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DOWNS & DUNES

THEIR PLANT LIFE AND ITS ENVIRONMENT

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THEIR PLANT LIFE AND ITS ENVIRONMENT

By

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Illustrated with 74 photographs,
93 line drawings and diagrams,
together with 54 distribution maps

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PREFACE

THE combination in one volume of an account of the conditions of plant life of the Chalk Downs and Sand Dunes is, as these pages will show, logically justified by the various features they have in common, whilst their many striking differences merely tend to accentuate the significance of these resemblances.

This work had its origin in two courses of Lectures delivered by the writer as Fullerton Professor of the Royal Institution. As the outcome of many requests that these should be published, much of their substance has been embodied here. Biological Notes respecting most of the more abundant or characteristic species have been added since it is felt that these will be of interest alike to the general reader and the student. These notes are, in general, supplementary to the information provided by floras and make no attempt to provide the criteria of critical identification, but striking features of morphology are often mentioned where these can help those unfamiliar with wild plants to recall the flowers referred to.

It should perhaps be emphasised that the sections dealing with the fauna of these two habitats are not intended to be accounts of the animal life as such, but to serve as an indication of the specialised character of this aspect of the environments.

The observations and data which are here dealt with were obtained over a period of many years, mostly prior to 1943 and I would record my indebtedness to the assistance given by my students in obtaining the large amount of data concerning the water content and temperatures of dunes on which the generalisations here recorded are based.

The text figures and plates are with a few exceptions from the author's own drawings and photographs, but I am indebted to Dr. P. D. Wilson for permission to reproduce the photograph of *Romulea columnae* in Plate XXV and part of Fig. 9 is taken from a drawing by Dr. Violet Anderson. I am also indebted to colleagues for assistance in the preparation of Figs. 51, 57, 76 and 90.

I would wish to record my indebtedness to Professor F. W. Oliver, F.R.S., my predecessor in the Quain Chair at University College, to whose pioneer work on the dynamic aspects of ecology in relation to vegetation I owe my own initiation in this field. To Mrs. I. Evans I am indebted for assistance in the preparation of the Index.

E. J. S.

Kew
Spring, 1952

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I

THE DOWNLAND HABITAT

THE long-headed people of the megalithic civilisation, who probably came from the Mediterranean and south-western Europe, entered Britain about 2500 B.C. or possibly earlier. They were responsible for the great stone circles of Avebury and Stonehenge, which are standing witnesses to the early occupation of the chalk by man. The long barrows, perhaps of the same people and period, as also the round barrows of a later age (*ca.* 2000 B.C.), together with such camps as those at Whitehawk and Maiden Castle, show not only that early man tended to occupy the higher and drier ground but that he found the chalk downs particularly suitable in this respect. Neolithic man's advent in these islands was contemporaneous with the comparatively warm and moist conditions that obtained towards the close of the 'Atlantic period' during which the forests of Oak, Alder and Lime reached their maximum development. With the subsequent climatic fluctuation to the warmer and drier sub-boreal conditions of the Bronze Age the circumstances had become more favourable to species associated with a continental climate and it was about this time, some 3,000 years ago, that we first have evidence of the Beech tree in Britain, possibly then, even more than now, confined to the chalk by reason of the intolerance of this tree for ill-drained soils. The evidence from charcoals from the Neolithic deposits at Maiden Castle examined by the writer (cf. *Journ. Ecology*, XXVIII, p. 310, 1940) suggest that at that period the chalk hills were probably clothed with Oak-Hazel woodland, but it is obvious that forest destruction by man had already begun. He destroyed the trees and shrubs by fire and axe not only to permit of his primitive agriculture, but also to encourage the pasturage for wild animals. From the Neolithic camps at Whitehawk on the open downs near Brighton Dr. Kennard obtained evidence, furnished by shells of the land mollusca, that moister conditions than to-day then prevailed there; and the occurrence of shells of the snail

Acme lineata, a species of damp places in woodlands, is significant as also the frequency and large size of the shells of the snail *Arianta arbustorum*, a species of shady woodlands (cf. *Sussex Archaeological Collections*, Vol. LXXI, p. 84). Here too then the evidence suggests that in Neolithic times the downs were occupied by woodland, dwarf perhaps but not very open in character. Moreover in view of the marked tendency for these same hills to-day to become clothed again with scrub, and eventually with trees whenever grazing is prevented, there is no reason to doubt the inference that the bare, grassy character of these chalk hills is mainly an outcome of human activity. It is interesting to note that the Neolithic deposits at Whitehawk yielded numerous bones of oxen, pigs and either goats or sheep. We can then picture the provision by early man for these domesticated animals and for the culture of his crops as initiating the woodland clearance from the summits and, as the climatic conditions became drier and the permanent water table fell, the timber line receded like a falling tide in the face of human pressure associated with climatic and soil conditions less favourable to tree growth. Growing human needs for fuel, for crops and for pasturage combined to accelerate this forest clearance.

With the rise of the wool trade from the twelfth century up to the end of the nineteenth, the utilisation of the chalk as one of the chief grazing grounds for sheep increased. Farming on the chalk was prosperous till about 1890, producing mutton, wool and fat stock, with Barley as the chief light-soil corn crop. The downlands of Sussex alone gave pasturage for some 150,000 sheep and it has been the grazing over the centuries that in no small degree has imposed upon the downland turf its superficial uniformity and the prevalence of low-growing herbs that only attain any appreciable stature at the time of flowering. The downs thus share something of that beauty that Bacon admired in 'lawns of green grass kept finely shorn'; but their aesthetic appeal is due in large measure to the open, unconfined character and their unique topography, which Gilbert White so aptly described as the 'swell and heave of their broad backs into the sky.' Man and sheep have combined to ensure 'the green round bosom of the windswept wold' and this is as potent a factor in their wild life as the physical and chemical features of the soil and one which must be fully appreciated if the attractions and amenities of the downs are to be preserved.

The grassy swards that form so characteristic a garment of the North and South Downs are a feature of the chalk escarpments from Dorset in the south-west to the Lincolnshire and Yorkshire Wolds in the north-east. They have been the grazing grounds for sheep since Neolithic man first brought agriculture to these islands. Such grasslands together with the shrubby vegetation that is termed Chalk-Scrub and the woodlands that are called Beech hangers form the habiliments of semi-natural vegetation that clothe the calcareous soils derived from the lower, middle and upper chalk. Over much of East Anglia the chalk is covered with boulder-clay and other glacial deposits so that the soils formed here, though they may have in common many of the chemical characters of chalk soils, often exhibit a physical texture that is very different.

The distribution of chalk and other calcareous rocks is shown in the map (Fig. 1) on the next page, from which it will be noted that there is a marked preponderance in the south-east and the bulk of such rocks occur in the regions south of a line drawn from the Wash to the Bristol Channel. This has been shown to mark roughly the northern limit of many southern species even though not associated with calcareous soils (cf. Salisbury, E. J., *The East Anglican Flora*, Norwich, 1932). Indeed, it may be said that in this region soil conditions and climate combine to reinforce their respective influence. Nevertheless, as the map shows, calcareous rocks extend both westwards (e.g. Gower Peninsular in South Wales) and in the North, whilst the calcareous soils of sand dunes often provide coastal habitats which have both the chemical and physical characteristics required by calcium-loving plants even where the mainland soils are unsuitable for their growth.

The solvent action of rainwater and the denudations of past ages have in large part removed the upper and middle chalk from extensive areas and the residual clay-with-flints remains as a tribute to the great thickness of calcareous matrix that has been removed.

If we are adequately to appreciate the causes that have brought about the peculiarities of the plant life of Downland, scrub and Beech hanger, we must know something of the conditions which obtain in these habitats and how the environment is influenced by the climate, the soil, and the plants and animals which it supports.

The chalky soils are formed by physical and chemical changes combined with the action of diverse living organisms from the parent rock of chalk, which varies in its degree of impurity but usually consists of from 95% to over 99% of calcium carbonate ($CaCO_3$). Such calcium carbonate



FIG 1. Map showing distribution of chief calcareous areas.

will dissolve in pure water to the extent of only about 15 parts per million. Calcium carbonate hexahydrate is about twice as soluble (*Ca.* 0·03–0·04 gm. per litre). Since rainwater is often a near approach to pure water this would give us a fair approximation to the solution under rainfall were it not that

the raindrops dissolve carbon dioxide from the air and even more from the surface soil, as a result of which the water becomes converted into a weak acid ($H_2O+CO_2=H_2CO_3$); moreover, the CO_2 changes the carbonate into the bicarbonate. In water saturated with CO_2 the calcium bicarbonate is dissolved to an extent of 2,500 parts per million. It is thus seen that the carbon dioxide which is constantly being given off by the soil bacteria, by the protozoa that feed on them, by the roots of higher plants and in fact by all the living things in the soil as they respire, is the potent factor in bringing about the solution of the chalk, and an essential part of the conversion of this soft rock into soil. On relatively level ground or on gentle slopes we can obtain evidence of this gradual dissolving away of the chalk with the passage of time, which leaves behind the relatively insoluble material, by taking a series of soil samples at successive depths below the surface. The rate at which calcium is leached out of the soil by rainfall depends on a number of circumstances that differ from place to place. If there is a very large amount of chalk in the soil the total dissolved and washed away in any one season is understandably greater than when the original quantity is small, but the one is by no means proportional to the other. For example, in an experiment in which amounts of limestone were added to plots of soil in proportions such that one received 6·6 times the amount of the first and another 26·5 times as much, the rates of leaching were in the proportion of 1 is to 2·1, is to 2·6. So the law of diminishing returns here applies in a striking degree.

But as leaching proceeds the particles of chalk become smaller and smaller so that in proportion to their volume their surface increases. As a consequence, though the absolute amount of calcium leached away is steadily falling the percentage loss tends gradually to increase. The lysimeter ·experiments of Demelin and Batisse (*Soil Science*, pp. 1–7, 1938) give figures for the average annual loss of calcium carbonate from a bare soil which amounted to approximately 987 kilograms/hectare, or about 855 lb. per acre. Sir Daniel Hall estimated the annual loss of calcium carbonate from the unmanured plots on the clay at Rothamsted as about 1,000 lb. per acre, a rate of leaching that may be increased where ammonium sulphate has been added to the soil by an amount roughly equivalent to the

quantity of NH_3SO_4. Since the capacity of rainwater to dissolve the chalk and the solubility of the latter are both dependent upon combination with carbon dioxide, the effect will be greatest near the surface where organisms are most abundant and will diminish with depth. Actually, as the analyses from chalk downs in Hertfordshire given below show, the proportion of calcium steadily augments with increasing depth till the solid chalk is reached. It is important to realise that the presence of a close carpet of vegetation accelerates this leaching of the chalk because the living roots near the surface, the teeming bacteria, the microscopic animal life as well as larger organisms such as earthworms all give off carbon dioxide continuously whilst they are active, as we have already noted, and when dead the same gas is liberated during the processes of decay. Thus the rainwater percolating through the surface layer is enriched by the gas that enables it to function as an efficient solvent. This feature helps us to understand why it is that a bare chalk surface may undergo erosion yet changes but little in character and does not form a soil until it is colonised by vegetation. So too, if we look at a section of a chalky soil, as when a new road is cut or a fresh excavation made at the edge of a chalk pit, we can see that where roots penetrate there leaching is most pronounced, each root being surrounded by a sheath of clayey residue to the creation of which its own respiration has in no small degree contributed. The zone of influence around roots, the so-called rhizosphere, is thus a region of active leaching.

If is of course true that the roots tend to follow the fissures of the rock, which are the drainage channels, but it is the presence of the living roots in these fissures that replenishes the supply of carbon dioxide without which the efficiency of the drainage water as a solvent would not be maintained. By this process the fissure is enlarged and becomes a clay pocket supporting still more roots and thus promoting its own extension.

TABLE I. SOIL PROFILE ON CHALK DOWN, TRING

Depth in inches	*Percentage $CaCO_3$ (Averages)*
0–3	55
6–9	75
12–15	94
30	96

The much greater ease with which the calcium is leached out compared with the other soil constituents has the natural outcome that certain of the other nutrient chemicals present in the parent rock become more concentrated. For example, in one area examined the rock at a depth of 3 ft. (90 cms.) contained only 0·28% of magnesium oxide whereas at a depth of 4 ins. there was over 0·3% and in the top 2 ins. there was 1·24%. It is evident from these figures that the surface soil was derived from at least four times its volume of parent rock, and when we allow for the fact that the magnesium itself has also undergone some leaching an appreciably larger volume was probably represented.

If the leaching occurs on a slope the residual material may be removed almost as fast as it is formed and the leached particles being carried downwards form the soil at the foot of the slope instead of accumulating *in situ*. Further, under these conditions, unleached particles are likewise eroded downwards and so the soil that is formed is an alkaline calcareous one. If, however, the leached soil is not washed downwards but accumulates where formed the surface layers tend to become wholly depleted of their calcium carbonate and with the accretion of organic material may even become highly acid. This helps us to understand why patches of acid-loving plants such as Heather may often be found on the level crests or the gentler slopes of a chalk down and why the chalk grassland is often something of a mosaic of soil patches differing in chemical characteristics and physical texture. This has often misled observers into thinking that the soil preferences of species are less pronounced than they in fact are. Patches of leached soil on the crest of chalk downs are sometimes found to have developed markedly acid conditions (pH 5 or less) such that if attempts were made to grow clover crops, sugar beets, mangold and barley or even wheat they would fail unless the soils were heavily limed.

Even under conditions most favourable for leaching various factors militate against the rapid culmination of this trend towards acidity. Diverse animals, small and large, such as ants, earthworms, moles and rabbits stir up the unaltered subsoil and mix it with the leached particles. Earthworms are an important influence in retarding the attainment of the acid condition since they often feed on the surface soil, where

acidity tends to be highest, and by means of their calciferous glands reduce the soil's acidity as it passes through the worm's digestive tract. Moreover, as the soils on chalk downs are often very shallow and, especially on southern slopes, attain a high temperature in summer, evaporation from the surface after rain may bring about sufficient capillary rise from the unleached layers beneath to carry back to the surface some proportion of the basic substances carried down by drainage.

From all this we can understand why it is that the more characteristic chalk flora is associated with the slopes of the chalk downs rather than their level crests, for on the steeper of these slopes the influence of erosion greatly retards if it does not actually counteract the secular changes due to leaching. The presence of a high proportion of chalk in the soil not only means a copious supply of calcium ions but it also implies an alkaline reaction. Thus plants which either benefit by or are markedly tolerant of calcium will be favoured at the expense of those to which a large amount of calcium or an alkaline reaction is unfavourable.

Calcareous soils are very apt to be deficient in phosphorus. There would indeed appear to be an antagonism between the intake of calcium and phosphorus ions, since it was found by J. Greaves, who examined seventeen forage plants from this point of view, that when the content of phosphorus was high that of calcium was low and vice versa. Indeed as the farmer well knows these chalky soils often benefit more by the application of phosphatic manures than by any others. If we add lime to a soil in appreciable quantity the elements iron, manganese and boron, all of which are essential to plant growth, may become no longer available, or are only obtained with great difficulty. As an illustration we may quote the experiments carried out by Miss Heintz on the effect of liming of the soil on the amount of exchangeable manganese (*Journ. Agric. Sci.*, XXXVI, pp. 227–38, 1946). As the figures quoted below show the exchangeable manganese falls steadily with the

pH	5·5	6·3	7·5	7·9
Lime/acre, tons	1	3	8	12
Manganese %	10·0	8·4	5·0	2·0

increasing alkalinity of the reaction brought about by greater and greater additions of lime.

The neutral reaction is at pH 7·0 when the acid and alkaline

ions just balance one another. It is only below the neutral point that manganese becomes readily available, so that the leached surface layer of a chalk down may yield five times as much manganese as the unleached subsurface. It follows that species which are particularly efficient in obtaining the above-mentioned elements and which do not require them in so large amounts as others will inevitably be at a relative advantage when growing on the chalky soils. But it is possible that some of the perennial chalk plants which have root systems that consist of both shallow and deeply penetrating roots make as it were the best of both worlds, exploiting the leached layer with the one part of the root system and the unleached with the other (cf. Fig. 16). Indeed, artificial cultures of chalk-loving plants using identical volumes of leached and unleached soil either stratified with acid soil above and chalky soil below or mixed may exhibit a marked benefit from the stratification (cf. p. 17).

Most of the more typical chalk soils have an appreciably alkaline reaction. This is frequently about pH 7·5 and the normal range is pH 7 to pH 8·4. Since the carbon dioxide derived from the plant roots under a closed turf may be considerable the reaction is commonly just above the neutral point and immediately around the roots may be actually on the acid side. The leached surface layer may however be slightly or even appreciably acid (pH 5·5 or even less). But whilst the chemical characteristics are distinctive the physical features are also quite marked. In particular these soils are well aerated partly by reason of the friable nature of calcareous soils and the good drainage that the porous and fissured rock provides, but also because the CO_2 emitted by the respiring organisms does not attain a high concentration but combines to form the bicarbonate and is removed by the excellent drainage. Thus the accumulation of this heavy gas in the soil interstices, which is a marked feature of many soils, below the depth at which temperature fluctuations ensure mixing with the atmospheric air, is greatly diminished and deep root penetration is not only normal but conditions are favourable for respiration by the roots.

Though the surface soil may be temporarily wet, it is rarely, if ever, waterlogged. This and the good aeration to which reference has already been made implies that conduction of heat by the soil is poor and that radiant energy from the sun received

at the surface is not quickly dissipated by rapid conduction to the cooler soil below. The chalk soil is in fact what gardeners describe as a 'warm soil,' and this feature is accentuated by the southern aspect of the slopes, where the most distinctive chalk plants are usually to be sought.

The data obtained over a period of eighty-four years, from Chilgrove in West Sussex, respecting the rainfall and saturation level in the chalk below show clearly that there is a considerable time-lag. Thus for the average of the whole period the lowest level of saturation occurs in September whilst the minimum average rainfall is in April and May. The average rainfall attains its maximum in October, but the highest saturation level is not reached till February. These data indicate a time-lag of about four months and the flow of the intermittent streams of the chalk country which are called 'bourns' suggest a time lag of the same order. There is some evidence of a secular fall in the level of saturation in the chalk, but a study of the ratios between saturation level and total rainfall at Chilgrove during successive twenty-year periods shows but little if any significant difference until the late 'nineties.

TABLE II. RATIO OF SATURATION LEVEL TO RAINFALL, CHILGROVE

1836–1855	Ratio S/R	4·72
1856–1875	,,	4·76
1876–1895	,,	4·80
1896–1915	,,	4·33

In general the saturation level in the chalk follows the contours of the ground with a normal gradient towards the valleys of about 12 to 15 ft. (3·6 to 4·5 m.) to the mile in the middle chalk and some 15 to 20 ft. (4·5 to 6 m.) to the mile in the upper chalk. The Chilgrove data indicate fluctuations of the order of 130 ft. in the depth of the water table from the surface. Rise of water in chalk by capillary action can occur up to 16 ft., but at a very slow rate so that water supply by this means is only effective for vegetation where the water table is quite shallow. The capacity of the chalk soil to retain water is mainly determined, as in other types of soil, by the proportion of organic material, chiefly of vegetable origin, which it contains. It is also affected by the amount of clayey material and to a slight degree by the chalk itself. If the capacity of the calcium

carbonate to retain water is represented as unity, then an equal weight of the clay fraction would have a water-retaining capacity of about three, whilst the same weight of organic material would have a value of nearly nine; but since the organic material is far lighter than clay the water-holding capacity for equal volumes of these two constituents is not so very different.

The nature of the changing structure and physical composition of a downland soil as it affects water retention is well shown by a series of samples taken from a level area near Aldbury, Hertfordshire, after a period of heavy rainfall.

