly treated plants at intervals, usually a week or multiples of a week. RGR and NAR are then estimated as mean rates over the successive intervals. Fisher (1921) showed that, if W_1 and W_2 are the total dry weights at times t_1 and t_2 respectively, the mean value of RGR for the time interval t_2-t_1 is given by

$\frac{(\log_e W_2 - \log_e W_1)}{(t_2 - t_1)}$ whatever the form of the growth curve. Following Gregory (1926) it has been usual to calculate NAR as

$$\frac{(W_2 - W_1)(\log_e L_2 - \log_e L_1)}{(t_2 - t_1)(L_2 - L_1)}$$

where L_1 and L_2 are total leaf area at times t_1 and t_2 respectively, but Williams (1946) has pointed out that this expression gives an accurate estimate of mean NAR only if the relationship between L and W is linear over the interval $t_2 - t_1$. For short intervals (1–2 weeks) it appears that this condition is approximately satisfied, and the errors introduced are negligibly small, at least for field crops, in comparison with those due to sampling variation in W and L. Estimates of NAR made by this method for longer sampling intervals may have serious positive or negative bias depending on the direction in which the relation between L and W deviates from linearity.

In a field crop the measurements of total dry weight and total leaf area are made on random samples of plants, from which mean values for the plant population are estimated, and the accuracy of the estimates depends on the size and structure of the samples. It is not intended to discuss the statistical problems of sampling here; in practice, the size and number of the samples is likely to be limited by the labor involved, and it is therefore essential to use efficient sampling methods. A procedure for improving the accuracy of estimation of growth increments designed to eliminate errors due to initial differences between samples taken at the beginning and end of an interval was used by Goodall (1945) and has been fully investigated statistically by McIntyre and Williams (1949). Measurements or ratings of a size attribute highly correlated with the growth function to be estimated are made on both samples at the beginning of the interval (the measurement must not, of course, involve destruction or injury of the plants), and the mean values of the growth function for the samples taken at the beginning and end of the interval are corrected to the mean value of the initial measurement or rating. This procedure may permit economy of effort in sampling, but greatly increases the labor of computation.

There is no direct method of measuring the leaf area of a plant in one operation. If the number of plants in a sample is small the total leaf area can be obtained by summing the separately determined areas of individual leaves. Various methods are available for this purpose: printing the leaf outline on blueprint paper and measuring the area with a planimeter, or by cutting out the leaf print and weighing it; measuring appropriate linear dimensions and computing the area from the geometry

of the leaf shape (Gregory, 1921); using an area photometer, which measures the reduction in the light falling on a photoelectric cell when a leaf is placed in the incident beam (e.g., Kramer, 1937; Milthorpe, 1942); estimating the area of each leaf by matching with one of a graded series of standards made by tracing or photographing a suitable set of leaves (Bald, 1943). With larger samples of plants such as are necessary for studies on field crops, it is impracticable to measure the area of each leaf, and the total leaf area must then be estimated indirectly from total leaf weight and the leaf area to leaf weight ratio. This ratio may be determined by weighing and measuring the areas of a small subsample of leaves, but in computing the mean ratio for the whole population of leaves in the sample, allowance must be made for the fact that the ratio varies inversely with leaf weight (Watson, 1937). For plants with large undivided leaves, like sugar beet, a less laborious method is to punch out disks of known area from the bulked leaf laminas of the sample, taking steps to ensure that all parts of the lamina have an equal chance of being sampled. By counting the number of disks in a sample of known weight, the mean area to weight ratio for the whole population of leaves can be estimated.

The samples taken from a field crop may be based on a fixed number of plants or a fixed area of crop. The latter is the only practicable method for cereal crops, for after the onset of tillering it is difficult to distinguish individual plants. It may also be desirable for widely spaced crops, because, in the later stages of growth, interplant competition is likely to make dry weight and leaf area per unit area of crop less variable than per plant. Unit area of crop is also the appropriate basis for comparisons between differently spaced crops.

Much of the remainder of this article is concerned with the analysis of yield in terms of the two attributes NAR and total leaf area, which may be regarded, respectively, as measures of the efficiency and of the capacity of the photosynthetic system. One advantage of this form of analysis is that it effects at least a partial separation of those aspects of growth which are controlled by internal factors from those which depend on external factors, for according to Gregory (1926) "Relative leaf growth rate [and hence total leaf area] is largely dependent on internal factors and is relatively independent of external conditions; whereas, in contrast with this, net assimilation rate has been shown to be wholly controlled by external factors." Though other workers maintain that NAR shows time drifts that cannot be accounted for by change in external factors, the distinction made by Gregory appears to be

broadly true. Before discussing experimental results, however, it is desirable to consider the significance of NAR in greater detail.

It may be noted here that agricultural yield usually refers to the weight, not of the whole plant, but of particular organs, tissues, or chemical constituents that have economic value, such as the grain of cereals, the tubers of potatoes, the fiber of flax, the hairs on the seed of cotton, or the sucrose of the sugar beet root. Comparisons of agricultural yield in this sense between crops would be meaningless, for the definition of yield varies with the crop. The only suitable basis for such comparisons is total dry weight. It is possible for crops of the same species to have equal total dry weights at harvest and yet differ in agricultural yield; this might occur, for example, with different varieties of a species. For a complete analysis of agricultural yield, it would therefore be necessary to examine the causes of variation in the distribution of dry matter between organs and tissues as well as in the total weight of dry matter. This phase of the yield problem will not be discussed here, though it is obviously an important aspect of the special physiology of individual crop species.

III. Limitations of the Concept of Net Assimilation Rate

It is important to bear in mind that NAR is not a pure measure of photosynthesis, but, as the adjective "net" implies, depends on the excess of dry matter gain by photosynthesis over loss by respiration. Consequently, it is not safe to assume that all changes in NAR originate from variation in the rate of photosynthesis. Thomas and Hill (1949) showed by direct measurement of the CO_2 exchange of alfalfa grown in sand culture, but in conditions otherwise similar to those of a field crop, that the loss of CO_2 by respiration of the tops and roots, including that of the tops during the day, amounted to about 40 per cent of the total CO_2 uptake in photosynthesis; for successive cuts of alfalfa, the value increased from 33 per cent to nearly 50 per cent. The total respiration of sugar beets was relatively smaller, about 30 per cent of total photosynthesis. Assuming that respiration is of a similar order relative to photosynthesis for field crops in general, there is evidently plenty of scope for NAR to vary through change in respiration rate independently of the rate of photosynthesis.

When we consider NAR as a resultant of photosynthetic gain and respiratory loss, it is apparent that it involves the expression of respiration rate as the total respiration of the whole plant per unit leaf area. Now, respiration of the whole plant per unit leaf area will vary with leaf area ratio, independently of change in the respiratory activity of

the tissues, merely because the respiration of a varying weight of plant material is referred to unit leaf area. For example, as leaf area ratio falls with advancing age, the rate of respiration per unit leaf area must tend to increase, and hence NAR to decrease, independently of any change in the rate of photosynthesis or of respiration rate per unit dry weight. However, the rate of respiration (per unit dry weight) may also fall with age and so offset the direct effect on NAR of change in the leaf area ratio. These considerations make it difficult to assess the significance of change in NAR with age, or of lack of change, because a time drift in NAR, independent of external factors, might originate from a drift in the rate of photosynthesis, or in the rate of respiration (per unit dry weight), or in leaf area ratio, and absence of a time drift in NAR might arise from opposing drifts in these three attributes.

The same considerations are relevant to the question of what is the best basis on which to express NAR. Ideally, the basis of reference should be a precise measure of the capacity of the system responsible for dry matter accumulation, that is of the "internal factor" or "growing material" of the plant. NAR expressed on such a basis would then vary only with external factors and would be independent of age, nutritional state, and species. Heath and Gregory (1938) maintained that NAR shows these characteristics when expressed on the basis of leaf area, and this would imply that leaf area is a close approximation to the ideal basis. However, as photosynthesis occurs mainly in the leaves, whereas respiration proceeds throughout the whole plant, it seems to be impossible for any one attribute to be a precise measure of the "internal factor" for both processes. Since NAR depends on both photosynthesis and respiration, it follows that there can be no ideal basis of reference for net assimilation that will render NAR wholly independent of the internal factors. The best course seems to be to use a basis of reference appropriate for photosynthesis, since this must be the dominant process whenever increase in dry weight is taking place.

It is conventional to express photosynthesis on the basis of leaf area; textbooks take this for granted and do not explain why leaf area is to be preferred to other attributes such as leaf weight. Presumably the reason is that both diffusion of CO_2 into the leaf and absorption of light are likely to be more closely dependent on leaf area than on any other easily measured attribute. During the greater part of the day, photosynthesis of field crops is probably limited by CO_2 concentration, and in these conditions the rate of diffusion of CO_2 into the leaf is probably not affected by the thickness of the leaf, but depends only on its surface area.

There is obviously a need for uniformity in the basis of expression

of NAR, so that the results of different workers can be compared directly, and this is a strong argument for the continued use of leaf area. Some workers have expressed NAR on the basis of leaf dry weight, solely to avoid the labor of estimating leaf areas. Although this may be satisfactory for comparisons between treatments in particular experiments, the results lose their value for broader comparisons.

Williams (1939) preferred to express NAR on the basis of leaf protein-nitrogen * instead of leaf area or leaf dry weight. The protein-nitrogen content of the leaves was used as a rough measure of the content of cytoplasm, and it was assumed that variations in this content largely determine the time drift of both respiration and photosynthesis. In a later paper, Williams (1946) maintained that the time drift of E_P in experiments by a number of workers conformed more closely with trends in environmental factors than did the time drifts in E_A or E_W and concluded that in a constant environment E_P would be constant over a large part of the growth period, implying that leaf protein-nitrogen is a good measure of the "internal factor" for NAR. If so, E_P should be independent of the nitrogen status of the plant, but, on the contrary, Williams found that E_P varied significantly with nitrogen supply. To account for this he supposed either that part of the leaf protein in plants with a high nitrogen status is present in an inactive storage form or that the effectivity of the cytoplasm as a whole decreases with increasing nitrogen supply. Assuming the first possibility to be correct, Tiver and Williams (1943) suggested that cytoplasmic protein, rather than total leaf protein, would be a more adequate basis of computation though its use would have the practical disadvantage of requiring elaborate analytical procedures. The second possibility, that the effectivity of the cytoplasm varies with nitrogen supply, is merely an alternative way of saying that cytoplasmic protein is not a satisfactory measure of the "internal factor" for NAR. A priori, neither photosynthesis in the leaves nor respiration of the whole plant, the two determinants of NAR, would be expected to depend closely on the amount of cytoplasm in the leaves, because photosynthesis is not a property of the cytoplasm but only of the chloroplasts, and the total respiration of the plant depends on the protoplasmic content of all the organs and not merely the leaves. Instead of attempting to devise a basis of reference

* In the remainder of this paper, NAR will be used to signify net assimilation rate on a leaf area basis. Where comparisons are made with other bases of reference, the notation of Williams (1939) will be used, as follows:

E_A=net assimilation rate on a leaf area basis.

E_W=net assimilation rate on a leaf dry weight basis.

E_P=net assimilation rate on a leaf protein-nitrogen basis.

for NAR that conforms more closely to the ideal, it is better to continue to use the leaf area basis for the sake of uniformity, especially as, for reasons already stated, it appears that no single plant attribute can be a precise measure of the "internal factor" for NAR. The leaf protein basis appears to have no practical advantage, because the estimation of total leaf protein or cytoplasmic protein involves even more labor than the estimation of leaf area.

A source of error in the estimation of NAR of field crops is that the whole root system cannot be recovered, and often NAR has to be estimated from the dry weight of the tops of the plant alone. This will result in an underestimation of NAR, at times when the root system is increasing in dry weight. Williams (1946) has shown that the error introduced may be large in the very early stages of growth, later decreasing and becoming negligible. He concluded that, especially during early stages, the exclusion of the root system may obscure or exaggerate the real effects of a given treatment on NAR because fertilizer and other treatments frequently have differential effects on root and shoot growth; for example, the underestimation of NAR was much greater at a low level of phosphate supply than at a higher level.

Another limitation of the NAR concept arises from the fact that photosynthesis is not entirely restricted to the leaf lamina, but occurs also in other green parts of the plant, in stems and petioles, and in the leaf sheaths and ears of cereals. Consequently NAR is not an exact measure of the efficiency of the leaves in producing dry matter, but overestimates it to an extent depending on the relative amounts of photosynthesis in the leaf laminas and in the rest of the plant. The error is probably small for plants in a vegetative state, but may become serious after flowering. Thus, nearly half the dry weight increase of barley plants after ear emergence is the result of photosynthesis in the ears (Watson and Norman, 1939; Porter, Pal, and Martin, 1950). It should be noted here, since the matter will not be referred to again, that variation in the amount of photosynthesis in the inflorescence may be of some importance in determining variation in cereal yield. Asana and Mani (1950) have shown that varieties of wheat differ in the extent to which the ears contribute toward dry matter production and have suggested that this may have a bearing on varietal differences in loss of yield caused by rust infection.

IV. Experimental Results

1. *Variation of Net Assimilation Rate*

a. Changes with Time. (1) *Smooth trend.* Variation of NAR with time can, for convenience, be considered as made up of two parts, the smooth trend persisting over long periods, and short period deviations from smooth trend.

If NAR were wholly determined by external factors, the smooth time trend of NAR would follow the seasonal trend in climatic conditions. But it is possible that NAR may also vary with time independently of external factors, in so far as the basis of reference fails to be an adequate measure of the internal factor for dry matter accumulation. If the magnitude of the internal factor per unit of the basis of reference changes steadily throughout the growth of the plant, then NAR will show a time drift depending on the age of the plant, even if external conditions are held constant. The time drift observed in a varying environment will then be determined partly by the smooth trends of environmental factors and partly by change in the internal factor with age.

Figure 1A shows smoothed curves of E_A for four species of crops grown in the field at Rothamsted in southeastern England, plotted against time throughout the year. Though values for any one species cover only part of the year, it is evident that E_A undergoes a periodic change; from low values in winter it increases through the spring and summer to a maximum at the end of June, subsequently falling again during the late summer and autumn. The data for only one of the four crops, sugar beet, extend over both the rising and falling phases, but the results for this crop show a peak in midsummer, and this is evidence that the rising and falling trends are not characteristic of different crops, but represent a response to change in the environment, reflecting the seasonal climatic cycle. Though there is no rigid proof, any other explanation seems improbable. It follows that if E_A varies with age, the age effect must be relatively small and insufficient to obscure the time trend induced by seasonal change in external factors. Which of the possible factors, e.g., temperature, day length, light intensity, are responsible for the seasonal variation in NAR cannot be determined from the data, because all the factors are highly correlated in their seasonal trends.

If the time trend of NAR is determined by external factors, the curves of the seasonal cycle of NAR for crops in the northern and southern hemispheres should be opposite in phase. No data exist on NAR of

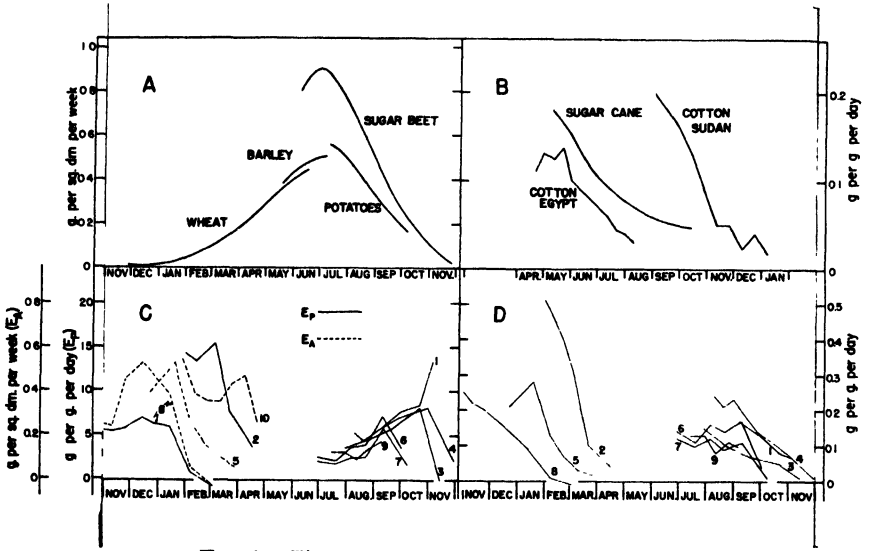


FIG. 1. Time trends in net assimilation rate.

A. Smoothed curves of E_A, averaging results of several field experiments on each of four crops at Rothamsted, England (Watson, 1947a).

B. E_W of field crops of cotton in the Sudan (average of 11 years' data) and in Egypt (average of 10 experiments in 2 years) (Crowther, 1944), and of sugar cane in North Bihar, India (smooth curve drawn through results of 6 experiments in 4 years; Asana, 1950).

C. E_P and E_A in single experiments on plants grown in pot culture at Adelaide, South Australia (experiments 1 to 9) and at Sydney, N. S. W. (experiment 10). (1) wheat and (2) Sudan grass (Petrie and Ballard, 1936); (3) and (4) oats (Williams, 1936; E_P values for experiments 1 to 4 taken from Williams, 1939); (5) tobacco (untopped plants, Petrie, Watson, and Ward, 1939); (6) flax (high-moisture treatment; Tiver, 1942); (7) linseed (high-moisture treatment; Tiver and Williams, 1943); (8) tobacco (untopped plants, high-moisture treatment; Petrie, Arthur, and Wood, 1943); (9) *Phalaris tuberosa* (Williams, 1946); (10) flax (unshaded plants; Milthorpe, 1945).

D. E_W for experiments 1 to 9 at Adelaide.

field crops grown south of the equator, but Fig. 1C shows the changes with time in E_P and E_A for ten experiments on six species grown in pot culture in unheated glasshouses at Adelaide, South Australia (lat. 35°S, compared with 52°N for Rothamsted) and at Sydney, N.S.W., (lat. 34°S). E_P and E_A increased during November and December to high values at the end of December and in January, subsequently decreasing through March and April. There are no records for May, but from the end of June onward all the experiments show a rise in NAR continuing until November, except that in experiments 3, 4, 6, and 7 the

final values fall away sharply from the previous rising trend. These values refer to very late stages of growth, after the emergence of the panicle of oats (experiments 3 and 4) and during the ripening of flax and linseed (experiments 6 and 7) when the leaves were in a state of senescence. Values of E_A for the corresponding stages for wheat and barley were omitted from Fig. 1A. The results plotted in Fig. 1A and C thus agree in showing that in both northern and southern hemispheres NAR on a leaf area or leaf protein basis follows the seasonal climatic trend, fluctuating between high summer values and low winter values.

By an extension of the same argument, it would be expected that crops grown near the equator would show little seasonal trend in NAR. The only extensive series of determinations made in the tropics or subtropics are those of Crowther (1944) on cotton in the Sudan (lat. 14°N) and in Egypt (lat. 30°N), and of Asana (1950) on sugar cane in northern Indian (lat. 25°N). Both these workers computed NAR on the basis of leaf dry weight. The results, plotted in Fig. 1B, show in all three cases a steady fall of E_W with time, except for a short initial rise for cotton grown in Egypt.

Figure 1D shows the time trends of E_W derived from the experiments at Adelaide, for which the E_P and E_A data are given in Fig. 1C. Like those of Fig. 1B all the experiments show a steady fall of NAR with time, irrespective of the time of year covered by the growth period. The contrast between the time trends of E_P (Fig. 1C) and of E_W (Fig. 1D) between July and October is very striking. The fact that, in the experiments during this period, the time trend of E_P follows the climatic trend, while that in E_W does not, has already been noted by Williams (1946).

The conclusions to be drawn from Fig. 1 are that the time trend of NAR, expressed on the basis of leaf area or leaf protein, is determined by seasonal trends in climatic factors and is little affected by age, but that NAR on a leaf weight basis is much more dependent on internal factors, which cause a marked decline with advancing age, sufficient to obscure any time trend induced by change in external factors.

The existence of an age effect on NAR has long been the subject of controversy, which has not yet been settled by critical experiments. Gregory (1926), Heath (1937, 1938), and Heath and Gregory (1938) maintained that E_A and E_W are independent of age up to the time of maximum leaf area. Williams (1937) held, on the contrary, that the leaf dry weight basis gives values that fall steadily with increasing age. Williams (1946) also put forward the view that NAR on a leaf area basis falls with age except during a short phase early in the growth period, but that, on a leaf protein basis, it is independent of age over

almost the whole of the period of growth, except in conditions of high nitrogen supply.

The crucial test would be to make measurements of NAR on plants growing in constant environments. This has not yet been done, presumably because the elaborate equipment necessary for growing large numbers of plants in controlled conditions has not been available to workers interested in the matter. An alternative method is to compare the NAR of plants of different ages, i.e., sown on different dates, growing in the same conditions. This was attempted by Watson and Baptiste (1938), in a field experiment on sugar beet and mangolds, but no significant effect of sowing date on E_1 was established. In another experiment (Watson, 1947a) on three varieties of sugar beet, E_1 of two varieties was significantly increased by later sowing, but that of the third was unaffected. In both experiments, the average effect of sowing one week earlier, that is, of an increase of one week in age, was to decrease E_A by 0.012 g. per square decimeter per week. The mean E_A of all sowings fell steadily with time, the mean rate of decrease per week being 0.054 g. per square decimeter per week in the first experiment and 0.043 g. in the second. These experiments support the view that NAR on a leaf area basis declines with age independently of external factors, though they do not provide conclusive proof, but they also show that the age effect was much too small to account for the whole of the time trend.

Goodall (1945) has determined the time trend in E_W for tomato by a method that avoids any effect of age. He measured the dry weight change of tomato plants at a constant stage of development (the eight-leaf stage) during a twenty-four hour period, and repeated the experiment at intervals of about two weeks throughout a year. E_W increased from low values in December to a maximum in midsummer, and then decreased again through the autumn to a winter minimum. These results show that E_W is subject to a time trend induced by the seasonal change in climate, similar to that in E_A (Fig. 1A), although as already shown, if measurements are made at successive stages of growth of the same crop the seasonal trend is obscured by the much greater age effect. Leaf area was measured on a few occasions, and for these, approximate estimates of E_A were made. The mean estimates for the winter and for the summer, respectively, were 0.12 and 0.48 g. per square decimeter per week, a considerably smaller range than that shown in Fig. 1A, presumably because the plants were grown in a glasshouse, where the range of external factors, at least of temperature, between summer and winter values was not so great as in the field.

(2) *Short period deviations from smooth trend; the effect of climatic*

factors. It is unlikely that internal factors controlling NAR will fluctuate within short periods of time, and it is therefore reasonable to attribute deviations of NAR from smooth time trend to short-period changes in climatic factors. Experimental estimates of NAR will, of course, also show deviations due to random errors. In so far as the deviations in different climatic factors are uncorrelated, it should be possible to estimate the independent effects of different factors by the method of partial correlation. This has been attempted by Briggs, Kidd, and West (1920), Gregory (1926), and Watson (1947a). Briggs *et al.* and Gregory included the whole variation of NAR and of climatic factors in their correlations, and did not eliminate time trend, for they assumed that over the periods examined by them NAR varied only about a mean value and was free from trend. Briggs *et al.* concluded that NAR of maize was correlated more closely with temperature than with any other environmental factor. Positive correlations of NAR with weekly mean temperature and with mean maximum temperature were established. The data for one year provided estimates of the duration of light of different intensities relative to full sunlight, and Briggs *et al.* concluded that the best correlation was obtained when light intensity was assumed to be limiting up to one-fifth full sunlight. In computing these correlations with light intensity, the simultaneous variation in other factors was not eliminated.

Gregory (1926) found that NAR of barley was positively correlated with mean day temperature (or mean daily maximum) and negatively correlated with mean night temperature (or mean daily minimum). His interpretation of this result was that high night temperatures increase respiration loss and so reduce NAR, whereas high day temperatures increase NAR by increasing the rate of photosynthesis. It follows from these relations to day and night temperature that NAR increased with increase in the daily temperature range but was not much affected by variation in daily mean temperature. Gregory (1926) also found a significant positive partial correlation of NAR with total radiation but not with hours of bright sunshine.

Watson (1947a) obtained similar results for field plantings of potatoes and wheat, though the partial regressions were not significant. For sugar beet, however, the signs of the temperature regressions were reversed; NAR was negatively correlated with mean daily maximum and positively with mean daily minimum, so that increase in the daily temperature range depressed NAR, whereas, as before, change in daily mean temperature had little effect. It was considered unlikely that the relationship shown by the regressions on maximum and minimum temperatures represented direct effects of temperature on NAR, and it was

suggested that they arose indirectly from a dependence of NAR on leaf water content. The leaves of field crops of sugar beet often show severe wilting on sunny days during the summer, and this might be expected to reduce photosynthesis by stomatal closure. The daily range of temperature tends to be smaller in cloudy and wet periods than when the sky is clear; a small daily temperature range may, therefore, be an index of conditions favoring maintenance of turgidity in the leaf, and wide daily range of conditions favoring high transpiration rate and wilting. Unfortunately, no records of the degree of wilting were kept, and measurement of leaf water content were made too infrequently to allow a critical test of the hypothesis.

Goodall (1945) attempted to correlate E_W, measured on tomato plants at a constant stage of development on a number of occasions throughout the year, with environmental factors in the glasshouse. The partial regression of E_W on mean daily light intensity was positive and significant, but none of the other factors tested had significant effects. The regression coefficients on day and night temperature were both positive, and that on night temperature was the greater.

The results of these four investigations are sufficient to show that temperature is an important controlling factor for NAR, but the nature of the temperature effects observed is surprisingly variable, suggesting that there are important interactions between temperature and other factors.

The use of partial regression analysis to determine the relation of NAR to environmental factors is an insensitive method for several reasons. The errors of estimation of NAR, especially in field plantings, are often high, so that only very large effects of climatic factors can be detected. NAR is usually determined over rather long intervals, of two weeks or more, and the use of mean values of climatic factors over these intervals involves considerable smoothing of the short-term variations. To test the possibility of any more complex relationship than a linear one involves great labor in computation, nor is it possible to take into account the interactions between different factors that certainly exist. Another difficulty is that some of the standard meteorological measures of climatic factors, e.g., hours of bright sunshine, are not appropriate measures of the environment in relation to plant growth. To obtain precise information on the effects of climatic factors and their interactions on NAR it will be necessary to grow plants in controlled environments, so that the intensity of each factor can be varied independently of the others.

Blackman and Rutter (1948) made an experimental study of the effect of varying light intensity on the growth of bluebell (*Scilla non-*

scripta) and sunflower (*Helianthus annuus*) by subjecting plants to different degrees of shading. They found that NAR increased linearly with increase in the logarithm of light intensity, expressed as a fraction of full daylight. Blackman and Wilson (1951a) have confirmed this result in nine other species at all stages of growth except late in the autumn when the growth rate was very low. The straight line relationship between NAR and log light intensity was found to hold over a long period of the year, (Fig. 2) although NAR in full daylight varied widely (between 0.30 and 0.76 g. per square decimeter per week for sunflower). It was found that shading had no after effect on NAR; plants shaded during April and unshaded plants had the same NAR in May, when compared in the same light intensity. Incidentally, this result implies that NAR is independent of the thickness of the leaves. Shading had little effect on total leaf weight per plant, but increased the area of the leaves and reduced their thickness, i.e., increased the leaf area to leaf weight ratio. The thinner leaves of the shaded plants were

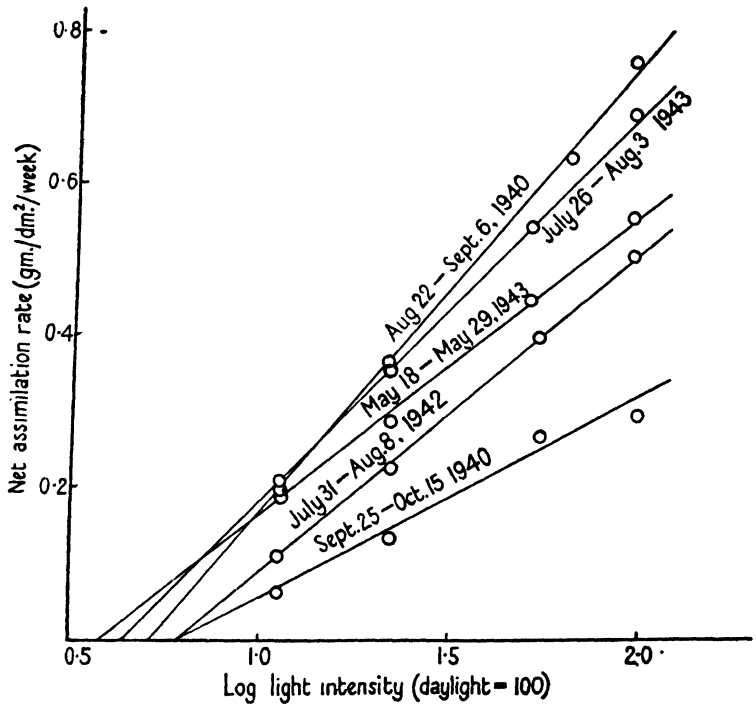


FIG. 2. The effect of varying light intensity on the net assimilation rate of sunflower seedlings *(Helianthus annuus)* at different periods in the summer. (Blackman and Rutter, 1948.)

just as efficient in dry matter production per unit area in May as the thicker leaves of the plants not shaded in April. This is a strong argument in favor of leaf area as a basis of reference for NAR in preference to leaf weight. Watson and Baptiste (1938) similarly found that though late sowing reduced the thickness of the leaves of sugar beet and mangold it had little effect on NAR.

Milthorpe (1945), working on flax, has also shown that shading reduced NAR, but as his experiment tested only two light intensities it gave no information on the form of the relation between NAR and light intensity. Monselise (1951), on the other hand, found that E_A of citrus (Sweet Lime) seedlings was unaffected when the light intensity was reduced by shading to 30% or less of full daylight, but E_W was slightly though not significantly decreased.

Nutman (1937) measured the rate of photosynthesis of coffee leaves in natural conditions and found that the rate varied directly with light intensity when this was low, soon after sunrise or just before sunset or in cloudy periods, but was reduced by the high intensity of full mid-day sunlight, through stomatal closure. The total daily assimilation of leaves on a coffee tree growing in shade was greater than in the sun. It is probable, therefore, that NAR of coffee decreases with increase in light intensity in the region near to that of full daylight, showing that the relationship found by Blackman and Rutter (1948) may not apply to all species.

The sensitivity of NAR to variation of light intensity may play a part in determining the effect of spacing on crop yield. Crowther (1937) found that closer spacing of cotton decreased E_W and attributed this to increased shading of the lower leaves.

b. Variation between Species. Heath and Gregory (1938) collated results reported by various workers on a number of species of plants growing in different environments and concluded that all of them showed practically the same mean NAR during the vegetative phase, and, therefore, that mean NAR is constant for all species and environments. The tabulated values of mean NAR range from 0.12 to 0.72 g. per square decimeter per week, and though reasons are given for rejecting some of the low values, the remainder still cover a considerable range. The evidence for the constancy of mean NAR is not convincing, and the results can more reasonably be interpreted as showing that mean NAR varies with species or environment or both. It has already been shown that the NAR of a species varies with the seasonal climatic trend, and it therefore seems probable that if measurements were made on the same species grown in different places, differences in NAR would be found

corresponding to the differences between local climates, but this has not yet been tested.

Watson (1947a) determined the mean NAR of several species of crops growing in neighboring fields over the same period of the year, so that comparisons between species could be made in nearly identical environmental conditions. Differences were found that were consistent from year to year. The largest was that between wheat and sugar beet; the mean NAR of the latter was nearly twice that of the former. Significant differences were also found between wheat and barley, barley and sugar beet, and potatoes and sugar beet. Some of these comparisons were not independent of age, but there was almost as great a difference in mean NAR between wheat and sugar beet sown within a few days of each other as between autumn-sown wheat and spring-sown sugar beet. An unpublished experiment at Rothamsted in which wheat, barley, and oats sown on the same date in spring were compared, showed the following differences in mean NAR over the period April 27 to June 21:

Mean NAR	Wheat	Barley	Oats	S.E.
Grams per square decimeter per week	0.358	0.312	0.287	±0.0065

Goodall (1950), in West Africa, determined the NAR of cacao seedlings over a period of thirty weeks from planting and obtained values that fall much below any of those tabulated by Heath and Gregory (1938); the mean NAR was only 0.072 g. per square decimeter per week. The seedlings were grown under shade trees in about 20 per cent of full daylight, but though this may partly account for the low values observed, it is probable that cacao has inherently a much lower NAR than the other species for which data exist.

There is also evidence that NAR may vary within a species. Small but significant differences have been found between varieties of potatoes, and high-sugar content strains of sugar beet appear to have a greater NAR than strains bred for high yield (Boonstra, 1939; Watson, 1947a). Cacao seedlings grown from the progeny of four trees differed in NAR during the early stages of growth (Goodall, 1950); mean NAR for thirty weeks after planting ranged between 0.058 and 0.082 g. per square decimeter per week. The existence of interspecific differences in NAR is thus well established, and there is also strong evidence of intraspecific variation.

c. Effect of Variation in Supply of Mineral Nutrients and Water. Gregory (1926) found that a fourfold increase in nitrogen supply to barley grown in pot culture had no effect on NAR in the period up to the attainment of maximum leaf area. Crowther (1934) similarly concluded that E_W of cotton grown in the Sudan was unaffected by nitro-

gen supply, but his results give some indication of a nitrogen effect, and later work (Crowther, 1937) on the same crop in Egypt showed a steady increase in E_W with increasing nitrogen supply. Crowther considered that part of this increase may have arisen from branch elongation across the spaces between the rows, exposing more leaves to high light intensity, but it is difficult to accept the suggestion that the large plants receiving high-nitrogen supply were less subject to mutual shading than the smaller plants receiving low-nitrogen supply. Ballard and Petrie (1936) found that varying nitrogen supply to Sudan grass had no effect on E_W, but wheat grown with 1 g. $NaNO_3$ per pot gave values of E_W consistently less than when the rate of application was 3, 6, or 10 g., and after ear emergence differences in E_W also developed between the higher rates. Similarly, Williams (1946) found that nitrogen supply had no effect on E_W of *Phalaris tuberosa* in the early stages of growth, but later there was a divergence between the nitrogen treatments, and by the end of the experiment, which terminated before flowering and while the weight and presumably the area of the leaves was still increasing, increased nitrogen supply caused a significant increase in E_W.

Using material from the long-continued field experiments at Rothamsted, where differences in nutrient supply have been intensified by repeated annual applications of varied fertilizer treatments on the same plots over many years, Watson (1947b) found that nitrogenous fertilizer increased the NAR of barley in the period before maximum leaf area and that of mangolds throughout the whole growth period. In an experiment on sugar beet grown in sand culture (Morton and Watson, 1948), NAR was unaffected by nitrogen supply, except that, after a change from a low to a high water regime, the NAR of high-nitrogen plants was considerably greater than that of low-nitrogen plants.

The conditions in which a nitrogen response occurs are not yet defined. It may be that NAR is affected only by severe nitrogen deficiency and that over a wide range of higher levels of nitrogen supply it is nearly constant. Gregory (1937) held that variation of NAR with nitrogen supply occurs only in the later stages of growth when leaf area is decreasing owing to senescence and death of the leaves and that it is attributable to more rapid senescence caused by nitrogen deficiency. However, this explanation is inadequate, for several workers have reported responses to nitrogen occurring at early stages of growth while leaf area was still increasing, and when presumably only a small fraction of the total leaf area was in a senescent state.

The data on the effect of phosphate are contradictory. Phosphorus deficiency depressed E_W of oats in the early stages of growth, but later caused an increase (Williams, 1936), attributed in part to delayed se-

nescence of the plants with low phosphate supply. On the other hand, Gregory and Baptiste (1936) reported that phosphorus deficiency had no effect on NAR during the first six weeks of the growth of barley, but subsequently caused a reduction, and Gregory (1937), in a discussion of these results, stated that phosphorus deficiency leads to more rapid senescence of leaves. However, there is evidence that the rate of senescence of leaves may be affected by varying phosphate supply without accompanying change in NAR, and this throws doubt on the hypothesis that variation in NAR caused by change in phosphorus supply is an indirect consequence of effects on senescence. Thus Petrie, Watson, and Ward (1939) showed that increased phosphorus supply delayed yellowing in the five oldest leaves of tobacco, but hastened it in the younger leaves, and topping the plants also delayed senescence, but they were unable to detect any effects of phosphorus or topping on NAR. Watson (1947b) recorded results similar to those of Williams; the NAR of field crops of barley and mangolds was reduced by phosphorus deficiency in the period before maximum leaf area.

Information on the effect of potassium on NAR is scanty. Results reported by Gregory and Baptiste (1936) for barley show that potassium deficiency caused a reduction through the whole period of observation. This was confirmed by Watson (1947b) for the early stages of growth, but in mangolds application of potassium increased NAR only at a low level of nitrogen supply. Potassium is generally supposed to play a special role in relation to photosynthesis, and it is surprising that in these field experiments the effect of potassium on NAR was small compared with those of nitrogen and phosphorus.

Application of farmyard manure increased NAR of barley and mangolds in the period before maximum leaf area was attained (Watson, 1947b) and showed negative interactions with fertilizer applications. These interactions may be interpreted as indicating curvature in the response to increased nutrient supply, but that between farmyard manure and nitrogenous fertilizer may be a consequence of the supply of potassium by the farmyard manure, for the $N \times K$ interaction was also negative, as noted above. With this exception, the interactions between mineral nutrients were small and positive; each of the nutrients increased NAR, the effect of nitrogen being the greatest, and each had a greater effect in the presence of the others. In the period after maximum leaf area, however, the interactions were large compared with the main effects. The significance of these interactions is doubtful, because the designs of the old experiments used as source of plant material provide no estimate of error, and it is possible that the apparent interactions resulted from the lower accuracy of estimation of NAR in the

later stages of growth. However, the results at least suggest that, after leaf area ceases to increase, the effect on NAR of variation in one nutrient becomes more dependent on the supply of other nutrients than in the previous growth phase. If the interactions are real, they may reflect differences in the rate of senescence of leaves. In the barley experiment NAR was low where two of the three nutrients (N, P, and K) were applied and the third omitted; these are the conditions likely to produce the most severe deficiency symptoms in the leaves and the greatest differences in senescence rate. However, it seems that too much emphasis has been placed on the possible role of senescence in determining the effect of nutrient supply on NAR, and there is no doubt that nitrogen, phosphorus, and potassium can all affect NAR of fully functional leaves.

Several workers have found that NAR was depressed by reduction in water supply (Tiver, 1942; Petrie, Arthur, and Wood, 1943; Tiver and Williams, 1943; Morton and Watson, 1948), but there is no trace of such an effect in the results of Milthorpe (1945). The reason for the discrepancy is not obvious, for the severity of the restriction on water supply appears to have been similar in all the experiments. The low-water treatments permitted variation in moisture content of soil or sand between field capacity and the wilting point, while in the high-water treatment the moisture content was held close to field capacity. Drought seems to have no cumulative or after effects. The NAR of plants subjected to drought after a period of high-water supply fell to that of plants grown throughout in a low-water regime, and on return from a low- to a high-water supply NAR recovered completely and became equal to that of plants receiving continuous high-water supply. As the fall in NAR lasted only as long as the drought conditions, it seems reasonable to attribute the decrease of NAR to stomatal closure associated with wilting, and not to a change in leaf structure or composition, because such changes would persist for some time after restoration of full water supply. However, Petrie *et al.* (1943) have suggested other explanations.

d. Conclusion. An earlier review of the literature led Heath and Gregory (1938) to conclude that NAR in nature is not a very variable quantity, and Gregory (1950) apparently still holds this view. The present survey gives a decidedly different impression, for it shows that NAR varies between and within species, with mineral nutrition and water supply, and, very widely, with seasonal climatic conditions. However, the significance of this variation in relation to dry matter accumulation and yield depends on its magnitude in comparison with the variation in leaf area, and this will be discussed in a later section.

2. *Variation in Leaf Area*

Agricultural yield is usually measured in terms of weight of crop per unit area of land. In an analysis of the causes of variation in dry matter yield, it is therefore appropriate to express the leaf area of a crop on the same basis as yield, that is, as the area of leaf surface per unit area of land surface, rather than as leaf area per plant, especially if comparisons are to be made between different species of crop. The term leaf area index (LAI) has been proposed (Watson, 1947a) for this measure of leaf area. If leaf area and land area are expressed in the same units, LAI is a pure number independent of the units of area measurement. For a single species, grown at approximately constant spacing, variation in LAI depends mainly on change in leaf area per plant. The spacing of different species, however, varies widely in agricultural practice, being adjusted in accordance with experience or the results of field experimentation to give maximum yield. Differences between species in LAI therefore depend on differences in plant population as well as in leaf area per plant.

a. Changes with Time. The variation with time in LAI has been measured in a number of field crops grown at Rothamsted (Watson, 1947a); the results are shown in Fig. 3. For autumn-sown wheat, LAI remained very small, less than 0.1, throughout the winter, but began to increase in March. The rate of increase in LAI at first increased with time, but later decreased, falling to zero in early June when LAI reached its maximum. Subsequently, LAI fell steadily until harvest in early August. It is evident that LAI of wheat changed continually throughout the growth period and did not assume a steady value at any stage. The maximum values of LAI ranged from 1.5 to 4 in the three wheat crops investigated.

The prolonged initial phase of low and very slowly increasing LAI of autumn-sown wheat was not shown by spring-sown barley; presumably it was a consequence of winter climatic conditions. The curves for barley and wheat were otherwise similar, except that the maximum value for barley occurred later, at the end of June. The maximum LAI, about 2.5, fell within the range of values found for wheat.

The graphs of LAI of potatoes show an initial rise and a final fall, but the peak was more flattened than in the cereals, and occurred later. There was a period during August and September when almost steady values of LAI were maintained, at about 1.5 for the 1937 crop and between 2 and 2.5 for the 1938 crop.

The data for sugar beet are more extensive and give some indication of the range of variation in LAI between crops of the same species

grown in different seasons in the same locality and with similar agricultural treatment. The graphs for the early phase of increasing LAI are concave upward, showing that the rate of increase of LAI tended to increase with time as in the cereals. The spread between the results for

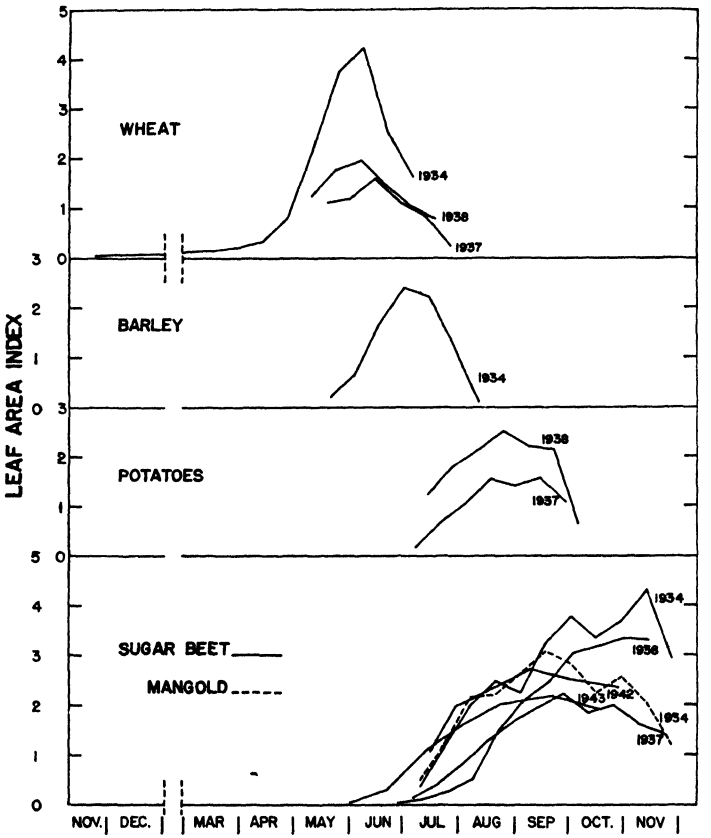


FIG. 3. Change with time in the leaf area index of field crops grown at Rothamsted. (Data from Watson, 1947a, replotted.)

different crops in this stage is accounted for largely by variation in the date of sowing. From the end of August onward the graphs flattened off to nearly steady values, so that for the whole growth period they had an S-shaped form. However, there was a tendency for LAI to fall during October and November. This fall was more pronounced in the single crop of mangolds for which data are given in Fig. 3 than in sugar beet. The maximum values of LAI varied between 2 and 4 and

occurred still later than for potatoes, in September, October, or November.

Boonstra (1929, 1937) has published data on the leaf area of field crops of oats and sugar beet which show variation with time similar to that described above. Other workers on growth analysis have either used material grown in pot culture or, if they have used field material, have preferred to measure leaf weight instead of area.

The variation with time in LAI is mainly ascribable to change in leaf area per plant, though changes in plant number also play some part. The plant population of field crops tends to decrease with time through deaths from disease and other causes. In winter wheat, for example, the loss of plants between germination and harvest may be as high as 25 per cent of the initial population (Russell and Watson, 1940). In other crops, such as sugar beet, that are thinned to a prescribed spacing at any early stage, the subsequent losses are usually small.

The initial increase of LAI in wheat and barley is associated with tillering. During this phase the number of meristems producing leaves increases. Shoot number reaches its maximum when LAI is still small, and many of the younger shoots subsequently die. The growing points of surviving shoots eventually cease to produce leaves and become inflorescence initials. The large increase of LAI that occurs in May for wheat and in June for barley (Fig. 3) takes place during the phase of stem elongation and is the result of expansion of existing leaves. LAI reaches its maximum at about the time when the shoots have attained half their final height. The decline in LAI which follows is due to senescence and death of the leaves in succession from the base of the stem upward.

In other crops, the developmental sequence that gives rise to changes in LAI with time may be much simpler than in the cereals. For example, sugar beet plants remain in a vegetative state in their first season's growth and continue to produce new leaves until harvest. The changes in leaf area here depend almost entirely on the activity of a single apical meristem, and on the growth and longevity of the leaves it produces. Lateral buds may also develop, to a varying extent on different plants, especially in the late stages of growth, but they produce only small leaves, unless the apical growing point is damaged, and contribute little to total leaf area.

General descriptions of the changes in plant population and in the morphology of the crop plants, such as those outlined above, can be amplified and made quantitative by means of census and developmental studies (Sec. II), but they give no information on the physiological

causes of variation in leaf area. Much of the information derived from developmental studies has little relevance to leaf area considerations, because the selection of growth attributes for measurement has usually not been made with this purpose in mind.

Variation in the total leaf area of a plant may be brought about through change either in leaf number or leaf size. The number of leaves present at any time is the difference between the total number of leaves produced up to that time and the number which have died; it therefore depends on the number of growing points, the length of time during which they produce leaves, the rate of leaf production during this period, and the length of life of the leaves. Variation in leaf size may arise from effects on cell division, resulting in differences in cell number, or on cell extension. Physiological analysis of variation in leaf area must therefore take account of the effects of internal and external factors on the following aspects of leaf growth:

(1) Those involving meristematic activity; the division of shoot meristems, leading to increase in the number of growing points; the rate of production of leaf primordia; induction of flowering, terminating the production of leaves at a shoot growing point.

(2) Those concerned in leaf expansion; the rate and extent of cell division and cell extension.

(3) Those determining senescence and death of leaves.

It is not yet possible to account for variation of LAI with time or between species in these terms. Some rather fragmentary information exists on the relative importance of the different aspects of leaf growth in determining differences within a species between strains or varieties and on the relationships of particular aspects to internal and external factors. These will be discussed in the following sections.

b. Intraspecific Differences. European varieties of sugar beet include strains selected for the highest fresh-weight yield of roots consistent with reasonable sugar content, usually known as *E* types, and others selected for the highest sugar content, known as *Z* types. *E* types have larger leaves with a higher water-content than *Z* types. Boonstra (1937) compared two such strains (*A* and *Z*) of the variety Kuhn, and found that the rate of production of leaves was lower in the high-yielding strain (*A*) than in the high-sugar content strain (*Z*). Leaves of *A* also had a shorter life than corresponding leaves of *Z*, although they continued to expand over a longer period. Consequently, *Z* had more living leaves than *A*, except in the early stages of growth, and the difference tended to increase as growth proceeded. The higher leaf number of *Z* was insufficient to counterbalance the greater leaf size of *A*, so that *A* had the higher leaf area per plant, but the superiority

of A over Z decreased from mid-August onward and fell to zero at harvest in late October.

Similar results were found in a comparison between an E type sugar beet strain and a variety of mangold (Watson and Baptiste, 1938). The mangold had larger leaves, but the sugar beet had a greater leaf number, resulting from a higher rate of leaf production and a lower death rate. In this case, higher leaf number outweighed smaller leaf size and produced a greater leaf area per plant in sugar beet than in mangold. These results suggest that, over the range of agricultural varieties of *Beta vulgaris,* leaf size tends to fall and leaf number to rise as sugar content and dry matter content increase and that the rise in leaf number depends both on more rapid production and on longer life of leaves. There is evidence of a similar inverse correlation between leaf number and leaf size in comparisons between varieties of wheat and potatoes (Watson, 1947a).

The possible significance of variation in the vitality of leaves in relation to yield was first pointed out by Boonstra (1929); he used "vitality" to signify "continuance of function" or "lebensdauer," and this is probably better described by the term "longevity." He showed that four varieties of oats differed considerably in the length of life of corresponding leaves, and found some evidence of an association of long life with high yield. Differences in leaf size and in the number of leaves produced also contributed to determine the differences in total leaf area responsible for the varietal differences in yield, but his data are inadequate to determine the relative importance of these and of variation in longevity of the leaves.

c. Effect of Climatic Factors. Gregory (1921) investigated the changes with time in total leaf area of cucumber plants grown in a glasshouse at approximately the same temperature at different times of year. The rate of expansion of leaf area was greater in summer than in spring or winter, and this was attributed to higher light intensity and longer photoperiod. The average leaf area over the growth period (about thirty days) in the different experiments was found to be proportional to the total radiation received. The same result was found for plants grown in continuous artificial light of intensities comparable to daylight in the glasshouse in December, but at a higher temperature. In the spring and summer glasshouse experiments, relative leaf growth rate (RLGR) was approximately constant throughout the growth period, but in the December experiment and in artificial light RLGR fell steadily with time, and this was attributed to a detrimental factor associated with the low-light-intensity, high-temperature conditions.

In continuous artificial light, total leaf area increased with increase

in temperature up to about 25°C., but decreased with further rise in temperature (Gregory, 1928). The initial rate of expansion of the cotyledons increased with rise in temperature, but their final area was reduced at supraoptimal temperatures by inhibition of cell division. At temperatures in the suboptimal range, RLGR calculated for the foliage leaves alone decreased with time through the operation of a detrimental factor associated with low-light intensity, but was independent of temperature. The effect of temperature in this range on total leaf area was therefore wholly determined by the time taken for the first foliage leaf to unfold, that is to say, by an effect on development of the apical bud; this effect had a normal temperature coefficient (Q_{10}) of 2.5. RLGR decreased with rise of temperature above the optimum, and the rate of fall of RLGR with time increased. The accelerated fall of RLGR with time was attributed to change in distribution of material between stem and leaf and to a check in cell division in the leaf primordia. These results led Gregory to postulate that leaf expansion depends on the production of a "leaf forming" substance by a photochemical reaction, independent of carbon assimilation, acting on a nitrogenous substrate in the leaves or on a precursor stored in the cotyledons. This hypothesis would account for the absence of any effect of temperature in the suboptimal range on RLGR and for the observed increase of RLGR with increased light intensity and duration. It also implies that RLGR is independent of the rate of carbon assimilation.

Very different conclusions were reached in a study on barley grown in pots and exposed to natural summer weather conditions (Gregory, 1926). The relation of deviations of RLGR from a smooth time trend to various climatic factors was examined. In contrast with the results of the cucumber experiments it was found that RLGR was correlated positively with mean day temperature and negatively with mean night temperature and with total radiation. The deviations of RLGR from smooth trend were found to be independent of NAR. The partial correlation of RLGR with evaporating power of the air was not significant though fairly large; contrary to expectation its sign was positive, and this was thought to be an indirect effect arising from an association of low evaporating power with waterlogging or leaching caused by high rainfall.

Blackman and Rutter (1948, 1950) found that plants of *Scilla nonscripta* grown in the open under shades produced a larger total leaf area than plants grown with full daylight illumination. The weight of leaves was little affected by shading. The ratio of leaf area to leaf weight decreased linearly with increase in the logarithm of light intensity, expressed as per cent of full daylight. The ratio of leaf area to total plant weight also showed a linear relation to log light intensity.

Similar effects of shading on leaf-area ratio were found in experiments on other species, including some economic plants (Blackman and Wilson, 1951b). Monselise (1951) also showed that the leaf area of citrus (Sweet Lime) seedlings was increased by shading, and as NAR was unaffected, the rate of increase of dry weight was greater in shaded than in unshaded plants. Milthorpe (1945), on the other hand, found that shading reduced the leaf area of flax by decreasing both leaf number and leaf size. His plants were grown in a glasshouse with a mean day temperature about 80°F. and a mean night temperature about 70°.

It is reasonable to conclude that growth in leaf area in open-air conditions is decreased by increase in illumination, whether continuous or temporary, and is also affected by temperature. However, the results of Gregory and of Milthorpe indicate that in some circumstances, possibly when temperature is high, leaf area may increase with increase in illumination.

Watson and Baptiste (1938) showed that the rate of leaf production from the apical growing point of sugar beet or mangold increased with rise in temperature and concluded that both the smooth time trend and short-period deviations in the rate were determined chiefly by temperature variation. The temperature coefficient (Q_{10}) of the rate of leaf production, calculated from the regression of the logarithm of the mean rate for sugar beet and mangold on mean temperature for successive weekly periods, was 2.4 and was not significantly altered when time trend was eliminated. There was evidence of an after effect of low-temperature exposure, for on return to a higher temperature the rate of leaf production was temporarily higher than would be expected from the magnitude of the temperature rise. The rate of death of leaves could not be shown to depend on temperature, except that late in the year it increased as the result of injury by frost. There was no obvious seasonal trend in the death rate, and this suggests that it was not greatly affected by environmental conditions.

There is evidence from Gregory's experiments on cucumber that external conditions at or soon after germination may have a continued effect on the subsequent course of leaf area development; variation of temperature in the suboptimal range had no effect on RLGR of the foliage leaves, and the differences in total leaf area between plants grown at different temperatures were wholly determined by the time of unfolding of the first foliage leaf. The effect of variation in date of sowing on the leaf area of sugar beet and mangold (Fig. 4) may have a similar explanation. Delay in sowing reduced leaf area per plant (and also LAI since the plant populations were similar for all sowings) in July

and August, but late-sown plants eventually developed a larger leaf area than early-sown plants (Watson and Baptiste, 1938; Watson, 1947a). This was brought about by an increase in leaf size, because the late sowings had a smaller number of leaves than the early sowings throughout the growth period. The larger leaves of the late-sown plants

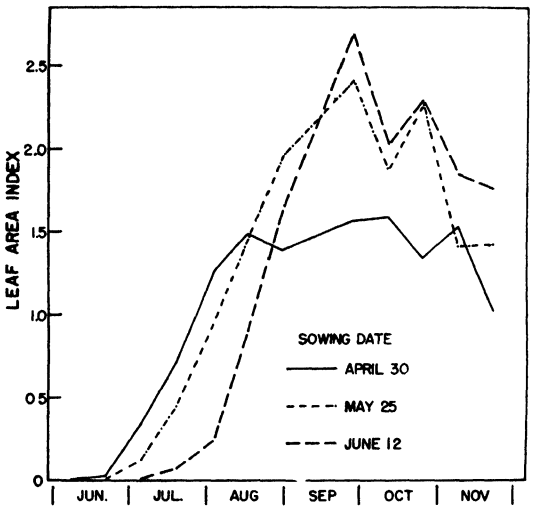


FIG. 4. Effect of date of sowing on leaf area index of sugar beet (Means of three varieties. Data from experiment 5, 1937; Watson, 1947a.)

were also thinner and had a higher area to weight ratio. Thus, in the later stages of growth leaves initiated at the same time attained a much larger size in the late-sown plants than in the early-sown. Since the climatic conditions during their growth were identical, the external cause of the difference in leaf expansion must have operated at an earlier stage. The intensity of climatic factors at and soon after germination varied with the date of sowing because of the seasonal trend in climate, and it seems necessary to assume that this variation in climate at the beginning of the growth period induced differences in the internal factors controlling leaf expansion that persisted throughout subsequent growth. Variation in the date of sowing also affected the relative growth of stem and root and the distribution of assimilate between them, but whether this was a cause or a consequence of the change in leaf expansion is not clear. Nor is it known which climatic factor was the operative one.

Temperature and light may greatly influence the ontogenetic drift in

leaf area through the control of flowering by vernalization and photoperiodism. According to Konovalov (1944) vernalization of wheat accelerates the rate of production of leaves and shortens their period of growth but not their functional life. In consequence the leaf area of the plant at any given stage of growth is increased, although the final size of individual leaves is little affected. When an inflorescence develops at a growing point, production of leaves ceases, and in addition, the presence of the growing inflorescence has an inhibitory effect on the expansion of the young leaves immediately below it. This fact is utilized in the commercial practice of topping tobacco plants; removal of the inflorescence causes the upper leaves to grow larger than in intact plants (Avery, 1934; Petrie, Watson, and Ward, 1939). The inflorescence affects cell extension in the upper leaves and not cell division, for the increase in leaf area produced by topping is the result of increase in cell size, and there is no effect on cell number except in the vascular tissue. Another consequence of flowering that may affect leaf area is the breakdown of apical dominance, permitting lateral buds to develop.

Temperature may affect the leaf area of perennial plants through control of bud dormancy. An interesting example of this is found in cacao. This species, like many other tropical trees, shows periodic renewal of bud development, leading to the production of new leaves in a succession of "flushes," so that growth in leaf area follows a stepwise course (Goodall, 1950). In young seedlings, flushing appears to be independent of external factors, but in mature trees it occurs only when the daily maximum air temperature rises above 83°F. and is inhibited at lower temperatures. (Humphries, 1944; Greenwood and Posnette, 1950).

d. Effect of Variation in Supply of Mineral Nutrients and Water. It is a familiar fact requiring no documentation that the leaf area of plants, in common with other size attributes, is greatly dependent on nutrition. The way in which the different aspects of leaf growth listed at the end of Sec. IV,2a are influenced by the supply of mineral nutrients is far from being fully analyzed. The following account of some of the effects involved is based on observations on material from field experiments at Rothamsted (Watson, 1947b), except where other authors are quoted.

Variation in nitrogen supply affects all the phases of leaf growth. Increase in leaf area produced by application of a nitrogenous fertilizer results from increase in both leaf number and leaf size. The higher leaf number may be caused either by an increased rate of production of leaves from each growing point, as, for example, in sugar beet or mangold, or by increase in the number of growing points, as in cereal crops,

the tillering of which is greatly dependent on nitrogen supply. Morton and Watson (1948) found that the larger leaves of sugar beet plants receiving a high-nitrogen supply had more cells and larger cells than corresponding leaves of low-nitrogen plants, showing that nitrogen supply affects both cell division and cell extension in the leaf. Because of this multiplicity of effects, application of nitrogenous fertilizer tends to increase leaf area throughout the whole growth period.

In contrast with the effect of nitrogen, those of phosphorus and potassium appear to be more transitory. Phosphate application was found to increase the leaf area of cereal crops mainly by increasing tillering, and its effect was greatest near to the time of maximum shoot number. Subsequently it declined, falling to zero at about the time of maximum leaf area. This suggests that leaf size in cereals is not increased by increase in phosphorus supply. Indeed, it may be reduced; Morton and Watson (1948) found that the area of the penultimate leaf on the main shoot of barley was consistently less on plots receiving phosphate than on plots where phosphate was omitted. Potassium had little effect on leaf area of wheat or barley during the tillering phase, but increased leaf area during the subsequent phase of shoot extension, presumably by increasing leaf size or by delaying senescence. A similar difference between phosphate on the one hand and potassium and sodium salts on the other was found in experiments on mangold and sugar beet; phosphate increased the number of leaves per plant, whereas potassium and sodium had no effect on leaf number but caused greater leaf expansion. However, in mangold phosphate also increased leaf size. Petrie, Watson, and Ward (1939) also found that increase in phosphorus supply to tobacco increased leaf size, and in this case the effect on leaf number was small.

Information on the effect of nutrition on the length of the functional life of leaves is scanty. Application of nitrogenous fertilizer slightly increased the death rate of leaves of mangolds, but the increase was smaller than that in the rate of production, and this may indicate an increase in the longevity of the leaves. As already noted (Sec. IV,1c) the evidence on the effects of phosphorus supply on the senescence of leaves is contradictory. As the effect of potassium in increasing the leaf area of barley was most marked during the period when leaf area was decreasing from its maximum, it is possible that increased potassium supply delayed senescence of the leaves.

In general, restriction of the water supply reduces leaf area. Petrie, Arthur, and Wood (1943) found, however, that this was true only for the earlier part of the growth period of tobacco. Drought conditions delayed senescence of the leaves, causing a slower decline of leaf area

from its maximum, so that plants grown with a continuous high-water supply ultimately had a smaller leaf area than plants subjected to drought. In experiments on flax (Milthorpe, 1945), drought reduced leaf area throughout the whole period of growth, by reducing leaf number. This was largely the result of the more rapid death of the lower leaves of plants receiving a restricted water supply and partly because there were fewer tillers. There was no reduction in leaf size by drought. Maximum leaf area was attained earlier in droughted plants, and this also was a result of earlier and greater dying off of leaves. The effect of drought on senescence of the leaves was thus the opposite of that found for tobacco. Variation of water supply had little effect on the rates of production or death of leaves of sugar beet, (Morton and Watson, 1948) ; the reduction in leaf area by drought was therefore the result of decreased leaf size, mainly due to a reduction in cell number. The effect of drought on leaf area increased with increase in the supply of nitrogen.

Wadleigh and Gauch (1948) showed that the rate of elongation of leaves of cotton decreased with increasing soil moisture stress. Leaf growth ceased when the soil moisture stress rose to about 15 atmospheres, and the same limiting value was obtained for different irrigation cycles during the growth of a given leaf, for different leaves on the same plant and for leaves on different plants, although these varied widely in growth rate at lower moisture stresses. No data on the effect of varying soil moisture stress on final leaf size are given.

3. *The Relative Importance of Variation in Net Assimilation Rate and in Leaf Area in Determining Yield*

When Heath and Gregory (1938) put forward their hypothesis that mean NAR during the vegetative phase is constant for a wide range of species and environments, they also pointed out its implication that, since dry matter increase is determined by NAR and leaf area, differences in dry matter accumulation must arise mainly from variation in leaf area. Although later work has not upheld the constancy of NAR, it has confirmed that, in general, dry matter yield does depend more on variation in leaf area than in NAR.

The variation between years in mean leaf area of the same species grown in the same situation and between varieties in the same year was relatively much greater than the variation in mean NAR (Watson, 1947a). Throughout the comparisons between years and between varieties, increase in dry matter yield was associated with increase in mean leaf area, but there was no obvious correlation between yield and mean NAR. Similarly, varying the supply of nutrients affected dry matter

production mainly by causing changes in leaf area, and variation in NAR was of secondary importance (Watson, 1947b). This is illustrated in Fig. 5 which shows the dry matter increment of mangold plants grown with a wide range of fertilizer treatments on the Barnfield experiment,

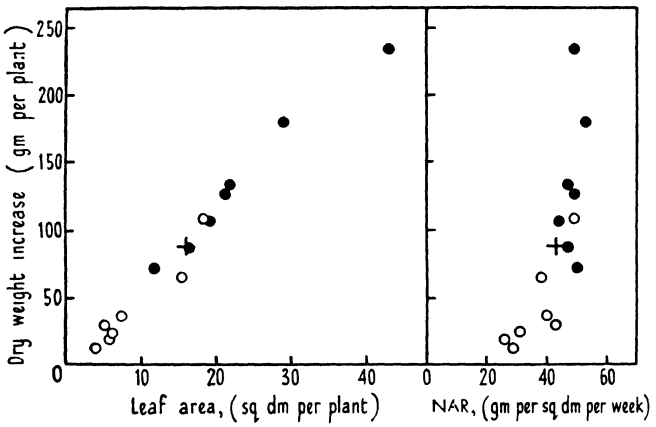


FIG. 5. The relation of dry weight increase per plant in the experimental period to mean leaf area per plant and to mean net assimilation rate for plants grown on plots receiving varied fertilizer treatments in the Barnfield experiment on mangolds, Rothamsted (Watson, 1947b). The scales of leaf area and NAR are adjusted so that the abscissas of the mean values (represented by crosses) are approximately equal. Open circles represent plots which received no nitrogenous fertilizer and black circles plots which received sulfate of ammonia (in addition to varying combinations of other nutrients).

Rothamsted, plotted against mean leaf area per plant and mean NAR. Dry matter production increased almost linearly with increase in mean leaf area over the whole range. Mean NAR was relatively much less variable than mean leaf area and showed no consistent trend over the greater part of the range of dry weight increase, between 100 and 230 g. per plant. The lower values of dry weight increase, below 100 g. per plant, on plots receiving no added nitrogen, were associated with a marked reduction in NAR, but the effect of nitrogen on leaf area was still relatively greater than that on NAR.

An assessment of the relative importance of variation in leaf area and in NAR as determinants of the difference in dry matter yield between species must take account of the different lengths of the growth period, that is, of variation in the persistence of leaf area in time as well as in its mean magnitude. The appropriate measure for this purpose is the integral of leaf area index over the growth period; this has

the dimension of time, and has therefore been termed leaf area duration (LAD). The LAD of a crop is a measure of its ability to produce leaf area on unit area of land throughout its life and hence of its whole opportunity for assimilation. In conditions of constant NAR, dry matter production by different crops would be proportional to LAD.

The mean yields of dry matter for wheat, barley, potatoes, and sugar beet grown in several seasons at Rothamsted were found to be approximately proportional to mean LAD, so that the ratio of dry matter yield to LAD was nearly the same for all crops (Watson, 1947a). This ratio is an estimate of dry matter increase per unit leaf area per unit time, that is, of mean NAR over the whole growth period, the value of NAR at any time being weighted by the magnitude of LAI at that time. The ratios for wheat and barley were slightly higher than those for potatoes and sugar beet, but the differences were partly attributable to dry matter production by photosynthesis in the ears of the cereals. These results indicate that differences in dry matter accumulation between the four crops were almost completely accounted for by differences in leaf area. At first sight the constancy of the weighted mean NAR for the four crops appears to contradict the earlier conclusion (Sec. IV,1b; Fig. 1a) that these crops differ in NAR when compared in the same conditions. The reason for the discrepancy is that while wheat and barley produced their maximum leaf area in June or early July (Fig. 3), near to the time when NAR was also maximal, potatoes and sugar beet failed to profit from the high NAR in midsummer because their leaf areas were small at this time and did not reach high values until later in the year when NAR had fallen to a much lower level, and this was sufficient to offset the inherently higher NAR of the potatoes and sugar beet. In the estimates of weighted mean NAR, the higher NAR of sugar beet and potatoes was counterbalanced by the greater weighting of the high summer values of NAR for the cereals, resulting in similar values of the weighted mean for all the crops.

It is evident that variation in dry matter production between different species of annual crops grown in the same situation, like that between varieties of the same crop, between years and between different fertilizer treatments, was mainly brought about by variation in leaf area, and that variation in NAR was relatively unimportant, but this conclusion rests on comparison of only four species.

Some of the factors that influence growth affect leaf area and NAR in the same direction; for example, increase in nitrogen supply or water supply in some conditions increases both NAR and leaf area. Other factors, of which light is the best example, may have opposite effects on NAR and leaf area, and in such cases the resultant variation in dry

matter production with change in the factor will tend to be small. Gregory (1926) noted that "the positive and negative correlations of net assimilation rate and relative leaf growth rate respectively with total radiation [observed in his experiments on barley] provide a mechanism whereby the yield of the plant tends to remain within fairly narrow limits, in spite of climatic variation." Similarly, it follows from the linear increase of NAR and linear decrease of leaf weight ratio with increase in the logarithm of light intensity, expressed as percentage of full daylight, (Blackman and Rutter, 1948; Blackman and Wilson, 1951b), that RGR increases with increase in light intensity from low values to a peak in the neighborhood of full daylight, presumably falling again at higher light intensities, so that variation of light intensity in the range close to full daylight produces only slight change in RGR Consequently, it is likely that yield is little affected by fluctuations in natural illumination. Gregory refers to this situation as an example of adaptation of the plant to change in its environment, ensuring equal facility for growth in a range of climatic conditions, but it is fair to point out that as yet there is no evidence of such adaptation to other factors than light.