TABLE III. LEVEL AREA OF CHALK DOWN, ALDBURY

Reaction pH	*Depth* *ins.*	*Water content* *% of dry weight*	$CaCO_3$ %	*Organic material* %	*Ratio W.C./organic*
7·4	0–1	103·0	3·0	35·05	2·9
7·5	1–2	66·4	6·7	23·0	2·9
7·6	2–3	55·6	7·8	19·04	2·9
7·6	3–4	54·4	9·9	18·9	2·8
7·6	4–6	41·3	23·0	—	
7·6	6–8	38·8	44·0	—	

The ratio of water retained to the amount of organic material in the soil is seen to be wellnigh constant. The very large amount of water retained by the surface soil is noteworthy and can be contrasted with the much lower values on the slope (cf. Table IV) of the same down sampled on the same day. Here too the effect of erosion on the slope is manifest in the diminished evidence of leaching as the surface is approached. On the level crest the amount of calcium carbonate even at a depth of six inches scarcely attains to that in the first inch of the soil on the slope. The total volume of living roots for these four soil

TABLE IV. SLOPE OF CHALK DOWN, ALDBURY, AFTER HEAVY RAINFALL

Depth in inches	*Range of water % content*	*Range of* $CaCO_3$ %	*Percentage volume of living roots*
0–1	69–80	41·0–46·2	12·3–12·5
1–2	51·9–74·6	48·0–52·0	4·7–5·5
2–3	50·8–51·4	56·2–60·5	0·8–3·3
3–4	47·8–48·9	61·5–64·0	1·0

zones sampled was also determined, and these data show how quickly the amount of root development diminishes with depth in the shallow soils of the slopes representing, in this locality, only about one-twelfth of that close to the surface whereas at

the corresponding depth in a level area the living roots would probably be almost half as numerous as near the surface. This diminished penetration implies a less effective obstacle to climatic erosion and is an added factor in the slow rate of soil development. The natural water contents of a chalk down in Surrey were studied over a period of two years by Dr. V. Anderson (*Journ. Ecology*, XV, p. 72, 1927) and the data she obtained are summarised below:

TABLE V. NATURAL WATER CONTENT OF CHALK DOWN SOILS (from V. Anderson)

Depth in inches	*Mean*	*Percentage Water Content* *Min.*	*Max.*	*Range*
0–3	37	8·6	61	52
6–9	27	11·5	36	24
12–15	26	10·7	34	23
27–30	27	15·3	35	19

The supply of water to the plant by the soil can be thought of as a sort of tug-of-war in which the forces of retention by the soil are in opposition to suction exerted by the plant. But though the osmotic pressure of the cell sap and thus the suction can be augmented through, for example, conversion of complex into simple sugars, the law of diminishing returns soon applies when any sudden increase of water loss by the leaves brings about wilting.

Determinations of the amount of water remaining in the soil when wilting of the vegetation that it bears takes place, though subject to variation with the rate at which the soil dries out and with the external conditions at the time of wilting, indicate that so far as the chalk is concerned the amount of water which is non-available, being held by physical forces greater than can be readily overcome by the plant, is about 4–5% whilst near the surface it is probably between 10% and 11% (cf. V. Anderson, *loc. cit.*, and G. H. Locket, *Journ. Ecology*, XXXIII, pp. 222–9, 1946). It will be apparent that only for very shallow-rooted species is the risk of drought appreciable, since the fluctuations at the surface are marked, whilst for deeper-rooted species the supply of water is unlikely to fall below the wilting point and moreover the risk of waterlogging and inadequate aeration is negligible below the first 3 ins. Anderson's data showed that the supply of water was relatively steady at depths of half a meter or more (over 20 ins.) at which levels even in the

height of a summer drought there was still from 11–15% of water, and of this only about 4% was held so firmly by the physical forces of the soil as to be of little value to the plant. On the other hand the surface soil (0–7·5 cms. or 0–3 ins.) showed striking fluctuations with a maximum of 61% and a minimum of 8·6%. In the very severe summer drought of 1945, it was noteworthy that the shallow-rooted species were badly scorched and in some instances killed, whereas deep-

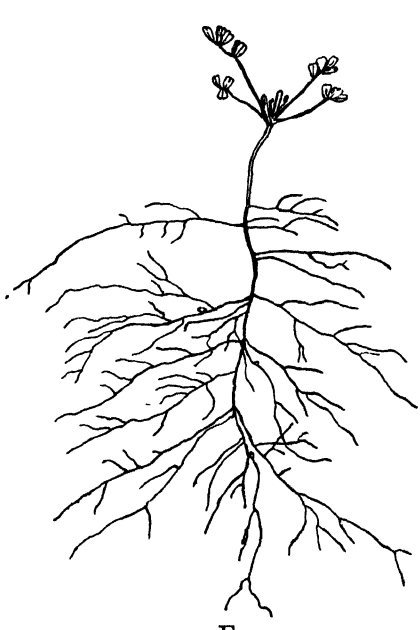


FIG 2

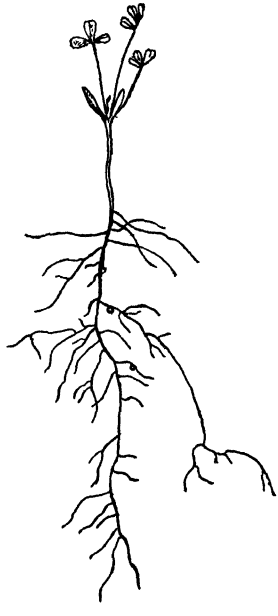


FIG 3

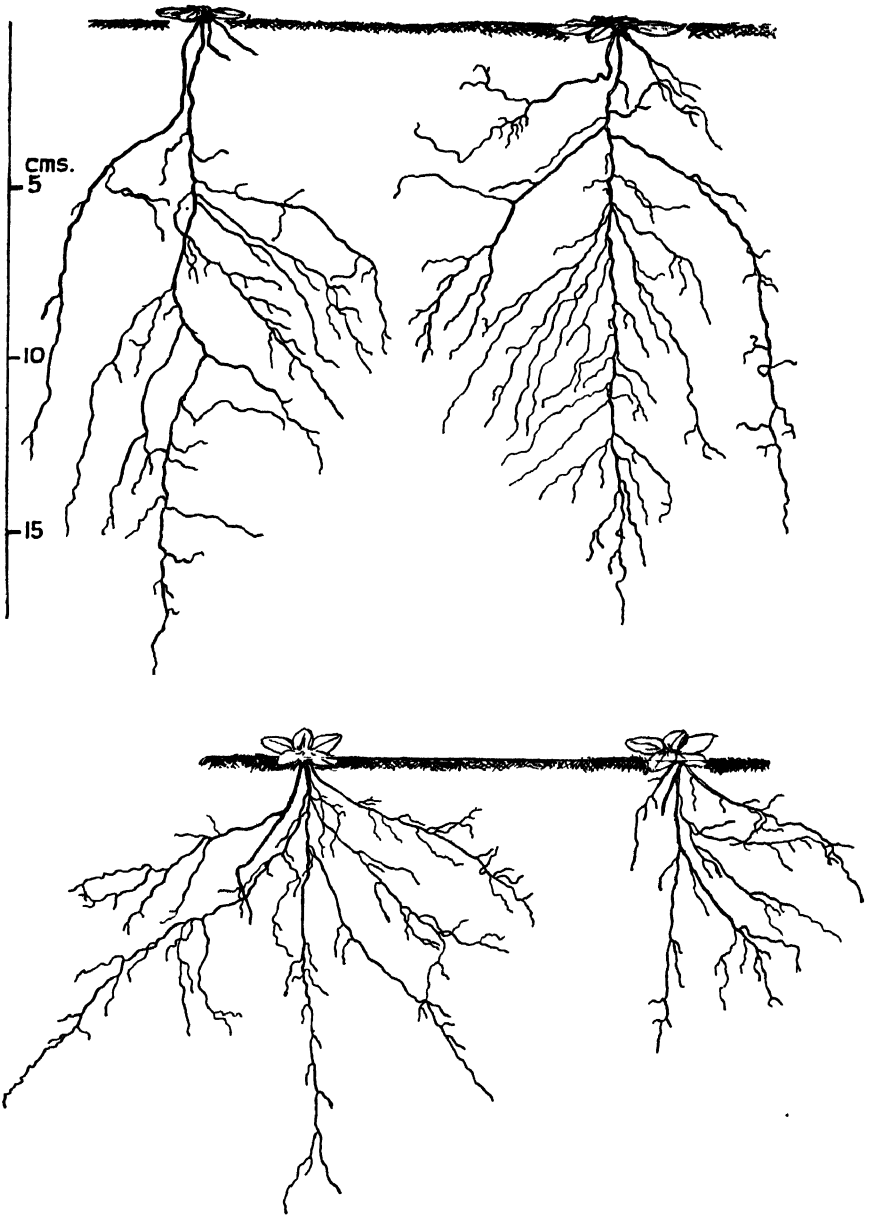
FIGS 2 and 3. Two typical seedlings of Horseshoe Vetch (*Hippocrepis comosa*) from a replicated experiment. FIG 3. Plant grown in non-calcareous soil. FIG 2. Plant raised in similar soil to which chalk was added. The roots of both bore nodules.

rooted species such as the Rock Rose (*Helianthemum nummularium*), the Squinancy-wort (*Asperula cynanchica*) and the Salad Burnet (*Poterium sanguisorba*) remained green or only exhibited a browning of the edges of the leaves.

The effect of the calcium ions in stimulating root development has been observed in water cultures, and as little as 1 part in 40,000 would appear to be adequate to induce root growth. Striking differences in root development were observed in seedlings of *Blackstonia* (*Chlora*) *perfoliata* when raised on a sandy loam

devoid of free carbonates and on the same soil to which chalk was added. Other similar experiments carried out by the writer in which *Seseli libanotis* (Pl. III), *Senecio integrifolius* and *Hippocrepis comosa* were raised from seed on non-calcareous soil and on the same soil with added chalk all demonstrated a strikingly increased root development in the more calcareous and more alkaline soil. It is obvious that in these experiments the beneficial effect of the added chalk may have been due to a combination of various factors, for, though there is no doubt as to the stimulating influence of the calcium ions themselves on root development, the beneficial influence of the lower acidity (higher pH) of the soil upon its contained micro-organisms must not be overlooked, nor its prevention of aluminium toxicity. Nevertheless, the fact that the plants in the soils without added chalk were rooted in an acid medium whereas those in the chalked soil were growing in an alkaline one would in the latter inevitably render the ions of boron, manganese, phosphorus and iron less readily available, were it not that the far larger absorptive surface of the living root is probably by its respiration creating its own immediate environment and thus in part, if not wholly, compensating for the alkalinity of the general soil mass.

In the experiments just referred to the root systems of the plants were carefully floated out on glass plates and the total length of all the ramifications were measured. The specimens of Horseshoe Vetch (*Hippocrepis comosa*) only six weeks old grown in the soil with added chalk had an average total root length of 277·1 cms. compared with an average length of 77 cms. for the plants in the soil without chalk (Figs. 2 and 3). Assuming a mean root diameter of 0·5 mm. the respective surfaces would average 43·46 sq. cms.±8·7 and 12·0 sq. cms.±5·8, a ratio of 3·6 in the presence of chalk to 1 in its absence. Thus, even ignoring the root hairs, the absorptive surface would be over three times as great for the seedlings grown in calcareous soil as for those in the non-calcareous. If the surface created by the root hairs were also taken into account the difference in absorptive capacity would be considerably accentuated. In similar experiments with the Field Fleabane (*Senecio integrifolius*) (see Fig. 4) the differences though not so marked were considerable. Thus the total root lengths of two seedlings six weeks old grown on the non-calcareous soil were 57·5 cms. and 128 cms. respectively whilst the seedlings grown in similar soil



FIGS 4. Field Fleabane (*Senecio integrifolius*). *Below* typical plants grown on a 'non-calcareous' soil, and *above* on similar soil with added chalk. Note stimulating effect of the calcium ions on root development.

with added chalk had roots that were 138 cms. and 179 cms. in length. In other terms the roots of the plants in the chalky soil were on the average nearly one and three quarter times the length of those grown on the same soil without chalk. It is not surprising therefore to find that the root systems of chalk plants are in general both extensive and richly branched. This copious root development is favoured by the frequently extensive fissuring of the chalk and the hinderances to accumulation of high concentrations of CO_2 to which reference has already been made.

The effects upon plant life consequent upon the chalky character of the rooting medium are diverse, both advantageous and deleterious conditions accrue and the same effect may be beneficial at one time and under certain conditions and harmful at another and in altered circumstances. Such an equivocal effect is the rapid decomposition of organic matter that occurs in the presence of carbonates, due in large measure to the alkaline reaction of the soil favouring an abundant and active bacterial population. Amongst the latter the nitrogen-fixing bacteria *Azotobacter* are markedly favoured by the presence of calcium carbonate. There is also neutralisation of any organic acids formed and the clay particles tend to be flocculated with consequent maintenance of the texture of the soil. The alkaline reaction of the soil moreover renders the trace element molybdenum more readily available. This may well have a particular significance in relation to the prevalence of many members of the Pea tribe (Leguminosae) in the chalk down flora. It has been shown that many species of this group are benefited by molybdenum and that further the fixation of nitrogen by the bacteria inhabiting the nodules on their roots is promoted by traces of this element. These nodule organisms have a free existence in the soil during part of their life-history and the calcium ion itself has been shown to be beneficial to

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PLATE I. Chalk flora. BELOW. Frog Orchis, *Coeloglossum viride*. The inflorescence to the right is that of the Chalk Scabious, *Scabiosa columbaria*, Tring. $\times\frac{1}{1}$. TOP LEFT. Two uncommon plants of open habitats on chalk, in foreground, Ground Pine, *Ajuga chamaepitys*, in background *Teucrium botrys*. Between the two are plants of the hairy Violet; above the lump of chalk is the Thyme-leaved Sandwort. $\times$*ca.* $\frac{1}{3}$. TOP RIGHT. Chalk Milk Vetch, *Astragalus danicus*, showing mat-like habit. $\times$*ca.* $\frac{1}{3}$.













this phase of their existence so that, whether in the free state in the soil itself or within the nodule, the chalk provides a favourable environment for these bacteria. It may be added that molybdenum markedly benefits also the capacity of *Azotobacter* to fix the free nitrogen of the atmosphere. The effect on the availability of some other nutrients is however not so favourable. Thus although the alkaline reaction increases the *proportion* of available phosphorus there is, as already mentioned, apparently an antagonism between the intake of calcium and phosphorus so that in fact phosphatic fertilisers are usually one chief requirement of calcareous soil.

Just as the availability of molybdenum is promoted by the alkaline reaction so too the availability of other nutrient elements, namely boron, manganese, iron and aluminium, is diminished. Heart-rot of sugar beet, which is a symptom of boron deficiency, is a frequent complaint on highly calcareous soils. Here too may occur 'grey speck' of oats, a manganese deficiency symptom, and the yellowing of foliage due to iron deficiency known as Chlorosis. Excess lime limits not only the uptake but also the utilisation of boron; moreover, boron deficiencies are accentuated when the potassium supplies are high, and since calcareous soils are often well supplied with potash the liability to boron deficiency is thus even greater, so that on chalk soils species with low boron requirements will tend to be favoured.

Attention has however been called to the fact that owing to the surface leaching the soil of a chalk down may, and often in the more level areas does, comprise a surface soil which is appreciably acid and lower layers which are alkaline. Experiments were carried out by P. L. Gile and J. O. Carrero (*Journ. Agric. Sci.*, XXI, pp. 545–73, 1921), in which plants of Maize were grown with the different roots of the individuals passing into three separate vessels each supplying either nitrogen, potassium, or phosphorus, and the resultant growth showed that

* * *

PLATE II. Chalk flora. TOP LEFT. Clustered bellflower, *Campanula glomerata*, a single flower of the common harebell, *C. rotundifolia* is also seen in the foreground. The grass in the background is the Cat's tail, *Phleum pratense*. × *ca.* ½. TOP RIGHT. Bee Orchis, *Ophyrs apifera*. × *ca.* ⅔. BOTTOM. Self-heal, *Prunella vulgaris*, a common species forming mat-like aggregates of rosettes. × *ca.* ⅓.

a healthy plant can be produced when the diverse nutrients essential for growth are obtained separately by different parts of the root system. It would therefore seem probable that when a calcicole species has part of its root system in a leached surface soil and part in an unleached substratum it would be

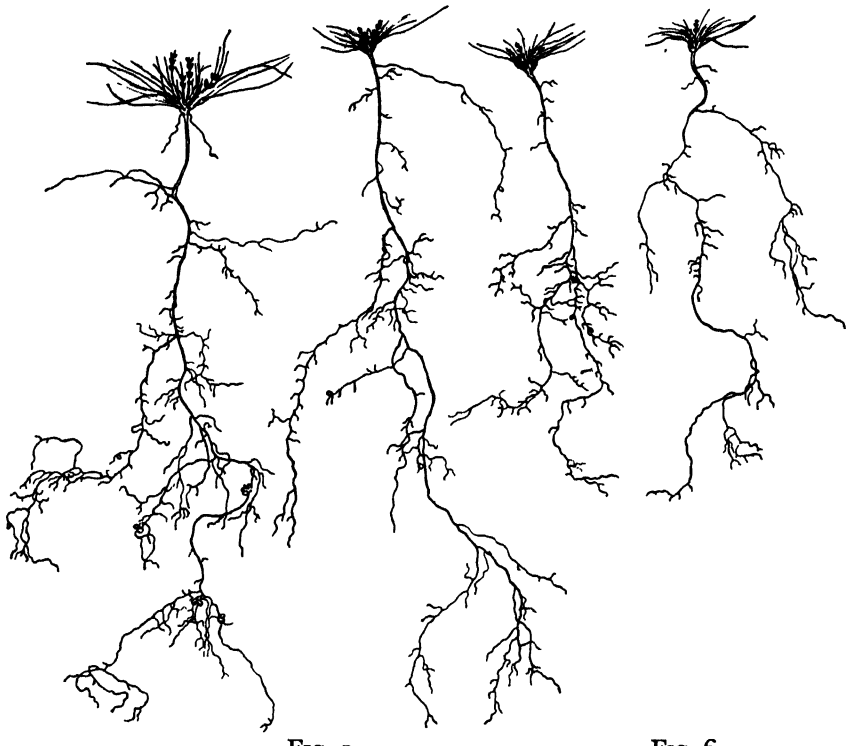


FIG 5 FIG 6

FIGS 5 and 6. Seedlings of Wild Sanfoin (*Onobrychis viciaefolia*). FIG 6. Two plants grown in a uniform mixture of calcareous and 'non-calcareous' soils. FIG 5. Two plants grown in similar soils of the same total volume but with the non-calcareous portion above and the calcareous portion below. The plants grown in the stratified soil have more extensive root systems. Each pair consists of the largest and smallest plant from corresponding treatments.

able to obtain such elements as are most easily available in an acid medium from the one and those most readily available in an alkaline medium from the other. Thus iron, manganese and boron might be largely derived from the more superficial layers and molybdenum through the deeper-penetrating roots. Experiments carried out with pronounced calcicoles and

facultative calcicoles indicated a markedly beneficial effect from stratified soil (cf. Figs. 5, 6 and 7).

The soil conditions have a marked influence on the character of the soil inhabitants, thus whilst bacteria are more common

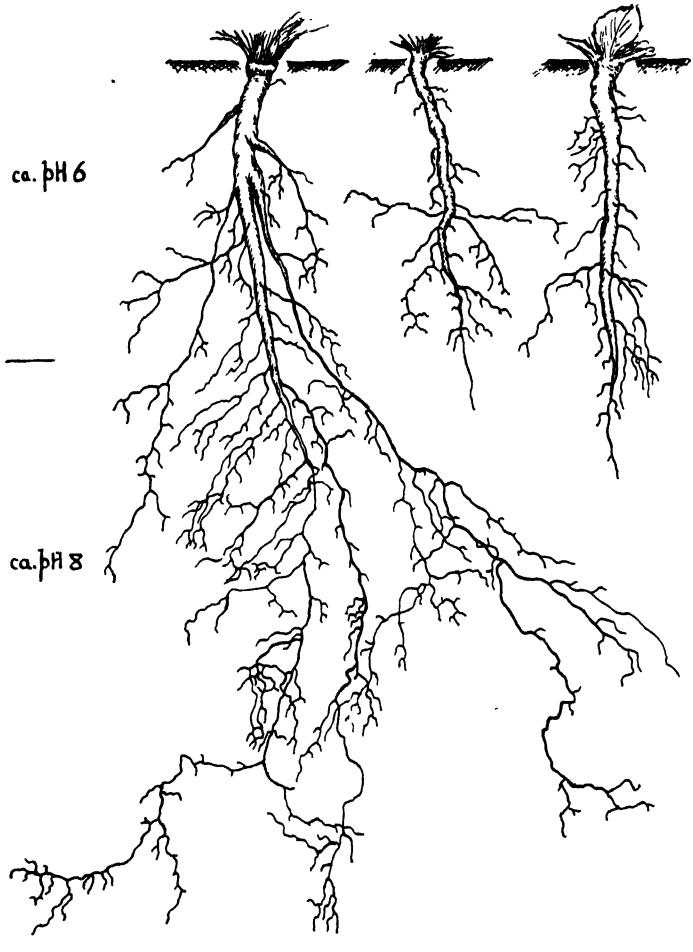


FIG 7. One-year-old plants of Spotted Cat's-ear (*Hypochoeris maculata*). The two smaller on the right grown in a uniform mixture (pH 7·8) of calcareous and 'non-calcareous' soil. The larger plant was grown in the same total volume of soil but with the non-calcareous constituent (pH 6) above and the calcareous constituent (pH 8) below.

in alkaline than in acid soils fungi are less so. The slime-fungus (*Plasmodiophora*) that causes the disease known as 'club-root' or 'finger-and-toe' in Cabbages and other Crucifers is rarely present

since it requires an acid environment to flourish, whereas the disease known as Potato Scab is liable to be serious. The prevalence of wireworms, moles and rabbits are probably concomitants of the physical conditions of soil texture rather than of the chemical qualities, and the excessive lightness and puffiness of some agricultural land on the chalk is a symptom of the same attributes. In uncultivated chalk land the surface may be compacted and the soil atmosphere often occupies a much smaller proportion, but Dr. V. Anderson found that the pore space in the top inch of an old downland soil ranged from 12 to 26% by volume. At a depth of between 1 and 2 ins. the pore space was 10·5 to 22%, whilst between 3 and 4 ins. it represented 9·6 to 12%.

The combined effect of all these circumstances is a medium eminently fitted for root development and offering little mechanical resistance to such since the growing root-tip can readily dissolve its way through the carbonates or enlarge the fissures that already exist.

II

THE FLORA OF THE CHALK DOWNS

AS we wander over the open downland the feature that probably attracts our attention most of all is the short turf of fine-leaved grasses which has for centuries past provided permanent pasturage for the grazing sheep. The clearance of woodland and scrub, which Neolithic man begun, has probably continued almost without interruption during the past four millennia and the trees and shrubs that man removed by fire and axe have been prevented from returning by the browsing flocks of sheep and, since Roman times, by the rabbits also. Because grasses are pre-eminently tolerant of repeated mowing, whether by machine or ruminant, the preponderance of such plants in the turf is natural, but it is especially the narrower leaved and more drought-resistant types that here find their appropriate environment.

But the variety of other plants that are to be found in any area is markedly associated with the average height of the herbage. For just as Daisies, Plantains, Dandelions and Cat's Ear are liable to be most troublesome on the closely shaven lawn and tend to diminish when a lawn is left uncut for a few years, whilst such are normally inconspicuous or even absent in the tall herbage of a lush meadow, so too the flora of the down is usually richest where the herbage is low in stature and poorest where the grasses are tallest and most dense. This is largely, though by no means entirely, a matter of competition, especially for light.

The height of the growth is chiefly dependent upon the intensity of grazing and the nature of the soil. The grazing itself operates both directly and indirectly. For where the browsing is continuous and intense not only is the herbage kept short, but the more robust types of grass that could grow to an appreciable height in the absence of grazing are in fact killed out, just as the taller kinds of grass disappear when meadowland is continuously mown and do not in fact persist in an abbreviated state.

But where the soil is shallow and poor, as, for example, on the slopes of the chalk hills, where removal of soil particles by erosion is in conflict with the soil-forming factors previously considered, the herbage is naturally dwarfed and here a much lower intensity of grazing will suffice not only to keep the herbage very short but to prevent that almost complete protection of the soil surface by vegetation that is termed a 'closed' community. Indeed, it is generally true to say that the steeper the slope of the chalk down the more 'open' the character of the vegetation and the more frequent and larger are the patches of bare soil, though this generalisation is of course only applicable when we compare areas that are subject to the same degree of grazing. If we look at the steep slopes of railway cuttings through the chalk, the vegetation is, as we should expect, rather open but taller than where grazing occurs; but the annual mowing of these slopes does impose a certain artificial restriction on height and in particular retards even if it does not entirely preclude the development of trees and shrubs. The floral displays that such railway banks often present in early July bear witness to the diversity of the plant life which they support mingled with the grasses.

Amongst the most characteristic of the grasses of the chalk are the Sheep's Fescue (*Festuca ovina*) (Pl. IX) and the Red Fescue (*Festuca rubra*). The former is commoner on the sloping, shallower and more calcareous soils and is easily distinguished by its rather tufted habit, its fine slightly glaucous foliage, and above all by the minutely rough surface of the angular flowering stem just below the first branch of the inflorescence. If we have no magnifying glass we can easily detect this roughness with the tip of the tongue. The Red Fescue is usually most abundant where the soil is deeper and more leached, especially on the more level tops of the downs. The habit of this grass is spreading, the leaves are not so fine as those of the Sheep's Fescue, and the flowering stem just below the first branch of the inflorescence is smooth instead of being rough. Two of the Oat Grasses (*Helictotrichon pratensis* and *H. pubescens*) are common and widespread. Both have the prominent awns twisted at the base characteristic of all the Oats, but the former has leaf-sheaths that are smooth, whereas those of the latter are hairy. The Quaking Grass (*Briza media*) and *Koeleria gracilis* (*cristata*) are two species very characteristic of the chalk, both of which have a

pronouncedly tufted habit. The heart shaped flower-heads of the Quaking Grass are unmistakable and their slender attachments to the branched inflorescence results in their almost perpetual movement in the breeze which accounts for the popular name. By contrast the inflorescences of *Koeleria* appear stiff and spear-like but when the branches spread apart at the time of flowering they possess a grace peculiarly their own. Both these grasses have glaucous bluish foliage, but the leaves of *Briza* are smooth, whereas those of *Koeleria* are hairy. Very characteristic also but rather less tolerant of heavy grazing is the Chalk Brome Grass, a tall species that in flower attains to some 3 ft. in height, and in full bloom its large yellow stamens with purple-brown marking render it a handsome plant that is sometimes the predominant species of large stretches of down. This is true also of another chalkland grass, *Brachypodium pinnatum* (Pl. XI), which is a coarse-growing plant intolerant of heavy grazing, but in its absence rapidly spreads to the almost entire exclusion of any other plants. This grass is therefore something of a chalkland weed, since it suppresses those many other species which are the particular charm of the downland vegetation.

Although it is true that the leaves of the Sheep's Fescue are in a sense permanently folded, since the two halves never spread out flat, yet the space between the two halves is wider in moist air than in dry, and a similar change is observed with leaves of the Red Fescue (cf. Fig. 8). The blades of the Oat Grasses (*Helictotrichon*) are almost flat when the supply of moisture is abundant, but in dry weather the two halves of the grass-blades are brought together by the shrinkage of the thin-walled 'motor' or 'hinge' cells that extend along two lines on either side of the midrib for the length of the blade. On the upper surface of the leaf of the False Brome (*Brachypodium pinnatum*) there are a number of lines of such motor cells which occupy the grooves between the parallel ridges so that as the leaf loses water the blade becomes rolled up (cf. Fig. 8), and this occurs also with the leaves of the Quaking Grass (cf. Fig. 8) and the Chalk Brome Grass (*Bromus erectus*).

If, as in very dry weather, the loss of water from the leaves is in excess of the intake from the roots the thin-walled motor cells shrink and leaves such as those of the Oat Grasses fold and of the Brome Grass become rolled. But when, as in rainy and humid conditions, the intake of water is in excess of the loss from the

leaf surface the lines of thin walled cells expand and the leaves flatten. As most of the pores (stomata) through which the water escapes from the leaves are situated on the upper surface of the leaf-blades the approach of the two halves to one another tends to check the rate of water loss. For, when contraction is

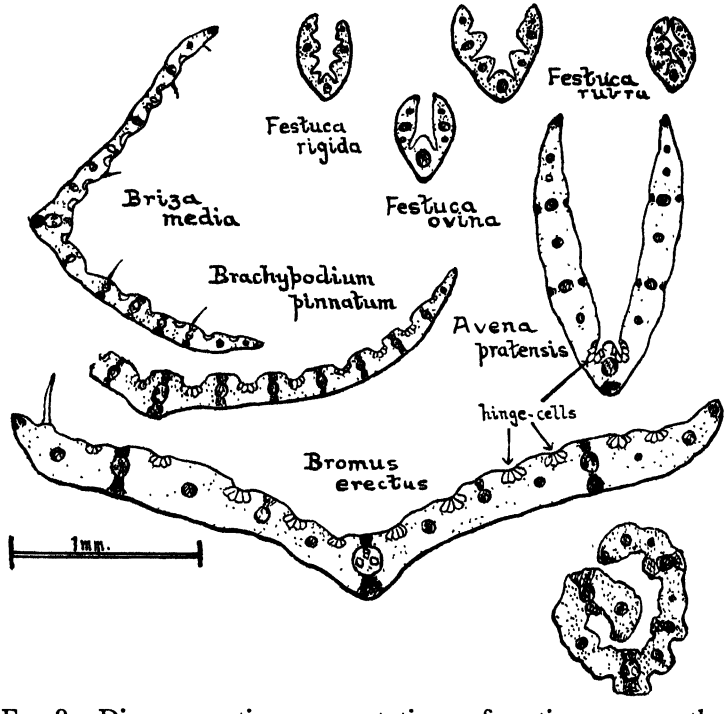


FIG 8. Diagrammatic representations of sections across the leaves of various chalkland grasses. Below, leaf of the Chalk Brome (*Bromus erectus*) expanded as in damp weather, and, on right, rolled as in dry conditions. The position of the thin walled cells ('hinge' or 'motor' cells) that bring about these changes is shown. At top right the Red Fescue (*Festuca rubra*) is shown in dry (R.) and moist (L.) condition. The other leaves shown are Quaking Grass (*Briza media*), False Brome (*Brachypodium pinnatum*), Oat Grass (*Helictotrichon* (*Avena*) *pratensis*), the Sheep's Fescue (*F. ovina*) and the Chalk Fescue (*Scleropoa* (*Festuca*) *rigida*).

extreme, water vapour can only escape through the narrow slit between the two edges. This structure thus constitutes an automatic mechanism for regulation of the rate of loss in relation to the rate of water supply.

It is a natural outcome of the well-drained soil conditions and the continual grazing that the prevalent plants of the chalk

downs are low-growing perennials, and indeed some 90% of the species have their resting winter buds in or on the surface layer (*Hemicryptophytes*). The number of annuals and biennials is correspondingly few. Where the community of plants is open and frequent bare patches of ground permit of the easy establishment of seedlings, such annuals and biennials may represent nearly 10% of the total number of species present but the denser the vegetation and the greater its average height the smaller the proportion of these plants that must be continually replaced by seed (*Therophytes*), and this is true both in respect to the number of species and to the number of individuals. The most characteristic of the annuals is the Chalk Fescue Grass (*Scleropoa* (*Festuca*) *rigida*) which is particularly met with on the miniature erosion slopes below the numerous diminutive terraces that follow the contours on steep gradients. Sometimes it is an abundant weed on derelict arable land on chalky soils. The plants are often erect, sometimes semi-prostrate, but rarely more than 6 ins. in height, with narrow folded leaves like those of the Sheep's Fescue and stiff green or purplish green inflorescences. On similar situations the Purging Flax is quite common but is also sometimes abundant on almost flat areas where the soil is shallow. Another characteristic annual is the Spring Felwort *Gentiana anglica* (=*G. lingulata*), which is like a small autumnal Felwort with usually four petals instead of five and flowering in June or July instead of September. There are several species of Eyebright, including the endemic *Euphrasia anglica*, which are normally annual but the seeds of which sometimes germinate in the autumn and may then live for more than a year. This is true also of the Felwort (*Gentiana amarella*) whereas its close ally *G. germanica* is normally biennial. The Eyebrights are usually semi-parasites on the roots of grasses but under wet conditions appear to be able to live an independent existence, which suggests that they parasitise their hosts for water and water-soluble nutrients alone.

The Ground Pine (*Ajuga chamaepitys*) or Yellow Bugle and the Yellow Centaury (*Blackstonia perfoliata*=*Chlora perfoliata*) (Pl. IV) are both winter annuals, or perhaps technically biennials, the plants of which can be seen in the winter bearing little rosettes of leaves, a habit which is, as we shall see, a marked feature of many of the perennial species in the non-flowering state. The Ground Pine is so called because of the pine-like appearance

of its crowded, narrow leaves (Pl. I) and affording so striking a contrast to its perennial woodland relative the Bugle (*Ajuga reptans*).

LIST OF CHARACTERISTIC CHALK FLORA ANNUALS (A) AND BIENNIALS (B) (P=Perennial)

(For annuals of Cornfields etc., see p. 123)

Ajuga chamaepitys	Ground Pine (Southern continental type winter A)
Anthyllis vulneraria	Kidney Vetch (B)
Blackstonia perfoliata	Yellow Centaury (Southern oceanic A or B). Pl. IV
Carlina vulgaris	Carline Thistle (B)
Euphrasia spp	Eyebright (A)
Gentiana amarella	Felwort (Northern continental A)
Gentiana anglica	Spring Felwort (A)
Gentiana germanica	Greater Felwort (B). Pl. III
Linum catharticum	Purging Flax (A)
Scleropoa rigida	Chalk Fescue (A)
Teucrium botrys	(A). Pl. I
Thesium humifusum	Bastard Toadflax (Oceanic; ? A or short-lived P). Pl. VI
Trifolium (campestre) procumbens	Hop Trefoil (A)

Less characteristic are *Trifolium minus*, *Lathyrus nissolia* (Pl. XII), *Myosotis arvensis* and *M. collina* and the semi-parasites, the Yellow Rattle and Red Bartsia, *Rhinanthus crista-galli* and *Odontites rubra*.

Ecologists who have studied plant communities have attempted to characterise each by the extent to which particular kinds of plants are to be found as constituent members of any one kind of vegetation (constancy) and by the presence of species in a community that do not occur in others (exclusive species). Unfortunately this means of characterisation was, from the outset, doomed to have a very limited value the reasons for which are clearly exhibited by the plant community of chalk grassland but apply also in smaller or greater measure to the vegetation of other types of habitat. Firstly, as we have seen, the soil of a chalk grassland is undergoing continual change and in any area this process continues at unequal rates. So we are confronted at once with the problem as to when chalk pasture ceases to be such. For our characterisation we must in fact draw an arbitrary line that nature does not recognise. Moreover, in vegetation that appears typical there are quite commonly patches intermingled that are less typical, presenting a

mosaic of parts that in respect to the physical conditions and the organisms that these support are by no means entirely comparable. It is true that there are species of plants which by reason of their physiological specialisation are restricted to the chalky soil through the peculiar conditions this presents. But it is obvious that the more highly specialised the requirement of a species the more restricted will be its occurrence, so that inevitably the higher the degree of exclusiveness of the species the greater will tend to be its scarcity, and thus its degree of constancy will be low. In other words the more valuable this kind of plant as an indicator the less likely we are to find it, except under conditions that are unequivocal. A high degree of specialisation renders a species valuable as an indicator of environmental conditions, especially since the plant's capacity for differentiating habitats is probably much greater than our own; but as already noted the chalk soils are marked not only by very distinctive chemical features but by physical conditions also, and some species are common on the chalk mainly by reason of the former, some mainly by reason of the latter, still others mainly by the conditions imposed by continual grazing, and most species to some extent perhaps by the combination of all three.

If the chief condition that determines the presence of a particular plant is plenty of calcium carbonate in the soil we shall expect to find the same plant not only on the chalk down but on other soils with this same quality. For example, the Yellow Centaury (*Blackstonia perfoliata*) (Pl. IV) which is a marked feature of our chalk downs is also to be met with on the limestones, on calcareous dunes and even chalky boulder clay. It is to be found on soils that are dry and even on wet soils that are calcareous, as in the dune slacks at Southport, in company with the Grass of Parnassus (*Parnassia*). It grows also on soils that are light and soils that are heavy, but all the habitats appear to have this in common: that they are well supplied with bases, particularly calcium. Thus the Yellow Centaury, though highly characteristic of the chalk down, is far from being an exclusive species.

As a wild species the Field Sage (*Salvia pratensis*) (Pl. VIII), a very rare British plant, is almost confined to the chalk, but its exclusiveness is probably an expression mainly of its liking for well-drained warm conditions, since on the Continent it occurs,

in the milder southern climate, on non-calcareous soils. It is evident then that restriction is chiefly of importance in relation to other communities in which the salient habitat conditions are similar, and the fact that a particular species occurs in other plant communities (low exclusiveness) where the same master factors operate in reality enhances its significance. The species that occurs in one plant community and never in any other is apt to be so rare and local that for most people it is but a name and presents a specialised problem, perhaps peculiar to itself, which may help but little towards an understanding of the habitat that it occupies. So it is that the general structure and physiognomy of a plant community is often of more import than the precise species of which it is composed. The forest remains a forest whether the trees be

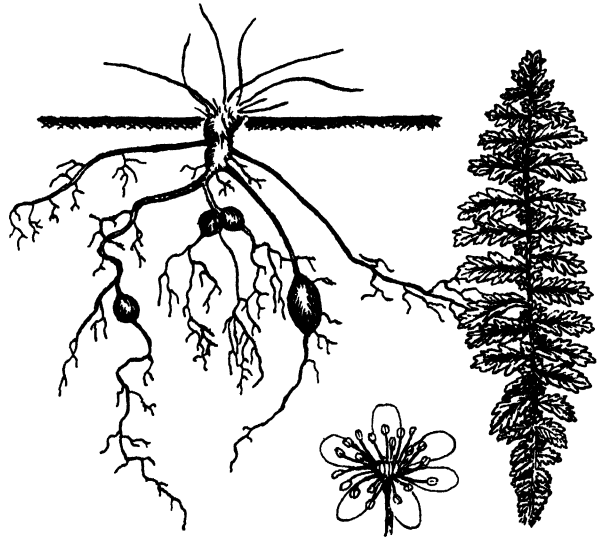


FIG 9. Dropwort (*Filipendula hexapetala*). Root system (after Anderson) on left, showing the food-storage organs. On right, leaf showing the characteristic alternation of large and small leaflets. Below, a single flower showing the six petals and numerous stamens.

Oaks or Beeches, and we recognise the fundamental similarity of the carpet of plants whether it be on the Downs of Sussex or Wiltshire, the Chilterns or the Lincolnshire Wolds, despite the fact that some of those plants which grow commonly in one area are rare or absent from another.

All these areas just mentioned are characterised, for instance, by the prevalence of kinds of plants which, in the non-flowering stage at least, bear their leaves close to the ground in a rosette, a feature well exemplified by the plantains, of which both the Black Plantain (*Plantago lanceolata*) and the Grey Plantain (*Plantago media*) are common; but whereas Black Plantains are to be found wherever grazing or cutting permits such rosette plants to flourish, the Grey Plantain with its sweet-smelling pale grey spikes is more particularly associated with chalky soils.