The different strains of sugar beet provide another instance of an association of increase in leaf area with decrease in NAR; the large-leaved *E* types have a lower NAR than the small-leaved *Z* types. It is unlikely that this inverse correlation is the result of selection for maximum yield, for such selection would retain strains that combine large leaf area with high NAR, if it were possible for these to occur together, though it would eliminate strains having both small leaf area and low NAR.

V. Discussion

We may now consider how far the results reviewed in the preceding sections throw light on the efficiency of field crops as producers of dry matter and whether they indicate that changes in cultural practice might lead to improved efficiency. Much of the following discussion relates to crops grown in England, partly because these are the ones with which the author is familiar, and also because data for crops in other countries are lacking, but the principles involved may have a wider application.

There appears to be little opportunity for increasing yield through increase of NAR. Variation in nutrient supply over a wider range than is normal in agricultural practice has only small effects. There is some evidence that change in NAR with nutrient supply occurs only at low nutrient levels, so that increase in rates of fertilizer application above those used at present is unlikely to lead to appreciable increase in NAR.

The fact that NAR varies between and within species suggests the possibility of finding new crops with higher NAR than those now grown, or of increasing the NAR of existing crops by plant breeding. However, the variation within species so far observed is not great, and the opinion of Gregory (1950) that "there is little hope that the efficiency of the photosynthetic process can be increased by selection or breeding" is probably justified, especially if the association of high NAR with low leaf area, shown by the sugar beet strains, occurs generally in other species.

It has been shown that the time trend of NAR in natural conditions follows the seasonal climatic trend and that short-period deviations from smooth trend can be related, to some extent at least, to fluctuations in climatic factors. If NAR could be determined more accurately and the climate specified precisely by more appropriate meteorological measurements, it is probable that much more and perhaps most of the variation of NAR with time would be accounted for by variation in environmental factors. Assuming this to be true, NAR of a field crop at any time is determined by the weather conditions at that time and by the genetic constitution of the crop plant, but is not much affected by nutrition or age. As weather conditions cannot be controlled on a field scale, it follows that little can be done by cultural means to improve yield through increase in NAR. The factor of water supply must be excepted from this statement for it can be controlled by irrigation, and increase of yield by irrigation is probably attributable in part to increase in NAR. It should be noted here that in places where there is wide seasonal fluctuation in rainfall, the water supply factor may be an important determinant of seasonal variation in NAR. For obvious reasons, this is unlikely to be true of the changes in NAR (Fig. 1A) of crops grown in England.

If NAR is fixed by weather conditions and cannot be increased by cultural treatment, efficiency in dry matter production must depend on making the best use of the period during which the climate favors high NAR. From this point of view, barley was the most efficient of the four crops for which data are given in Fig. 3, because its maximum LAI coincided with the midsummer peak of NAR. Wheat was somewhat less efficient; its LAI attained an earlier maximum, at the beginning of June, and decreased rapidly in June and July during the period when NAR was greatest. However, photosynthesis in the ears at this time must have helped to offset the decline in LAI. Potatoes and sugar beet were much less efficient than the cereals, for they produced their greatest leaf area too late to profit from the high NAR of the summer months.

These considerations indicate that the yield of sugar beet could be increased by inducing a greater development of leaf area during the

summer months, and the obvious way of doing this is by earlier sowing. Figure 4 shows that early sowing of sugar beet has the desired effect, though at the expense of a reduction in leaf area later in the year. However, this reduction occurs when NAR has much lower values than in midsummer, and so the loss of dry matter production that it causes is less than the gain obtained from the increased leaf area in June and July. In recent years there has been a steady trend toward earlier sowing of the sugar beet crop in eastern England, and no doubt this change is one of the chief causes of the continuing rise in yield. Previously, most of the crop was sown in April or early May, but now much is sown in March, and February sowings are not uncommon. The mean date of the experimental sowings for which data are given in Fig. 3 was May 7, but some of these crops were deliberately sown later than in normal practice. Similar arguments suggest that earlier planting of main crop potatoes would be advantageous. There is good evidence that delay in planting leads to serious loss of yield (Rothamsted Report, 1950) but as yet the leaf area changes involved have not been investigated. There are, of course, practical limits to earliness of sowing or planting, set by the time when the soil becomes dry enough for cultivation and by the risk of frost injury to potatoes or of excessive bolting in sugar beet caused by prolonged low-temperature exposure.

There is a possibility that the yield of winter wheat might be increased by delaying the whole sequence of leaf area development, or at least the phase of declining leaf area, so that the maxima in LAI and NAR would be more nearly synchronized. The time of onset of the fall in leaf area probably depends on the time of formation of the inflorescence, and to delay it would presumably require the temperature and photoperiodic responses of the plant to be changed by breeding. The same result might be achieved by spring sowing of suitable varieties, but hitherto the varieties of spring wheat grown in England have not yielded so well as winter wheat. However, new higher-yielding varieties such as *Atle* and *Bersée* are now available, and the area under spring wheat is rapidly increasing. It is possible that spring wheats inevitably have a lower LAD than winter wheats and this would offset any advantage to be gained from more efficient use of the high NAR of the summer months. There is also the practical objection that any change designed to make the different cereals more uniform in development would tend to make them mature simultaneously and so concentrate the work of harvest into a shorter period.

As the possibility of increasing NAR appreciably by plant breeding or cultural means appears to be small, improvement in yield must be sought mainly through control of leaf area. The extent to which dry

matter production could be increased by increase in leaf area depends on whether NAR is affected by increase in LAI. If LAI were increased indefinitely, at some stage NAR would be expected to decrease through reduction in the average light intensity at the leaf surface caused by mutual shading of the leaves, and possibly through decrease in CO_2 concentration of the atmosphere in the neighborhood of the lower leaves due to increased uptake of CO_2 in photosynthesis. The value of LAI beyond which further increase begins to have an appreciable adverse effect on NAR is not known. If it occurred within the range normally found in field crops, NAR would be expected to vary with age, but the results of the experiments in which the date of sowing of sugar beet and mangolds was varied indicate that the effect of age was small. Comparisons of the same species grown in different seasons also suggest that NAR is independent of variation in LAI; variation in the mean LAI of wheat in May-June over the range from 1.3 to 3.1, and of sugar beet in July-October from 1.3 to 2.5, was not accompanied by any systematic change in NAR (Watson, 1947a). This evidence, though far from conclusive, suggests that it would be necessary to increase LAI considerably beyond the highest values (about 4) shown in Fig. 3 before serious reduction in NAR occurred. It follows that if such an increase in LAI could be achieved, there would be a corresponding increase in dry matter production.

During the greater part of the life of annual crops, LAI has very low values. Figure 3 shows that for wheat, barley, and potatoes LAI exceeded unity only for ten to twelve weeks of the growing season; for sugar beet the period was longer, but the extension was of little significance for dry matter production because it occurred late in the season when NAR was very low. During three-quarters of the growth period between sowing and harvest of winter wheat and about half of the growth period of the spring-sown crops, LAI was less than unity. So long as the leaf area of a crop is less than the area of land on which it is growing, that is, when LAI is less than 1, some of the incident solar radiation cannot be intercepted by leaves but must fall on bare soil. This situation holds for a large part of the life of annual crops and accounts in part for their very low efficiency of utilization of solar energy. An indication of the extent to which dry matter production is limited by low LAI can be obtained by calculating from the values of NAR given in Fig. 1A (with suitable extrapolation) what the dry matter production would be if LAI could be maintained at a value of 4, the maximum in the data plotted in Fig. 3, for the six months from April to September. The calculated yields are 14 tons dry matter per acre for wheat, and 24 tons for sugar beet, compared with the maximum yield of 4 to 5 tons

dry matter that has been obtained at Rothamsted from these crops in the most favorable conditions. These figures have a bearing on projects to use large-scale cultures of green algae for food production, for they indicate the possibility of very high yields of dry matter per unit area, if a photosynthetic system equivalent to a field crop with maximal LAI could be maintained continuously throughout the period of the year when NAR is high.

In a crop grown from seed, an initial period of very low and slowly increasing LAI is inevitable. The length of this period could possibly be shortened, and the development of a high LAI hastened, by selection and breeding of plants with a high initial RLGR. Application of fertilizers may produce a similar result, and field observations suggest that phosphate is particularly effective in hastening leaf growth in the stage immediately after germination. Size of the seed, and especially of the embryo, is likely to be an important factor determining the initial leaf growth rate. Perennial plants are presumably capable of more rapid leaf area development in spring than annuals, and an investigation of pasture grasses from this point of view would be of interest.

It has been shown that nutrition has a greater influence on leaf area than on NAR, and the beneficial effects of fertilizer applications are therefore to be ascribed mainly to increase in LAI. It is probable that most agricultural practices designed to increase yield have the same physiological basis, and that the development of successful systems of crop husbandry largely depends on discovering empirically the optimal conditions for leaf area production in a particular environment. Increase of yield through measures taken to control disease, such as the rotation of crops or the use of fungicides and insecticides, probably results mainly from the prevention of loss of leaf area, though unpublished work has shown that some virus diseases cause a reduction in NAR as well as in leaf area. Hitherto growth analysis has been applied mainly to the investigation of plant growth in relation to environmental factors, but the same methods could profitably be used to throw light on the physiological effects of attack by pathogenic organisms on crop plants.

It will be apparent from this review that, though a considerable amount of work has been done on growth analysis since the methods were outlined by Gregory and by Briggs, Kidd, and West more than thirty years ago, only a small part of it relates to field crops, or specifically to the physiological basis of variation in yield. Much more attention has been devoted to investigation of the causes and significance of variation in NAR than in leaf area, though the latter appears to be of far greater importance in relation to yield. There is now a need for the steady accumulation of data on agricultural crops, covering as wide a

range of species and environments as possible, to test on a broader basis the conclusions already reached, often on slender evidence, and to elucidate the contradictory results, of which several instances have been noted. Such data could be obtained without much additional labor, if whenever a growth study involving intermittent sampling of a crop is undertaken, measurements of leaf area are made in addition to the other determinations, for example, of chemical composition, for which the investigation may primarily be intended. As Heath and Gregory (1938) have pointed out, "much of the information which might have been gained [from past growth studies] was not forthcoming owing, presumably, to a lack of appreciation of the possibilities of growth analysis."

The conclusion of Heath and Gregory (1938) that mean NAR during the vegetative phase is constant for all species and environments was based on comparisons in which species differences were confused with differences in environment. It has been shown not to hold for different species grown in the same environment, but a critical test of the constancy of mean NAR in different environments still requires to be made by determining the NAR of the same species grown in a number of situations with widely varying climate. This could most conveniently be done in a country with a wide latitudinal and climatic range, such as the United States; the range available in Britain is too small for this purpose. Apart from its bearing on Heath and Gregory's hypothesis, information on the seasonal trend of NAR in different situations, similar to that given in Fig. 1A for southeastern England, would be of great interest, especially if obtained for the same group of species, for it would provide a quantitative basis for comparing the potentiality of the climate for dry matter production by crops in different parts of the world.

Another problem requiring investigation is the dependence of NAR of field crops on LAI, and this involves finding a method of varying LAI experimentally. The obvious way is by varying the plant population, but it is possible that LAI would be limited by nutrient supply and would not be greatly affected, except in the early stages of growth, by change in plant number. This, rather than a decrease of NAR offsetting an increase in LAI, is probably the reason why yield becomes almost independent of plant number as the plant population is increased. A growth analysis study of the effect of varied spacing on yield would throw light on the nature of interplant competition, even if it failed to provide information on the effect of NAR of variation in LAI.

To solve many of the problems which have been discussed, it will be necessary to experiment on plants grown in controlled environments. The controversy as to the existence of an age effect on NAR can be settled only by making measurements throughout the growth period of

the NAR of plants growing in constant conditions. The effects of climatic factors and their interactions on NAR and on leaf growth can be fully elucidated only if means of varying the factors independently over a wide range are available. Interpretation of the results of growth studies on crops growing in natural environments will be made easier if comparisons can be made with the same crop grown in a range of controlled environments, where the climatic factors are held constant or made to vary in simple, systematic ways.

Finally, there is a need for more work on the physiology of leaf growth. This aspect of plant physiology has hitherto received too little attention. Since it has been shown that leaf area is the major determinant of crop yield, it is clear that a better understanding of the causes of variation in yield depends on a fuller knowledge of the processes that control leaf production and leaf expansion and set a limit to leaf size.

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Copper in Nutrition

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I. Introduction

From supposed poison to nutrient in twenty-five years. How rapidly theories are altered and values changed in the light of advancing scientific knowledge. This is the story of copper, which, along with cobalt and one or two other elements, has quickly leaped from obscurity to prominence in the field of nutrition.

Formerly, we were apprehensive about the possible toxic effects of Bordeaux spray residue, or the harmful consequences we thought might occur when we found that the infant son had been mouthing a penny. At present, we are more concerned in determining whether our crops are getting enough trace elements, our livestock the correct mineral,

protein, and carbohydrate ratio, and ourselves a balanced diet. Copper is now acknowledged to play a very important part in each of these nutritional relationships.

Although the presence of copper was demonstrated in some plants and animals early in the nineteenth century, the metal was long believed to be carried about passively. For a hundred years, scientists did not challenge this assumption. About 1920, however, copper was accepted, rather suddenly, as an essential constituent of all living material, and interest in determining its necessity and possible nutritive role expanded rapidly. The essentiality of copper is now unquestioned, but much research lies ahead before a complete knowledge of its function in living organisms can be obtained.

Copper compounds are used extensively throughout the world for the control of plant disease. Most reports have been on the use of the old copper fungicide, Bordeaux mixture. The story of this fungicide, starting with its accidental discovery by Millardet, near Bordeaux, France, in 1882, makes an intriguing chapter in the history of plant disease control, but is outside the scope of this work.

II. Historical

Copper is believed to be the first metal employed by man. This is undoubtedly due to the fact that it occurs in quantity in the free state. There is no way of determining, within a period of centuries, when copper was first used, but the Copper Age followed the Stone Age, and artifacts, weapons, and utensils of the metal were made before the dawn of written history. The American Indian worked the copper of the Lake Superior region prior to the arrival of the white man.

The occurrence of the element in plant tissues was reported in 1816 (Dawson and Mallette, 1945), and a few years later its presence in animal tissues was also demonstrated. For a long time it was generally believed that the copper present in biological material was merely accidental and had no definite function. The amounts in living tissue are at best very small, and early analytical methods were not particularly sensitive. It is understandable, therefore, why the first reports were often conflicting, and occasionally, erroneous.

Copper research with invertebrate animals developed much earlier than with vertebrates. This was perhaps due to the fact that most invertebrate blood contains relatively larger amounts of copper. The metal was detected in the blue blood of snails in 1847 as part of a protein complex which was established as a definite respiratory pigment.

The pigment behaved with oxygen in a manner similar to that of hemoglobin, and was given the name hemocyanin.

About the same time, the presence of copper was demonstrated in the human body, but it was considered to be quite accidental. Little interest was created, and studies of copper in vertebrates languished for nearly a century. It was not until after 1920 that copper was accepted as a definite constituent of vertebrate as well as invertebrate tissue. An important milestone in copper research on vertebrates was the work conducted at the University of Wisconsin and initiated about 1924. This research revealed the fact that copper plays an important role in the formation of hemoglobin. The findings naturally led to a close examination of the distribution of copper in all living tissues and food and to studies of the relationship of copper to certain enzyme systems. The development of research on copper in animals has been covered a number of times in recent literature (Elvehjem, 1935; Rawlinson, 1943; Redfield, 1934; Schultze, 1940; Sheldon, 1932).

Early in the present century it was suspected that copper might be essential to plants. Investigations about this time showed that all plant material examined contained from three to forty or more parts per million of the element, and applications of Bordeaux sometimes increased yields even when no disease was present (Lutman, 1911). Lutman (1916) and later Cook (1923) reviewed the various reports of the stimulating effect of copper on plant growth, usually in connection with the use of Bordeaux mixture. In these two reviews, however, the essentiality of copper, and therefore, the possibility that the stimulating effect might be due to a deficiency of the element in the soil, was apparently not considered.

The success of early experiments was hindered, not only by impurities in the nutrient salts used, but also by the traces of copper in water from stills with metal condensers (Stout and Arnon, 1939). Thus, Brenchley (1914) found only toxic effects when copper was added to solution cultures. Sommer, in 1931, however, used special purified salts, and water redistilled in Pyrex, and became the first to demonstrate that, without a minute amount of copper, plant growth cannot take place. Her work was corroborated the same year (Lipman and Mackinney, 1931), and the status of copper as a plant nutrient was firmly established.

The effects of lack of available copper in the soil appear not only in vegetation growing on these soils but also in animals feeding on this vegetation. The symptoms in both plants and animals may range all the way from slightly reduced growth to definite pathological symptoms, depending on the severity of the deficiency. Two main groups of plant diseases caused by a lack of copper are recognized. The first comprise

those affecting fruit trees, especially citrus, and are referred to as "die-back" diseases or "exanthema." They are widely distributed and have been described many times (Anderssen, 1932; Floyd, 1910, 1917; Oserkowsky and Thomas, 1938). The second group affects cereals chiefly and is made up of the disorders covered by the term "reclamation disease." Such disorders have been noted for many years in a wide range of crops on the heath soils of northwestern Europe.

Long before a lack of copper in any soil was suspected, a wasting disease of cattle, commonly known as "Lechsucht," was prevalent in Europe. It was not until 1933 that it was shown to be caused by a lack of copper in the forage eaten (Sjollema, 1933). In the meantime, similar bovine troubles were reported from other parts of the world. Symptoms were not the same in every case, which suggested that other factors might be involved, even though copper therapy always resulted in improvement. Various sheep troubles were also traced to a lack of copper, but here again, symptoms varied somewhat in different countries.

Soils high in organic matter, particularly newly cultivated peat soils, are most frequently discussed in connection with copper deficiency. There are many reports of the successful use of copper sulfate or other forms of copper on such soils (Allison *et al.*, 1927; Felix, 1927).

Recently, it has been found that applications of copper to mineral soils increased production even where these soils apparently contained enough copper for normal growth (Berger and Truog, 1949; Gilbert, 1948a; Manns *et al.*, 1937; Swanback, 1950). The conclusion was reached (Swanback, 1950; Willis and Piland, 1936) that copper, in addition to its nutritive value, acts as an oxidation catalyst in rendering other elements available. Such results indicate that copper and possibly other trace elements have considerably more value as soil amendments than is suggested by the slight amount taken up by the plant.

Because copper is essential to both plants and animals and because deficiencies of the element are widespread in the soils of the world, it was chosen as the subject of the first symposium of the McCollum-Pratt Institute held at Johns Hopkins University, June 14-16, 1950. The symposium covered many phases of copper nutrition, including its enzymatic functions, the effect of its deficiency on plants and animals, and the interrelationships between copper and other nutritive elements. The papers and discussions presented at this symposium have been published (McElroy and Glass, 1950).

III. Value of Copper to the Plant

All plants contain copper. Early reports were concerned chiefly with the possible health danger of an excessive amount in food (Carles, 1917). However, this concern gradually disappeared when it was found that even fruit with copper spray residue usually contained less of the element than many food materials which had been consumed for years without ill effects (Anonymous, 1923).

The amount of copper in a plant varies, depending on species, soil, the amount of fertilizer used, and other factors. However, similar foods, under the same circumstances, contain approximately the same amount of the element. In descending order of copper content, some different classes of plant foods are arranged as follows: nuts, dried legumes, cereals, green legumes, roots, leafy vegetables, fruits, and nonleafy vegetables (Lindlow *et al.*, 1929). A summary of the published copper analyses of crops has been recorded up to 1941 (Beeson, 1941).

The amount of copper in a plant may be increased by copper fertilization (Colman and Ruprecht, 1935; Elvehjem and Hart, 1929; Miller and Mitchell, 1931). By this means, in sand culture, the writer increased the copper content of the corn ear from 5 to 28 parts per million. Bacon and associates (1950) found that copper was taken up by the leaves of tobacco plants in amounts varying directly with the amounts applied to the soil. However, even when a greater yield results from the use of copper, an increase in copper content does not always take place. For example, Swanback (1950), in a series of experiments covering a period of three years, obtained substantial weight increases in tobacco by soil treatments with copper. With one exception, there was less copper deposited in leaves with copper sulfate supplied in the soil than without it, indicating that active copper in the soil is not always synonymous with absorbable copper.

The methods of determining available copper in soils are not entirely satisfactory at present, and can be expected to give only approximate results. Therefore, leaf analysis is coming into greater use in an effort to indicate the actual amount of soil copper available to the plant. We are warned, (Steenbjerg, 1948), however, that leaf analysis of the copper content of plants is not an infallible guide in the diagnosis of copper deficiency. When growth is severely stunted, as it usually is under conditions of severe copper deficiency, the copper content of the plant material (as per cent of dry matter) may not be unduly low.

Bordeaux mixture has been found many times to increase the yield of potatoes even where the control of disease was not a contributing factor (Cook, 1923; Lutman, 1911; Whetzel *et al.*, 1936). This has

been attributed in part to the lengthened life of the plant, and, in part, to a favorable influence on tuber composition. Tubers from sprayed vines were usually higher in solids, starch, and nitrogen than tubers from unsprayed vines (Cook, 1923). The increased yield and increased solids of the tubers apparently depended on the presence of copper in the spray, since yields of tubers were decreased when a lime spray containing no copper was used. In the writer's experiments, tobacco on land treated with copper sulfate tended to ripen somewhat later than tobacco on land not so treated, and this has been found to be true also for other crops (Russell and Manns, 1934).

Copper has some function in chlorophyll formation, although the chlorophyll molecule contains no copper. This function is presumably indirect, since plants may cease to grow as a result of copper deficiency and still show no signs of chlorosis (Sommer, 1945). Spraying with copper has been found to increase the chlorophyll content of wheat (Okuntsov, 1946a), cranberries (Bergman and Truran, 1933), citrus (Orth *et al.*, 1934), and other plants. A copper treatment may not only increase the amount of chlorophyll in a plant, but it may also have a protective effect against chlorophyll destruction (Anderssen, 1932; Bergman and Truran, 1937; Okuntsov, 1946b). This would retard the physiological aging of the plant and result in a longer life. Chlorophyll is extracted with more difficulty from copper-sprayed plants than from unsprayed ones (Lutman, 1916).

From a physiological point of view, copper is important as a constituent of at least three enzymes: ascorbic acid oxidase, laccase, and tyrosinase. The latter may be taken to include monophenol and polyphenol oxidases. Ascorbic acid oxidase catalyzes the oxidation of ascorbic acid (vitamin C) in the presence of oxygen (Stotz *et al.*, 1937). Laccase will oxidize various phenolic compounds (Keilin and Mann, 1939, 1940). It is similar-to tyrosinase, but differs in that it does not oxidize tyrosine or *p*-cresol.

Tyrosinase is the best known of the copper enzymes. In 1937, as polyphenol oxidase, it was obtained from potato juice (Kubowitz, 1937), and since that time it has been purified from a number of plant sources (Dalton and Nelson, 1939; Keilin and Mann, 1938; Parkinson and Nelson, 1940). In chard leaves, the enzyme was found to be located in the chloroplasts, since the cytoplasm did not show any appreciable oxidase activity, Arnon, 1949). In studying the tyrosinase activity of potato tubers in relation to enzymatic blackening, it was found that tubers from plants grown on soils poor in copper, although making an entirely normal appearance, had a tyrosinase activity less than one-tenth that of tubers from plants with a normal copper supply. As a result of

the low tyrosinase activity, blackening of bruised potatoes deficient in copper was slight in comparison with tubers supplied normally with the element (Mulder, 1949).

IV. Effects of Copper Deficiency in Plants

The effects of copper deficiency in plants range all the way from slightly reduced growth to disease symptoms so severe that death eventually ensues. In the case of copper deficiency of woody plants, a more or less chronic condition known as "dieback" or "exanthema" frequently occurs. This disease may kill the tree, but more often merely results in unthriftiness. "Dieback" occurs in many parts of the world, on many kinds of trees. A large number of the published reports have been in connection with citrus (Camp and Fudge, 1939; Cipola, 1937; Floyd, 1917; Fudge, 1939; McCleery, 1929), but tung (Dickey *et al.*, 1948; Drosdoff and Dickey, 1943; Gilbert *et al.*, 1946), avocado (Ruehle and Lynch, 1940), olive (Smith and Thomas, 1928), apple (Anderssen, 1932; Dunne, 1938), pear (Oserkowsky and Thomas, 1938), and plum (Cahill, 1929) are among other trees affected.

"Dieback" was first described on oranges in Florida in 1875 (Fowler). The causal agent, at that time, was believed to be a fungus. It was recognized in California in 1896 and is now known to occur in most of the citrus-growing areas of the world. Copper was used as a corrective for many years before lack of the element was proved to be the actual cause.

An early symptom of copper deficiency is an unusually dark green color of the foliage, indicative of a high nitrogen concentration. This symptom is characteristic of copper deficiency in other plants also and has been observed under controlled conditions in the laboratory.

In acute copper deficiency of citrus plants, the twigs start to die, and the leaves soon turn a yellow-green color, drop quickly, and leave the twig denuded (Camp and Fudge, 1939). Gum pockets may form between the wood and bark of the twig near the leaf bases, and the twig is often covered by a typical, reddish brown, gummy excrescence. Multiple buds form below the injured twigs, but the growth that develops from these buds also dies back.

The quality of the fruit on copper-deficient trees deteriorates even before the appearance of leaf and twig symptoms, and an overly large proportion of the crop is thrown into the lower grades. In more severe cases, splitting of the fruit is common, and the brown gummy excrescence also appears on the rind. Such fruit is usually shed before the period

of normal maturity. Affected trees may bloom profusely in the spring and set a heavy crop of fruit, which is shed by midsummer.

In stone fruits, copper deficiency restricts growth considerably, and the trees are small and underdeveloped. Vigorous spring growth is produced, but the leaves soon turn yellow and drop, and there is serious twig dieback. Eruptions of the bark and swollen multiple buds occur as in citrus.

As has been mentioned, herbaceous plants may also be affected by copper deficiency and symptoms are even more severe than on woody plants. The "reclamation" disease of small grains and other crops, due to insufficient amount of available copper in the soil, commonly occurs on newly cultivated organic soils (Brandenburg, 1935; Hoffmann, 1939; Melchers and Gerritsen, 1944; Nicolaisen and Seelbach, 1938; Proskura, 1940; Smith, 1927), but has also been found in alkaline calcareous areas (Piper, 1938, 1940). The trouble was originally attributed to the toxic action of a contituent of the peat, but Sjollema (1933) showed that the disease could be cured by the addition of copper sulfate to the soil, and his results were soon confirmed by others (Brandenburg, 1935; Nicolaisen and Seelbach, 1938).

The disease produces very characteristic and easily recognized symptoms in oats and other cereals, and many descriptive names have been given to it, including "yellow tip" and "wither tip." In general, the plants make fairly normal growth for several weeks, but with the approach of spring, a marginal chlorosis appears and the leaf tips wither, droop, and become yellowish gray. The tips of newly emerging leaves become chlorotic, wither, and die without unrolling. The lower leaves may remain green for a considerable time, and numerous secondary tillers develop freely from the base of the plant, but these also show leaf symptoms at a later stage. No inflorescence is produced in severe cases, although secondary tillers continue to form. The withered leaf tips, bushy growth, and greenness at the base of such copper-deficient plants present a striking contrast to normal plants.

An inflorescence is formed in less severe cases, but the chaff is whitish, and practically no grain is produced. Deficient grain formation is one of the most characteristic features of the disease in the field, since it may result from a copper deficiency, which is not sufficiently severe to affect the vegetative growth. This has also been demonstrated in the laboratory (Piper, 1940).

Smith (1927), in studying the reclamation disease in Holland, isolated an organic substance, which, he claimed, produced symptoms of the disease in normal pea and oat plants. He concluded that the beneficial effect of copper in soils which produced plants with reclamation

disease was due to the formation of an insoluble compound of copper with the organic substance. Other investigators (Brandenburg, 1935; Piper, 1942), however, confounded Smith's theory by obtaining symptoms of reclamation disease in copper-free solutions to which no toxic substance had been added.

Copper-deficiency symptoms in tomato plants under greenhouse conditions have been described several times (Arnon and Stout, 1939; Bailey and McHargue, 1943; Gilbert, 1948b; Piper, 1940, 1942; Reed, 1939; Sommer, 1931). The dark green color of the somewhat smaller leaves whose margins curl upwards and inwards and the permanent wilting of the entire top of the plant are characteristic. Similar symptoms are shown in tobacco (McMurtrey and Robinson, 1938) and sunflower (Sommer, 1931). The wilting characteristic, even under ample moisture conditions, seems to be a constant symptom, but others, such as chlorosis as found in sugar beets (Van Schreven, 1936), may vary in different species and under different conditions.

Some crops are much more sensitive to copper deficiency in the soil than others. For instance, wheat and oats are less tolerant of a lack of copper than rye and may fail entirely on a deficient soil which produces good crops of rye.

Tobacco (Gilbert, 1948a; Swanback, 1950), sweet corn (Berger and Truog, 1949), and onions (Felix, 1927; Knott, 1936), in most cases, make much better growth on copper-treated soil than on untreated soil, although, with the possible exception of onions, copper-deficiency symptoms in these plants have never been noticed in the field. Copper was found in at least two cases to increase the duration of burn in tobacco (Swanback, 1950; Tisdale, 1930), but one other experiment reported by O. E. Street of the Pennsylvania tobacco experiment station in 1949 (personal correspondence) was not in accord. It seems safe to assume that there is no retarding effect.

Fertilization not only increases crop yields, but it decreases frost damage (Davis, 1950). When trace elements, especially copper, are added to the fertilizer, even more protection is afforded (Harris, 1948). This point has been well illustrated in Florida citrus orchards after certain severe freezes (Lawless and Camp, 1940). Little or no damage was done to the completely fertilized trees, but considerable defoliation and fruit drop occurred on trees not receiving the minor elements.

V. Copper in the Soil

1. Amount

Copper is generally estimated to range from one to over fifty parts per million in normal agricultural soils (McMurtrey and Robinson, 1938). Holmes (1943) studied the copper contents of a large number of United States soils and obtained similar results. His range was from two to sixty-seven parts per million. As might be expected, the severely weathered, leached, and more acid soils of the South Atlantic states averaged much lower in total copper than soils from more western states, such as Missouri and Oklahoma.

The intensity of soil acidity and the composition of the parent material have considerable influence. For example, Cecil and Decatur soils from southeastern United States differs widely in copper content, although they belong to the same great soil groups, and have similar pH values, texture, and color. They are, however, derived from different parent materials. The Cecil soil is from granite, which was probably weathered under more acid conditions than the Decatur, derived from limestone. Consequently, since copper is more soluble under acid conditions, the Cecil soil retained less of the copper of the parent rock than the Decatur. It was assumed that the content of the element was nearly the same to start with.

Collington and Norfolk soils are both of coastal plain origin and have similar texture and pH values The Collington, however, which is derived from green-sand marl, contains approximately three times as much copper as the Norfolk soil, which is derived from the more common coastal plain materials.

It should be understood that the total quantity of copper in a soil constitutes an inventory only and does not indicate the amount available to plants growing on that soil. Brun (1945) found that the copper contained in Norwegian humus soil could be divided into three categories: water soluble, absorbed, and fixed. The last could not be removed without chemical destruction of the soil, and, of course, would be unavailable to plants. It is quite possible for a soil to be high in total copper and yet be low in available copper.

2. Factors Influencing Availability

Many factors influence the degree to which soil copper is available to the plant. These include pH value, humus content, nature of the previous crop, amount of clay and sand, and effect of other elements (Steenbjerg and Boken, 1950). Frequently several factors are effective

at the same time. Most workers report that copper availability lessens with decreased acidity of the soil. Peech (1941) and Piper (1942) found that a decrease in acidity for any given level of copper reduced the availability somewhat when measured either chemically or by total copper absorbed by plants. In soils of high organic content, such as peat soils, however, the reverse may be true—the more acid the peat, the greater may be the relative response to copper, and the greater the number of crops that are likely to benefit by the copper application (Harmer, 1946).

The amount of organic matter present in a soil exerts a great influence on the availability of soil copper. In fact, many highly organic soils can be made profitable only after large amounts of copper have been applied to them (Browne, 1950; Comin, 1944; Harmer, 1941, 1946). The most striking example, perhaps, is the saw-grass peat of Florida, where almost useless soil was made to produce good crops by copper fertilization (Allison, 1930; Allison *et al.*, 1927). Truck farmers on the Carolina coastal plain usually apply 200 lb. of copper sulfate per acre to newly cleared peat soils and may apply as much as 50 lb. per acre per year thereafter, if justified by results.

It has been suggested (Steenbjerg and Boken, 1950) that the great copper deficiency that appears in newly cultivated peat soils must be explained by the original low content of available copper and that this is aggravated by dressings of nitrogen, phosphorus, and potassium—hence the continued use of copper on these soils.

3. Effects on Crop Yields

Although copper deficiency occurs, particularly on peats and other soils with a very high humus content, it is also common on very sandy or gravelly soils with a low humus content (Anderssen, 1932; Riceman *et al.*, 1938). It is less common, but sometimes occurs in mineral soils with a fair amount of organic matter (Isaac, 1934; Rohrbaugh, 1946).

A copper deficiency severe enough to cause disease symptoms insures remedial measures, but if less severe, usually attracts little attention. The result is that maximum growth is not obtained with many crops for lack of a pound or two of copper which could be supplied at slight cost per acre. Greenhouse and field plot tests have shown that the first slight indication of the need for the element is demonstrated by a retardation of growth, which occurs long before any visible symptoms are apparent. Since areas of marginal deficiency will outnumber areas of acute deficiency, it is difficult to estimate the amount of potential yield actually lost.

In addition to the instances where borderline copper deficiences have

been demonstrated, there are many where applications have resulted in marked crop increases, even though the copper content of the soil appeared to be ample. In the United States, an impetus was given to the use of copper on the Atlantic coastal plain soils during the period from 1934 to 1937. An analysis of twenty-five of these soils demonstrated that while none were extremely low in copper, in only four did the copper content exceed twenty parts per million (Manns and Russell, 1935).

Remarkable results were obtained by adding copper sulfate to the fertilizer. In field experiments carried out in North Carolina, South Carolina, and Virginia in 1935, the average yield of tobacco was increased 43.9 per cent, and the quality, 10.4 per cent. The yield of cotton was increased 20.23 per cent (Churchman *et al.*, 1936, 1937). In Delaware, the average values of sweet potatoes, tomatoes, and lima beans were increased 4.45, 9.65, and 43.55 per cent respectively (Manns *et al.*, 1936a).

In Wisconsin, on Miami silt loam (Berger and Truog, 1949), the yields of usable corn ears were 5 to 40 per cent greater when copper sulfate was added to the fertilizer. Several investigators have found that copper increased tobacco production. In Pennsylvania, O. E. Street of the tobacco experiment station at Lancaster obtained a weight increase of 27 per cent in cigar-filler tobacco (personal correspondence, 1949). In Florida (Tisdale, 1930), copper increased the percentage of uniformly colored leaves of flue-cured tobacco. In Connecticut (Swanback, 1950), in experiments with Havana seed tobacco covering a period of three years, it was found that copper gave an increase of from 13 to more than 26 per cent in crop value.

F. A. Gilbert (1948a), over a period of eight years, conducted more than two hundred field experiments, primarily on tobacco. The purpose was to determine the value of copper on soils which were not considered to be actually deficient in the element. The tests were made with Burley tobacco in four Ohio valley states, and with flue-cured tobacco, in Virginia and the Carolinas. Available copper in these soils ran from one part per million in a few coastal plain soils to sixteen parts per million in some of the Ohio valley soils. The majority were between five and ten parts per million.

In approximately 80 per cent of the tests, an increase in the weight of tobacco, in the quality of the leaf, or in the two together, was obtained. No satisfactory correlation between available soil copper and increased yields were found except at the extreme levels of the soil copper. In some cases, identical procedure on the same soil type on near-by farms gave quite different results. The greatest increase in production was 35 per cent, and the average was about 8 per cent, which did not equal

the results obtained by Churchman and his associates (1936) over much of the same territory.

The only similar set of experiments on copper sulfate was conducted in Denmark, primarily on cereals (Steenbjerg and Boken, 1950). Six hundred and forty trials were conducted over a period of nineteen years, and the results were quite similar to those obtained by Gilbert—87 per cent of the copper-treated plots yielded increases as compared to Gilbert's 80 per cent.

4. Comparison of Different Forms of Copper for Use as a Soil Amendment

Copper sulfate is the form of copper most frequently employed for soil-amendment purposes and until recently was used exclusively. During the past few years, however, continuing experiments have shown that copper in other forms, including finely ground copper minerals, might be used to correct deficiencies of the element in the soil. Several of these minerals in a comparatively impure state contain more of the metal than copper sufate, and it is not difficult to concentrate it even farther by a flotation process.

Among the forms of copper that have been tested are pyrites ash, malachite, copper flake, cupric oxide, cuprous oxide, oxide mixtures, copper acetate, copper carbonate, copper chloride, and several copper-bearing sulfide ores, including chalcopyrite. Pyrite ash, which contains from 1 to 2 per cent of copper, is obtained in the production of sulfuric acid by roasting pyrite. The ash has been used experimentally as a copper fertilizer in Denmark (Steenbjerg and Boken, 1950), but will never be of any importance in competition with other forms of copper because of transportation costs.

Teakle and his associates in Australia (1941, 1943a, 1943b) compared oxidized copper ore, roaster residues from pyrites burners, and copper sulfate as sources of fertilizer copper and found all to be of value. No one form was better than others under all conditions. However, the sulfate was at a disadvantage in the Australian experiments. It alone did not contain zinc and possibly other undetermined constituents, which Teakle admitted may have affected the results, since there was evidence pointing to a need for zinc on some of the soils used in the tests.

In Denmark (Steenbjerg and Boken, 1950), finely ground copper pyrites containing 12.8 per cent copper and considerable zinc were found to be inferior to copper sulfate as a soil amendment, but could be used were it economical. No response of the soil to zinc was demonstrated. In the United States, copper flake, the copper oxides, and other copper salts have compared favorably with copper sulfate as a soil amendment

in a few experiments which are being continued, but have seldom surpassed the sulfate in effectiveness.

On peat soils in which soluble copper is quickly "tied up," the small crystal form of copper sulfate is preferred to the powdered form, since it remains available longer. On such soils, after the immediate copper needs have been met, the use of finely ground minerals of high copper content, because of their slow solubility, might be preferable to a form of copper quickly soluble which has to be applied at frequent intervals. Another advantage claimed for the less soluble forms of copper is that there is no danger of a toxic effect with very large dressings (Wild and Teakle, 1942).

The application of a soil amendment depends not only on its effect, but also on its price. A refined industrial product is more expensive than the raw material from which it is produced—in this case some copper mineral. On the other hand, in fortifying high-analysis fertilizer with copper or other trace elements, a high metallic content is of prime consideration in order not greatly to change the percentage of NPK.

5. *Residual Effects*

Copper has considerable residual effect in mineral soils—much less in organic soils. Copper applications must be made more frequently, therefore, on heavier soils and on extremely sandy soils subject to excessive leaching. The residual value of as little as 3 to 10 lb. of copper sulfate on sandy Australian soils was sufficiently substantial so that no response was obtained with additional amounts the following year (Teakle, 1942). Danish experiments (Steenbjerg and Boken, 1950) showed that approximately 40 lb. per acre was effective for at least three years, and the writer, in experiments continuing since 1946 on mineral soils, finds that beneficial effects are still obtained from original applications of 20 and 40 lb. of copper sulfate per acre. In Florida (Harris, 1948), it was found that a 30-lb. application of copper sulfate was effective for at least five years, and in California the beneficial effect of copper sulfate soil treatments for "exanthema" of pear trees lasted over three years (Oserkowsky and Thomas, 1938).

Copper in organic soils is held tenaciously in the zone of placement (Allison, 1931; Lucas, 1948), and preliminary experiments at Battelle Institute have shown that a similar tendency exists in a clay loam with a fair amount of organic matter. Organic soils collected five years after receiving a 50-lb. application of copper sulfate showed that an approximate equivalent of 48 lb. remained in the upper 8 in. This explains why shallow-rooted crops are more responsive to copper applications than deep-rooted crops and why copper spraying of fruit trees affected by

"exanthema" is often more effective than soil applications. Although the copper in organic and heavy mineral soils is leached slowly, and with difficulty, the "fixing" power of such soils is so great as to offset this advantage, and such soils usually require more copper than the lighter types.

6. *Possible Toxic Effects*

In spite of the many successful experiments on the use of copper, it has not been generally accepted as a soil amendment to the extent that it is included as a general fertilizer ingredient. In areas of extreme copper deficiency, its use is imperative, but in regions where soil treatments are not 100 per cent successful, little copper is used. In fact, there is considerable opposition to its inclusion in general fertilizer mixtures on the grounds of its cost, and its possible toxicity over a period of years.

The writer found that the growth of tomatoes in nutrient solution was depressed by a concentration of as little as one part per million, but some growth was obtained in acid-washed sand when a nutrient solution containing five parts per million was applied. Copper toxicity occurred on certain extremely sandy western Australian soils with applications of as little as 10 lb. of copper sulfate per acre (Teakle, 1942), but this appears to be an exceptional case.

All agree that there is not the slightest danger of copper toxicity on peat soils; in fact, the chief concern is in getting enough of the metal. Ten thousand pounds of copper sulfate per acre has been applied to plots of Florida peat with but temporary injury (Allison, 1931), while in pot tests on peas (Bobko and Panova, 1945), growth was still obtained on peat containing 1280 mg. copper per kilogram, or the equivalent of 10,280 lb. of copper sulfate per acre.

Most mineral soils can fix substantial amounts of copper over a period of years. In France, Bordeaux mixture has been used yearly on vineyard soils since 1886 without toxic effects. It is estimated that 130 kg. of metallic copper per hectare fell on the soil during each ten-year period (Rolet, 1934), or the equivalent of approximately 2770 lb. of copper sulfate per acre for a sixty-year period. An average of 80 lb. of copper sulfate per year for thirty-two years has been added as Bordeaux mixture to some Long Island potato soils, but the limit of toxicity has not yet been reached (Skaptason, 1940). In one experiment on a sandy cranberry bog with a peat subsoil (Bergman and Truran, 1933), the equivalent of 2400 lb. of copper sulfate per acre was applied without injury to the vines and with no reduction in yield. Large amounts of

copper pyrites have been applied to a calcareous soil without injury (Smith, 1930).

In one Ohio experiment, still in progress on Miami soil, the writer has added 20 lb. of copper sulfate per acre per year since 1946. The treated vegetable plots thus far have slightly outyielded the untreated plots and there is no evidence of toxicity. In a greenhouse experiment, tomato plants were set in pots of Miami soil mixed with sand to which was added copper sulfate sufficient to injure, and eventually kill, the young seedlings. After two weeks, other seedlings planted in the pots from which the dead plants had been removed, grew and eventually bore fruit.

In view of the foregoing experiments, there would seem to be little possibility that copper toxicity would ever occur on ordinary agricultural soils, by accrued copper from fortified fertilizer even if it contained as much as 1 per cent of the element. The objection to adding copper sulfate to general fertilizer mixtures because of cost is more valid. Not only the cost of the copper but the expense of mixing it with the fertilizer has to be considered.

A preliminary survey of eastern fertilizer companies showed that the majority contacted did not use copper in their product; some used it on special demand orders, and a minority included it in at least one grade or brand. Most companies reasonably follow the recommendations of their experiment stations or repeated demands of their customers. The use of copper as a soil amendment is increasing, although it is difficult to obtain tonnage figures. There are at least five companies advertising on a national scale that produce copper-containing trace-element mixtures, where there were none scarcely more than a decade ago. The number of independent farmers who use copper as the sulfate or in mixtures is increasing also. However, the majority, as yet, give little thought to the possible need for any minor elements or do not consider that their insurance value is sufficient to warrant their added cost.

7. *Effect on Availability of Other Elements*

It has been proved many times that the absorption and utilization of one element is profoundly affected by the concentration of other elements present, both in the soil and in the plant. For example, one element may prevent the excessive intake of a second that is toxic in too great an amount. On the other hand, it may increase the availability of the second element.

Copper may function either way. It is known to affect or be affected by several other elements. The copper-nitrogen balance is an outstanding example. As early as 1914 (Lipman and Burgess), it was found

that copper exerted marked stimulating effects on the nitrifying flora of a mineral soil, and frequently more than doubled the normal nitrate yield. However, Jensen (1916) obtained a reduction in the amount of nitrates with soil applications of copper sulfate at the rate of 100 lb. per acre. It has been suggested that such a high rate kills some of the nitrifying organisms. Apparently a low rate does not, since Swanback (1950), with applications of 18 lb. per acre, consistently obtained a higher rate of nitrogen production from his test plots than from the check plots.

Where copper deficiency occurs, an increase of the nitrogen level increases the severity of the deficiency symptoms (Camp and Fudge, 1939; Dickey *et al.*, 1948; Gilbert *et al.*, 1946; Hamilton and Gilbert, 1947). Chemical analyses of tissues (Camp and Fudge, 1939; Fudge, 1939) from citrus trees exhibiting copper-deficiency symptoms have shown a much higher nitrogen content than have analyses of comparable tissues from trees which give no indication of the deficiency. A decline in nitrogen content has been found following the application of copper treatments to deficient trees. This condition might be classified as either an excess of nitrogen as compared to copper, or a deficiency of copper as compared with nitrogen. The latter point of view is more practical since it is quite easy to supply a deficient element, but difficult to remove an excess. In most cases, the term "deficiency" must be considered as relative, as is brought out not only in the relation of copper to nitrogen, but also to several other elements.

In the past several years, the relation of copper to molybdenum has attracted considerable attention, especially since the latter element is now considered to be essential to plant life. In 1938, by spectroscopic examination, a high molybdenum content was found in the herbage of pastures on which sheep and cattle were affected by a "scouring" disease, known as "teartness" (Ferguson, 1943; Ferguson *et al.*, 1938, 1943). It was soon found that copper was a specific remedy for the disease (Russell, 1944) and "teartness" could be eliminated by administration of copper sulfate directly to the affected animals or by applying it to the pastures.

Analysis of forage grown in some Florida areas, long recognized as copper deficient, show a high molybdenum content (Comar *et al.*, 1948). Forage containing five parts per million of copper on a dry matter basis has been found to be adequate for ruminants under certain conditions, but up to ten to fifteen parts per million may be inadequate if the ration contains considerable molybdenum, lead, or zinc, or if the calcium-phosphorous ratio is wide.

Lucas (1946), among others, has found a copper-zinc relationship.

Zinc sulfate on organic soil increased plant growth only when copper was present, and zinc injury is reduced by the presence of copper. Laboratory experiments have demonstrated a copper-zinc antagonism in rats (Gray and Ellis, 1950; Smith and Larson, 1946). The feeding of excessive zinc produced an anemia which was corrected by copper feeding. The presence of lead is possibly a factor contributing to copper deficiency where the lead content of the forage is found to be high and copper low, but in most cases is not believed to be of prime importance (Shearer and McDougall, 1944).

Copper has the same effect as potash in correcting excessive absorption of iron (Erkama, 1949; Willis and Piland, 1934), and an excess of copper can induce iron chlorosis (Chapman *et al.*, 1939; Shkol'nik and Makarova, 1950). Corn grown on an unproductive peat soil became chlorotic when a large amount of copper sulfate was added to the soil, but a green color again developed in the leaves when they were treated externally with a 1 per cent solution of ferrous sulfate (Willis and Piland, 1936).

Antagonism of copper and manganese (Schropp, 1948) and of copper and boron (Shkol'nik and Makarova, 1949) has also been reported. In a South Carolina experiment (Bacon *et al.*, 1950), no increase in weight of tobacco was obtained on Marlboro fine sandy loam by additions of copper sulfate. However, when potash deficiency symptoms were observed and the amount of potash was increased from 48 lb. to 80 lb. per acre, a pronounced increase in weight was obtained in favor of the copper-treated plants over the controls. The variation in the results of copper sulfate applications to mineral soils of the same copper content may be partly explained by these interrelations or antagonisms between elements.

8. *Aspergillus niger*

By the use of specially purified media, it was found that the fungus *Aspergillus niger* needs copper, zinc, and iron in its nutrition. The black pigment in the spores was found to be a mixture of humins dependent on copper and iron for their formation (Bortels, 1927). When receiving sufficient copper, the spores of this fungus are black; when receiving no copper, they are white; and with slightly increasing amounts, the color ranges from cream through yellow and brown. The fungus has a copper sensitivity as low as 0.1 part per million, and, therefore, may be used as a criterion of the amount of available copper in the soil (Mulder, 1937, 1938, 1939).

On many mineral soils, the amount of available copper determined by *Aspergillus niger* bioassay agrees quite closely with the amount ex-

tracted by Morgan's "Universal" solution * and determined chemically or spectrographically. With organic soils, however, *Aspergillus niger* is much more sensitive and extracts a proportionally greater amount of copper than can be obtained by leaching with Morgan's solution.

VI. Copper in Animals

1. Use in the Body

Copper is necessary to animal life, although its essentiality, or even its presence in all animal tissues, was questioned for many years (Rose and Bodansky, 1920; Willard, 1908). It is now recognized, that for the proper utilization of iron, small quantities of copper are needed (Hart *et al.*, 1928; *Sheldon*, 1932). Without the copper, iron is assimilated and stored in the liver, but is not converted into hemoglobin (Elvehjem and Sherman, 1932). Such a conversion does take place only in the presence of copper.

Several naturally occurring, animal organic substances contain copper. One of them, hemocyanin, a copper-protein complex, is found in the blood of certain invertebrates. In the crab, spider, and snail, for example, the hemocyanin functions as an oxygen carrier, similar to hemoglobin in man. A red pigment, turacin, containing 7 per cent copper, is found in the feathers of the turaco, a South American bird. Turacin is a derivative of the normal porphyrin pigments generally found in animals and plants. Certain other copper-bearing proteins have been isolated, including hemocuprein from the red blood corpuscles of mammals and hepatocuprein from liver; but as yet, little is known of their physiological significance (Dawson and Mallette, 1945).

The enzyme tyrosinase is found in animal tissues. This enzyme, in a series of changes, converts tyrosin to melanin, a black pigment (Cunningham, 1931). Thus, copper is claimed to play a role in skin and hair pigmentation (Singer and Davis, 1950; Smith and Ellis, 1947). Pigmented cat and dog hair, and to a lesser degree, the skin underlying pigmented hair, have a higher copper content than white hair and underlying skin (Sarata, 1935).

Anemia in the rat, accompanying a severe copper deficiency, was found to be further accompanied by a decrease in the cytochrome oxidase activity of the bone marrow—a loss which was offset when copper was again fed to the animal (Comar, 1948; Schultze, 1941; Schultze and Simmons, 1942). The bone marrow is one of the chief centers of blood

* One hundred grams of sodium acetate, 30 ml. acetic acid, water to a total volume of 1 liter.

formation from food products (hematopoiesis), and it would seem that copper plays an essential part in this reaction.

Milk produced by cows on a normal ration contains about 0.15 mg. of copper per liter (Elvehjem *et al.*, 1929). Efforts have been made to increase this ratio by feeding large amounts of the metal (Elvehjem *et al.*, 1929; Hamilton *et al.*, 1929). However, the cow, and also the hen, with few exceptions, thwart the efforts of man to change the mineral composition of their products.

2. *Deficiency Symptoms*

The original Wisconsin work in which anemia was produced in rats by means of a diet low in copper has been repeated and confirmed a number of times, both with rats and with other animals (Comar, 1948; Cunningham, 1931; Elvehjem and Hart, 1932; Teague and Carpenter, 1951). Symptoms of copper deficiency are anemia, diarrhea, cessation of growth, depigmentation of hair, poor reproduction, abnormalities of bone formation, nervous disorders, and general debility. In sheep, the wool is affected. However, all these symptoms are not always present in deficient animals, either in laboratory experiments or in the field.

Borderline copper deficiency, due either to a low copper intake or to a deficiency induced by the addition of molybdenum or other toxic elements to the diet, is one of the causes of poor breeding performance in cows. If a copper deficiency in the feed of a herd continues for some time, the cows may fail to come in heat. If bred, they produce a high percentage of dead or weak, sickly calves.

In copper-deficient cattle, a condition sometimes develops which resembles X-disease (hyperkeratosis) very closely. Many skin sores develop and fail to heal. There is a loss of hair and a roughening and thickening of the skin in more advanced cases. The careful observer can distinguish this copper-deficient condition from true hyperkeratosis in that the sores in copper deficiency are at the actual sites of injury and there are no lesions in the mouth, gullet, or bile duct. Furthermore, if the animal is fed small amounts of copper, the condition clears promptly.

Copper deficiencies in domestic animals, especially ruminants, are found in many parts of the world. Much of the trouble is complicated by various factors including superabundance of other elements, and, therefore, the deficiency symptoms vary widely and are known by different names. In Australia, a nervous disorder of cattle is known as the "falling disease." Sheep are affected by a staggering disease called "enzoötic ataxia," and by a wool abnormality as "stringy" or "steely wool." In the "falling" disease, the affected animals lack muscular

coordination, especially of the hind legs, stagger, and frequently fall. The disease is usually terminated by sudden death. A positive correlation was found between hemoglobin and copper values of blood, both in copper-deficient, staggering cattle, and those receiving copper supplements (Bennetts *et al.*, 1942a).

"Stringy wool" appears to be the earliest and frequently the most obvious sign of copper deficiency in sheep, occurring even when the disorder is not sufficiently severe to cause manifestations of ataxia (Bennetts, 1942). "Enzoötic ataxia" most commonly affects lambs from one to two months old. They become unthrifty, stiff in gait, and their growth is retarded. The ataxia progresses rapidly, and the lambs usually die within a few weeks. Ewes with "stringy" wool always drop lambs with ataxia.

A very low copper status of pastures and animals is constantly associated with these diseases, and optimal response in health and production is obtained by the administration of copper supplements to the animals or by topdressing the unhealthy pastures with copper sulfate (Bennetts and Beck, 1942; Bennetts *et al.*, 1941, 1942b). Additions of copper to the diet of sheep have also been found to make better wool even where the animals were apparently not copper deficient.

A disease similar to "enzoötic ataxia" has been investigated in England. This disease, described in 1932 (Stewart), is called "swayback," "swingback," or "warfa," and was widely distributed throughout Great Britain. The disease is confined almost exclusively to young lambs. Most are affected at birth and are unable to raise themselves to suckle. Others manage to struggle to their feet, but sway and collapse if they attempt to walk. The mortality rate of affected animals is nearly 100 per cent. It was shown that the disease was not due to a copper deficiency of either soil or herbage (Shearer and McDougall, 1944; Stewart *et al.*, 1946), but nevertheless the affected animals suffered from a copper deficiency and responded to copper medication (Dunlop *et al.*, 1939). Just what conditions prevent the grazing ewes from utilizing the natural copper of "swayback" herbage is not yet known, but high levels of other elements, such as zinc and lead, may be a contributing factor (Gray and Ellis, 1950). The first case of a copper deficiency in cattle was reported in England in 1946 (Jamieson and Russell, 1946), and in Ireland in 1949 (O'Donovan, 1949). In both cases, the trouble was connected with a low copper content of the pasture forage.

In continental Europe, a copper-deficiency disease of cattle is also found, and for years has been known as "Lecksucht" or "licking disease." In areas where this disease occurs, the copper content of the vegetation is usually very low, unlike conditions in "swayback" areas.

"Lecksucht" is cured by administration of copper sulfate or by copper treatment of pasture soils.

In the United States, copper deficiency in cattle is known as "salt sick," and is most severe in Florida (Becker *et al.*, 1931; Neal *et al.*, 1931), where it is frequently complicated by deficiencies of iron and cobalt.

The antagonism of copper and molybdenum has already been mentioned. This antagonism, causing the disease known as "teartness," where the copper content of the forage is low in proportion to the molybdenum content, is not uncommon in England (Ferguson, 1943; Ferguson *et al.*, 1943; Russell, 1944). A similar condition in cattle was described from California and was correlated with forage high in molybdenum (Britten and Goss, 1946).

The effect of copper sulfate as an antidote for molybdenum toxicity in cases of "teartness" has been explained as follows (McGowan and Brian, 1947): The activity of bacteria in the gastrointestinal tract is believed to be controlled by catechols. Molybdates reduce the effective concentration of catechols by formation of complexes. As a result, uncontrolled bacterial activity becomes excessive and causes the condition manifested by extreme diarrhea. The therapeutic effect of copper is suggested as being due to its toxic effect on the bacteria. The complete story of copper-deficiency diseases to 1944 has been reviewed (Russell, 1944).

The demonstration of disease in animals caused by a mineral unbalance in the feed emphasizes the necessity for a consideration of the levels of all minerals in the diet before determining the requirement of any one. A deficiency disease may not reflect merely a low level of a dietary essential, but may also indicate an excess of one or more other minerals which interfere with the normal metabolism of that essential dietary constituent.

Any attempt to arrive at a conclusive statement regarding the occurrence of copper deficiency in man, or the human requirements of copper, would be premature at this time, and would, therefore, be controversial. It has been estimated that human daily needs of copper are in the neighborhood of 2 mg. per day, and the adult body is said to contain from 100 to 150 mg. of the element (Cuthbertson, 1948) stored, for the most part, in the liver (Flinn and Inouye, 1929).

3. Use as an Anthelmintic and in Mineral Supplements

Copper sulfate has been used as an anthelmintic for gastrointestinal parasites of sheep (Rietz, 1935, 1936; Stewart, 1934; Wood, 1931).

However, its use has not been uniformly successful, and it has largely been replaced by phenothiazene.

Copper sulfate is one of the important components in most mineral supplements for cattle, sheep, swine, and poultry. There is a growing use of such supplements. Their prime purpose is insurance against possible deficiencies in the regular feed. Granted that such a purpose is met, is there any value in the extra amounts of minerals that are consumed? Little research has been done on this subject.

Braude (1945) reported that the addition of five parts per million of copper as the sulfate, to the diet of fattening pigs, did not increase their weight, although the copper content of the livers was higher in the treated pigs than in the controls. However, Carpenter (1949), in a series of field trials, found that raising the copper content of the diet of growing swine from eleven parts to forty-five parts per million increased the average weight of five-month-old pigs 13 to 15 per cent. The growth-promoting effect of the copper did not appear to be attributable to any effect on the microbial or parasitic populations of the intestinal tract.

4. Toxicity

Copper in small amounts is not now considered to be very toxic to animals, but on occasion, overdoses have proved fatal. There is one report of chronic copper poisoning near a smelter (Bisset, 1934), and long ingestion of salt mixtures sold as a preventive for stomach worms has also proved fatal to sheep (Boughton and Hardy, 1934; Rietz, 1936).

In New Zealand (Cunningham, 1946b), a study was made of the poisoning effects of varying amounts of copper in animal feed. Doses up to 80 g. of copper sulfate were not poisonous to yearling heifers or to adult cows. The lethal single dose ranged between 200 and 400 g. From these figures, it has been estimated that the amount of copper sulfate that would be fatal to an adult human being in a single dose would probably be around 50 g.

Somers (1947) estimated that a fatal dose of supposedly harmless ferrous sulfate would require the ingestion of several hundred 0.2-g. tablets, or at least 40 g. of the material, although as little as 6 to 10 g. have produced death when accidentally swallowed by children. Thus, copper, which has been considered poisonous by most people, is scarcely more toxic than iron as ferrous sulfate, which is ordinarily thought of as innocuous.

VII. Regions of Copper Deficiency

Local areas of copper deficiency are widespread throughout the world. As has been mentioned, soils high in organic matter, especially newly

cultivated peat soils, are most likely to be deficient, but very sandy or gravelly soils with a low humus content have, in many cases, been reported to require copper before a satisfactory crop can be grown on them.

1. *Europe*

The "reclamation disease" of cereals, beets, and leguminous crops occurs on reclaimed heath and moorland soils in Denmark, Holland, Germany, Russia, and other parts of Europe. Sjollema (1933) connected this disease with the animal trouble known as "licking disease" or "Lecksucht" and demonstrated that the two had a common cause—too little copper. The "licking disease" also occurs in Sweden (Sandberg and Svanberg, 1943) and Norway (Ender, 1942), where it is known as "Pica." The location of the copper-deficient soils in Europe has been mapped by Rademacher (1937).

In England, "swayback" of sheep (Dunlop *et al.*, 1939) and "scours" of cattle (Jamieson and Russell, 1946) have been cured by copper treatments. A soil actually low in the element was not reported until 1946 (Jamieson and Russell), and the first case of an "exanthema" in fruit trees was not recorded until 1950 (Bould *et al.*, 1950; Jones, 1950). In Ireland, spraying with Bordeaux not only has been of fungicidal value, but large crop increases attributed to the correction of copper deficiency have been observed over a twenty-year period (Muskett, 1950). There has been one record where copper treatments restored to normal, emaciated cattle which had been fed on poor hay from a peaty soil, or had been kept on bare moorland pasture (O'Donovan, 1949).

2. *South Africa and the Antipodes*

In South Africa, copper deficiencies of sheep similar to "swayback" and "enzoötic ataxia" have been reported (Madsen, 1942). A chlorotic condition of deciduous fruit trees also occurs. Analysis of the chlorotic material showed a consistent deficiency of copper, and additions of copper sulfate to the soil around the trees prevented or cured the trouble (Anderssen, 1932; Isaac, 1934). Treatments with salts of various other elements or with manure had no effect.

Severe copper deficiencies occur on the geologically ancient soils of Australia and New Zealand. In Australia, both "reclamation disease" of cereals (Piper, 1940) and "exanthema" of fruit trees occur (Cahill, 1929; Dunne, 1938; McCleery, 1929), and copper-deficiency troubles with sheep and cattle are prevalent (Bennetts, 1943; Bennetts *et al.*, 1941). The low copper content of Australian soils does not appear to be localized, but is general over the continent, from New South Wales in the

east, where citrus has been affected for many years (McCleery, 1929), through South Australia (Riceman and Donald, 1938; Riceman *et al.*, 1938), to Western Australia (Beck, 1941; Bennetts, 1943; Teakle, 1942).

Unlike conditions in many other parts of the world, copper troubles here are due to the low content of the element in the soil rather than to the fact that copper is made unavailable by organic matter. The Australian soils, in which copper deficiency occurs, are leached sands or gravels, frequently calcareous, and have a low organic content.

In New Zealand, reclaimed peat soils are deficient in copper, especially peat-pumice and peat-sand mixtures (Cunningham, 1944, 1946c). Certain cattle and sheep troubles, such as peat scours, anemia, unthriftiness, and difficulty in rearing young, all appear to result from this deficiency. Top-dressing such deficient areas with 5 lb. of copper sulfate per acre per year is recommended for preventive purposes (Cunningham, 1946a,b).

3. America

No cattle troubles attributed to a lack of copper are known to occur in South America, but conditions similar to "swayback" and "enzoötic ataxia" in sheep have been reported from Peru (Madsen, 1942). "Exanthema" of fruit trees also occurs, and copper sulfate is recommended for its control (Cipola, 1937). Dr. H Evans, plant physiologist of the cocoa research scheme in Trinidad reported at the cocoa industry conference held in London in 1950 that practically all cocoa growing in Trinidad is suffering from faulty trace-element nutrition, and deficiencies of copper are of frequent occurrence.

In North America, copper deficiency occurs chiefly on high organic soils, but heavy soils in California (Oserkowsky and Thomas, 1938), light sands in Florida (Dickey *et al.*, 1948), and sandy loam in North Carolina (unpublished report from North Carolina Experiment Station) have also been shown to be deficient.

The largest area of severe copper deficiency in North America is in Florida, where the use of copper amendments on the soil is standard practice (Allison, 1930a,b). Not only is "exanthema" of citrus, "dieback" of stone fruits, and "leaf burn" of tung prevalent, but in some locations, the production of any agricultural crop is virtually impossible without the use of copper. Cattle restricted to grass forages on certain Florida soils suffer from a nutritional anemia known locally as "salt sick" (Becker *et al.*, 1931; Neal *et al.*, 1931). This disease, which has been mentioned previously, is due primarily to too little copper in the forage, although iron and cobalt deficiencies are complicating factors, and treatment ordinarily consists of therapy with all three elements.

The luxuriance of the native vegetation on deficient areas cannot be taken as an index of the amount of copper in the soil, since many of these plants are adapted to such conditions. Before remedial measures were taken, cattle were frequently found to be starving for copper and other trace nutrients on native pastures where the thick grass grew knee-high.

Copper deficiency extends up the Atlantic coastal plain in more or less scattered areas, both on organic and mineral soils. Copper is usually applied to crops on the organic soils, but is used infrequently on the mineral soils, even though results have shown that, in many cases, excellent results may be obtained by so doing (Manns *et al.*, 1936a,b). Some of the deficient coastal plain mineral soils are poor soils in other ways. Such marginal soils are occasionally farmed, but are usually in pine forest, and the need for trace elements, which may be greater than realized, does not attract attention.

Local areas of copper deficiency occur practically everywhere, where peat and muck soils are farmed, for example, in New York (Felix, 1927; Knott, 1936), Indiana (Conner, 1933), Ohio (Comin, 1944), and Michigan (Harmer, 1941, 1946). In Michigan, slightly more than 12 per cent of the land is classified as organic (Davis, 1950), and is spread over every one of the eighty-three counties in the state. The areas range in size from less than one to more than 5000 acres. On such land, copper is recognized to be just as important as the major plant foods, and the recommended application of copper in the form of the sulfate is 25 to 50 lb. per acre annually, until a total of 250 to 300 lb. has been added, or until no further benefit is shown.

On the Pacific coast, areas of copper deficiency have been found in California and Washington. In both states, an "exanthema" of pears occurs, and in California, other fruit, including citrus, is affected. Copper has been applied by introducing copper sulfate crystals into holes bored in the trunk of the tree a few inches above the root crown (Thomas, 1931), by spreading the crystals around the base of the tree, and by Bordeaux spray. The first method has been the most effective. Spraying is of value, but must be continued each year, and the action is localized. Ground treatments result in slight improvement only, and, in California at least, are not effective for two or three years after the treatment. This is not surprising in view of the fact that the soil in many of the treated orchards is very heavy with presumably a large capacity for fixing copper (Rohrbaugh, 1946). Furthermore, these orchards were not irrigated, and the precipitation is only about 20 in. As a result, in most cases, the copper sulfate dissolves very slowly, and large crystals of the salt may be found around a treated tree for several years after application. In the more humid east, soil applications of

copper on orchards have been more successful and trunk applications are seldom made.

At the present time, the localities mentioned are recognized as being copper deficient. There are other local areas where crops will respond to copper additions (McLean *et al.*, 1944) even though the total amount in the soil is not excessively low.

There are an increasing number of cases where poor crop growth appears to be due to mineral unbalance, rather than to an actual deficiency of any one element. Additions of pure, highly concentrated salts or fertilizer serve to aggravate the condition. The remedy would be, of course, to avoid excessive use of such materials or to balance them with the lacking major and perhaps minor essentials.

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Ecological and Physiological Factors in Compounding Forage Seed Mixtures*

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I. Problems with Artificial Seed Mixtures

With the advent of livestock enterprises and their incorporation into farming systems, the use of artificial mixtures of grasses and legumes has been encouraged. A map prepared by Vinall (1935), Fig. 1, shows that the forage species used in mixtures in the more humid or in irrigated areas were introduced from other countries. The introduced for-

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age plants that are adapted to various sections of the United States are usually of either northern or southern origin.

The forage plants used within a region also respond differentially to the factors that influence the rate of growth. These differential growth responses among species are not well understood, thus it is difficult to maintain a balance of grasses and legumes in mixtures. Through

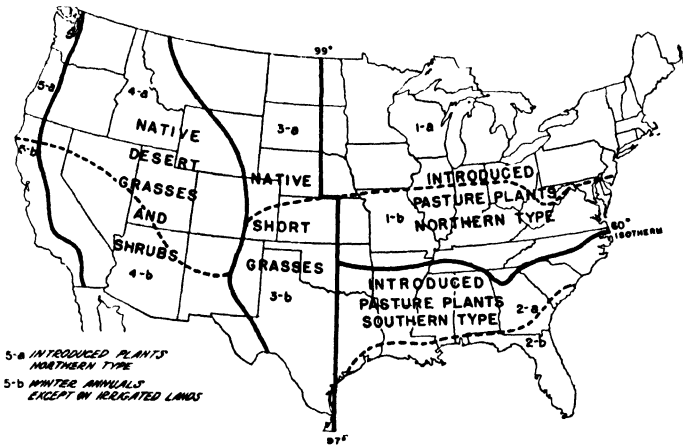


FIG. 1. On the basis of climate the United States may be divided into five general regions. The kind of plants that furnish most of the pasturage in each region are indicated. (From *U.S. Dept. Agr. Misc. Pub.* **194**, 1934.)

trial and error and fundamental research much has been learned about the behavior of species in mixtures. However, physiological and ecological data needed to interpret the life histories of species in mixtures are so limited that cause and effect are often misinterpreted.