FIG 10. Horseshoe Vetch (*Hippocrepis comosa*) showing leaf base with stipules and glandular swelling (a), pod (b), an inflorescence and a prostrate shoot in the winter condition, showing the branches orientated in one plane.

The rosette plants comprise about 35% of the entire chalk down flora and are representative of a great diversity of families, which emphasises that it is not the prevalence of plants of any particular affinity that is responsible for so high a proportion. It is, however, true that the terrestrial Orchids that are such a feature of the chalk and of which a number of species occur

are all rosette plants in the non-flowering condition, and by virtue of their tubers can resist a remarkable degree of desiccation to which, owing to their shallow depth of rooting, they are very liable. The most widespread is the Spotted Orchis (*Orchis fuchsii*) which occurs on other basic soils; but the Sweet Scented (*Gymnadenia conopsea*) (Pl. XVII), the Bee Orchis (*Ophrys apifera*) (Pl. II), the Pyramidal Orchis (*Anacamptis pyramidalis*) (Pl. V) and the Frog Orchis (*Coeloglossum viride*) (Pl. I) find with us their main home on the chalk. There are a number of others which are confined to the chalk, but they are local or even very rare. It is significant that most of these Orchids are characteristic members of the flora of areas with a continental climate and probably find a congenial home in our oceanic climate only on the well-drained warm soils of the chalk (cf. p. 36).

The Ranunculaceae are represented amongst the rosette plants by the Pasque Flower (*Pulsatilla vulgaris*), sometimes known as Dane's Blood because it so often frequents the warm southern slopes of Neolithic or other prehistoric earthworks attributed by our forefathers indiscriminately to the Danes (Pl. VI).

The Dropwort (*Filipendula hexapetala*) (Fig. 9 and Pl. VIII) is a Rosaceous rosette species, whilst the Pea tribe are represented by the biennial Kidney Vetch (*Anthyllis vulneraria*), more especially found on erosion slopes.

The Compositae are represented by a number of rosette species well exemplified by the Dwarf Thistle (*Cirsium acaulos*) and *Senecio integrifolius*, the former a deep-rooted and long-lived perennial, the latter a shallow-rooted and short-lived perennial that is liable to die after flowering. Whilst the population of Dwarf Thistles remains relatively constant, that of *Senecio integrifolius* shows striking fluctuations. Two other yellow flowered members of the Compositae which exhibit the rosette habit merit comment as being far commoner on the chalk than elsewhere. The first, the Hoary Ragwort (*Senecio erucifolius*) is a more erect tidier plant than the common Ragwort (*S. jacobaea*) with larger flower-heads and ribbed hairy fruits instead of smooth ones. The second is the Ox-tongue (*Picris echioides*) a biennial plant which is readily distinguished by the bristle-like hairs which beset the leaves and the two types of bracts around the flower-head of which the outer are heart-shaped and spreading

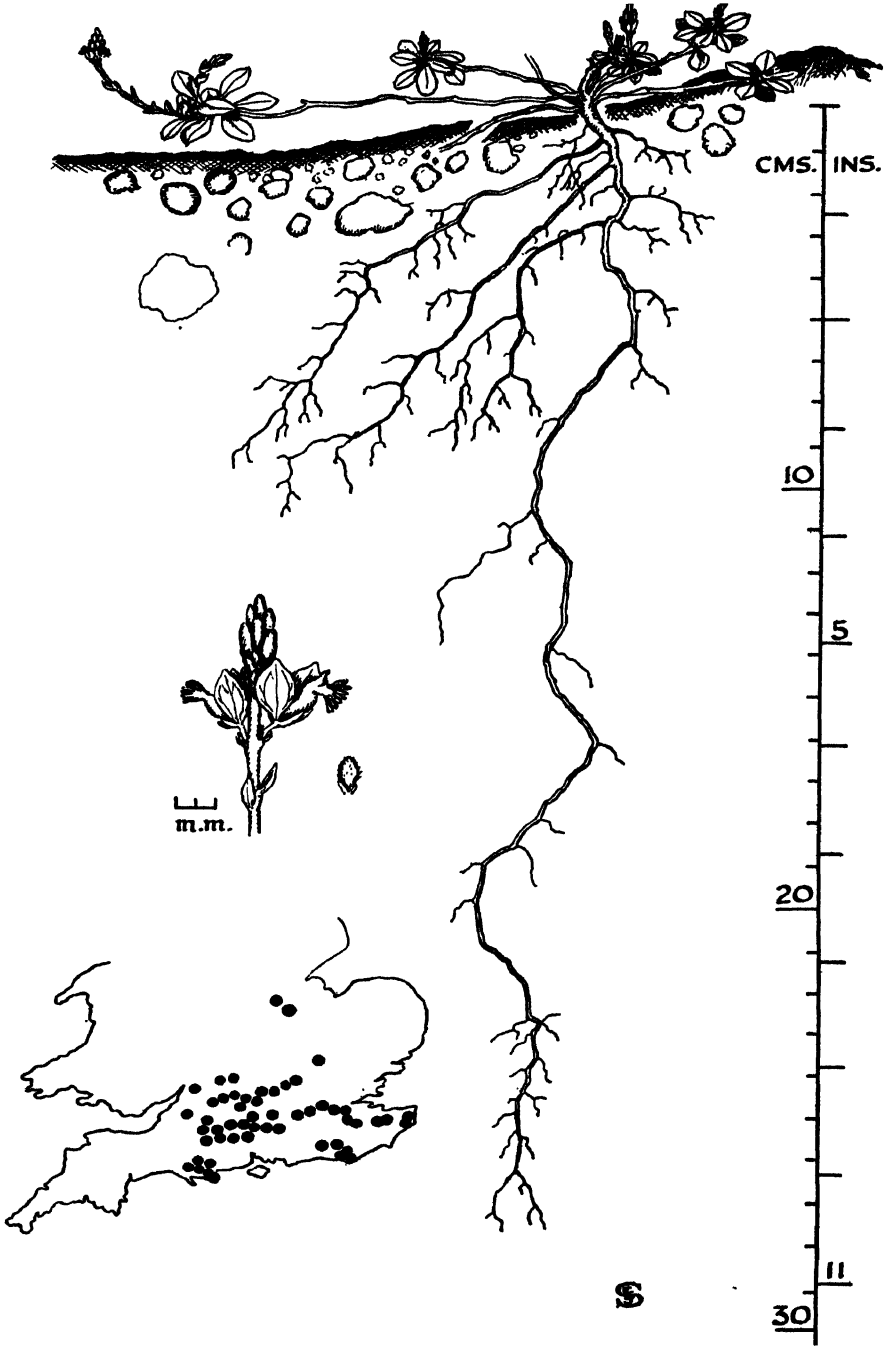


FIG 11. The Chalk Milkwort (*Polygala calcarea*) showing the characteristic rosettes of leaves in the early summer condition, the root system, also an inflorescence and a map of the English distribution. Gloucestershire.

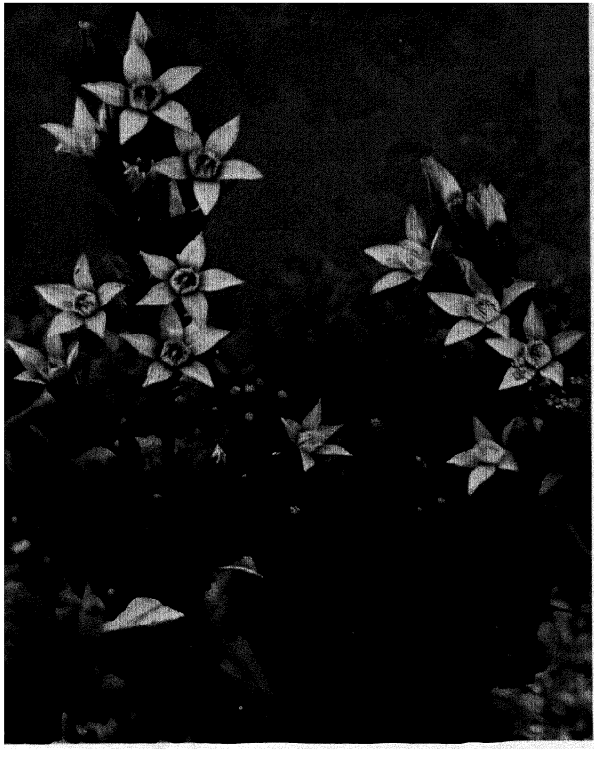
and the inner erect. The ox-tongue is noteworthy as producing two types of fruit in the same flower-head, those opposite the inner series of bracts being far larger and more tumid than those produced from the bulk of the florets. The Carline Thistle, (*Carlina vulgaris*) is a biennial rosette species. The Chalk Scabious (*Scabiosa columbaria*) represent this habit in the Dipsaceae, whilst the Clustered Bell Flower (*Campanula glomerata*) (Pl. II) and the Rampion (*Phyteuma tenerum*) (Pl. VIII) are examples from the Campanulaceae. A number of Gentianaceae are also rosette plants, notably the Yellow Centaury, the Gentians and the less characteristic, but often common, Pink Centaury (*Centaurium umbellatum*).

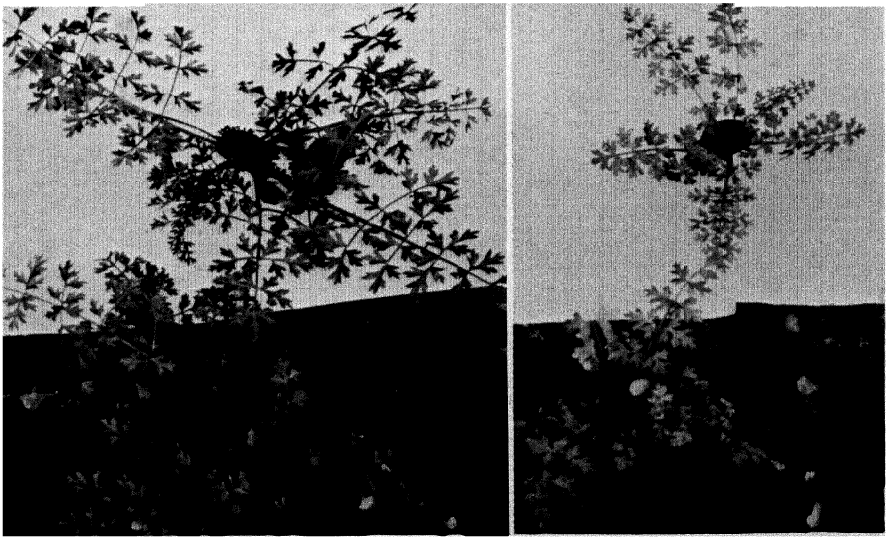
One of the most striking of the biennial rosette plants is the great Cotton Thistle (*Cirsium eriophorum*), the rosettes of which can attain a diameter of nearly 1 yard whilst the flowering stems with their magnificent heads of flowers may attain to a height of 6 or 7 ft. (Pl. XIX). The winter rosettes of this thistle illustrate in a marked degree a feature that is common to other rosette species, namely their capacity to weaken or even kill the surrounding plants over which the rosette leaves spread. This is mainly, though probably not entirely, an effect of shading, and is enhanced by the positive pressure exerted by the rosette leaves which maintains them in intimate contact with the herbage or soil on which they rest. This downward pressure can be demonstrated if we cut off a rosette from beneath, close to the ground, whereupon the leaves will be seen to bend downwards. The higher rate of growth on the upper than underside of the leaf stalk that exerts the downward thrust is apparently conditioned by the combined stimuli of gravity and high light intensity which together determine the operation of the growth hormones.

Just as the rosettes of the Dandelions and Daisies on our lawns in large measure escape the blades of the mechanical mower, so

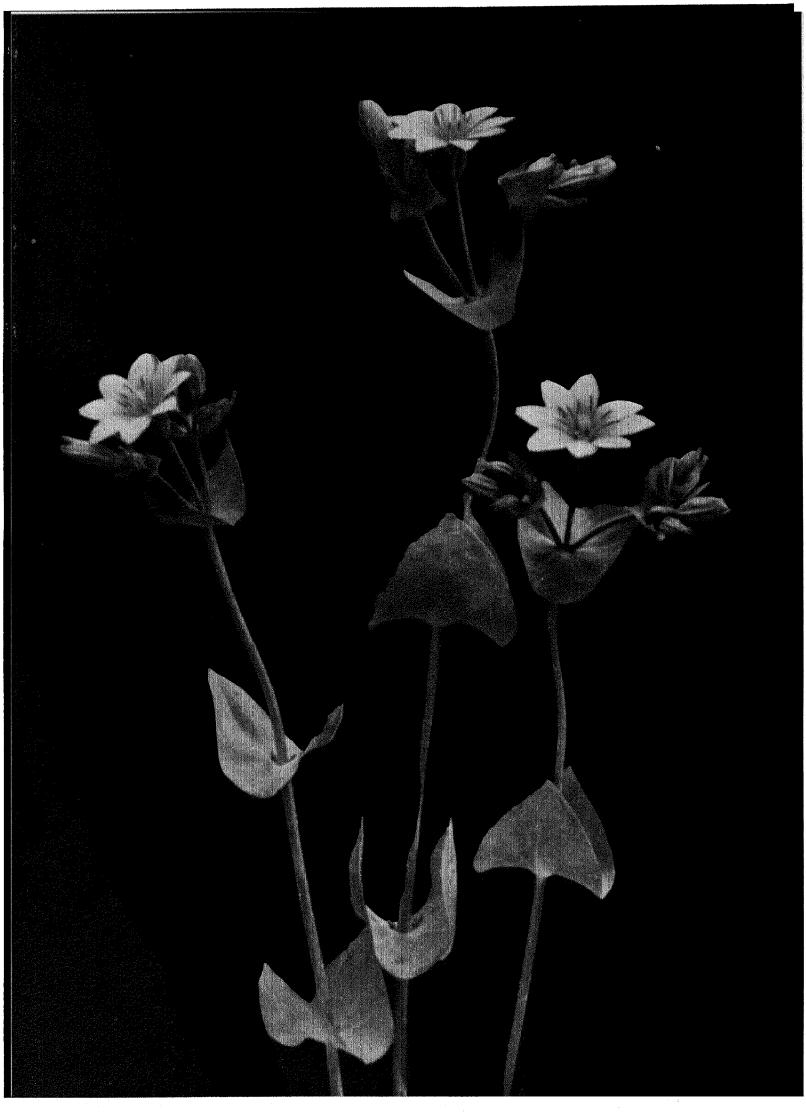
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PLATE III. Chalk down plants. BELOW. First year plants of the rare carrot-like *Seseli libanotis* grown, on the right, without chalk and on the left in similar soil with chalk added. Note the rosette habit and that the plants on the chalky soil are twice as large. ABOVE. The Greater Felwort (*Gentiana germinaca*), a biennial with rosette habit before flowering, growing on a chalk down in Buckinghamshire. The small seed-vessels are those of the Purging Flax. Life-size.





IV



too the rosettes of the chalkland pasture plants remain in considerable degree immune from the teeth of the browsing animal which, by pruning the grasses around, brings about a preferential selection in favour of the rosette species. It is not surprising therefore that this growth form is so marked a feature of the downland vegetation. No less characteristic and prevalent, and for much the same reasons, are the mat plants which develop a low-growing carpet of foliage from a laterally-spreading shoot system that tends to suppress surrounding competitors in much the same manner as a rosette. An excellent example of this type of growth is afforded by the Horseshoe Vetch (*Hippocrepis comosa*) (Pl. IX) so named because the pods break across when ripe into one-seeded segments that have the form of horseshoes (see Fig. 10). The flowers resemble those of the Bird's-foot Trefoil, except in their smaller size, but the leaves have a number of leaflets instead of only three as in the latter species. An old plant of the Horseshoe Vetch may have developed a mat of branches and foliage more than a square metre in area, although this is liable to be pruned severely back in a hard winter. Such a mat can be lifted off the ground, but in the Milk Vetch (*Astragalus danicus*) (Pl. I) the mat is formed by the extensive branching of the underground stems in the upper layers of the soil, a type of growth which is shared by the Bird's-foot Trefoil (*Lotus corniculatus*), the Mouse-ear Chickweed (*Cerastium arvense*) and the Harebell (*Campanula rotundifolia*). All three of these are common on the chalk but only *Cerastium arvense* is far more common here than on other types of soil. The Squinancy-wort (*Asperula cynanchica*) is a mat plant restricted to calcareous soils, especially chalk downs and also dunes with a high lime content (Pl. XXX), and it is instructive to compare its habit and leaf structure with that of its woodland relative the Woodruff (*Asperula odorata*). The Rock Rose (*Helianthemum nummularium*) (Pl. IX) furnishes an example of a mat-forming shrub which attains its greatest frequency on the chalk. The very characteristic Chalk Milkwort (*Polygala calcarea*) is a mat-forming perennial which is also a rosette plant in that the leaves at the base of each flowering shoot are crowded

* * *

PLATE IV. The Yellow Centaury (*Blackstonia perfoliata=Chlora*), a common plant of the chalk down. Nearly life-size.

together in a rosette-like manner (see Fig. 11). It is perhaps not without significance that the Common Milkwort (*P. vulgaris*) that occurs on a wide variety of soils and in a diversity of habitats exhibits no such rosette tendency, whereas *P. calcarea*, which is confined to chalk downs, has the rosette tendency in a marked degree. It may be added that some of the rosette species, such as the Clustered Bell Flower (*Campanula glomerata*) and the Dropwort (*Filipendula hexapetala*), by virtue of the production of lateral buds develop an aggregation of rosettes that approximates to a mat type of growth. The same tendency is seen in the Greater Knapweed (*Centaurea scabiosa*), the Salad Burnet (*Poterium sanguisorba*) (Pl. IX) and the less characteristic but common Self-heal (*Prunella vulgaris*) (Pl. II).

CHARACTERISTIC ROSETTE SPECIES OF CHALK

C.=Continental; C.N.=Continental-Northern; N.C.=Northern-Continental; S.C.=Southern-Continental

Aceras anthopophora (S.C.)	Man Orchis
Anacamptis pyramidalis (S.C.)	Pyramidal Orchis
Gymnadenia conopsea	Sweet Scented Orchis
Herminum monorchis (N.C.)	Musk Orchis
Himantoglossum hircinum (S.C.)	Lizard Orchis
Ophrys apifera (S.C.)	Bee Orchis
Ophrys aranifera (S.C.)	Spider Orchis
Orchis militaris (S.C.)	Soldier Orchis
Orchis simia (S.C.)	Monkey Orchis
Orchis ustulata (C.)	Dwarf Orchis
Spiranthes spiralis	Lady's Tresses
Anthyllis vulneraris	Kidney Vetch
Campanula glomerata	Clustered Bell Flower
Carlina vulgaris	Carline Thistle
Centaurea scabiosa	Great Knapweed
Cirsium acaulos	Dwarf Thistle
Cirsium eriophorum v. britannica	Cotton Thistle
Filipendula hexapetala	Dropwort
Phyteuma tenerum (Oceanic)	Rampion
Plantago media	Grey Plantain
Poterium sanguisorba	Salad Burnet
Pulsatilla vulgaris (C.)	Pasque Flower
Salvia pratensis	Field Sage
Scabiosa columbaria	Chalk Scabious
Senecio integrifolius	Chalk Ragwort
Seseli libanotis (C.)	

OTHER FREQUENT ROSETTE SPECIES, LESS RESTRICTED TO THE CHALK

Agrimonia eupatoria	Agrimony
Bellis perennis	Daisy
Carduus nutans	Mush Thistle
Daucus carota	Carrot
Leontodon hispidum	Rough Hawkweed
Orchis fuchsii	Spotted Orchis
Pimpinella saxifraga	Burnet Saxifrage
Plantago lanceolata	Black Plantain
Primula veris	Cowslip

ANNUAL AND BIENNIAL (ROSETTE PLANTS BEFORE FLOWERING)

Ajuga chamaepitys (S.C.)	Ground Pine
Anthyllis vulneraria	Kidney Vetch
Blackstonia perfoliata (=*Chlora*)	Yellow Centaury
Carlina vulgaris	Carline Thistle
Centaurium umbellatum	Pink Centaury
Gentiana amarella	Felwort
Gentiana anglica	Spring Felwort
Teucrium botrys (S.C.)	

CHARACTERISTIC MAT PLANTS FOUND MAINLY ON CHALK

Asperula cynanchica (S.C.)	Squinancy-wort
Astragalus danicus (C.N.)	Milk Vetch
Hippocrepis comosa (S.C.)	Horseshoe Vetch
Helianthemum nummularium	Rock Rose
Origanum vulgare	Marjoram
Polygala calcarea (S. Oceanic)	Chalk Milkwort

GRASSES

Helictotrichon pratensis	Oat Grass
Helictotrichon pubescens	Oat Grass
Brachypodium pinnatum	
Bromus erectus	Chalk Brome

OTHER MAT PLANTS FREQUENT ON CHALK BUT ALSO ON OTHER SOILS

Achillea millefolium	Yarrow
Campanula rotundifolia	Harebell
Carex flacca	Glaucous Sedge
Cerastium arvense	Mouse-ear Chickweed
Festuca rubra	Red Fescue
Galium verum	Yellow Bedstraw
Hieracium pilosella	Mouse-ear Hawkweed
Lotus corniculatus	Bird's-foot Trefoil
Medicago lupulina	Black Medick
Prunella vulgaris	Self-heal
Thymus serpyllum	Thyme

Consideration of the soil conditions has shown us that the chalk is a peculiarly favourable habitat for leguminous plants.

MEMBERS OF THE PEA TRIBE MOST CHARACTERISTIC OF THE CHALK

Anthyllis vulneraria	Kidney Vetch
Astragalus danicus	Milk Vetch
Hippocrepis comosa	Horseshoe Vetch
Onobrychis viciaefolia	Wild Sanfoin

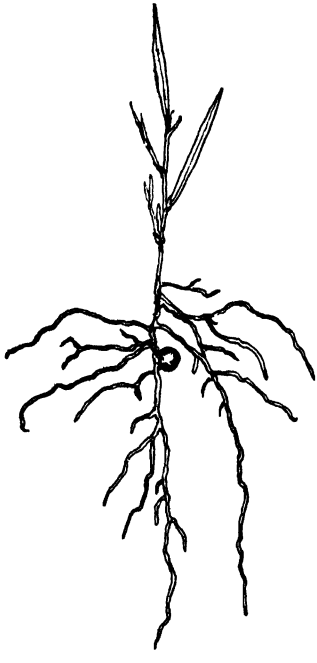


FIG 12. Seedling of the biennial Grass-leaved Vetch (*Lathyrus nissolia*) in the winter state with one large bacterial nodule on the root system.

Less restricted to the chalk, but common there, are the Bird's-foot Trefoil (*Lotus corniculatus*), the Red Clover (*Trifolium pratense*), the Hop Trefoil (*T. campestre*) and the Wild White Clover (*T. repens*). The Black Medick (*Medicago lupulina*) is also common, whilst the semi-shrubby Rest-harrow (*Ononis repens*) is more local in its occurrence. The Grass-leaved Vetch (*Lathyrus nissolia*; see Fig. 12 and Pl. XII) is an annual that is also local but sometimes abundant in certain seasons.

GEOGRAPHICAL ELEMENTS IN THE CHALK FLORA

The most characteristic chalk plants are usually to be found on the south facing slopes. Here the natural warmth of the well-drained soil is accentuated by the greater amount of radiant energy which a given area receives from the sun owing to the angle of the soil surface. Here also erosion removes the leached soil crumbs and so maintains the peculiar physical and chemical features which the chalk plants prefer. Such a habit is clearly more favourable than most for the growth of species characteristic of warmer southern climes, and it is therefore of interest to find that species which, on the European mainland, have a southern trend in their geographical distribution constitute a conspicuously large part of the kinds of plants which occur exclusively or mainly in the chalk.

The Southern-continental element of the chalk flora includes several orchids, namely the Man Orchis (*Aceras anthropophora*, Fig. 13), the Lizard Orchis (*Himantoglossum hircinum*, Fig. 13), the Bee Orchis (*Ophrys apifera*), the Spider Orchis (*Ophrys aranifera*=*O. sphegodes*, Fig. 13), and the Pyramidal Orchis (*Anacamptis pyramidalis*). To this category belong several Labiatae, notably the rare Field Sage, a deep-rooted perennial with a rosette habit and tall flowering stems which bear bright blue flowers (Pl. VIII). The rare white-flowered Self-heal (*Prunella laciniata*, Fig. 13) with toothed leaves has a curiously patchy distribution in England, possibly due to its recent arrival from the Continent since it was first recorded from the limestone of the Mendip Hills in 1906. (Cf. J. W. White. *Journ. Bot.*, XLIV, 365, 1906). There are also two annual species of the Dead Nettle tribe that have a Southern-continental distribution, namely the yellow-flowered Ground Pine (*Ajuga chamaepitys*, Fig. 13) and the purple flowered *Teucrium botrys*, both as we might expect plants of the shallow soils and open communities (Pl. I). To the Southern-continental class also belong two mat-forming species, the Squinancy-wort (*Asperula cynanchica*, Fig. 13) and the Horseshoe Vetch (*Hippocrepis comosa*, Fig. 13), the Quaking Grass (*Briza media*) a tussock perennial, and the Broomrape (*Orobanche elatior*) which parasitises the roots of the Greater Knapweed (*Centaurea scabiosa*) (Pl. VII).

A few of the characteristic chalk plants though also southern are associated with oceanic rather than continental climatic conditions. This is so for the Yellow Centaury (*Blackstonia perfoliata*, Fig. 14), the Chalk Milkwort (*Polygala calcarea*, Fig. 11) and the Rampion (*Phyteuma tenerum*, Fig. 13), both blue flowered deep-rooted perennials. Another oceanic southern species is our variety of the biennial Cotton Thistle (*Cirsium eriophorum v. britannicum*, Fig. 15), which becomes commoner as we pass westwards, an endemic variant of the continental type, *C. eriophorum* itself (Pl. XIX). The same geographical class is also represented by the Bastard Toadflax (*Thesium humifusum*) a perennial parasitic plant (Fig. 13 and Pl. VI).

Several chalk species are definitely plants of continental climatic conditions, exhibiting a preference for areas of hot summers and cold winters and a dry rather than a humid atmosphere. Such are the Dwarf Orchis (*Orchis ustulata*), the Pasque Flower (*Pulsatilla vulgaris*, Fig. 13) and *Senecio integrifolius*,

Fig. 13, all three perennial rosette plants. Two biennials belong to this category, namely the Greater Felwort (*Gentiana germanica*, Fig. 13) (Pl. III) and the very rare carrot-like *Seseli libanotis* (Pl. III). Other continental species, but with a definitely northern trend (Northern-continental) are the Musk Orchis (*Herminium monorchis*), the Milk Vetch (*Astragalus danicus*, Fig. 15) and the annual Felwort (*Gentiana amarella*).

The proportion of species which are more or less confined to calcareous soils tends to augment as one passes further northwards, and to a less marked degree westwards, so that one can infer that the physical and chemical features of chalky soils tend to ameliorate the climatic effects of low temperatures and high humidities. The prevalence of southern species is therefore to be expected, as also that of the continental element. So too we are scarcely surprised to find that some species which we do not regard as particularly chalk lovers in England exhibit this soil preference in Ireland, such plants, for instance, as the perforate St. John's Wort (*Hypericum perforatum*) and the yellow Oat Grass (*Trisetum flavescens*). Both these occur in England on calcareous soils but are common on other soils also. As the maps showing the distribution of some of the more characteristic British calcicole species indicate, their occurrence as wild plants in Britain shows the same trend as on the Continent itself and an appreciable number of the southern types do not occur, even in the calcareous areas, much beyond the line joining the Wash to the Bristol Channel (e.g. *Thesium humifusum*, Fig. 13, *Senecio integrifolius*, Fig. 13, *Salvia pratensis*, *Iberis amara*, Fig. 15, *Polygala calcarea*, Fig. 11). The Yellow Centaury has a more extended range reaching into Scotland and is common over a wider area in Ireland than in England. Since this species is to be found growing even in shallow water in base-rich slacks of calcareous sand dunes its tolerance of moist conditions is manifest, so that its extension into the more humid conditions of the north and west is to be expected. Both the Milk Vetch and the Pulsatilla Anemone are absent from the Irish mainland, but whereas the latter Continental species occurs from Gloucestershire in the south-west to Yorkshire in the north and Norfolk in the east, the northern-continental Milk Vetch, *Astragalus danicus*, extends from the south of England to the north of Scotland (Fig. 15) and also occurs on the island of Arran off the west coast of Ireland. The Squinancy-wort occurs as far north as

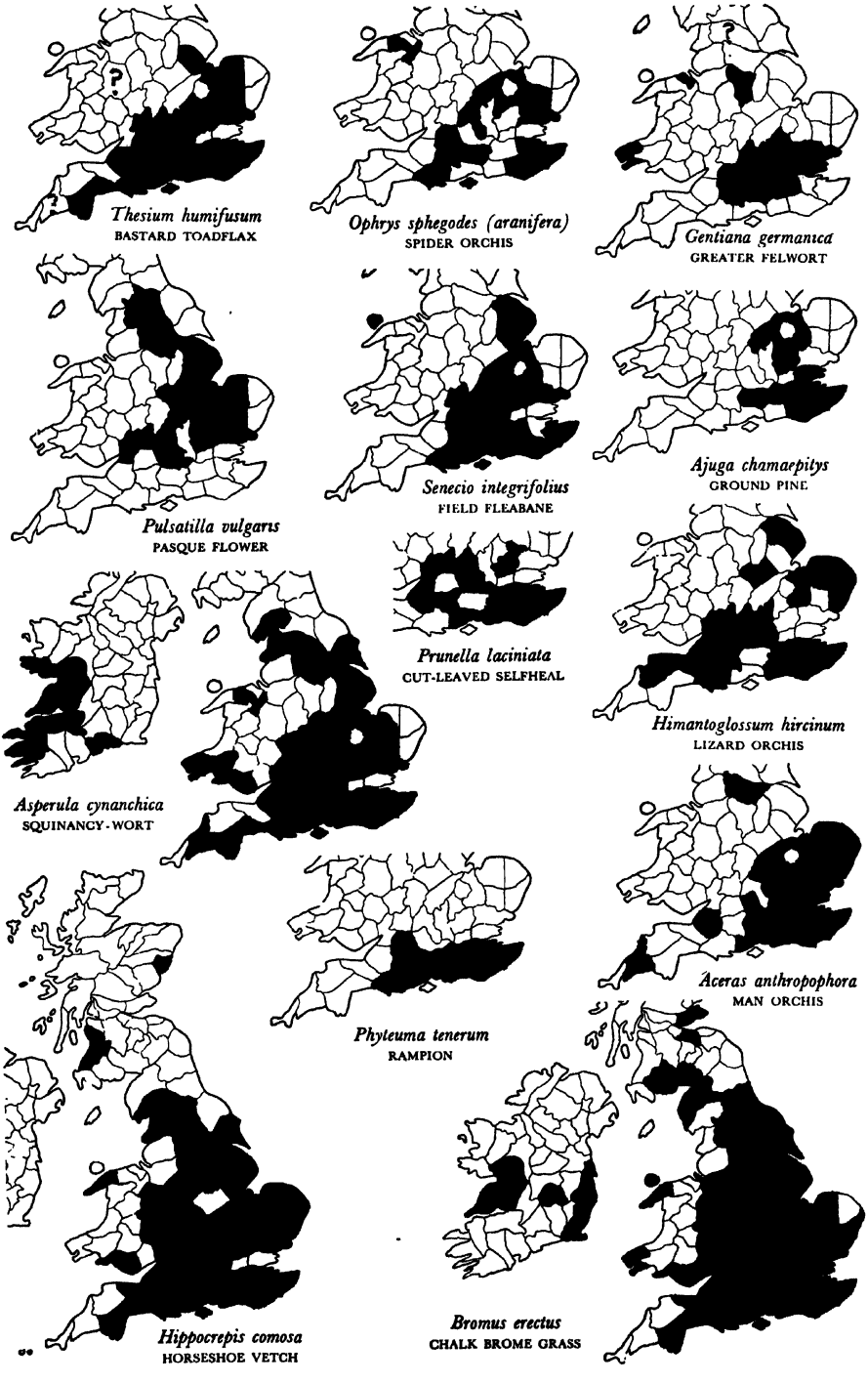


FIG 13. Distribution maps of Chalk Downs species. Prevailing Southern and Eastern distribution.

Westmorland and in the west of Ireland, and *Brachypodium pinnatum* occupies a similar but more restricted range, and in Ireland only occurs in Waterford.

The Bee Orchis has a wide distribution both in England and Ireland, whereas the Spider Orchis (Fig. 13) is absent from Ireland, and except for a locality in Denbigh does not extend north west of the line from the Wash to the Severn.

Of the kinds of plants which we shall scarcely ever find except on the chalk down or similar calcareous habitats none are more characteristic than the orchids. Some of these are extremely rare, as for instance, the Monkey Orchis (*O. simia*), perhaps now extinct owing to unfortunate ploughing. The Lizard Orchis though also very rare had in fact been found in a number of new localities during the nineteen-thirties (Fig. 13), whereas most of our British Orchids have tended to become rarer. The reason for this is that most of them are short-lived perennials, and indeed many individuals of some, fruit but once. It is obvious, therefore, that unless there is constant replacement by seedlings there is bound to be a diminution of the population. So many people never refrain from picking an Orchid when they see one; and though each person may only gather a few, yet the so-called moderation of the many adds up to devastation of the species. But, why, if this be so, has the Lizard Orchis been found in new places even though the total population of plants in Britain may not have appreciably increased? The answer is, I think, that during the nineteen-thirties there was an appreciable import trade of plants of this species from the Continent, and it is not improbable that the seeds of these garden-grown individuals have been responsible for the appearance of the Lizard Orchis in fresh localities.

Curiously enough, three of the most characteristic of the chalk Orchids have green flowers, namely the Lizard Orchis, the Musk Orchis and the Man Orchis. The last-named though by no means common is not infrequent in some localities. Its popular name is due to the fancied resemblance of the flower to a green man, the two mid lobes of the lip representing the legs, the two lateral lobes the arms, whilst the body of the flower suggests a head.

The Dwarf Orchis, a charming species usually 6 ins. or less in height with dark buds and pale pink flowers, has sadly diminished, but is still not infrequent in a few localities.

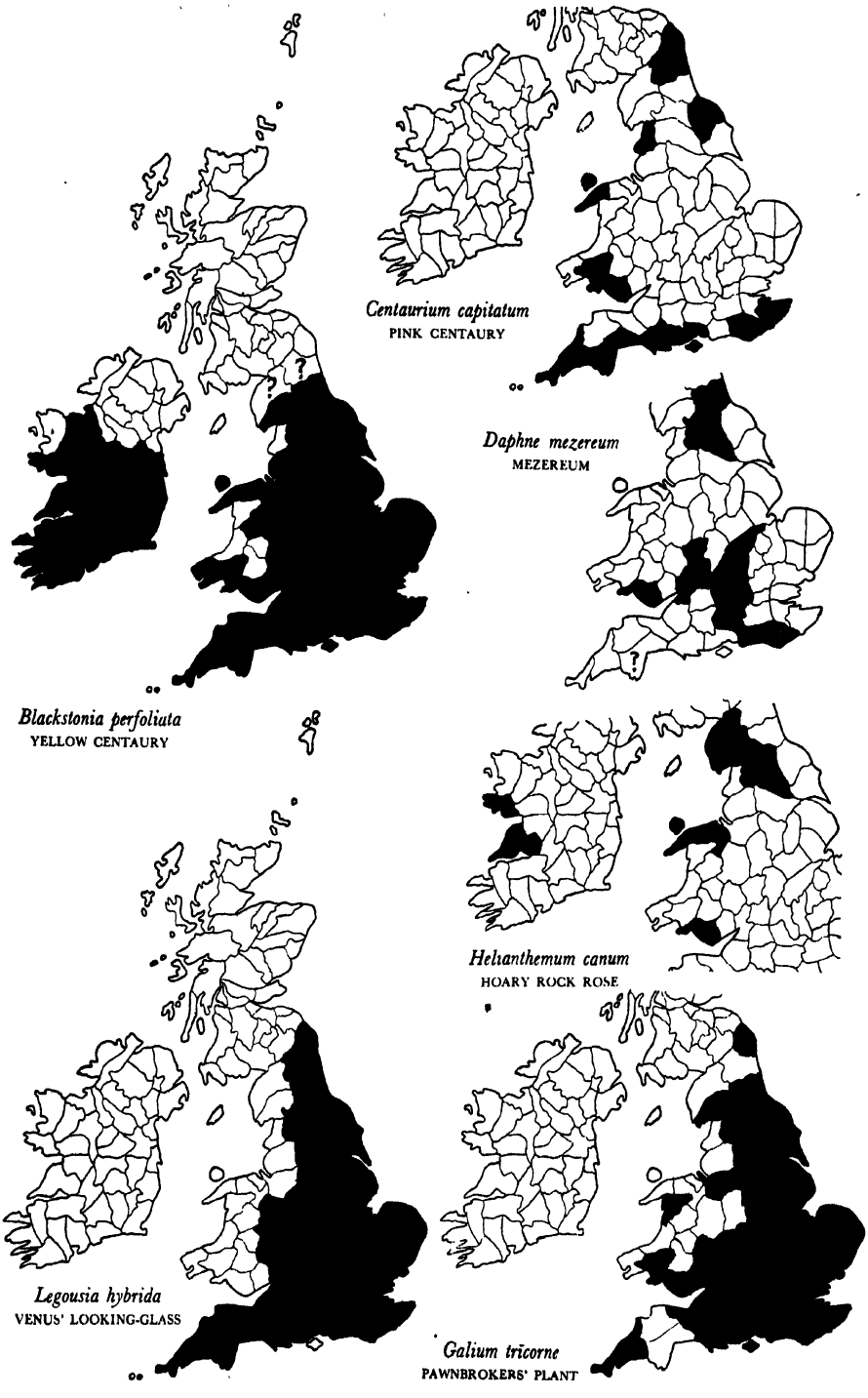


FIG 14. Distribution maps of calcicolous species.

The truly wild Sanfoin (*Onobrychis viciaefolia*) is probably confined to the chalk. It is a true perennial and in this differs from its coarser relative the commonly cultivated fodder plant, which is usually biennial or at most a very short-lived perennial. The wild plant has deeper-coloured and more beautiful flowers, whilst the leaflets are narrow like those of a vetch and the entire plant is more prostrate. Three blue-flowered plants we shall only find here. The greater Felwort (probably an abbreviation of Fieldwort), a beautiful Gentian (*Gentiana germanica*, Pl. III) that is technically a biennial and passes the winter in a rosette stage. The Rampion (*Phyteuma tenerum*), a deep-rooted, rosette perennial with a very restricted range in the south east (Fig. 13 and Pl. VIII). It is a member of the Harebell family (Campanulaceae), but unlike most members of the group the small deep blue flowers are borne in compact heads which subsequently give place to almost spherical groups of fruits. In common with other members of its family, the stems and leaf stalks show a milky juice when broken. The third is the Chalk Milkwort (*Polygala calcarea*, Fig. 11) easily recognised by its inflorescence of very blue flowers which spring from rosettes of spathulate blunt leaves. Unlike the Gentian and the Rampion, which are both late summer flowers, the Milkwort is a flower of the early summer or late spring. The black seeds bear a small oily white appendage known as a caruncle which is attractive to ants and they often play a part in the dispersal of its seeds.