Benedict (1941) conducted an experiment in which dried bromegrass, *Bromus inermis,* Leyss, roots were mixed with sand and sown with the same grass. Bromegrass growth was inhibited, and the cause was attributed to some harmful substance or substances from the dried roots. Myers and Anderson (1942) found that bromegrass seedlings grew better in the soil of a four-year-old nitrogen-starved bromegrass sod, if nitrogen was added, than in a cultivated soil. The writers concluded that the highly carbonaceous organic matter tied up available nitrogen and that the toxic substances, if present, were destroyed by nitrogen fertilizer.

Ahlgren and Aamodt (1939) found that the top and root weights of two species used in a mixture were less for both species in the mixture

than for pure stands. This retarded growth among both species, when growing in association, was attributed to harmful root interactions. Such a reduction in growth by two species in a mixture was not found to exist in other experiments. Stapledon and Davies (1928) grew forage species in mixtures to study the influence of one species on another. The ryegrasses, particularly Italian ryegrass, *Lolium multiflorum,* Lam., had a depressing effect on the growth of orchardgrass, *Dactylis glomerata,* L., timothy, *Phleum pratense,* L., and rough stalked meadow grass, *Poa trivialis,* L Tall oatgrass, *Arrhenatherum elatius,* (L.) Mert. and Koch., also tended to retard the development of certain other grasses. When grown with timothy, orchardgrass was the aggressor species. In another experiment five grasses (Italian ryegrass, perennial ryegrass, *Lolium perenne,* L., orchardgrass, tall oatgrass, and timothy) were grown with clovers (broad red, *Trifolium pratense,* L., late flowering red, white, *Trifolium repens,* L., and alsike, *Trifolium hybridum,* L.). Orchardgrass and tall oatgrass produced the highest yields in competition with clover and retarded the clover the most. Timothy retarded the growth of clover the least. Late flowering red clover was retarded less by grasses than broad red clover and all red clovers were aggressive toward white clover.

Åberg, Johnson, and Wilsie (1943) grew red clover, alfalfa, *Medicago sativa,* L., timothy, and bromegrass in all combinations in a field experiment to measure species behavior in different mixtures. They found that bromegrass was more aggressive when grown in various mixtures than the other three species. Alfalfa yielded less in a mixture with bromegrass and red clover than when grown in pure stands. From a greenhouse experiment, these workers reported that bromegrass yielded less when grown in mixtures with orchardgrass, timothy, and red clover than in pure stands. Orchardgrass and timothy each produced higher yields when grown with bromegrass than when grown in pure stands. Timothy yields were lower when grown with orchardgrass than in pure stands. Alfalfa yields were reduced when grown with orchardgrass and increased when grown with bromegrass. The individual plant yields of red clover were lower in pure stand than the yields for individual plants grown with mixtures of other species.

Roberts and Olson (1942) measured the yield of individual plants of red clover, sweet clover, *Melilotus alba,* Desr., alsike clover, Wisconsin white clover, lespedeza, *Lespedeza striata,* Thunb., H. and A., and alfalfa when grown alone and with each of red top, *Agrostis alba,* L., and Kentucky bluegrass, *Poa pratensis,* L. There was no evidence of simultaneous yield decreases of both species in a mixture.

It should not be denied that there may be plant associations in which

species in mixtures are mutually harmful to each other because of toxic excretions or some antagonistic effect. However, a careful examination of literature concerning forage plant mixtures indicates that there is generally no gain or loss in the herbage or root yields of all species in a mixture. When growing aggressive and nonaggressive species in a mixture, the increased yields of the aggressive plants were counteracted by decreases in yield of the nonaggressive plants. There was a compensating rather than a mutually beneficial or antagonistic relationship among species grown in association.

Plant populations resulting from sowing grasses and legumes are dynamic; the prominence of a given species in a mixture is depleted or augmented, depending upon the relative growth of each species under imposed or natural environmental factors. Plants used in forage mixtures vary morphologically, genetically, and physiologically, and thus respond differentially to climatic, soil, biological, and other factors. Information that interprets the variable growth responses of plant species under different environmental conditions could be used in designing mixtures and imposing desirable management practices.

Specific data on the relative growth responses of forage plants to simple and many interrelated growth factors is fragmentary. In this manuscript an attempt is made to piece together the available data on growth factors and to discuss their single and combined effects on the growth of species in mixtures. This report obviously shows the acute need for more fundamental research to gain a better understanding of the behavior of plant species and genotypes in mixtures.

II. Plant Adaptation as Related to Compounding Seed Mixtures

It is difficult to maintain the stands and production of species components in mixtures. New seedings of mixtures of the taller growing grasses and legumes often produce the highest yield the year after sowing, thereafter the productivity declines (Stapledon and Davies, 1930; Ahlgren *et al.*, 1944, 1946). The cause of this decline is not well understood, but is usually attributed to loss of the leguminous associate and the concurrent low supply of available nitrogen. Legumes are usually more vulnerable to injury and stand depletion than the grasses.

Although it is not generally acknowledged, grasses alone, when adequately fertilized, are more productive than grass-legume mixtures. It would be much simpler to maintain grasses or mixtures of grasses than grass-legume mixtures. However, the utilization of legumes in mixtures is of great practical significance because the magnitude of production is

related to available nitrogen supply. Nitrogen manufactured by well-adapted legumes is less expensive than commercial nitrogen fertilizer.

The growth behavior of species in mixtures can often be interpreted by growth factors. The first parts of this section deal with the adaptation of plant species as influenced by single climatic, soil, and biological factors. This was done to simplify the presentation; although the growth of plants, alone or in mixtures, is influenced by the combined effect of many factors. The last portion of this section deals with some competitive effects among plants in mixtures as interrelated to growth factors and plant succession.

1. Climatic Factors

a. Temperature-Plant Relationships. Temperatures are intricately related to the growth behavior of species and strains of forage plants and determine, to a considerable extent, their adaptation and amount of growth that may be expected at different seasons of the year. Temperature is also associated with the sowing date of forage species because of its effect on germination and seedling development.

Species differ in their temperature requirements for germination. Chippindale (1949) has shown that a continuous low temperature of 5° C. to 10° C. did not affect germination of Italian ryegrass, was only slightly depressive to perennial ryegrass and orchardgrass, but was very depressive to timothy, tall fescue, *Festuca elatior,* var. *arundinacea* and Kentucky bluegrass. Alternating temperatures (18° C. for 18 hours; 27° C. for 6 hours) were without effect on the germination of Italian ryegrass, perennial ryegrass, and timothy, but were very favorable for germination of orchardgrass, tall fescue, and essential for Kentucky bluegrass.

Field germination of some species of grasses and legumes was compared with laboratory germination by Stapledon *et al.* (1927). The results indicate that temperatures below 44° F. retard germination. At these low temperatures clovers germinated quicker than grasses. Alfalfa required higher temperatures for germination than red clover, and night frosts retarded alfalfa germination. For optimum germination of alfalfa the mean soil temperature should exceed 45° F. for a 30-day period after sowing.

In another experiment the emergence and early seedling growth of eight species of forage grasses and legumes were measured under daily alternating temperatures of 40°–55° F., 55°–70° F., 70°–85° F., and 85°–100° F. (Sprague, 1943). Sudan grass, *Sorghum vulgare,* Pers., emerged readily at temperatures of 85°–100° F., but the emergence of all the other species in the test (bromegrass, orchardgrass, meadow fescue,

Festuca elatior, L., timothy, Kentucky bluegrass, ladino clover, *Trifolium repens,* L., and colonial bentgrass, *Agrostis tenuis,* Sibth.) was reduced. The seedling emergence of Kentucky bluegrass, colonial bentgrass, timothy, orchardgrass, and ladino clover was seriously inhibited at 85°–100° F. Although seedlings of bromegrass and meadow fescue emerged at high temperatures, the seedlings died or made little growth during a six-week period. The growth rate of seedlings differed with temperatures. Bromegrass and ladino clover seedlings made the best growth at 70°–85° F. temperatures. The yields of Sudan grass seedlings were about the same at 70°–85° F. and 85°–100° F. All the other species produced the highest yields at temperatures ranging from 55°–70° F

The rate of emergence and development of seedlings, as influenced by temperatures, should be associated with planting date The differences in responses of species to temperature can enable certain species to become aggressive in mixtures at a very early stage of growth. For example, tests in Virginia show that alfalfa seedlings (relatively high-temperature species) are competitive to orchardgrass seedlings (relatively low-temperature species) when sown in late summer. The reverse occurs with spring sowings.

Northern and southern forage plants respond differently to temperatures. E. M. Brown (1939) found that the optimum temperatures for herbage production was between 80° and 90° F. for Kentucky and Canada bluegrass, *Poa compressa,* L., and 60°–80° F. for orchard grass. For Bermuda grass, *Cynodon dactylon,* L., Pers , the herbage yields were higher at 100° F. than at other temperatures. The highest root and rhizome yields for species were obtained at temperatures as follows: Kentucky bluegrass 60° F., Canada bluegrass 50° F., orchardgrass 60°–70° F., and Bermuda 100° F. High soil temperatures seemed to be more harmful than high air temperatures to the cool season grasses. The harmful effects from high day temperatures on growth of orchardgrass were counteracted by low night temperatures.

In comparing Dallis grass, *Paspalum dilatatum,* Poir, Bermuda grass, carpetgrass, *Axonopus compressus* (Swartz) Beauv., and Kentucky bluegrass, Lovvorn (1945) found that the first three grasses, which are used in southern regions of the United States, produced more top and root growth at 85° F., than at 65° F. Kentucky bluegrass produced more roots at the lower temperature, but herbage yields at the two temperatures were similar.

Temperature per se often limits the regional adaptation of plants. The pasture plants of southern origin such as the genera, *Paspalum, Cynodon, Axonopus, Lespedeza,* and *Digitaria,* do not survive in temperate regions. The regional adaptation of grasses of northern origin

is also largely affected by temperatures. For example, orchardgrass is used in warmer regions than Kentucky bluegrass and timothy, and tall fescue is adapted to warmer regions than orchardgrass. Field plantings indicate that tall fescue varieties are adapted to a wide range of temperature conditions. They are used in latitudes from Florida to Maine, however, Alta and Kentucky 31 fescue do not grow vigorously during the warm summer months in the lower south.

Temperatures have a pronounced effect upon the succession of species in a mixture. White clover varieties are commonly used in mixtures with timothy, orchard, Kentucky bluegrass, or other grasses and during the spring months the clover stand is often seriously reduced due to grass competition (Johnstone-Wallace, 1937; A. B. Brown, 1939; Dodd, 1941; Sprague and Garber, 1950). The grasses of northern origin grow at lower temperatures than white clover, hence their early spring growth is aggressive toward white clover. In some of northeastern states where bromegrass is adapted, it is apparently used with ladino clover because bromegrass starts growth later in the spring than orchardgrass. For this reason bromegrass is less aggressive toward ladino clover than orchardgrass. The species in a mixture that responds similarly to a given temperature would be expected to be least aggressive toward each other, if other physiological differences are eliminated.

Injuries due to low temperatures vary with species and strains of forage plants. Tysdal and Pieters (1934) found cold resistance of alfalfa and red clover seedlings to be greater than for crown vetch, *Coronilla varia,* L., and that of crown vetch to be greater than for lespedeza. Of the lespedezas, Korean, *Lespedeza stipulacea*, Maxim., was injured more than common, *Lespedeza striata*, Thunb., H. and A.; perennial lespedeza, *Lespedeza sericea*, Thunb Benth., being the most tolerant of low temperatures. Cold tolerance differed with stage of growth; red clover and alfalfa seedlings were more cold tolerant at stages of growth beyond the two-leaf stage than at earlier stages of seedling development. Korean lespedeza was more cold tolerant at the two leaf stage than at later stages of seedling growth.

Ruptured plant tissue, encountered during low-temperature periods, is often indirectly associated with plant mortality because the injured tissue becomes diseased. Jones (1928) described injuries in the phloem, xylem, central parenchyma and other injuries in roots and crowns of alfalfa due to low temperatures during the winter months. Such severe injuries appeared to shorten the life of plants because parasitic disease organisms, such as *Aplanobacter insidiosum*, (L.) McC., which causes bacterial wilt, enter at the points of ruptured tissue. Weimer (1930) isolated five parasitic strains of Fusaria and three of bacteria at points

where the phloem was injured by heaving and alternate freezing and thawing during the winter.

Not only do species differ in their temperature adaptation, but Rogler (1943) found that strains within a species also differ in this respect. For a given species, seedlings of northern origin were found to survive in a greater proportion after artificial freezing than seedlings of southern origin. In another experiment, four clones of bromegrass were grown at soil temperatures of 20°, 26°, and 31° C. (Dibbern, 1947). The three clones of northern origin produced the highest herbage yields at 20° C., whereas the clone of southern origin produced the highest herbage yields at 26° C. Root growth was retarded more by the higher soil temperatures than top growth, and at 31° C. one northern clone did not survive.

The ability of a species to survive under low temperatures (winter hardiness) is related to genotypes, grazing or cutting management, and other factors. Sprague and Fuelleman (1941) and others report that winter hardiness is associated with the degree of dormancy after cutting in the fall. Ladak alfalfa, a very winter-hardy variety, recovered much more slowly after cutting for hay as compared with less hardy varieties such as Grimm, Hardistan, and common alfalfa.

Some of the combined effects of temperature and other factors on the growth and behavior of plant associations are discussed in Sec. II, 4.

b. Light-Plant Relationships. The light factor, photoperiod and intensity, has a profound influence on the adaptation and growth rate of pasture plants and their behavior in mixtures under field conditions. Latitude has a great influence on the length of day, the longest day at Gainesville, Florida, being 14.1 hours as compared with 16.7 at Saskatoon, Saskatchewan, Canada.

In California, various mixtures of forage species were tested under different cutting intensities where water was adequate under irrigation (Peterson, 1951). The magnitude of the yields was associated with light conditions and temperatures (Fig. 2). Even though temperatures were favorable for high yields, the productivity of all mixtures decreased in the latter part of the growing season because of the shorter days and a decrease in light intensity.

Blackman and Templeman (1938) conducted experiments to measure the effect of light intensity upon the growth of red fescue, *Festuca rubra*, L., bentgrass, *Agrostis* spp., and white clover. In greenhouse and field experiments three light intensities were studied: 100 per cent daylight, 60 per cent of daylight, and 40 per cent of daylight. The yields of herbage of all three forage species were diminished as the light intensity was reduced, the effect being approximately linear. In greenhouse experi-

ments with white clover the relative yields at 40 per cent daylight were approximately 40 as compared with 100 for daylight conditions. In a field experiment the relative herbage yields of clover under 40 per cent daylight intensity ranged from about 60 to 80 per cent of the yields for full daylight. A reduction in light intensity on red fescue and bentgrass affected leaf production similarly to that reported for white clover. The plots were clipped frequently in these experiments.

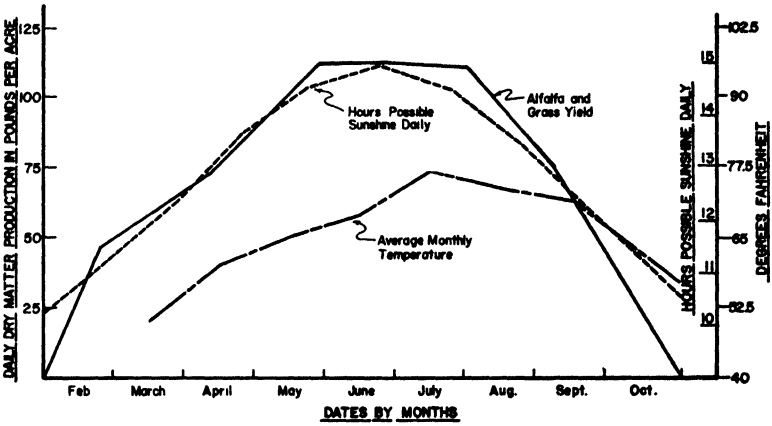


FIG. 2. The effect of light intensity and temperature on the yield of an Alfalfa-grass mixture (Peterson, 1951).

In measuring the effect of light intensity on bromegrass, twenty-three clones of different origin were grown under relative light intensities of 5, 14, and 46; the light intensity outside of the greenhouse being 100 (Dibbern, 1947). After about twelve months all the clones died at a relative light intensity of 5, more than half of the clones died at a light intensity of 14, and about one-fourth of the clones died at a light intensity of 46.

Photoperiod was found to have a great effect on the growth rate of eight forage seedlings (Sprague, 1943). For every species the dry matter production, number of leaves, and plant height were lower under the 9-hour than the 16-hour day length. The amount of roots produced in proportion to the tops was also found to be less for the 9-hour than the 16-hour day. The higher top-to-root ratio at the short day photoperiod was apparently attributed to a slow rate of carbohydrate synthesis under short day lengths. In an experiment with three southern grasses, Bermuda, Dallis, and carpetgrass, photoperiod had little effect on the yield,

but the trend was for higher production with a longer day (Lovvorn, 1945).

Photoperiod influences the vegetative growth development of forage plants. During the short photoperiods which occur in the autumn and spring the leaves of Kentucky blue, Canada blue, orchard, brome, and other grasses are short and prostrate in habit of growth (Stuckey, 1942; Peterson and Loomis, 1948; Evans and Watkins, 1939; Watkins, 1940; Keller and Peterson, 1950). As the length of the photoperiod increases, the leaves grow longer and more erect. At the end of a test period with orchardgrass, the plants were 744 mm. high under a 16-hour day as compared with 450 mm. for an 8-hour day (Stuckey, 1942). The internal structure of orchardgrass was also altered by light, the walls of fibers being noticeably thicker in the long day plants.

Flower induction and flowering of many forage plants is associated with photoperiod and temperature. In a test with perennial ryegrass, orchardgrass, bromegrass, timothy, meadow fescue, and Kentucky and Canada bluegrass, no flowers developed under a 10-hour day, and the best heading was obtained under a 16-hour day (Sprague, 1948). Flowering was satisfactory when the plants grown under 10 hours of daylight received 1 or 2 hours of supplementary light during the middle of the night, indicating that the length of the dark period affects flowering. Increasing the intensity of supplementary light above 75 foot candles did not affect flower development of the grasses. Some combined effects of temperature and photoperiod are given in Sec. II, 4.

The local adaptation of strains of a given species is apparently greatly influenced by photoperiod. An early maturing strain of bromegrass produced about the same number of panicles per plant under 15- and 18-hour photoperiods. Of a late maturing strain only 60 per cent of the plants flowered under a 15-hour day while all the plants flowered under an 18-hour day (Evans and Wilsie, 1946). Strains of timothy that differed greatly in maturity were tested in different latitudes (Evans *et al.*, 1935). A very early maturing strain of timothy bloomed 24 days earlier at Washington, D. C., than at the most northerly station at Guelph, Ontario, Canada. For the latest maturing selections the dates for heading were reversed, i.e., blooming occurred 16 days later at Washington, D. C., than at Guelph. Since the temperatures favor earlier spring growth at the more southern latitude, the late blooming date of late maturing timothy at more southern latitudes is attributed to the comparatively short photoperiod. Early maturing strains are those that flower under shorter days than the late maturing strains.

Temperature alone has been reported to influence the photoperiodic response of certain forage plants (Roberts and Struckmeyer, 1938, 1939).

Alfalfa, typically a long day plant, did not produce flowers at a temperature of 70° to 75° F., but at an intermediate temperature (63° to 65° F.) flowered only in the long day environment. In the cool environment (55° F.) the temperature induced flowering under short day conditions, but the typical photoperiodic response occurred under the long day conditions.

Red clover and white clover did not flower under short day conditions at any temperature, but produced a few flowers at 63° to 65° F. under long day conditions and showed a typical photoperiodic response at 55° F. and long day. Louisiana white clover flowered under all conditions except warm temperatures and short days.

The potential yielding capacity of a timothy variety is apparently associated with photoperiod (Evans, 1939). Late maturing varieties grown at more southern latitudes in North America will not produce high yields because the culms will remain short and dwarfed as compared to earlier maturing varieties. Very early maturing (short day) varieties, would be expected to mature so early in the northern latitudes that low temperatures would retard growth. The productivity would be low unless such strains excel in aftermath growth.

The dry matter production and maturity of strains and species as influenced by photoperiod will influence their aggressiveness in a mixture. Early maturing grass and legume varieties are those that produce elongated leaves and flower under shorter photoperiods than the later maturing plants. If an early maturing grass variety is sown with a later maturing variety, the early one will become the aggressor because the culms and erect leaves will shade and retard growth of the late varieties Keller and Peterson (1950) measured the growth behavior of strains of timothy and red clover that differ in maturity when grown in pure stand and various mixtures. The dry matter production of red clover was not altered by photoperiod. Timothy yields were increased as the length of day was increased. When timothy-red clover mixtures were grown under a 10-hour day, the timothy in the mixture was not benefited; however, with a 14-hour day the yield of timothy in the mixture increased by 47%. The proportion of timothy to red clover growing in a mixture increased with increasing day lengths, thus making timothy more aggressive or better able to compete with red clover under long days.

Ladino clover and other white clover genotypes of northern origin flower under long photoperiods and fail to flower under the shorter photoperiod in Florida (Blaser and Boyd, 1940). Since white clover generally behaves as a winter annual in Florida, ladino is not used in that region, because it does not produce seed. The white clover geno-

types of southern origin flower readily under the shorter photoperiod encountered in that region. Genotypes of other annual legumes from northern and southern origin such as black medic, *Medicago lupulina,* L., and annual sweet clover, *Melilotus* spp., responded similarly to white clover genotypes to photoperiod, (Blaser and Stokes, 1946, and unpublished results).

Certain legumes, such as Korean lespedeza, fruit readily under a short photoperiod, but a photoperiod of more than 14 hours will prevent fruiting (Smith, 1941). In Missouri, Korean lespedeza is apparently better adapted to southern Missouri than to the northern part of the state. In northern Missouri the rate of seedling growth is slower than in southern Missouri during early spring because the short days and low temperatures retard vegetative growth. In the fall of the year, long days delay flowering; hence plants are often killed by frost before reseeding (Smith, 1941).

In experiments conducted in Florida, Korean lespedeza made very poor vegetative growth when compared with common lespedeza (Warner and Blaser, 1942). Under the short day lengths during January and February, when lespedeza germinated, Korean lespedeza plants were dwarfed and matured seed in spring. Because of this dwarfness and early maturity, Korean lespedeza not only made poor growth, but it was not able to compete with other species in the mixture.

2. *Soil Factors*

a. Moisture and Aeration. Deficiencies and excesses in soil moisture are acute agricultural problems because these factors are difficult and often impossible to regulate. Grasses are generally less vulnerable to injury from excesses and deficiencies in soil moisture than legumes. The natural grasslands in the United States are devoid of legumes (Weaver and Clements, 1938). Grasses survive serious droughts because the axillary buds are below the soil surface where they apparently escape extreme xeric conditions and because they assume a dormant condition during dry periods. Grass species in the prairie region differ in their adaptation to soil moisture. The taller grass species, such as big bluestem, *Andropogon furcatus,* Muhl., are dominant in prairie regions where soil moisture is most favorable; the short grasses such as buffalo grass *Buchloë dactyloides,* Nutt., are predominant where moisture is less favorable.

According to investigations by Dillman (1931), the drouth tolerance of plant species is not associated with water requirements (pounds of water required to produce a pound of dry matter). The range of water requirements varied widely for crop plants, sorghums and millets having

a low water requirement as compared with alfalfa and perennial grasses. To manufacture 1 lb. of dry matter, bromegrass, crested wheatgrass, *Agropyron cristatum* (L.) Beau., and western wheatgrass, *Agropyron smithii,* Rydb., required 784, 853, and 1183 lb. of water, respectively. Water requirements varied with season, for example Grimm alfalfa harvested at three dates required 469 lb. of water per pound of dry matter for the early summer cutting, 817 lb. for the mid-summer cutting and 1115 lb. for the late summer crop. The use of alfalfa, in the dry land regions, is attributed to the growth that is made during the early season when water requirements are apparently at their lowest point.

Since the water requirements of plants adapted to regions of low rainfall are not necessarily low, it appears that the root volume and depth is important. The capillary water movement in soils to roots of plants is too slow to meet water requirements for growth, hence root growth is important in supplying the water needs of the plants (Baver, 1948). Burton (1943) found that the maximum root depth of seven southern grasses did not differ greatly, but the distribution of roots within the rooting zone was very great. Three-fourths of the roots of carpet and vaseygrass, *Paspalum urvillei,* Steud., known to be adapted to wet soils, were found in the upper 8 in. of soil. With strains of Bahia grasses, *Paspalum* spp., three-fourths, of the roots were found in the upper 20 in. of soil. The root weights in the upper 16 in. of soil amounted to 10.97 g. of roots per 100 sq. in. of surface soil for common Bahiagrass, *Paspalum notatum,* Flügge, as compared with 3.77 g. for carpetgrass.

Bahia grasses were much more drouth tolerant and more productive during dry periods than carpetgrass in Florida (Blaser, unpublished results). Stephens (1942) found that Dallis grass and carpetgrass require moist soils as compared to Bermuda grass, and Lovvorn (1945) and Mayton (1935) report that Dallis grass is less susceptible to drouth injury than carpetgrass.

Gist and Smith (1948) measured the root mass and depth of penetration of grasses of northern origin. For the 0- to 3-in. depth they found the root weights in pounds per acre for various grasses to be: Kentucky bluegrass, 1126; orchardgrass, 1247; bromegrass, 718; timothy, 680. At the 12- to 18-inch soil layer the root weights for grasses were as follows: Kentucky bluegrass, 3 lb.; orchardgrass, 30 lb.; timothy, 6 lb.; and bromegrass, 106 lbs. per acre. The data indicate that the expected productivity of these grasses during dry periods, from highest to lowest yields, would be in the following order: bromegrass, orchardgrass, timothy, and Kentucky bluegrass. Lamba *et al.* (1949) studied root growth of timothy, red clover, alfalfa, and bromegrass. The average

root weights of seedling plants increased steadily during the first year, but increases were much larger during the second year. Alfalfa and bromegrass produced more root growth than timothy and red clover. These investigators report that timothy obtains most of its water and nutrient supply from the upper 8-in. layer in silty loam soils.

During dry periods the reserve supply of soil moisture is utilized readily and growth is subsequently retarded. Chamblee (1951) found that the depth at which moisture was depleted was associated with plant species and root characteristics. The moisture supply in the upper 12 in. of soil was depleted as fast by orchardgrass as by alfalfa, but at lower depths the moisture was much lower and often at the wilting point for alfalfa.

In dry years the highest herbage yields are obtained from species that have deep and extensive root systems. During 1951 the summer and fall seasons were very dry in Virginia. At Blacksburg an orchardgrass-ladino clover mixture produced 3405 lb. of dry herbage as compared to 6891 lb. for an alfalfa-orchardgrass-ladino clover mixture The herbage yields for an orchardgrass-alfalfa mixture was 7489 lb. as compared to 6812 for alfalfa without a grass (Table I). A mixture of birdsfoot trefoil-white clover-Kentucky bluegrass produced a yield of 3690 lb. per acre. Mixtures with alfalfa and birdsfoot trefoil produced more herbage during the summer months than mixtures with ladino clover during this dry year. In two grazing experiments in Virginia a Kentucky 31 fescue-ladino clover mixture was more productive than a ladino clover-orchardgrass mixture during the drier summer months Kentucky 31 fescue pastures in pure stand were more productive than orchardgrass pastures. In plot experiments orchardgrass and Kentucky 31 fescue were more productive than Kentucky bluegrass during the deficient rainfall period.

The application of supplemental moisture during dry summer periods has increased yields by as much as eightfold in Pennsylvania (Robinson and Sprague, 1947). Other experiments also show that low summer yields are augmented by water supply.

The root and top growth of forage plants is intricately related to soil environment; soil drainage and aeration being critical factors in soils in the humid section of the United States. Sprague (1933) and Farris (1934) studied root development of various grasses and crop plants in New Jersey. It was found that the root systems of plants grown in soils in this humid region were decidedly less extensive than in soils of midwestern states. Boynton and Reuther (1938) found that the oxygen in the soil air was as low as 0.1 per cent in the second foot of a silty clay loam during early spring. Carbon dioxide was found to be much higher

TABLE I

Seasonal Yields of Various Forage Mixtures in Virginia, 1951

Mixtures in Pounds per Acre	Yields in Pounds per Acre				Total for Season
	May 29	July 10	Aug. 20	Oct. 9	
Alfalfa 20 orchardgrass 3	3459	2389	945	696	7489
Alfalfa 10, ladino clover 1, orchardgrass 3	3658	2165	546	522	6891
Alfalfa 20	3322	1881	1030	579	6812
Ladino clover 2, orchardgrass 8	1927	1001	477	—	3405
Kentucky bluegrass 10, Virginia white clover 1, and birdsfoot trefoil 10	1003	2264	423	—	3690

TABLE II

Root and Herbage Growth of Leguminous Plants as Influenced by Soil Moisture

Moisture Level * (Per cent)	Black Medic (*Medicago lupulina*)		California Bur (*Medicago hispida*)		White Clover (*Trifolium repens*)		Persian Clover (*Trifolium resupinatum*)	
	Herbage	Roots	Herbage	Roots	Herbage	Roots	Herbage	Roots
25	32	75	33	53	18	48	10	46
50	108	88	75	77	82	113	69	91
75	100	100	100	100	100	100	100	100
100	15	15	74	69	92	74	106	94

* One hundred per cent equals moisture level after a Leon fine sand was saturated with water and permitted to drain 10 hours

in the soil atmosphere than in the above-ground atmosphere. Lamba *et al.* (1949) found that root growth of alfalfa, timothy, red clover, and bromegrass was better in a sandy soil than in a silty loam soil. Artificial aeration of a silt loam stimulated the depth of penetration and amount of root growth of alfalfa and bromegrass.

The root development of plants is dependent upon the combined effects of soil environment and genetic characteristics of species (Farris, 1934; Burton, 1937; Weaver and Clements, 1938; Baver, 1948; Lamba *et al.*, 1949, and others).

In an experiment conducted by Volk and Blaser (unpublished results, University of Florida) legume species displayed differential responses when grown at four moisture levels, approximately 25, 50, 75, and 100 per cent of field capacity (Table II). The relative yields of black medic were 32, 108, 100, and 15 as the moisture increased from a low to a high level. White clover growth was not retarded by high moisture levels; the relative yields being 18, 82, 100, and 92, respectively, for low to

high water levels. The yields of tops were associated with root growth. For black medic clover the relative root yields were 75, 88, 100, and 15 as compared with 48, 113, 100, and 74 for white clover when the soil moisture ranged from 25, 50, 75, and 100 per cent field capacity, respectively. The adaptation of Persian clover was similar to white clover, but yields of California bur clover, *Medicago hispida*, Gaertn., were slightly diminished by high moisture levels.

White and Persian clovers produced numerous short, fine, surface roots under the highest moisture level, but black medic had short coarse roots (Fig. 3). The development of many fine surface roots in Persian and white clovers apparently increased the surface area of roots which increased the oxygen availability to the plant at high moisture levels where lack of oxygen usually limits metabolic activity.

Burton (1937) crossed alfalfa species with inherent tap- and branching-tap root systems. The alfalfa genotypes with the more branching roots were found to produce higher herbage yields than the less branching genotypes when grown in a poorly aerated soil.

Since soil moisture and aeration are difficult to control, the plant species that are best adapted to these localized soil conditions should be used in mixtures. In general, forage plants are most productive on reasonably well-drained soils, but certain species, such as redtop, meadow fescue, tall fescue, tall oatgrass, carpetgrass, birdsfoot trefoil, alsike, white, and red clovers, will grow on imperfectly drained soils.

b. Soil Fertility and Soil Reaction. Perhaps the earliest work in the United States which associated plant population changes in pastures with the fertility status of soils was reported by Carrier and Oakley (1914). They reported that fertile soils had fewer weeds and better stands of cultivated grasses than poor soils. Experimentally, they treated small plots with manure and various combinations of mineral fertilizers in 1909. A marked decrease in broom-sedge, *Andropogon virginicus*, L., and an increase in Kentucky bluegrass and white clover were associated with superphosphate or nitrate of soda treatments. The white clover population was increased the most on plots which received superphosphate without nitrogen. Cooper (1932) reported various degrees of degeneration of Kentucky bluegrass-white clover pastures in New York. The best pastures were made up of Kentucky bluegrass-white clover mixtures and the poorest pastures were made up of poverty grass, *Danthonia spicata*, (L.), Beauv. There was little correlation between pH and species components in various stages of succession, and the degeneration of desirable species was attributed to depletion of soil nutrients. It has been clearly established that the productivity and maintenance of cultivated grasses and legumes in the humid area of the United States

cannot be attained without applying mineral nutrients (Johnstone-Wallace, 1937; Dodd, 1941; Brown and Munsell, 1943; Mott, 1943; Blaser *et al.*, 1945; MacDonald, 1946; Sprague *et al.*, 1947, and many others).

Information on the relative growth responses of species components to the mineral nutrient status of soils should be useful in compounding seed mixtures. It is generally assumed that leguminous plants require

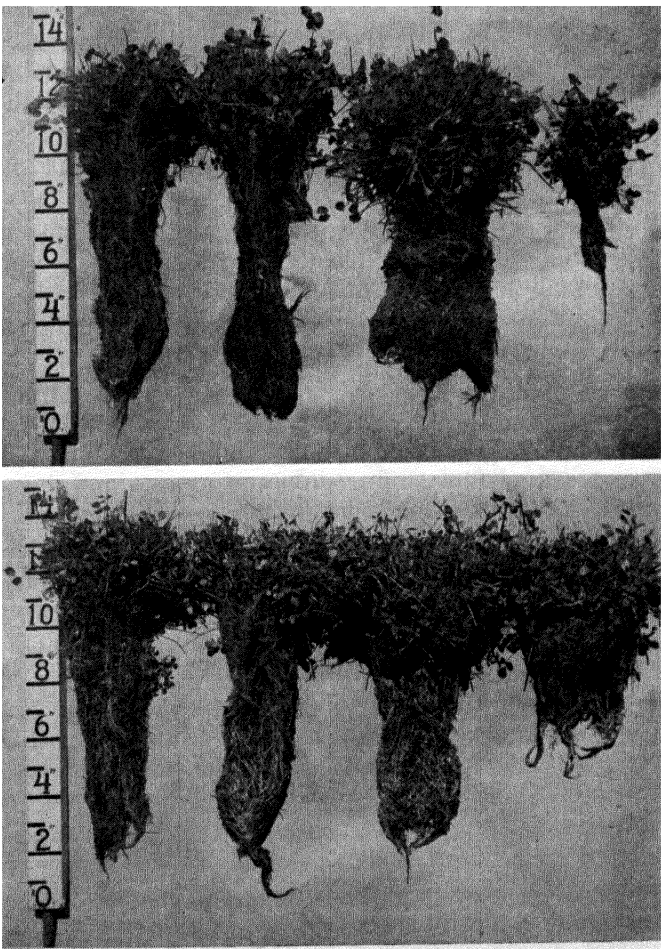


FIG. 3. Effect of soil moisture level on roots of clover. Upper, black medic clover; lower, white clover. Left to right: approximately 25, 50, 75, and 100 per cent of field capacity. White clover produced many fine surface roots and made good growth under high moisture conditions. Black medic had short coarse roots under high moisture conditions and made poor growth.

higher nutrient levels than grasses. Grasses and certain legumes respond quite differently to the nutrients sulfur, boron, and molybdenum. Under sandy soil conditions in Florida, the leguminous plants red clover, black medic, and white clover growing with grass mixtures were stunted and yellowish in the absence of sulfur supplements (Bledsoe and Blaser, 1947; Neller *et al.*, 1951). Sulfur influenced the rate of grass growth indirectly through improving the available nitrogen supply. Data reported in various annual reports in Virginia show that ladino clover does not respond to borax applications whereas alfalfa induces pronounced responses on certain Virginia soils. In the absence of boron supplements, alfalfa cannot compete with associated grasses and weeds, hence the stand of alfalfa degenerates. Grasses have not been found to respond to supplemental applications of borax in field experiments. Experiments conducted in Florida (Killinger *et al.*, 1943, and unpublished results) showed that under very similar soil conditions leguminous plants in the genera, *Medicago* and *Melilotus* responded to boron, whereas *Trifolium* spp. did not respond. However, the seed production of crimson clover, *Trifolium incarnatum*, L., was increased when soils were supplemented with borax in Alabama (Naftel, 1942). Experiments on certain soils show that legumes such as subterranean clover, *Trifolium subterraneum*, L., and alfalfa often respond in growth when molybdenum is applied (Anderson and Thomas, 1946; Evans and Purvis, 1951).

Robinson (1944) found that seedlings of grasses and legumes produced more dry matter as increments of phosphorus were added. The leguminous seedlings made relatively better growth at low levels of phosphorus than the grass seedlings. In a field experiment with an orchard grass-ladino clover mixture grown on a soil low in phosphorus, the relative phosphorus absorption from phosphate fertilizers containing P^{32} was measured by Blaser and McAuliffe (1949). During the first four weeks more than 22 per cent of the phosphorus absorbed by orchard grass and ladino clover seedling plants came from the fertilizer. Approximately two weeks later 15 and 25 per cent of the phosphorus in orchardgrass and ladino clover, respectively, came from the fertilizer. The herbage from a second harvest also showed that orchardgrass utilized more soil phosphorus than ladino clover.

In experiments in Virginia, phosphorus absorption was measured among species for two plant associations (alfalfa-orchardgrass and ladino clover-orchardgrass mixtures) in two locations (Rich unpublished data). Superphosphate at the rate of 53 lb. per acre containing P^{32} was applied in spring on replicated plots treated the previous year with 0, 100, 200, and 400 lb. of P_2O_5 per acre. For all species the amount of phosphorus absorbed from the fertilizer increased as the

residual phosphate applications decreased (Table III). For alfalfa-orchardgrass mixtures the orchardgrass absorbed as much phosphorus from the fertilizer as alfalfa. Ladino clover absorbed more phosphorus from the fertilizer than the orchardgrass component in the mixture. These results with P^{32} suggest that orchardgrass and alfalfa species are better adapted to absorb phosphorus from the less available sources of soil phosphorus than ladino clover. Yields of the grass and legume fractions of mixtures in these experiments indicate that the leguminous associate is more competitive to the grass associate under the higher levels of phosphorus fertilization.

TABLE III

Phosphorus Absorbed by Forage Components in Two Grass-Legume Mixtures under Four Levels of Fertilization in Virginia, 1951*

Pounds per Acre of P_2O_5 Applied in 1950 and Disked in	53 lb. per acre of Radioactive P_2O_5 Broadcast in Spring 1951			
	Alfalfa-orchardgrass mixture		Ladino-orchardgrass mixture	
	Alfalfa	Orchardgrass	Ladino clover	Orchardgrass
	Per Cent P Absorbed from Fertilizer			
400	24.0	26.2	29.2	16.0
200	31.5	32.7	42.0	22.1
100	32.7	32.9	48.8	25.9
0	38.6	42.9	45.1	37.5
Mean	31.7	33.6	41.2	25.3
	Per Cent P in Plant			
400	0.31	0.40	0.31	0.36
200	0.28	0.37	0.29	0.37
100	0.28	0.36	0.29	0.36
0	0.26	0.38	0.29	0.35
Mean	0.28	0.37	0.29	0.36

* Average of two locations

In experiments conducted in North Carolina, Woodhouse (1947) found that the increases of Korean lespedeza due to liming ranged from −1 to 226 per cent during a three-year period (Table IV). Lime was more beneficial to alfalfa than to lespedeza; the yield increases for alfalfa ranged from 212 to 802 per cent. Growth of both alfalfa and lespedeza was improved with phosphate fertilizer. The yield increases ranged from 36 to 43 per cent for alfalfa as compared with 2 to 24 per

TABLE IV

Relative Growth Responses of Alfalfa and Lespedeza to Lime, Superphosphate, and Potash at North Carolina

		Percentage Yield Increases		
Legume	Treatment	1945	1946	1947
Alfalfa	Yield increases due	43	43	36
Lespedeza	to phosphorus (%)	2	18	24
Alfalfa	Yield increases due	6	16	14
Lespedeza	to potassium (%)	—12	—3	17
Alfalfa	Yield increases	212	802	494
Lespedeza	due to lime (%)	—1	33	226

cent for lespedeza. When treated with potassium fertilizer, alfalfa yields were increased from 6 to 16 per cent as compared with —12 to 17 per cent for lespedeza.

The effect of nitrogen and potassium on plant succession due to differential absorption and growth rate of species components in mixtures is given in Sec. II-4c.

Plant species also respond differently to soil acidity. In a greenhouse experiment, York (1947) found that alfalfa and perennial lespedeza responded quite differently to levels of liming and pH. A soil was limed to approximately pH 5.0, 6.0, 7.0, and 8.0. The yield of alfalfa was 5.1 g. per pot at pH 5.0 and 8.8 g. at pH 6.0, beyond which there was no further yield increase. With lespedeza the yield was 9.3 g. for the unlimed soil at pH 5.0, as compared with a decrease in yield to 6.9, 4.5, and 0.4 g. when the soil was limed and the pH values were about 6.0, 7.0, and 8.0 respectively.

On a sandy acid soil in Florida the production of six *Trifolium* species and four species in the genera *Medicago* and *Melilotus* were tested at two levels of lime (Blaser *et al.*, 1941). The yield of the *Trifolium* species was increased slightly by liming whereas the yields of *Medicago-Melilotus* species were increased greatly when the rate of lime was raised from 1 to 2 tons per acre. When growing white clover and California bur clover in a mixture, the proportion of bur clover in the forage was increased by adding lime and that of white clover was reduced. It was concluded that the *Trifolium* species remained productive under a lower lime and pH level than *Medicago-Melilotus* species.

3. Biological Factors

a. Morphology of Plants. The establishment, maintenance, and propagation of species in mixtures is related to morphological character-

istics. Plants that grow erect, such as many grasses of northern origin, are generally aggressive to plants with a prostrate habit of growth, such as white clover. It is generally more difficult to maintain short prostrate strains than taller prostrate strains of white clover in an association with erect growing grasses unless very close or intensive clipping or grazing is practiced. In an experiment at Middleburg, Virginia, four varieties of white clover were grown alone and separately in mixtures with each of two grasses, Kentucky bluegrass and orchardgrass. From the standpoint of size, the strains of white clover may be classified from tallest to shortest in the following order: ladino, S-100, Virginia, and Kent wild. Ladino clover was the most productive clover when grown either in pure stand or in a grass mixture, and Kent wild was the least productive (Table V). In 1950 the mean yields of mixed herbage (legumes and grasses) for one harvest were: ladino clover, 2496 lb., and Kent wild clover, 1237 lb. per acre. In 1951 the yields were relatively

TABLE V

Herbage Yields and Botanical Composition as Influenced by Four Varieties of White Clover Grown in Different Mixtures, Middleburg, Virginia *

White Clover Varieties and Grass Mixture	Herbage Yields—1950				Herbage Yields—1951			
	Total Lb.	Clover Lb.	Clover %	Weeds %	Total Lb.	Clover Lb.	Clover %	Weeds %
Ladino-orchardgrass	2461	1296	53	2	2186	839	38	1
Ladino-Ky. bluegrass	2690	1548	58	2	1942	862	44	3
Ladino alone	2337	2235	96	4	1254	1073	86	14
Mean	2496	1693	68	3	1794	925	52	5
S-100-orchardgrass	1633	507	31	3	1700	359	21	6
S-100-Ky. bluegrass	2077	936	45	5	1398	596	43	6
S-100 alone	1323	1122	85	15	1304	860	66	33
Mean	1677	855	51	7	1467	605	41	14
Virginia-orchardgrass	1588	365	23	10	1501	328	22	6
Virginia-Ky. bluegrass	1567	490	31	13	1159	479	41	10
Virginia alone	1084	514	47	53	1293	731	57	43
Mean	1413	456	32	22	1318	513	39	19
Kent wild-orchardgrass	1324	147	11	10	1420	97	9	9
Kent wild-Ky. bluegrass	1699	328	19	29	834	211	25	21
Kent wild alone	689	277	40	60	1150	372	32	56
Mean	1237	251	20	25	1134	227	20	28

* Yield data include last harvest in 1950 and first harvest in 1951.

the same. S-100 clover was somewhat more productive than Virginia white clover in both years.

Botanical composition data show that the growth of clover varieties is influenced by grass association. During 1950 in ladino clover-orchard grass and ladino clover-bluegrass mixtures, the herbage was made up of 53 and 58 per cent of ladino clover, respectively. When Kent wild clover was grown with orchardgrass only 11 per cent of the yield was made up of clover as compared with 19 per cent clover for the bluegrass-white clover mixture. In 1951, S-100, Virginia white clover, and Kent wild clover were less productive and constituted a lower percentage of the mixture when grown with orchardgrass than when grown with bluegrass, whereas the ladino clover yields were of similar magnitude when grown with either of these two grasses.

It may be concluded that shorter growing clover varieties such as Kent wild, Virginia, and S-100 are less competitive when grown in mixtures with tall aggressive orchardgrass than with short and less aggressive bluegrass Species grown in mixtures that are similar in height would be expected to be reasonably compatible if they respond similarly to other physiological factors.

Competition among plants is probably not influenced by root morphology. Davies (1928) found that Italian ryegrass was aggressive toward rough stalked meadow grass (shallow roots), meadow fescue, (deeper roots), red clover (deep roots), and alfalfa (very deep roots). Competition was attributed to aerial shading.

Rate of aftermath growth is influenced by morphological characteristics of plants. Orchardgrass, which produces much higher aftermath yields than does timothy, also produces numerous lateral shoots at the base of each culm even before the first spring growth is grazed or mowed (Fig. 4). These lateral shoots develop quickly after the spring growth is removed. In timothy there are only one to three buds per corm, and these buds do not usually develop into shoots until the spring growth is removed. The differential rate of aftermath development of these two species is also influenced by temperature and moisture (See Sec. II, 1a,2a).

Stoloniferous or rhizomatous grasses generally form dense sods which are more aggressive toward legumes than are bunch grasses. When bunch grasses are seeded heavily, they are also competitive and leguminous species do not usually survive in the bunchy grass growths. With sparse stands of bunch grass, associated species grow in the open areas. Bunchy growth habits are very undesirable when palatability among species differs. With ladino clover, a palatable species, and Kentucky 31 fescue, an unpalatable species, cattle overgraze the palatable clover and

undergraze the unpalatable fescue. Selective grazing of fescue is encouraged because of its bunchy growth.

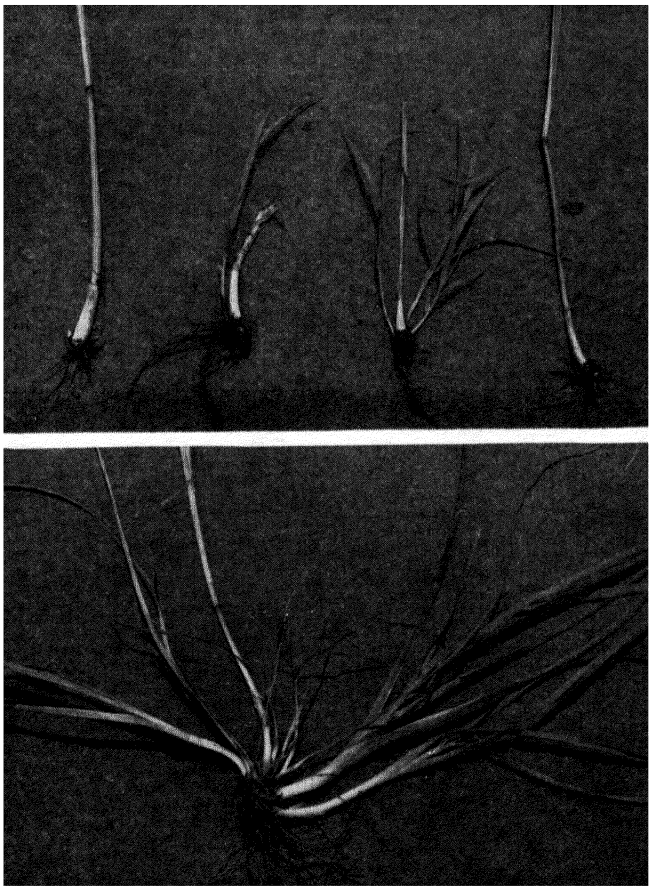


FIG. 4. Comparative shoot development of orchard grass and timothy. Upper, timothy; lower, orchard grass. Owing to the development of many shoots at the base of each culm, orchard grass produces high aftermath yields.

Some stoloniferous grasses, such as carpet and centipede, *Eremochloa ophiuroides*, Munro., Hack., form an extremely dense sod. It is very difficult to maintain other grasses and clovers in mixtures with such sods, even under close grazing management practices. In the southern region where seedlings of winter or spring annual legumes volunteer, seedling mortality is often high because of the dense grass sods, (Hollo-

well, 1938; Blaser *et al.*, 1945; Stewart and Rogers, 1947). Stephens (1942) and Lovvorn (1944) report that it is easier to grow legumes with Dallis grass (a bunch grass) than carpet grass (a stoloniferous grass), because the latter has a more open sod. The reconstruction of pasture species as related to morphology is given in Sec. II, 4b.

The degeneration of pastures from three to five years after seeding has been reported by Bates (1948), Pollitt (1947), and others. No great changes in botanical composition of the herbage occur, but the yield, protein, and carotene content sharply decreases. This has been associated with the formation of a mat of roots immediately under the surface of the soil. Under grazing conditions, the grasses developed more but smaller tillers, as they became older.

b. Palatability. In general, the palatability of a forage species is primarily associated with growth stage, i.e., mature herbage is decidedly less palatable than young leafy herbage (Watson, 1951). Likewise, the differences in palatability due to differential growth stage within a species are usually larger than the differences in palatability among forage plants when growth stage is similar. Palatability varies with animals; cattle usually prefer orchard grass in a vegetative stage of growth to Kentucky bluegrass herbage in a similar growth stage, yet the reverse usually occurs with sheep.

From the viewpoint of herbage quality, mixtures should be made up of forage plants that are highly nutritive and palatable. According to Garrigus (1950), the dry matter intake from palatable species is apparently higher than from less palatable ones. With a fecal bag technique, he found that sheep and steers consumed less herbage when grazing Kentucky 31 fescue than when grazing other grasses and legumes. The dry matter intake when grazing leguminous species was higher than grass species. No data were reported for mixtures.

In Virginia, the palatability of species and mixtures was measured with beef animals. Small areas of the experimental plots were sampled immediately before and after grazing. The animals were removed before any species or mixture was grazed too closely so as to avoid a confounding of availability and palatability. During a two-year period, when animals had access to all species or mixtures, 48 per cent of a pure stand of orchardgrass herbage was consumed as compared to 27 per cent for herbage from a pure stand of Kentucky 31 fescue (Table VI). When ladino clover was grown with the grasses, 44 per cent of the mixed herbage from Kentucky 31 fescue-ladino clover was consumed as compared with 64 per cent of the available herbage of a ladino clover-orchardgrass mixture. Orchardgrass was more palatable than Kentucky 31 fescue, and ladino clover improved the palatability of both grasses.

In the palatability experiment the clover population in the clover-grass mixtures was maintained with palatable orchardgrass, and the less palatable fescue because the plots were mowed closely after each grazing trial (Table VI). In an adjacent grazing experiment with beef cattle, the ladino clover population was high in both mixtures for the first year. During the second year ladino clover made up 40 per cent of the herbage in the orchardgrass-ladino clover mixture as compared with only 16 per cent ladino clover in the Kentucky 31 fescue-ladino clover mixture. At Blacksburg, Virginia in an experiment with dairy cattle, the ladino clover population is also much lower when grown with Kentucky 31 fescue than with orchardgrass.

TABLE VI

Yields, Relative Palatability, and Botanical Composition of Four Pasture Mixtures (Middleburg, Virginia, 1950-51)

Mixtures *	Means for 1950 and 1951		Ladino Clover in Mixtures			
			1950		1951	
	Yields Lb./acre	Herbage consumed %	Grazed %	Clipped %	Grazed %	Clipped %
Orchardgrass	4153	48	—	—	—	—
Ky. 31 fescue	4442	27	—	—	—	—
Orchardgrass and ladino clover	3908	64	48	49	26	53
Ky. 31 fescue and ladino clover	4127	44	40	44	16	33

* Seeding rates in pounds per acre grasses in pure stand 14 lb., with clover 8 lb and clover at 2 lb. The experiments were sown in September, 1949.

In grazing experiments, the low population of ladino clover in relatively unpalatable fescue herbage as compared with orchardgrass is attributed in part to selective grazing, but is more directly attributed to closeness of grazing. Cattle refused to graze Kentucky 31 fescue closely, unless pasturage was scarce. Kentucky 31 fescue also produces more herbage during the late summer and fall and this competitive effect also is thought to be harmful to ladino clover.

c. Diseases and Insects. Insect and disease injuries often reduce the stand, productivity and/or longevity of forage plants. Disease and insect pests may attack and injure plants during seedling development or after establishment (Graber and Jones, 1935; Chilton and Garber, 1941; Dickson, 1947; Hanson and Allison, 1951; and others).

When growing mixtures of forage plants, the species that are highly

susceptible to prevailing diseases or insects are retarded and consequently the resistant species becomes dominant. The differential susceptibility of strains within forage species to disease and insects offers much inducement for developing disease and insect-resistant strains (Painter and Grandfield, 1935; Hermann and Eslick, 1939; Burton, 1948; and others).

Although a plant that is resistant to a disease or an insect usually becomes aggressive to an associated plant that is susceptible to the pest, Burton *et al.* (1946) found an inverse relationship. On sandy soils of the Southeast annual lespedezas often disappear because they are very susceptible to injury from root-knot nematode, *Heterodera marioni* (Cornu). Among twenty-eight strains of lespedeza grown on a nematode-infested soil, all strains died at the end of the first summer. Out of 147 Bermuda grass selections certain strains were found to be both highly susceptible and resistant to nematodes. Root-knot susceptible lespedeza grew well and was found to be practically free of nematodes when grown with five root-knot resistant strains of Bermuda grass.

d. Variety. Crop varieties are plants within a species that differ in genetic constitution. The adaptation of varieties differ because of the differential response between genotypes and environmental factors. An ideal variety would be one that is superior in yield, longevity, and quality when considering all climatic, soil, and biological factors.

Varieties and strains were often considered in the previous sections when discussing plant adaptation, and hence those relationships will not be repeated. The previous reviews suggest that all factors which affect yield and quality should be carefully considered in formulating a breeding program which is directed toward the improvement of varieties. If this is done the isolation of varieties that are superior with respect to some growth factors and inferior to others can be avoided.

The voluminous data pointing out the superiority of certain varieties for local or regional conditions will not be given. In the evaluation of varieties, yields are often overemphasized and information on the life history is neglected. The improved strains of grasses developed at Aberystwyth are apparently very superior in longevity and leafiness under close grazing, but seedling vigor and productivity during the early life were apparently sacrificed in comparison with commercial varieties (Stapledon and Davies, 1930; Davies, 1939).

Experiments conducted in Virginia show that Virginia commercial orchardgrass produced more aggressive seedlings than the S-143 Aberystwyth) variety (Table VII). By expressing the relative yield of Virginia commercial seedlings as 100, the yield of S-143 seedlings was 36 when seeded on September 4 and sampled 38 days later. When seeded

TABLE VII

Relative Rate of Seedling Development of Two Orchardgrass Varieties, Virginia 1950-51

Sowing date	Days after Sowing	Weight of 25 Seedlings (g.)		Relative Seedling Weight	
		S-143	Virginia	S-143	Virginia
September 4	38	0.20	0.56	36	100
March 15	65	0.62	0.72	86	100
April 15	65	1.66	2.25	74	100

on March 15 and April 15 and sampled 65 days later, the relative yields of S-143 were 86 and 74, respectively.

Seedlings of forages that become established quickly are more likely to survive than seedlings which grow slowly, under common hazards of field conditions. Since slow developing seedlings are subjected to more hazards than rapid growing seedlings, it becomes apparent that higher seed rates to obtain stands are required for the species that develop relatively slowly. This may account for the high rates of seeding orchard grass recommended in England as compared to the United States.

4. Plant Succession—An Interrelationship of Climatic, Soil, and Biological Factors

In mixed plant associations, the differential growth responses of species to artificial and natural environmental factors determine plant succession. The processes of plant succession are exceedingly complex, because of the interacting relationships among factors that affect growth In spite of insufficient fundamental data, a description and interpretation of several examples of plant succession as influenced by various growth factors is given in the subsequent sections.

a. Grazing Management of Grass-Legume Mixtures. The kind of grazing management practices used are dependent upon the morphological characteristics of species (Klapp, 1937; Jones, 1939; Moore *et al.*, 1946). Species with tall and erect habits of growth, such as alfalfa-bromegrass mixtures, can be almost completely defoliated under heavy continuous grazing. Frequent and rather complete removal of foliage causes a drastic reduction in yield because of depleted organic food reserves in the roots, stolons, rhizomes and/or stubble (Graber *et al.*, 1927; Graber, 1931; Rather and Dorrance, 1938; McCarty and Price, 1942; Smith and Graber, 1948; Dotzenko and Ahlgren, 1950; Tesar and Ahlgren, 1950). Tall erect growing species may be maintained under rotational grazing where grazing periods are of short duration and are

followed by long rest periods. Close grazing is not especially injurious to stand and yield if the period of grazing is short. With grasses that store food reserves in the stubble close grazing may be more injurious to the grasses than to the legume in mixtures (Sullivan and Sprague, 1943; Sprague and Sullivan, 1950).

Mixtures made up of short, erect, and/or prostrate species have survived and produced as high or almost as high yields under continuous as under rotational or intermittent grazing (Carrier and Oakley, 1914; Comfort and Brown, 1933; Hein and Cook, 1937; Hodgson *et al.*, 1934; Woodward *et al.*, 1938; Moore *et al.*, 1946; Peterson, 1947; Mayton *et al.*, 1947). With the shorter and/or prostrate species complete defoliation does not usually occur, even under close intensive grazing; hence, production can be maintained under either rotational or continuous grazing.

During the spring season there is usually a critical period of competition among grass-clover associations because of temperature and light interrelationships. In Sec. II, 1a. it was pointed out that grasses of northern origin start active competitive growth earlier in the spring than clover because of their adaptation to lower optimum temperatures. White clovers are further retarded by the erect reproductive growth of grasses during spring months, which is attributed to the combined effects of temperature and photoperiod. With grasses, like Kentucky bluegrass, orchardgrass, and bromegrass, a short photoperiod accompanied by cool temperatures has been found to stimulate flower induction. After the flower primordia are laid down, the combined effect of long days with cool temperatures, encountered during the spring, stimulates shoot elongation and flowering of grasses (Peterson and Loomis, 1948; Gardner, 1950; Newell, 1951). Since flower primordia are laid down during the fall of the year under short day low temperature conditions, most grasses of northern origin usually flower only once during the growing season.

Because of the combined effects of temperatures and photoperiod, the grass blades and culms elongate rapidly as the days lengthen in spring, making grasses aggressive toward white clover. When temperatures become optimums for clovers, their growth is usually restricted because of the low light intensity. The species in mixtures also compete for moisture or nutrients, Sec. II, 4c.

Nitrogen fertilization also augments grass competition. The earliness of grass growth is often limited because of a low level of available nitrogen. By adding nitrogen the earliness and magnitude of grass growth relative to the clover in the mixture is accentuated, thereby making the grasses even more aggressive toward prostrate white clover associates.

The aggressiveness of grass associates can be offset by imposing early spring grazing. Early grazing apparently favors the predominance of white clover in the sod because of the improved light intensity and higher soil and air temperatures at the clover level. By grazing to remove the insulating herbage, higher soil temperatures and better clover growth would be anticipated.

b. Improving Degenerated Kentucky Bluegrass-White Clover Pastures. Permanent pastures in the more humid northern and northeastern states that are poorly managed and not given proper cultural treatments are often composed of broom-sedge, povertygrass, hawkweed, *Hieracium pratense*, Taush., dwarf white clover, and Kentucky bluegrass plants. By fertilization, an environment is created whereby the desirable species are encouraged and the undesirable ones are discouraged. Fertilizers are not toxic to undesirable species. This was shown by MacDonald (1939), who found that the growth of certain undesirable plants found in degenerated pastures was stimulated by fertilizers.

At this stage where the soil has been supplemented with needed nutrients, species respond differently to temperatures. Bluegrass and white clover grow at lower optimum temperatures than do most of the undesirable plants, hence, these desirable plants become aggressive because of their spring growth. This early spring growth of the desirable species as compared with the undesirable plants brings into effect the growth factor, light. The early spring herbage of the desirable plants reduces the light intensity and photosynthesis at the growth level of the undesirable plants. When temperatures in late spring become optimum for growth of undesirable plants, their rate of growth is restricted because of the low light intensity and its effect on organic foods.

At this stage morphology and palatability become factors. Hawkweed, with its prostrate leaves, begins to grow erect as the sod thickens. This erect habit of growth restricts light absorption and some hawkweed foliage is also consumed with the palatable herbage of desirable species which further retards its growth.

Morphologically broom-sedge is a robust, erect-growing species with a bunchy growth habit. Carrier and Oakley (1914) found that mowing and close grazing shifted the plant population from broom-sedge to bluegrass and white clover. Under close grazing and rather complete defoliation, the growth rate of broom-sedge is retarded more than that of desirable species components. As the rate of growth of undesirable species diminishes, white clover and bluegrass encroach because these species are propagated vegetatively by stolons or rhizomes.

This type of plant succession, without nitrogen fertilizer, requires some two to five years because the growth of grass is dependent upon a

legume for nitrogen. The succession to desirable plants may be realized in a much shorter time by applying nitrogen fertilizer with lime and minerals. This stimulates the growth of bluegrass which is usually limited by soil nitrogen.

Unproductive permanent pasture areas where the population of desirable species is very low can be brought into a productive status much faster by renovation and reseeding with suitable mixtures than by surface broadcasting of fertilizer and regenerating the stoloniferous species (Sprague *et al.*, 1947). Obviously, unproductive pastures and meadows can be reconstructed without renovation or reseeding only when the desirable species are propagated by rhizomes or stolons.

c. Competition for Potassium. Plants grown in mixtures often compete for potassium. Blaser and Brady (1950) found that weeds absorbed higher percentages of potassium than grasses and that grasses absorbed higher percentages of potassium than clover. Bear and Wallace (1950) found that certain weeds growing in alfalfa were higher in potassium content than alfalfa. In Virginia experiments, the mean potassium content of species fractions of seventeen grass-legume mixtures grown on five fertilized soils was 3.28 per cent for grasses as compared with a mean of 2.32 per cent for legumes.

The critical percentage, at which potassium affects rate of grass growth, has not been established, but it is thought that grasses have a lower potassium requirement than legumes and yet the luxury consumption of potassium is higher for grasses than for legumes. Drake *et al.* (1951) found that plant species, such as grasses, with roots of a low base exchange capacity absorbed more potassium than plants with roots high in base exchange capacity.

Temperature, as related to growth of species, influences competition for nutrients. Since grasses of northern origin grow at lower temperatures than legumes, grasses are aggressive competitors for potassium during the spring season. Ladino clover is often potassium deficient and stunted because of the low available potassium when grown with grasses. Alfalfa and ladino clover populations have been almost eliminated in one year in grass association where potassium fertilizer was not supplied.

Nitrogen fertilization is also intricately associated with potassium competition among grasses and legumes. The earliness of grass growth is often limited by available nitrogen rather than by temperature. By supplying nitrogen fertilizers in early spring, the augmented grass growth and concurrent high absorption of potassium reduces the supply of potassium for the leguminous associates. Consequently, on soils low in potassium, the clover population and growth diminishes.

Further evidence of nutrient competition among grasses and legumes

as related to nitrogen and potassium fertilization was obtained from an experiment in Virginia (unpublished). In a soil rather low in available potassium, ladino clover was grown in pure stand and with several grasses. The ladino clover yields in pure stand were not retarded by nitrogen fertilizer, and the responses from potassium fertilization were low. When ladino clover was grown with grasses, the clover stand and growth was very poor when treated with nitrogen alone, but quite satisfactory when both potassium and nitrogen fertilizers were applied. Ladino clover in grass mixtures made the best growth when potassium was used in the absence of nitrogen. Even though high levels of potassium were supplied with nitrogen to ladino clover-grass mixtures, the ladino clover population and yields were smaller where nitrogen fertilizer was applied than in its absence. This suggests the presence of other competitive factors, such as light and water.

Evidence of competition for potassium between grasses and legumes suggests that grass-legume mixtures may require higher levels of potassium than pure stands of legumes. On soils low in potassium, applications of potassium after the flush spring growth of grasses would probably encourage the leguminous associate in the aftermath growth.

d. Seedling Competition. When a mixture of seeds of forage species are seeded together, a struggle for survival develops immediately after the first seeds germinate. At this stage the mixture of plants enters into a dynamic biological community because of the differential reaction and responses among species to various environmental growth factors.

The influences of germination on seedling growth and competition can have an important bearing on seedling competition because the early plants will have a definite advantage over the later ones. Chippindale (1949) showed that seeds of grass species differ in the time required for germination. Under identical environmental conditions, Italian ryegrass germinated in five days, while orchard grass required fourteen days. In the field, Stapledon *et al.* (1927) found that the percentage establishment of orchardgrass seeds sown was 39 to 44 per cent while for Italian ryegrass, it was 52 to 70 per cent. The rate and time of germination of seed of different species is influenced by the combined effect of the factors, temperature, moisture, and light. Some viable seeds fail to germinate readily because seed coats are impermeable to water or oxygen, or because the seed contain dormant or rudimentary embryos (Meyer and Anderson, 1939). Some seeds, such as common Bahia grass, will not germinate rapidly regardless of environment because their tough waxy seed coats restrict water absorption (Burton, 1940). With sulfuric acid scarification quick germination is attainable.

The combined effect of moisture and temperature influences the rate

TABLE VIII

Yields of Dry Matter Expressed in Pounds per Acre of Two Varieties of Birdsfoot Trefoil *(Lotus corniculatus)* When Grown with Various Mixtures in Two Locations in Virginia, 1951

Trefoils Seeded with Other Species in Pounds Per Acre	Birdsfoot Trefoil, Varieties				Mean Yields		Relative Yields of Birdsfoot Trefoil Varieties
	Empire (New York)		Italian seed				
	Mixture yield	Trefoil yield	Mixture yield	Trefoil yield	Mixture yield	Trefoil varieties yields	
Orchardgrass, 4	1941	484	2326	641	2133	563	47
Ky. bluegrass, 12	2287	1138	2631	1276	2459	1207	100
Ky. 31 fescue, 4	2431	834	2298	908	2365	871	73
Ky. bluegrass, 8, timothy, 3, Va. white clover, 1	2241	722	2605	1280	2432	1001	83
Ladino clover, orchardgrass, 4, alfalfa, 5, red clover, 2	3001	127	2898	114	2950	121	10
Mean for species or variety of trefoil	2381	660	2551	843	2468	753	—

Note The varieties of birdsfoot trefoil were seeded at the rate of 10 lb. per acre

and degree of germination of some species. Blaser and Killinger (1950) found that alternating temperatures in a moist environment stimulated germination of hard white clover seeds. Scarified seeds germinated readily without alternating temperatures. Chippindale (1949) determined the moisture requirements of various grass seeds by placing seeds in a soil at different levels of available moisture. The data indicate that the moisture requirements of orchardgrass are very high, those of perennial ryegrass and Kentucky bluegrass are high, and those of timothy and tall fescue are low.

Light in the presence of optimum temperatures improved the percentage germination of Kentucky bluegrass and tall fescue. Anderson (1931) reported that light improved the germination of Canada bluegrass, but a combination of light and nitrate resulted in additional germination.

Although the rate and time of germination, as related to environmental factors, is an initial phase that may determine the aggressiveness of species in mixture toward each other, other factors also become operative. The rate of seedling growth after emergence is often associated with size of seed or caryopsis. Seeds of ryegrasses have a large caryopsis as compared with redtop which may partially account for the rapid development of ryegrass seedlings as compared with redtop. Redtop has a very small caryopsis as compared to Kentucky bluegrass and chewings fescue; yet Erdmann and Harrison (1947) showed that redtop is aggressive in relation to the other species. In several experiments conducted in Virginia with white clover varieties, ladino clover seedlings developed faster than S-100 clover, which in turn developed more quickly than Kent wild clover. Stapledon *et al.* (1927) associated the rate of tillering with aggressiveness of species. Perennial ryegrass tillered more profusely than other grasses included in the study.

Apparently rate of seedling growth after emergence is partially dependent upon stored food reserves in seeds, and also on genetic factors which determine the various rates of growth of species under different environments. An approximate classification of the aggressiveness of forage seedlings during establishment, which is based on observations and experiments in Virginia and New York and data reported by Stapledon and Davies (1930), is given on page 212. The species with the lowest numbers are the most aggressive.