The Field Fleabane (*Senecio integrifolius*) is a rosette plant which in summer sends up a single unbranched stem bearing at its summit from three to five yellow flower heads. These later give place to wind-borne fruits. The plant is a short-lived perennial and it is probably due to this that its numbers are subject to very marked fluctuations. I have known chalk pastures where it is normally a rare plant, or in some years extremely so, yet for two or three years only it occurred in large numbers to decline again as abruptly as it increased.

The perennial parasite *Thesium humifusum*, which is confined to calcareous pastures, is also a very fluctuating species. Its yellow-green foliage and small, inconspicuous pale flowers are quite distinctive but easily overlooked in 'poor' seasons. It is a member of the Santalaceae, a family of parasitic trees, shrubs and herbs mainly tropical in their distribution and only represented in Britain by this one species (Pl. VI).

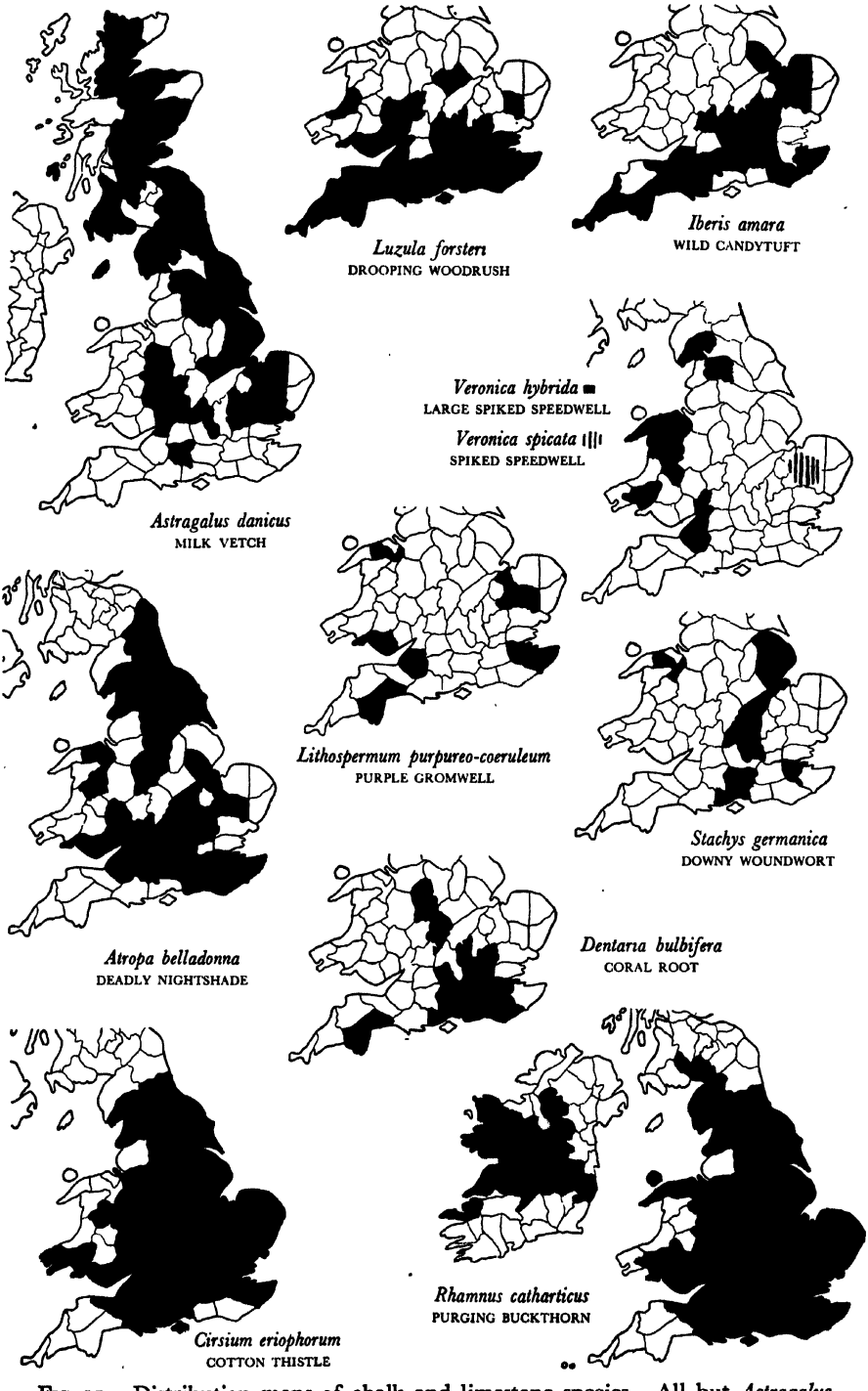


FIG 15. Distribution maps of chalk and limestone species. All but *Astragalus* prevailingly Southern.

One of the commonest of the rosette plants of the chalk is that charming member of the Carrot tribe, the Burnet Saxifrage (*Pimpinella saxifraga*). The root beneath the rosette can be readily seen to be encircled by a number of ridges and furrows (cf. Fig. 17). These puckerings are due to longitudinal contractions which take place each season and amount to a shortening by about 9%, as a result of which the rosette leaves are maintained in close contact with the surface. Perhaps, however, the most striking feature of this species is the variation in its foliage. Two kinds of rosette leaves are met with (cf. Fig. 17), some plants bearing leaves that are not unlike those of the Salad Burnet (*Poterium sanguisorba*) with a number of oval-toothed leaflets on either side of the leaf-stalk, whilst other plants bear leaflets which are deeply cut. The difference between the two varieties is analogous to that shown by the foliage of the two kinds of Hogweed that are to be seen in our hedgerows, though in this plant the contrast is less marked.

The duration of the chalk plants is very varied, some few, such as the Purging Flax and the Felwort, are summer annuals that germinate in the spring and complete their life-history by the autumn of the same year, thus having a life-span of 6–7 months; others, such as the Ground Pine (*Ajuga chamaepitys*) and the Spring Felwort (*Gentiana anglica*) are winter annuals that germinate in the autumn and pass the winter as small rosette plants, the first-named flowering in the spring and the latter in the summer, their respective life spans being about 10 and 12 months. The Greater Felwort, *Gentiana germanica*, is a true biennial, since the seeds usually germinate in the spring and the rosettes do not send up flowering stems till the summer of the following year, so that the life-span is about 18 months. The wild Mignonette (*Reseda lutea*) is something between a biennial and a perennial for though normally it passes the first season as a rosette plant, flowers in the summer and dies in the late autumn, frequently there are developed upon the roots, buds, from which shoots arise and may thus be said to prolong the life-span and, if recurrent, this leads to repeated vegetative multiplication. The true perennials may be short-lived, like the Field Fleabane (*Senecio integrifolius*) which flowers for perhaps two or three years and then dies, or such may be of prolonged duration, as, for example, the local Rampion (*Phyteuma tenerum*) and the very rare but beautiful Field Sage (*Salvia pratensis*),

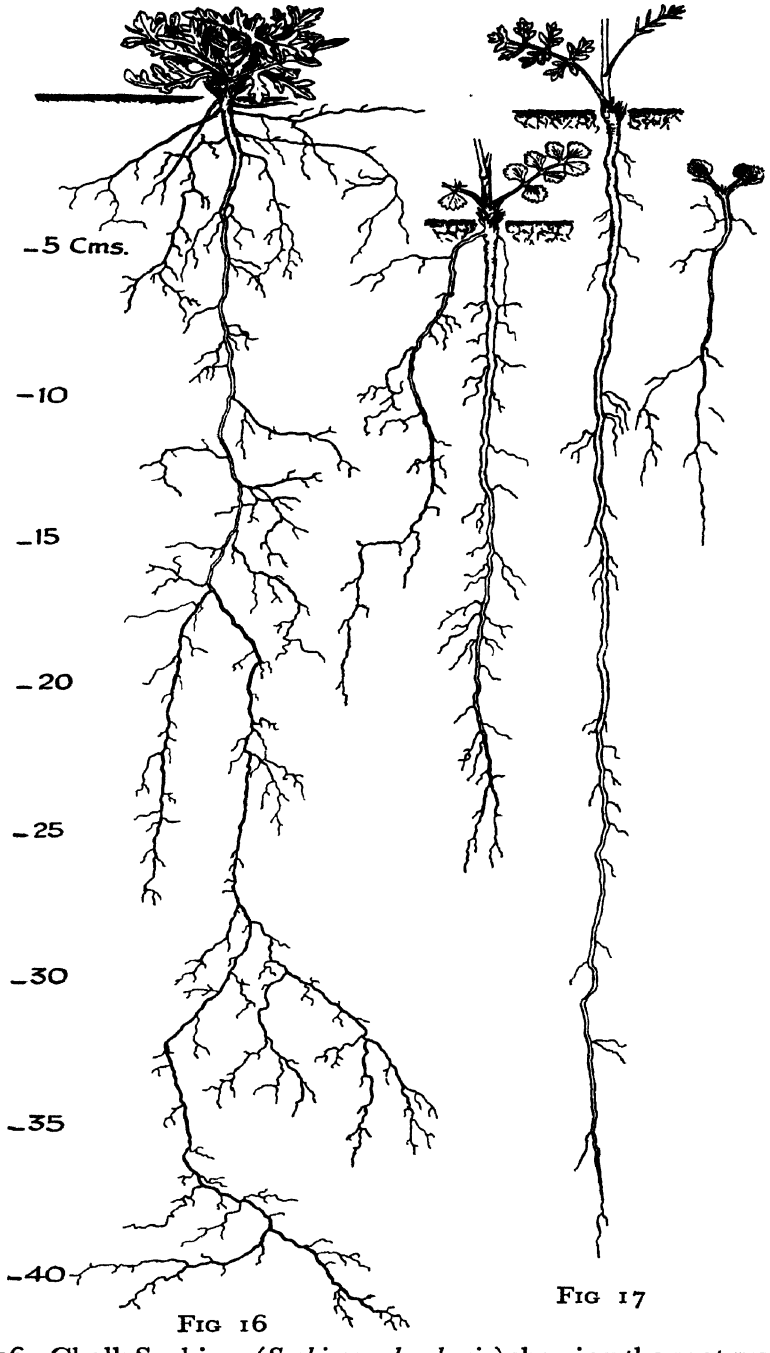


FIG 16 FIG 17

FIG 16. Chalk Scabious (*Scabiosa columbaria*) showing the root system with shallow and deeply penetrating roots and the lobed radical leaves. FIG 17. Burnet Saxifrage (*Pimpinella saxifraga*) showing the root system of two adult plants bearing the two types of foliage and a seedling.

both of which will survive for many years, dying down each year after flowering and producing new leaves each spring in late March or early April.

The populations of particular kinds of plants show fluctuations that are in general the more marked the shorter the normal life-span of the species. The annuals, for example, are apt to show this in an extreme form, since a species may be abundant one year in a season unfavourable to seed production, or the seed shed may exhibit poor germination, or again there may be a high rate of mortality amongst the seedlings. The weather may be responsible for such failures either directly, as a result of frost or excessive dampness at critical seasons, or indirectly, by favouring the development of a fungal disease or an insect pest. Whatever the circumstances responsible, a large population of the Annual Felwort in one year may be followed by a great scarcity the next, and large numbers of individual plants of the Yellow Centaury in any area one season are rarely succeeded by many plants the next. The same is sometimes true of short-lived perennials (e.g. *Senecio integrifolius*), but in respect to long-lived perennials that fruit repeatedly it is quite improbable that during the succession of yearly crops of offspring those either of one season or the aggregate of all will not suffice to maintain the population at a level exhibiting changes of a far less abrupt character. Thus with annual and biennial plants the fluctuations in the number of individuals are often spectacular whereas the conspicuous fluctuations in regard to the longer-lived perennials are not so much in relation to the size of the population as to the ages of the individuals forming it.

SPECIES PRACTICALLY CONFINED TO CHALK PASTURES (EXCLUSIVE)

Aceras anthopophora	Man Orchis, rosette perennial
Ajuga chamaepitys	Ground Pine, rosette annual
Carex ericetorum	mat perennial
Carex humilis	Dwarf Sedge, mat perennial
Gentiana germanica	Greater Felwort, rosette annual
Herminium monorchis	Musk Orchis, rosette perennial
Himantoglossum hircinum	Lizard Orchis, rosette perennial
Onobrychis viciaefolia	Sanfoin, mat perennial
Ophrys sphegodes	Spider orchis, rosette perennial
Orchis simia	Monkey Orchid, rosette perennial
Orchis ustulata	Dwarf Orchis, rosette perennial
Phyteuma tenerum	Rampion, rosette perennial
Polygala calcarea	Chalk Milkwort, mat perennial

SPECIES PRACTICALLY CONFINED TO CHALK PASTURES (EXCLUSIVE)—*contd.*

Prunella laciniata	White Self-heal, mat perennial
Pulsatilla vulgaris	Pasque Flower, rosette perennial
Salvia pratensis	Field Sage, rosette perennial
Senecio integrifolius	Field Fleabane, rosette perennial
Seseli libanotis	rosette biennial
Thesium humifusum	Bastard Toadflax, annual parasite

CHARACTERISTIC SPECIES IN THAT THEY COMBINE A HIGH DEGREE OF RESTRICTION TO CALCAREOUS PASTURES WITH A HIGH FREQUENCY

Anacamptis pyramidalis	Pyramidal Orchis, rosette perennial
Anthyllis vulneraria	Kidney Vetch, rosette biennial
Asperula cynanchica	Squinancy-wort, mat perennial
Blackstonia perfoliata	Yellow Centaury, rosette biennial
Brachypodium pinnatum	spreading perennial
Bromus erectus	Chalk Brome, mat perennial
Campanula glomerata	Clustered Bell-flower, rosette perennial
Carlina vulgaris	Carline Thistle, rosette biennial
Cirsium acaulos	Dwarf Thistle, rosette perennial
Filipendula hexapetala	Dropwort, rosette perennial
Helianthemum nummularium	Rock-rose, sub shrub
Helictotrichon pratensis	Oat Grass, tussock grass
Hippocrepis comosa	Horseshoe Vetch, mat perennial
Linum catharticum	Purging Flax, annual
Ophrys apifera	Bee Orchis, rosette
Poterium sanguisorba	Salad Burnet, rosette perennial
Scabiosa columbaria	Chalk Scabious, rosette perennial

The chalk downs also have their distinctive toadstools as for instance the autumnal *Lepiota mastoidea* or the St. George's Mushroom (*Tricholoma gambosum*) of late Spring.

ROOTS OF CHALK PLANTS

The root systems of the plants of the chalk belong to two main classes, namely the shallow-rooted species and those with deep roots. To the former category belong such annual plants as *Festuca rigida*, the Purging Flax (*Linum catharticum*) and the Ground Pine (*Ajuga chamaepitys*), in which the depth of the roots rarely exceeds 6 ins. whilst most of their roots occur within the first 3–4 ins. from the surface. Such plants have usually completed their period of activity by the middle of the summer and thus evade the drought conditions liable subsequently to ensue. The perennial orchids are also shallow-rooted plants, but these pass into a dormant state during the summer drought and rely on the moisture in the tubers for survival.

We have previously seen that the water content at a depth of over a foot into the chalk is normally adequate even during the summer drought to maintain plants in a non-wilted state, so it is of interest to note that most of the perennial species have root systems that extend to or beyond this level.

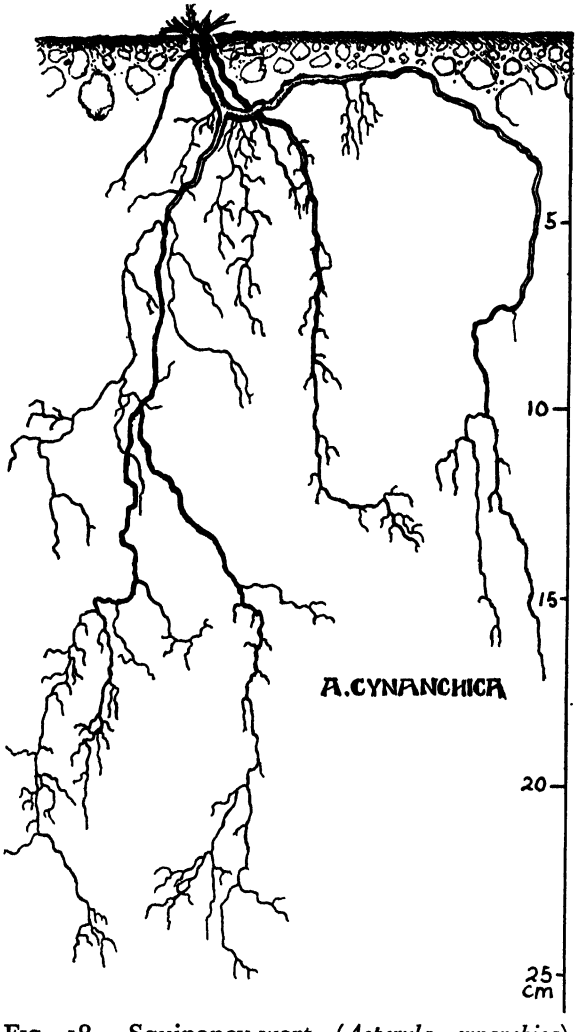
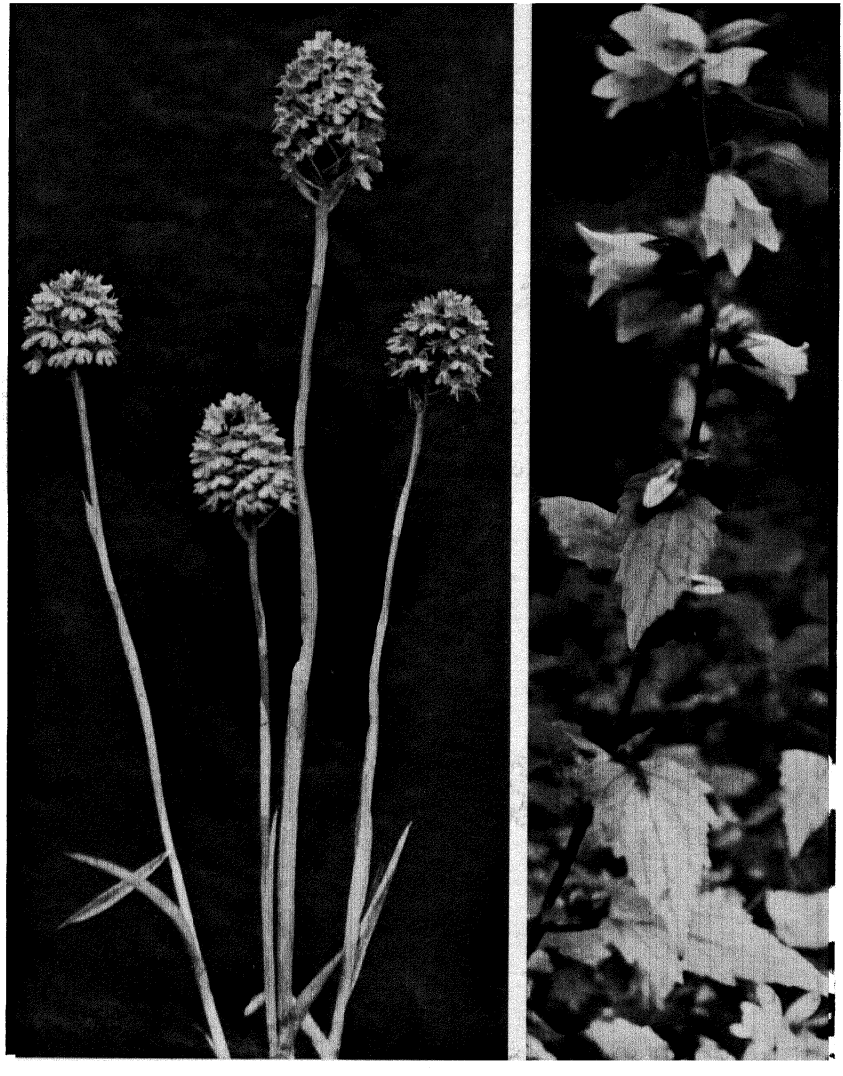


FIG 18. Squinancy-wort (*Asperula cynanchica*) showing the root system with superficial roots and branches penetrating to 9¾ in. (25 cm.).