Information as to the relative rate of seedling development can be quite useful in compounding seed mixtures. An experiment was established in Virginia to measure the adaptation of varieties of birdsfoot trefoil. The trefoils were seeded with grass and/or legume mixtures at two locations (Table VIII). When birdsfoot trefoil (slow seedling de-

Rank	Grasses
1.	Italian ryegrass, *Lolium multiflorum*
2.	Perennial ryegrass, *Lolium perenne*
3.	Tall oat grass, *Arrhenatherum elatius*
4.	Orchardgrass, *Dactylis glomerata*
5.	Tall fescue varieties, Alta and Kentucky 31, *Festuca elatior var. arundinacea*
6.	Bromegrass, *Bromus inermis*
7.	Meadow fescue, *Festuca elatior*
7.	Orchardgrass, S-143
8.	Timothy, *Phleum pratense*
8.	Meadow foxtail, *Alopecurus pratensis*
9.	Redtop, *Agrostis alba*
10.	Red fescue, *Festuca rubra*
11.	Canada bluegrass, *Poa compressa*
11.	Kentucky bluegrass, *Poa pratensis*
12.	Bent grass, *Agrostis* spp.

Rank	Legumes
1.	Red clover, *Trifolium pratense*
1.	Sweet clover, *Melilotus alba*
2.	Alfalfa, *Medicago sativa*
3.	Alsike clover, *Trifolium hybridum*
4.	Ladino white clover, *Trifolium repens*
5.	Birdsfoot trefoil, *Lotus corniculatus* Seed sources from Italy, France, and Germany
6	S-100, white clover
7.	Birdsfoot trefoil, Empire (New York)
8.	Common white clover

velopment) was sown with a light rate of orchardgrass (fast seedling development) the relative yield the subsequent year was 47 as compared with 100 when birdsfoot trefoil was sown with Kentucky bluegrass (slow seedling development). Kentucky 31 fescue seedlings are more aggressive than Kentucky bluegrass; hence the relative yield of birdsfoot trefoil varieties was less with fescue than for seedlings grown with Kentucky bluegrass. When the trefoils were sown with a complex mixture of aggressive species (alfalfa, orchardgrass, red clover, and ladino clover) the relative yield was only 10. With this complex mixture the aggressive species reduced the stand and yield of trefoil even though seeding rate adjustments were made. The birdsfoot trefoil produced a relative yield of 83 when grown with a complex mixture made up of species components that develop comparatively slow during seedling development.

III. Compounding Mixtures as Related to Use

1. Yields and Quality as Influenced by Mixtures.

The yields of several species grown in mixtures are generally higher than the yields of individual species. Stapledon and Davies (1928) conducted an experiment to test the yields of forage plants due to association. The first year after sowing, the relative yield of legumes grown alone was given a value of 110. With perennial ryegrass-legume mixtures the relative yield was 133 as compared with 139 for orchardgrass-legume mixtures. In another experiment, Stapledon and Davies (1930)

report that two grass-legume mixtures produced a mean yield of 82.8 cwt. as compared with an average of 39.4 cwt. for seventeen grass species grown in a pure stand. The yields of the legumes in pure stand were also less than the yields of the grass-legume mixtures. At Ottawa, Canada, the yield of herbage from ten cultivated grasses grown separately for a period of three years varied from 1077 to 2415 lb, of herbage per acre, as compared to yields ranging from 4016 to 5712 lb. per acre for the ten grasses in legume mixtures (Kirk, 1937). Other work conducted in more humid areas of the United States shows that the use of legumes with grass in mixtures resulted in increases in dry matter production (Fergus, 1935; Johnstone-Wallace, 1937; Brown and Munsell, 1943; Blaser *et al.*, 1948; Sprague *et al.*, 1947; and others).

Wilsie (1949) conducted experiments with alfalfa-grass mixtures in a region where alfalfa is well adapted. During a period of five years, alfalfa seeded in pure stand produced as much herbage as alfalfa-grass mixtures. Toward the end of the experimental period, the stand of alfalfa was depleted by bacterial wilt and the alfalfa-grass mixtures began to produce higher yields than pure alfalfa.

In the above experiments the soils were supplemented with minerals other than nitrogen so as to create a reasonably favorable mineral nutrient status for the legumes. By supplying minerals other than nitrogen, legume-grass mixtures would be expected to produce higher yields than grass mixtures, the growth of which would be limited by the low level of nitrogen. With liberal nitrogen applications very high yields can be obtained for mixtures with or without legumes (Johnstone-Wallace, 1937; Robinson and Pierre, 1942; Fink, 1943; Robinson and Sprague, 1947; Blaser and Brady, 1950; Burton and DeVane, 1951). It is also possible to regulate seasonal growth by nitrogen fertilization (Frankena, 1937; Giöbel, 1937).

If the utilization of grass mixtures supplemented with nitrogen fertilizer was economically sound, management practices would be greatly simplified since leguminous plants in mixtures are much more vulnerable to stand depletion than are grasses (Davies, 1928; Brown, 1939; Dodd, 1941).

High quality herbage may be characterized by low fiber and lignin contents and high digestibility, and high contents of protein, minerals, and vitamins (Morrison, 1949; Watson, 1951). The quality of a given species is best when in a leafy vegetative growth condition and poorest when in a stemmy growth condition (MacDonald, 1946; Watson, 1951). There is usually a greater difference in quality between the extreme growth stages of a single species than between species at the same stage

of growth. Herbage quality depends primarily on management and secondly on species components in mixtures.

a. Top vs. Bottom Species. Morphologically forage plants may be classified into either top or tall and bottom or short species. Bottom species, such as Kentucky bluegrass, bent grasses, rough stalked meadow grass and the shorter white clover phenotypes, become dominant under hard and continuous grazing.

Whether the sod should be made up of short, dense herbage of bottom species or of taller less dense herbage of top species, has been a much debated topic. The choice between bottom and top species depends quite largely upon the method of utilization and use. For heavy continuous grazing, bottom species may be superior to top species when considering longevity and yield. A reverse relationship would be expected under rotational grazing or hay management practices.

Stapledon and Davies (1928) conducted an experiment to measure the influence of species on each other. With various mixtures of top grasses and legumes, it was found that the yields of herbage declined each year during a four-year period. The decline in production was associated with the encroachment of bottom species such as bent grass. Ahlgren *et al.* (1946) also attributed declining yields of tall species to an increase in bottom grasses such as redtop and Kentucky bluegrass.

In Pennsylvania, an unproductive bluegrass-white clover pasture was top-dressed with lime and fertilizer and renovated (limed, fertilized, and sown with top grasses and legumes). After the bottom species (bluegrass and white clover) were well established, this mixture produced 3700 lb. as compared with a yield of 5200 lb. of herbage per acre for the top species (Sprague *et al.*, 1947).

R. B. Musgrave of Cornell University (unpublished data) tested the productivity of mixtures with top species, bottom species, and mixtures of top and bottom species. The yields of mixtures with ladino clover were higher than the yields with Kent wild clover in the mixture. Mixtures with top grasses (tall oats, orchard, or timothy) produced higher yields than mixtures with bottom grasses (redtop, Kentucky bluegrass, or red fescue). Nowosad and Stevenson (1947) found that a mixture of three top grasses (brome, timothy, and slender wheat) with three bottom grasses (Kentucky blue, Canada blue, and redtop) with legumes, gave a yield of 4440 lb. of herbage per acre. When the bottom grasses were excluded from the mixture the yield was 4413 lb. of herbage per acre.

It may be concluded that top species have a greater capacity for production if favorable grazing or cutting management practices are used.

b. Simple vs. Complex Mixtures. The number of species components to use in mixtures has been a controversial issue. In European countries and England rather complex mixtures have been used in comparison to those recommended in the United States. Johnstone-Wallace (1927) and Stapledon and Davies (1928) concluded that mixtures should be reasonably complicated—the whole aim being to combine early and late species and strains so as to obtain a long and reasonably uniform herbage supply. Stapledon and Davies (1928) suggested a type mixture made up of six grass and three leguminous species; within this mixture a total of eight strains was also suggested.

In a more recent publication Milton (1939) showed that yields of mixtures composed of two or six grasses with given legumes were of similar magnitude. Willard (1951) suggested that forage seedings should be made up of at least one grass and one legume and that the employment of more species is good insurance against failure. Results obtained during the last two years in Virginia indicate that the yields of mixtures with ladino clover can be improved during the first harvest year by adding alfalfa or red clover to the mixture.

The compounding of mixtures with many species, with the idea of obtaining both high yields and a good distribution of herbage, has apparently not been successful in practice. The writers were unable to find a publication which showed that complex mixtures were superior to simpler ones. The trend, in compounding mixtures, has been altered toward using a few species that are particularly well adapted to localized environments and imposing specialized management utilization practices, such as cutting for hay and then grazing, cutting for silage and then grazing or grazing alone (Stapledon and Davies, 1930; Willard *et al.*, 1947; and Cornell University, unpublished data). When considering plant adaptation as related to growth factors, it is obviously much easier to manage simple mixtures, hence, the employment of special management and utilization practices with special purpose, simple mixtures seem to be practical.

2. Developing a Forage Cropping System

Hein and Cook (1937) found that over one-half of the total herbage was produced during the first one-third of the grazing season at Beltsville, Maryland. In northern as well as southern latitudes, a flush growth of herbage is invariably produced in early spring which is followed by seasonal periods of low herbage yields, (Brown and Munsell, 1936; Blaser *et al.*, 1945). High herbage yields during the spring season are attributed to favorable temperature, rainfall, and light conditions.

In practice a reasonably uniform supply of herbage, with some re-

serve pasturage, should be available throughout the grazing season. If a given acreage and mixture is used only for pasture, there will either be an excess of herbage which will be wasted at one season or an acute shortage at another season.

Since many of the growth factors cannot be controlled, it seems logical to manipulate mixtures and management practices with the objective of developing a more uniform herbage supply during the grazing season. Instead of using one mixture solely for grazing, and other mixtures entirely for silage or hay; mixtures might be managed flexibly for combinations of hay, silage, and grazing uses.

For such flexible forage cropping systems, mixtures can be compounded: (1) for grazing; (2) for silage and aftermath grazing; (3) for silage, hay, and aftermath grazing; (4) for early, mid, late season, and/or winter grazing. The acreage used for grazing or preserved crops can be varied so as to use the mixtures to furnish the feed supply that is most needed.

The employment of several mixtures in cropping system seems logical because the relative growth of forage species varies with seasons. This is true because species respond differentially to environmental factors. When considering morphological characteristics, species are best suited for certain uses, i.e., for grazing, hay, or silage. However, the productive status of species, when utilized flexibly, can be maintained under appropriate grazing or cutting management.

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Soil Manganese in Relation to Plant Growth

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I. Introduction

Among the earlier workers who studied the so-called stimulating effect of manganese on plant growth the names of Loew (1903), Bertrand (1905), and particularly Mazé (1914) must be mentioned. The last named carried out nutrient solution experiments with corn (*Zea mays* L.).

Of much importance was the discovery by Sjollema and Hudig (1909) (see also Hudig, 1911), that oat plants suffering from an unknown "soil disease" could be cured by the addition of 50 kg. of manganese sulfate per hectare. This "disease" was found to occur in the northern part of the Netherlands, particularly on reclaimed peaty soils which had become neutral or slightly alkaline through liming or application of Chilean nitrate as a nitrogen fertilizer. Hudig was unable to decide whether the beneficial effect of manganese had to be attributed to neutralization of some unknown injurious soil constituent or to its "stimulating influence" on plant growth.

A number of papers, mostly by Western European authors, appeared subsequently to Hudig's paper. It was shown that the "Dörrfleckenkrankheit" ("Gray Speck disease," as the oat disease was called first by Clausen, 1910), was common on many neutral sandy and peaty soils. One of the most remarkable of these papers was published by Hiltner (1924). He showed that the "Dörrfleckenkrankheit" is not limited to oats growing on neutral or alkaline soils, but may also be found in plants growing in acid nutrient solutions. In both cases it was cured by manganese. These experiments were very important for they demonstrated that the disease was not primarily caused by organic substances or by an alkaline reaction. Although these results may be considered as evidence that the gray speck disease is brought about by manganese deficiency, this conclusion was not drawn by Hiltner. Since carbon dioxide treatment of oat plants suffering from gray speck disease was found to

have a similar effect as supplying manganese to the nutrient medium, Hiltner (1924) attributed the beneficial effect of manganese to improved carbon dioxide assimilation by the plants, so that the disturbed equilibrium CO_2 assimilation-mineral substance uptake, which was supposed to be the cause of the disease, thereby would be corrected.

The essentiality of manganese as a micronutrient element for green plants became apparent shortly after 1920 (McHargue, 1922). The first authors who recognized that the symptoms of gray speck disease are essentially the symptoms of manganese deficiency were Samuel and Piper (1928). They carried out culture solution experiments with oats in comparison with pot and field experiments with "sick" soils. Very low values for manganese were found in diseased plants in comparison with healthy plants from sterilized "sick" soil or from "healthy" soil. Although clear differences in soil manganese were found, the methods used were inadequate for determining the plant-available manganese in soil, so that no explanation was given of the fact that plants growing on soils which contain large amounts of total manganese are unable to absorb the small quantities of this element that are required for normal development. Apparently Samuel and Piper were unaware of the important investigations by Beijerinck and Söhngen, who as early as 1913 and 1914, respectively, carried out a number of microbiological experiments concerning the oxidation of manganous salts to manganese dioxide. From his investigations Söhngen (1914) concluded that the unavailability of manganese in neutral or alkaline soils was due to the conversion of Mn^{++} to insoluble manganic oxides. In a later paper Piper (1931) demonstrated the importance of both soil reaction and oxidation-reduction equilibrium in rendering manganese unavailable to plants. The papers of Beijerinck and Söhngen were overlooked by soil scientists until their experiments were repeated and extended by Gerretsen (1936, 1937). Since that time a considerable number of papers have appeared dealing with the various aspects of soil manganese. Some of the investigators, for example, Gerretsen (1937), Leeper (1947), Quastel *et al.* (1948) are of the opinion that the conversion of available Mn^{++} to insoluble Mn^{+++} or Mn^{++++} is brought about by soil microorganisms; others believe that this is not the case because of the great rapidity with which this process takes place (Fujimoto and Sherman, 1948).

The fact that manganese, when supplied to plants in excessive amounts may cause toxic symptoms, has appeared to be of great importance in agriculture and horticulture. It has been shown, particularly during the last decade, that many acid soils may contain amounts of plant-available manganese large enough to bring about manganese

toxicity of the plants growing on it. In fact, manganese injury has been shown to be one of the main causes of soil acidity damage in many plant species on many acid soils. Since many papers deal with this subject, a relatively large portion of this review is devoted to the topic of manganese toxicity.

Many authors have considered the function of manganese in living organisms, plants, bacteria, and fungi, as well as animals. It appears that manganese plays the role of an activator in many enzymatic reactions. Practically all these investigations have been carried out *in vitro* so that it is as yet impossible to decide which enzymatic reactions are involved when manganese deficiency occurs *in vivo*. There is increasing evidence that manganese plays an important role in the photosynthetic apparatus of green plants and together with iron controls the oxidation-reduction potentials in the cells during illumination and in the dark.

II. Manganese Determination

Manganese in soils and plants can be determined by colorimetric, spectroscopic, polarographic, and biological methods Plant material is generally ashed or wet-digested, though in some cases spot tests are used, which aim to estimate the manganese content of leaves, stems, fruits, etc., directly. The determination in soils is complicated by the fact that the several manganese compounds differ widely in availability, which to a great extent depends on the pH and the redox potential of the soils. Moreover, microorganisms take a very active part in transforming soluble manganese compounds into insoluble oxides and vice versa; consequently the manganous-manganic equilibrium in the soil depends largely on the activity of the soil flora, a fact which often has been overlooked by soil chemists.

Microbiological transformation may affect the amount of available manganese in a very short time, so storage of wet samples has to be avoided. Also purely physical treatments, such as drying or sterilizing, can effect drastic changes in the available manganese content of a soil; these facts should be born in mind when taking soil samples for manganese determination. Sherman and Harmer (1942) stress the point that samples should be analyzed immediately and in their natural field condition, especially because some soils release larger amounts of exchangeable manganese if they are air-dried before extraction. Boken (1952) showed that not only the amount of exchangeable manganese increases considerably when wet soil samples are dried at higher temperatures, but also that this is the case during storage of air-dried soil samples even at room temperature. The increase in the manganese

values is a function of both the length of the storage period and of the storage temperature.

1. *Colorimetric Methods*

In many cases the original method of Willard and Greathouse (1917) as modified by Richards (1930) is still used; it involves the destruction of the organic material by ashing, the removal of the chlorides by digesting with sulfuric acid, the elimination of the disturbing effect of iron by addition of phosphate and finally the oxidation of the manganese to permanganate by means of periodate. The red color of the permanganate is measured photometrically. Strickland and Spicer (1949) have made an extensive study of the kinetics of the formation of permanganate using periodic acid as an oxidant and give a detailed account of the probable mechanism of the oxidation, at the same time recommending suitable conditions for an effective absorptiometric method.

According to de Wael (1941) Richards' method does not give correct results; digestion with sulfuric acid causes errors (up to 18 per cent) due to evaporation, whereas the ash retains some manganese because of the formation of insoluble manganic oxides. Coppenet (1949) showed that the silicic acid in the ash of cereal straw combines with manganese causing 27.4 to 40.5 per cent of the manganese present to escape determination. To avoid this the author dissolves the silicate in 2–3 ml. hydrofluoric acid. Strickland and Spicer (1949) found permanganic acid in the distillate from boiling sulfuric acid containing manganese solutions. This error can be avoided by the substitution of 85 per cent H_3PO_4 for the 12 N H_2SO_4 commonly used.

Smith (1950) emphasizes the point that the oxidation to permanganate by means of periodate is less rapid than is generally believed. He recommends holding the temperature of the solution near the boiling point for at least thirty minutes after the addition of KIO_4. Nydahl (1949) claims that by using ammonium peroxidisulfate instead of periodate the oxidation is completed in a few seconds, whereas with periodate no more than 86 per cent of 1 μmol manganese is converted into permanganate after boiling for one hour.

As the accuracy of the colorimetric determination of permanganate diminishes markedly at very low concentrations, several authors attempted to revise existing methods or to perfect new ones. Sideris (1937) uses the formaldoxime reagent (H_2C : NOH) of Deniges, (1932) which instantaneously develops a wine red color directly proportional to the amount of manganese in the solution. After some improvements with regard to the interfering ions of iron and phosphate (Sideris, 1940), amounts of manganese varying from 0.005 to 0.01 mg. in a 10-ml. sample

can be determined with an accuracy of approximately 2 per cent. The same reagent is used by Waldbauer and Ward (1942) and Kniphorst (1946), whereas Wiese and Johnson (1939) prefer benzidine ($NH_2 \cdot C_6H_4 \cdot C_6H_4 \cdot NH_2$) which gives a blue color with permanganate, quickly changing into a stable yellow-green color.

The most sensitive reaction for manganese is the oxidation of 4,4'-tetramethyldiaminodiphenylmethane by $KMnO_4$. According to Gates and Ellis (1947) the organic material is ashed at 600°C., dissolved in a HNO_3-H_3PO_4 mixture, oxidized with KIO_4, and methane base added. Chlorides, vanadium, and cerium interfere; recoveries of manganese added to various materials ranged from 90–112 per cent. The sensitivity range according to these authors lies between 0.05 and 0.5 μg. Mn. According to Cornfield and Pollard (1950) this method is 300 times as sensitive as the permanganate method; they were able to determine the manganese content in the ash of 0.05–0.1 g. oven-dried plant material.

In the widely used Morgan soil testing system (Lunt *et al.*, 1950) manganese is determined in the soil extract either with benzidine and NaOH or with KIO_4 and methane base (tetra-base); the resultant blue color is compared with a standard color chart, rating from 5 to 40 p.p.m. in soil.

Chemical tissue tests are very useful to reflect the nutrient status of the plant. Leaf analysis for practical diagnostic purposes was introduced by Lagatu and Maume (1932). Roach (1944, 1946) at the East Malling Research Station in England applied the method for the detection of manganese deficiency: 25 mg. of dried leaf were burned directly in an acetylene flame, and the line intensity was determined with a flame spectrometer. Roach and Roberts (1945) used an ingenious method for diagnosing manganese deficiency in leaves by injecting or spraying a growing leaf with a solution of $MnSO_4$ (0.025 per cent). Deficient leaves respond by improving the chlorotic color of the tissues in a few days.

Nicholas (1948) has developed a quick and more-or-less precise quantitative determination of the manganese content of crop plants which may be used for the diagnosis of deficiencies in the field, as well as for the detection of cases where excess may be expected. With Morgan's acetate-acetic acid buffer at pH 4.8 0.5 g. of leaf is extracted. The reagents used for the test are trioxymethylene sulfate and NaOH, when manganese is in excess, or KIO_4 with methane base for deficiency levels. In the latter case the sensitivity ranges from 1 to 100 parts per 1000 million.

2. *Spectrochemical Methods*

The desirability of greater rapidity, permitting analyses of large numbers of soil samples, has resulted in the development of spectrochemical procedures for manganese. Flame spectrography has been perfected by Lundegårdh (1951) to such an extent that a number of important elements can be quantitatively determined by means of an automatic robot machine of very ingenious construction. Of biological interest is the high sensitivity in the flame of heavy metals, e.g., manganese. The manganese line (4030 Å) can be separated from the near-by potassium line (4044, 2 Å) by means of a spectrographic slit with a width of 0.005 mm. The accuracy of the determination in leaves is approximately 3 per cent, and the error is in general definitely less than 5 per cent. Heidel (1946) also uses a spectrochemical procedure for the determination of manganese.

3. *Polarographic Methods*

A promising method seems to be the polarographic determination which has been used by Zàk (1942) in an investigation of the fluctuation of the manganese content of lucerne during the season. Manganese shows a pronounced step in the polarographic curve at -1.53 v. and may be determined in this way with an accuracy of 0.01 mg. per cent. Zàk shows that the silicic acid of the ashed plant material binds up to 20 per cent of the manganese present, and repeated evaporation to dryness with HCl is necessary to avoid these losses. The polarographic method has the advantage that in a single polarogram different ions can be determined one after another.

Riches (1946) proposes to isolate different trace elements from a mineral acid digest by the use of synthetic resins. With a small column packed with granules of Amberlite 1 R 100 it was possible to retain quantitatively copper, cadmium, zinc, nickel and manganese. Recovery after elution with *N* HCl followed by polarographic determination amounted to 87–96 per cent.

4. *Biological Procedures*

The objection that the crude ways in which soils are generally extracted for chemical determinations differ very much from the progressive mild extraction exercised by the plant roots does not hold true for biological tests, which come much nearer to natural conditions.

As early as 1912 Bertrand and Javillier demonstrated the favorable influence of manganese ions on the growth of *Aspergillus niger*. Niklas and Toursel (1941) showed that 0.001 per cent of $MnSO_4$ increased the

weight of the mycelium as much as 83 per cent. Steinberg (1936) obtained an increase in weight of the mycelium of *Aspergillus niger* of approximately 30 per cent by the addition of manganese. He showed, however, that the optimal heavy metal concentration varies with the acidity of the solution, being approximately twentyfold in the solution at pH 8.01 as compared to that at 7.35. Löhnis (1944-45), who made a very thorough investigation of the influence of manganese on yield and sporulation of *Aspergillus niger,* came to the conclusion that, though *Aspergillus* is quite sensitive to traces of manganese under highly acid conditions, an *Aspergillus* standard will not be suitable for soil tests. Nicholas (1950), however, uses the *Aspergillus* method for the determination of manganese in soils, but adjusts the basal solution to pH 7.5 with dilute ammonia before addition of the soil sample. The effective range per 50-ml. culture solution lies between 0.01 and 10 μg.

An interesting microbiological method has been developed by Bentley, Snell, and Phillips (1947). *Lactobacillus arabinosus* responds to manganese by producing more lactic acid, which is measured by titration. The basal medium is freed from traces of manganese by preabsorption with the test organism. Within 73 hours 0.3 μg. manganese causes an increase in acid production of 6 ml. 0.1 *N* acid. Recovery of added manganese was quantitative within the experimental error of approximately 10 per cent.

III. Manganese in the Soil

Manganese occurs in the soil in different forms with widely divergent solubilities. Therefore one has to distinguish between total manganese and available manganese. The former, which may be determined by treating the soil with strong acids (Alten and Weiland, 1933, even use *aqua regia*), is of secondary importance for plant growth. Of much more significance is the available or "active" manganese as it is called by Leeper (1935, 1947). It includes water-soluble and exchangeable Mn^{++} and those forms of manganic oxide which are easily reducible by hydroquinone at pH 7. Those oxides which oxidize hyposulfite at pH 7 and hydroquinone at pH 2, but not at pH 7 are considered by Leeper moderately active, whereas the rest of the manganic oxides, which require more drastic treatment for solution may be considered inert and of no value for plant growth.

1. Effect of pH on Soil Manganese

The occurrence of manganese in various forms depends on a number of factors of which pH and organic matter content are the most im-

portant. Soils with pH values lower than 5.5 may contain a large amount of their manganese in water-soluble or exchangeable form. With increasing pH Mn^{++} will be converted into manganic oxides (Mn^{+++} and Mn^{++++}), as a result of which it becomes far less available to plants so that under certain circumstances manganese deficiency may occur. This conversion presumably depends largely either directly or indirectly on the activity of microorganisms. The oxidation of Mn^{++} which in the test tube takes place at pH values above 8, proceeds in the soil at much lower values probably owing to the presence of hydroxy acids and perhaps pyrophosphate (Söhngen, 1914; Heintze and Mann, 1947). Mattson *et al.* (1948) were unable to observe a stimulating effect of hydroxy acids on Mn^{++} oxidation. Since the experiments of Söhngen have been confirmed by the present authors a more detailed investigation of this problem seems urgent. Microorganisms appear to be able to oxidize Mn^{++} at pH values of the soil above 5.5.

Fixation of added manganese in an unexchangeable form in many neutral or alkaline soils proceeds rapidly. Wain *et al.* (1943) observed fixation of the bulk of the added manganese within a few days after its application. Similar results have been obtained by Sherman and Harmer (1942). The rapidity with which the exchangeable manganese content of a soil can fall after liming is clearly shown in Table I derived from Heintze (1946). Increasing amounts of lime were added to a clay loam and after one week's incubation pH values and exchangeable manganese were determined.

TABLE I

Exchangeable Manganese of a Clay Loam after One Week's Incubation with Lime (After Heintze, 1946)

Treatment	pH	Manganese (mg. %)
Control	4.5	10.2
1 ton lime per acre	5.5	10.0
3 tons lime per acre	6.3	8.4
8 tons lime per acre	7.5	5.0
12 tons lime per acre	7.9	2.0

In the light of these facts it becomes intelligible that the application of manganese sulfate to manganese-deficient soils generally has only a transitory effect, unless at the same time measures are taken to reduce the pH of the soil.

In this connection it is of interest to note that the application of lime, not as $CaCO_3$ but as CaO, to manganese-deficient clay soils rich in organic matter may result in a temporary improvement and even in

a complete recovery (Maschhaupt, 1934; Popp *et al.*, 1934). The former author even used from 15,000 to 20,000 kg. CaO per hectare which fully suppressed the deficiency symptoms on a so-called Roodoorn soil, a sea clay soil, devoid of $CaCO_3$, with a pH of 5.7 and a humus content of 12.5 per cent. In a couple of years, however, on this soil wheat showed severe manganese-deficiency symptoms. A similar beneficial effect of treating manganese-deficient soils with high amounts of CaO on growth and health of oats was noted by Gisiger and Hasler (1948). At high pH values soil organic matter apparently may reduce higher manganese oxides to Mn^{++} (Mattson *et al.*, 1948).

The reduction of manganic oxides to Mn^{++}, may proceed either by direct reaction with organic matter or by biological processes. Reduction by organic matter is more likely at low pH values since the oxidizing power of the higher oxides increases rapidly with acidity. Hydroxy acids again play an important part in this reduction (see below). Biological reduction can take place in acid as well as in alkaline soils if the oxygen tension is low through waterlogging.

2. *Availability of Soil Manganese and Its Estimation by Chemical Analysis*

Initially it was thought by Leeper (1935, 1947) as well as by Sherman and Harmer (1942) that the active manganese brought into solution by 0.2 per cent hydroquinone in normal ammonium acetate of pH 7.0 would be a reliable measure of plant-available manganese and thus for distinguishing between healthy and deficient soils. In alkaline soils easily reducible manganese should be at least 100 p.p.m. in order to maintain an adequate level of exchangeable manganese for plant growth. In such soils the quantity of exchangeable manganese should be > 3 p.p.m.

Heintze (1946) in an extensive study of "marsh spot" in peas failed to distinguish between soil samples from healthy and diseased parts in the same fields when using Steenbjerg's method (1935) for the determination of exchangeable manganese or Leeper's method with hydroquinone and calcium nitrate.

Dion, Mann, and Heintze (1947) investigated the factors controlling the reducibility of higher manganese oxides. Estimation of the easily reducible manganese appeared to be dependent on the pH of the system, the nature of the salt solution, the nature of the reducing agent, the time of contact in addition to the amount and nature of the higher oxides of manganese present. Pyrolusite (MnO_2) and a synthetic preparation of $Mn(OH)_3$ were found to be easily reducible. Manganite ($MnO(OH)$) and hausmannite ($MnMn_2O_4$) are apparently difficultly reducible forms.

The substitution of hydroxylamine hydrochloride for hydroquinone in Leeper's procedure was found to avoid the troublesome destruction of hydroquinone prior to the colorimetric manganese determination.

Jones and Leeper (1950, 1951a), investigating the availability of manganese in various synthetic manganese oxides, could not correlate the response of oats and peas obtained in pot experiments with the quantities of manganese in the soil as determined by means of a solution of hydroquinone in normal ammonium acetate. With this reagent the amounts extracted from manganite, hausmannite, and pyrolusite were of the same order. Yet the manganite and pyrolusite when added to manganese-deficient soils gave healthy plants, whereas hausmannite failed. The combined action of a concentrated electrolyte and a reducing agent seemed to be too drastic. Much better results were obtained with 0.05 per cent watery hydroquinone solutions (one-hour contact). The method as adopted by these authors includes stirring of the soils with 50 per cent alcohol containing 0.05 per cent hydroquinone, the alcohol being used to flocculate the colloids Hydroquinone is removed by washing with 50 per cent alcohol, and the manganese now present as the exchangeable ion is replaced with a semimolar calcium nitrate solution at pH 7. The results obtained by this method by Jones and Leeper (1951a) have given the best correlation with plant response.

Electron microscope photographs of a number of synthetic manganese oxides showed that all the beneficial manganese oxides consisted of very small particles. Obviously a large specific surface is needed to ensure activity. This was found to be true of several highly oxidized forms: manganite, pyrolusite, cryptomelane, and manganous manganite; hausmannite, however, was found to be inert and unavailable to oats even when the particles were as minute as those of the active forms. X-ray analysis showed that the latter was highly crystalline, whereas in the others the degree of crystallinity was low. Difference in crystallinity was suggested by Jones and Leeper (1951a) to be also the cause of the divergent results with respect to manganite, for which Dion, Mann, and Heintze (1947) reported a low reducibility in hydroquinone solutions.

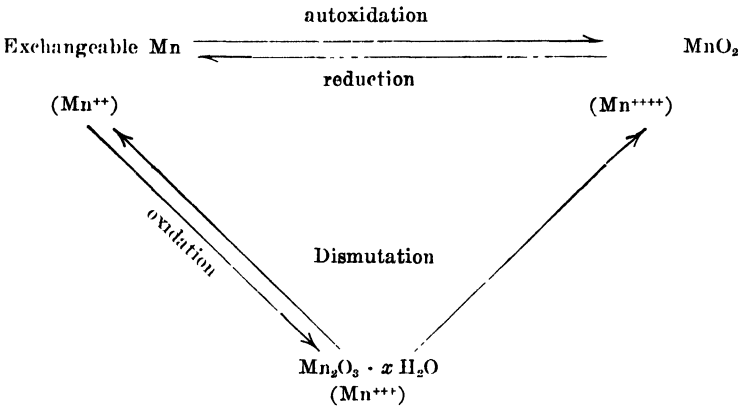
Curing manganese-deficient soils with active oxides did not increase the content of exchangeable manganese of the soils. This shows clearly that a reserve of the bivalent manganese is not needed for healthy plant growth.

In experiments with Australian soils active manganese oxides were found to preserve their activity for a considerable number of years (Jones and Leeper, 1951b). Presumably they have to be reduced to Mn^{++} at the root surface before the manganese can be absorbed. Re-

version of active oxides to a less available form is thought to be due mainly to aging, i.e., the surface becomes more ordered and less active.

3. Occurrence of Trivalent Manganese in Soil

An important contribution to our knowledge of the different states in which manganese may be present in the soil comes from Dion and Mann (1946). They showed that in alkaline soils a significant part of the soil manganese may be present in the trivalent state, which exists as the more or less highly hydrated manganese oxide $Mn_2O_3 \cdot xH_2O$. This is considered to be the first product of oxidation of divalent manganese in soils. According to these authors the following manganese cycle may be represented:



Autoxidation of divalent manganese to MnO_2 will probably be of significance only at pH values above 8. In less alkaline soils oxidation of divalent manganese is assumed to result in the production of trivalent manganese. In a percolation experiment with three soil samples 80.3 to 98.5 per cent of the added manganese sulfate which had been circulated for two weeks through the soil was recovered as trivalent manganese.

In acid solutions manganic hydroxide dismutes to give an ion of divalent manganese and a molecule of MnO_2, according to the following equation:

$$2Mn(OH)_3 + H_2SO_4 \rightarrow MnSO_4 + MnO_2 + 4H_2O$$

Under soil conditions Dion and Mann (1946) expect the same dismutation to take place. To show the effect of pH on this process they carried out an experiment to measure the amount of Mn^{++} produced in one week as a result of storage of $Mn(OH)_3$ at different pH values. At pH

7.50, 10.7 per cent dismutation was observed after one week, whereas at pH 6.18 a value of 82 per cent was found.

With sodium or potassium pyrophosphate the trivalent manganese may be extracted from the soil forming a stable complex to which the formula $Na_3(Mn(H_2P_2O_7)_3)$ may probably be ascribed.

The results of Mattson *et al.* (1948) confirm the concept of Dion and Mann as to the occurrence in alkaline soils of a large part of the soil manganese in the trivalent state.

4. *Effect of Organic Matter on Soil Manganese*

The role which organic matter plays in the conversion of the Mn^{++} to insoluble manganese compounds in the soil is not clear. That the presence of a certain amount of organic matter is required for the appearance of manganese deficiency of the plants has been shown by many workers. In the Netherlands manganese deficiency will be found on sandy soils containing a certain amount of organic matter and on reclaimed peaty soils when the pH becomes higher than 6 or 6.5. On neutral or alkaline clay soils, however, manganese deficiency is seldom found, unless they contain a certain amount of organic matter.

It may be possible that the effect of organic matter is due to the presence of hydroxy acids which according to Söhngen (1914) and Heintze and Mann (1946) play an important part in the conversion of soil manganese.

Heintze and Mann (1949) advance the hypothesis that manganese deficiency of plants on neutral and alkaline soils of high organic matter content and of adequate total manganese content is due to the formation of complexes of Mn^{++} with the organic matter which are dissociated only to such a slight extent that the available manganese in the soil is insufficient for the needs of the plants. The formation of such complexes was shown by these authors. Jones and Leeper (1951b) found no evidence for the existence of such complexes in their experiments.

Hudig (personal communication) made the interesting observation that in the northern part of Holland, on the borderline between acid sandy peat soil and clay soil, gray speck disease of oats was a common phenomenon, whereas on both sides of this line oats were perfectly healthy. The most plausible inference is that in the diseased area the pH of the peaty soil had been raised by the clay to a level at which manganese is made insoluble. The question, however, as to why on alkaline clay soils manganese is much more available than on sandy soils of the same pH needs further elucidation.

5. *Manganese in Calcareous Soils*

The French workers Boischot and Durroux (1949) have studied the fate of manganese in calcareous soils; manganese was found to be fixed by adsorption on the surface of the calcium carbonate particles. In contact with a 0.1 per cent neutral solution of ammonium humate the adsorbed manganese was set free in a form accessible to plants. This would explain why crops growing on calcareous soils generally do not suffer from manganese deficiency; if it does occur on such soils it is not caused by adsorption of the manganese on the calcium carbonate, but, according to these authors, has to be ascribed to biochemical oxidative processes.

IV. The Role of Microorganisms in Transforming Manganese Compounds

1. *Oxidation of Manganous Compounds*

The oxidation of manganous compounds to brown manganic oxides by bacteria and fungi was first shown by Beijerinck (1913). A small micrococcus and motile rods were isolated, forming small brown colonies on agar with 0.05 per cent manganous lactate as sole carbon source (*Bacillus manganica*). Amongst the fungi were representatives of Botrytis, Mycogone, Tricholadium; one of the most active fungi was *Papulospora manganica*, which feeds on traces of organic substances present in plain agar and which is able to oxidize manganous carbonate at relatively large distances from the mycelium.

Söhngen (1914) made a very valuable contribution to the problem and showed that a great variety of microorganisms, including *Pseudomonas fluorescens, Azotobacter chroococcum, Escherichia coli, Oidium lactis* and different species of Saccharomyces were able to transform soluble manganous compounds into insoluble, brown manganic oxides, when grown on agar media containing neutral salts of hydroxy acids (gluconic, malic, citric, lactic, and tartaric acids). However, the same oxidation could be performed by applying a drop of a sterile Na_2CO_3 or $NaHCO_3$ solution to the surface of these agar media.

On the other hand, it was shown by this author that in agar plates, containing sugars or cellulose and MnO_2, the latter compound is transformed into soluble manganous salts through the intermediary of the hydroxy acids produced by different cellulose or sugar-decomposing microorganisms. Whether manganous salts will be converted into manganic oxides or the reverse reaction will take place largely depends on the pH of the medium.

The agricultural aspect of the problem rested for a quarter of a century until Gerretsen (1936, 1937), by using soil agar plates in the center of which agar with 1 per cent $MnSO_4$ was placed, showed that brown rings of MnO_2 were formed, which consisted of numerous small colonies of bacteria and of fungi in which MnO_2 had been precipitated. The intensity of the precipitation rapidly diminished when the pH of the agar was raised or lowered, the limits lying between pH 6.3 and 7.8.

Leeper and Swaby (1940) using Gerretsen's technique, slightly modified, confirmed his results. Though brown spots generally developed most rapidly in plaques of pH between 6 0 and 7.5 they also observed brown spots due to microbial oxidation on plaques of which the final pH ranged from 4.8 to 8.9, the initial pH being 5.5. MacLachlan (1941) by means of the same soil agar plaque method was able to isolate a greater number of manganese oxide-precipitating bacteria from a manganese-deficient soil than from a normal soil and attributed manganese deficiency in the soil in question to the activity of microorganisms. According to Bromfield and Skerman (1950) neither the agar used by Beijerinck nor that by Gerretsen to isolate the active bacteria was satisfactory for the purpose, because pure cultures of bacteria isolated from Gerretsen's medium failed to oxidize Mn^{++} on plain soil agar media. Bromfield and Skerman, however, used meat infusion agar as an intermediate culture medium when isolating these bacteria and overlooked the fact that according to different authors most manganese oxidizing bacteria either do not thrive on such media or lose their ability to oxidize manganous compounds (Beijerinck, 1913; von Wolzogen Kühr, 1927). Bromfield and Skerman (1950) isolated two bacteria which were unable to oxidize manganous compounds separately, but did so in association on soil agar plaques. In contrast to these statements Timonin (1950a) isolated several microorganisms on Gerretsen's calcium citrate-manganous sulfate agar which were capable of oxidizing manganous salts on artificial media as well as on soil agar manganese sulfate plaques without further addition.

The present situation with regard to the microbiological oxidation of manganous compounds to insoluble manganic oxides is not yet sufficiently cleared up. There is positive evidence that microorganisms of widely divergent origin are able to produce hydroxy acids from cellulose and other substrates of vegetable origin and that the manganous salts of these acids are readily oxidized chemically by the oxygen from the air when the pH is above 7. In accordance with this fact the application of organic material may result in inducing manganese-deficiency symptoms or in aggravating them, with lower yields of grain than on untreated soil. Hudig and Meyer (1919) in their fundamental experiments

on gray speck disease incorporated different organic materials in their sand cultures (cotton, glucose, filter paper, etc.) which resulted in the appearance of severe manganese deficiency symptoms which could be prevented in some cases by applying $MnSO_4$, indicating that by the addition of organic material available Mn^{++} had been immobilized. Timonin (1946) using straw mulch obtained similar results and de la Lande Cremer (Agricultural Experiment Station, Groningen, private communication) using aqueous extracts of wheat straw observed distinct symptoms of manganese deficiency in his pot cultures.

However, the nature of the organic material incorporated in the soil seems to be of great importance. When Hudig and Meyer (1919) added oat leaves instead of cellulose to their pot cultures, the plants remained healthy; extracting the leaves with sodium hydroxide or with acids annulled the effect, and the disease symptoms were as heavy as with cellulose. Fujimoto and Sherman (1948) observed a considerable increase in available manganese of Hawaiian soils after treatment with sucrose, ground pineapple leaves, and sugar cane leaves with a high carbon nitrogen ratio. Hurwitz (1948) in studying the effect of applying oat straw and alfalfa meal at a carbon-nitrogen ratio of 30:1 to a soil observed a considerable increase in exchangeable manganese which after three days' incubation at 37° and 47°C. reached a maximum value. Thereupon it decreased to about the initial value after about two weeks' incubation. The increase in exchangeable manganese as described by these authors apparently has to be attributed to the very rapid breakdown of the organic matter as a result of which the oxygen supply became limited and the redox potential was lowered. In the case of sucrose a decrease in pH may also have occurred.

Mann and Quastel (1946) percolating neutral or slightly alkaline soils with 0.02 *M* $MnSO_4$ showed that the manganese usually disappears at an increasingly rapid rate and is found in the soil in an oxidized form. Biological poisons such as sodium azide (0.001 *M*) inhibit the oxidation. They concluded that oxidation under the given experimental conditions is wholly or almost wholly accomplished by proliferating microorganisms.

Though the oxidation of manganese compounds is exothermic, there is as yet no evidence of the existence of true autotrophic manganese oxidizing bacteria. The precipitation of the manganic oxides has been observed inside the bacterial and fungal cells as well as outside (Beijerinck, 1913; von Wolzogen Kühr, 1927; Gerretsen, 1936). Whether in all cases oxidation takes place through the intermediary of hydroxy acids and an accompanying rise of the pH or that a more direct oxidation by means of special enzymes occurs as well is still to be investigated.

As manganese-oxidizing microorganisms of the former class require only small quantities of organic materials and representatives are to be found among the most common groups of soil microbes, it is evident that in most soils the conditions for microbial immobilization of manganese will be fulfilled as soon as the pH rises above neutrality. Moreover organic compounds excreted by the roots may favor the development of manganese-precipitating microorganisms in the rhizosphere. Timonin (1946) showed that a susceptible variety of oats harbored in its rhizosphere five to thirteen times as many manganese-oxidizing bacteria as a resistant variety. The application of cyanogas as a soil disinfectant reduced the numbers of bacteria in the rhizosphere to about 7 per cent of their original value and tripled the yield of the plants.

It is interesting to note that according to von Wolzogen Kühr (1927) the removal of manganese from dune water in the filter beds of the waterworks is essentially a bacteriological process, analogous to that described above for the soil. This author attributes to the precipitated manganic oxide the property of absorbing manganous compounds on its surface which are readily oxidized by microorganisms; in this way manganic concretions of increasing size are built up. It is alluring to suppose that a similar process takes place in the soil by which manganese deposits grow in size and gradually become less available to the plants. The formation of iron-manganese concretions in the A_2 horizons of certain poorly drained prairie soils which are waterlogged for a considerable part of the year, perhaps may be attributed to a similar process. These concretions which may have diameters from 0.1 to 15 mm. contain from fifteen to seventy-five times as much manganese and from two to more than four times as much iron as the surrounding soil in which they are found; the manganese is present as the higher oxides (Drosdoff and Nikiforoff, 1940).

2. Solubilization of Manganic Oxides

The solubilization of unavailable manganic oxides can be accomplished by microorganisms in different ways: by changing the redox potential or the oxygen tension of the soil, or eventually by producing reducing organic substances which cause the manganic-manganous equilibrium to shift in the direction of the latter compounds. The favorable effect of waterlogging on manganese-deficient soils is to be ascribed to these activities of microorganisms. In addition to a high water content which greatly limits the entrance of oxygen from the air, a certain amount of assimilable organic matter is necessary for the growth of the microorganisms to enable them to accomplish their diverse metabolic activities. Söhngen (1914) has convincingly shown that precipitated

brown MnO_2 may be brought into solution by hydroxy acids, produced by microorganisms, e.g., from cellulose, but not by fatty acids, such as acetic, propionic, or butyric acids. Similar results have been obtained by Heintze and Mann (1947). They found, however, a sharp difference between $Mn(OH)_3$ and MnO_2, the former being dissolved to a large extent by various hydroxy acids whereas the latter was practically unattacked.

The pH may influence manganese availability in different ways. The reduction of higher manganic oxides by organic matter is more important at low pH values, since the oxidizing power of these oxides increases rapidly with acidity. The production of strong inorganic acids especially sulfuric acid by the sulfur-oxidizing bacteria and nitric acid and sulfuric acid by nitrifying bacteria favorably influences the amount of manganese available to the plants.

3. *Microorganisms in Relation to Leaf Spots of Manganese-Deficient Oats*

Microorganisms may play another important role in connection with the development of the typical symptoms of manganese deficiency. Gerretsen (1937) carried out extensive studies with sterile cultures of oats, in soil, sand, and nutrient solutions containing inadequate quantities of manganese for normal growth and showed that, when these cultures were kept sterile, the plants did not show typical symptoms of gray speck disease, though generally they remained smaller than normal plants.

Infection of these cultures, either with a small quantity of the original diseased soil (5 per cent) or even with a diseased root tip of a diseased plant resulted in the appearance of the typical symptoms. Alkaline products produced in the decaying roots by the infecting saprophytic microorganisms are carried in the transpiration stream to the leaves, where they produce the gray spots.

According to Gerretsen it is necessary to distinguish between the direct physiological effect of manganese deficiency (etiolation, reduced photosynthesis, necrosis) and the typical leaf spots related to the infection of the roots.

In the light of these facts one aspect of the distinction between susceptible and resistant varieties of oats might be traced back to an increased unspecific resistance of the roots toward invading microorganisms, hereditary "axeny," as Gäumann (1946) calls it, which is a common quality of resistant varieties in general. On the other hand, diminished photosynthesis is the reason why manganese-deficient plants contain less carbohydrates than normal plants (see Sec. X,4), and it

is to be expected that in consequence the roots not only remain smaller but also have a lower degree of resistance to invading microorganisms.

In accordance with this view Timonin (1946) succeeded in growing healthy susceptible oats on a diseased plot which had been treated with cyanogas, a soil fumigant. He ascribes the improvement, however, to the eradication of the manganese-oxidizing bacteria in the soil. Hasler (1951) showed that the dry weight of the roots of a number of grasses was much more depressed than that of the leaves on manganese-deficient soils, the ratio of the dry weights of the roots of the diseased plants as compared to those of the healthy ones being 1 : 5, whereas that of the leaves was 1 : 2.5.

4. Resistant Oat Varieties

The fact that the resistant varieties do not show the typical gray speck disease symptoms may point to an increased resistance of the roots toward invading saprophytic microorganisms.

There is no doubt that the resistant varieties need manganese too for normal growth, though they might be adapted to a lower level of this element than the ordinary varieties. Accordingly the yield of the resistant varieties is also unfavorably affected by manganese deficiency. Rademacher (1935) growing a resistant variety on a manganese-deficient soil obtained a lower yield (45 per cent) than on a healthy soil. Though in Timonin's experiments (1946) the resistant variety ACTON produced 40 per cent more grain than the susceptible variety on a diseased plot, the yield of the former was doubled by fumigating the soil with cyanogas. It is supposed that in this case the oat plants have had more manganese at their disposal, as, according to Timonin, the greater part of the manganese-oxidizing bacteria had been killed by the soil disinfectant. It is the impression of the authors that there is as yet insufficient evidence to draw a definite conclusion with regard to the real causes of the resistance of certain oat varieties to manganese deficiency.

V. SYMPTOMS OF MANGANESE DEFICIENCY IN PLANTS

Cereals, oats (Wallace, 1944; Samuel and Piper, 1929). Among cereals, oats is the most susceptible crop. Marginal gray-brown colored necrotic spots and streaks appear first on the third highest leaves, particularly on the basal half. The streaks tend to elongate and coalesce. At the distal ends of the affected basal part the necrotic spots may soon extend across the blades so that the upper half or two-thirds of the leaf falls over with a sharp kink at the collapsed portion. The distal ends of the leaves remain green for a considerable time. On older leaves

the collapse may be confined to the lower quarter, and oval spots of necrotic tissue may appear irregularly on the leaf blade, though less frequently toward the tip end. Streaks of tissue collapsing at the margins of the leaves are also very characteristic. The root system is poorly developed and is more affected by microorganisms than is the case with an adequate manganese supply.

In *wheat* and *barley* the symptoms are not so characteristic as in oats. The leaves are somewhat pale green and may show only faint chlorotic streaking and yellowing. In severely affected barley irregular brown necrotic spots occur on the leaves running especially between the veins. In some cases these necrotic spots may be situated on the middle parts of the leaves with falling over of the distal halves similar to oats. In other cases the spots are located on the basal half and sometimes on the distal half. In wheat interveinal white lesions and streaks may develop. In rye and maize the necrotic tissues are also white colored. In severely attacked rye large parts of the leaves may collapse. The general appearance of manganese-deficient cereals is very limp. In the field rye is considerably less susceptible than the other cereals. Of ten varieties of winter and spring wheat tested by Gallagher and Walsh (1943) three appeared to be nearly immune to manganese deficiency, six others were particularly sensitive, and one was intermediate. Similar large differences were noted in oats.

Grasses. Grasses growing on soils where oats showed severe symptoms of manganese deficiency did not exhibit the typical leaf symptoms (Hasler, 1951). Some leaves had brownish tips while grayish spots were situated on the leaf blades. Of the fifteen species tested by Hasler, *Alopecurus pratensis*, *Arrhenatherum elatius*, and *Bromus erectus* gave the highest increases in yield upon manganese treatment. *Anthoxanthum odoratum, Cynosurus cristatus, Festuca pratensis* and *Trisetum flavescens* gave intermediate responses. The following species responded slightly or not at all to added manganese. *Agrostis alba, Dactylis glomerata, Festuca rubra, Lolium italicum, Lolium perenne,* and *Poa pratensis.* The root systems of manganese-deficient grasses were poorly developed.

Beans (*Phaseolus vulgaris*) (Townsend and Wedgworth, 1936). At first the trifoliate leaves show a faint mottled pattern, the tissue near the veins remaining green longer than that between the veins. The cotyledonary leaves remain green until late in the development of the disease. A few days after the appearance of the first mottling the entire leaf blade may turn golden yellow. Small necrotic brown spots can be seen parallel to each side of the midrib and principal veins which may extend to the tips and margins of the leaves. Subsequently, the under-

surface of affected leaves appears to be cupped between the veins, while the upper surface of the same areas appears water-soaked and soon breaks down. New growth from the apical bud becomes slower as the disease progresses, and the buds eventually die. All leaves become brown and withered by the time the bud dies. Frequently there is secondary growth from lateral buds.

Peas (Wallace, 1944). The plants may appear quite healthy or, with a severe deficiency, may show a somewhat chlorotic condition in the foliage. In the seeds a very characteristic condition of the seed occurs, known as marsh spot. When the seed coat is removed and the two cotyledons are separated, small brown specks or larger circular brown areas are seen on the flat surfaces. The areas may become hollowed out in very severe conditions.

More severely affected plants show a brownish discoloration of the young tendrils and the youngest internodes at the top of the stem (Samuel and Piper, 1929). The youngest leaves fail to expand, becoming yellowish with small discolored areas between the veins. Slightly older but not fully expanded leaves acquire a characteristic mottled appearance due to the mesophyll between the small veins becoming yellow, whereas the veins themselves remain green. The lower leaves retain their normal green color. The growing tips and the youngest leaves will be completely dead in a short time.

Potato (Wallace, 1944). The tip leaves lose their luster and turn pale. They tend to be small and rolled toward the upper surfaces. Small blackish brown spots may be developed on the leaves along the veins, and although these are more numerous on the pale leaves near the tips of the shoots, they may also be present on older leaves which are still green. In severe conditions the plants show much browning and yellowing, especially in the young foliage.

Tobacco (McMurtrey, 1944). The first visible symptom is a loss of color in the young leaves. Between the veins the tissue is light green to almost white while the veins themselves remain darker. The leaf has a checkered appearance, because of the contrast between the green veins and the tissues that have lost their color. In the latter tissues necrotic spots may develop which may drop out giving the leaf a ragged appearance. Usually this spotting is not confined to the tip and margins, as in the case of potassium deficiency, but involves parts scattered over the entire leaf. The plant as a whole may be considerably dwarfed.

Tomato (Skinner, 1944). The earliest symptom is a lightening of the green color, which gradually turns to yellow in the leaf areas farthest from the major veins. As the condition progresses the yellow becomes more marked and extensive. The veins remain green, which gives a char-

acteristic mottled appearance to the leaf. Eventually the foliage may become completely yellow, and in many cases necrosis sets in, appearing at first as small brown pinpoints centering in the yellow areas farthest from the veins and expanding until larger dead areas indicate complete breakdown of the tissue. Growth is spindling, little or no blossoming takes place, and no fruits form.

Sugar beet and mangold (Wallace, 1944). The leaves tend to be more upright than usual and somewhat triangulate in outline, due to curling of the margins toward the upper surfaces The interveinal tissue becomes chlorotic. Brownish spots may appear in the interveinal areas and the brown tissue may die and fall out leaving small holes.

In *Brassica* crops (Wallace, 1944), the symptoms first appear as an interveinal chlorotic marbling With severe deficiencies the whole of the leaves may be practically bleached, only the veins remaining green (kale) or some necrosis may develop in the mottled tissue, when it takes on a dull brownish gray appearance (savoy cabbage).

Other vegetable crops. The general foliage symptoms are a chlorosis between the veins, in many cases extending from the margin inward. The tissue along the veins and midrib remains green much longer.

Ornamental plants. Dickey and Reuther (1938) describe manganese deficiency symptoms in a great number of ornamental plants. In most cases the affected leaves show a yellow green chlorosis extending inward from the margins between the primary veins, the tissue immediately surrounding the midrib and primary veins remaining green.

Fruit plants (apples) (Wallace, 1944). The leaves develop an interveinal chlorosis which begins near the margins and extends toward the midrib, and finally only the veins remain green Strongly growing young shoots may be only little affected, which is a point of difference from iron deficiency, in which the chlorotic condition is always most severe in the young tip foliage. In pears, plums, peaches, and cherries the symptoms are similar to or only slightly different from those of apple (see Wallace, 1944). In citrus the leaf pattern is also that of a network of green veins on a lighter green background (Camp *et al.*, 1944).

VI. Manganese Content of Plants

1. *Normal Plants Growing under Natural Conditions*

The manganese content of plants grown under natural conditions varies enormously. This is mainly due to the fact that the availability of soil manganese varies in much the same way. Since the latter has been shown to be dependent to a large extent on soil pH and oxidation-

reduction potential (see Sec. III), it may be expected that plants growing on acid soils and on waterlogged soils are rich in manganese.

Olsen (1934) determined manganese in leaf blades of *Holcus lanatus, Oxalis acetosella, Asperula odorata,* and beech (*Fagus silvatica*) growing on Danish soils at a wide range of pH values. A close correlation was found between soil pH and manganese content of these plants. Above pH 7 values lower than 100 p.p.m. were found, whereas on the most acid soils the leaves contained more than 1600 p.p.m. in the dry matter. Plants growing on swampy soils contained high manganese values even at pH values higher than 7. The uptake of manganese by different plant species growing under the same conditions may differ widely. This appears from the extensive investigations of Erkama (1947), who analyzed a great number of naturally occurring plant species.

The analytical data of Mayer and Gorham (1951) show that the manganese content of naturally occurring plants varies with the individual species, the pH of the soil, and the water content of the soil. The correlation with pH, as observed by these authors was less pronounced than was the case in the investigation of Olsen (1934).

2. *Manganese Content of Healthy and Manganese-Deficient Plants*

There is little agreement in the literature as to the critical amount of manganese in plants below which deficiency symptoms may be found. Samuel and Piper (1929), Piper (1931), and Leeper (1935) found 14 to 15 p.p.m. in the whole plant at the flowering stage to be the lowest value in healthy cereals. Rye, ryegrass, and a tolerant barley variety were found to be healthy when containing only 10 to 11 p.p.m. manganese on the dry basis. Gerretsen (1937) succeeded in growing healthy oat plants in sterile culture media very low in available manganese. Values as low as from 5 to 10 p.p.m. Mn in such plants were found.

In manganese-deficient winter wheat (tops) analyzed in early spring Coïc and Coppenet (1949) found values of 20.3 and 22.5 p.p.m. and in healthy plants 34.5 and 48.5 p.p.m. Goodall (1949) determined manganese in various parts of wheat plants at different growing stages. He found no response to manganese treatment when the manganese content of the older leaf blades at the beginning of shooting was higher than 34 p.p.m.

Nicholas (1949) determined manganese in the leaves of a number of crop plants grown on a soil poor in available manganese. Oats with 7 p.p.m. Mn had the lowest value and showed pronounced deficiency symptoms; wheat and barley containing 14 and 12 p.p.m. of Mn respectively

were slightly deficient, whereas maize on the same soil containing 15 p.p.m. Mn in the dry leaves was healthy. From the other plants investigated, peas with 8 p.p.m. and sugar beet and mangold both with 10 p.p.m. showed moderate deficiency symptoms. In flax, radish, carrot, and lucerne with 15 p.p.m. or over, visual signs of the deficiency were absent. These values are much closer to those of the Australian workers than to those of Goodall and Coïc and Coppenet.

Hasler (1951) found the following concentrations of manganese in manganese-deficient grasses: *Arrhenatherum elatius,* 37 p.p.m.; *Festuca pratensis,* 44 p.p.m. A large variation in the manganese content of various grass species grown on the same soil has been recorded by Beeson *et al.* (1947). Under the conditions of their experiments *Agrostis alba* contained 815 p.p.m. Mn whereas *Poa pratensis* had values of 108 and 164 p.p.m. Seekles (1950) determined manganese contents of grass grown on different soils in the Netherlands. Grass from clay soils had the lowest manganese content viz. 114 p.p.m. in the dry matter that from peaty soils had 152 p.p.m. and that from sandy soils 191 p.p.m. These values are averages of a great number of analyses in samples originating from different parts of the country.

VII. Correcting Manganese Deficiency

Manganese deficiency can be corrected in a number of ways.

1. Application of Manganese Sulfate to the Soil

Amounts from 50 to 100 kg. per hectare are being recommended by various authors, although on alkaline peat soils larger amounts may be required for obtaining healthy plant growth. Since on many manganese-deficient soils the added manganese sulfate will be readily converted into practically unavailable oxides, the duration of the improvement is often very short. This was already noted by Hudig (1911), who had to apply manganese sulfate simultaneously with the sowing of oats in order to be sure that the plants did not suffer from gray speck disease.

2. Spraying the Foliage with a Dilute Solution of Manganese

This method is more economical since much smaller amounts can be employed. From 0.2 to 0.5 per cent manganese sulfate solutions are being used (from 500 to 1000 l. per hectare). Gallagher and Walsh (1943) employed 1 per cent manganese sulfate sprays in correcting manganese deficiency in oats. Harmer and Sherman (1943) added manganese sulfate to Bordeaux mixture at the rate of 1 kg. $MnSO_4$ per 500 l. Bordeaux mixture. Manganese deficiency in fruit trees was cor-

rected by Thompson (1944) by injecting a solid manganese salt into the trunk.

3. *Treating the Soil with Acidifying Substances*

The beneficial effects of treating the soil with acidifying substances such as sulfur or sulfate of ammonia are often due to the formation of pockets of relatively high acidity in which the manganese becomes much more soluble than in the bulk of the soil. That this statement is true may be concluded from the experiments of Hudig (1911) in which mixing of a peaty soil with sulfuric acid or acetic acid in amounts equivalent to those present in ammonium sulfate had no effect on the deficiency symptoms of oats, whereas a treatment with sulfate of ammonium gave practically healthy plants. Similar results have been obtained by Gerretsen in an unpublished experiment with sulfur of a different degree of fineness. The best results were obtained with coarse particles.

Treating the soil with acid peat may also give good results.

A method which has given perfect results is mixing the applied manganese sulfate with one of the above mentioned substances.

4. *Flooding*

The flooding of soils sometimes may give a much improved manganese supply to the plants due to the reduction of part of the manganic oxides to available manganese. Under certain circumstances, however, flooding may have the reverse effect This has been demonstrated in the Dutch and Belgian sea polders which were inundated during World War II. After the flooding manganese deficiency was more frequently observed than before.

VIII. Manganese Nutrition and Fertilizer Interactions

The effect of compounds which bring about considerable changes in pH (lime, sulfur) will not be considered here, since their effect has been discussed in detail in Sec. III,1.

1. *Nitrogen Applications*

The beneficial effect of ammonium sulfate as contrasted to the harmful influence of nitrate, particularly sodium nitrate, on the availability of soil manganese is well known. This effect is entirely indirect and results from the changes in pH which accompany the uptake of NH_4^+ and NO_3^- by the plants. Since the shift in pH is greater with sodium nitrate than with calcium nitrate, the former affects the availability of soil manganese more strongly.

It may be expected, however, that the nitrogen compounds will exert a direct effect on the uptake of manganese. Furthermore the change in pH of the nutrient medium may also affect the uptake of manganese ions.

Several authors have observed that nitrate nitrogen may favor the manganese uptake by plants. Olsen (1934) growing barley in nutrient solutions of pH 6–7 found 90 p.p.m. in the dry matter of the leaf when the plants had been supplied with nitrate and 23 p.p.m. when ammonium nitrogen had been employed. Coïc *et al.* (1950) studying manganese deficiency in cereals in Brittany obtained much more healthy plants when the crop was treated with calcium nitrate than in the absence of added nitrogen. The manganese content of the grain from manganese-deficient plants was 14 p.p.m. without nitrogen fertilization and 19.4 p.p.m. when treated with a moderate amount of calcium nitrate. When treated with manganese the values were 15.5 and 21.3 p.p.m. of manganese respectively.

Timonin (1950b) reports a beneficial effect of calcium nitrate in correcting manganese deficiency under field conditions.

The favorable effect of nitrates on manganese uptake by plants is also apparent from papers reporting on studies of manganese excess (Millikan, 1950; Löhnis, 1951).

Manganese uptake in relation to pH of the nutrient medium was studied by Olsen (1934) in culture solution experiments with barley, mustard (*Sinapis alba*), *Zea mays*, and *Lemna polyrrhiza*. An optimal uptake was found to take place at pH 6 and 7. Similar results were obtained by Burström and Boratynski (1936) in nutrient solution experiments with wheat. From pH 3.5 to 6.5 a clear increase in manganese uptake was observed.

The increased uptake of Mn^{++} (or other cations) at decreasing hydrogen-ion concentration of the nutrient medium may be explained by an enhanced affinity of Mn^{++} for the root surface as a result of the increased Ca/H ratio on the root surface exchange complex (complementary ion effect). If under similar conditions of decreased hydrogen-ion concentration a base-adsorbing solid substrate, e.g., clay, is present, two systems are operating with opposite effects on the availability of Mn^{++}. The release of Mn^{++} from the surface of the solid exchange material will be diminished, whereas the affinity of Mn^{++} for the root surface is enhanced. Epstein and Stout (1951) studying the uptake of manganese from bentonite-containing suspensions observed an increased absorption of manganese with increasing Ca/H ratio on the bentonite. Apparently the increased affinity of Mn^{++} toward the root surface at increased Ca/H ratio outweighed the diminished exchangeability of manganese on

the bentonite. Under soil conditions the complementary ion effects will be obscured by changes in the concentration of available manganese.

2. *Effect of Phosphate Fertilization*

A beneficial effect of superphosphate on uptake of applied manganese was observed by Steckel *et al.* (1948) when both fertilizers were mixed together. The beneficial effect is stated to be due to the precipitation of the manganese as the manganous phosphate, which would retard the oxidation of the manganese and would provide a constant though small supply of divalent manganese. The somewhat increased acidity caused by the superphosphate surrounding the manganese would also be of some importance in preventing rapid oxidation of the added manganese.

On the sandy soils of central Florida which are almost exclusively composed of siliceous sand, application of large amounts of phosphate at pH values from 5.5 to 6.0 may give rise to the accumulation of calcium phosphate, presumably "hydroxy apatite" which retains applied manganese and magnesium so that they are not so readily leached by high rainfall as is the case from these soils without the presence of accumulated phosphate. Both manganese and magnesium thus adsorbed are available to citrus (Wander, 1950)

Albrecht *et al.* (1941) in studying the effect of calcium carbonate and phosphate applications to a well-weathered prairie soil of pH 5.5 found that calcium carbonate when mixed throughout all the soil lowered the manganese content of sweet clover, lespedeza, *Poa pratensis*, and notably *Agrostis alba*, as might be expected. Mixing the carbonate into the surface one-fourth of the soil and leaving three-fourths untreated gave a considerably higher manganese content of the crop as compared with the untreated plants. Phosphate dressings were found to exert a beneficial effect on manganese uptake of the plants.

3. *Effect of Copper on Manganese Nutrition*

Hudig *et al.* (1926) have stated that copper treatment of neutral soils on which the crop suffered from copper deficiency would correct the copper deficiency but would promote the occurrence of manganese deficiency.

Mulder (1938) studying the phenomena related to copper nutrition of plants and copper treatment of soils has carried out a few experiments, the results of which tend to confirm the above statement of Hudig *et al.* (1926). The microbiological oxidation of manganous salts to MnO_2 by fungi was found to be clearly stimulated by the addition of a trace of copper to the nutrient medium of the microorganisms. The copper-manganese relationship in green plants was studied in nutrient

solution experiments with cereals. In one experiment with rye an increased demand for manganese was observed with increased copper supply. In a similar experiment with barley such a copper-manganese interaction did not occur. In the presence of an excessive amount of manganese, however, the barley roots of copper-supplied plants showed an intensive browning presumably due to MnO_2, particularly in the upper parts, which was absent when the plants suffered from copper deficiency. Although the plants were not growing under sterile conditions, the browning occurred so uniformly that it was improbable that microorganisms were involved. The results of these experiments show that copper may activate the biological oxidation of manganous compounds by fungi and probably by root cells from barley plants.

Kenten and Mann (1949) were able to extract from horseradish roots an enzyme system which may oxidize manganese in the presence of hydrogen peroxide to Mn^{+++} or Mn^{++++}. The system consists of peroxidase and peroxide substrate (Kenten and Mann, 1950). Although it is unknown whether the system may accumulate MnO_2 *in vivo*, it is probable that at a high concentration of Mn^{++} this may be the case. It is unknown whether this system may be less active in copper-deficient plant roots.

The effect of copper sulfate on the oxidation of manganese in acid soils treated with calcium carbonate was studied by Sherman *et al.* (1942). In contrast to the biological oxidation reported above, a retarding effect of copper on manganese oxidation was demonstrated, as a result of which oat plants were suffering much less from manganese deficiency than in the absence of applied copper sulfate. Both soils used by Sherman *et al.* (1942) were clay soils which presumably were not deficient in copper. The results of Ødelien (1948), working on copper-deficient soils are in agreement with those of Hudig *et al.* (1926).

4. Iron-Manganese Relationships

According to Shive (1941), Somers and Shive (1942), Somers, Gilbert, and Shive (1942), and Stiles (1946), the ratio of iron to manganese in the nutrient medium of soybean plants and presumably also of other plant species should lie between 1.5 and 2.5 to assure optimal plant growth. If the ratio is above 2.5, symptoms of iron toxicity (= manganese deficiency) would occur; if it is below 1.5, the plant would suffer from manganese toxicity (= iron deficiency). Since the values for active (soluble) manganese and iron within the plant tissues associated with good growth covered about the same range of values as did those in the external medium, the observed phenomena were thought

to be due to the existence of a close interrelationship between iron and manganese within the living cell.

In a large number of papers either published earlier than those of Shive and collaborators, or later, the existence in plants of a more or less pronounced iron-manganese interdependency has been reported (see the review by Twyman, 1946). According to most authors, however, the range of iron-manganese ratios of the nutrient medium at which normal plant growth is possible is much wider than that mentioned by Shive *et al.* In contrast to the statement of these authors that more importance should be attached to the ratio of manganese to iron than to their absolute concentrations in the nutrient medium, Hewitt (1948c) found that the growth of oats and sugar beet was affected by absolute levels of these elements rather than by their ratios. Similar results were obtained by Morris and Pierre (1947) in nutrient solution experiments with lespedeza. Increase of the concentrations of both iron and manganese caused pronounced symptoms of manganese toxicity notwithstanding that the ratio of iron to manganese in the nutrient solution was unchanged. Ouellette (1951) found both the concentration of iron and manganese in the culture solution and their ratio of importance in attaining optimal growth of soybeans. Although iron chlorosis due to manganese excess is reported by many authors, there is sufficient evidence available in the literature to state that manganese excess is not identical with iron deficiency and that iron excess is not identical with manganese deficiency (see Sec. IX).

Some authors have presented clear evidence that an increased iron supply to the plants may depress the uptake of manganese (Somers and Shive, 1942, for soybeans; Morris and Pierre, 1947, for lespedeza; Burström, 1939, for wheat). An increased manganese supply may also depress the uptake of iron, but the effect is less clear than the reverse (Somers and Shive, 1942). Friederichsen (1944) studied the effect of increasing manganese concentration of the nutrient solution on the iron content of roots and leaves of spinach and barley plants. With nitrate as the nitrogen source high concentrations of manganese did not affect the iron content of the leaves. The roots, however, were much lower in iron. When the plants were supplied with ammonium nitrogen, manganese depressed not only the iron content of the roots but also that of the leaves.

IX. Manganese Toxicity in Plants

It has been shown, mainly during the last decade, that excess of manganese in the nutrient medium may cause toxicity symptoms. Since the concentrations of manganese at which the toxicity symptoms become

visible are relatively low, many acid soils may be found on which the manganese supply to the plants is high enough to bring about some crop injury. From the results of several investigations which will be discussed below, it has appeared that manganese toxicity is one of the main causes of soil acidity injury to plants. Aluminum toxicity and lack of available calcium, magnesium, or molybdenum may also affect plant growth on certain acid soils.

Before excess of available manganese was recognized as the cause of injury to plants growing on certain acid soils (Jacobson and Swanback, 1932; Bortner, 1935; Wallace *et al.*, 1945; Hewitt, 1945; Hale and Heintze, 1946; Löhnis, 1946, 1951), manganese toxicity of plants had been studied by soil scientists working on manganiferous soils, i.e., soils rich in manganese. Such soils have been described as early as 1909 by Kelley (see Sherman *et al.*, 1949; Jacobson and Swanback, 1932) in the drier regions of the Hawaiian Islands. Manganese contents ranging from 1 to 4 per cent may be found in such soils. Kelley (1909) indicated the relationship between the poor growth of pineapple in these regions and the high manganese content of the soils. Extensive pot experiments with similar soils have been carried out in Puerto Rico by Hopkins *et al.* (1944).

That manganese toxicity may be the cause of injurious effects observed on acid soils was shown by Jacobson and Swanback (1932) working with tobacco on Connecticut soils, and Bortner (1935) studying abnormally growing tobacco in Kentucky. Extensive investigations have been carried out by workers of the Long Ashton Research Station in England (Wallace *et al.*, 1945; Hewitt, 1945, 1946, 1947, 1948a). They compared the visual symptoms of acidity injury of different plant species growing in the field with those of sand cultures at different levels of certain added micronutrient elements. A striking resemblance was found to exist between field symptoms of acidity and excess of manganese in the sand cultures, particularly at low calcium levels. This was found to be true of several agricultural and horticultural crops (including runner bean (*Phaseolus vulgaris*), cauliflower, savoy cabbage, swede, and kale). In potato, calcium deficiency was also frequently seen as an acidity symptom. Oats, barley, celery, carrot, beet, and particularly sugar beet and mangold appeared to be much more sensitive to excess of aluminum than to excess of manganese so that acidity injury to these crops may resemble aluminum toxicity. Hale and Heintze (1946), studying cases of field acidity from various parts of England came to conclusions similar to those of Wallace *et al.* (1945).

The poor growth of legumes on many acid prairie soils in the United States appeared to be due to high amounts of soluble manganese in these

soils (Morris and Pierre, 1947, 1949; Morris, 1948). On certain acid soils of northern Wisconsin potatoes may suffer from "stem streak necrosis," a disease which Berger and Gerloff (1947a,b) showed to be due to excess of available manganese. Schmehl *et al.* (1950) growing alfalfa in an acid soil from New York observed symptoms of manganese toxicity According to these authors the poor growth of their plants was only partly due to manganese excess. Aluminum toxicity apparently was of more importance. Similarly Heslep (1951) found phosphorus deficiency, manganese toxicity and presumably a third factor as the causes of poor growth of lettuce in two acid Californian soils.

Although magnesium deficiency is often found to be the cause of acidity damage of cereals and potato on sandy and peaty soils in the Netherlands (Smit and Mulder, 1942), manganese toxicity may also occur (Löhnis, 1946, 1950, 1951). In 1940 the disease was observed for the first time in *Phaseolus vulgaris* growing on a sandy soil which had been fertilized with ammonium sulfate for a number of years as a result of which the pH had dropped to a very low value. Its cause remained unknown until 1943 when visual symptoms identical with those noted in the field were induced by the addition of excess manganese to plants growing in nutrient solutions or in neutralized soil. To obtain more evidence as to the cause of the disease, young full grown leaves of *Phaseolus vulgaris* from both injured and normal plants, grown on the same soil treated with lime, were analyzed for manganese. The values found in a large number of samples from injured plants, collected during three successive years, ranged from 1104 to 4216 p.p.m. Mn in young foliage and from 40 to 904 p.p.m. in healthy plants of the same age. Although in different years apparently owing to different climatic conditions widely varying concentrations of manganese were found, the threshold values above which the foliage was always visibly affected was almost constant in the successive years, that is approximately 1200 p.p.m. on a dry weight basis. This value depends on a number of various factors, and it may be expected that changing the circumstances under which the plants are growing also will change the amount of manganese at which toxicity symptoms become visible. Temperature was found by Löhnis to have an important effect. Bean plants containing manganese in such amounts that severe symptoms of injury might be expected at moderately high temperature remained healthy at a high temperature. Millikan (1951) in nutrient solution cultures of peas found a remarkable difference in tolerance between older and younger leaves of the same plant. Manganese concentrations much higher than those which

were found in the affected younger leaves did not cause injury to the lower leaves.

Of further plant species tested by Löhnis (1951), vetch and lucerne appeared to be very susceptible to excess of manganese. The minimum amount of manganese in affected plants (field experiments) was for vetch 500 p.p.m. in 1948 and 1117 p p.m. in 1949 and for lucerne 477 p.p.m. in 1948 and 1083 p.p.m. in 1949. White and red clover and flax were found to be slightly susceptible. Mangold was depressed in growth in acid soils but appeared to be insensitive in nutrient solutions. This agrees with the results of Hewitt (1948a) that the injury by acidity in sugar beet and mangold is often due to aluminum toxicity. Potatoes, tobacco, mustard, oats, and strawberry appeared insensitive in field tests. In contrast to the results of Löhnis potatoes have been found to suffer from manganese toxicity on certain northern Wisconsin soils [stem streak necrosis, Berger and Gerloff (1947a,b)], while tobacco growing on certain acid soils in Kentucky was found to show typical manganese toxicity symptoms (Bortner, 1935). Whether these different results in potatoes and tobacco have to be attributed to the different environmental conditions under which the plants were growing or to varietal differences is unknown.

Morris and Pierre (1949) working with nutrient solutions found lespedeza and sweet clover to be much more sensitive to manganese toxicity than peanuts. Cowpeas and soybeans held intermediate positions. Since the peanuts contained much lower amounts of manganese than the other plant species supplied with the same amount of manganese, the tolerance of this plant apparently is due to a limited absorption of manganese. Lespedeza absorbed large amounts of manganese, whereas the sensitiveness of sweet clover apparently was due to its inability to endure relatively low amounts of manganese.

In accordance with these results Löhnis concluded from the manganese contents of the various plants tested for manganese toxicity that a tolerance for a high level of available manganese in the soil may be due (1) to a weak absorption of manganese (oats, mustard, mangold) and (2) to a strong tolerance within the plants (tobacco, flax, strawberry, potato, and presumably broad bean). Striking examples were found to be oats, which contained only 325 p.p.m. of Mn when growing in an acid soil, and tobacco, which contained nearly 3000 p.p.m. Both plant species showed no visual symptoms of manganese toxicity. Jacobson and Swanback (1932) recorded values of 5250, 6470, and 11670 p.p.m. of manganese in affected tobacco grown on acid soils.

1. *Manganese Toxicity in Relation to the Supply of Some Nutrient Elements*

a. Effect of Nitrogen Compounds. The effect of nitrogen nutrition on manganese toxicity was studied in detail by Millikan (1950) in nutrient solution experiments with flax. With nitrate and urea as the nitrogen sources severe symptoms of manganese injury were noted which were absent in the case of ammonium nitrate and ammonium sulfate and in plants subjected to nitrogen deficiency. Toxicity symptoms were affected by these treatments in the following range of increasing severity nitrate>urea>NH_4NO_3>$(NH_4)_2SO_4$>nitrogen deficiency. Although the manganese content of the plants was much higher in the case of nitrate nutrition than when supplied with ammonium compounds, it was presumably not the only cause of the large difference in toxicity symptoms. The beneficial effect of the presence of ammonium ions in the nutrient solutions on the appearance of manganese toxicity symptoms was also observed by Löhnis (1951). The foliage of beans treated with nitrate alone contained five times as much manganese as in the presence of ammonium nitrate.

b. Effect of Phosphorus. A beneficial effect of phosphate fertilization of acid soils on tobacco plants suffering from manganese toxicity was found by Bortner (1935). In nutrient solutions with high manganese, phosphate gave a similar effect. These results were not confirmed by Morris and Pierre (1947), who found a greater depression of growth of lespedeza owing to excessive manganese in culture solutions with a higher phosphate concentration. Walsh *et al.* (1950) observed a favorable effect of applications of superphosphate and basic slag in preventing manganese toxicity of swedes.

c. Effect of Calcium. There is no agreement in the literature as to the effect of calcium ions on manganese injury. Hewitt (1945) considers calcium as an element that clearly antagonizes the intake of manganese under sand culture conditions. With increasing calcium supply (as the sulfate) the symptoms of manganese toxicity became less severe.

Morris and Pierre (1947) in culture solution experiments with lespedeza were unable to show an alleviation of manganese toxicity by the addition of calcium. If acid soils were treated with calcium sulfate, the symptoms of manganese deficiency in lespedeza and sweet clover were found to be aggravated (Morris, 1948). This was shown to be due to a lowering of the pH as a result of which the content of water-soluble manganese in the soil increased. Water-soluble rather than exchangeable manganese of the soil was found to be a reliable indicator of manga-

nese toxicity. A similar unfavorable effect of calcium sulfate application on soil pH and manganese toxicity was found by Berger and Gerloff (1947a) with potato and by Schmehl *et al.* (1950) in pot experiments with alfalfa.

The well-known beneficial effect of liming (increase of pH) on manganese toxicity is due to the conversion of soluble manganese to unsoluble manganese oxides (see Sec. III). The uptake of Mn^{++} by the plants is favored, however, as was shown by Olsen (1934) in nutrient solution experiments with barley, *Zea mays,* mustard, and *Lemna polyrrhiza.* Optimal absorption was found to occur at pH 6 to 7.

d. Manganese Excess in Relation to Iron Deficiency. If the statement of Somers and Shive (1942) that normal plant growth depends on a certain iron-manganese ratio within the plant would appear to be true, it may be expected that manganese toxicity is identical with iron deficiency. Several authors have discussed this problem; some of them agree to a certain degree with Somers and Shive, others do not give support to their views.

Evidence that excess of manganese may produce symptoms of iron deficiency comes from those authors who have studied manganese excess in pineapple on manganiferous soils in Hawaii and Puerto Rico. On these soils growth of pineapple is very poor apparently owing to a large absorption of manganese. The plants become very chlorotic, and they respond clearly to sprays of ferrous salt solutions. (Johnson, 1917; Hopkins *et al.,* 1944; Sideris and Young, 1949). When Phaseolus beans were planted in such soils, they showed severe chlorosis within ten days, and no further growth of the plants took place (Hopkins *et al.,* 1944). Applications of iron as humate or liming the soil to pH 6.2, which precipitated a great deal of the soluble manganese, gave normal plant growth. In addition to these experiments with soil, Hopkins and collaborators carried out extensive investigations with beans, tomato, and pineapple, growing in culture solutions in order to elucidate the iron-manganese relationship. They presented substantial evidence that under the conditions of their experiments the injurious effect of excessive manganese might be counteracted by iron. This was found to be true not only of the chlorosis but also of necrotic spotting which occurred on the leaves.

Similar results were obtained by Millikan (1947, 1949), who studied the effect of a number of heavy metals, including manganese, on the growth of flax in nutrient solutions. Although his main interest lay with the antagonizing effect of molybdenum on manganese toxicity, Millikan carried out treatments with iron salts to show that the chlorosis and top

necrosis of his flax plants were due to iron deficiency. Other symptoms of excessive manganese, such as the dwarfed growth and the lower leaf necrosis were not prevented by iron. Warington (1951) confirmed Millikan's results with flax in foliage painting tests with dilute ferrous sulfate solutions.

The results of Hopkins *et al.* (1944), Millikan (1947, 1949), and Warington (1951) indicate that at least part of the symptoms of manganese toxicity may be considered as manganese-induced iron deficiency.

Morris and Pierre (1947) were unable to confirm these results with lespedeza. Symptoms of iron deficiency were found to differ widely from those of manganese toxicity. Nevertheless they observed a considerable alleviation of manganese toxicity by addition of iron. This was found to be due to an approximate 50 per cent reduction in the manganese content rather than to an increase of total iron in the plant. In a further set of experiments (Morris and Pierre, 1949) it was shown that the symptoms of manganese toxicity in soybeans, cowpeas, and peanuts were entirely different from those of iron deficiency.

Manganese toxicity of potato (stem streak necrosis) was found by Berger and Gerloff (1947a), to be entirely different from iron deficiency, and it was unaffected by treating the plants with dilute ferrous sulfate solutions.

Although Hewitt (1948b) in a single case reports the occurrence of iron deficiency (in sugar beet) upon treatment with several heavy elements, including manganese, he was unable to obtain any response to ferric citrate when painted on the leaves of Phaseolus showing manganese toxicity symptoms (1945). Similarly, Löhnis (1951) in her extensive studies on manganese toxicity did not observe a beneficial effect of ferrous sulfate treatments of manganese-injured plants. Symptoms of iron deficiency in beans when grown in an iron-deficient nutrient solution appeared to be entirely different from those of manganese toxicity. In a single experiment, however, in which the manganese injured bean plants grew at a high temperature, a clear response to iron treatment was found. The appearance of the plants was whiter than usual. Since Hopkins *et al.* (1944), who obtained a very clear response of manganese injured Phaseolus to ferrous sulfate, were working under tropical conditions, it may be possible that the temperature factor can explain the controversy between various workers as to the relation between iron deficiency and manganese toxicity.

e. Manganese Toxicity in Relation to Molybdenum Supply. In a large number of nutrient solution experiments Millikan (1947, 1949, 1950, 1951) has investigated the effect of molybdenum on toxicity symp-

toms caused by excess of some heavy metals, including manganese. In flax plants a marked reduction in the severity of the injury was observed. Ammonium molybdate appeared to be more effective than sodium molybdate (Millikan, 1947, 1949).

In a further set of experiments Millikan (1951) studied the effect of sodium and ammonium molybdates on manganese uptake from high and low manganese solutions by flax, peas, cabbage, and tomato and its distribution in the plant tissues, using a tracer technique. A marked accumulation of manganese in the tops of the leaves of flax at both manganese levels was observed. This concentration corresponds with the lower leaf necrosis which commences at or near the tip of the leaf. The presence of excess of molybdenum appeared to have a marked effect not only on the total manganese content, which was much reduced, but also upon its distribution in the leaves. The manganese content of the leaf ends was relatively much more depressed than that of the base of the leaves. In peas, cauliflower, and tomato similar relationships were found to exist between manganese content, manganese distribution in the leaves, occurrence of toxicity symptoms, and addition of molybdates.

From the results of his experiments and from the similarity of visual symptoms of manganese excess and molybdenum deficiency, Millikan concludes that a narrow relation exists between both phenomena. It should be stressed, however, that comparatively large amounts of molybdenum are required to affect manganese toxicity in Millikan's experiments, whereas in molybdenum studies extremely small amounts of this micronutrient element have been found to give normal plant growth. In contrast to Millikan's results with flax, Hewitt (1948c) found that molybdenum may accentuate chlorosis caused by excess of manganese in sand cultures of sugar beet. Löhnis (1951) was unable to show any effect of molybdenum on manganese toxicity of flax growing in nutrient solutions. Warington (1951) showed that molybdenum in amounts similar to those employed by Millikan may intensify the chlorosis induced by manganese excess in flax and soybean. These results are in agreement with those of Hewitt with sugar beet. In contrast to molybdenum, vanadium was found to be able to alleviate the symptoms of manganese toxicity.

To test Millikan's hypothesis as to the relation between manganese toxicity and molybdenum deficiency the senior author carried out the following experiment (unpublished). Manganese determinations were carried out in white clover grown in acid soils in a number of which the plants responded clearly to small amounts of added molybdenum. If a relation between manganese toxicity and molybdenum deficiency exists, it would be expected that plants which responded to added molybdenum

would have higher manganese contents than those which did not so respond. This appeared not to be the case.

*2. Symptoms of Manganese Toxicity in Some Crop Plants.**

Beans (*Phaseolus vulgaris*) (Löhnis, 1951; Hewitt, 1945). The first symptoms in younger leaves appear as marginal and later smooth interveinal chlorosis between major veins. When older, the leaves become somewhat crinkled and are spotted with small yellowish and later whitish areas. Finally minute brown necrotic spots appear. Petioles of the seed leaves and of the first trifoliate leaves are speckled with small superficial purple brownish spots. Severely injured plants remain stunted and produce hardly any flower or seed. Less injured plants may recover later in the season, when only traces of the initial injury still occur in the older leaves.

Peas (Millikan, 1951). First symptoms, necrosis along the edges of the third or fourth leaflets in the form of small grayish spots in the interveinal tissues. These marginal spots soon coalesce, and the necrotic edge may inroll. The tendrils of the affected leaves show a necrosis at the tips. The upper leaves of the plant may show symptoms like iron deficiency chlorosis followed by necrosis.

Vetch (Löhnis, 1951). The young leaves are chlorotic and a very marked dark purplish discoloration occurs along the margins of the full grown leaves. Sometimes small orange-red sunken spots may be found in the leaf margins, and the upper surface of the leaves may be speckled with minute dark spots. The plants remain small and spindly.

Soybeans and cowpeas (Morris and Pierre, 1941). In soybeans pale green irregular areas occur between the main veins of the leaves. Most of the affected areas become brown. In cowpeas small reddish purple spots are distributed uniformly over the leaf area. In both plant species growth is markedly decreased.

Alfalfa (Hewitt, 1948a). Growth is reduced and there is marginal paling of midstem leaves, followed by pale brown or buff spotting near margins; younger leaves are distorted at tips, with wavy margins or twisting of lamina. Later a yellow-green or gray-green paling at leaf tips occurs; margins become brown or bronzed and irregularly speckled.

Red clover (Hewitt, 1946). Marginal chlorosis of leaves. When older, leaflets show marginal crinkling and forward curling, slightly cupped; paling becomes yellow-green, spreading interveinally; light brown necrotic spotting appears between veins around inner border of pale marginal regions.

* This list covers only the most important agricultural and horticultural crops of which a rather clear-cut description has been found in the literature.

Sweet clover (Morris and Pierre, 1949). The distal leaf margin shows marked chlorosis, usually accompanied by a definite crimping of the leaf; no spotting.

Lespedeza (Morris and Pierre, 1949). Dark reddish brown leaf spots, very distinct on the underside of the leaves, cover in more severe cases as much as 50 per cent of the leaf area. Leaf margins are chlorotic. Considerable shedding may occur.

Potato (Berger and Gerloff, 1947b). First symptoms are the appearance of dark brown streaks on the lower stem at the base of the petioles. A pale yellow chlorosis develops in areas between the veins on the lower leaves although the veins themselves remain green. Quite often small brown necrotic areas, irregular in shape, appear between the veins near the midrib on the leaflets. As the necrosis becomes more severe, many long, narrow brown streaks are found on the lower portions of the stem and even on the petioles. The necrotic streaks also affect the inner tissues of the stem. The affected parts become very brittle, the petioles break off with a slight touch, and the chlorotic leaves finally dry and fall from the plant. The streaking of the stem and subsequent leaf dropping progress upward on the plant until the terminal bud becomes necrotic and the plant dies prematurely.

Cauliflower (Hewitt, 1946). There is marked forward cupping of margins of middle and older leaves. A marginal paling occurs, spreading interveinally between major veins, followed by dark brown spotting in pale areas. There is also severe marginal and interveinal crinkling and distortion.

Savoy cabbage (Hewitt, 1946). Growth is stunted. Expanding leaves show a marked paling in a narrow marginal zone ("rim effect"), becoming cream or dull white. Occasionally a slight mottling spreads inward interveinally for a short distance. Slight forward cupping of first affected older leaves may occur, but is absent in later leaves. Older leaves later develop indigo or black tinting along margins and in veins in marginal zone, and there is interveinal dark brown necrotic spotting.

Flax. Although this plant may tolerate relatively large amounts of manganese without any harmful effect, severe damage is affected by excessive amounts. The growth of the plants is stunted, and a severe apical chlorosis occurs. A brown necrosis may develop at the middle of one or both edges of the second lowest pair of leaves. This necrosis soon involves the whole of the distal half of the leaf. Other lower leaves will also become damaged, the necrosis mostly commencing at the tips of the leaves and extending downward, so that soon the top half of the leaf will be involved. The lower halves of the leaves will remain normal green in color. Sometimes numerous dark brown necrotic spots may be

found on the lower leaves. On the stems sometimes numerous small brown spots may be found, which may coalesce to form larger areas.

Carrot (Hewitt, 1948a). Growth is slightly reduced; chlorosis of leaf margins is followed by bronze necrotic speckling along leaf margins and scorching.

Lettuce (Hewitt, 1948a). Growth is reduced. Foliage is pale and dull yellow around leaf margins.

Peach (Thornberry, 1950). Excessive manganese causes "internal bark necrosis," i.e., occurrence of necrotic lesions localized internally without any observable change on the surface. These lesions may converge into necrotic areas which tend to advance until the trunk or bark is girdled. At later stages of the disease there is surface darkening and subsequent splitting of the outer bark along with the production of gum.

X. Function of Manganese in Plants

Manganese plays an important role as a cofactor in various enzymatic reactions. Many of these reactions have been studied *in vitro* with more or less purified enzymes obtained from normal organisms, plants as well as animals. Control experiments employing tissues or enzymatic preparations derived from organisms deficient in manganese are missing in most of these investigations.

In several enzyme studies concentrations of manganese far higher than those required in nutrition experiments with plants or microorganisms have been employed. Another fact which deserves more attention is the specificity of the metals. In many enzymatic reactions *in vitro* manganese may be replaced my magnesium, cobalt, nickel, or still other metallic ions. Although it may be possible that in the living organisms this replacement also occurs, little is known of it so far. The fact that manganese deficiency of green plants occurs mainly on neutral or alkaline soils in which the magnesium supply is ample and magnesium deficiency on acid soils in which available manganese is present in large amounts is not in favor of the replaceability of both metals in their major functions in higher plants. Whether a tendency in that direction occurs in any "natural" enzymatic reaction may only be decided by experiments in which different combinations of manganese, magnesium, cobalt, etc., have been supplied. The tissues of such plants will have to be used for enzymatic studies.

The only experiments of this type of which the authors are aware are those of Nilsson *et al.* (1942), who studied the replacement of magnesium by manganese in a number of enzymatic reactions and in some growth studies with three species of bacteria, namely, *Azotobacter chroo-*

coccum, *Bacterium radiobacter*, and *Bacterium prodigiosum*. Although the results obtained demonstrate that under the conditions of these experiments manganese may be substituted for magnesium in Azotobacter and presumably also in *B. radiobacter* and *B. prodigiosum*, the time during which the rate of growth of these bacteria was ascertained was so abnormal, that is, two and five months respectively, that the conclusions have only limited value A further objection to these experiments is that no cultures with both manganese and magnesium added were included, so that it cannot be concluded to what extent the growth in the solution with either magnesium or manganese may be considered as normal.

Although it is not the purpose of the authors to give a detailed review of all the enzymatic reactions described in the literature in which manganese may function as a cofactor, some of the reactions which are of fundamental importance in higher and lower plants will be reported here. In addition an attempt will be made to connect the results of these enzymatic studies with those of plant physiological and bacteriological investigations

It has been shown that manganese catalyzes not only various reactions of carbohydrate breakdown and organic acid metabolism but also a number of important conversions involved in nitrogen metabolism and phosphorus metabolism

1. *Manganese in Relation to Carbohydrate Breakdown*

a. Glycolysis. The breakdown of carbohydrates to tricarbonic acids (glycolysis) by the cells of higher plants, microorganisms, and animal cells occurs in a number of graded steps, each of which is catalyzed by different enzymes. Some of these reactions are activated by manganese, magnesium, or cobalt ions, namely, phosphoglucomutase, which catalyzes the interconversion of glucose-1-phosphate and glucose-6-phosphate, and enolase, which catalyzes the formation of phosphoenolpyruvate from D-2-phosphoglycerate. Mg^{++}, Mn^{++}, or Zn^{++} are active as a cofactor in this case (see the review of Lardy, 1949). In fermentation experiments with purified apozymase from *Saccharomyces cerevisiae*, Nilsson *et al.* (1942) observed practically no breakdown of glucose to ethanol and carbon dioxide in the absence of either manganese or magnesium. Both metals gave about the same activation Optimal activity was obtained with 0.01 *M* $MnCl_2$.

b. Organic Acid Metabolism. It is a well-known fact that organic acids play an important role in cell respiration as well as in the reverse process, carbon dioxide assimilation. The former process, the breakdown of the end products of glycolysis to carbon dioxide and water, proceeds

through a number of enzymatic reactions involving different organic acids known as the Krebs cycle (Green, 1949; Bonner, 1950). Although these reactions have been studied in detail mainly in animal tissues and tissue extracts and in microorganisms, there is both direct and indirect evidence available that similar reactions occur in higher plants.

One of the important enzymes of the tricarboxylic acid cycle of Krebs, isocitric dehydrogenase, which catalyzes the transformation of isocitric acid to α-ketoglutaric acid, requires either Mn^{++} or Mg^{++} (von Euler *et al.*, 1939; Adler *et al.*, 1939; Ochoa, 1948). This conversion proceeds in two steps:

$$\text{D Isocitric acid} + TPN_{ox} \xrightleftharpoons[\text{oxalosuccinic carboxylase}]{\text{isocitric dehydrogenase}} \text{Oxalosuccinic acid} + TPN_{red} \quad (1)$$

$$\text{Oxalosuccinic acid} \xrightleftharpoons[+Mn^{++}]{} \alpha\text{-Ketoglutaric acid} + CO_2 \quad (2)$$

Reaction (1) depends on the presence of triphosphopyridine nucleotide (TPN). According to Ochoa, Mn^{++} is required for reaction (2) and not for (1). Since both reactions (1) and (2) are reversible, this system perhaps can play an important part in the biological fixation of carbon dioxide as a first step in photosynthesis.

The experiments of Ochoa have been carried out with extracts from animal tissues. Von Euler *et al.* (1939) have found the isocitric dehydrogenase system in animals, yeasts, and higher plants. In the absence of Mg^{++} or Mn^{++} the reaction does not proceed. The activity of Mg^{++} was found to be less than that of Mn^{++}. The optimal concentration of Mn^{++} is 5.10^{-4} *M*, and that of Mg^{++} is $2.5.10^{-3}$ *M* (extract of animal tissues). Berger and Avery (1944) investigated the isocitric dehydrogenase of the Avena coleoptile. It was shown to be activated by Mn, Mg, and Co ions and to a lower extent by Zn and Ni. In accordance with von Euler *et al.* (1939) a Mn concentration of 5.10^{-4} *M* was found to be optimal.

A further example of a carboxylase depending for its activity on manganese is the oxalacetic carboxylase studied in detail by Vennesland *et al.* (1949). This enzyme, which splits oxalacetic acid in pyruvate and carbon dioxide has been found in parsley root. Its activation by various cations has been studied by Speck (1949). In the absence of metal ions oxalacetic carboxylase from parsley roots was found to be nearly inactive. The optimal effect was obtained with Mn^{++} at a concentration of 0.01 *M*. Ca^{++}, Co^{++}, Cd^{++}, and Zn^{++} showed also a notable effect while Pb^{++}, Ni^{++}, Fe^{++}, Mg^{++}, Cu^{++}, and Ba^{++} acted only slightly.

The preparation of oxalacetic carboxylase from a number of different

plants (wheat germ, carrot, beet, spinach, parsley, parsnip, peas) invariably showed the capacity of catalyzing the reversible reaction:

$$\text{L-Malate} + \text{TPN}_{ox} \rightleftharpoons \text{Pyruvate} + \text{CO}_2 + \text{TPN}_{red} \qquad (3)$$

an activity referred to as "malic enzyme." This reaction, which may be of great importance in the fixation of carbon dioxide, is catalyzed by Mn^{++} as well as Co^{++} (Conn, Vennesland, and Kraemer, 1949).

A manganese-activated "malic enzyme" system in animal tissues has been described by Ochoa *et al.* (1948; see also Salles *et al.*, 1950).

The malic enzyme system has recently been studied in connection with carbon dioxide assimilation of green plants (Vishniac and Ochoa, 1951; Tolmach, 1951; Arnon, 1951). It was shown that illuminated isolated chloroplasts may greatly enhance the carbon dioxide fixation in the malic enzyme reaction (3). This effect apparently is due to the photochemical reduction of TPN by the illuminated chloroplasts as a result of which reaction (3) is shifted to the left. It is questionable, however, whether this reaction represents a true model of photosynthesis since the photochemical reduction of TPN or DPN may also be coupled with other reactions which require the presence of the reduced pyridine nucleotides.

In addition to the enzymatic reactions described above many more dealing with organic acid metabolism which are activated by manganese may be found in the biochemical literature.

2. *Manganese in Relation to Nitrogen Metabolism*

The activity of manganese as a cofactor in enzymatic reactions is not limited to the carbohydrate and organic acid metabolism, but is of similar importance in the nitrogen metabolism of plants and animals. Many of the simple peptidases of plants, microorganisms, and animals do not operate in the absence of metallic ions. These may be manganese ions but also cobalt, ferrous, or magnesium ions. L-Leucine-aminoexopeptidase, a peptidase which splits L-leucylglycine and other L-leucine containing di- and tripeptides is activated by manganese and magnesium, (Smith and Bergmann, 1944; Smith, 1951). Apparently high concentrations of these cations are required to give full operation of the reaction. It was observed that the effect of manganese on the activity of peptidase was considerably greater when enzyme and cations were incubated together for some time before the substrate was added. This indicates that the metal reacts with the enzyme protein in forming the active enzyme.

The peptidase which hydrolyzes glycylglycine is specifically activated by cobalt and to a much smaller degree by manganese (Maschmann,

1941; Smith, 1951). In this case, however, no time lag in the activation of glycylglycine dipeptidase by cobalt has been observed. It was found that cobalt formed a complex with the dipeptide. From these and a number of similar observations it was suggested (Smith, 1951) that the role of the metal ion in the enzyme system could be explained by assuming an interaction of this ion with the substrate on one hand and with the protein on the other.

Very interesting is the observation by Bamann and Schimke (1941a, b) that the "L-peptidase" activity of animal and plant tissues may be increased by both Mn and Mg ions whereas the "D-peptidase" reaction is activated by Mn^{++} but not by Mg^{++}. In their experiments the authors tested seedlings of lentil, peas, oats, wheat, barley, and rye; leucylglycine was used as the substrate in the enzyme reactions. (For a review of the literature on metal activated peptidases see Smith, 1951 and also Hewitt, 1951).

Further manganese-activated enzymes which play a part in the nitrogen metabolism of plants are arginase and glutamyl transphorase. Arginase splits the amino acid arginine into ornithine and urea. It may be activated by Mn^{++}, Co^{++}, Ni^{++}, or Fe^{++} (Hellerman and Perkins, 1935; Stock, Perkins, and Hellerman, 1938; Anderson, 1945; Folley and Greenbaum, 1948; Greenberg, 1951).

Glutamyl transphorase plays a part in the amide metabolism of plants. It has been found to catalyze the reaction:

$$\text{Glutamine} + \text{Hydroxylamine} \longrightarrow \text{Glutamohydroxamic acid} + \text{Ammonia}$$

ATP (adenosinetriphosphate) or ADP (adenosinediphosphate), phosphate or arsenate, and manganese (not replaceable by magnesium, zinc, copper, ferrous iron, aluminum, or cobalt) are essential components of the complete system. The enzyme has been isolated from seedlings of *Cucurbita pepo* (Stumpf *et al.*, 1951). It has been found present in a wide variety of algae and plants, particularly in nodules of clover and lupine. The same enzyme system has been found to catalyze the exchange of isotopic ammonia with the amide group of glutamine (Delwiche *et al.*, 1951).

The question may be raised whether the observed effect of manganese on the above-mentioned enzymatic reactions may explain the results of those investigations in which the relation between manganese nutrition and nitrogen metabolism has been studied *in vivo*. In experiments with excised roots of wheat plants and with macerated roots, Burström (1939, 1940) has shown that the rate of nitrate assimilation may be increased considerably by addition of small amounts of manganese to the nutrient solution. Since manganese has an activating effect on the

so-called basal respiration of wheat roots (Lundegårdh, 1939), the beneficial effect of added manganese on both nitrate assimilation and basal respiration of roots may be a result of a manganese-activated enzymatic reaction of the glycolysis or tricarboxylic acid system.

Nance (1948), in experiments with wheat roots, failed to demonstrate a stimulating effect of manganese on nitrate reduction. This may have been due to a higher manganese content of the seed than was the case in the experiments of Burström (1939). Jones *et al.* (1949) in culture solution experiments with soybeans observed an accumulation of nitrite in the nutrient solution when no manganese was added. The plants developed yellow leaves, ascribed by the authors to nitrogen deficiency. Supplied with small amounts of manganese, no nitrite accumulated, and the plants were green and healthy. These results would indicate that manganese activates the reduction of nitrate to nitrite. The presence of nitrite in culture solutions of plants deficient in manganese has also been observed by Eversmann and Aberson (1927) and Gerretsen (1937). The latter author, however, ascribes its presence to the fact that the roots and especially the root tips of manganese-deficient plants are easily attacked by microorganisms which in the presence of decaying organic material easily reduce nitrate to nitrite.

From the fact that spinach plants, growing in nutrient solutions with either ammonium or nitrate nitrogen, showed no substantial difference in manganese deficiency, Friederichsen (1944) concluded that manganese plays no part in nitrate reduction of this plant. Alberts-Dietert (1941) studied the effect of manganese on growth of *Chlorella* in culture solutions with different nitrogen compounds. In the absence of added manganese, nitrate and ammonium nitrogen gave the same effect when *Chlorella* was grown under autotrophic conditions. In the presence of glucose, however, nitrate was found to be inferior to ammonium salts, apparently owing to a poor nitrate reduction. Supplied with manganese this difference was not observed. These results would indicate that under autotrophic conditions the effect of manganese deficiency on nitrate reduction was overshadowed by its effect on carbon dioxide assimilation.

High concentrations of nitrate in manganese-deficient plants have been recorded by Leeper (1941) and Hewitt *et al.* (1949). Although these results in accordance with those of Burström (1939) may indicate a possible function of manganese in nitrate reduction, it may also be explained by assuming a reduced carbohydrate content in manganese-deficient plants as a result of a poor carbon dioxide assimilation (see Gerretsen, 1949).

Hewitt *et al.* (1949) in the case of manganese-deficient cauliflower

found an accumulation of nitrate as well as of amino acids, particularly aspartic and glutamic acids, in young leaves. These results are hard to reconcile with the postulated role of manganese in nitrate reduction. They may indicate, however, that the function of Mn may be sought in catalyzing some reaction in the chain between amino acids and protein, e.g., the above-mentioned peptidase activity or the glutamyl transphorase The accumulation of nitrate possibly might result from the accumulation of amino acids. The results of Hewitt *et al.* (1949) are in agreement with earlier investigations by Friederichsen (1944) who showed that manganese-deficient spinach leaves had a considerably higher ammonia and amino acid content than leaves from normal plants; nitrate was also higher in manganese-deficient leaves, but the difference was much less pronounced than in the roots. The protein content was slightly lower in manganese-deficient plants Gerretsen (1936, 1937) found also a higher ammonia content in manganese-deficient leaves of oats than in normal plants.

The effect of manganese in comparison with that of iron and molybdenum on the assimilation of nitrate in excised wheat roots has been studied recently by Burström (1949) in inhibition experiments with di-n-amylacetic acid This substance in concentrations as low as 10^{-6} *M* was found to be able to inhibit nitrate assimiliation almost completely. Addition of manganese or iron in amounts of 5 p.p.m. restored the nitrate assimilation, whereas molybdenum had no effect. From these experiments it may be concluded that manganese activates a reaction in wheat roots essential for the nitrate assimilation which may be blocked by di-n-amylacetic acid These results need not to be in conflict with the view of the senior author that molybdenum has to be considered as an essential element in the reduction of nitrate by *Aspergillus niger*, denitrifying bacteria, and green plants (Mulder, 1948). Molybdenum which exerts its activity in concentrations a thousand times smaller than those employed for manganese has undoubtedly been present in adequate amounts in the roots employed by Burström. At least two views exist: (a) both manganese and molybdenum are essential for nitrate assimilation in roots of wheat; (b) the mechanism of nitrate assimilation of roots is different from that of leaves of higher plants and that of microorganisms. The latter concept apparently holds for *Aspergillus niger*, which according to unpublished experiments by the senior author does not require Mn for nitrate reduction.

The view that at least two different mechanisms of nitrate assimilation exist in green plants is in accordance with the results of recently published investigations by Mendel and Visser (1951). These authors demonstrated that the nitrate reduction which occurs in tomato leaves

in the dark is dependent upon respiration for a source of energy, while in the light the reduction may well be independent of respiratory processes with the necessary energy supplied by light. This was concluded from the fact that iodoacetate, a well-known inhibitor of cell respiration, almost completely inhibited nitrate reduction in the dark, whereas it was completely without effect in the light.

3. Manganese Nutrition and Ascorbic Acid Content of Plants and Animals

The question whether manganese may affect the formation of ascorbic acid in plants and animals cannot be answered definitely. In a number of investigations pronounced differences in ascorbic acid content between manganese-deficient and normal plants have been found. Several other workers, however, were not able to confirm these results.

The first observation of a beneficial effect of manganese on the ascorbic acid content of plants was made by Rudra (1939a) He investigated the effect of dilute solutions of manganese sulfate and manganese chloride on germinating seeds of *Cicer arietinum*, *Phaseolus mungo*, wheat, barley, and oats. After six days germination considerably higher values for ascorbic acid were found in the manganese-treated seedlings of Cicer and the cereals than in those germinated in water. The optimal concentration of manganese was found to be 0.001 per cent in the case of Cicer and 0.01 per cent with the cereals. In a further paper the same author (1939b) claims that the inability of guinea pigs to synthesize ascorbic acid may be attributed to insufficient manganese in the tissues of these animals. Simultaneous injection of mannose and manganese was found to increase the ascorbic acid content of some tissues, particularly liver and jejunum. Without manganese, mannose would not affect the ascorbic acid content (see also Rudra, 1944). These experiments have been repeated by Skiñner and McHargue (1946) with scorbutic as well as normal guinea pigs. No effect of injections of mannose and manganese on the scorbutic condition of the animals nor on the amount of indophenol-reducing substances of their livers was observed by these authors.

In another paper Rudra (1943) described on slender evidence the occurrence of a manganese-activated hexose dehydrogenase in the small intestines of animals, which would be able to produce ascorbic acid from aldohexoses.

In experiments with tomatoes growing on manganese-deficient soils Hester (1941) observed an increased content of ascorbic acid in the fruits from plants treated with manganese. These results have not been confirmed by Lyon *et al.* (1943), who in carefully controlled nutrient

solution experiments found manganese-deficient tomatoes as rich in ascorbic acid as fruits from control plants. A similar negative effect was obtained by Gum *et al.* (1945). The ascorbic acid contents of neither the foliage nor the fruit of tomatoes, growing in nutrient solutions, showed any consistent differences with manganese treatment. In contrast to these results, von Bronsart (1950) in Germany obtained consistently higher values for ascorbic acid (sum of reduced and oxidized forms) in tomatoes from manganese-treated plants than in the fruits from untreated control plants.

A positive effect of manganese additions or sulfur treatments of manganese-deficient soil on growth and ascorbic acid content of spinach, Sudan grass, and oats has been reported by Harmer and Sherman (1943). In Sudan grass and oats the reduced form of ascorbic acid was affected mainly, whereas in spinach the oxidized form was increased to a very large extent by an improved manganese supply. Rangnekar (1945) found a notably higher concentration of ascorbic acid in the leaves of manganese-treated *Amaranthus gangeticus* than in the leaves of control plants.

Maton (1947), working in Hoagland's laboratory, found a remarkable effect of the manganese supply to some plants growing in culture solutions on the ascorbic acid content of their leaves. In sunflower 42 μg. ascorbic acid per gram fresh weight of leaves was found in the absence of manganese against 74 μg. in leaves of plants supplied with 0.125 p.p.m. of Mn. In tobacco the differences were even more pronounced: 20 μg. per gram fresh weight of Mn-deficient leaves against 145 μg. in leaves of manganese-supplied plants. Tomatoes on the other hand did not show any difference in ascorbic acid content of the leaves at different manganese levels notwithstanding the occurrence of great differences in total yield.

No correlation was found by Hivon *et al.* (1951a) between manganese nutrition of soybeans grown in the field and ascorbic acid content of the leaves. In an extensive nutrient solution experiment with green pod beans the same authors (1951b) determined ascorbic acid (reduced form) in the leaves of manganese-deficient and normal plants at 27, 34, 41, 48, 55, 62, and 69 days from planting. At 30 days the plants with restricted manganese showed definite chlorosis which became increasingly severe at later sampling date. No effect of manganese supply on ascorbic acid content occurred.

The discussion of the above-mentioned papers clearly demonstrates the great lack of uniformity in the results obtained by the various authors. Although several workers have reported definitely negative results, the number of papers in which a positive effect has been shown

is too large to deny the effect which, under certain circumstances, manganese may have on the ascorbic acid content of green plants. Since weather conditions, notably illumination, have been shown to be of great importance in controlling ascorbic acid content of plants, it may be possible that they play an important part in affecting the manganese-ascorbic acid relationship. This point is also stressed by Hamner (1945) in a discussion of minor element-vitamin relationships in plants. The fact that some authors are working under field conditions and others under greenhouse conditions, either with nutrient solution cultures or with soils, may also be considered as a point which deserves more attention.

The relationship between manganese and the content of some other vitamins or vitaminlike substances has been studied in a few cases only. Gum *et al.* (1945) found lower concentrations of carotene in manganese-deficient tomato leaves than in those from normal plants. The fruits of these plants showed no differences For riboflavin slightly lower values were found in the leaves and fruits from manganese-deficient tomato These results are in accordance with those of Burger and Hauge (1951), who analyzed manganese-deficient and normal soybean plants for carotene, choline, and tocopherol (vitamin E). Plants from manganese-deficient soil which exhibited symptoms of chlorosis and necrosis were found to be notably lower in carotene and tocopherol, but higher in choline. A similar beneficial effect of manganese treatment on carotene content of the leaves was found in wheat and oats.

1. The Role of Manganese in Photosynthesis

The evidence is increasing that manganese is an essential constituent of the photosynthetic apparatus in green plants. In this connection it is interesting to note that as early as 1924 Hiltner in his extensive investigations on gray speck disease of oats relates two remarkable experiments, which hitherto received little attention. (1) Increasing carbon dioxide assimilation of oat plants by enriching the surrounding atmosphere with carbon dioxide was found to prevent the outbreak of the gray speck disease on a manganese-deficient soil; reducing the carbon dioxide content of the air aggravated the symptoms (see Table II). (2) Reducing the carbon dioxide assimilation by shading the plants also intensified the Mn-deficiency symptoms, whereas the effect of manganese additions was much more pronounced on the shaded plants than on the plants grown in normal daylight. Both experiments point to an intimate connection between carbon dioxide assimilation and manganese activity in the plant.

A quarter of a century later Gerretsen (1949) showed that CO_2

TABLE II
(After Hiltner, 1924)

Treatment	Number of Grains	Total Dry Weight, g.	Symptoms
0 Mn, no CO_2 added *	0	3.12	Pronounced Mn-deficiency symptoms
+ Mn, no CO_2 added *	23	5.73	No symptoms after the appearance of the fourth leaf
0 Mn, CO_2 added	168	10.97	No symptoms at all
+ Mn, CO_2 added	138	9.53	No symptoms at all

* Reduced CO_2—content of the air.

assimilation of leaves from oat plants, grown on manganese-deficient soil or in culture solutions poor in manganese, is reduced to 25–40 per cent of the normal rate. As special care had been taken not to use leaves which were chlorotic or which showed any pronounced outward signs of manganese deficiency, it is unlikely that in this case chlorosis had been the cause of a reduction of the photosynthetic activity by 60–75 per cent.

To investigate the role manganese eventually plays in photosynthesis, Gerretsen (1950a, 1951) used cell-free watery suspensions of crushed oat leaves in which he determined the redox potential in the dark and during illumination.

It was shown that the change of the E_h upon illumination was much more pronounced with normal leaf material than was the case with manganese-deficient leaves. The addition of small amounts of manganese as $MnSO_4$ in the latter case restored the E_h changes to normal values. Addition of manganese to normal leaf extracts in the dark had no effect, but upon illumination the potential rose with 100 to 150 mv. to values which make the formation of peroxides and in particular hydrogen peroxide highly probable.

Addition of trivalent iron had the opposite effect—the equilibrium $Fe^{+++} \rightleftarrows Fe^{++}$ was shifted to the right by illumination and to the left in the dark. Gerretsen concluded that in the plant a photosensitive oxidation-reduction system exists in which manganese and iron act as complementary oxidation-reduction agents. They keep each other in equilibrium at a fixed potential during illumination and at another potential in the dark. As the potential of such a combination is determined in the first place by the ratio of the components and much less by the absolute quantities, it is evident that an excess of one element over the other is likely to disturb the oxidation-reduction equilibrium

in the plant. As early as 1930 Hopkins suggested that manganese tends to control the ratio $Fe^{+++} \rightleftarrows Fe^{++}$ in the cell, and in a more recent paper he and his co-workers are led to believe that the interaction of manganese, iron, and light controls to a large extent the oxidation-reduction potential of green plants (Hopkins *et al.*, 1944). Thatcher (1934) grouping the elements according to their function in the plants placed Mn and Fe amongst the oxidation-reduction regulators and called them "mutually coordinating catalysts for oxidation-reduction reactions."

In this connection the observation of Shive (1941), Somers, Gilbert, and Shive (1942), and Somers and Shive (1942) that the dry weight of their soybean plants was related to the iron-manganese ratio and not so much to the absolute concentrations of the elements seems to fit very well into this scheme.

Although several workers repeating the experiments of Shive and his collaborators were unable to confirm their results as to the narrow ratio of iron to manganese required for optimal growth, most of them observed an antagonizing effect of manganese on iron (see Sec. VIII).

The scope of this review does not permit us to go into details of the complicated photochemical reactions which constitute photosynthesis. It will suffice to say that by virtue of his experiments Gerretsen (1950a) assumes that in the dark manganese and iron exist respectively in the divalent and trivalent forms. Owing to illumination, under absorption of light energy, the situation becomes reversed and now Mn^{+++} and Fe^{++} cooperate in the photolysis of water, which is regarded as the first step in photosynthesis. The ultimate effect is that Mn^{+++} accepts one electron from OH^-, ($H_2O \rightleftarrows OH^- + H^+$) which becomes a $\overline{OH}$ radical. The manganese ion is reduced to Mn^{++}, whereas the $\overline{OH}$ radical finally gives rise to the evolution of oxygen ($2\overline{OH} \rightleftarrows \frac{1}{2}O_2 + H_2O$). At the same time, by light induced electron transfer, Fe^{++} cedes an electron to H^+, which becomes a highly reactive $\overline{H}$ atom, the iron being oxidized to Fe^{+++}. The $\overline{H}$ atom immediately combines with an intermediate acceptor to a more stable $\overline{HX}$ reduction product, which will be used in the formation of carbohydrates. Manganese and iron are now back in their original valency states, and the process can start anew.

It should be stressed that other workers demonstrated the importance of manganese in the fixation of carbon dioxide in certain light-induced reactions. Apparently the reduced carbon dioxide assimilation as observed by Gerretsen in manganese-deficient oat leaves may be due to reduced primary photochemical reactions or to reduced activity of enzymes of the tricarboxylic acid cycle or to both.

The fact that manganese deficiency, iron deficiency, and manganese

toxicity are all accompanied by chlorosis does not imply that the cause of this chlorosis is the same in all these cases. In the latter two cases the junior author is inclined to ascribe the chlorosis to photooxidation of chlorophyll, which is a secondary effect of the rapid destruction of the protective protein substances surrounding the chloroplasts, in consequence of the high redox potentials which are characteristic for the illuminated Mn-Fe redox systems in the plant, when Mn is in excess (Gerretsen, 1950b).

This view is supported by the fact that injury due to manganese excess is greater in more intense light, which has been observed by different workers, McCool (1913, 1935), Hopkins *et al.* (1944), Morris and Pierre (1949), whereas Gericke (1925) reports that wheat plants growing in solutions deficient in iron showed excellent growth and normal green color in the shade and little growth and chlorosis in bright sunlight.

Accepting reduced carbon dioxide assimilation as one of the main consequences of manganese deficiency enables us to interpret a number of divergent characteristic symptoms from a central point of view.

1. The reduced content of sugar and starch in the leaves of oat plants (McHargue, 1926) and of tomatoes (Eltinge, 1941) deficient in manganese is a direct result of reduced photosynthesis.

2. The same holds true for the retardation of growth, the smallness and slackness of the leaves, the weakness of the leaf ribs which causes the leaves to drop over with a kink.

3. Reduced frost resistance (Gerretsen, 1949; Lloyd Frisbie, 1947) is closely related to the turgescence of the cells and the latter to the content of sugars in the cell sap.

4. The presence of large quantities of nitrates in the leaves of manganese-deficient oat plants and canary grass as observed by Leeper (1941) fits well into the scheme, as it is obvious that accumulation of inorganic nitrogen must take place in leaves, in which insufficient carbohydrates are synthesized to combine with the nitrogen to build up proteins.

5. The entrance of toxic substances into the cells of manganese-deficient oat leaves (Gerretsen, 1937) with subsequent loss of turgescence and poisoning of the protoplasts is closely linked with increased permeability of the cell walls and the reduced size of the protoplasts due to lack of assimilates.

6. The reduced volume of the root system (Gerretsen, 1937; Hasler, 1951) and the susceptibility to invading saprophytic microorganisms can also be traced back to shortage of carbohydrates, the multiplication of the cells in the meristematic zone being much slower, as well as the

rejuvenation of the root cap tissue, which determines its protective function.

7. By increasing the carbon dioxide content of the surrounding air gray speck disease symptoms may be reduced or even disappear (Hiltner, 1924); in this case the increase of carbon dioxide assimilation neutralizes the decrease due to manganese deficiency.

8. Manganese-deficiency symptoms are aggravated by shading the plants; in this case reduced photosynthesis is further reduced by diminishing light intensity, which inevitably leads to a change for the worse.

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Atomic Energy and the Plant Sciences *

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I. Introduction

The Atomic Energy Commission supports research in the plant sciences along three broad lines: (1) The effects of radiation on plant growth, both physical effects and biochemical effects, are of primary concern to the Commission. (2) Of equal importance are the uptake of fission products and other radioactive material, their movement and distribution in the soil, their uptake by plants and utilization by animals. (3) The AEC is also responsible for applying atomic energy products and techniques to fundamental research with plants.

In the implementation of this program the AEC carries on a considerable amount of work in the plant sciences at its national laboratories, particularly on plant genetics, radiation effects, uptake of fission products, and biosynthesis. This paper discusses only the unclassified part of the AEC program in the plant sciences. In addition, the AEC has forty-one cost-sharing contracts for plant science research at twenty-nine universities, colleges, and research institutions. Apart from such direct support, the AEC produces isotopes at incentive prices and sponsors courses in the use of isotopes in research.

In this review of AEC-supported research in plant sciences there is

* A major portion of the *AEC Semiannual Report to Congress* dated January, 1952, is a less technical and more detailed discussion of this same subject. The report is available from the Superintendent of Documents, U.S. Government Printing Office, Washington 25, D. C.

not always a distinction made between work in a national laboratory and that supported in universities and colleges. Although much of the work in the AEC national laboratories is fundamental in nature, it is directed specifically toward the determination of effects of radiation from the piles, accelators, and fission products upon plant and animal life. Research projects at institutions that receive AEC assistance are carried out under cost-sharing agreements with the institutions. Several factors are considered in granting allotments from AEC's available research funds: (1) the relation of the proposed work to AEC's statutory purpose; (2) how the work will supplement the research at the AEC national laboratories; and (3) projects which give promise of developing new techniques in the use of isotopes.

The atomic energy program, involving plants and soils, includes studies of the effects of both internal radiation (absorbed radioisotopes and fission products) and external radiation upon the development, growth, yield, and biochemical changes in plants. In addition, fundamental, cytological, and plant genetic studies are applicable to plant science and the possibility of plant breeding. The first part of this report is primarily concerned with the more programmatic aspects while the latter part will describe more general and fundamental work supported by the AEC, most of the latter being done at universities and colleges.

To make clear how a great diversity of projects fit into an overall scheme two tables listing the various AEC research projects in the plant sciences have been prepared. All the work which is largely supported by the AEC is listed in Table I. University research agreements dealing more with the use of isotopes in plant sciences are outlined in Tables II and III. To get a complete picture of the research in some areas it will be necessary to look at two tables at once. For instance the Soil, Fertilizer, and Mineral Nutrition research at AEC laboratories and major projects is listed in Table I while in Table II are listed other projects in this same field which are partially supported at universities and colleges. Many of the projects listed in the tables are not mentioned in this short review, but the tables by themselves should furnish an overall picture of AEC support in plant sciences at this time. Other plant science projects in the United States also get indirect aid from the AEC by being able to purchase radioisotopes at a nominal cost, but none of this work is mentioned here. Portions of the review have been taken from the AEC national laboratories quarterly progress reports, and some of this work has not been completed and published.

II. Effects of Radiation on Plants

The effect of radiation on biological material depends upon (1) type of radiation—internal, external, gamma, alpha, beta, or neutrons, (2) rate of exposure, and (3) variable species resistance. In general, it takes several thousand roentgens (r) of external radiation to cause visible plant damage but only several hundred roentgens to injure animals. It is a universal observation that the higher forms of life are more sensitive to radiation damage than the lower forms. However, plants are affected by low levels of radiation such as that from P^{32} because of the facts that P^{32} accumulates in the growing tips and that the dividing cells there are the most sensitive to radiation.

External radiations may be administered in a variety of ways. Using the same source, the dose may be given slowly or rapidly, continuously or intermittently. Using different sources one may vary the character of the radiation (different energies, charges, or masses) or compare the effect of different radiations given simultaneously with that of each radiation type used alone. Increase in effectiveness with increased specific ionization is usually seen in studies of higher forms—seed plants, mammals, and insects. Such a complex system might be expected to consist of many similiar units (cells), many of which must be destroyed before a whole effect can be seen.

1. External Radiation and Plant Development

The principal work in this field has been done at Brookhaven National Laboratory by A. H. Sparrow and W. R. Singleton. For three years various plants, especially corn and potatoes, have been grown in concentric circles around a 16-curie source (in 1951, 200 curies) of Co^{60} placed in the center of a three-acre field (Fig. 1). The gamma rays from this source are similar to x rays except that the gamma radiations are harder and more penetrating. The source is raised and lowered through a steel pipe into a lead "pig" in the ground by means of a remote control mechanism 70 meters away. The source was in the "up" position all the time, except when necessary to enter the field for cultivation, note-taking, hand pollination, etc.

The intensity of radiation is varied by the distance of the various rows from the source. Since the intensity of radiation is inversely proportional to the square of the distance from the source, extreme differences in radiation are obtained. For example, plants at 1 meter from the 16-curie source received 500 r per day while those at 10 meters received only 5 r per day. At 60 meters only 0.084 r per day was received.

Most plants can tolerate a very high level of external radiation con-

tinuously without visible damage as compared to the higher forms of animal life. Although plants vary in radiation sensitivity, all plants are affected by sufficiently high exposure. It is important to note that no stimulation has been observed at any radiation intensity. At high radiation intensities hypertrophic growth in certain structures was frequently noted in some species; in others tumor-like growth, as well as somatic



FIG. 1. Genetic stocks of corn growing in the 200 curie Co^{60} radiation field. Signs mark distance in meters from the radiation source in the center of the field. Plants in 3M row killed by radiation of approximately 700 r/day. Plants in 4M row very abnormal (approximately 400 r/day). Plants in 5M circle (250 r/day) almost normal in appearance but produced few seeds and small amount of pollen. Many mutations induced in pollen from this row. Photo taken August 21, 1951.

mutations, were observed. Tomato plants that received 20,000 r at a rate of 150 r per hour decreased in chlorophyll content and were retarded in development. Removed from the radiation, they resumed normal growth. Spiderwort was allowed to grow in a field varying from 5 r to 128 r per day. Growth was normal at 10 r per day, but at higher exposures growth declined but was accompanied by physical abnormalities until at 128 r per day there was no growth. Corn produced apparently normal growth at 125 r per day, and the growth was almost normal at 250 r per day, but at this level very few seeds were produced on each ear. At 390 r per day the plants were severely stunted.

Growth and flower development of lily plants were inhibited if exposed to more than 60 r per day, but no structural abnormalities were obvious. In the broad bean, growth and fruiting seemed normal under exposures of 5 r per day; at 22 r per day the plants flowered but bore no fruit, and at 34 r per day the seeds germinated, but growth and flowering were inhibited.

Dosages which cause extensive morphological changes also produce a considerable number of chromosomal aberrations. Since recovery to a normal growth pattern occurred in many plants which had previously shown severe radiation damage, it would seem that most of the morphological aberrations were not of a genetic nature.

Potatoes have been used to study the effects of acute doses of x rays and fast neutrons and of continuous chronic gamma irradiation from cobalt-60 upon germination and growth of plants (Sparrow and Christensen, 1950). For the potato tuber various dosages of radiation to the tuber before planting resulted in a decrease in the yield. Continuous gamma radiation at equivalent levels had no adverse effect on growth. Tubers were cut into seed pieces and given x ray doses before planting from 75 r to 38,400 r. The date of emergence and consequently height of young plants were adversely affected by 300 r or higher (Fig. 2). Yield was significantly reduced by 1200 r, and 4800 r was near the lethal dose. At 1200 r and above the leaves in young plants seemed to be unusually thick and glossy with an uneven or slightly wrinkled appearance.

One as-yet-unexplained phenomenon was revealed when, during the harvest, seed potatoes that failed to sprout were dug up. Those tubers, heavily exposed to radiation, had not rotted as would ordinarily have occurred but were still fairly firm.

Recovery of the tubers from x ray irradiation occurred when F_1 tubers were planted the second year. Yield data indicated no apparent relationship to the original dosage. These plants included both high- and low-yielding lines that are being studied further. Thus, one may speculate that the radiation effect on the first year's yield and growth may be due in large part to physiological effects, and the effect observed on the F_2 crop could be attributed to long-lasting or permanent genetic change.

In comparison with the acute x ray irradiation of the potato seed, the field cobalt-60 source was used for chronic gamma irradiation studies over the whole growing season by planting potatoes at varying distances from the cobalt source. Dosage rates were 0.26, 1.15, 4.8, 19.5, and 79.7 r per day to give accumulated season totals of approximately 28, 123, 516, 2086, and 8529 r. No consistent relationship between dosage and yield was observed. Plants near the center of the field averaged as

high yields of potatoes as those planted at greater distances from the source of radiation. There was no visible difference in size or apparent vigor of the plants. The biological destructiveness of continuous gamma irradiation would thus appear to be much lower (not greater than 14



FIG. 2. Thirteen pieces of potato tuber were irradiated by x ray at each dosage of 0, 75, 150, 300, 600, 1200, 4800, 9600, 19,200, and 38,400 r and planted in rows as shown; 4800 r is a near lethal dose.

per cent) than acute irradiation of the potato tuber. No evidence of stimulation was obtained.

These observations in the cobalt field indicate that potatoes are relatively resistant to ionizing radiation. Two possibilities suggest themselves. One is the fact that cultivated potatoes are polypoid ($4n$-48) and hence should be more resistant than diploid plants. The other is the small size of their chromosomes which may make them less radiosensitive. Work with plants with large chromosomes, such as *Trillium, Tradescantia,* and *Lilium,* show that these are much more sensitive to radiation than plants with small chromosomes, such as tomatoes, sunflower, most grasses, corn, marigolds, snapdragon, and various weeds (Sparrow, 1950).

That chronic radiation is much less damaging physiologically than the same amount of radiation delivered in a short exposure is well established with animals. Several explanations are possible, but they all stem from the basic fact that density of ionization does not reach a very high level in the chronic exposure. Thus, the plant has a much better chance to recover from the damage than if given a single heavy exposure. This is true not only of physiological effects but for "2-hit" chromosome aberrations as well. It would not be expected to hold for mutations however.

A third type of irradiation damage is that from neutrons. Potato tubers have been exposed to neutrons from a pile with dosages similar to the x ray treatments described earlier. A tentative estimate is that fast neutron acute irradiation of plants is probably at least four times more effective than acute x irradiation. The more severe effect of fast neutrons supports the hypothesis of the importance of ionization density, since fast neutron irradiation produces very dense ionization tracks. The passage of a single track through or very near a chromosome would therefore be expected to cause a serious, if not a lethal effect.

2. Internal Radiation Effects

Although heavy radiation is damaging to plant life, there have been claims that radioactive fertilizers would increase crop yields, but these have not been confirmed (Alexander, 1951). Even the lowest levels of internal and external radiation appear to cause adverse changes in the plant, histologically and biochemically. Fortunately, at the levels normally used in radioactive isotope tracer experiments *in vivo*, such low levels of radiation result that the physiological effect is essentially nil. However, it has been necessary to determine under what conditions the damage produced from isotopes is serious enough to affect the validity of the conclusions.

Probably the most extensive use of tagged elements in plant science research has been with phosphorus-32. In the case of P^{32} it is concentrated in the meristematic regions such as the growing root and stem tip where its radiation effect is thus concentrated and where the newly forming cells are more sensitive both biochemically and genetically. In animals the accumulation of P^{32}, Ca^{45}, and fission products in the bone and their effect on the hematopoietic system is an analogous situation. In plant sciences the effects of internal radiation have not been studied extensively and there has been no utilization of this tool in plant biochemical studies. For instance, the production of plant tumorous growth by radiation is unexplored. The exact mechanism which operates in the damage of living tissue by radiation is not completely understood.

It is known that cell division is affected and that irradiation injury may be accompanied by chromosome breakage.

Gross determination of internal radiation damage has been carried out under a joint USDA-AEC project. Plants (barley and alfalfa) are grown in nutrient solutions containing various amounts of the radioisotope, i.e., P^{32}. The length and dry weight of the tops and roots are used as the criteria of injury caused by radioactive material (Fig. 3).

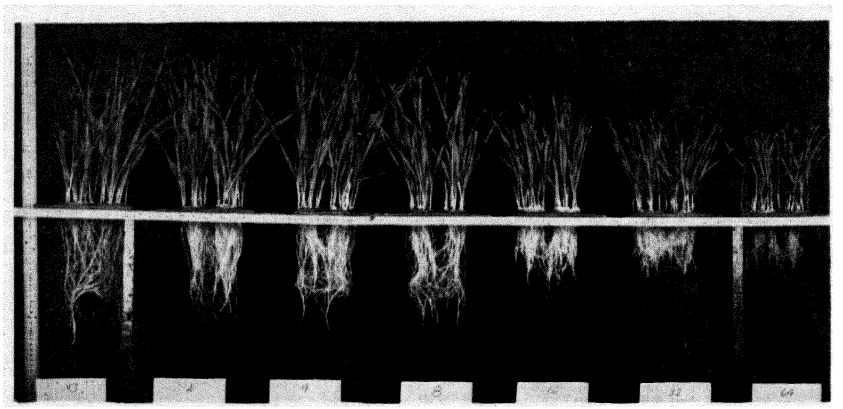


FIG. 3. Barley grown in nutrient solution 2×10^{-5} molar in phosphate and containing left to right: 0, 2, 4, 8, 16, 32, and 64 microcuries P^{32} per liter.

Damage to the tops is more severe than damage to the roots, and the injury is primarily due to radiation from the P^{32} accumulated within the plant. Injury is associated with a high specific activity of the isotope in the nutrient solution, i.e., ratio P^{32}/P^{31}. This condition allows a higher specific activity of the isotope to accumulate in the plant, or in reverse one might say the plant can be partially protected from a radioactive isotope by abundance of the inactive form. Blume, Hagen, and Mackie (1950), using barley growing in nutrient solution, found that the lowest level at which any damage was produced was at 5.6 millicuries P^{32} per gram of P_2O_5. When plants were grown in soils with surface application of P^{32} from 0 to 12.5 millicuries P^{32} per gram of P^{31}, the damage was too small to be statistically significant (Blume, 1952). These and similar results indicate that concentrations of isotopes much higher than those usually used in plant nutrition studies are necessary to get visible damage to plant growth.

Histological changes induced in barley plants by radiation from P^{32} can be detected at much lower levels than amounts causing a decrease in plant growth (Mackie, Blume, and Hagen, 1952). The size of the outer-

most cells of the terminal meristem of barley growing in P^{32} nutrient solutions were measured and related to the specific activity of the P^{32}. The cells of barley growing in nutrient solution containing as little as 2 microcuries P^{32} and 2 x 10^{-5} mole P^{31} per liter were larger in the epidermal layer of the stem apices compared to the nonirradiated controls. Measurement of these apex cells of the growing points of the stem gave no indication of the existence of a threshold value which divides damaging from nondamaging doses of radiation It does not follow that this injury would be reflected in a permanent symptom of abnormality, and at the lowest radiation levels apparent injury to the root tip was not followed by damage to the apical meristem. At levels of radiation where there was apparent injury to the root tip, histological examination showed that cell division ceased, the cells of the growing points enlarged, the cytoplasm became less dense, and the cell walls thickened.

3. Genetic Effects and Plant Breeding

Radiation has served as a useful adjunct in the study of genetics, not only because it has afforded more mutations for study, but also because the frequency of an otherwise extremely rare event can be increased to the point where the processes or mechanisms of the mutational change can be conveniently studied under various conditions. In addition, the analysis of genetic and cytogenetic effects of radiation has given valuable data from which general theories on the mechanism of radiation effect have been postulated.

The frequency of spontaneous mutation varies considerably, but is generally of the order 10^{-5} or 10^{-7} for any particular gene (10^{-8} for bacteria). Data now being gathered at Brookhaven indicate that the rate in corn may be much higher, in the order of 10^{-3} to 10^{-6}. In spite of this, when all types of mutation for all genes borne by any one individual are considered, mutation becomes almost commonplace. Muller (1950) has estimated that approximately one in every twenty germ cells contains a new mutation that has arisen during the life of the organism. The application of any mutagenic agent, even in small amounts, will obviously increase the frequency of mutation. If an estimate of a doubling of mutation rate with every 50 r is assumed (this is the figure for Drosophila; estimates range from 3 r to 300 r for man), it is apparent that a dosage of 200 r would increase the frequency of new mutations to roughly one in every four gametes. Fortunately, however, a fair proportion of these would be so minute as to be almost undetectable although most of them would be undesirable. A few might be useful, or potentially so, under somewhat changed environmental conditions. Thus, a

long-range possibility of actual benefit lies in the genetic effects of radiation on the heredity of plants and animals.

The AEC is conducting genetic research at three of its national laboratories, Brookhaven, Oak Ridge, and Argonne, and twenty-one genetic research projects at cooperating universities throughout the country are directly supported by the AEC. Most of these projects are designed to reveal the mechanisms by which radiations cause genetic changes. In Table III is a list of university projects specifically concerned with agricultural genetics.