* * *

PLATE V. Pyramidal Orchis (*Anacamptis pyramidalis*) a common orchid of the chalk down. ON RIGHT. Nettle-leaved Bell-flower (*Campanula trachelium*) a plant of chalk-scrub and beechwood clearings. Both ×*ca.* ½.







Thus as shown in Fig. 16 the root system of the characteristic Chalk Scabious (*S. columbaria*) extends to a depth of over 40 cms. (15·7 ins.) and is freely branched, thus effectively exploiting the volume of soil which it occupies. The root system of the Burnet Saxifrage (*Pimpinella saxifraga*), a characteristic chalk perennial (cf. Fig. 17), may extend more than 2 ft. deep (75 cms.). This plant occurs in two forms, one with a leaf superficially like that of the Salad Burnet (*Poterium*, Fig. 21) and the other with leaflets which are deeply cut (Fig. 17), but both exhibit similar rooting depths and seem to have the same physiological requirements.

The root system of the Squinancy-wort (*Asperula cynanchica*, Fig. 18) is only somewhat shallower, attaining to about 21 ins. (53 cms.), but here too the extensive branching ensures efficient exploitation of the soil and the very narrow leaves present but a small exposed surface for water loss by transpiration, the more so that the prostrate habit ensures, as for other mat plants, a considerable measure of protection from the wind. The Chalk Milkwort (*Polygala calcarea*), also a mat plant, has a root system penetrating less deeply (*ca.* 11 ins. = 28 cms.) (cf. Fig. 11) and in very severe drought has been seen to exhibit partial wilting. The roots of seedling plants of Horseshoe Vetch (cf. Fig. 2) are already extensive in relation to the size of the plant, and the roots of adult specimens that were excavated in their entirety had main roots penetrating to over 24 ins., so it is

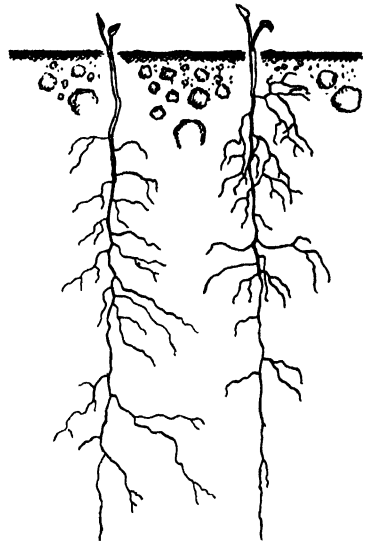


FIG 19. Two first-year seedlings of Rampion (*Phyteuma tenerum*), half-natural size, showing the root system mainly developed downwards. (Depth *ca.* 5 in. (12 cm.).)

* * *

PLATE VI. Chalk-down plants. ABOVE. The Pasque Flower (*Pulsatilla vulgaris*) growing in short-turf on the chalk. BELOW. Turf of down in Hertfordshire showing the prostrate shoots of the Bastard Toadflax (*Thesium humifusum*), growing parasitically on the grasses. Most of the other foliage is that of the Salad Burnet and on the left is a Dwarf Thistle (*Cirsium acaulos*). Both about life-size.

hardly surprising to find that even in the most severe drought the Horseshoe Vetch does not appear to suffer. The early development of a deeply penetrating root system is seen in the characteristic chalk plant, the Rampion (*Phyteuma tenerum*), where seedlings only a few weeks old will have roots over 5 ins. deep (Fig. 19), whilst roots of adult plants were measured penetrating to depths of from 1 ft. to over 18 ins.

The perennials can be grouped in two categories: (1) Those with relatively shallow roots less than 1 ft. in depth (under 30 cms.). Such are the following:

Anemone pulsatilla	Pasque Flower
Filipendula hexapetala	Dropwort (Fig. 9)
Campanula glomerata	Clustered Bellflower
Salvia pratensis	Field Sage
Senecio integrifolius	Field Fleabane (Fig. 4)
Linum anglicum	Wild Flax
Origanum vulgare	Marjoram
Polygala calcarea	Chalk Milkwort (Fig. 11)

(2) Those usually deep-rooted and penetrating to over a foot (30 cms.). The figures in brackets indicate the maximum depths actually measured.

Asperula cynanchica	Squinancy-wort (to > 53 cms.) (Fig. 18)
Astragalus danicus	Milk Vetch
Centaurea scabiosa	Greater Hardheads
Cirsium acaulos	Dwarf Thistle (to > 51 cms.)
Helianthemum nummularium	Rock Rose (to 76 cms.) (Fig. 20, p. 69)
Hippocrepis comosa	Horseshoe Vetch (to > 90 cms.)
Onobrychis viciaefolia	Sanfoin (> 40 cms.)
Ononis spinosa	Rest Harrow (to 92 cms.)
Phyteuma tenerum	Rampion (to 45 cms.)
Pimpinella saxifraga	Burnet Saxifrage (to > 75 cms.) (Fig. 17)
Poterium sanguisorba	Salad Burnet (to 56 cms.) (Fig. 21, p. 77)
Scabiosa columbaria	Chalk Scabious (>40 cms.) (Fig. 16)

The characteristically aromatic scent of the trodden downland turf is due not so much to any great diversity of scented plants as to the prevalence of a few. Yarrow, Burnet Saxifrage, Wild Carrot, Germander Speedwell, Agrimony, St. John's Wort and Rest Harrow all contribute to the bouquet, but it is the Self-heal, Calamint, Marjoram and above all the Thyme which provide the pot-pourri that delights our sense of smell. The thyme indeed often empurples the short turf in June since its flower-buds escape all but the closest browsing, so that its abundance can be realised.

III

THE ANIMAL LIFE OF THE CHALK

THE animal life of a chalk down is a constituent dependent upon the plant life for its existence and itself contributing to the characteristic features of the living community. Here it is for instance that we find such chalk-loving snails as the Whelk-like *Cyclostoma elegans*, with its pyramidal shell and distinctive operculum, flourishing in the friable soil of the chalky banks, whilst the flattened black-and-white shells of *Helicella itala* and *H. virgata* are frequent upon the short turf of the sheep walks. The flattened, banded shells of *H. itala* are usually met with on the steepest and sunniest southern slopes, where the angle of the ground ensures the maximum warmth. *H. virgata* is commonly the food of the beetle larvae which we call glow-worms (*Lampyris notiluca*), whose fairy lamps on a warm moist June evening are more abundant on the short turf of the chalk than anywhere else. On the Downs, too, occur *Helicella caperata*, *H. heripensis*, *H. cartusiana*, *H. cautiana*, *Pupa secale*, and *P. marginata*. The investigations of A. S. Kennard brought to light the interesting fact that though the snails *H. virgata*, *H. caperata* and *H. cautiana* are common on the Kentish chalk of to-day, there is no evidence of their presence there in Roman times, possibly because the area of open grassland was then meagre compared with what obtains now.

The Downs also are peculiarly the home of the blue butterflies; indeed, the Chalkhill Blue (*Lysandra corydon*) takes its name from this fact, which is scarcely surprising, since the caterpillars during part of their life history feed upon the buds and foliage of the Horseshoe Vetch (*Hippocrepis comosa*). The larvae of the far rarer Adonis Blue (*Lysandra bellargus*) devour the same food plant, whilst those of the charming Little Blue (*Cupido minimus*) are nourished on the flowers of the Kidney Vetch (*Anthyllis vulneraria*), in the heads of which the small larvae can be found in June, to develop into butterflies some ten months later. The Large Blue (*Maculinea arion*) has larvae with a remarkable life-history. The eggs are laid by the

female on the buds of the Thyme, which the larvae resemble both in colour and hairiness and upon which they feed for about three weeks; but at a later stage in their life-history they are to be found in ants' nests, usually those of the Red Ant feeding upon the larvae of the ants, the butterfly emerging about a year after the eggs hatch. The association of this very rare species with chalk downs is due partly to the greater frequency of the food plant in chalk country, but perhaps mainly to the prevalence here of old, but still inhabited, ant-hills clothed in a mantle of Thyme.

The caterpillars of the Large Blue are known to be taken into the ants' nest by the ants themselves, and the attraction is the sweet liquid which the larvae of this and some other blue butterflies secrete. Far from injuring the larvae, the ants in some degree protect them, and it is interesting to note that the larvae of the Chalk Hill Blue have been found associated with the ant *Acanthomyops flavus*, and those of *Lysandra alcon* have been observed in nests of *Tetramorium caespitosum* and to feed on the eggs and larvae of this ant.

The Silver-spotted Skipper (*Hesperis comma*) is another butterfly of the chalk, although the caterpillars feed on grasses that are not confined to calcareous soil. The Brown Argus (*Aricia agestes*) is chiefly found in chalky districts and calcareous sand dunes, the food of the caterpillars being usually the Rock Rose, but also the common Stork's Bill. The chalk scrub is the especial home of the Brimstone Butterfly, whose larvae feed upon the Purging Buckthorn, and here too we particularly find the Green Hairstreak (*Callophrys rubi*); but though the larvae of this butterfly may feed on such calcicolous species as the Rock Rose and Buckthorn it is stated to feed also on the calcifuge Whortleberry, so that the greater prevalence of this butterfly in chalk scrub is probably not due to the distribution of the food plants.

Of the moths of the chalk perhaps the most familiar is the diurnal Six-spot Burnet, the cocoons of which can often be seen upon the grass stems. The food plants of the larvae are such leguminous herbs as Clovers and Kidney Vetch, and the Clearwing (*Dipsosphecia scopigera*) is similarly partial to the Kidney Vetch and the Bird's-foot Trefoil.

Some nocturnal moths are more or less features of the chalk country, such, for instance, as the Small Emerald (*Hemistola*

chrysoprasaria), the larva of which feeds on the Wild Clematis. The Barred Hooktip (*Drepana cultraria*), *Cosymbia linearis* and the Lobster Moth (*Stauropus fagi*), so-called from the remarkable lobster-like caterpillar, all have larvae which feed on Beech leaves and this is true also for those of the Barred Sallow (*Tiliacea aurago*), though the Maple may serve equally as food. *Eupithecia denotata* has caterpillars that feed on the Wild Canterbury Bell (*Campanula trachelium*), a plant of Beechwood clearings and margins.

The Scarce Forrester (*Procris globulariae*) has larvae which feed on species of Hardheads (*Centaurea scabiosa* and *C. nigra*) those of *Cucullia lychnitis* on the Black mullein (*Verbascum nigrum*), those of the Flame moth (*Euphyia rubidata*) on the Bedstraw and those of the Rustic moth (*Agrotis cinerea*) on the wild Thyme. Since all these food plants are much commoner on the chalk than elsewhere, it is natural that the predator caterpillars that depend upon them are likewise commonest here. However, there are two other moths associated mainly with the chalk country whose larvae feed on plants almost if not quite as common elsewhere. Thus the Feathered Ear Moth (*Pachetra sagittigera*) has caterpillars that feed on grasses, and those of the Chalk Carpet Moth (*Ortholitha bipunctaria*) feed on clovers.

Although the larvae of *Philereme vetulata* and *P. transversata* feed only on the Purging Buckthorn, the moths are by no means especially characteristic of chalk country. However, the Carpet Moths, *Epirrhoe galiata* and *E. rivata*, the larvae of which feed on the Bedstraws, are both commoner on the chalk than elsewhere, especially the former species, although the food plants are less markedly calcicoles than the Purging Buckthorn.

The chalk downs also have their characteristic beetles, such as *Brachinus crepitans* and *Oedemeea lurida*, to mention but two; whilst the particular coleopterous fauna of the Beechwood may be exemplified by *Orchestes fagi*.

The high frequency of Wireworms, Moles and Rabbits has already been alluded to and the abundance of the Harvest Bug, here and on other base-rich soils, is often irritatingly emphasised. This last feature perhaps more than any other makes us apprehend that the fauna of the chalk is a distinctive one.

IV

BIOLOGICAL NOTES ON CHALK GRASSLAND PLANTS

Thesium humifusum	Bastard Toadflax (Map, Fig. 13, p. 39)
Ophrys apifera	Bee Orchid
Pimpinella saxifraga	Burnet Saxifrage
Orchis ustulata	Burnt Orchis
Carlina vulgaris	Carline Thistle
Hypochoeris maculata	Cat's Ear
Bromus erectus	Chalk Brome (Map, Fig. 13, p. 39)
Polygala calcarea	Chalk Milkwort (Fig. 11, p. 31)
Scabiosa columbaria	Chalk Scabious
Cichorium intybus	Chicory
Campanula glomerata	Clustered Bell-flower
Primula veris	Cowslip
Filipendula hexapetala	Dropwort
Cirsium acaulos	Dwarf Thistle
Carex humilis	Dwarf Sedge
Euphrasia spp.	Eyebright
Gentiana amarella (*G. axillaris*)	Felwort
Senecio integrifolus	Field Fleabane (Map, Fig. 13, p. 39)
Gentiana campestris	Field Gentian
Salvia pratensis	Field Sage
Erigeron acris	Fleabane
Coeloglossum viride	Frog Orchis
Lathyrus nissolia	Grass-leaved Vetch
Gentiana germanica	Greater Felwort (Map, Fig. 13, p. 39)
Ajuga chamaepitys	Ground Pine (see p. 25)
Centaurea scabiosa	Hardheads
Picris hieracioides	Hawkweed
Plantago media	Hoary Plantain
Trifolium campestre (*T. procumbens*)	Hop Trefoil
Hippocrepis comosa	Horseshoe Vetch (Map, Fig. 13, p. 39)
Anthyllis vulneraria	Kidney Vetch
Spiranthes spiralis	Lady's Tresses
Himantoglossum hircinum	Lizard Orchis (Map, Fig. 13, p. 39)
Aceras anthropophora	Man Orchis (Map, Fig. 13, p. 39)
Astragalus danicus	Milk Vetch (Map, Fig. 15, p. 43)
Orchis simia	Monkey Orchid
Herminium monorchis	Musk Orchis
Carduus nutans	Musk Thistle
Pulsatilla vulgaris	Pasque Flower (Map, Fig. 13, p. 39)
Linum catharticum	Purging Flax

BIOLOGICAL NOTES ON
CHALK GRASSLAND PLANTS—*contd.*

Anacamptis pyramidalis	Pyramidal Orchis
Briza media	Quaking Grass
Phyteuma tenerum	Rampion (Map, Fig. 13, p. 39)
Ononis spinosa	Rest Harrow
Arabis hirsuta	Rock Cress
Helianthemum nummularium	Rock Rose
Poterium sanguisorba	Salad Burnet
Festuca ovina	Sheep's Fescue
Ophrys sphegodes (*aranifera*)	Spider Orchid (Map, Fig. 13, p. 39)
Veronica spicata	Spiked Speedwell (Map, Fig. 15, p. 43)
Gentiana anglica (*praecox*)	Spring Felwort
Asperula cynanchica	Squinancy-wort (Map, Fig. 13, p. 39)
Gymnadenia conopsea	Sweet-scented Orchis
Thymus serpyllum	Thyme
Cirsium tuberosum	Tuberous Thistle
Echium vulgare	Viper's Bugloss
Daucus carota	Wild Carrot
Linum alpinum v. anglicum	Wild Flax
Onobrychis viciaefolia	Wild Sanfoin
Blackstonia perfoliata	Yellow Centaury (Map, Fig. 14, p. 41)
Carex ericetorum	
Gentiana baltica	
Koeleria gracilis (*K. cristata*)	
Seseli libanotis	

*

THE MAN ORCHIS, *Aceras anthropophora.* Orchidaceae. 2n=42.

The tubers are oval in shape and bear at the summit a few narrow leaves and a stem about 6 to 10 ins. in height with small rather crowded green flowers somewhat resembling those of the Frog Orchis and with a similar edging of reddish pigment; but the yellowish green lip in the Man Orchis has no spur and has four lobes, two at the tip and two at the sides producing a fanciful resemblance to legs and arms, hence the popular name. Pollination is probably affected by hymenoptera and ants. Capsules are not infrequently produced.

This is a winter-green species, the new leaves being formed in September.

The Man Orchis is a continental-southern type extending in Britain as far north as S.W. Yorkshire, and is absent from Ireland (cf. map, Fig. 13, p. 39).

PYRAMIDAL ORCHIS, *Anacamptis pyramidalis*. Orchidaceae. 2n=36. (Pl. V)

From the two oblong tubers arise several narrow leaves about 4 ins. long (10 cms.) and a stem usually about 1 ft. high with dense-flowered spike that is strikingly pyramidal at the apex when young. The flowers are rosy pink with a broadly three-lobed velvety lip and a long spur.

Pollination is effected both by butterflies and moths and capsules are formed freely. Flowering does not usually occur until about seven or eight years after germination. The seeds were counted in two pods and numbered 1,935 in one and 4,440 in the other.

Widely distributed in Europe, it has a definitely continental-southern trend and in Britain does not occur in north-east Scotland but has its northern limit in the Western Isles. Even in the South of England it is especially associated with slopes having a southern aspect.

KIDNEY VETCH, *Anthyllis vulneraria*. Leguminosae. (Pl. IX)

Perennial, but often short-lived and frequently, in good soil, biennial only, with simple, long-stalked basal leaves followed by pinnate ones the leaflets of which are oval, have entire margins and are dark green and smooth above but bear silky hairs beneath. The dormant buds are situated just above the soil surface. The inflorescence is characteristic and consists normally of a pair of oval flower-heads (hence the north country name of 'Twins'), each of up to twenty or more closely set, stalkless, pale yellow, pea-like blossoms of which the most conspicuous feature is due to the numerous hairs, developed from the swollen calyces, from the whitish downy bed of which the yellow flowers appear to emerge. Sometimes the flowers are red, as on some of the calcareous dunes of the west, rarely they are white or purple. For genetics of colour races cf. Marsden-Jones and Turrill, *Journ. Genetics*, p. 261, 1933. The pod is quite small and only contains 1–3 seeds (*ca.* 0·0023 gm.) of which about 8%, the 'soft seeds,' germinate almost at once. The rest germinate after a shorter or longer delay, yielding from 80% to 100%. From the observations of Marsden-Jones and Turrill (*Journ. Ecology*, XXI, 1933) the seeds appear to germinate throughout the spring, summer and autumn, and large plants, subject to little competition, may produce some

5,000 seeds. The cotyledons are large and fleshy and the first few leaves are simple.

The plant overwinters as a flat dome-shaped rosette.

ROCK CRESS, *Arabis hirsuta*. Cruciferae. 2n=32.

A biennial or short-lived perennial forming a dense rosette of basal leaves from which the erect flowering stems are produced and attain 12–24 ins. (30–60 cms.). The whole plant is covered with branched hairs. The small white flowers are succeeded by slender pods up to 2 ins. long (5 cms.) containing numerous small seeds with a narrow wing. Particularly associated with calcareous soils, though not confined to them, and especially frequent on the limestones and the more calcareous dunes. Also found on the mortar joints of old walls. Germination continuous, often rather poor.

SQUINANCY-WORT, *Asperula cynanchica*. Rubiaceae. 2n=44 (var. *montana*, 2n=22). (Pl. XXX)

A mat-forming prostrate perennial easily distinguished by the narrow linear 'leaves,' usually four at a node, of which those of one pair (the fused stipules) are smaller than the other pair (the true leaves with axillary buds). The flowers are small (about 4 mm. in diameter), pink outside and white inside. The fruit is very small and covered with minute protuberances.