In a fundamental study of radiation genetics, Brookhaven is growing corn under continuous radiation in its gamma-ray field. Corn is being studied intensively because more is known about the genetics and cytology of corn than of any other farm crop plant. The mutation rate of four endosperm characters *Su, Pr, Sh,* and *R* has been studied in both megaspore and microspore (Singleton, 1950a,b). At the highest radiation given in 1950 (125 r / day) slightly more than 1 per cent of mutations were obtained from 6400 seeds studied. Lower intensities of radiation produced fewer mutations. No increase over the spontaneous mutation rate was found with intensities less than 5 r per day. A total of 275,000 seeds were examined through 1950. Although endosperm characters were studied primarily, there is reason to suppose other plant characters will respond similarly to radiation. Attempts are being made to induce such plant characters as the short stalk *rd*, and the shorter stalk br_2. Pollinations made in the radiation field in 1950 gave sufficient seed for about 10 acres of corn which is being examined for short types this year. It seems likely that such induced plant characters can be inbred and isolated in a hybrid within two or three years, which is much less than required by a crossing and backcrossing program. It is this feature of the gamma radiation that is of interest to plant breeders. There is a good chance that a greater diversity of genes responsible for hybrid vigor may be induced by radiation, thus giving the plant breeder many more genes with which to work. Such an eventuality might make it unnecessary to comb various parts of the world for specific genes of disease resistance and drought resistance.

At the University of Minnesota the effects of radioactive substances on plant pathogens and other microrganisms are being investigated in an attempt to determine the biological significance and usefulness of changes induced by radioactive materials. In the corn smut fungus, *Ustilago zeae,* many mutants have been obtained by growth on media containing uranyl nitrate. Detailed comparative studies of such mutants have shown that they differ from the parental lines in morphology, physiology, and pathogenicity.

A similiar project on the physiology and genetics of plant pathogenic microorganisms grown in the presence of various radioisotopes is being supported at the Ohio Experiment Station. Corn breeding experiments and effects of atomic bomb exposures on corn seed is a continuing project at the California Institute of Technology.

In a series of experiments somewhat similar to the Brookhaven project, 75,000 peanut seeds were exposed to x rays at dosages of 10,000 r, 16,000 r, and 18,500 r at North Carolina State College. One major plant breeding objective was to produce a mutant resistant to leaf spot disease which causes serious loss in peanut crops. In the summer of 1951 there were raised 13,600 progenies of the X_3 generation. The peanut plants range from normal or slight variability to plants of variability of every description as a result of the radiation in 1949.

Although the X_3 progeny has not been completely analyzed at the time of this report, mutants of a wider range of variability in resistance to leaf spot have been obtained. There are also many other variants which may be of economic importance.

4. Biochemical Effects of Radiation

The nature of radiation damage in plant tissue is probably as complex as that in animal tissue, but with plant material few investigations have been made. Cytogenetic investigations of radiation effects have been made on plant material, but relatively few biochemical studies have been reported. Much more work is needed in all fields before an adequate understanding of the mechanisms of radiation damage can be achieved.

Fundamentally the initial physical, chemical, and biochemical effects should be the same in all biological systems. Ionizations, excitation, and the production of activated molecules, H_2O_2, HO_2, and OH radicals should lead to a wide array of unusual chemical by-products and actual destruction or inactivation of many molecules, leading to a general disturbance of the more sensitive metabolic processes.

It is possible that important labile enzymes are easily destroyed even in the presence of the usual complex cell constituents which should exert a considerable protective influence. Although enzymes are not found in dilute pure solution *in vivo,* Dale (1943) believes that enzyme inactivation plays a large role in radiobiological injury. It is not definitely known which systems are the critical ones in plant metabolism, although it is known that certain enzymes and plant hormones are susceptible to radiation damage (Skoog, 1935).

Physiological and cytological consequences of irradiation of plants and plant materials are being carried on at Brookhaven National Labora-

tory and in collaboration with investigators at other institutions. For example, at the University of Pennsylvania investigations are in progress on the tyrosinase activity in potato tubers, and in preparations of the enzymes from the tubers.

The phytoradiology work at Argonne National Laboratory under S. Gordon was initiated to study the effects of radiation on higher plants and has developed into a major project on biochemical effects of ionizing radiation. A number of the observed effects of high-energy radiations on plants are similar to those caused by changes in auxin level, and thus the effect of such radiation on auxin (indoleacetic acid) and auxin economy becomes pertinent to research upon the mechanisms of radiation effects. One of the major controlling factors of plant growth and development are the growth hormones or auxins and the chief site of auxin synthesis is the growing terminal bud of the higher plant.

Investigation at Argonne Biology Laboratory has dealt with the effect of ionizing radiation (1) on auxin in *in vitro* and *in vivo* systems, (2) on the biosynthesis of auxin in the living plant tissues, and (3) on physiological processes controlled by auxin.

In aqueous solutions x-ray irradiation inactivates auxin with apparent first order kinetics. Added organic compounds are able to protect free auxin against inactivation by ionizing radiation. Such protective action was shown by ethanol, glucose, ascorbate, cysteine, glutathione, and citrate—all possible components of a plant cell.

Auxin levels have been determined immediately after various single doses of x-ray irradiation were given to kidney bean, cocklebur, and cabbage plants. Radiation doses as low as 25 to 100 r cause an immediate drop in free auxin levels. As the radiation dose is increased, the absolute amounts of free auxins in the tissue progressively decrease. Depending on the plant material, it takes from 50 to 1000 ionizations produced in the tissues to inactivate one molecule of auxin. Auxin is present in very minute amount in the cell and when one considers the tremendous excess of molecules in the cell which could compete with indoleacetic acid for the radiation-induced oxidizing groups, the efficiency of free auxin inactivation by ionizing radiation is surprisingly high.

Continued production of auxin after irradiation is likewise inhibited by low radiation doses. Kidney bean and cocklebur plants were irradiated in single doses from 25 to 10,000 r, their auxin levels being followed by periodic sampling after irradiation. Auxin formation is inhibited in the kidney bean by as little as 25 r, with progressive inhibition by higher doses. Recovery of the capacity to synthesize auxin after irradiation is attained in from several days to two weeks, depending on the dose. Doses

of 10,000 r result in increasingly depressed biosynthesis, with no recovery.

The effectiveness of low doses of ionizing radiation can be interpreted as being due to its action upon molecules which affect multimolecular turn over, i.e., the enzymes. If the enzyme system involved in auxin supply is radiosensitive, the free auxin reservoir would be rapidly lowered and made manifest by reduced auxin level.

Biochemical investigations are underway dealing with the effect of ionizing radiation directly on the system involved in growth hormone synthesis. Exposure of the plants to radiation causes decreased growth and auxin concentration. The effect of the low radiation doses can be reversed by applying synthetic growth hormone to the plant following irradiation. The effect of higher radiation doses cannot be reversed, implying that a more profound biochemical injury has taken place such as on the enzymes.

Morphological changes due to irradiation can likewise be shown to be due, in part, to radiation sensitivity of the hormone system. Plant workers are familiar with the phenomenon of apical dominance. The terminal growing point, or bud, suppresses the growth of lateral buds. When the terminal meristem is cut off, or severely injured, the lateral buds immediately leave their "dormant" state and begin growing. This process was shown to be specifically controlled by the auxin produced by the terminal bud. Thus, when the stem tip is removed and auxin alone is applied to the stump, the laterals stay suppressed as long as the auxin source is allowed to remain. If the applied source is in turn removed, normal growth of the laterals is immediately initiated.

Terminal growing points of the cocklebur were irradiated with single low doses of x-ray irradiation; the remainder of the plant being shielded with lead. Lateral bud growth ensued, the buds increasing over 100 per cent in size within two days. When auxin was applied to the tips immediately after irradiation, lateral buds stayed suppressed.

Argonne investigators have concluded that these apical dominant responses to irradiation are chiefly, if not wholly, due to radiation sensitivity of the auxin supply system. Apparently the process of auxin formation is relatively sensitive to radiation, and this provides an explanation, in part, for changes in growth and development of higher plants exposed to relatively intense, low doses of ionizing radiation.

5. Biological Chains

The purpose of such programs are to determine the extent and manner of concentration of radioactive materials in plants and in aquatic organisms of our rivers. This function is necessary in order to deter-

mine (1) why certain forms concentrate particular isotopes to such a high degree, (2) how the concentration of radioactivity in these organisms can affect higher forms of life such as animals and fish, which ingest them, and (3) whether the concentration of radioactive isotopes present on the land and in the rivers can be decreased in order to reduce possible hazards.

Several projects are specifically designed for this purpose. At the Hanford Laboratory the concentration of radioactive materials in the aquatic organisms of the Columbia River is monitored at frequent intervals as a check on the safety of Hanford operations. More than 500 samples of vegetation, soil, and mud are assayed each month for radioactivity. In addition, the organisms occupying important links in the food chain of the river as well as fish are reared in pile effluent or subject to individual isotopes which may contaminate the river. The organisms are then fed to higher forms which would normally consume them. The pattern of deposition of the activity in both of the forms is studied.

Radiobiological ecological surveys of the Columbia River project have disclosed the particular biological chains in need of continuing study. Ecological surveys of the Savannah River Project Area are to be undertaken with support from the AEC by universities and colleges in the states most directly concerned.

It has been found that in the Columbia River radioactive phosphate is taken up extensively by both the fauna and flora and constitutes a greater biological hazard than other radioactivity in the river. It is produced from the natural phosphates in the river water when the water is used for cooling the pile. Algae in the river have the ability to build up phosphorus concentrations thousands of times that present in the river water. The fish feed on the algae and over 85 per cent of the activity deposited in trout is assimilated from food organisms. Thus, the longer-lived isotopes deposited in the fish originate principally from the food while shorter-lived isotopes are accumulated directly from the water. Activity concentrated in animal forms is therefore dependent upon feeding habits as well as upon the activity density of the surrounding water. These studies designed to measure biological chains indicate that the level of activity in the Columbia River has been maintained at levels that have no adverse effects on the fauna and flora of the river. The levels in the water below the piles and in the fish are far below tolerance for man and are entirely safe for food.

Hanford has operated a small experiment station in which a variety of fruits and vegetables were irrigated with water drawn from the Columbia River below the reactor cooling outlets. At no time has any

significant or, in fact, measureable amount of radioactive material appeared in the soil and crops.

Annual surveys have been made of the soil, plants, and animals collected in the area of the first atomic bomb detonation site at Alamogordo, New Mexico, in order to obtain some concept of what role the low level contamination of the soil may play in the metabolism and life cycles of the plants in this area. The data may serve to indicate what can be expected from bomb areas of much higher activity.

III. Uses of Isotopes in Plant Sciences

Although the changes that radiation causes in living matter are of great scientific interest, the AEC also sponsors fundamental research in the broad fields of soil science, plant nutrition, plant biochemistry, and physiology, and plant genetics. Generally these projects involve the use of radioactive isotopes in their research programs. In Table I Part II are listed the projects at AEC national laboratories and AEC university projects which receive a major part of their support for this type of research from the AEC. In Tables II and III are listed forty-one projects in plant sciences which are partially supported by the AEC at universities and colleges. It is impossible to discuss these diversified projects in a single review, but the descriptive titles in the tables will serve as a guide, and in many cases publications of the investigators will provide further information.

1. Soil, Fertilizer, and Mineral Nutrition

The AEC has a broad field of interest in soils and fertilizers, mineral metabolism, and plant nutrition. Table II lists research projects which the AEC is partially supporting in this field at universities. Various processes of the atomic energy industry create radioactive materials that might become available to growing plants. Research topics associated with the soil and plants are but a segment of a diversified group of research projects built around the theme of fission products in the life cycle—from soil, to plants, to animals or man. It is necessary for the AEC in its research to evaluate (1) the state and availability of minerals (fission products) in the soil, (2) the absorption of minerals by the roots and thus the physiology of the root, (3) translocation and deposition of various elements in plants, and lastly (4) the role of minerals in plant biochemistry. That much fundamental research must precede the completion of this Herculean task is obvious, and the AEC Act provides for some of the support of this research.

Many of the AEC research projects in soil and plant nutrition in-

volve work in more than one of the three divisions indicated in Table II. Most of the projects utilize radioisotopes, and it is hoped they will stimulate research in fields beyond that supported directly by the AEC.

The AEC is interested in the movement in the soil and uptake by plants of radioactive bomb debris and fission products such as strontium, yttrium, cesium, columbium, ruthenium, tellurium, ionium, barium, sodium, potassium, lanthalum, cerium, plutonium, and uranium as well as some nonradioactive elements used in its program such as beryllium. All these minerals are taken up by plants, but many do not present a problem because they are either not taken up in significant quantities or else their half life is too short to make them much of a hazard. Strontium and yttrium are potentially the most biologically hazardous of the fission products. Strontium-90 has a 25-year half life and strontium-89 a 55-day half life. Both are beta emitters, are absorbed and concentrated out of the soil by plants as if they were an isotope of calcium, and they are likewise absorbed and utilized by man and animals in lieu of calcium.

Strontium-yttrium absorption by both plants and animals has been the subject of numerous investigations (Table I and II), such as those of Jacobson and Overstreet (1948). Tests by the Hanford botany group have shown that red kidney bean plants take up strontium in proportion to its concentration in a nutrient solution over a broad range of 0.0001 to 100 parts per million. Plants build up concentrations of strontium in their leaves five to ten times as great as that present in the nutrient solution. Abnormally high concentrations of calcium in the soil will partially prevent strontium uptake by plants.

Strontium likewise is readily translocated to the leaves and all other parts of the plant including edible fruits. In one experiment 1.6 per cent of the initial dose of strontium applied to the soil appeared in leaves of barley and peas, whereas only 0.00045 per cent of a dose of trivalent plutonium was translocated to the leaves.

Radioisotopes are proving to be of greatest value in fertilizer research. A major effort has been a joint AEC-U.S. Department of Agriculture project in the Bureau of Plant Industry, Soils, and Agricultural Engineering for developmental work on the safe and extensive use of radioisotopes in the field. There are several phases of this program such as (1) development of procedures for use of radioisotopes in general soil and plant research, (2) development of procedures for preparing and handling labeled fertilizers and ascertaining levels of possible injury to the plant from radioactive fertilizers, (3) investigation of the role of trace elements, particularly in relation to chlorosis, (4) performance of basic soil research with P^{32}, Ca^{45}, Zn^{65}, K^{42}, S^{35}.

2. *Plant Metabolism*

Radioactive tracers can be successfully utilized in almost all phases of plant biochemistry and physiology, but the number of investigators and the amount of work in these fields are surprisingly small compared to animal biochemistry. The projects listed in Table III cover a rather broad range of subjects in plant metabolism.

Research in photosynthesis is an excellent example of an old problem being attacked with successful results with a radioisotope, C^{14}. A major AEC project in this field at the Radiation Laboratory of the University of California has used the two tools C^{14} labeled CO_2 and paper chromatography in the study of the mechanism of the utilization of light energy in carbon dioxide reduction (Calvin *et al.*, 1951).

Experiments with $C^{14}O_2$ of high specific activity have allowed a great number of observations on this hitherto almost impenetrable system of reactions. The advantages of such a method lie first in its sensitivity; intermediates of concentrations of less than 10^{-6} *M* may be readily determined in a few milligrams of plant material. Secondly, when labeled carbon dioxide is added the reservoirs, the intermediate products are consecutively labeled with C^{14}. Analysis of the products of photosynthesis in $C^{14}O_2$ by two-dimensional paper chromatography has allowed separation of most of these compounds.

As the length of exposure of an actively photosynthesizing plant to $C^{14}O_2$ was shortened, the labeled carbon fixed by the plant was found in fewer and fewer compounds. Thus by rate curves, it was found that the $C^{14}O_2$ was first incorporated into the carboxyl group of phosphoglyceric acid. It was further confirmed that this carbon dioxide reduction is accomplished entirely by dark reactions and that the reducing power formed during photosynthesis in the light had a half life of several minutes in the dark.

Present investigations by the University of California group are concerned with the sequence of organic intermediates on the pathway to sugars in the photosynthesis process. In addition progress is being made upon elucidation of a photosynthesis organic cycle necessitated for continuous generation of the two-carbon compound which is carboxylated by the CO_2 to give phosphoglyceric acid.

Biochemists are using radioisotopes to study the action of the well-known weedkillers, such as 2,4-D. Much is known of the practical use of 2,4-D; little is known of its biochemical action. Radioactive labeled 2,4-D is being used to study its rate of absorption by susceptible and resistant plants, its translocation in various species, its destruction and break-down products, and the specific biochemical steps blocked by its action.

In Table II are listed several projects dealing with mineral movement and metabolism in plants which bear upon various mineral deficiencies. Chlorotic plants are found in all parts of the country and occur when trace minerals such as iron, zinc, copper, and manganese are not absorbed by the plant or are naturally deficient. In one of these projects at Washington State College, studying the mechanism of mineral translocation in plants, it has been found that movements of the minerals can be easily influenced by pH and concentration of phosphates. Iron is absorbed best under more acid conditions, and its mobility in the plant decreases at higher phosphate concentrations and pH. It appears to be precipitated as ferric phosphate and hence metabolically becomes nonfunctional.

TABLE I

AEC Research in Plant Sciences at Its National Laboratories and Totally Supported University Projects

I. Effects of Radiation on Plants
  1. External Radiation Effects
    a. Brookhaven National Laboratory
      (1) Genetics and Physiological Effects of Ionizing Radiation on Plants: Killing, Stunting of Growth, Abnormal Growth Patterns, Change Yields — W. R. Singleton
  2. Internal Radiation Effects
    a. Argonne National Laboratory
      (1) Growth and Development of C^{14}-Labeled Plants — N. J. Scully
    b. Hanford National Laboratory
      (1) Levels of Radioactive Elements Which Will Cause Damage to Plants and Microorganisms — J. W. Porter
    c. USDA Bureau of Plant Industry, Soils, and Agriculture Engineering
      (1) Radiation Injury to Plants Grown on Nutrient Solutions Containing P^{32}
  3. Genetic Effects
    a. Brookhaven National Laboratory
      (1) Cytological and Cytochemical Effects of Radiation in Plants — A. H. Sparrow
      (2) Genetic Effects of Ionizing Radiation (Corn Breeding Program) — W. R. Singleton
  4. Biochemical Effects
    a. Argonne National Laboratory
      (1) Radiosensitivity of Growth Hormone and Its Biogenesis — S. A. Gordon
  5. Biological Chains
    a. University of California at Los Angeles Medical School
      (1) Radiological Survey of Soil and Biological Material from Continental Atomic Bomb Detonations — K. H. Larson, S. Warren
    b. Hanford Biology Laboratory
      (1) Concentration of Radioactive Materials in Aquatic Organisms of the Columbia River — R. F. Foster

(2) Radiobiological Ecological Survey of the Columbia River R. F. Foster
(3) Radioactivities of Soil and Plants Irrigated with Columbia River Water below the Reactors at Hanford

c. Oak Ridge National Laboratory
(1) Ecological Survey of Oak Ridge Pile and Processing Wastes on Plants and Animals in the Immediate Vicinity

d. Washington University, Applied Fisheries Laboratory
(1) Bikini and Eniwetok Biological Surveys

II. Use of Isotopes in Plant Sciences

1. Soil, Fertilizer, and Mineral Nutrition

a. USDA Bureau of Plant Industry, Soils, and Agricultural Engineering
(1) Improvement of Soil Management and Crop Production through Investigations with Isotopes
(Furnishes labeled fertilizers to 25 state agricultural stations)

b. University of California at Los Angeles
(1) Uptake of Ce, Cs, Sr, and Pu by Various Crops from Representative Soils K. H. Larson

c. Hanford Biology Laboratory
(1) Absorption and Translocation of Radioelements (Y^{91}, Sr^{90}, Cs, I^{131}, Pu) by Plants J. W. Porter
(2) Mechanisms Involved in Retention and Release of Radioactive Isotopes by Soils

d. Schenectady Area
(1) Permeability and retention of Radioactive Materials in Local Soils

e. University of Tennessee AEC Project
(1) Incorporation of Ca^{45} into Soil and Relation of Soil Types to Availability of Nutrients C. L. Comar

2. Plant Biochemistry and Physiology

a. Argonne Biology Laboratory
(1) Synthesis of C^{14} Labeled Indolacetic Acid R. Stutz

b. Brookhaven National Laboratory
(1) Metabolism and Photosynthesis in Plants M. Gibbs

c. University of California Radiation Laboratory
(1) Path of Carbon in Photosynthesis M. Calvin, A. A. Benson

d. Hanford Biology Laboratory
(1) Plant Metabolism of Radioelements J. W. Porter

e. Oak Ridge Biology Laboratory
(1) Biochemical and Biophysical Investigations in Photosynthesis with Particular Attention to the Light Reaction W. A. Arnold
(2) Nucleic Acid Metabolism of Plant Tissue G. R. Noggle

3. Biosynthesis

a. Argonne National Laboratory
(1) Biosynthesis of C^{14}-Plant Products—Labeling of Plant Species and Isolation of Sugars, Dextran, Organic Acids, Alkaloids, etc.
N. J. Scully

b. Brookhaven National Laboratory
(1) Biosynthesis with Plants M. Gibbs

c. Oak Ridge
(1) Separation, Identification, and Role of Sugars and Saccharides in Plant Tissue G. R. Noggle

TABLE II

AEC Partially Supported Research in Soils, Fertilizer, and Plant Nutrition at Universities and Colleges

Institution	Title	Investigators
	State and Availability of Minerals in the Soil	
University of Arizona	Utilization of Phosphorus from Biological Materials	W. H. Fuller and W. T. McGeorge
Idaho State College	Radioactive Materials in Water and Soil Adjacent to Reactor Testing Station	A. E. Taylor
North Carolina State College	Movements of Ions through Soil Systems	N. S. Hall
	Absorption of Minerals by Plants	
University of Arizona	Uptake of Strontium by Various Types of Crops	W. H. Fuller and W. T. McGeorge
University of California	Internal and External Factors Affecting Ion Absorption by Plants	L. Jacobson and R. Overstreet
Duke University	Factors Affecting Absorption of P^{32} by Mycorrhizal and Nonmycorrhizal Roots of Pine	P. J. Kramer
University of Idaho	Absorption and Translocation of Minerals in Diseased and Healthy Western White Pine	T. S. Buchanan, W. K. Ferrell and E. T. Hubert
Michigan State College	Absorption and Utilization of Radionuclides Applied to the Leaves of Plants Including Strontium	H. B. Tukey
University of Texas	Biological Accumulation of Inorganic Materials by Algae	J. Myers

Washington State College	Rate of Movement of Ions into Plant Tissues	N. Higinbotham
Washington State College	Zinc Nutrition of Plants in Calcareous Soils	O. Biddulph
	Translocation and Deposition of Elements in Plants	
University of Missouri	Translocation of Radiophosphorous in Squash Plants	J. Levitt
North Carolina State College	Rate of Movement of Organic and Inorganic Compounds in Intact Trees	D. B. Anderson
Utah State Agricultural College	Radioisotopes in Studying Lime-Induced Chlorosis	D. W. Thorne
Washington State College	Absorption, Translocation, and Deposition of Various Elements in Plants	O. Biddulph
University of Wisconsin	The Role of Root Grafting in Translocation of Water, Nutrients and Disease Among Trees	A. J. Riker and J. E. Kuntz

TABLE III

AEC Partially Supported Research in Plant Biochemistry, Physiology, and Genetics at Colleges and Universities

Institution	Title	Investigators
	Photosynthesis Research	
University of Arkansas	Intermediary Metabolism of Photosynthetic Bacteria	J. M. Siegel
Smithsonian Institute	Biochemical Investigation of Photomorphogenesis in Green Plants	R. Withrow
University of Utah	Studies of Photosynthesis Processes in Cell-free Preparations	R. Lumry and J. D. Spikes
	Plant Metabolism	
University of California	Tracer Studies of the Metabolism of Plants and Bacteria	H. A. Barker, W. Z. Hassid and C. C. Delwiche
Iowa State College	Metabolism and Physiology of Roots	S. Aranoff
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Oklahoma Agricultural and Mechanical College	Mechanism of Nitrate Reduction	R. MacVicar
University of Wisconsin	Studies of Biological Nitrogen Fixation	R. H. Burris and P. W. Wilson

Institution	Title	Investigators
	Plant Agricultural Genetics	
California Institute of Technology	Radiation Genetics	G. W. Beadle
University of Minnesota	Radioactive Substances on Plant Pathogens and Other Microorganisms	E. C. Stakman
University of Nebraska	Thermal Neutron Irradiation of Crop Seed	E. F. Frolik
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Vegetation Control on Industrial Lands

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I. Scope and Nature of the Problem

Agronomists generally recognize that the control of weeds by one means or another constitutes a major portion of the effort involved in crop production. The magnitude of the job of controlling vegetation on nonagricultural land is not so well appreciated. Until recently this has been largely accomplished by manual or mechanical methods with scythes, brush hooks, and mowing machines. During the past decade there have been many developments in killing or suppressing plant growth by chemical means. This chapter will be largely devoted to advances in the use of herbicides for the control of unwanted vegetation.

Lands may be divided into five groups for the purpose of considering problems related to the control or eradication of plant growth: (a) crop

land, (b) pasture and range, (c) forests, (d) recreational areas including home lawns, and (e) industrial lands.

It is with group (e), industrial lands, that this discussion will deal. Among the lands that may be considered as industrial in nature are the following:

railroad right-of-ways and switching yards
highway right-of-ways
pipeline right-of-ways
electric line right-of-ways
telephone and telegraph right-of-ways
transmitter and transformer stations
drainage and irrigation ditches
canals and waterways
grounds surrounding factories, mills, and refineries
lumber and pole yards
oil tank farms
airfields
parking lots
water reservoirs

Military lands may be included in the above list for purposes of this review. Problems of vegetation control at arsenals, ammunition dumps, and firing ranges are often very similar to those encountered on industrial property.

The needs of industry for vegetation control vary with the use to which the land is to be put. The vegetation control objectives peculiar to railroads, highways, and other industrial lands will be discussed under various headings in Sec. III.

Each situation presents its own problems. Species composition is an important consideration, and a plant census is essential to efficient vegetation control by chemical means. Ecological factors must be studied in determining practical objectives. Only by a working knowledge of plant taxonomy and ecology in addition to the new technology related to herbicides can the most efficient vegetation control be accomplished.

II. Chemicals Used for Vegetation Control

Herbicide research is being undertaken on such an extensive scale at the present time that it is difficult, if not impossible, to mention in a review of this nature all the compounds referred to in the literature as showing promise for one or another industrial vegetation control problem. Discussion will be confined to those herbicides that have already found a place.

Knowledge of a chemical tool is as essential to its proper use as knowledge of a mechanical device. Understanding of the nature of the physiological effect of an herbicide on the plant, variation in species response, the importance of the condition of the plant and various soil

and climatic factors constitute the basic information needed for efficient use of an herbicide.

1. *Chlorophenoxyacetic Acids*

Two members of this family of plant growth regulators have come into wide use for industrial vegetation control, 2,4-dichlorophenoxyacetic acid (hereafter called 2,4-D) and 2,4,5-trichlorophenoxyacetic acid (hereafter called 2,4,5-T).

a. Derivatives and Formulations. The acids themselves are seldom employed because certain salts and esters are more readily formulated. Early in the development of 2,4-D it became evident that under ordinary conditions its alkyl esters were more effective herbicides than its salts. The alkyl esters of both 2,4-D and 2,4,5-T came into use for industrial vegetation control and particularly for control of woody plants.

Recently esters of higher molecular weight have virtually replaced the alkyl esters in the United States for industrial vegetation control purposes. The lower vapor pressure of such materials reduces the likelihood of sufficient volatilization occurring from sprayed surfaces to result in damage to unsprayed vegetation (Allen, 1950). Mullison *et al.* (1951) have shown that the herbicidal activity of certain glycol ether esters of 2,4-D is greater on many plant species than the common alkyl esters of 2,4-D.

Commercial formulations are generally emulsifiable, although they may be diluted with straight oil for certain uses. Many formulations have an acid equivalent concentration per gallon of 4 lb. of either 2,4-D, 2,4,5-T or a fifty-fifty mixture of these two.

b. Some Physiologic Aspects. The physiology of the action of 2,4-D and the influence of various environmental factors has been discussed in an earlier review in *Advances in Agronomy* (Crafts and Harvey, 1949) and also by Mitchell (1948). 2,4,5-T appears to operate by much the same mechanism and is probably subject to the same internal and external influences (Linder *et al.*, 1949). A few points bear emphasis because of their relationship to successful use of these compounds.

Spraying operations must necessarily extend over as long a season as possible to make industrial use of herbicides a practical proposition. There is often a tendency to begin spraying brush and rapidly elongating herbaceous perennials at an early date, but experience has shown this practice to result in relatively poor kill. This phenomenon appears to be related to the transport of the herbicide from leaves to stems and roots, which Mitchell and Brown (1946) have found occurs in association with organic food materials within the plant. Spraying foliage of woody plants before it is fully developed and is providing excess products of photosyn-

thesis for movement downward frequently gives inferior results in terms of root and crown kill. Likewise applications early in the growth of an herbaceous perennial frequently result in a poor kill of underground parts, apparently because it is still drawing on underground reserves and has not yet begun to return an excess of food materials to storage organs.

Experiments with perennial weeds, such as Canada thistle, indicate that as maturity approaches poor results are obtained, again probably because of limited transport. Such principles should be considered in spraying mixed vegetation on industrial grounds. Late growing season treatments of herbaceous weeds are generally profitable only where earlier mowing has induced resumption of vegetative growth.

Tree saplings or suckering growth of woody plants that have previously been cut off do not reach physiological maturity in the sense that an herbaceous plant does at time of seed formation. Spraying operations on woody vegetation have proved successful throughout the summer (Durr, 1950).

The effects of atmospheric and soil conditions on the performance of an herbicide is an important consideration in planning the continuous spraying operations essential for many industrial uses. Weaver *et al.* (1946) found that 2,4-D in oil solution was not removed from foliage by simulated rain. Rainfall soon after spraying with emulsions appears to have no adverse effect when esters of chlorophenoxyacetic acids are used. Once the water has evaporated the residual ester is removed from the leaf with difficulty.

The herbicidal effectiveness of chlorophenoxyacetic acids has been observed in the field to be correlated to some degree with growth rate (Marth and Davis, 1945). Lee (1949) reports that corn is most likely to suffer injury from 2,4-D applications when moisture and temperature conditions are favorable to good growth. The more tolerant weeds and woody plants appear to be influenced in their response in a similar manner. Low temperatures, such as may occur in the early spring, are not conducive to good weed kill apparently because of retarded growth. Kill of the more tolerant species, for example white ash and cattail, has been observed to be much more complete during hot weather than when cool weather follows spraying. Soil moisture deficiencies that materially retard growth appear to inhibit the kill of woody as well as herbaceous species (Durr, 1950).

c. Compound Specificity. Both woody and herbaceous plants are being controlled with these compounds on industrial lands. The use of 2,4-D for control of herbaceous weeds is too well known by agronomists to call for extensive discussion in this review. In general the principles

of herbaceous weed control on roadsides, mill and factory grounds, etc., are similar to those established for perennial weed control in cultivated fields.

Hamner and Tukey (1946) were among the first to point out the possibilities of killing a variety of woody species with 2,4-D. The use of 2,4-D for woody vegetation control on electric utility right-of-ways dates from 1945. From the beginning of this work certain woody species appeared resistant to 2,4-D, and the success of the chemical for controlling right-of-way brush growth appeared very much in doubt. Thus Ashbaugh and Barrons (1946) listed hickory, maple, oak, and members of the genus *Rubus* as being difficult to kill. Early in 1947 the writer observed that highway right-of-way plots sprayed with an ester of 2,4-D in 1945 and again in 1946 were becoming increasingly populated with blackberry. Elm, willow, sumac, and elderberry had been eliminated. Although blackberry may be acceptable on some industrial grounds it is generally considered undesirable.

The specific action of derivatives of 2,4,5-T on many plants that are tolerant to 2,4-D was first reported by Tam (1947) who found it to be more active than 2,4-D on a number of species in Hawaii including eucalyptus and lantana, and also by Barrons and Coulter (1947a), who found it very active on blackberry and other members of the genus *Rubus*. Subsequently 2,4,5-T has been observed to be more active than 2,4-D on a number of woody plants including mesquite, osage orange, maples, and poison ivy.

Mixtures of esters of 2,4-D and 2,4,5-T containing one-third to one-half of the latter were soon placed on the market, frequently under the name of "brushkillers." Such mixtures have been widely used for woody plant control since 1948. Where the objective is the control of a single species known to be susceptible to one or the other component, 2,4-D or 2,4,5-T may be used alone. For mixed woody populations, so prevalent on right-of-ways, mixtures of the two compounds have proved best. Most species appear to be at least as susceptible to a mixture of 2,4-D and 2,4,5-T as to 2,4-D alone, willow being one established exception (Butler, 1950).

Where control of herbaceous weeds is the primary objective, 2,4-D formulations generally prove adequate or even superior to 2,4-D–2,4,5-T mixtures. Some herbaceous species, such as horsenettle and ground cherry, are considerably more susceptible to 2,4,5-T than to 2,4-D. Regardless of the objective there is much to recommend a careful species census prior to a choice of spray material.

d. Application Methods. Five methods are being employed for the application of chlorophenoxyacetic acid weed killers to woody growth.

1. Foliage spraying during the season of active growth in relatively large volume of water from ground equipment.

2. Low volume foliage application with ground equipment using oil or water as a carrier.

3. Low volume foliage application by aircraft with oil or oil-water emulsions as a carrier.

4. Application to bark at the base of the plant (basal application) during either the dormant or growing season using oil as a carrier.

5. Application in oil to cut stumps at any season of the year.

Smith (1946) found that 2,4-D was absorbed and translocated when applied as a coarse discontinuous spray thus permitting low volume application. Although low volume spraying is now almost a universal practice in agriculture, high volumes are commonly utilized in applying chlorophenoxyacetic acids for industrial vegetation control. High volume spraying minimizes risk from drift and provides maximum coverage of dense vegetation often growing at different levels. This method is by far the most important at the present time and constitutes the basis of most control programs, particularly where plant populations are large (Ashbaugh, 1950). Other methods may be employed to meet specialized problems and conditions.

Much foliage spraying is done with a concentration of 3 to 4 lb. acid equivalent per 100 gallons of spray applied in a volume adequate to wet the foliage. The experience of many operators indicates the importance of wetting all sides of a woody plant and driving the spray into dense growth in order to wet the stems (Suggitt, 1950). The relative importance of stem *vs.* leaf wetting by high volume aqueous sprays has not been clearly established, although the work of Mullison (1952) on beans has shown that absorption of lethal doses can take place through succulent stems.

Low volume spraying by airplane or ground equipment has a definite place where water is difficult to procure or on land inaccessible to spray trucks. Low volume treatment is most successful where vegetation is not dense. There is inherently more drift hazard from a low volume, highly concentrated spray than from a high volume spray, and the sensitivity of crops adjacent to areas to be treated should be carefully considered.

Hamner and Tukey (1946) first reported experiments in which 2,4-D was applied to cut surfaces. Early field results on stump treatment were promising (Anonymous, 1946). Barrons and Coulter (1948) reported good results with stump treatment at all times of the year, and pointed to preliminary results on application to uncut bark. Subsequently a number of workers have reported experiments on stump and

basal application (Barrons and Coulter, 1947; Egler, 1949; Coulter, 1950, 1951; Beatty, 1950). 2,4,5-T has given superior results on most species for basal or stump treatment. Applications during summer and at varying times during the dormant season have proved successful; however, Coulter (1950) points to the field experience of a number of users who have obtained best results in late winter and spring.

Oil is used as a carrier for 2,4,5-T or 2,4-D in stump and basal application. Fuel oils and kerosene have proved as effective as other oils (Barrons and Coulter, 1947c). The concentration of 2,4,5-T generally recommended by manufacturers for stump and basal spraying varies from 12 to 20 lb. per 100 gallons. Coulter (1950) states that 16 lb. per 100 gallons of oil is the most practical concentration. Adequate volume must be applied thoroughly to saturate the bark from the ground line to the cut surface of the stump or up about 2 ft. when uncut brush is being treated.

Certain species, including red maple, appear more susceptible to basal or stump treatment than to foliage sprays (Beatty, 1950). Klingman (1950) has listed a number of additional advantages of basal treatment. Currently basal bark treatment seems to be desirable under the following circumstances:

1. Where original stands are thin or where earlier spraying has greatly reduced stands.
2. Where adjacent sensitive plants make blanket foliage spraying risky.
3. Where lack of suitable power equipment precludes conventional foliage application.
4. Where labor is lacking during the summer or where it is desirable to extend the season of operations to reduce seasonal variations in labor requirements.
5. Where species such as red maple predominate which may be more readily controlled by a basal treatment.

Stump treatment appears to be profitable wherever trees must be cut before building new lines or where, for esthetic reasons, visibility, or fire breaks it is not desirable to leave dead trees or brush standing.

e. Application Precautions. Spray operators must exercise due caution in using chlorophenoxyacetic acids because of the hypersensitivity of certain crop and ornamental plants which may be growing adjacent to treated areas. Cotton, grape, tomato, and papaya are plants that have most often shown responses when growing near treated land. Malformed leaves do not necessarily indicate a reduction in productivity of these crops; however, sound public relations policy dictates great caution on the part of spray operators.

Three ways in which chlorophenoxyacetic acids may reach unsprayed areas are recognized.

1. Drift of spray particles.
2. Blowing of dust from soil and plant surfaces following spraying.
3. Drift of vapor volatilizing from sprayed surfaces.

In the writer's opinion the likelihood of their occurrence is in the order named.

Close observation will reveal very tiny droplets arising from spray guns or booms and moving vertically in thermal currents as well as laterally in the wind. Reduction of pressure to ensure large droplets, careful handling of spray guns and booms, and due consideration for wind direction and velocity will materially aid in avoiding trouble from drift. Dormant basal treatment or late season foliage spraying may often be safely practiced on areas that must be skipped during the regular season of operations. Drift from oil solutions as used for dormant spraying must not be overlooked when hypersensitive woody plants such as grapes are growing nearby.

Salts of 2,4-D and 2,4,5-T are so low in volatility that it is unlikely that vapor drift can cause foliar effects on the most sensitive plants (Mullison, 1949). The alkyl esters are considered to be sufficiently volatile to account for some of the responses that have occurred on unsprayed areas (Tafuro *et al*., 1950). The higher molecular weight esters are of very low volatility and it appears unlikely that they vaporize sufficiently to cause trouble out-of-doors when, even in closed containers, the biological effects of their vapor is negligible (Allen, 1950; King and Kramer, 1951). Blowing of chlorophenoxyacetic acid derivatives adhering to soil dust, leaf hairs, and other particles undoubtedly occurs and can account for effects on plants that were upwind at the time of spraying. The prevalence of this mode of movement as a source of trouble is difficult to ascertain. Airplane spraying presents special hazards, and Raynor (1950) has offered suggestions for safe use.

2. *Sodium Chlorate*

The use of sodium chlorate for the eradication of noxious perennial weeds on crop land is well known to agronomists. It has also been widely used for many years for roadbed spraying on railroads in the United States and Canada.

Sodium chlorate kills top growth by contact action and is systemically toxic following root absorption. It is a powerful oxidizing agent and presumably kills by some oxidizing action. It is nonselective, although some species require higher dosages than others for a lethal effect. Moderate dosages may give a contact kill of all top growth of herbaceous

vegetation, but fail to kill underground parts of tolerant species. It is a common observation on railroad beds following a few years spraying with the dosages frequently used that many herbaceous non-grasses are eliminated whereas perennial grasses such as quack, Johnson, and Bermuda grass persist. Woody plants, such as Virginia creeper and trumpet vine that invade the roadbed, and certain herbaceous broad-leaved perennials, such as bouncing bet, are difficult to eradicate with economic rates of application. Vegetation control, through contact foliage burning and limited systemic stunting, is the most common accomplishment on the more tolerant plants. Higher doses than commonly employed will result in eradication.

The success of a particular rate of application of sodium chlorate varies with soil moisture. Excessive rainfall leaches the compound readily. Crafts (1935) found no evidence of adsorption by soil colloids. His studies indicated that chlorate distribution in soils is largely determined by the amount of water that passes through the soil following application of the chemical.

Soil fertility factors in relation to chlorate absorption by roots have been studied extensively. Crafts (1939) found that for the same degree of plant kill on fertile soils higher dosages were required than on soils low in fertility. Nitrate ions were found by Crafts to inhibit absorption of chlorate. Even on railroad beds, where soil fertility is not ordinarily considered, because of stone or cinder ballast, it is frequently observed that poorer results are obtained where the underlying soil is of a fertile nature.

3. Sodium Trichloroacetate

Among the most recently developed herbicides to come into wide use for industrial vegetation control is sodium trichloroacetate, often called sodium TCA. This compound, which has a growth-suppressing and at suitable dosages a lethal effect on many grasses, is widely used as a component of mixed sprays for railroad beds and other areas where complete vegetation control is desired. Special problems such as control of phragmites grass, cattail, and Johnson grass are currently being handled with sodium TCA or with a mixture of this herbicide with other compounds.

Sodium TCA enters plants primarily through the root system although under some conditions limited foliar translocation may take place (Haygood, 1951; Barrons and Hummer, 1951). The compound, which is very soluble in water, is subject to leaching and decomposition in the soil (Loustalot and Ferrer, 1950).

Barrons and Hummer (1951) have discussed the various plant responses to sodium TCA. Buds of many perennial grasses exhibit a pro-

found dormancy which is followed by death or recovery, depending on dosage and various other factors. Many non-grasses are tolerant of sodium TCA while others are inhibited in growth.

Rates found useful for perennial grass control vary from 50 lb. per acre upward, depending on species and various external factors. Because sodium TCA has little effect on many non-grasses, it is frequently applied in combination with other herbicides. In some instances, investigators have observed superior results when the grass was in a weakened condition as a result of prior mowing or spraying. Barrons and Hummer (1951) presented data indicating a relationship between lowered carbohydrate reserves and good grass kill. When combined with a phenolic contact herbicide which burned grass foliage to the ground the writer has, in some instances, observed a better kill than when sodium TCA was applied alone. Barrons and Hummer (1951) found that sodium TCA was absorbed by all plants tested but the limited amount present in grass foliage compared with that in foliage of TCA-tolerant plants suggests that it may be decomposed readily within the susceptible species. These authors suggest that a reduction in grass top-growth, by mowing or by a contact herbicide, insures a greater concentration of TCA in the cambial regions where it apparently has its greatest effect.

Sodium TCA is sold in dry form to be made into a spray or, in some instances, to be mixed with a suitable diluent for dry application. A concentrated solution is also available for railroads or other users of tank car quantities. It presents no particular hazards to warmblooded animals, does not support combustion and, although corrosive to certain metals on long exposure, it appears to present no corrosion problem to rails or fences that may be wet with a spray. Furthermore, a corrosion inhibitor is usually incorporated in commercial sodium TCA powder and concentrated solutions.

Soil moisture is the important external factor governing the effectiveness of sodium TCA. Moisture is needed to put the chemical in the soil solution. Excess rainfall may promote leaching below the zone of active root absorption.

4. Substituted Phenols

Many chloro and nitro substituted phenols are acutely phytotoxic. Pentachlorophenol is now widely used as a fortifying agent for herbicidal oils (Sherwood, 1950). Crafts (1945) found dinitro-ortho-secondary butyl phenol (called DNOSBP) to be the most phytotoxic of the substituted phenols, and this compound is now used in formulating general contact sprays. According to Crafts and Reiber (1948), DNOSBP is approximately four times as phytotoxic as pentachlorophenol. It is

now available under proprietary names as a general contact weedkiller.

The nature of the effect of DNOSBP has recently been reviewed by Barrons (1951). Little if any translocation of the toxicant occurs within most plant tissues. Where sufficient oil is present in the spray to move through plant tissues, DNOSBP will also be moved in oil solution. The effect of pentachlorophenol is also largely confined to tissues wet with a spray or reached by the oil component (Barrons, 1949).

Although these phenolic compounds may be used to fortify straight oil sprays they are more frequently applied as oil water emulsions with the phenolic toxicant in the oil phase. According to Sherwood (1950) pentachlorophenol-fortified oil may be used at one-fifth the volume of a straight oil with equivalent results. Crafts and Reiber (1948), who investigated the quantitative relationships of oil and phenolic fortifying agents, concluded that for broadleaved weeds there was little advantage in using more than 3 per cent oil as a carrier for DNOSBP in the final spray. Increasing the oil content to around 10 per cent improved the kill of grasses. It is a common practice in preparing contact sprays either of pentachlorophenol or DNOSBP to use about 20 per cent oil in order to ensure adequate penetration to the growing points of grasses.

DNOSBP is very soluble in oil and the commercial formulations available may be mixed with most oils in any proportions. Oils in the boiling range of the fuel oils, diesel oil, and kerosene are commonly employed. Pentachlorophenol is considerably less oil soluble and an oil solvent high in aromatics is essential for the preparation of a satisfactory spray. There are on the market concentrated emulsifiable pentachlorophenol formulations to which additional oil must be added.

The use of phenolic herbicides in fortified oils or oil emulsions is limited to specialized vegetation control problems because of their temporary contact or "chemical mowing" effect. Where perennial vegetation predominates and rainfall is prevalent repeated applications are required for continued control. Annual plants may be killed with phenolic sprays especially when young. In semi-arid sections where annuals predominate and dry soil prevents emergence of more seedlings, one spraying will have a lasting effect. Thus in California, much roadside vegetation control for fire protection and also ditchbank weed control is accomplished with emulsions containing pentachlorophenol or DNOSBP.

5. Herbicidal Oils

Various petroleum fractions have been used for many years for the control of herbaceous vegetation particularly in the western United States. Creosote oil and other coal by-product oils have occasionally been used.

Straight oils, like phenolic-fortified emulsions, are contact herbicides. Only tissues actually wet by an oil spray or reached as a result of internal movement are affected. Most plants are susceptible to the action of herbicidal oils; however certain species, notably members of the *Umbelliferae* family, are quite tolerant.

Minshall and Helson (1949), in a study of the effects of herbicidal oils on the physiology of plants, confirmed earlier reports that internal movement is largely through intercellular spaces. Using a dye dissolved in oil they failed to find evidence that oil moved into living cells. Crafts (1946) suggests that plants differ in the manner in which their protoplasm reacts to oil, thus postulating cellular absorption. Dallyn and Sweet (1951) report that aromatic oils actually penetrate cells of oil-susceptible plants, but in tolerent species the oil remains in intercellular spaces.

Crafts and Reiber (1948) distinguish between the acute oil toxicity resulting in a rapid burning of foliage and chronic toxicity resulting in a yellowing of leaves, stunting, and subsequent death. The lower boiling aromatic fractions are responsible for acute plant responses, whereas higher boiling components which persist within plant tissues often have a chronic effect. Minshall and Helson (1949) found that a cessation of photosynthesis and transpiration followed oil treatment. Oil-tolerant plants later resumed these processes whereas the susceptible plants died. Greene (1936) found that in most instances respiration was lowered following oil spraying. Minshall and Helson (1949) postulate that oils kill by disrupting internal water relations which in turn affect transpiration and other processes.

The observations of early users of oils as herbicides indicated that crude fractions were more toxic to plants than refined fractions. Treatments that removed unsaturates and aromatics reduced toxicity. Gray and de Ong (1926) found that the sulfonation test, which indicates the proportion of unsaturated compounds present, may be used as an index of phytotoxicity. However, Crafts and Reiber (1948) have shown that certain unsulfonatable residues are often toxic.

In recent years a number of highly phytotoxic petroleum oils have been placed on the market especially for weed control purposes. Crafts and Harvey (1949) list fourteen proprietory weed oils for general contact weed control on sale in California in 1948. These special oils vary to some degree although all are high in aromatics.

The choice of straight oil or a phenolic-fortified oil emulsion where contact killing of weeds is desired is largely a question of economics. Crafts and Harvey (1949) express the view that since the use of fortified

oil emulsions greatly extends the service of a given volume of oil they will probably become widely used as their properties become known.

Emulsifiable aromatic petroleum fractions high in xylenes are currently used for the control of submerged plants in irrigation canals and ditches. (Anonymous, 1949). They have essentially a contact action on aquatic vegetation, and regrowth from roots of anchored aquatics occurs freely.

6. *Boron Compounds*

The phytotoxic effects of excesses of boron in the soil have been recognized for many decades and much experimental work on the subject has been conducted by plant nutrition and fertilizer investigators. The use of borax, a hydrated sodium tetraborate, and other boron compounds for vegetation control was apparently an outgrowth of such work.

Unlike sodium chlorate and the organic compounds used as herbicides, chemicals in this group owe their herbicidal effect to a phytotoxic element, boron, rather than to a particular molecular structure of otherwise nontoxic elements. The borate ion is absorbed by the roots and becomes systemically toxic.

A coarse grade of sodium borate sold under the proprietary name Borascu has been used for several years for soil sterilization of areas to be kept free of vegetation such as parking lots and driveways. Recently a form higher in boron content, designated as concentrated Borascu, has become available.

Boron compounds have a low level of toxicity to warmblooded animals and do not support combustion. They are relatively cheap, but large quantities are required for effective control of vegetation. As most boron-carrying ores are mined in California, transportation is a major cost factor when used in eastern or midwestern United States or Canada.

Soil properties and rainfall are the important factors in the success of boron compounds for soil sterilization. Crafts (1939), who studied the response of plants to borax in three soils at two nutrient levels, concluded that it was most effective in the lighter and more porous soils. He found that soil fertility per se had no effect on borax toxicity as it does with sodium chlorate.

Crafts and Raynor (1936) found that the toxicity of borax applied at herbicidal dosages on a given soil varies with the rate of fixation and leaching. Soil moisture is essential to move the slightly soluble borax into the zone or root growth. Fixation tends to hold the borax near the surface particularly in clay soils, but on porous soil it may be leached below the zone of maximum root growth. That fixation accounts for loss of toxicity was shown by Crafts and Raynor (1936), who observed a

gradual decrease in the toxic properties of soil in cans even though no boron was lost from the cultures. The rate of toxicity loss was greatest in clay soil high in lime and was lowest in a sandy loam.

During a season of high summer rainfall the writer has observed complete failure of two ton of borax per acre on a clay loam while the same dosage on an adjacent sandy soil gave a complete kill of existing herbaceous vegetation. Boron compounds appear to have the greatest initial effect and to give the longest period of control on light soils in areas of moderate to light rainfall.

Plants vary considerably in their boron tolerance. Grasses as a group are relatively tolerant, however, certain broadleaved species also require very heavy dosages for effective control.

7. *Sodium Arsenite*

For many years sodium arsenite was used for soil sterilization of railroad beds and other industrial grounds; however, its high degree of toxicity to animals has been a cause of considerable livestock loss. It is considered safe only on well-fenced areas where there is no chance of stock eating sprayed vegetation or drinking water that may be contaminated by leaching from sprayed areas. Great care must be exercised in handling arsenite solutions to avoid contact by the operator or inadvertent spillage where stock may have access to it.

Like borax, sodium arsenite owes its herbicidal properties to a toxic element, in this instance arsenic. Solutions sprayed on foliage have a contact herbicidal effect; however, the killing of established plants results from systemic poisoning following absorption of the arsenite ion from the soil.

As the highly soluble sodium arsenite must be present in the root zone to be absorbed, rainfall and the textural grade of the soil are important factors in toxicity. (Crafts and Rosenfells, 1939). In addition to the kaolinitic colloids of the soil, the presence of red iron oxide was found by these authors to reduce arsenic toxicity. Like borax, sodium arsenite tends to be most successful on light soils in areas of moderate to light rainfall.

As with other herbicides, plant species vary in their tolerance. Deep-rooted perennials growing on soils where much of the arsenite may be fixed in the surface layer are often difficult to kill. Certain summer annuals that are natives of arid or semi-arid regions show considerable physiologic tolerance (Robbins *et al.*, 1942).

Dosages of sodium arsenite required for soil sterilization vary from about 4 to 8 lb. per square rod, depending on soil and rainfall factors.

Lower rates applied as a foliage spray will kill top growth by contact but root kill may be limited.

8. *Ammonium Sulfamate*

This herbicide has a systemic effect on most plants and is translocated from foliage to the stems and underground parts of many species. The use of ammonium sulfamate on industrial lands is primarily for woody plant control. Grasses and other herbaceous plants adequately wet with the spray will be killed.

Jacobs (1950) has reported extensive commercial scale comparisons between ammonium sulfamate and esters of the chlorophenoxyacetic acids for brush control on utility right-of-ways. He reports that at a somewhat higher initial cost ammonium sulfamate gives a more complete kill of mixed woody species than the chlorophenoxyacetic acids, and less frequent applications thus need to be applied. Jacobs points out that ammonium sulfamate gives a superior kill of oaks, hickories, maples, and wild cherries, whereas certain other species are more sensitive to 2,4-D and 2,4,5-T. He suggests the use of ammonium sulfamate on mountainous and relatively inaccessible right-of-ways where cost of application is high and where the most effective killer will lengthen the period between sprays. Greco (1951) has reported successful eradication of a variety of marshland woody species with ammonium sulfamate.

9. *CMU 3-(p-chlorophenyl)-1,2-dimethyl urea*

A discussion of the many new experimental herbicides now being investigated for various industrial vegetation control problems is beyond the scope of this review. One of particular note is 3-(*p*-chlorophenyl)-1,1-dimethyl urea, called by its manufacturers CMU.

Bucha and Todd (1951) and Wolf (1951) have presented data on the nature of the herbicidal effect of this compound. It is toxic to most plants. It is absorbed from the soil by the roots and appears to be transported to above-ground parts. CMU is very persistent in the soil.

Young and Loomis (1951) reported that effective vegetation control was obtained for one season on railroad cinder ballast with the use of 20 lb. of CMU per acre. The vegetation controlled included quackgrass and miscellaneous annual and perennial plants. Comparable results were obtained when 10 lb. of CMU were applied in combination with 80 lb. of sodium chlorate or 30 lb. of sodium TCA. Viehmeyer *et al.* (1951) reported successful control of mixed vegetation along an irrigation ditch with CMU. Further work will be required before the place of CMU in various vegetation control programs can be determined.

10. Mixtures of Herbicides

Because of variation in response of plant species to different herbicides many vegetation control problems must be handled with mixtures. The common use of 2,4-D and 2,4,5-T esters for control of woody plants has already been described.

Mixtures of sodium chlorate and boron compounds are being used for killing existing vegetation and providing a germination-preventive residue. Chlorax and Polybor-chlorate are proprietary products of this type. Taylor (1951) found a mixture of sodium chlorate and sodium TCA to be among the most successful treatments for railroad beds, and this combination is now used on some railroads.

A mixture of borax and sodium TCA has shown promise for complete vegetation control and sodium 2,4-D added to this combination has improved the kill of deep-rooted perennials In the mixtures referred to above sodium TCA serves primarily as a grass-controlling agent. Whenever employing sodium TCA for grass control another herbicide such as 2,4-D must also be used if non-grasses are present. An effective mixture for the control of established vegetation consists of a phenolic-fortified oil emulsion with a 2,4-D ester in the oil phase and sodium TCA in the water phase.

III. Special Problems on Various Industrial Lands

So many industrial vegetation control problems have only recently been attacked with chemical tools, that further experience must be gained before the most efficient and economic methods for each type of problem will be fully known. Variations in soil, rainfall, length of growing season, and species composition all have their influence on choice of chemicals as well as methods and timing of application. Supply and cost of labor is another vital factor. No blanket programs can be suggested in a review of this type, however certain problems and their solution will be described.

1. Some Ecological Considerations

The old saying "nature abhors a vacuum" is never more evident than following certain herbicide applications. The most persistent soil sterilants are eventually leached or inactivated below the phytotoxic level. Reinvasion then takes place and plant successions may be observed influenced by species tolerance to the chemical and prevailing ecological factors.

The continual elimination of all vegetation essential for certain lands such as railroad beds is difficult and expensive, particularly in humid

regions. Before deciding on the need for a vegetation-free condition in any situation one should consider the practicability of a grass cover maintained relatively free of non-grasses by chlorophenoxyacetic acid sprays. Many people have killed all existing vegetation only to find reinvasion occurring sooner than anticipated, frequently with species more objectionable than those which occupied the area before treatment. Wherever a cover of a short-growing perennial grass will serve the purpose, it is generally less expensive to maintain than a sterile soil. Mowing soon after flowering will keep most grasses at a reasonable level. Where mechanical mowing is impractical a contact spray of a pentachlorophenol or DNOSBP-fortified oil emulsion will provide a "chemical mowing" as required. Modest dosages of sodium TCA may be used for suppressing grass growth. When using a selective grass suppressing agent, such as sodium TCA, it is very necessary to include an herbicide, such as 2,4-D, to control the non-grasses; otherwise they may grow rampant because of reduced grass competition.

Although grassland is usually considered the most desirable cover for right-of-ways, Egler (1951) has pointed out that reinvasion with certain woody plants will readily occur in grass communities in New England. He further reports that several types of shrub communities have persisted for many years without reinvasion with tree species. Where tall woody plants cannot be tolerated but a shrub cover is acceptable, the studies of Egler (1951) may have particular significance. He proposes conversion from a mixed tree-shrub community to a shrub or a shrub-grass community by spot treatment with chlorophenoxyacetic acids rather than a blanket spray.

The ease of establishing and maintaining grassed land in humid areas where woody plants are normally present varies with soil factors. In poor acid soils, where grass has difficulty in becoming established, reinvasion with woody plants and non-grass herbaceous species may occur quite readily. Where a thick turf develops, as competitive plants are eliminated reinvasion is frequently rather slow

2. Utility Right-of-Ways

Potential savings by the use of chemical brush control methods as compared with repeated hand cutting have been estimated by a number of right-of-way maintenance engineers with whom the writer has discussed the subject to vary from 50 to 75 per cent. Costs during the first year or two while the area is being converted from brush to grassland are not necessarily higher than the cost per annum for cutting. Savings are realized during ensuing years when only an occasional maintenance treatment is required.

Many of the factors one must consider in deciding on a program for brush control on right-of-ways have already been discussed. Foliage applications of a chlorophenoxyacetic acid brush killer are generally used for the conversion program to eliminate the bulk of the woody plant population. Basal dormant treatment may be desirable where risks from summer spraying are great or where woody plant populations are relatively small. Ammonium sulfamate may have a place on inaccessible land, as suggested by Jacob (1950). The choice of basal *vs.* foliage spraying for maintenance of an area after much of the brush has been eliminated is a subject currently being investigated by a number of public utilities. Stump treatment has proved especially useful when new lines are being established through wooded areas.

Ashbaugh (1950) has discussed a program for brush control on utility right-of-ways which has proved successful in the mountains of western Pennsylvania. Two foliage sprays of a chlorophenoxyacetic acid brush killer at yearly intervals have reduced the number of woody plants from between 4000 and 8000 per acre to less than 1000. During ensuing years basal spraying is employed for adequate maintenance. Ashbaugh reports that the West Penn Power Company with which he is associated has converted 5000 acres of right-of-way from brush land essentially to grassland. The frequency with which a maintenance spray is required will depend on many environmental factors that influence rate of growth and rate of reinvasion.

Alternating herbicides in the maintenance program as suggested by Jacob (1950) may prove desirable.

3. Highways

Much roadside spraying has been aimed at woody plants, the prime vegetation control problem in humid areas. In general the problems of woody plant control along highways are similar to those on utility right-of-ways. Accessibility with power equipment makes a high volume foliage spray highly practical in most situations. Basal applications have proved desirable in some instances for maintenance once the mass of woody vegetation has been eliminated. This method may also prove valuable where foliage spraying would jeopardize sensitive plants. Sylwester (1950) has pointed out that brush control is essential on highways to improve visibility, to provide good drainage, and to minimize drifting snow. He reports considerable savings by the use of chemicals as contrasted to hand cutting which permits rapid regrowth.

In many instances highway maintenance authorities are responsible for the eradication of noxious perennial weeds growing in the right-of-way. Local weed control research has established the best methods for

each species under varying environmental conditions. Bruto (1950) has discussed the use of herbicides for noxious weed control in Missouri. In areas where agricultural land is relatively free of ragweed, roadside spraying to kill this species is now practiced as a public health measure. (Anonymous, 1950; Vintinner, 1951).

Vegetation near guard rails and traffic signs where mowing cannot be accomplished mechanically presents a special problem. The objective here is to eliminate tall-growing non-grasses and retard grass growth. Complete elimination of vegetation in such situations is not desirable in areas of high rainfall because of erosion and the inevitable reinvasion with weeds. No proved chemical program is being used, however Iurka and Pridham (1950) have reported progress with several herbicide mixtures. In arid sections where annuals predominate, contact sprays of oil or fortified oil emulsions are widely used around signs and guard rails as a fire preventive measure.

Overall weed control for the sake of beautification is not a primary objective on most highways, but there are areas where it is being practiced, particularly along parkways in metropolitan areas. In this connection 2,4-D is the most useful herbicide. By eliminating tall growing weeds with this herbicide a single mowing after grass flowering is often adequate to keep the vegetation short for the balance of the season.

In humid areas where elimination of non-grass vegetation is desired, late spring and early summer spraying will often provide maximum kill of tall growing perennials such as golden rod, wild aster, and thistles. The same spray may fail to control other species which are low in growth at this time of the year, i.e., wild carrot, because grass and taller herbaceous plants protect them from spray interception. Mowing after grass flowering followed by spraying after some weed regrowth has occurred is a recognized method of providing maximum kill.

4. Railroads

Complete elimination of vegetation on the roadbed is the universal objective of maintenance engineers. The width of this strip usually extends from 4 to 6 ft. beyond the edge of the ballast. Vegetation in this area causes slippage if it should lodge on the tracks. It impedes good drainage, shortens tie life, and endangers train crewmen who must often mount and dismount moving cars.

For many years some spraying of roadbeds has been practiced and today a large proportion of the heavily traveled track in the United States and Canada is treated with herbicides. At one time sodium arsenite was widely employed, but livestock losses have discouraged its use by most railroads. Sodium chlorate is widely used for railroad

spraying. Because this compound renders sprayed vegetation highly flammable calcium chloride is frequently included in the spray solution as a fire preventive measure. Several of the mixtures as discussed earlier are also employed (Rake, 1950).

Much special equipment has been built by railroads and by contract spray operators for roadbed treatment. Rapid sectional controls that permit heavy application where vegetation requires and which may be quickly shut off where there is no vegetation are common to good equipment. When 2,4-D is to be included in the spray, an injection system

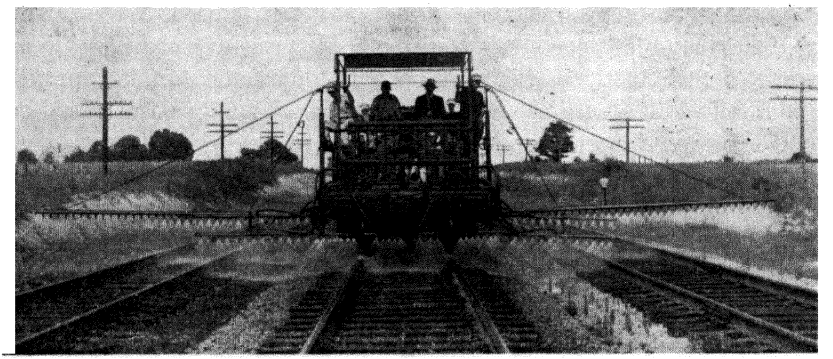


FIG. 1. Roadbed sprayer in operation. This is the lead car of a spray train consisting of tank cars and a locomotive. Note the series of valve handles in front of the operators used to control the various boom sections.

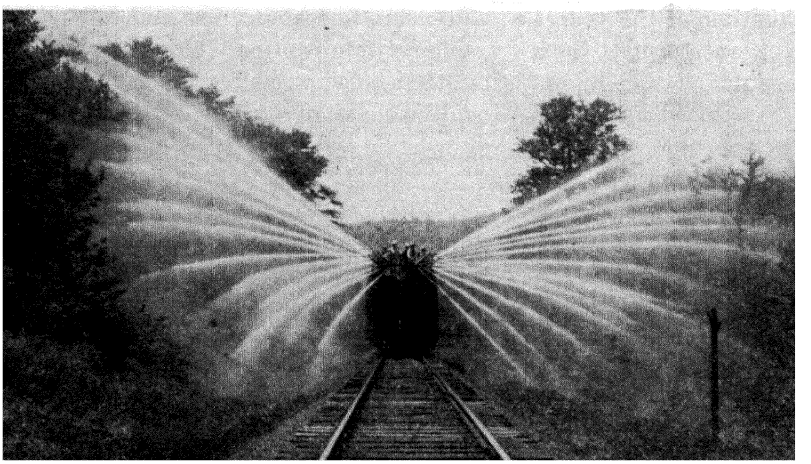


FIG. 2. A railroad brush sprayer in operation. Ahead of this spray car are several tank cars all being pulled by a locomotive.

which permits introduction of this herbicide into a mixture where safe to use and quick shutoff where hazards to adjacent plants dictate has been found useful.

The control of vegetation between the roadbed and the fence by mowing or other mechanical means has long been a major section crew task. Railroads are taking an increasing interest in adapting the woody plant control methods so widely used on utility right-of-ways. Several special pieces of on-track equipment that permit spraying brush from a moving spray train have been constructed and are now in use. Foliage application of chlorophenoxyacetic acid brushkillers are employed. Gillingham (1951) has discussed such equipment and its use.

Certain areas where fire hazard is great, such as under wooden trestles, are often treated with borax at high rates to provide a relatively vegetation-free condition for as long a period as possible.

5. Miscellaneous Problems

Only a portion of the many programs now employed for vegetation control on various industrial lands have been reported in the literature. A few that have come to the writer's attention will be mentioned.

For adequate fire protection oil tank farms require sparce vegetation throughout the area with bare soil near tanks. Grazing by cattle or sheep has proved useful for large areas while various chemical treatments are often used adjacent to the tanks. Herbicides may also be used for the elimination of unpalatable species in the grazed area.

Problems of complete vegetation control are handled with various herbicides frequently in combination (Rake, 1950). Pole yards, transformer stations, lumber storage areas and grounds near wooden buildings are examples. Such areas should be covered with crushed rock, gravel, or cinders to prevent water and wind erosion. Contact sprays of phenolic herbicides have been used to keep vegetation at a minimum in ammunition storage areas without creating an erosion problem.

Egler (1950) has reported the successful use of a chlorophenoxyacetic acid brushkiller for vegetation control on transmitter sites. By selective basal application species especially valuable for wildlife food or cover were preserved while less desirable species were eliminated.

Both submersed and emergent aquatic plants may be a problem in irrigation ditch and canal channels and terrestial plants must be properly managed on the banks. Methods of vegetation control on irrigation systems in the western United States have been thoroughly discussed in a recent bulletin (Anonymous, 1949). Burning, mowing, controlled grazing, and herbicides are all employed. The injection of emulsifiable

petroleum fractions high in xylenes for the control of submerged aquatics in irrigation ditches is one of the more recent developments.

Cattail in irrigation ditches of the Imperial Valley have been successfully killed with a spray containing an amine salt of 2,4-D, sodium TCA, and a wetting agent. Other emergent aquatic weeds being successfully controlled with 2,4-D are lotus and alligator weed (Hess, 1946). This herbicide is now employed for the control of water hyacinth in canals and waterways in Florida and Louisiana (Hitchcock *et al.*, 1949).

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Soil and the Growth of Forests

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I. Introduction

In the humid parts of the United States the area occupied by forests is greater than that occupied by field crops. Most of the mountain land in both the East and the West will be in forests or grass indefinitely because of topography and climate. Many other geographic units are committed to forest use because of poor drainage or extreme soil properties such as sandiness which preclude their use for field crops in the foreseeable future.

Agronomic research here and abroad has resulted in the accumulation of a vast amount of information on the relationship between soil properties and the growth and yield of field crops. In contrast, most of the significant research in this country on the relation between soil and the growth of forests has taken place during the last 15 to 20 years. Results that can be used in the field, in the estimation of land quality for forests, have been obtained only in very recent years.

Soil characteristics which affect the growth and yield of field crops can be greatly modified and improved by artificial drainage, cover crops and green manure crops, appropriate crop rotation, tillage, and the proper use of fertilizers. Irrigation has long been practiced to make fertile dry-land soils productive for field crops, and it is being used more and more in humid climates. In contrast, little can be done in the way of increasing the productivity of the vast acreage of soils supporting forests. The rotation, or time that an individual forest occupies an area, may vary from 30 years for pulpwood to over 100 years for saw logs. Even if appreciable increase in growth could be obtained from the application of fertilizer, it would not ordinarily be economically feasible.

In this review significant contributions to our knowledge of the relation between soil profile features and the growth of various forest types or tree species will be presented on a regional basis. This seems necessary because the economic range of various tree species is limited regionally as are also soil groups and the climates under which both the soils and the forest vegetation have developed. Soil properties which may be significantly correlated with forest growth in one region may not be significant in another region because of differences in tree species, climate, length of growing season, length of day, or action of other limiting soil factors.

1. *The Problem*

If all forest land was covered with well-stocked stands of sufficient age for the entire solum and the upper substratum to have affected their growth, there would be little practical need for studying the relation between soil properties and growth because the volume of wood per acre at a given age would be a direct measure of productivity. However, this situation obtains only in isolated cases east of the Great Plains, and in some second-growth and virgin forests in the West. Moreover, most of the accessible virgin forests of the West will eventually be cut and subsequent stands will be managed on a much shorter rotation than at present; hence, even for these lands, information on the productivity of the soil for various species is needed.

Most forest land does not support stands of such stocking and age as to reflect soil productivity in terms of height, growth, or yield. The principal object of studies of soil properties and the growth of forests should be the development of methods for evaluating the productive potential for various tree species of non-forest land (abandoned crop land), cut-over, partially cut timberlands, or land that supports very young or very old decadent stands.

2. *Measures of Forest Growth*

Measures of forest growth include annual and periodic volume increases in cords, cubic feet, and board-foot units per acre. Yield at a given age is also expressed in these units. However, in evenaged stands, the total height of trees in the dominant crown canopy is the best measure of soil productivity because it is least affected by stand density or the number of trees per acre at any given age. Stand density is usually expressed as basal area (the sum of the cross-sectional areas of the tree stems 4.5 ft. from the ground expressed in square feet per acre), or stocking in milacres (Chisman and Schumacher, 1940).

In forestry a *site* may be defined as an area of land with a characteristic combination of soil, topographic, climatic, and biotic factors. *Site quality* refers to the productive capacity of an area of land for a tree species or a mixture of species (a forest type). It may be expressed in terms of total height of trees in the dominant crown canopy at an index age (50 years for many species). When site quality is expressed in terms of height of trees at a given age, it is called *site index*. Typical site index curves are shown in Fig. 1.

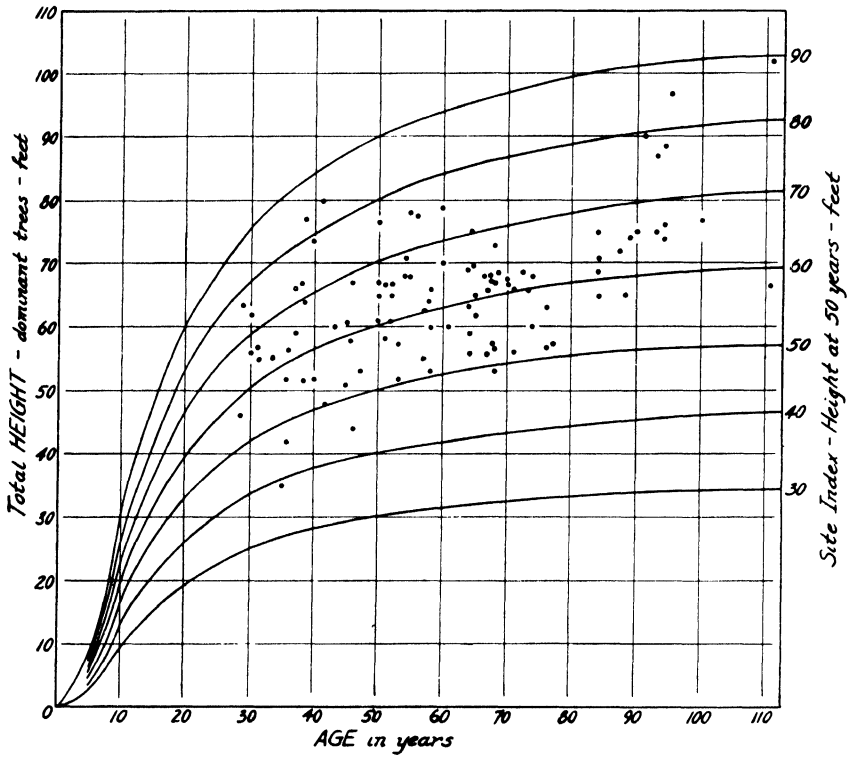


FIG. 1. Typical site index curves.

3. *Soil Properties Related to Forest Growth*

Numerous studies have been conducted to test the relationship between physical, chemical, and biological properties of soil and the growth of forests. Site quality is largely determined by soil properties, or other features of site, which influence the *quality* and *quantity* of growing space for tree roots. Success or failure in demonstrating significant relationships between soil properties and plant growth depends largely on the investigator's ability to select for measurement and statistical tests the independent variables that are initially limiting or most limiting.

II. SOIL AS AN ENVIRONMENT FOR TREE ROOTS

The factors that affect root distribution in forest stands may be listed as climate, soil, topography, and inherent rooting habits of different tree species.

1. *Climate: Effectiveness and Distribution of Precipitation*

A considerable amount of the total precipitation occurring over forested land never reaches the mineral soil. In the pine and hardwood forests of the Southeast approximately 0.25 in. of precipitation is intercepted by the tree crowns and is lost through evaporation, and as much or more is absorbed by the unincorporated organic matter (A_0 horizon). Hence, any individual rain must be in excess of approximately 0.5 in. before it may contribute to the moisture supply in the upper mineral soil. Under climatic conditions characterized by periodic precipitation during the growing season the uppermost part of the mineral soil is repeatedly moistened to the field capacity and dried to near the wilting point. In contrast, the soil below this zone may be at or near the wilting percentage for longer periods of time because the water retention capacity of the upper zone must be satisfied before water will move under the force of gravity to lower depths. If the total annual precipitation occurs mostly as snow or as rain during the winter months, the entire soil mass will start the growing season at the field capacity, and its moisture content will be gradually reduced during the growing season. In the former case, small tree roots will be concentrated in the upper part of the soil which is repeatedly moistened, whereas in the latter case the roots will be more uniformly distributed in depth.

Roots will grow whenever conditions of temperature, aeration, moisture, and fertility are favorable. In the South, lateral roots of pine trees grow throughout the year with intermittent periods of dormancy whenever the soil moisture content approaches the wilting percentage or when soil temperature drops to the freezing point (Reed, 1939). Granted that the fertility level of any soil is sufficient to support tree growth, then the distribution of tree roots and their concentration vertically in stands will be influenced by water availability and aeration. Soil aeration decreases markedly from the surface downward in well-differentiated soils; hence, a high concentration of small roots, the tips and relatively young tissue near the tips of which represent most of the absorbing area, is not to be expected at great depths below the surface. Under conditions where subsurface irrigation is not a factor and precipitation is uniformly distributed throughout the year, as in humid temperate climates, small roots tend to be concentrated in the uppermost part of the mineral soil as well as in the F and H layers of the A_0 horizon if they are present. These zones afford maximum aeration and are the first to benefit by the average rain of 0.75 to 1.50 in. during the growing season. The penetration of precipitation of this magnitude is limited and conditioned primarily by the water-holding capacity of the

soil which is determined by texture and organic matter content. Within a given climatic regime, the average penetration of moisture from periodic rains is greater in coarse-textured than in fine-textured surface soils, and this is reflected in the vertical distribution of small roots.

In regions where the annual precipitation occurs largely as snow, factors of soil, substratum, and topography that influence moisture infiltration, storage, and subsurface flow determine the relative position of roots in the soil profile.

2. *Soil Properties: Texture, Permeability, Aeration, Infiltration, Stoniness, and Organic Matter Content*

Small roots are uniformly distributed to greater depths in coarse-textured soils than in fine-textured soils where the amount and distribution of rainfall is of the same order. For example, on Lakewood sand in the Ocala National Forest in Florida, roots less than 0.1 in. in diameter in stands of sand pine (*Pinus clausa*, Engelm. Vasey) are rather uniformly distributed in the mineral soil to a depth of 17 to 20 in. In contrast, roots of this size class in mature pine stands or oak-hickory forests on fine-textured soils (silt loams and clay loams) in the Piedmont Plateau region are concentrated in the top 3 in. of mineral soil. In both cases, this depth indicates the average penetration of 1.5 in. of rain when consideration is given to interception, absorption by surface organic matter, and the water-holding capacities of the mineral soils. Water penetrates deeper into soils which contain an appreciable amount of stone than it does into those of the same textural grade without stone.

Permeability of soil to water and air is correlated with other soil properties and affects root growth markedly. Coile and Gaiser (1942a) found that the foliation and subsequent growth of black locust (*Robinia pseudoacacia* L.) seedlings growing in a heavy plastic impermeable clay were markedly increased by the presence of a screen cylinder containing sand. This device improved soil aeration.

Soil aeration, difficult to measure directly, is highly correlated with other soil properties such as volume changes (swelling and shrinking) that occur with changes in moisture content. Soils which exhibit large changes in volume with moisture changes tend to be poorly aerated when they contain adequate amounts of water for root growth, the noncapillary pore space (air space) being greatly reduced by internal swelling. Coile (1942), Slade (1949), and McClurkin (1951) have found that volume changes of fine-textured soils measured as shrinkage from a saturated state to the oven-dry state are highly correlated with the moisture and xylene equivalents of the soil. On the basis of 31 ob-

servations on the subsoils of 16 widely different soil series of the Piedmont region, Slade developed the following equation for shrinkage:

$$Y\,(\text{Shrinkage in \% vol.}) = -0.413 + (0.179 \pm 0.040)\,(\text{M.E.} + \text{X.E.}) + (0.951 \pm 0.153)\,(\text{M.E.} - \text{X.E.}) \quad (1)$$

where M.E. = moisture equivalent, weight basis
X.E. = xylene equivalent, weight basis, corrected to specific gravity of water
M.E. − X.E. = imbibitional water value (I.W.) (Fisher, 1924)

Both variables are significant at the 1 per cent level.

McClurkin's data were based on 21 observations on 11 different soil series in the same region. The following relationship between volume shrinkage and other physical properties of the soil was developed:

$$Y\,(\text{Shrinkage in \% vol.}) = 11.265 + 1.021\,(\text{I.W.}) - 0.0575\,(2\,\text{sand \%} - \text{silt plus clay \%}) \quad (2)$$

The first independent variable (I.W.) is significant at the 1 per cent level, whereas the second, mechanical composition, is significant at the 5 per cent level. The former is correlated with the amount and the crystal structure of clays, whereas the latter is a direct measure of amount of various particle size classes.

Soil permeability, expressed in terms of pore space drained under 60 cm. tension, can be estimated if the imbibitional water value and mechanical composition of the soil are known (Diamond, 1951). Analysis of 116 observations of permeability paired with the two independent variables yielded the following equation:

$$Y\,(\text{Permeability}) = 23.15 - 11.23\,(\log.\ \text{I.W.}) - 0.07\,(\text{silt plus clay \%}) \quad (3)$$

A similar study of permeability pore space drained under 60 cm. tension in 15 hours, made by Maple (1951) on 113 samples from 53 profiles, yielded the following equation:

$$Y\,(\text{Permeability}) = 11.23 - 6.17\,(\log.\ \text{I.W.}) \quad (4)$$

Curle (1951) found root and shoot growth of slash pine (*P. caribaea* Morelet) seedlings to be lower in subsoil of low permeability and high imbibitional water value, such as the Orange series, in comparison with contrasting soil series such as Davidson, Georgeville, and Cecil whose permeability is higher and whose imbibitional water values are relatively low. In this study the Orange subsoil was water-logged for 18 months and consequently was poorly aerated.

Humus, either unincorporated and in the form of an H-layer or incorporated in the mineral soil as an A_1 horizon, exhibits favorable characteristics for holding water that is available to plants. Thick

H-layers are associated with a high concentration of small roots, which condition may be attributed in part to the high water-holding capacity of the humus coupled with the fact that in an ordinary rain the humus may absorb all the water, thus leaving little or none for gravitational flow to the mineral soil below it (Coile, 1938a).

Organic matter increments in coarse- and medium-textured soils increase the moisture equivalent or field capacity more than they increase the wilting percentage; hence, they increase the amount of water available for root growth in the A_1 horizon as compared to the A_2 horizon. This tends to cause the development of a concentration of small roots in the A_1 horizon if rainfall occurs intermittently during the growing season (Coile, 1938b; Coile and Gaiser, 1942b).

3. Topography: Slope, Subsurface Irrigation, and Water Table

Degree of slope and extent of slope influence both surface and subsurface movements of water. Lower slopes have a greater potential supply of water than upper slopes and ridges with the same precipitation.

Subsurface irrigation is an important source of soil moisture and hence influences root distribution in steep mountain soils when relatively impervious rock formations approach the surface of the land. This is especially significant in areas such as the Northern Rocky Mountain region where most of the annual precipitation may occur as snow. Following the snow melt, water in excess of the water-holding capacity of the soil and substratum tends to move down the slope along relatively impermeable rock strata and may be observed as seepage where the impermeable material approaches the surface. Thus an important source of moisture for root growth under such conditions of climate and terrain is a subsurface supply which entered the soil at some distance from and above the place where it is finally absorbed by roots. Under such conditions small roots of trees tend to be uniformly distributed to a greater depth than is the case in soils on gentle slopes that receive appreciable quantities of water directly on the surface during the part of the year when temperatures are sufficiently high for plant growth both above and below ground.

A permanent water table close to the surface of the ground causes tree roots to be concentrated above the saturated zone. This condition is often seen in coastal regions.

4. Inherent Rooting Habits of Forest Trees

A considerable volume of material has been written into textbooks of forest ecology and silvics in attempts to classify the root systems of trees into deep-rooted, shallow-rooted, with or without tap roots, and

intermediate classes. This has been done without much quantitative evidence. The position in three-dimensional space of the root systems of most forest trees is subject to great modification by the root environment i.e., physical properties of the soil, water availability, and aeration.

In young well-stocked forest stands a concentration of roots near the surface becomes evident at about the time a closed canopy has been formed and competition for growing space above the ground (light) becomes marked. This appears to be between 18 and 24 years for southern pines. This condition may be considered the beginning of a forest soil root profile which culminates in the greatest amount of absorbing root surface in the A_0 and upper A horizon under the climax forest (Coile 1937, 1940).

The root patterns of seedlings are relatively distinct by groups of seedlings. Large seeded species tend to develop relatively deeply penetrating root systems before shoot growth becomes significant. For example, the tap roots of the oaks, hickories, and walnuts may grow a foot in length before the cotyledons appear above the surface of the soil. In contrast, most of the pines other than longleaf pine have a more balanced ratio of roots to shoots. As young trees develop to maturity, their root systems are more and more modified by their environment, i.e., the soil.

A great many of the controlling factors in forest succession, which culminates in a stable and perpetuating forest community, hinge upon the development of a zone of high root concentration near the surface, which precludes the reproduction of species whose juvenile root system is inherently superficial or whose reduced photosynthetic efficiency under a closed forest canopy results in the manufacture of insufficient food for adequate root development extending below the zone of greatest competition from established vegetation.

III. Northeastern Region

1. Conifer Types

Haig (1929) reported a study of the relation between the site index of young red pine (*Pinus resinosa* Ait.) plantations in Connecticut and the "colloidal" content of the various soil horizons. He found that the site index of red pine increases as the percentage of the finer fractions (silt plus clay) increases in the A horizon. Presumably the textural grades of the A horizons studied ranged from sands to loams, and the textural profiles of the soils were not greatly differentiated. Haig's data indicate that red pine has higher site index values on sandy loam and

loam soils than on loamy sand or sands (Fig. 2). This generality also holds in the Lake States region, where it has been found that jack pine (*P. banksiana* Lamb.) does better on the coarser soils than either red pine or white pine (*P. strobus* L.). Another study of the relationship between soil properties and the site index of young red pine plantations in Connecticut was made by Hickock *et al.* (1931). The plantations were

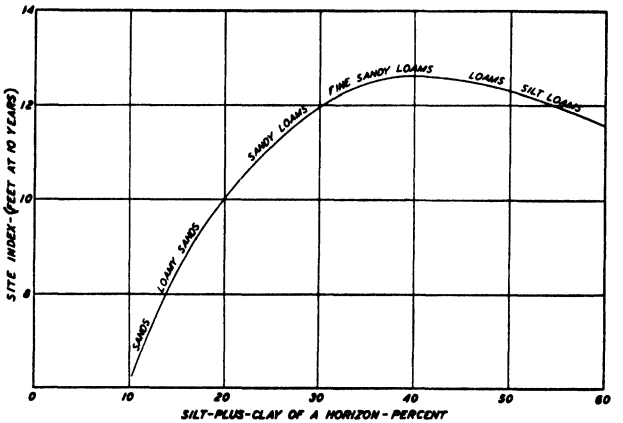


FIG. 2. Relation of site index of red pine plantations to amount of fines in the surface soil (Haig, 1929). Correlation index is 0.58 ± 0.07; standard error of estimate is ± 1.32.

from 12 to 30 years of age and occurred on a rather wide range of soil types. They found a low degree of correlation between site index and individual soil attributes such as soil series, texture, and the character of the A_0 horizon and of the subsoil. No relation was found between the acidity of any soil horizon and site index of red pine. Silt plus clay content of the A horizon showed a fairly good correlation with site index for values of silt plus clay up to 25 per cent, which is in line with Haig's results.

Total nitrogen content of the A horizon showed a better correlation with site index than did any other factor analyzed (Hickock *et al.*, 1931). With respect to total nitrogen content of the surface soil in this study, it should be appreciated that other factors of the soil-site and vegetation complex affect it; for example, soil nitrogen should increase with increasingly favorable moisture conditions for the growth of vegetation and the subsequent decay of organic matter formed by the vegetation.

It is believed that the absence of stronger correlations between site

index of red pine and soil characteristics was due to the age of the plantations, which was under 30 years. It is probable that subsoil characteristics, parent material, and the moisture regime as influenced by topography are most effective in conditioning growth of forest stands after they have reached the developmental stage when competition for growing space, moisture, and nutrients becomes marked. Unless forest stands are greatly overstocked when they start, they do not develop a conspicuous concentration of small roots near the surface until they are 20 to 25 years old. When this concentration of surface roots occurs, which can be called a forest soil root profile, competition for moisture and nutrients obtains in the surface zone, and trees must depend partly on roots at lower depths in the soil and substratum for the absorption of water. If subsoil or substratum characteristics are unfavorable for root growth, then the growth of the trees is reduced when the roots in the surface-soil zone compete strongly for available water and nutrients.

Remarkable response in growth of young red pine to application of slash and humus on deep sands in Warren County, New York, has been reported by Heiberg and White (1950). The plantings, made in 1928, showed retardation of growth when only 5 or 6 years old. The stagnated trees were characterized by general chlorosis, dying of needles, decrease in the number of years that the needles persist on the tree, shortening of the needles, and decreased height and diameter growth. Application of fresh slash in the spring of 1934, obtained from nearby white pine (*P. strobus* L.) stands on good soils, resulted in immediate response in the form of improved color and needle length followed by increased height growth the next year. In control plots glass wool was used to obtain the same mulching effects as slashing, but no response in tree vigor occurred. The effect of a 2 in. application of the H-layer from a white pine-hemlock (*Tsuga canadensis,* L. Carr.) stand, which was spaded into the soil, on the growth of red pine, white pine, white spruce (*Picea glauca,* Moench Voss.) and red spruce (*P. rubra* Link.) was striking. In 15 growing seasons the average heights by species for humus-treated and control plots were: red pine 14.7 and 7.2 ft.; white pine, 9.9 and 5.2 ft.; white spruce, 6.6 and 4.4. ft.; and red spruce, 6.1 and 1.8 ft. The tree spacing was 2 ft. by 2 ft.

Studies were later made of the effects of various applications of mineral fertilizer on the growth of red pine. The amount and kind of fertilizer applied per acre were: 500 lb. 5-10-5, 100 lb. ammonium sulfate, 500 lb. calcium oxide, 200 lb. potassium chloride, 200 lb. tricalcium phosphate, and 300 lb. sodium nitrate. Increase in tree vigor and response in height growth occurred only in the treatments containing potassium and sodium. Mean annual height growth for the seven growing

seasons of these two treatments was 104 per cent and 41 per cent over the control respectively. The entire fertilizer experiment was repeated in 1946 with increased amounts applied and with potassium sulfate added. Results again indicated a marked growth response to potassium. The effect of fertilization on potassium content of the youngest foliage (one year old) and growth of the trees was still evident after 16 years.

Heiberg (1941) indicated that height growth of forest trees commonly planted in New York is greater on mull than on more humus types. This relationship can be partly attributed to favorable soil-site factors, such as good physical soil properties and favorable moisture conditions, which are conducive to mull formation as well as to rapid tree growth.

The inherent productivity of the wind-blown sandy soils derived from water-deposited sands of glacial origin in parts of the Northeast is extremely low. These soils are comparable in some respect to those of the sandhills of the Southeast and the deep sands of Michigan. When such soils were cleared, for either cultivation or pasturage, wind erosion frequently became severe and their productivity for forest plantations was further decreased by reduction in organic matter. Altpeter (1941), working in Vermont, has found mulches of organic matter such as manure, straw, hay, weeds, or tree slash to increase both survival and growth of conifers on these windblown sands. His observations are in accordance with those of Heiberg (1941), and Heiberg and White (1950), in the Adirondacks, and those of Wilde and Patzer (1940) in Wisconsin.

2. Hardwood Types

Hickock *et al.* (1931) also studied the relation between the composition of natural mixed hardwoods and soil properties in Connecticut. They found no strong correlation between the occurrence of the various species and the soil factors. In the case of lesser vegetation they found that both the frequency and total numbers of plants were higher on moist soils than on drier soils. They did not find any plants that were good indicators of soil types.

More recently Lunt (1939) reported on the relation between certain chemical characteristics of the surface soil to a depth of 5 in. and the site index of evenaged stands of oak in Connecticut. Essentially no correlation was discovered between site index of the oak and various soil characteristics associated with fertility, namely, total nitrogen, exchangeable calcium, available potassium, available phosphorus, and total exchangeable bases. This lack of correlation between the fertility factors and site index would be expected if no great difference between inherent

chemical composition of the soils occurred. Under such circumstances the composition of the surface soil would be conditioned primarily by the stand composition of the oak forest. In this study no observations were made on soil profile characteristics or physical properties. Although apparently no quantitative data were obtained on topography, Lunt concluded that there was a relationship between site index and topography, the best sites being on lower slopes. Lower slopes generally afford better growth conditions than upper slopes or ridges, for tree species that grow in well-drained soils, because of better moisture relations.

McKinnon *et al.* (1935) made a survey of the composition and stocking of cutover old field white pine lands in central New England and concluded that very light soils should be planted (presumably to pine) or allowed to grow hardwoods for cordwood, whereas better sites should be managed for hardwood sawlogs.

Diebold (1935) observed the relationships between soil types and forest site quality in the Northeastern Appalachian Plateau of east-central and south-central New York. The soils of the region are derived from glacial deposits; they are genetically young and strongly influenced by the nature of the parent material, which may be acid or alkaline. Sugar maple and beech were found throughout the area along with other species. On the basis of types of humus layers and occurrence of wind-throw, Diebold concluded that deep, well-drained soils with an alkaline influence in the subsoil were best for the natural hardwood forests, whereas shallow soils and those with poor internal drainage (as evidenced by subsoil mottling) were of low quality for the local hardwoods. Donahue (1939) observed that poor internal drainage was related to failures or to poor growth in coniferous plantations.

Studies of the relationship of depth to water table in various soils in south-central New York as it was influenced by kinds of soil were made by Diebold (1938) and later reported by Spaeth and Diebold (1938). Although they observed that occurrence of roots was markedly affected by the presence of a water table in the poorly drained soils, the few data they had on heights of trees showed no apparent correlations with presence of high water tables. On the basis of soil conditions in that area it appears likely that had proper data been obtained on height, age, volume, and stand composition, the expected relations between poor subsoil drainage characteristics and stand composition and site quality would have been revealed.

IV. Lake States Region

1. *Aspen Type*

The growth of aspen (*Populus tremuloides* Michx.) as affected by soil properties and fire has been studied by Stoeckeler (1948). Aspen is the most widespread type in the Lake States. There are nearly 20 million acres of this type which represent 39 per cent of the commercial forest area. Management of aspen in the Lake States is a problem of considerable importance to foresters in the region. As in the case of other forest types elsewhere, a significant amount of the area of the present or potential type is not made up of stands of such character that site index can be determined in the conventional manner; hence, the desirability of being able to estimate site quality from the soil is apparent. Stoeckeler (1948) measured several soil properties in 30 rea-

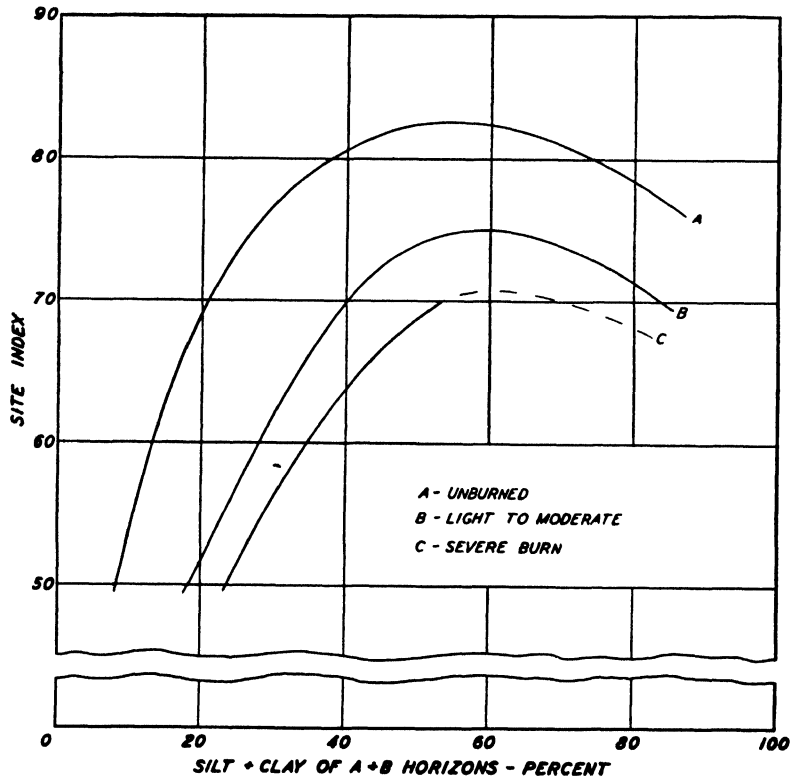


Fig. 3. Effect of soil properties and burning on site index of quaking aspen (Stoeckeler, 1948).

sonably well-stocked stands of aspen which ranged from 20 to 69 years of age. Soil texture, as measured by the amount of silt and clay in the A and B horizons combined, was found to be an important factor affecting site quality of aspen. Productivity increased with a rise of silt plus clay content to an optimum of 50 to 55 per cent and then dropped off somewhat in the finer-textured soils such as the poorly aerated clays. This relationship, along with the effect of burning on site index, is shown in Fig. 3.

Data from 29 plots were grouped on the basis of textural classes and abundance of calcium carbonate in the subsoil. The water table in the soils of these plots was too deep to affect tree growth. The texture of the soils ranged from coarse sands to silt loams. Volumes of the stands increased with increases in the amount of fines in the soil and the greatest volumes were found on medium-textured soils with limy substrata (Fig. 4). Stoeckeler suggested that site classes I, II, III be managed for

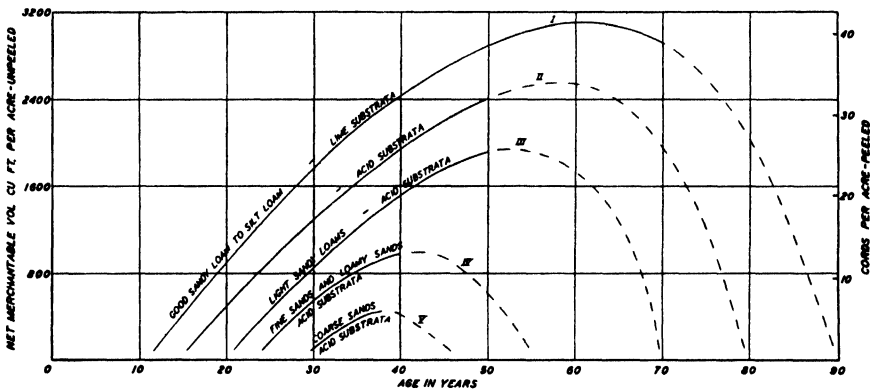


FIG. 4. Influence of soil properties on site class and yields of quaking aspen (Stoeckeler, 1948). Relation of site class to average site index is: I=86; II=77; III=68; IV=57; and V=45.

aspen, whereas the better soils of class IV might be converted to white pine, and the remainder of class IV and class V could be converted to jack and red pines. Aspen is replaced naturally on the first three site classes by hardwood, spruce, and fir. A relationship between former forest cover and the site index of aspen was found in the case of 37 plots which had not been seriously affected by repeated fires. Poor growth of aspen was found on land which previously supported jack pine or a poor growth of red pine. Areas which formerly grew good white pine produced fair aspen, and land which once supported the birch-beech-maple type is in site classes I or II for aspen. The height of mature bracken

fern is a fairly good indicator of site quality for aspen. Where bracken is only 1 to 2 ft. high, site quality for aspen is low, whereas land which will grow bracken to a height of over 3 ft. is of good quality for aspen.

Aspen stands growing on sandy loam containing 35 to 50 per cent silt-plus-clay contain much more reproduction of other hardwoods and of conifers than do stands on coarser-textured soils.

The prospects of profitable management of quaking aspen on various soils as affected by intensity of repeated burns is indicated in Table I (Stoeckeler 1948).

TABLE I

Management of Quaking Aspen as Affected by Soil and Fires (Stoeckeler, 1948)

Soil Class	Per Cent Silt plus Clay in Top 24 in. of Soil	Class of Product Expected of the Site	Prospects of Profitable Management Intensity of Burning			
			Not burned	Light burn	Moderate burn	Severe burn
Poor sands	0-10	———	No	No	No	No
Better sands and loamy sands	10-20	Pulpwood	Yes (light cut)	Usually not *	No	No
Light sandy loams	20-35	Pulpwood and box-bolts	Yes	Yes	Usually not *	No
Good sandy loams	35-50	Lumber, box-bolts, or pulpwood	Yes	Yes	Yes	Usually not
Loams, silt loams, and heavier † soils	Over 50	Lumber, box-bolts, or pulpwood	Yes	Yes	Yes	Usually not

* May produce a light pulpwood cut if there is a permanent water table within 3 to 7 ft of the surface.

† Excludes heavy clay soils whose growth potential is approximately the same as that indicated for light sandy loams

The effect of the distance from the soil surface to the prevailing ground water table, measured as the upper limits of the deoxidized zone (gley horizon), and the organic matter content of the upper 7 in. of soil on average annual height growth and site index of quaking aspen has been reported by Wilde and Pronin (1949). Working with poorly drained

siliceous gley sands in central Wisconsin they obtained conventional data on 22 stands that ranged in age from 22 to 27 years. Height growth and site index increased with increases in organic matter content between 1.5 and 4.5 per cent. Growth increased with increasing depth to the ground water table when it was between 16 and 32 in. Further increases in depth were associated with decreasing site quality.

A comprehensive study of the interrelationships of soil and site index of aspen was conducted by Kittredge (1938) in Minnesota and Wisconsin. The relation between site index of aspen and the following factors was studied: soil texture groups; geological formation groups; combined texture and geological formation groups; soil profile groups; and natural community plant indicator groups. Site index of aspen was found to be most closely related to soil profile groups, to natural community plant indicator groups, and to combinations of these two.

Conventional soil types were grouped by Kittredge into various classes on the basis of the character of the C horizon, extent of development of the A_2 horizon (leached zone) and the moisture regime under which it was developed, textural class of the A horizon, presence or absence of a gley zone, and the development of the A_1 and A_0 horizons. The correlation ratio was used as a measure of the relation between 22 soil profile groups and site index of aspen. Observations were made on 230 sample plots. No one profile feature alone had sufficient weight to enable prediction of habitat productivity. A correlation ratio of 0.795 was found for the relationship between site index and the 22 soil profile groups. The mean site indices of many of the groups were, however, not significantly different from each other. Xeric conditions tended to be unfavorable for the growth of aspen, especially if they were intensified by sandy surface soil and subsoil and associated with a poor development of the A_2 horizon. Mesic conditions tended to be favorable. Hydric conditions tended to be favorable except where they were accompanied by deficient drainage. Strong development of the A_2 horizon was associated with good growth and a weak A_2 with poor growth. A calcareous subsoil tended to be more favorable than a noncalcareous subsoil. Sandy C horizons combined with sandy surface horizons were unfavorable in xeric habitats but generally were favorable in hydric habitats. A clayey subsoil was favorable for the growth of aspen except when associated with deficient drainage. Rock substratum at shallow depths was generally unfavorable for the growth of the species.

Kittredge (1938) concluded that the site index of aspen is a more reliable measure of site quality than volume growth, and may be used satisfactorily for the evaluation of the differences and relative productivity of the aspen habitats. Conversely, the habitat groups, which may be

established most effectively on the basis of soil profiles, may be used within limits for prediction of the average growth. Individual plants of the aspen community do not indicate, with sufficient reliability, differences either in the habitats or growth rates of aspen. Groups of plant indicators, of which the most satisfactory were those based on maximum frequencies in natural communities other than aspen, together with the soil profile groups, are the most useful classifications for the differentiation and for the prediction of the productivity of the different aspen habitats.

2. Other Hardwood Types

The relation of soil characteristics to forest growth and composition in unevenaged northern hardwood forests of northern Michigan has been studied by Westveld (1933). No really satisfactory methods have been devised to estimate site index of unevenaged stands. In this study the heights of dominant trees, regardless of age, were taken as the site index. The 83 one-acre plots examined occurred on 25 soils types. Three site index classes, 70, 80, and 90 ft. were recognized, and 92 per cent of the plots were in the 80- or 90-ft. site index classes. It may be assumed that site index was based on height at maturity rather than height at some base age, such as 50 years in the case of eastern conifers. The narrow range in site index from the poorest to the best is not in accordance with the usual range in evenaged stands of other species. For example, site indices for various species have been found as follows: (basis 50 years) red spruce, 30 to 70; southern pines, 30 to 120; and (basis 100 years) Douglasfir, 80 to 210. In attempting to account for the narrow range of site indices, Westveld (1933) observed that in an oak yield study in Connecticut the range in site index was from 60 to 100, but 86 per cent of plots were in the 70- to 90-ft. classes. On the basis of this he suggested that hardwoods may have more exacting site requirements than conifers, and that the poor sites in these regions are usually not occupied by hardwood forest types. It is doubtful that such a generalization should be attempted, although it is agreed that certain hardwood types have relatively high site requirements. However, it is probable that in most of the earlier yield studies, extremely poor sites were not sampled because of such factors as apparent subnormal stocking. Furthermore, certain scrub oak types are typical of land of low site quality for any species.

The relation between soil characteristics and site index found by Westveld (1933) may be summarized as follows:

SOILS OF GROUP 1. Loams, sandy loams, and loamy sands with yellow sand substratum 15 to 30 in. below the surface. Ordinarily occur as site

class 80, although locally they may occur as class 90. Shallow or stony phases of any of these soils may occur as class 70.

SOILS OF GROUP 2. Loams and sandy loams with a sandy clay till, or drift, substratum 25 to 30 in. below the surface. Occur as site class 90, except where stony when they will occur as class 80 and where shallowness is combined with stoniness they may occur as class 70.

SOILS OF GROUP 3. Silt loams and loams with clay, or sandy clay, subsoils. Occur as site class 90 except in the case of very stony soils.

SOILS OF GROUP 4. Silt loams and loam with open coarse sand, gravel, and cobbles below 40 in. Occur as site class 90 except in cases of shallow or stony soils.

SOILS OF GROUP 5. Shallow soils resting on bedrock. Site class 80.

In 1941 Locke reported on the relation between soil conditions and other site factors and the annual growth of upland oak in the upper Mississippi Valley region. He concluded that the depth of soil horizons and their permeability, slope, and aspect were most important in determining the rate of growth under various conditions of stocking.

Einspahr and McComb (1951) studied the site index of oak in relation to soil and aspect in northeastern Iowa. Total depth of soil to impermeable subsoil or to bedrock was correlated with site index. The influence of soil depth on growth was greater on southerly slopes than on northerly slopes. Site index increased with increasing depth of soil. Site index of oak stands decreased with increasing slope per cent, and it was greater on southerly than on northerly aspects. The site index of white pine growing with the oaks averaged 8 ft. higher than that of the oaks, and the greatest difference was found on the poorer oak sites.

A subdivision of a part of the Upper Peninsula Experimental Forest in Michigan on the basis of soils and vegetation was made by Wilde and Scholz (1934). They indicated that classification of forest tracts on the basis of cover types, for management purposes, may not be entirely satisfactory because the cover types often represent a temporary condition and thus do not give a true expression of forest productivity. They recognized the following five soil conditions and associated forest types: (1) slightly podsolized loam with upland hardwood type (high productivity); (2) loam podsol with hemlock hardwood type (medium to high productivity); (3) swampy podsol with lowland hardwoods and some conifers (low productivity); (4) muck with hardwood conifer swamp type (low productivity); and (5) woody peat with cedar swamp type (very low productivity).

Youngberg and Scholz (1949) disclosed an apparent relationship between total replaceable bases in the upper 7 in. of soil and the growth of mixed oak stands in the unglaciated region of southwestern Wiscon-

sin. Growth or yield was expressed in rather arbitrary terms as volume of average dominant tree in cubic feet at 100 years. Growth increased on the average from 30 cu. ft. to 135 cu. ft. as the total replaceable bases increased from 2 to 10 me. per 100 g. When the latter values increased between 18 and 26 me. per 100 g. the growth was less than 30 cu. ft. Qualitative data on soil types and probable stand composition suggest that stand composition and physical properties of the soil (texture and depth) may be confounded with exchangeable bases and growth respectively.

3. Conifer Types

The importance of soil moisture in the occurrence and growth of black spruce has been emphasized by Westveld (1936). Black spruce will tolerate wet soils, but its growth there is inferior. Westveld found that on poorly drained mineral soils (fine sandy loams) where spruce constituted about 53 per cent of the stand and 10 species were represented, the 10-year diameter and height growth was 0.9 in. and 7.0 ft. respectively. On well-drained sandy loam soils where spruce constituted only about 5 per cent of the stand, the 10-year diameter and height growth was 1.6 in. and 12 ft., respectively, with 13 species represented. On poorly decomposed peat (Spaulding peat) the growth of spruce was only 0.4 and 3.0 ft. in 10 years, whereas on muck soil the 10-year growth was 2.4 in. and 13 ft., respectively. Because of the superior growth of spruce on soils where it constituted only a small percentage of the stand, Westveld suggested silvicultural treatment to favor spruce, especially when the associated species are of inferior commercial value.

A broad ranking of pine soils of northern Michigan into three classes was made by Donahue (1936). Conventional soil types, important in area, were ranked as follows:

1. FIRST-CLASS PINELAND. Ogenaw sandy loam: low-lying, smooth, moist, sandy loam surface soil underlain at 2 to 4 ft. with red clay. Roselawn sandy loam: sandy morainic deposits. Lenses of sandy clay or clayey sand in B horizon and in the parent material.

2. SECOND-CLASS PINELAND. Roselawn sand: coarse-textured surface soil and few clayey lenses in the subsoil. Rubicon sand: flat, well-drained, with yellow B horizon 6 to 22 in. from surface. Bridgeman fine sand: windblown deposits. Fine sand.

3. THIRD-CLASS PINELAND. Saugatuck sand: hardpan 6 to 12 in. from surface averaging 18 in. thick. Wallace fine sand: wind-blown with hardpan. Grayling sand: practically no fine sand, silt, or clay. Low water table.

Classification of Subsoil Properties by Code Number for Black Locust and Black Walnut Site Studies* † (Auten, 1945a)

Code No.	Internal Drainage	Code No.	Plasticity When Wet	Code No.	Compactness When Moist	Code No.	Color ‡
1	Very slow	1	Very highly plastic. Practically impossible to knead into a ball in hands.	1	Very compact. Breaks into lumps, very difficult or impossible to pulverize in hands.	1	Blue or drab-mottled below 8 in.
2	Slow	2	Highly plastic. Kneads into a ball with difficulty, very fatiguing to hands.	2	Moderately compact. Reduced only by considerable pressure to coarse granules which are pulverized only by considerable pressure.	2	Yellowish gray, mottled gray to rusty brown below 14 in.
3	Fair	3	Moderately plastic. Kneads stiffly.	3	Friable. Pulverizes with moderate pressure to mass of moderately resistant granules.	3	Grayish yellow to yellow mottled gray to yellow below 14 to 24 in.
4	Moderate	4	Slightly plastic. Kneads into a ball easily; can be rolled into a wire between palms.	4	Mellow. Pulverizes to mass of fine soft granules.	4	Grayish brown to yellow and mottled below 36 in.
5	Good to fast	5	Very slightly plastic. Wire barely formable between palms without crumbling.	5	Slightly coherent. Pulverizes completely with slight pressure.	5	Yellow brown to brown with little mottling.
6	Good to very fast	6	Nonplastic. Crumbles and cannot be rolled into a wire.	6	Noncoherent, loose.	6	Yellowish brown to reddish brown; no B horizon, no mottling.

* The field indices of plasticity and compactness are from the following sources: J. C. Russell, Report of the subcommittee on soil structure and consistency. In report of eighth annual meeting, American Soil Survey Association. Ames, Iowa. *Soil Survey Assoc. Bull* **9**, pp. 10-18. Mimeographed.

† The soil properties in horizontal order are often related but not invariably so.

V. Central Hardwood Region

On the basis of a study of physical and chemical soil properties and the growth of 135 black locust plantations and 120 black walnut (*Juglans nigra* L.) plantations, Auten (1936) concluded that the physical properties of the subsoil were most influential in determining site index. Plasticity, compactness, and structure of the subsoil gave the highest correlations with site index. Both species appeared to act similarly and unfavorably to insufficient or excessive drainage. Generally both species made their best growth on medium-textured soils such as sandy loams and silt loams. But little relationship was found between acidity, or chemical composition of the soil, and growth of either species.

In a re-examination of the 1936 data on site features and the growth of black locust and black walnut, Auten (1945a) found that physical properties of the subsoil and depth to the subsoil were correlated with height growth. Ratings were assigned to each subsoil by code number for drainage, plasticity, compactness, and color according to the description given in Table II. Thickness and texture of the A and B horizons were measured in the field. The following laboratory measurements were made: plasticity index, total nitrogen, organic carbon, and reaction.

Excessively dry sites were excluded from Auten's general analysis. Examples of these sites include excessively drained sandy soils, shallow soils over bedrock, and severely eroded soils with tight subsoils.

The relation between subsoil properties and site index is given in Table III.

TABLE III

Relation of Subsoil Properties to Site Index * (Auten, 1945a)

	Black locust						Black walnut					
Subsoil Property	1	2	3	4	5	6	1	2	3	4	5	6
Drainage	46	57	62	68	92	110	45	57	53	61	64	65
Plasticity	48	66	77	83	108	117	56	56	63	60	67	†
Compactness	56	69	79	97	101	117	56	61	61	62	63	69
Color	47	56	65	72	84	103	43	54	57	62	61	69

* Coded subsoil properties are given in Table II.

† Subsoil plasticity 6 is not represented here because all plasticity 6 subsoils were in the excessively drained group that was removed as explained in the section on dry sites.

The relation between site index of the two species and depth to the subsoil (least permeable horizon) is shown in Fig. 5.

No real difference was found between high and low sites with re-

spect to nitrogen and organic matter content of the soil. Similarly, no relationship could be demonstrated between soil reaction and site quality.

In 1937 Auten reported a study of the site requirements of yellow-poplar in the Central States. Seventy-eight sample plots in stands between 23 and 61 years of age were examined. Soil and other site features examined included: drainage of the land; soil texture; color of subsoil;

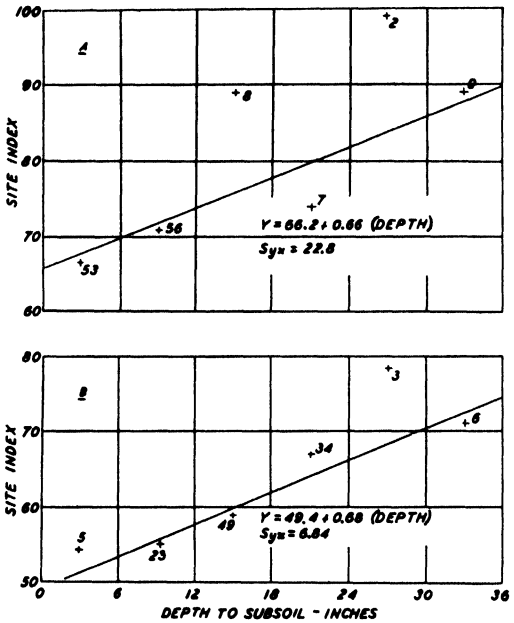


FIG. 5. Average relation between site index and depth to subsoil. A. black locust; B. black walnut. Plotted points are site index residuals (Auten, 1945a).

depth of horizons; depth of organic matter penetration (thickness of A_1 horizon); replaceable calcium; available magnesium; soluble phosphorus; available potassium; reaction; total nitrogen; exposure; topography; and aspect. Growth of trees was measured as average annual height growth for the most part. Many of Auten's results are of interest from the standpoint of the influence of yellowpoplar on the chemical properties of the surface soil. Yellowpoplar was found to make the best growth on deep, medium-textured, well-drained soils. An interesting relation between the depth of A_1 horizon and average annual height growth was found. The range of depths of A_1 horizons was 1 to 12 in., and the range of the height-age ratio was 0.64 to 4 ft. Auten (1937a,

TABLE IV

Coded Properties of Soil and Topography That Are Related to Site Quality of Land for Yellowpoplar (Auten, 1945b)

Subsoil Character				Surface Soil Character		Topographic Character	
No.	Color	No.	Drainage	No.	Texture	No.	Exposure
1	Blue-gray or drab Mottled below 8 in.	1	Very slow	1	Clay	1	Cove-sheltered
2	Drab and yellow Mottled below 14 in.	2	Slow	2	Silty clay	2	Cove-open
3	Yellow Mottled below 20 in.	3	Fair	3	Sandy clay	3	Slope-sheltered
4	Brown-yellow No mottling above 36 in.	4	Moderate	4	Silt loam	4	Slope-open
5	Yellow-brown Little or no mottling	5	Good to fast	5	Sandy loam	5	Flat-open
6	Red-brown No mottling	6	Good to very fast	6	Sand, shale, gravel	6	Ridge

Note: Horizontal rows do not necessarily define any specific soil or site All categories as designated by numbers were used independently of each other.

1937b) concluded that "yellowpoplar will not grow successfully on sites whose original A_1 horizon is less than one inch deep." It appears, however, that yellowpoplar will become established and grow rapidly in old field coves whose soil has no A_1 horizon if the soil has good physical properties and is well drained. If a soil has properties such that a luxuriant growth of yellowpoplar develops, the large annual fall of litter high in calcium results in the incorporation of humus so that a deep A_1 horizon is formed. The writer has observed A_1 horizons of up to 12 in. in depth under yellowpoplar of site index 120 in northern Georgia. Auten found no clear-cut relationships between fertility attributes of the soil and the growth of yellowpoplar. Exposure, topography, and aspect as they influence precipitation, temperature, and evaporation were related to its annual growth.

A method for predicting site quality of land for yellowpoplar on the basis of soil and topography was developed by Auten (1945b). This was based on a reanalysis of data from his earlier reports (1937a, 1937b). Chemical and physical properties of the soil as well as topographic features of aspect and exposure were either measured or described. Aspect referred to slope-facing direction, and exposure to absence of protection from drying winds.

Descriptive terms used to judge some features of soil or topography are given in Table IV.

Large differences in quantity of replaceable mineral nutrients were found among the soils studied. Calcium content per unit weight of soil in the A_1 horizon was higher on good sites than on poor sites. However, this may be a reflection of the large amount of litter, high in calcium, produced on such sites. No relation could be demonstrated between site index and the amount of nitrogen, magnesium, phosphorus, or potassium in the soil.

Site index averages for the subsoil color groups 1 to 6 in Table IV were respectively 57, 59, 90, 84, 91, and 84. Most of the yellowpoplar stands (65 out of 77) were on well-drained soils. Average site indices for combinations of drainage groups 1 and 2; 3, 4, and 5; and group 6 were 56, 83, and 95 respectively. Since 66 of the 77 soils were either sandy loams or silt loams little could be concluded about soil texture and site index. Depth to a tight subsoil rather than the thickness of the morphological A horizon was found to be correlated with site index (Fig. 6). An interesting relationship between the depth or thickness of the A_1 horizon (Fig. 7) and site index of yellowpoplar was demonstrated. This relationship is valid only on areas of undisturbed soil. Depth of organic matter incorporation was correlated with soil moisture conditions.

The regression is:

$$\text{Height of trees} = 1.125\ (\text{age}) + 2.62\ (A_1) + 23.06 \qquad (5)$$

and, the standard error of an estimate is 12.12 ft.

Average site indices for exposure classes 1 to 6 were 101, 94, 89, 77, 72, and 65, respectively. Southerly facing slopes had an average site

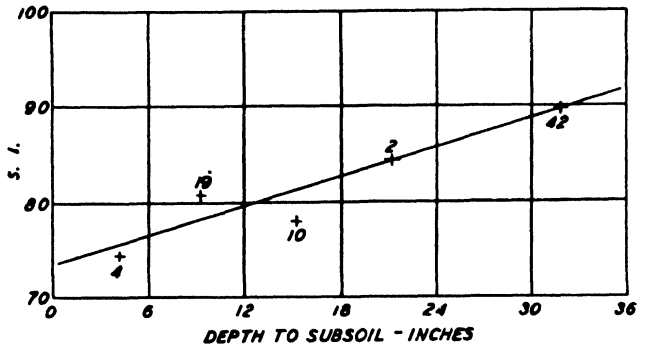


FIG. 6. Average relation between site index of yellowpoplar and depth to subsoil. Each plotted point is the average of site index residuals accumulated by 6-in. intervals of depth to subsoil from 0–36 in. (Auten, 1945b).

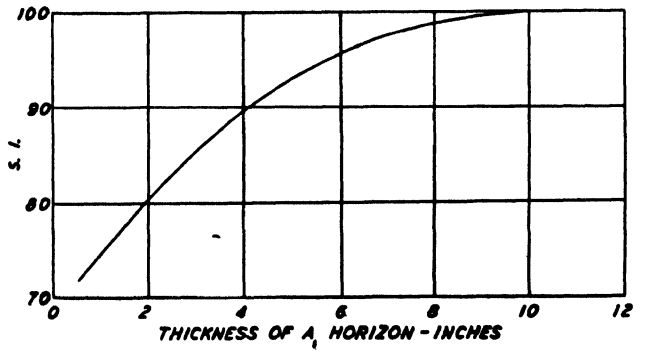


FIG. 7. Relation of site index of yellowpoplar to thickness of the A_1 soil horizon (Auten, 1945b).

index of 89, whereas northly facing slopes had an average site index of 72. Upper slopes and ridges were of lower site quality than lower slopes and coves.

The influence of topographic features of site index are shown in Table V.

TABLE V

Site Index Points to Subtract from 100 for Aspect, Exposure, and Position in Hilly to Steep Terrain (Auten, 1945b)

Site	Aspect	Exposure	Position	Negative Index Points
Cove	——	Sheltered	——	0
Cove	——	Open	——	3
Slope	Cool	Sheltered	Lower	6
Slope	Cool	Open	Lower	9
Slope	Cool	Sheltered	Upper	12
Slope	Cool	Open	Upper	15
Slope	Hot	Sheltered	Lower	18
Slope	Hot	Open	Lower	21
Slope	Hot	Sheltered	Upper	24
Slope	Hot	Open	Upper	27
Ridge	——	Sheltered	——	30
Ridge	——	Open	——	33

The effects of soil and topography on site index of yellowpoplar are summarized in Table VI.

In a study of the relation between soil, topography, and the site index of white oak (*Quercus alba* L.) in southern Ohio, Gaiser (1951) found topographic position, exposure, and depth of surface soil to be correlated with height growth. The data consisted of tree and site measurements on 51 plots in evenaged oak stands. Variables tested were: (1) distance from ridge line (per cent), expressed as

$$X_1 = \log \frac{1}{\text{per cent distance from ridge line}}$$

(2) exposure as the sine of the azimuth taken clockwise from southeast and adding one

$$X_2 = \text{sine (azimuth from SE)} + 1$$

(3) depth of the A horizon in inches

$$X_3 = \frac{1}{\text{depth A in inches}}$$

The dependent variable, site index, was taken, as its logarithm to the base 10, $Y = \log$ S.I. Slope per cent and available moisture in inches in both the A and B horizons were also tested. The independent variables correlated with site index of white oak are given in the following equation whose error of estimate is 9 per cent:

TABLE VI

Yellowpoplar Site Index as Indicated by Soil and Topography (Auten, 1945b)

Surface Soil	Surface Gray	Surface Brownish Gray	Surface Grayish Brown	Surface Brown to Grayish Brown	Surface Brown	Surface Brown
Subsoil	Subsoil very tight and plastic; drainage very slow; drab or blue-mottled below 8 in.	Subsoil heavy; drainage slow, light yellow to yellowish gray mottled below 14 in.	Subsoil well developed; drainage fair; yellow mottled below 14 to 24 in.	Subsoil present; drainage average; brown or deep yellow mottled below 36 in.	Subsoil light; drainage average to fast very little or no mottling	Subsoil; no B horizon; drainage average to very fast, permeable throughout
Usual topography of terrain	Flat	Very little slope	Gentle slopes	Moderate slopes	Rolling to hilly	Hilly to steep
Profile number*	1	2	3	4	5	6
Negative site index points for soil†	50	30	15	10	5	0
Negative site index points for topography						
flat land	15	15	—	—	—	—
hilly land	—	—	—	0-33	0-33	0-33
Approximate site index	35	55	85	57-90	52-95	67-100
Recommendation	Submarginal; do not plant	Marginal and uncertain	—	Depending on topography	(See Table IV)	Marginal to excellent

Note Areas with estimated site indices below 75 are not recommended for yellowpoplar.

* Profile numbers as indicated by T. M. Bushnell in "Key to the Soils of Indiana."

† Soil descriptions from "A Key to the Soils of Ohio" by G. W. Conrey, A. M. Paschall, and E M. Burrage, and from "A Key to Kentucky Soils" by P. E. Karraker, and W. S. Ligon.

$$Y = 1.837 - 0.036X_1 - 0.020X_2 - 0.051X_3 \quad (6)$$

Site index of white oak increases with distance from the ridge line and with increasing depth of the A horizon. It was higher on northerly and easterly exposures than on southerly and westerly exposures. Site index increased with available water-holding capacity in inches of the A horizon; this was confounded with soil depth since the textures of the surface soils were similar.

VI. Prairie-Plains Region

Studies of the relation between soil characteristics and the growth of trees in semi-arid regions have been undertaken largely because of interest in establishing and maintaining shelter belts. The Shelterbelt Project of the mid-thirties, in the Prairie-Plains region from Texas to North Dakota, required information on soil features that were advantageous to the successful establishment of trees. Stoeckeler and Bates (1939) concluded that porous soils, coarse-textured ones, were most favorable for trees in regions of limited rainfall because: (1) a given amount of rainfall will penetrate to a greater depth in such soils than in finer-textured ones; (2) during periods of abnormal rainfall water is stored to considerable depths where it may subsequently be available to tree roots but is not susceptible to loss through evaporation; and (3) runoff during heavy rainfall is minimized in coarse-textured soils. The presence of natural growth of trees on sands in areas of low precipitation in the Great Plains is attributed to the periodic replenishment of moisture to great depths in the sands. Roots have been found in such soils to depths of over 20 ft.

Harper (1940) found that trees adapted to the climatic environment in central Oklahoma make good growth on upland soils when the surface layer does not contain more than 25 per cent of clay and the subsoil does not contain more than 30 per cent of clay. In western Oklahoma satisfactory growth of trees obtains where the soil is coarser textured than that indicated above. Fine-textured soils or shallow soils over unweathered rock preclude successful establishment of trees in central and western Oklahoma.

The relation between soil properties and the natural occurrence of forest and grassland communities in Colorado has been reported by Livingston (1949). In the Great Plains of central Colorado, ponderosa pine (*P. ponderosa* Laws.) occurs on coarse-textured soils with a conglomerate substrate, whereas mixed prairie communities occur on adja-

cent fine-textured soils. The former soil conditions ordinarily contain more available moisture than the latter.

VII. West Coast Region

Relatively little work has been done west of the Great Plains on forest soil properties as they affect tree growth.

1. *Pacific Northwest*

The most important tree species and forest type in this region is Douglasfir (*Pseudotsuga taxifolia,* Lamarck. Britt). The relation between certain soil profile characteristics and Douglasfir site quality in Lewis County, Washington, has been studied by Hill *et al.* (1948). Stands of Douglasfir and the soils which produced them were studied in that part of the county where the annual precipitation ranged from 45 to 55 in. The altitude varied from 150 to 1000 ft. The winter precipitation, in the form of rain, is heavy. One hundred forty-eight stands

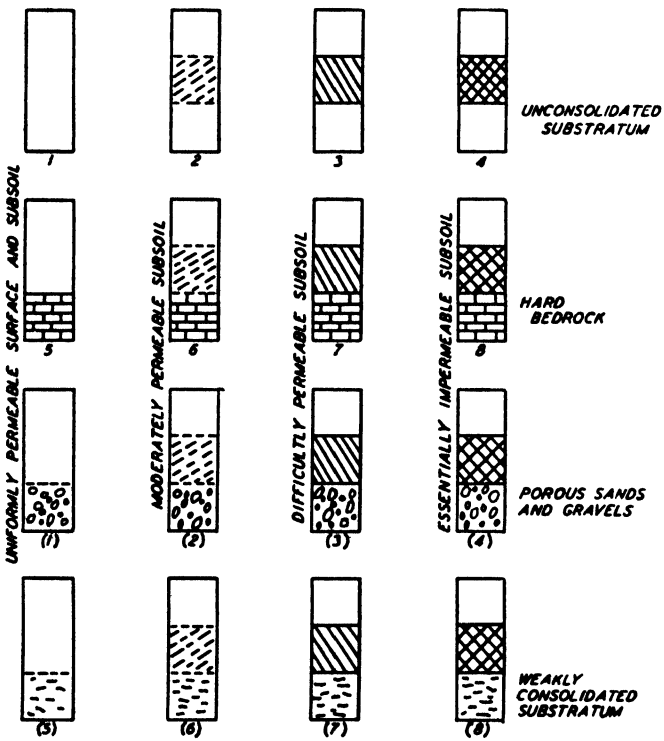


FIG. 8. Standard soil profiles (S.C.S., Washington).

which were mostly between 40 and 60 years of age were examined. Soil profiles recognized were 13 of the 16 basic profiles recognized by the Soil Conservation Service in Washington. Surface soil textures were grouped as coarse (C), light (L), medium (M), or heavy (H) and were used with the following profiles to form mapping units:

1. Deep soils, undifferentiated to a depth of several feet, allowing maximum water storage and root penetration.
2. Deep soils with subsoils or soil horizons which are slightly impermeable.
3. Soils with heavy, tight, impermeable subsoils.
4. Soils with hardpan subsoils, impervious to water and roots.

Of the four classes of profiles indicated above which differ in the permeability of the subsoil, each had four possible kinds of substrata: unconsolidated soil materials, hardrock, gravels, and semi-consolidated materials. Thus there were 16 basic profiles with four textural grades of surface soil possible in each. However, the 148 stands examined occurred on only 13 different soil profiles, or units. The basic soil profiles are shown diagrammatically in Fig. 8.

The relationship between the soil units and site quality for Douglasfir is shown in Table VII.

The results given in Table VII can be simplified as shown in Table VIII in which the soil and other site conditions are listed according to site quality classes.

It is evident from this work that the greatest growth of Douglasfir occurs on deep, permeable, medium-textured soils.

Gessel (1949) reported a study of soil profile features as they are related to site index of Douglasfir in northwestern Washington. Soil and site index measurements and methods of analysis were similar to those of Hill *et al.* (1948). Profiles with coarse-, light-, and medium-textured soils over open gravel in the 35 to 45 in. annual rainfall belt represented average site indices of 125, 150, and 176, respectively, at 100 years of age. The same types of profiles in the 45- to 60-in. rainfall belt supported stands with average site indices of 117, 143, and 170, respectively. Profiles with a hardpan or an impermeable zone were of higher site quality when the surface soil was medium textured than when it was light textured; also site quality was greater when the impermeable zone was more than 24 in. from the surface than when it was less than that. Gessel (1949) suggested that since most of the precipitation occurs when the trees are dormant, it may be assumed that an annual rainfall of 35 to 40 in. is sufficient to bring the profile to the field capacity, and any greater amount has little value for tree growth because it cannot be held in the porous substratum. For such profiles, the data appear to indicate

TABLE VII

Distribution of Douglasfir Plots by Soil and Site Classes and the Average Site Index by Soil Units, Lewis County, Washington (Hill *et al.* 1948)

Soil Group	Site Class IV			Site Class III			Site Class II			Site Class I			Average Site Index	Standard Deviation ±	Coefficient of Variation
	Site Index*														
	100	110	120	130	140	150	160	170	180	190	200	210			
(1) L			1	4	3								132	7.1	5.4
(1) M					1	3	2	1					154	9.9	6.4
1 L					1	4	1						150	6.3	4.2
1 M								2	5	5	1		184	8.9	4.8
1 H							1	1	3				174	9.4	5.4
2 M								2	1	1			178	10.5	5.9
2 H							5	2	1				161	6.4	4.0
3 M					1	3	1						150	5.0	3.3
3 H				3	1	1							136	9.4	6.9
6 H1 (deep)						1	8	4	2				165	8.5	5.2
6 H2 (shallow)				2	2	10	2						148	8.9	6.1
6 Ha-North Exposure					1	3	13	6	2				162	9.1	5.6
6 Ha †-South Exposure				1	11	5	2						144	7.8	5.4
6 Hb †-North Exposure						2	6	9	1				165	8.0	4.8
6 Hb-South Exposure				2	5	12	4	2					150	10.2	6.9
Grays Harbor County, Washington															
6 Hb-North										4	4		195	5.8	3.0
6 Hb-South							1	6	4	1			176	8.7	4.9
(1) GM									2	1			150	10.7	7.1
(1) GL				1	1	3	3								

* Average total height of trees in the dominant canopy when 100 years of age
† a = basalt.

TABLE VIII

Soil Groups Listed by Site Quality Classes for Douglasfir in Lewis and Grays Harbor Counties, Washington

Site Class III			Site Class II			Site Class I
Site Index						
130	140	150	160	170	180	190
(1), L	3H	(1)M, 1L,	2H,(6) H1	1H,	1M, 2M,	6Hb-North
	6Ha-South	3M, 6H2,	6Ha-North		6Hb-South	Grays Harbor
					Grays Harbor	
		6Hb-South	6Hb-South		(1) GM	
		(1) GL				

a lower site quality with 55 in. of rainfall than obtains where the precipitation is 40 in. The former occurs at slightly higher elevations. Perhaps the picture is confused by subsurface irrigation in the soils which occur in the lower topographic position and concurrent lower precipitation belt.

The relationship between Douglasfir site quality and soil fertility was studied in five localities in Oregon and Washington by Tarrant (1949). One plot in each site class from I to IV (site index 200, 170, 140 and 110 at 100 years) was examined in each locality making a total of 20 plots. Two soil pits were dug in each plot or stand and the various horizons were sampled and later analyzed. Physical and chemical properties of the soils measured were: silt-plus-clay, pH, total N, available P, available K, base exchange capacity, replaceable calcium, replaceable magnesium, and organic matter content. No significant relationships between these characteristics and Douglasfir site quality were demonstrated. The author suggests that the nutrient content of forest soils of the Douglasfir region appears to be too high to constitute a limiting factor in tree growth.

Acidity of the various soil horizons was between 5.0 and 6.0 pH units. Silt-plus-clay content of the soil was between 40 and 50 per cent. Total N ranged from 0.09 to 0.55 per cent. Available phosphorus in p.p.m. ranged from 10 to 44. Available potash in p.p.m. ranged from 105 to 572.

Base exchange capacity, replaceable calcium, and replaceable magnesium expressed in milliequivalents per 100 g. of soil ranged from 7 to 36; 1.0 to 12.0; and 0.6 to 2.1, respectively. Organic matter contents of

the A_1, A_2, and B horizons were approximately 15.0, 6.5, and 3.5, respectively.

2. *California*

Of the 100 million acres in California, over 45 per cent has been classified as commercial or noncommercial forest land. Soil site studies

TABLE IX

Timber Rating Chart for California (Storie and Wieslander, 1948)

Factor A: Depth, Texture	Rating in Per Cent	Depth Class
Over 72 in. deep	100	5
60-72 in. deep	90-100	5
48-60 in. deep	80-90	5
36-48 in. deep	70-80	4
24-36 in. deep	50-70	3
12-24 in. deep	30-50	2
0-12 in. deep	0-30	1
Factor B: Permeability		**Profile groups**
Permeable profiles	100	I, II, VII, VIII, IX
Slowly permeable profiles	80-90	III
Very slowly permeable profiles	30-70	IV, VI
Factor C: Chemical (alkalinity, salinity, etc.)		**Toxicity class**
None	100	—
Slight effect	80-90	S
Moderate effect	20-80	M
Strong effect	0-20	A
Factor D: Drainage, Runoff		**Drainage symbol**
Well drained	100	w
Excessive runoff	80-95	r
Imperfect drainage	40-80	i
Poor drainage	10-40	p

Factor E: Climate

CF—Coastal Fog (Redwood)		CR—Coast Range (Douglasfir)		WS—Westside Sierra (Pine)		ES—Eastside Sierra Pine (P.J.)	
Ppt.	Rating	Ppt.	Rating	Ppt.	Rating	Ppt.	Rating
45 in.	120%	45	100%	45	100%	40	90%
40	110	40	95	40	95	35	80
35	100	35	90	35	90	30	70
30	90	30	60-70	30	50-60	25	60
25	80	25	30	25	20	20	50
20	30					15	40

incident to the resource survey of California have been made by Storie and Wieslander (1948). Observations on forest stands and the soils which produced them were made at 163 locations in the Coast Range and Sierra Nevada areas. The elevations ranged from a few feet above sea level to 8000 ft.

Timber site quality at each location was determined by measuring the height and age of a dominant tree over 70 years of age and by reading the site class from appropriate site class curves based on height and age. In California, the customary curves used are those of Dunning (1942) which intercept 25-ft. height intervals at 300 years.

According to Storie and Wieslander (1948), four main soil factors appear to govern or limit the growth of conifers in California. These are: (a) depth and texture characteristics; (b) permeability; (c) chemical properties; (d) drainage and runoff. Table IX is a timber rating chart for sites and forests in California expressed under these headings.

The product of the factors A × B × C × D × E in per cent gives the site rating.

Examples: Use of rating chart.

1. Hugo loam; 60 in. to bedrock, permeable, no toxic conditions, well drained, CR region, 50-in. annual rainfall.

Factor A	Factor B	Factor C	Factor D	Factor E
90	100	100	100	100=90% high site

2. Gleason stony loam; 33 in. to bedrock, permeable, no toxic conditions, well drained, ES region, 25-in. annual rainfall.

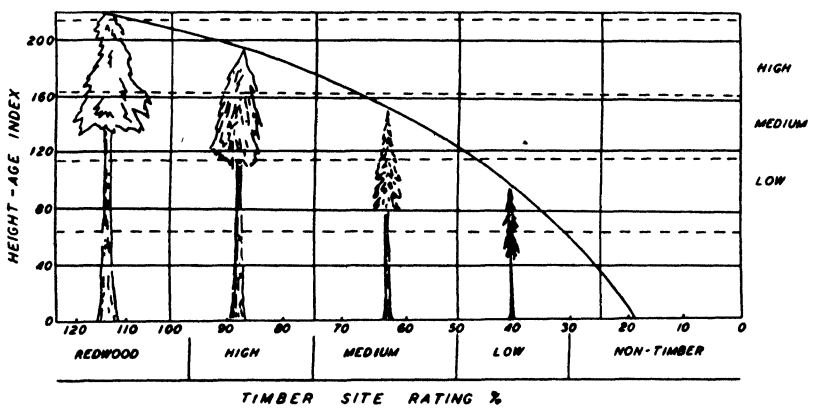


FIG. 9. Relation between site index and timber site rating based on soil and other factors in California (Storie and Wieslander, 1948).

$$70 \times 100 \times 100 \times 100 \times 60 = 42\% \text{ low site}$$

3. Maymen loam, 8 in. to bedrock, permeable, no toxic conditions, excessive runoff, CR region, 50-in. annual rainfall.

$$20 \times 100 \times 100 \times 80 \times 100 = 16\% \text{ nontimber site}$$

The relationship between timber site rating and height-age index is shown in Fig. 9.

VIII. Southern Appalachian Region

The relation between soil site characteristics and the survival and early growth of plantations on old fields in the Great Applachian Valley of Tennessee has been reported upon by Minckler (1941a, 1941b, 1941c). Soils of this area are derived from limestone, dolomitic limestone, shale, and sandstone. Steep slopes are characteristic of the shale areas, and in general the soils have been eroded and sometimes have a cover of briars or sassafrass (*Sassafrass variifolium*, Salis. Kuntze). Minckler observed that yellowpoplar, black walnut, and white ash (*Fraxinus americana* L.) make the best growth on the relatively steep and heavily vegetated northerly shale slopes, with northerly dolomite slopes second for yellowpoplar. White pine and shortleaf pine (*Pinus echinata* L.) did best on dolomite soil, with limestone and shale next in that order. However, he found that local differences in site, and especially in soil profile, influenced growth more than the general differences between soil types as a whole. On the basis of early observations, Minckler compiled a chart showing recommended species for different soil sites (Table X).

With respect to survival and growth, Minckler found that on site B yellowpoplar made a mean height growth in 2 years of 2.4 ft. as contrasted with 1.3 ft. on site G. Shortleaf pine had a survival of 43 per cent on sites A, C, and E, and 93 per cent on sites F, G, and H. Black walnut had reached heights of 3 to 6 ft. on sites A, B, and I, whereas on other sites its growth was negligible.

The importance of the condition of the B horizon was illustrated by the mean height growth of yellowpoplar in 2 years in sites A, B, C, and D. On friable, plastic, and stiff B horizons the growth was 2.5, 1.5, and 0.8 ft., respectively. A similar response was shown by white ash.

It is likely that the relatively poor response of shortleaf pine to good quality sites was related to the greater competition of native vegetation.

Minckler (1941c) found soil moisture to be related to aspect and slope position with a 1.5 per cent increase for each 190-ft. descent on slopes of 30 per cent. Depth of the A horizon on 82 old field areas was related to aspect, slope per cent, and slope position, with northerly,

gentle, and lower slopes having a deeper topsoil than the opposite conditions.

IX. Southern Region

1. Loblolly and Shortleaf Pines in Arkansas

Turner (1938) studied the growth of loblolly and shortleaf pines as influenced by soil properties on 222 plots in 22 soil types of the Coastal Plain region of southern Arkansas. His field data were adequate in number of plots and the stand data were sufficient. However, soil measurements were confined to thickness of horizons in the profile, mechanical composition, and acidity. Statistical treatment of the data was limited to simple correlation analysis and scatter diagrams. Thus the net effects of each soil property on site index and the interactions of various soil features were not tested. The various site classes can be described qualitatively as follows:

1. Superior sites. Site index 96 to 115. Located in flood plains of small streams. Fine sandy loam or silt loam soils without marked profile development and with good internal drainage.

2. Intermediate sites. Site index 76 to 95. Distinct profile development. Surface soil shallower than for superior sites. Some series are imperfectly drained.

3. Inferior sites. Site index 56 to 75. Shallow surface soils associated with previous accelerated erosion on slopes from 5 to 20 per cent and shallow surface soils on flat topography. Both of the above conditions of shallow surface soil were ordinarily associated with subsoils (B horizons) having a relatively high clay content. Some soil profiles with excessive internal drainage (sands) belong in this group.

2. Black Locust in Mississippi

The height growth of black locust 4 years old was found to be correlated with the depth of the surface soil by Roberts (1939) in Mississippi. The relationship was curvilinear and the data may be summarized as follows:

Depth of surface soil (in.)	1	5	10	15	20	25	30	35
Av. height of trees (ft.)	2.2	3.6	5.4	7.0	8.4	9.7	10.8	11.7

3. Redcedar in Arkansas

The site index and diameter growth of eastern redcedar (*Juniperus virginiana* L.) has been correlated with total depth of soil to unconsolidated parent rock material in the Ozark region of Arkansas by Arend and Collins (1948). Diameter growth, total and merchantable height,

TABLE X

Planting Chart[1]: Recommended Species for the Appalachian Valley and Adjacent Regions (Minckler, 1941b)

Aspect	Soil Depth[2]	Topographic Position	Desirable Soil Condition	[6] Species and Mixtures Recommended	
				Areas with very dense briars, weeds or brush	Areas with normal vegetative density or less (Includes all broomsedge)
Northerly slopes or well-drained bottoms[3]	The A horizon over 7 in.	Lower slopes, well-drained bottoms, and sink holes	A horizon friable. Upper half of B horizon friable to plastic, not stiff. [4] Well aerated soil	Yellowpoplar Black walnut Yellowpoplar-black walnut mixture A	Yellowpoplar Black walnut White ash Shortleaf pine-yellowpoplar mixture Yellowpoplar-black walnut mixture B
		Upper slopes	Same as above	Yellowpoplar White pine-yellowpoplar mixture C	White pine-yellowpoplar mixture Shortleaf pine-yellowpoplar mixture White ash D
	The A horizon 5 to 7 in.	Lower slopes	Same as above	White pine-yellowpoplar mixture E	White pine White pine-yellowpoplar mixture White pine-shortleaf pine mixture F
		Upper slopes	A horizon friable and well aerated. No special requirement for B horizon	[5]	White pine White pine-shortleaf pine mixture G
	The A horizon under 5 in., usually eroded	All positions		[5]	Shortleaf pine H

Aspect	Soil Depth[2]	Topographic Position	Desirable Soil Condition	[6] Species and Mixtures Recommended	
				Areas with very dense briars, weeds or brush	Areas with normal vegetative density or less (Includes all broomsedge)
Southerly slopes[6]	The A horizon over 12 in.	Extreme lower slopes, coves, and sink holes	A horizon friable. Upper half of B horizon friable or plastic, not stiff. Soil well aerated	Yellowpoplar Black walnut Yellowpoplar-black walnut mixture I	White pine-yellowpoplar mixture White ash Shortleaf pine-yellowpoplar mixture J
	The A horizon 7 to 12 in.	Slopes not steeper than 30 per cent and broad ridge tops	A horizon friable and well aerated. No special requirement for B horizon	[5]	White pine White pine-shortleaf pine mixture Shortleaf pine K
		Slopes over 30 per cent steepness	No special requirement	[5]	Shortleaf pine L
	The A horizon under 7 in.	All positions	No special requirement	[5]	Shortleaf pine M

[1] Start at left side of chart and progressively fit prospective planting site into proper compartments until recommended species are reached.

[2] If the soil of the upper half of the B horizon is friable (see footnote 4), the minimum depths of A horizon can be reduced. In general, 2 in. of friable B horizon can be substituted for 1 in. of A horizon. The presence of a deep friable B horizon in combination with a deep A horizon constitutes an excellent site. Areas long out of cultivation with sheet erosion arrested are superior to recently abandoned sites with a similar soil profile.

[3] Northwest, north, northeast, and east facing slopes.

[4] "Friable"—cannot be molded even at high moisture contents.
"Plastic"—can be molded into a soft adhesive ball when wet but is loose when moderately dry.
"Stiff"—impermeable soil.

[5] Very dense briars, weeds, or brush almost never occur on these site conditions.

[6] West, southwest, south, and southeast facing slopes.

and ages of 30 to 40 trees were measured in each of 91 different stands. The soils were classified as to parent material (limestone, dolomite, cherty limestone, mixtures of limestone and sandstone, sandstone, and first bottom alluvium) soil depth, topographic position, direction and degree of slope, and acidity of samples from 0 to 3 in. and 3 to 6 in. measured in pH units. Total depth of the soil was the only site feature found to be correlated with height growth. Understocked stands were shorter by about 5 ft. site index than well-stocked stands. Acidity in pH units was not related to rate of growth within the range of 4.7 to 7.8. Surface soil in redcedar stands was approximately one pH unit higher (6.6) than in adjacent open areas. This is in line with the observations of Coile (1933) in the Piedmont region of North Carolina. Site class, soil depth, and site index were summarized by Arend and Collins as follows:

Site I. Alluvial soils, deep and well drained. Site index 55-60.
Site II. Upland soils, 24 in. and over in depth. Site index 45-50.
Site III. Upland soils, 12 to 24 in. in depth. Site index 35-40.
Site IV. Upland soils, less than 12 in. in depth. Site index 25-30.

X. Southeastern Region

1. Piedmont Plateau Region

a. Loblolly and Shortleaf Pine on Residual Soils. In a study of soils with highly differentiated profiles derived from sedimentary rocks of Triassic age in the lower Piedmont Plateau of North Carolina, Coile (1935) found that site index of shortleaf pine was related to the texture-depth index of a soil profile. The texture-depth index is the ratio of the silt plus clay content of the B horizon to the thickness of the A horizon. Texture-depth indices less than 2 or greater than 8 indicated poor sites. Highest site indices were found where the texture-depth index of the soil was between 4 and 6. On the average this would represent a soil with 12 in. of A horizon and a B horizon containing 60 per cent silt and clay. On such soils shortleaf pine usually had a site index of 80 ft. Should the same kind of subsoil be covered with only 4 in. of A horizon, the texture-depth index would be 15 and the site index relatively low. The reasoning behind the development of the texture-depth index was based on the belief that site quality was a function of the amount and favorableness of growing space for tree roots in the soil. In the case of soils which have highly differentiated profiles with respect to texture, structure, and consistence, the depth of the surface soil and certain physical

properties of the subsoil become pertinent factors in determining the volume and quality of growing space for tree roots.

Because subsoils of the same textural class may have greatly different internal drainage, aeration, consistence, and structural characteristics, all of which affect root growth, the texture of the subsoil alone, or in conjunction with the depth of the surface soil, is not closely correlated to site quality for a wide variety of soil series.

An intensive study was made by Coile (1948) of the relation between soil features and the site index of loblolly and shortleaf pines in the lower Piedmont Plateau of North Carolina. The data consisted of 53 plots in loblolly pine, 75 plots in shortleaf pine, and 23 plots in mixed stands of the two species. The stands occurred on 27 soil types derived from sedimentary rocks of Triassic age, acidic and basic igneous rocks, the Carolina Slate formation, and alluvium and colluvium. On the basis of previous investigations of tree root distribution in these soils, only stands over 30 years of age were measured because competition for growing space in the soil is not particularly important in younger stands of average stocking.

Site index was assigned to each plot using the conventional total height and age relationships and appropriate curves in *U. S. Dept. Agr. Misc. Pub.* **50**, 1929. The contribution to site index (the dependent variable) of four primary soil variables, their joint effects, and their deviations from linearity were tested. The soil variables were:

X_1 = thickness (or depth) of the A horizon in inches.
X_2 = ratio of silt plus clay to the moisture equivalent of the B horizon.
X_3 = product of X_1 and X_2, hence (X_1X_2)
X_4 = second power of X_2, hence $(X_2)^2$
X_5 = product of X_1 and X_4, hence (X_1X_4)
X_6 = total depth of soil to the C horizon in inches.
X_7 = product of X_2 and X_6, hence (X_2X_6)
X_8 = product of X_4 and X_6, hence (X_4X_6)
X_9 = imbibitional water value of the B horizon.

Imbibitional water value is the difference between the moisture equivalent and xylene equivalent of a soil when the latter value is adjusted to a water equivalent on the basis of its specific gravity (0.86). The imbibitional water value is highly correlated with the properties of clayey soils which affect their permeability to water and air and hence their quality for the growth of roots.

The data were first classified and analyzed by three topographic position classes, i.e., ridges, middle slopes, and lower slopes and bottoms. No

significant differences in site were found between topographic position classes that were independent of the soil variables. Site index increased from ridge through slopes to lower slopes and bottoms but this was confounded with increasing depth of the surface soil (X_1).

Four soil variables, all significant at the 1 per cent level, were found

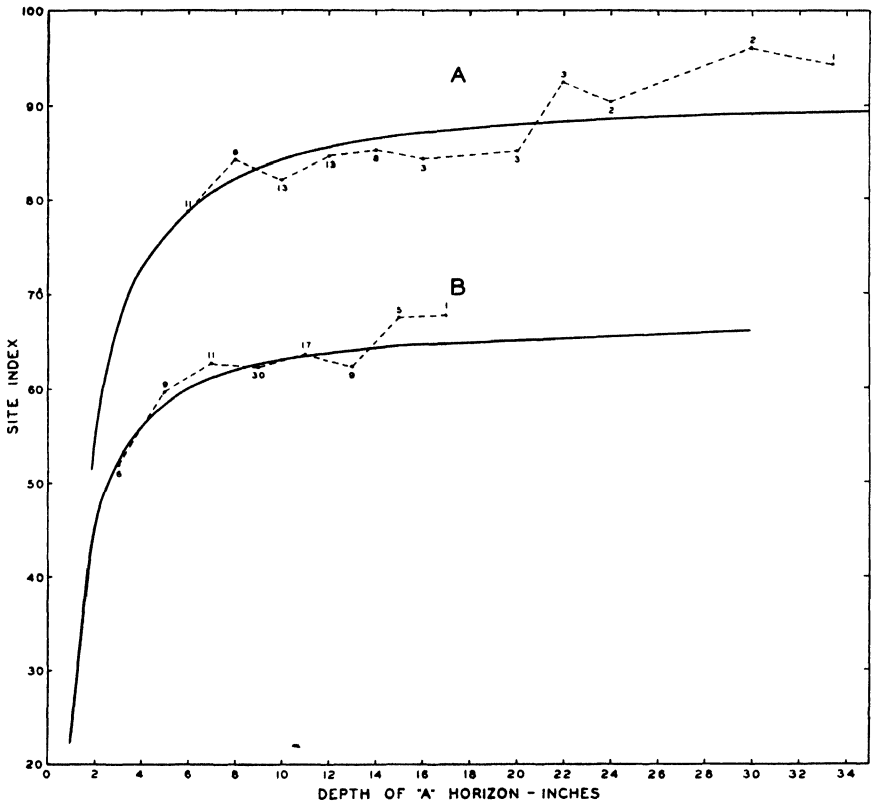


FIG. 10. Relation between site index and the depth in inches of the surface soil when the imbibitional water value of the subsoil is at the mean value for the group of plots involved. Curve A is for loblolly pine and was calculated from the regression

$$Y_L = 100.04 - \frac{75}{X_1} - 1.39X_9$$

Curve B is for shortleaf pine and was calculated from the regression

$$Y_S = 77.32 - \frac{45}{X_1} - 1.00X_9$$

The broken lines connect the mean residuals from regression; the number of plots upon which each is based is indicated by the number adjacent to the point.

to be correlated with site index and the following regression equations were developed:

$$\text{S.I.}_L = 38.71 - \frac{71}{X_1} + 40.27X_2 - 6.58X_4 - 1.17X_9 \qquad (7)$$

$$\text{S.I.}_S = 80.67 - \frac{44}{X_1} - 2.50X_2 - 1.08X_4 - 1.19X_9 \qquad (8)$$

Although soil variables X_2 and X_4 were statistically significant, estimates of site index using equations (7) and (8) did not differ appreci-

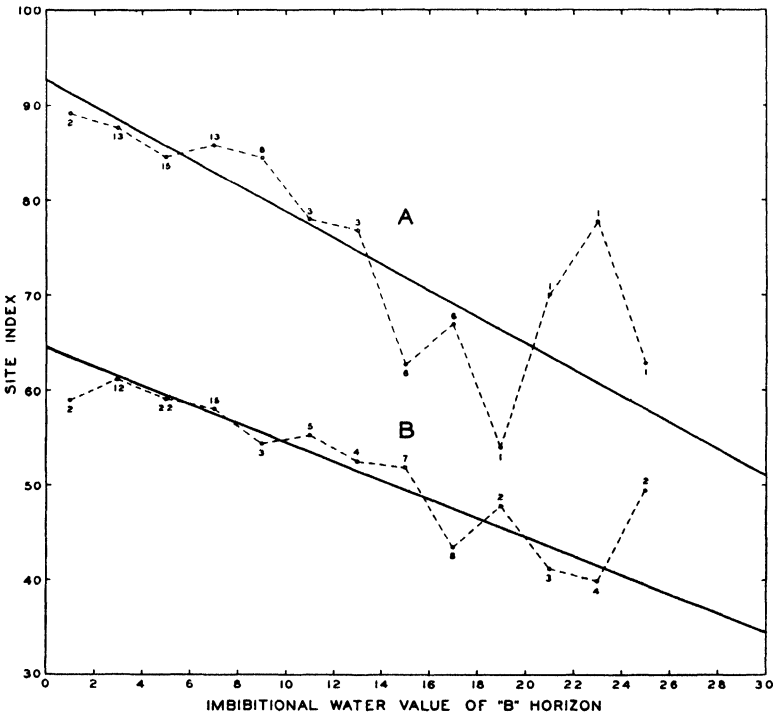


FIG. 11. Relation between site index and the imbibitional water value of the subsoil when the depth of the surface soil is at the mean value for the group of plots involved. Curve A is for loblolly pine and was calculated from the regression

$$Y_L = 100.04 - \frac{75}{X_1} - 1.39X_9$$

Curve B is for shortleaf pine and was calculated from the regression

$$Y_S = 77.32 - \frac{45}{X_1} - 100X_9$$

The broken lines connect the mean residuals from regression; the number of plots upon which each point is based is indicated by the adjacent number.

ably from those obtained by the use of equations (9) and (10) below in which these variables were omitted. Moreover, the inclusion of X_2 and X_4 required an additional laboratory measurement.

$$\text{S.I.}_L = 100.04 - \frac{75}{X_1} - 1.39X_9 \tag{9}$$

$$\text{S.I.}_S = 77.32 - \frac{45}{X_1} - 1.00X_9 \tag{10}$$

The error of estimate of a single observation in these equations is between 10 and 12 per cent of the estimated site index.

The net effects of depth of surface soil and imbibitional water value of the subsoil are given in Figs. 10 and 11.

It is of practical importance to note that the variable X_9 is characteristic of a soil series within rather narrow limits. Furthermore, soil series may be classified into relatively few groups according to their

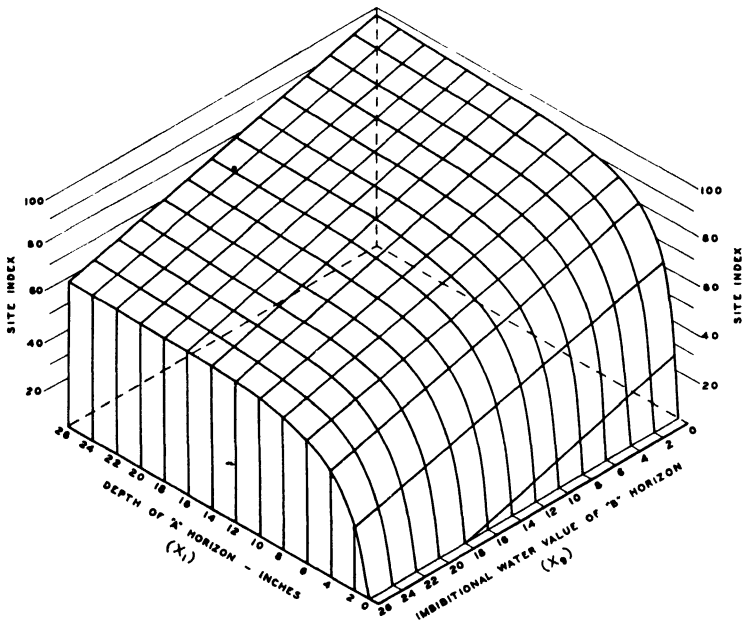


FIG. 12. Block diagram for the site index of loblolly pine as affected by the depth of the A horizon (X_1) and the imbibitional water value of the B horizon (X_9). The base of the three-dimensional figure can be considered as made up of soils with varying properties, while the curved upper surface can be visualized as the heights at 50 years of trees which the soils would produce. Calculated from the regression

$$\text{S.I.}_L = 100.04 - \frac{75}{X_1} - 1.39X_9$$

average X_9 values. Also, this value is highly correlated with soil consistence when moist and can be expressed in terms of relative plasticity. Hence, in estimating site quality of soil in the field, it is necessary only to measure the depth of the surface soil with an auger and to assign the X_9 value of the subsoil which is the average for the series or consistence class.

Figures 12 and 13 show the effects of both surface soil depth and subsoil properties on the site index of the two species.

Frequent fires in loblolly and shortleaf pine stands of the Piedmont Plateau reduce height growth of the trees (Stoehr, 1946). On the basis of soil and tree measurements on unburned versus frequently burned stands of loblolly and shortleaf pines in the Carolinas and Georgia it was found that burning lowered the apparent tree site index. The data consisted of 36 unburned and 21 burned stands of shortleaf pine and 21 unburned and 11 burned stands of loblolly pine. It was found that Coile's original equations (9) and (10) could be applied with confidence in the Carolinas and Georgia in unburned stands. However, tree site

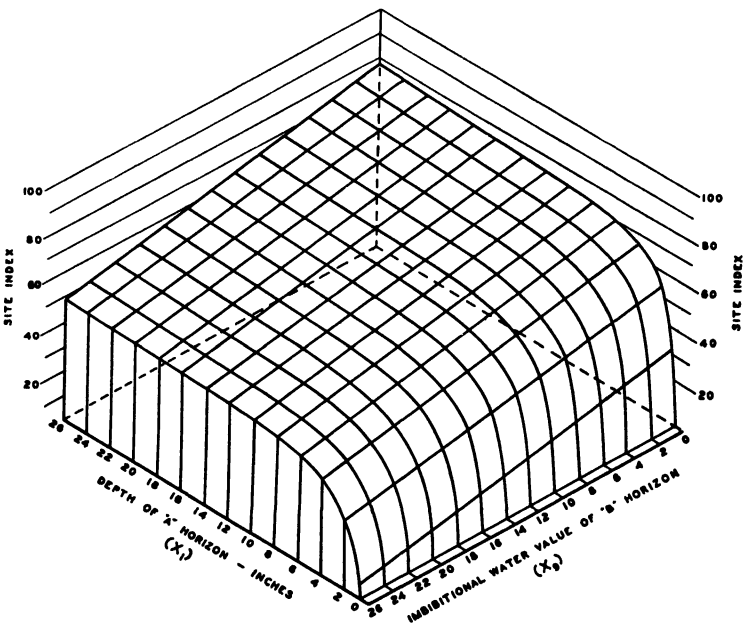


FIG. 13. Block diagram for the site index of shortleaf pine as affected by the depth of the A horizon (X_1) and the imbibitional water value of the B horizon (X_9). Calculated from the regression

$$S.I._S = 77.32 - \frac{45}{X_1} = 1.00X_9$$

index of recurrently burned stands was significantly lower than soil-site index as estimated from equations (9) and (10). Results of statistical tests showed that the effects of depth of surface soil (X_1) and physical properties of the subsoil (X_9) were not influenced by geographic location or burning, but the equation constant or level of the regression was significantly reduced by recurrent fires. Hence, new equation constants and their standard deviations were calculated for burned stands. They are given in equations (11) and (12) that follow:

$$\text{S.I.}_L \text{ (burned)} = (74.50 \pm 3.1) - \frac{75}{X_1} - 1.39X_9 \qquad (11)$$

$$\text{S.I.}_S \text{ (burned)} = (57.12 \pm 3.1) - \frac{45}{X_1} - 1.00X_9 \qquad (12)$$

It is believed that a large part of the reduction in tree site index associated with frequent fires is due to direct injury to the tree, such as defoliation and injury to the living tissues, rather than to changes in soil properties. In other words, if new stands were grown on previously burned areas their site indices would follow equations (9) and (10).

A revision of the earlier work of Coile (1948) on soil and the growth of loblolly pines in the Piedmont Plateau region has been made by Coile and Schumacher (1952). One hundred and sixty-one additional soil-site plots were measured in this physiographic region from North Carolina to Alabama. These new data were combined with the old, and new tests were made. Because of the appreciable latitudinal range in the Piedmont region and the possible effect of climate as well as past land use on height growth of pine, the data were classified as northern and southern Piedmont. The dividing line was on an east-west extension of the northern boundary of Stanley County, North Carolina.

TABLE XI

Number of Soil-Site Plots by Species, Geographic Location, and Fire History

		"North"		"South"		
Species	Data	Burned (B)	Not burned (NB)	Burned (B)	Not burned (NB)	Total
Loblolly pine	Old		73 *			73
	New	11	15	9	15	50
Shortleaf pine	Old		88 *			88
	New	4	48	25	34	111
Total		15	224	34	49	322

* Plots from which equations (9) and (10) were developed.

Whereas all of the old data (Coile, 1948) were from stands that had not been burned in recent years, the new data included some stands that had been burned frequently. The distribution of plots according to species, geographic location, burning, and "old" or "new" data is given in Table XI.

The combined data furnished 123 plots in loblolly pine and 199 plots in shortleaf pine. Soil factors tested were the following:

$1/X_1$ where X_1 = depth of A horizon in inches.

X_9 = imbibitional water value of the B horizon.

$1/X_9$ where X_9 = imbibitional water value of the B horizon.

Non-soil factors tested were burning (B) and geographic location (L).

Analysis of data for loblolly pine showed depth of surface soil (X_1) and imbibitional water value of the subsoil (X_9) both to be highly significant; but neither geographic location (L) nor the effects of burning (B) were of any significance.

The final regression equation for estimating site index of evenaged loblolly pine in the Piedmont region is as follows:

$$\log (\text{S.I.})_{\text{L}} = 2.0188 - \frac{0.399}{X_1} - 0.00843X_9 - \frac{0.0198}{X_9} \qquad (13)$$

Although the last variable on the right is not significant, it has been retained because a large amount of soil site data from the southeastern Coastal Plain indicates that if Piedmont and Coastal Plain data were combined, the net effects of imbibitional water values of the subsoil on site index would be curvilinear as indicated.

The standard error of estimate for loblolly pine was 11 per cent of the calculated site index.

Figure 14 is the graphic presentation of the net relationship between site index and the two significant variables for loblolly pine. The plotted points connected with broken lines represent residuals or average deviation of observed site index from computed site index.

Depth of the surface soil (X_1) and physical properties of the subsoil expressed as imbibitional water value (X_9) were highly correlated with the site index of shortleaf pine.

The equation for estimating site index of shortleaf pine throughout the Piedmont region is:

$$\log (\text{S.I.})_{\text{S}} = 1.8878 - \frac{0.1580}{X_1} - 0.00859X_9 - \frac{0.0408}{X_9} + 0.0053(\text{L}) \qquad (14)$$

where L is +1 if in the "North" and L is −1 if in the "South."

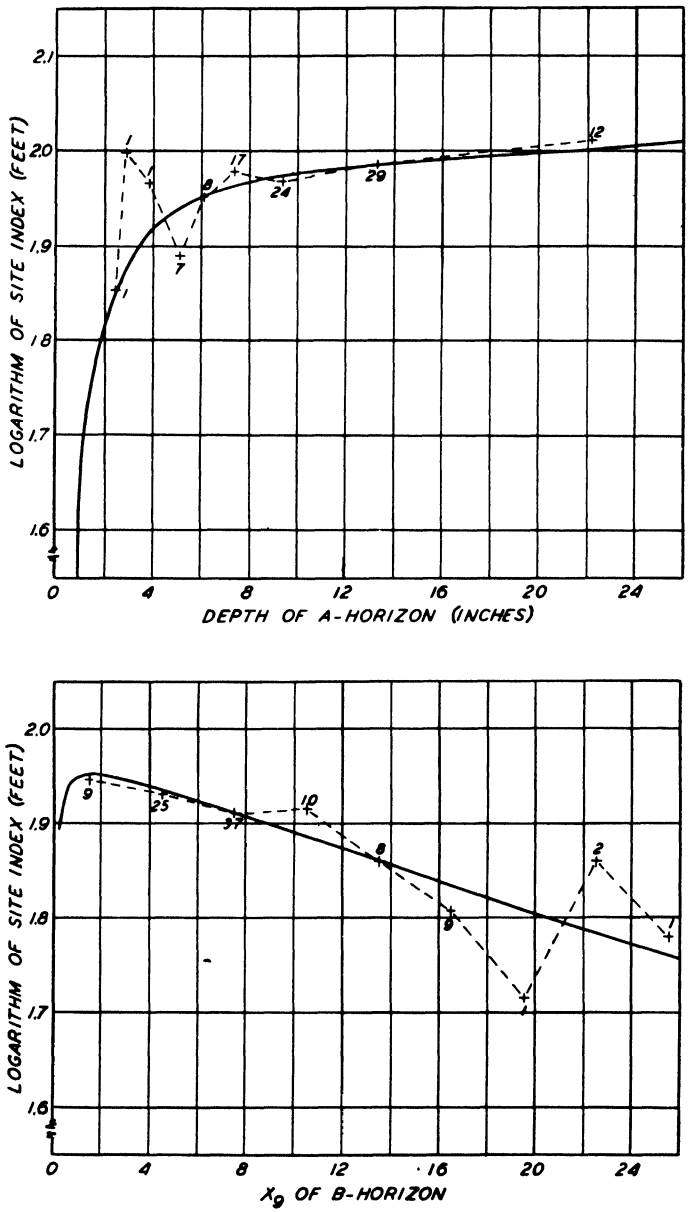


FIG. 14. Relation between site index of loblolly pine, expressed logarithmically, and the depth of the surface soil and the imbibitional water value of the subsoil. Broken lines connect the mean residuals from regression; the number of plots upon which each point is based is indicated by the adjacent number.

The standard error of estimate was 12 per cent of the calculated site index.

The net effects on site index of each of the two significant soil factors for shortleaf pine when one of the soils factors is held at its mean value is shown in Fig. 15.

Fortunately, for field application of results, the imbibitional water values of subsoils can be identified by broad classes on the basis of soil consistence when moist. For example, friable soils have relatively low

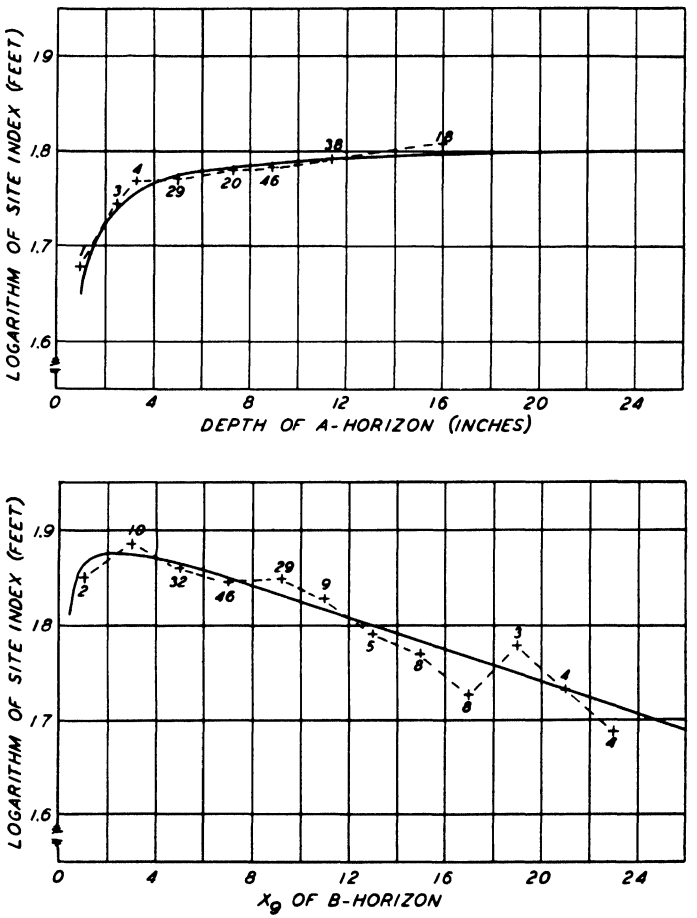


FIG. 15. Relation between site index of shortleaf pine, expressed logarithmically, and two important soil variables. Broken lines connect the mean residuals from the regression; the number of plots upon which each point is based is indicated by the adjacent number.

imbibitional water values whereas very plastic soils have high values. In the former case this characteristic is independent of the amount of clay.

Subsoils of the same series in the Piedmont are relatively constant with respect to their X_9 values, and hence, if a field man can estimate soil consistence or identify the soil series, he can assign the proper average X_9 value to a soil.

TABLE XII

Interrelations of Consistence, Texture, and Imbibitional Water Values of Piedmont Subsoils

Subsoil Class	Consistence When Moist	Texture	Class Range (X_9)	Number of Soil Samples n	Mean (X_9)	Standard Error of Mean
1	Very friable	Loamy sands and sandy loams	0–5	31	3.82	±0.54
2	Friable	Loams to clays	5–10	270	7.35	±0.18
3	Semiplastic	Sandy clay loams to clays	10–15	20	12.00	±0.67
4	Plastic	Sandy clays to clays	15–20	33	17.00	±0.52
5	Very plastic	Clays	20–25	34	21.80	±0.51

Consequently, the subsoils of the Piedmont may be classified according to their X_9 values, as in Table XII. Analysis of variance of these data showed that the variation among classes was so great that the standard error of the difference between neighboring class means based upon the fewest samples, classes 3 and 4, is 0.85, or less than one-fifth of the class difference.

The soil series and series variations which occur in the five subsoil classes are as follows:

Subsoil Class 1. *Very friable when moist.*

Durham, Altavista, Granville (very friable).

Subsoil Class 2. *Friable when moist.*

Georgeville, Herndon, Alamance (friable), Tirzah, Efland, Goldston, Durham, Appling, Cecil, Madison, Lockhard, Worsham, Wilkes, Davidson, Mecklenburg, Lloyd, Tatum, Congaree, Chewacla, White Store (azonal), Mayodan, Penn, Granville, all colluvium.

Subsoil Class 3. *Semiplastic when moist.*

Alamance, Colfax, Enon, Creedmore, Wehadkee.

Subsoil Class 4. *Plastic when moist.*
Helena, White Store.
Subsoil Class 5. *Very plastic when moist.*
Iredell, Orange, White Store (red phase).

Estimates of site index made with equations (9) and (13) and (10) and (14) have a maximum difference of only 3 ft. for each species. Because of this, Table XIII, based on the original equations (9) and (10), was developed and has been used throughout the Piedmont region.

TABLE XIII

Site Index Values for Loblolly and Shortleaf Pines in the Piedmont Plateau as Influenced by Soil (Coile, 1952)

Subsoil Class	Subsoil Consistence When Moist	Species	Depth to Subsoil (Inches) 2	4	6	8	10	12	18
1	Very friable	Loblolly	57	79	82	86	88	89	91
		Shortleaf	51	62	66	68	69	70	71
2	Friable	Loblolly	52	74	77	81	83	84	86
		Shortleaf	47	59	62	64	65	66	67
3	Semiplastic	Loblolly	46	68	71	75	76	77	79
		Shortleaf	43	54	58	60	61	62	63
4	Plastic	Loblolly	38	60	63	68	69	70	72
		Shortleaf	38	49	53	55	56	57	58
5	Very plastic	Loblolly	32	54	57	61	62	64	66
		Shortleaf	33	44	48	50	51	52	53

Numerous field tests of the soil site data given in Table XIII have been made in North Carolina and in parts of South Carolina. This table is based on equations (9) and (10). The field tests compared "tree site" index with "soil site" index. The former was obtained in the regular manner by measuring the total height and age of six to eight dominant trees in a well-stocked evenaged stand over 30 years old and by extrapolating site index from appropriate curves in *U.S. Dept. Agr. Misc. Pub.* **50**. A similar number of observations of surface soil depth and subsoil class (consistence) were made and their mean values used to assign soil site index from Table XIII. When several stands and soils are thus examined there is no significant difference between the average of the estimates obtained by the two methods.

The principal use for the indirect or soil method was originally visualized for land not supporting stands of suitable age, stocking, or species for direct site determination. Examples of this are cutover, abandoned fields, very young stands, unevenaged or partially stocked

stands, or land which presently supports other tree species. However, field tests with the soil method of estimating site potential show that it is just as precise as the direct method and requires only about one-third of the time needed to measure accurately total heights and ages and then obtain site index from curves or tables; hence, it is recommended for use even when stands suitable for tree measurements exist.

Many who use the direct method of site determination do not fully recognize the sources and magnitude of errors or inaccuracies involved therein. Common inaccuracies in measurement of total heights of trees with an Abney level are due to: (1) base line not properly measured, or not as long or longer than the height of the tree; (2) Abney level is not in adjustment; (3) tip of tree and its base are difficult to see because of understory or density of the stand; (4) total age of a tree cannot be obtained accurately because (a) tree center is not encountered, or (b) ring counts may be confused by "false" rings when a core is taken with an increment borer, or (c) when age is taken at 4.5 ft. the time required for the tree to reach that height may be misestimated.

Conventional site index curves contain errors of unknown magnitude because of certain basic assumptions with respect to the form of the curves and the relation of the distance between curves to age. This error is known to exist but it is not measurable from site index data alone.

Tests of the relation between site index as estimated from the soil and tree site index for stands 10 to 30 years of age have indicated that site curves for loblolly and shortleaf pine give overestimates for young stands.

It is suggested that those who wish to use the soil site method for estimating land quality would benefit by testing both methods (tree *vs.* soil measurements) in several existing stands on soils that are widely different. It should give the observer confidence when the soil method is applied to areas where suitable trees for direct site estimation do not exist.

b. Young Loblolly and Shortleaf Pine Stands on Residual Soils. An interesting application of the relation between soil profile features and site index of loblolly and shortleaf pines has been made in adjusting, or correcting, existing site curves (*U.S. Dept. Agr. Misc. Pub.* **50**, 1929) in the lower age classes, i.e., stands under 50 years of age (Coile and Schumacher, 1952). Using total height and ages of trees in the dominant canopy in conjunction with conventional site class curves for the species, site index estimates for young stands (10 to 30 years old) have been found to be much higher than site estimates for older stands on the same kinds of soil. This led to the conclusion that existing site curves

for southern pines give overestimates of site quality in young age classes. A correction factor for existing site curves was desired that would include the effect of age of stands on changes in the ratio of tree site index to soil site index. Equations for the two species were developed having the form

$$\log \frac{y}{Y} = b_1 \left(\frac{1}{A} - \frac{1}{50} \right)$$

where $\frac{y}{Y}$ = correction factor to be applied to existing curves

y = site index estimated from curves

Y = site index estimated from soil

$\frac{1}{A}$ = reciprocal of age

Since the index age is 50 years then $\log y = \log Y$ at that age. The equation for the ratio of tree site index (y) to soil site index (Y) for loblolly pine, based on 69 plots in stands 12 to 18 years of age and on 11 different soil series in the Piedmont region is the following:

$$\log \frac{y}{Y} = 1.2892 \left(\frac{1}{A} - 0.02 \right) \tag{15}$$

the standard error of 1.2892 is 0.1867. Thus for a stand 10 years of age

$$\text{S.E.} \left(\log \frac{y}{Y} \right) = (0.1 - 0.02)\ (0.1867) = 0.0149$$

which is equivalent to 3.4 per cent of the ratio y/Y at this age.

The relation between conventional site curves and curves adjusted according to equation (15) is shown in Fig. 16. It is evident that the former type gives overestimates in young stands.

Twenty well-stocked evenaged stands of the shortleaf pine type were examined. Their ages ranged from 12 to 29 years and they occurred on 10 different soil series of widely different properties.

Analysis of the shortleaf pine data, parallel to that of loblolly pine, provided the following ratio of tree site index to soil site index:

$$\log \frac{y}{Y} = 3.1746 \left(\frac{1}{A} - 0.02 \right) \tag{16}$$

The standard error of 3.1746 is 0.1467.

c. Loblolly Pine, Yellowpoplar, and Redcedar on Alluvium. Studies of the properties of well-drained first bottom alluvial soils and the horizontal distance to the stream channel as well as the vertical distance above the stream bed have been made with respect to the growth of loblolly pine (Ralston, 1947), and yellowpoplar and redgum (*Liquid-*

amber styraciflua L.) (Metz, 1947). Results showed site index values for loblolly pine and yellowpoplar were not dissimilar from estimates made by the use of the equation developed by Coile (1948) for loblolly pine in lower slopes and bottoms. This equation is:

$$(\text{S.I.})_{\text{L}} = 110.11 - \frac{101.0}{\text{depth surface soil}} - 1.98\ (\text{I.W.}) \qquad (17)$$

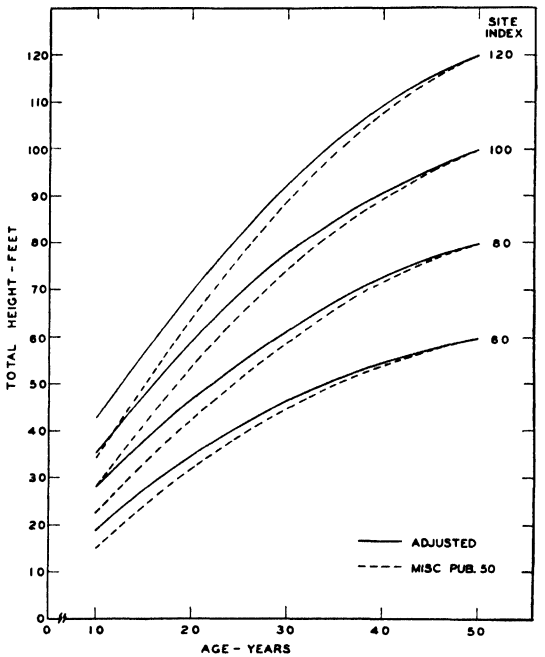


FIG. 16. Relation between conventional site index curves and adjusted site index curves.

The effect of distance to the stream channel on the site index of yellowpoplar was significant at the 5 per cent level. The equation expressing this relationship is:

$$(\text{S.I.})_{\text{YP}} = 86.91 + 0.102\ (\text{distance to stream in feet}) \qquad (18)$$

Site index of redgum was not found to be correlated with the soil characteristics or position with respect to the stream channel in these studies. The data for the three species studied were gathered from 75 plots.

d. Young Redcedar on Residual Soils. Ledford (1951) found that

the depth of the surface soil was highly correlated with the height growth of young redcedar (*Juniperus virginiana* L.) 10 to 14 years of age in the Duke Forest, Durham, North Carolina. On the basis of 73 observations of height growth of the species as related to the depth of the surface soil in inches (depth) and the imbibitional water value (I.W.) of the subsoil, he found that height growth was a function of age and depth of surface soil. Apparently, properties of the subsoil do not materially affect height growth in such young stands. Actually, however, subsoil properties measured as imbibitional water value are confounded with surface soil depth. Subsoils with high imbibitional water values would tend to be associated with shallow surface soils because of the low permeability to water of such very plastic soils and hence high rate of erosion under past cultivation.

The growth equation for young redcedar growing on seven different soil series is:

$$\log \text{ height} = 1.6525 - \frac{5.3514}{\text{age} + 1} - \frac{1.9518}{\text{depth to subsoil (in.)}} \qquad (19)$$

2. The Southeastern Coastal Plain

a. Loblolly Pine in Virginia, North Carolina, and Northeastern South Carolina. Gaiser (1948, 1950) reported on the relation between soil characteristics and drainage and the site index of loblolly pine in the Coastal Plain region of Virginia, North Carolina, and the northeastern part of South Carolina. Results were based on 202 plots in stands over 30 years of age. Drainage classes based on surface drainage were: good, imperfect, and poor (Lee, 1946). The soils were sampled to a depth of 4 ft. or more, and the following variables, all significant at the 1 per cent level, were found to affect site index: depth in inches of soil from the surface to the least permeable subsoil layer (depth) and the imbibitional water value (I.W.) of the subsoil. Equations for estimating site index were developed which have an error of estimate of 10 per cent. They are given below.

Good or imperfectly drained soils:

$$\log (\text{S.I.}) = 1.692 + 0.110 (\log \text{depth} + \log \text{I.W.}) \qquad (20)$$

Poorly drained soils with plastic subsoils:

$$\log (\text{S.I.}) = 1.715 + 0.110 (\log \text{depth} + \log \text{I.W.}) \qquad (21)$$

Poorly drained soils with friable subsoils:

$$\log (\text{S.I.}) = 1983 - \frac{0.772}{\text{depth}} \qquad (22)$$

Equations (20) and (21) differ only in the equation constant, the effect of soil variables not being unlike.

Tables XIV and XV have been developed for field use by Coile (1951) from equations (20), (21), and (22) and other information on the interrelations of soil consistence when moist, texture, and imbibitional water values.

TABLE XIV

Site Index of Loblolly Pine in the Coastal Plains of Virginia, North Carolina, and Northeastern South Carolina as Influenced by the Characteristics of Poorly Drained Soils (Coile, 1952)

Subsoil Characteristics			Depth to Subsoil in Inches						
Consistence	Texture	Imbibitional water value	6	12	18	24	30	36	42
Friable	Sandy loams to sandy clays	5	75	81	85	88	90	92	93
Semiplastic to plastic	Sandy clays	10	81	88	92	95	97	99	101
Very plastic	Clays	15	85	92	96	99	102	104	106

TABLE XV

Site Index of Loblolly Pine in the Coastal Plains of Virginia, North Carolina, and Northeastern South Carolina as Influenced by the Characteristics of Well and Imperfectly Drained Soils (Coile, 1952)

Subsoil Characteristics			Depth to Subsoil (Inches)					
Consistence when moist	Texture	Imbibitional water value	6	12	18	24	30	36
Very friable (noncoherent)	Sands	2	65	70	73	75	77	79
Friable	Loamy sands to light sandy loams	4	70	75	79	81	83	85
Friable	Sandy loams	6	73	79	82	85	87	89
Friable	Loams	8	75	81	85	88	90	92
Semiplastic	Sandy clay loams to clay loams	10	77	83	87	90	92	94
Plastic	Sandy clays	12	78	85	89	92	94	96

b. Loblolly Pine in South Carolina, Georgia, Florida, and Alabama. On the basis of stand and soil observations in 217 areas of evenaged loblolly pine over 20 years of age in the Coastal Plain regions of South Carolina, Georgia, Florida, and Alabama, Metz (1950) found the follow-

ing soil and topographic features to be significantly correlated with height growth of loblolly pine:

1. Product of depth of A horizon and the imbibitional water value of the B horizon.

2. Product of depth of A horizon and the silt content of the B horizon.

3. Product of depth of A horizon and the clay content of the B horizon.

4. Degree of surface drainage, i.e., well, imperfectly, or poorly drained.

The net effect of increasing imbibitional water value, silt content, and depth to B horizon was positive with respect to height growth, whereas increased clay content alone retarded height growth. Height growth increased with decreasing surface drainage. In this analysis the B horizon refers to the least permeable or finest-textured horizon, and the depth of the A horizon refers to the distance from the surface to the least permeable horizon. This was usually the B_2 horizon.

The general equation for estimating site index was:

$$\log (\text{total height}) = C - 6.97/age + [0.000420\ (\text{I.W. of B}) + 0.000021\ (\text{silt of B}) - 0.000077\ (\text{clay of B})]\ (\text{depth of A}) \qquad (23)$$

where $C = 2.0605$ for well drained soils

$C = 2.0729$ for imperfectly drained soils

$C = 2.0887$ for poorly drained soils

To calculate site index for loblolly pine with equation (23) the age to be used is 50 years, and the appropriate constant (C) for drainage is entered in the equation. Direct measurements of subsoil characteristics shown within the brackets may be employed, or mean values of these variables may be calculated for standard textural grades. The depth of the A horizon (actual distance in inches to the least permeable subsoil horizon) may be made in the field or calculated by convenient classes. The error of estimate for a single observation is 10 per cent.

Table XVI gives estimates of site index for loblolly pine in the Coastal Plain from South Carolina to Alabama as derived from equations for standard textural grades of subsoils, depth to the least permeable subsoil horizon, and surface drainage classes (Coile, 1952).

c. Longleaf Pine in the Coastal Plain. The height growth of longleaf pine (*P. palustris* Mill.) as influenced by soil properties and other factors was studied by Ralston (1949, 1951). Soil and mensurational data were analyzed from 303 plots in well-stocked evenaged stands of this type in the Carolinas, Georgia, and Florida.

TABLE XVI

Site Index of Loblolly Pine as Influenced by Depth to Least Permeable Horizon (Subsoil), Texture of Subsoil, and Drainage, Coastal Plain of South Carolina, Georgia, Florida, and Alabama, Based on 231 Plots (Coile, 1952)

Texture of Subsoil	Surface Drainage	Depth to Subsoil						
		6	12	18	24	30	36	42
Sand and loamy sand	Good	80	85	85	85	85	90	90
	Imperfect	90	90	90	90	90	90	95
	Poor	90	90	90	90	95	95	95
Sandy loam and sandy clay loam	Good	85	85	90	90	90	95	95
	Imperfect	90	90	90	95	95	100	100
	Poor	90	90	95	95	100	100	105
Loam, clay loam, sandy clay, and light clay	Good	85	90	90	95	100	105	105
	Imperfect	90	95	95	100	105	105	110
	Poor	90	95	100	100	105	110	115
Silty clay and heavy clay	Good	85	90	95	105	110	110	115
	Imperfect	90	95	100	105	110	115	120
	Poor	95	100	105	110	115	120	125
Silty clay loam and silt loam	Good	90	90	95	100	105	110	115
	Imperfect	90	95	100	105	110	115	120
	Poor	95	100	105	110	115	120	125

The equation for estimating height growth of 115 plots on imperfectly and poorly drained soils was:

$$\log \text{(total height)} = 1.886 - 11.20x_1 + 136.0x_1^2 + 0.00244x_2 + 0.00191x_3 + 0.000384x_4 - 0.00072x_5 \quad (24)$$

where $x_1 = \frac{1}{\text{age}}$ at 1.0 ft.

x_2 = moisture equivalent of the subsoil in per cent

x_3 = depth to mottling in inches

x_4 = stand density in number of stocked milacres

x_5 = +1 for plots in the Carolinas and −1 for those in Georgia and Florida

The latitudinal constant $_{(x5)}$ was significant at the 5 per cent point, whereas the other variables were significant at the 1 per cent level. The error of estimate for a single observation was 7.9 per cent. Tests of the effects of turpentining and turpentining latitude interaction did not reveal any significant relationships with growth.

Analysis of data from 188 plots on well-drained soils using the same independent variables that were tested for the imperfectly and poorly

drained soils, with the exception of depth to mottling, resulted in the following growth equation:

$$\log (\text{total height}) = 1.915 - 11.11x_1 + 136.0x_{1}^{2} + 0.00118x_2 + 0.000374x_3 - 0.014x_4 - 0.022x_5 + 0.008x_6 \quad (25)$$

where x_1, x_2, and x_5 are as stated in equation (24)

x_3 = number stocked milacres

x_4 = +1 for turpentine trees and −1 for "round" trees

x_6 = +1 for stands turpentined in the North or round in the South, and −1 for stands that are round in the North or turpentined in the South

The variables, x_{1}^{2} and x_6, were significant at the 5 per cent level; all other factors were significant at the 1 per cent point. The error of estimate of a single observation is 9.3 per cent for equation (25). Graphic illustration of the effects of turpentining and latitudinal distri-

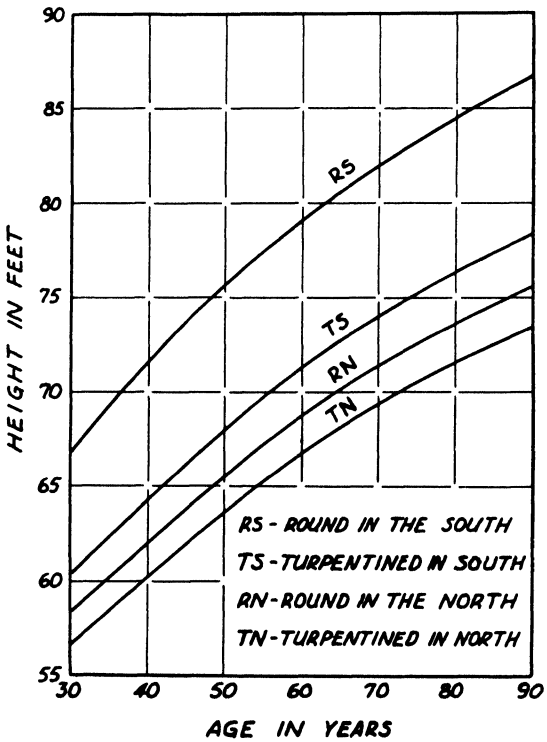


FIG. 17. Growth curves for longleaf pine on well-drained soils showing the effects of turpentining and latitudinal distribution.

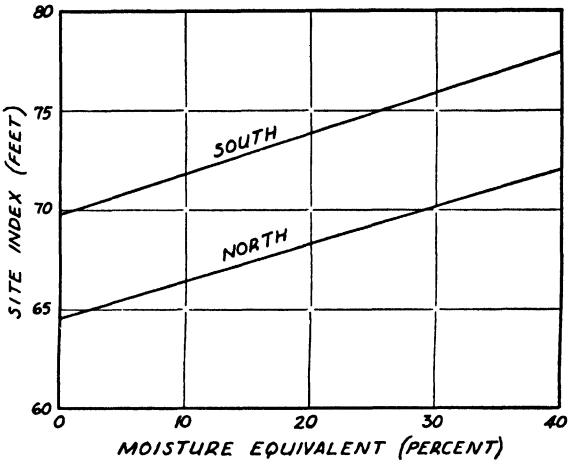


FIG. 18. Site index of longleaf pine on well-drained soils as influenced by moisture equivalent and latitudinal distribution.

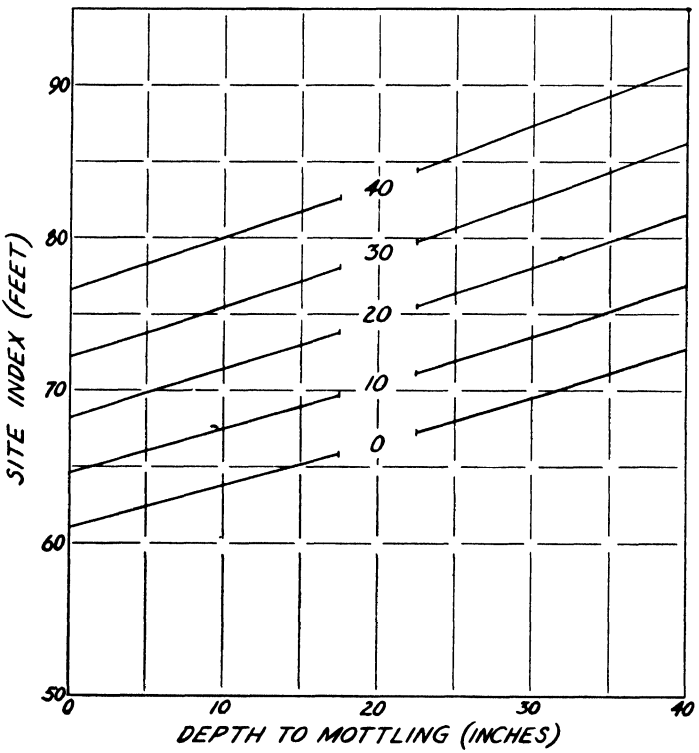


FIG. 19. Site index of longleaf pine on imperfectly and poorly drained soils as affected by moisture equivalent and depth to mottling.

bution on height growth when stand density and moisture equivalent of the subsoil are at their mean values is shown in Fig. 17.

Well-drained soils supporting longleaf pine tend to have rather uniformly deep surface soils hence the only soil factor related to growth was the physical nature of the subsoil measured as the moisture equivalent. The effect of this soil property and of latitudinal distribution on site index is illustrated in Fig. 18. In the case of imperfectly drained and poorly drained soils the properties related to height growth are the depth to mottling and the moisture equivalent of the subsoil (Fig. 19).

Analysis of the relation between silt plus clay content and the moisture equivalent (M.E.) of subsoils from 147 plots showed that these values were so highly correlated that either could be used for estimating site index (Fig. 20). The equation for the regression in Fig. 20 is:

$$Y \text{ (silt + clay of B horizon)} = 2.34 \text{ (M.E. of B horizon)} \quad (26)$$

On the basis of established relationships between the moisture equivalents and textural grades of subsoils supporting longleaf pine, Coile

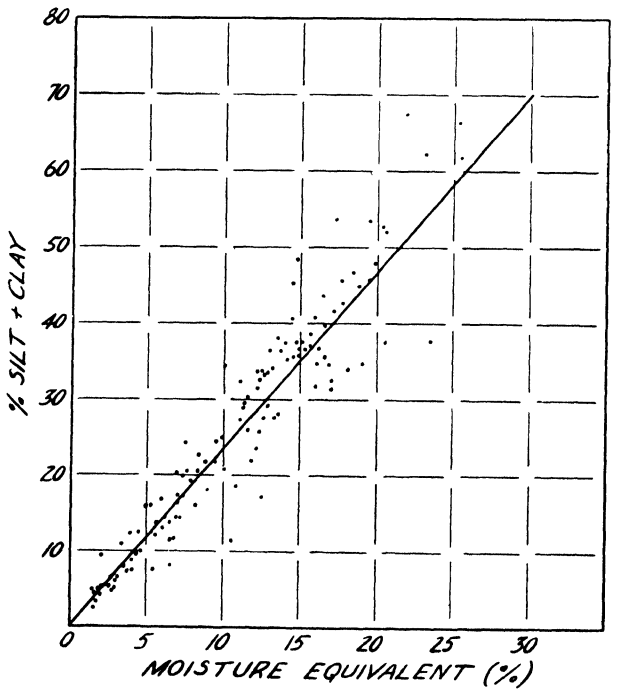


FIG. 20. The relationship between silt plus clay content and the moisture equivalent of the B horizon.

(1951) developed Tables XVII and XVIII for field use in estimating site quality of land for longleaf pine in the region.

TABLE XVII

Site Index of Longleaf Pine on Well-Drained Soils in the Southeastern Coastal Plain as Influenced by the Texture of the Subsoil

Subsoil Characteristics		Site Index	
Texture	Moisture equivalent	Well-stocked stands	Poorly stocked stands
Sand	2.7	64	58
Loamy sand	6.9	65	59
Sandy loam	13.3	66	60
Sandy clay loam	19.3	68	61
Sandy clay	25.0	72	62
Light clay	30.0	76	63
Heavy clay	35.0	77	64

TABLE XVIII

Site Index of Longleaf Pine on Poorly and Imperfectly Drained Soils in the Southeastern Coastal Plain as Influenced by Soil Characteristics

Subsoil Characteristics		Depth to Mottling (Inches)		
Texture	Moisture equivalent	18	30	48
		Site Index		
Sand	3.2	59	62	67
Loamy sand	6.6	60	63	69
Sandy loam	12.7	62	66	71
Sandy clay loam	18.6	64	68	74
Sandy clay	25.0	67	70	76
Light clay	30.0	69	72	78
Heavy clay	35.0	71	74	81

d. Slash Pine in the Coastal Plain. The effect of soil properties and other factors on the growth of natural slash pine (*P. caribaea* Morelet) stands over 20 years of age was studied by Knudsen (1950a). Soil and stand measurements were made on 231 plots in South Carolina, Georgia, Florida, and Alabama. Twenty independent variables were tested as to their effects on height growth. The soil variables included imbibitional water value of the B horizon, moisture equivalent of the B horizon, depth of the A horizon, mechanical composition of the A and B horizons, acidity (pH) of the A_2 and B horizons, and depth to mottling. Other independent variables were age of stands and turpentining. Appropriate tests of curvilinearity and interactions were also made. The only

soil property found to be correlated with site index of slash pine was the nature of the subsoil as reflected in its imbibitional water value. The net effects of turpentining were to reduce site index by 3 ft. The regression for slash pine site index is:

$$\log (S.I.) = 1.89153 + 0.0024423 (I.W.) + 0.0071144 (T) \quad (27)$$

where I.W. = imbibitional water value of the B horizon

T = +1 for "round" trees and −1 for turpentined trees

Equation (27) is shown graphically in Fig. 21.

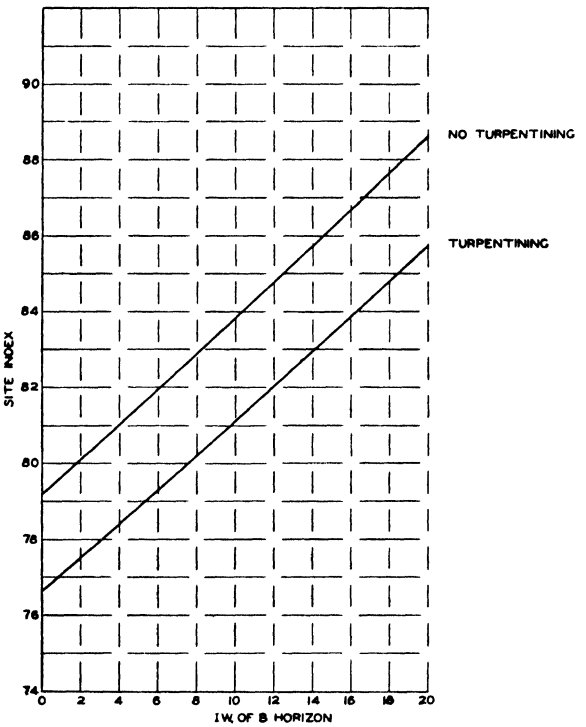


FIG. 21. Relation between site index of slash pine and imbibitional water value of B horizon as affected by turpentining.

Knudsen (1950b) examined the interrelation of some physical properties of Coastal Plain soils from 448 locations in the Southeast. One equation developed makes it possible to express imbibitional water value (I.W.) of the B horizon in terms of its silt and clay content (Si and C). The relationship is:

$$I.W._B = 0.28470 + 0.06936\ (Si)_B + 0.23610\ (C)_B \quad (28)$$

Both independent variables are highly significant.

Coile (1952) used arbitrary mean values of silt and clay for four broad classes of subsoil texture (Table XIX) to calculate their imbibitional water values with equation (27) and subsequently calculated site index for slash pine with equation (28). Table XIX gives estimates of site index for slash pine on the basis of subsoil texture which can be estimated in the field.

TABLE XIX

Site Index of Slash Pine Based on Texture of Subsoil (Coile, 1952)

Texture of Subsoil	Site Index (Round Trees)
Sands and loamy sands	75
Sandy loam and sandy clay loam	80
Loam, clay loam, sandy clay, and light clay	85
Silt loam, silty clay loam, silty clay, and heavy clay	90

e. Pond Pine in the Coastal Plain. Soils supporting stands of pond pine (*P. serotina* Michx.) have a wide range of profile characteristics. It occurs on mineral soils, organic loams, mucks, and peats. Hofmann (1949) studied the relation of soil properties to height growth of pond pine on 130 plots in the Carolinas, Georgia, and Florida. One hundred and one of these observations were on mineral soils, imperfectly and poorly drained; 29 observations were on organic loams, mucks, and peats all of which were poorly drained. The equation developed for estimating site quality of mineral soils is as follows:

$$\log\ (S.I.)_P = 1.6775 + 0.00347\ (M.E.) - 0.000276\ (\text{depth } A_1 \times O.M.) + 0.00071\ (\text{depth mottling}) + 0.000312\ (\text{length growing season}) \quad (29)$$

where M.E. = moisture equivalent of the subsoil

depth $A_1 \times$ O.M. = product of depth of A_1 horizon and its organic matter content

depth mottling = distance from surface to a zone of conspicuous mottling

length of growing season = average number of frost free days per year

In equation (29) the moisture equivalent of the subsoil was significant at the 2 per cent level, and the other independent variables were significant at the 5 per cent level.

Analysis of data from 29 organic soils (O.S.) indicated that stand

density, organic matter content of the surface soil, and the product of depth of A_1 and organic matter content affected height growth of pond pine. Equation (30) shows this relationship when stand density is at its mean level.

$$\log (S.I.)_{P(O S)} = 1.7917 - 0.00283 \text{ (depth } A_1 \times O.M.) \quad (30)$$

The relation between site index of pond pine and soil properties is shown in Table XX. This can be used for making estimates of site quality in the field.

TABLE XX

Site Index of Pond Pine in the Southeastern Coastal Plains as Influenced by Soil Characteristics (Coile, 1952)

Subsoil Texture	Depth to Mottling (Inches)	Mineral Soils *		Organic Loams	Muck and Peat
		($A_1 \times O M$) = 20†	($A_1 \times O M$) = 200	($A_1 \times O M.$) = 400	($A_1 \times O M$) = 1000
Sand	10	59	55	45	31
	40	61	58	48	34
Loamy sand	10	61	57	47	33
	40	63	60	50	37
Sandy loam	10	64	60	50	35
	40	67	64	53	38
Sandy clay loam	10	68	64	52	37
	40	71	67	55	40
Sandy clay	10	71	66	54	39
	40	74	70	57	42
Clay	10	74	69	56	40
	40	76	72	59	43

* Mineral soils: less than 15 per cent organic matter in the surface soil.
Organic loams. 15 to 35 per cent organic matter in the surface soil.
Organic soils: over 35 per cent organic matter in the surface soil (mucks and peats).
† Product of the depth of organic matter incorporation (A_1) and percentage of organic matter (O.M.) in the surface soil.

Zahner (1951) re-examined the data for 20 plots in organic soils previously studied by Hofmann (1949) and included some new variables; pH of surface soil, moisture equivalent, and imbibitional water value of the A_2 horizon, and its mechanical composition. Only the organic matter content of the surface soil was significantly related to site index. This relationship was expressed as:

$$\log (S.I.)_{P(OS)} = 1.8278 - 0.0035 \text{ (per cent organic matter)} \quad (31)$$

The error of estimate of a single observation using equation (31) is approximately 14 per cent.

Table XX shows estimates of site index for pond pine based on equations (29) and (30).

f. Sand Pine in Central Florida. The growth of sand pine on deep sands, mostly of the Lakewood series, in the Ocala National Forest in north-central Florida was studied by Barnes (1951). The data were based on sample plots in 54 evenaged stands. The soil was sampled and described to a depth of 9 ft. Mechanical analysis, separation of sands, and moisture equivalent determinations were made on all soil zones that appeared to differ in color or mechanical composition throughout the entire 9-ft. profile. In addition, the water-holding capacity of the soil to a depth of 9 ft. was calculated in inches of rainfall. None of the soil properties measured was found to be significantly correlated with height growth. Classification of the plots into two topographic position classes, (1) low flats and lower slopes and (2) upper slopes, high flats, and ridges, showed a difference in height growth that was significant at the 7 per cent level. Height growth of trees was greatest on the lower topographic position classes. This would indicate that data on depth to water table may be a useful measurement for deep sands in gently rolling topography. However, position of water table could not be deduced from profile observations to a depth of 9 ft.

The growth equation developed for the dominant stand in sand pine is:

$$\log (\text{total height}) = 1.9797 - \frac{10.577}{\text{age}} \quad (32)$$

XI. Résumé of Principal Soil Properties Related to Forest Growth

The productivity of soil for forest growth is conditioned by the quantity and quality of growing space for tree roots. Soil properties that may be classed under these two categories may have direct effects on growth, both direct and indirect effects (interaction), or only indirect effects.

The principal soil features and other factors related to forest site quality are:

1. Soil Factors

a. Depth of surface soil (A horizon), depth to least permeable layer, or depth to mottling. These measures of quantity of growing space

imply effective root depth for trees (small roots). The relationship of growth to these measurements is generally curvilinear. The net effects of increments of depth being great when depth is low. The effects of increasing depth on growth decreases beyond a certain point.

b. Total depth soil, and soil material functions as a measure of quantity of growing space in the case of immature or poorly differentiated profiles.

c. Physical nature of the subsoil, least permeable layer, or substratum as it influences water movement, water availability to roots, aeration, and mechanical hindrance to root growth. This factor may exhibit with either *a* or *b* above significant joint effects or interactions with tree growth. Physical properties of the subsoil that may be directly correlated with forest growth include texture, pore space distribution, imbibitional water values, water-holding capacity, and changes of volume with moisture content (shrinkage and swelling).

d. Physical properties of the surface soil, notably pore space distribution and texture may under certain conditions influence water infiltration and storage which is especially important to tree growth in semi-arid regions.

e. Organic matter in the form of either incorporated or unincorporated humus influences the moisture regime of soils as well as their structure and porosity to air. It serves as a direct source of energy for soil organisms and as a reservoir of nitrogen and other essential plant nutrients. In excessive amounts, organic matter may reflect poor drainage and be associated with low productivity.

f. Chemical characteristics involving nutrient supply may be a limiting factor in forest growth on deep excessively drained silicious sands in humid climates. In such cases the fertility factor is usually confounded with adverse physical soil properties and a low water table.

2. Other Factors

a. Climate and Length of Day. These two factors are confounded for tree species that have a wide latitudinal range. The relatively rapid growth of certain species of trees in northern latitudes can be attributed in part to long days during the frost-free period which offsets the short growing season. Climate, expressed as inches of rainfall, number of frost-free days per year, or defined indirectly by latitude and longtitude, has been found to be correlated with growth of forests independent of soil factors.

b. Aspect and Exposure. In regions or areas of marked relief, aspect of land (compass direction that a slope faces), and exposure (susceptibility of land surface to drying winds) greatly affect the local

climate as it is characterized by precipitation and temperature, wind movement (direction and rate), and evaporation. Northerly facing slopes (NW, N, and NE) are cooler and more moist than southerly facing slopes. A convenient way to express aspect is with an azimuth scale of 360° from North. Exposure may be stated in terms of the position of an area of land with respect to adjacent land as for example ridge *vs.* cove or draw.

c. Topography and Water Table. The relation of topographic position of land to forest productivity is primarily indirect. Relative topographic position and distance from the soil surface to the water table both influence water supply to the soil and tree roots. This moisture supply, modified by climate and soil properties may range from excessive to insufficient.

Subsurface irrigation resulting from seepage on mountain slopes and from fluctuating water tables in the alluvial flood plains of streams is an important factor in productivity that may be independent of soil profile features alone.

d. Surface Geology The permeability to water of rocks, rock formation, or unconsolidated geologic material may influence land productivity independent of the soil proper if the latter is shallow. Penetrability of substratum to tree roots may have an effect on tree growth independent of both its permeability to water and the properties of the overlying soil.

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