A. H. Volk (*Zeit. f. Bot.*, XXIV, pp. 81–185, 1931) gives the range of soil reaction where this species occurs as from pH 6·8 to pH 8·2 and the plant as exhibiting osmotic pressures from about 9 to 17 atmospheres.

The data as to rooting depths of this species are apparently very discrepant. If proper precautions are adopted to support a root system (cf. Fig. 18, p. 48) as it is excavated the chief source of error is the liability of breaking the finer roots and thus not following them to their limit so that the spread and depth is underestimated. Tansley and Adamson (cf. *Journ. Ecology*, XXIII, p. 207, 1925) from an area on the Sussex border record a rooting depth for this species of only 4 ins. 10 cms.). Anderson (*ibid.*, XXV, p. 91, 1927) from a shallow chalk soil in Surrey reported an average depth of 1½ ins. (3·7 cms.) and a maximum depth of 6 ins. (15 cms.). My own observations showed depths of penetration of 20 and 21 ins. (50–52·5 cms.), and these correspond more nearly to the data

furnished by Volk (*loc. cit.*), who records 25–50 cms. (10–20 ins.). The high degree of summer drought resistance which this species exhibits would suggest that at least normally the depth of penetration is appreciable.

The species is more or less winter-green. It does not occur north of Westmorland and is confined to the S.W. in Ireland (cf. map, Fig. 13, p. 39).

MILK VETCH, *Astragalus danicus*. Leguminosae. 2n=16. (Pl. I)

A perennial herb with a slender much-branched rootstock forming new leaves in mid-March or early April. The foliage forms a low mat-like carpet of pinnate leaves with narrow oblong leaflets covered with numerous soft white hairs intermingled on the upper surface with black ones.

The flower heads are oval, consisting of a number of crowded flowers with bluish-purple pea-like corollas and blackish hairs upon the calyx.

The very short pods are black when mature and beset with short white hairs. Each pod contains two oval seeds about 2·5 mm. in diameter which weigh about 0·001 gm. They are ripe by July and germinate freely in the autumn.

It is a northern-continental species occurring in both hemispheres and as a British species occurs on chalk downs, but on dunes is only found with any frequency in Scotland. It is absent from Ireland except on the island of Aran and does not occur in Wales (cf. map, Fig. 15, p. 43).

The dormant buds are situated in the surface layer of soil.

YELLOW CENTAURY, *Blackstonia* (*Chlora*) *perfoliata*. Gentianaceae. 2n=44. (Pl. IV)

Usually biennial forming a rosette of glaucous elliptical leaves in the first autumn and the following year sending up a stem from 6–18 ins. in height (15–45 cms.). This bears pairs of leaves joined in a cup-like manner which appear blue-green owing to their waxy bloom. The rooting depth is often shallow, only 4–5 ins. (10–12·5 cms.) on the chalk, but when growing in dunes the depth may be nearly twice as great. Anderson (*loc. cit.*, p. 92) calls attention to the presence of unbranched roots parallel to and near the surface as a characteristic feature. The plant if broken exudes a yellowish juice. The bright yellow flowers open in the early morning (about 6 a.m.) in

dry air, but close about three or four o'clock even if conditions are not wet; in darkness they exhibit a similar rhythm.

The capsules usually contain between 600 and 700 small black seeds (each *ca.* 11 mgms.), which germinate freely and more or less simultaneously in the autumn or following spring.

As can be seen from the map (Fig. 14, p. 41) the Yellow Centaury does not occur in Scotland and the north-eastern part of Ireland or in parts of Wales. As, however, these regions present few areas in which the soils are basic, still less calcareous, the absence is probably due to edaphic and not to climatic conditions. Wilting occurs if the water content of the soil falls below about 6%.

QUAKING GRASS, *Briza media*. Gramineae. 2n=14.

A tufted perennial grass with glaucous green foliage and characteristic heart-shaped spikelets, borne on a branched pyramidal inflorescence, that quiver in the slightest breeze. Fruits about 0·003 gm.

A continental-southern species widely, but often sparsely, scattered in calcareous pastures.

CHALK BROME, *Bromus erectus*. Gramineae. 2n=42.

A creeping perennial grass with hairy leaves the margins of which are rolled inwards. The inflorescences are tall, attaining to from 2–3 ft. (60–90 cms.). In full bloom the almost orange anthers are conspicuous. It is a self-incompatible species.

Areas in which *B. erectus* is the predominant grass can be seen on the chalk of the east with low rainfall and on the limestones of the west where the rainfall is high, and it is probable that freedom from grazing is the chief influence in determining the abundance of this grass.

Of wide distribution in Europe it is there also a feature of calcareous soils. In the British Isles it does not occur in Northern Ireland or Northern Scotland (cf. map, Fig. 13, p. 48).

CLUSTERED BELL-FLOWER, *Campanula glomerata*. Campanulaceae. 2n=34 or 68. (Pl. II)

A perennial, the basal leaves of which have long stalks and oval or long heart-shaped blades with a crenated margin and covered with short hairs. The stem, which in the early

stages of chalk scrub may reach over 2 ft. (60 cms.), is normally short and bears a terminal cluster, and often lateral clusters also, of erect bright blue flowers.

Three holes develop at the base of the capsule and the agitation of the stiff stem by the wind jerks the ripe seeds out intermittently. Each capsule usually contains from 60 to 100 seeds. These are oval and papillose, normally exhibiting rather low germination which takes place at intervals during May and June. Plants flower in their third year.

This species is widely distributed in Europe, but with a continental trend, as indicated by its rarity in Ireland and the West of England and its absence from the north of Scotland.

The plant overwinters as a rosette with the dormant buds almost at ground level protected by the surrounding turf.

MUSK THISTLE, *Carduus nutans*. Compositae. 2n=16.

A biennial rosette species that is far commoner on basic soils than elsewhere is easily recognised by its large nodding purple flower-heads which emit a pleasant perfume. Each head produces an average of 200 fruits.

Carex ericetorum. Cyperaceae. 2n=30.

A low-growing perennial Sedge with tufted habit spreading by means of the creeping stems which bear recurved and keeled leaves.

This sedge is a Northern-continental species confined in Britain to calcareous slopes in the Eastern counties.

DWARF SEDGE, *Carex humilis*. Cyperaceae. 2n=78.

A perennial early-flowering Sedge with a creeping habit. The inflorescences are pale-coloured and the narrow leaves are yellowish-green. It is an abundant constituent of the turf on the chalk in some areas, as, for example, Salisbury Plain. It is recorded from the Wye Valley, from Somerset, Wiltshire, Dorset and Hampshire. On the Continent it occurs in central and southern Europe associated with calcareous soils.

CARLINE THISTLE, *Carlina vulgaris*. Compositae. 2n=20.

A biennial forming a rosette of from about 5–10 ins. in diameter (12–25 cms.) of lanceolate spinous leaves which are cottony on the under surface. The stem is from 4–18 ins.

(10–45 cms.), erect and branched above, bearing heads with the outer bracts hairy and spreading and inner bracts straw-like both in colour and texture. These spread out in dry air and close together in wet conditions, becoming erect around the central disc of purplish tubular florets. The stout tap-root often penetrates to from about 8–12 ins. (20–30 cms.) and bears a number of branched lateral roots, but in the areas examined by Anderson the average depth of penetration was about 6 ins. (15 cms.).

The plant chiefly occurs on chalk downs and calcareous dunes, though occasionally on other dry and basic soils. The fruits normally germinate in the spring and the plants flower about sixteen months later.

HARDHEADS, *Centaurea scabiosa*. Compositae. 2n=14, 20 or 24.

A perennial herb with tufted stems 2–3 ft. (60–90 cms.) high with pinnatifid basal leaves and heads composed of a number of bracts with brown fringed tips, a series of conspicuous marginal flowers and numerous central tubular flowers, the whole head from 1½–2 ins. (3·7–5 cms.) across. The greyish fruits are frequently eaten by larvae of beetles so that of some seventy to eighty fruits that might be formed only about sixty-five usually develop. Adventitious shoots may develop from the roots. The fruits yield up to nearly 60% germination.

The leaves wither in autumn and develop in spring. The dormant buds are situated in the surface soil.

This is the host plant of the tawny-brown Broom-rape (*Orobanche elatior*, Pl. VII).

CHICORY, *Cichorium intybus*. Compositae. 2n=18. (Pl. X)

The wild plant is a perennial herb with dry twiggy angular stems and hispid oblong leaves which grows to a height of 1–3 ft. (30–90 cms.) and usually bears the sky-blue flower heads in pairs. All parts of the plant contain a milky juice.

The fruit weighs about 0·0015 gm. Germination is normally over 80%. Both self-sterile and self-fertile strains occur (cf. Stout, *Proc. Soc. Exp. Biol.*, 51, 1918).

DWARF THISTLE, *Cirsium acaulos*. Compositae. 2n=34. (Pl. VI)

A rosette perennial with dark green pinnatifid very shiny leaves pressed close to the surface, with, arising from the centre

a, usually stemless, flower head. The head is formed by numerous smooth bracts surrounding the crimson-purple flowers. The polished brown fruits each bear a dirty-white parachute of hairs. This pappus is hygroscopic, expanding in hot sunshine so that at maturity each rosette may be seen surmounted by a dome of thistle-down. Many of the parachutes that are seen air-borne do not, however, bear fertile fruits. Branching produces aggregates of leaf-rosettes and vegetative spread may occur by adventitious shoots from the roots which can penetrate more than 18–20 ins. (45–50 cms.), though in shallow soils the average depth may be only about 6 ins., as Anderson found (*loc. cit.*).

A widespread European species practically confined to calcareous pastures and often abundant. Its northern limit in Britain is in N.W. Yorkshire. It does not occur in Ireland.

Tuberous Thistle, *Cirsium tuberosum*. Compositae.

A spineless thistle that does not spread by underground runners, but has spindle-shaped roots. It spreads rather slowly and except for the smaller size of its purple flower-heads somewhat resembles the Gentle Thistle, *Cirsium dissectum* (*C. anglicum*, C. *pratensis*), of marshy habitats. It is a very rare oceanic type recorded from the chalk of Cambridge and Wiltshire and the limestone of Glamorgan.

The Frog Orchis, *Coeloglossum viride*. Orchidaceae. 2n=40.

A green flowered orchid commonly from 2–8 ins. high (5–20 cms.) sometimes quite common, though dwarfed, in the short turf by tracks on the chalk downs. The three to five bluish-green leaves arise from a pair of tubers that are usually two-lobed. The flower stalk bears a number of crowded green flowers with a very short spur like a flattened sphere, and a hood-like perianth, the outer segments of which are green with a brownish-red tinge and a thick yellowish-green lip, three-lobed at the tip and edged with red (Pl. I). Fruit appears to be freely produced. This orchid probably flowers in a few years after germination and the striking fluctuations in the number of plants in any locality may indicate a short life-span.

Like other orchids, its seeds are distributed by the wind, but the occurrence of the plant suggests that subsequent rain-wash may play a part, though the obvious preference of this species

for damper situations perhaps explains this localisation. It has a wide range in Europe from Asia Minor northwards and is also found in North America with a tendency to diminish in frequency towards its southern limit. In England it is also commoner in the north than in the south.

WILD CARROT, *Daucus carota*. Umbelliferae. 2n=18.

A hispid biennial passing the winter as a rosette of much-divided leaves from the centre of which a branched stem develops bearing umbels with a conspicuous 'beard' of bracts beneath. The mature fruit-head is cup-shaped like a bird's nest and the individual fruits bear rows of hooked spines. The roots are stout and woody, penetrating to a depth of some 9–15 ins. (22–37 cms.). The species is often common on shallower soils and erosion slopes where competition from perennial species is not severe.

Germination is up to nearly 70% in light, but only about 12% in the dark.

VIPER'S BUGLOSS, *Echium vulgare*. Boraginaceae. 2n=32.

A very hispid biennial forming rosettes of lanceolate leaves up to 18 ins. in diameter (45 cms.) and producing a bushy flowering stem in the second year. The numerous blue flowers set seed freely. The fleshy tap root may penetrate over 2 ft. (60 cms.).

The seeds germinate freely in spring and intermittently at other times but only if well illuminated. Mitchell (*Bot. Gaz.*, 1926) obtained 91% germination in light, but no germination in darkness.

Characteristic of dry soils, *E. vulgare* is more abundant on calcareous soils than any other type except sand, probably because of their well-drained character.

EYEBRIGHT, *Euphrasia* spp. Scrophulariaceae. 2n=22.

These semi-parasites are especially common on calcareous pastures and some of the segregates are confined to such, whilst others are equally characteristic of moorland soils (e.g. *Euphrasia minima*). Amongst the former the following are the chief:

Euphrasia nemorosa, a common small-flowered species of the early summer, and the var. *calcarea* is common on chalk downs. Germination in spring.

E. pseudo-kerneri is a large-flowered species of the chalk downs, probably endemic, flowering in late August and September.

E. salisburgensis is a distinctive species of the limestone of Yorkshire and Ireland.

E. curta f. *littoralis* is a dune plant.

Cf. H. W. Pugsley, *Journ. Linn. Soc.* (*Bot.*), XLVIII, pp. 467–543, 1930, where these and other segregates are figured and described.

FLEABANE, *Erigeron acris*. Compositae. 2n=18.

A hairy annual or biennial with basal rosette of ovate-lanceolate leaves and branched stems from 4 ins. to 18 ins. in height (10–45 cms.) bearing inconspicuous flower-heads, each with a disk of yellow florets and small pale blue ray florets. Fruits hairy below with a parachute of reddish hairs at the top.

Far commoner on calcareous soils than in siliceous habitats.

SHEEP'S FESCUE, *Festuca ovina*. Gramineae. 2n=14, 56 or 70. (Pl. IX)

A perennial grass forming erect almost cylindrical tufts with blue-green foliage. The leaves are narrow and grooved and the branches of the inflorescence all grow to one side, whilst the stem beneath is beset with minute teeth (the same region of the Red Fescue, *F. rubra*, found on deeper soil, is smooth).

A grass particularly associated with the drier erosion slopes and early phases of colonisation, with a rather shallow fibrous root system mostly in the first 3 ins. (7·5 cms.); nevertheless, very resistant to drought. Mycorrhiza has been recorded. According to Troll, from 10% to 20% of the plants of *F. ovina* are self-fertile. The grains yield a germination of from 20% to 70%. They weigh about 0·0007 gm.

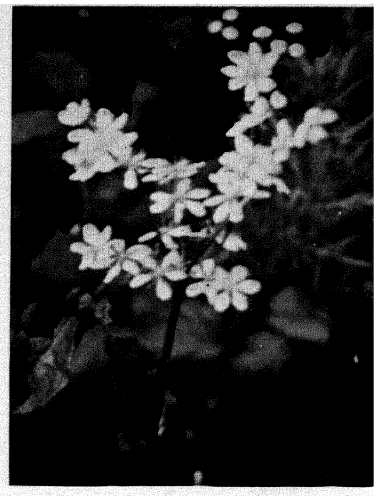
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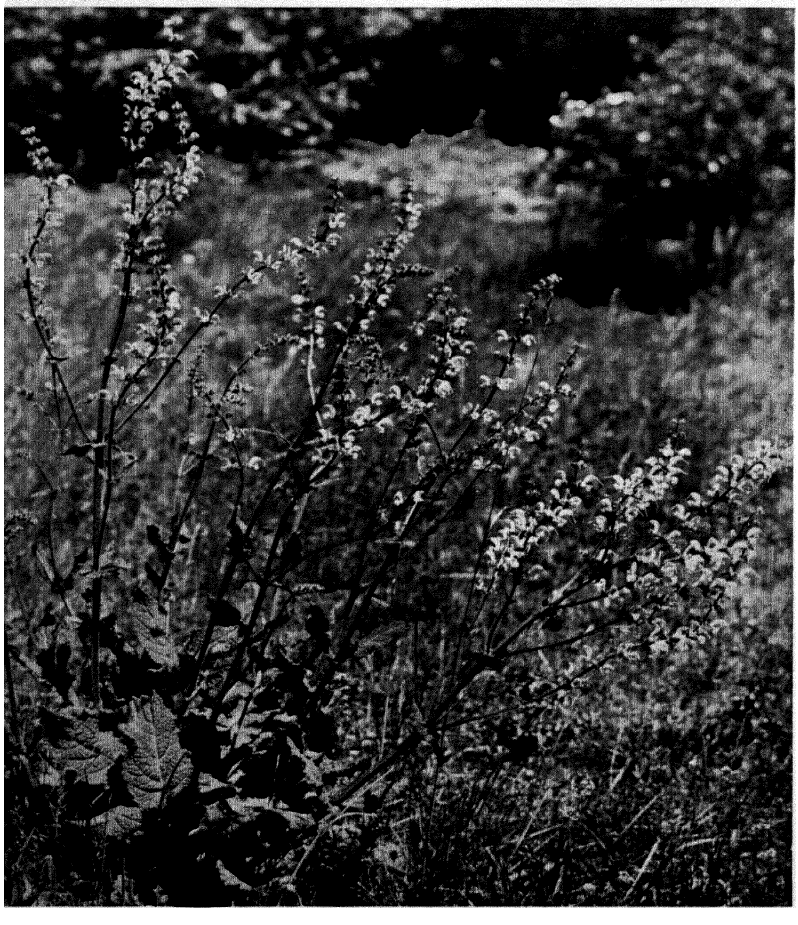
PLATE VII. Chalk flora. ABOVE. The Broomrape, *Orobanche elatior* growing parasitically on Hardheads (*Centaurea scabiosa*). Most of the foliage is of the latter plant and five inflorescences of the Broomrape, which has no leaves, can be seen at various stages of development. ×*ca.* ½. BELOW. Solomon's Seal (*Polygonatum multiflorum*) in Beechwood.











DROPWORT, *Filipendula hexapetala*. Rosaceae. 2n=14, 15. (Fig. 9, p. 29. Pl. VIII)

A perennial species with a somewhat shallow system of fibrous roots penetrating 4 or 5 ins. (10–12·5 cms.), many of which bear one or more oval swellings (cf. Fig. 9) which serve for food storage, chiefly starch. The foliage forms a rosette from 10–20 ins. (25–50 cms.) in diameter. The leaves are bright green with up to twenty pairs of large leaflets deeply serrated alternating with pairs of small leaflets (cf. Fig. 9). From the centre of the rosette arise the almost leafless flower stalks 6 ins. to 3 ft. high (15–90 cms.) which bear forked panicles of beautiful ivory-coloured flowers which when fully expanded are 10–20 mm. in diameter. A characteristic feature is the crimson flush on the outside of the petals which suffuses a brilliant colour over the unopened buds. Although the flowers have no nectar, they are faintly scented and visited by diptera. They are self-fertile. The fruits consist of a group of six to twelve erect two-seeded carpels. The rosettes are winter-green, forming a low dome. *F. hexapetala* (*Spiraea filipendula* of older floras) has a distribution ranging from southern Scandinavia and Siberia to Italy and Asia Minor. Absent from the west of Scotland and in Ireland only in S.E. Galway and Kildare.

FELWORT, *Gentiana amarella* (=*G. axillaris*). Gentianaceae.

A summer annual forming a small rosette of leaves before flowering. The bright yellow root-system is a shallow one occupying the top 3 or 4 ins. (7·5–10 cms.) of the soil and with a similar spread. The stem is branched above only and bears small purple tubular flowers. The erect capsules split into two valves and the contained seeds, numbering about fifty, are jerked out by the action of the wind on the stiff stem. The seeds, which weigh about 0·00017 gm., are almost spherical, hard and brown. They normally germinate in spring, rarely in the autumn. The flowers open or close rapidly in response to changes of temperature.

A continental-northern type.

* * *

PLATE VIII. Flowers of the Chalk down. TOP LEFT. Rampion (*Phyteuma tenerum*). ×*ca.* ½. TOP RIGHT. Dropwort (*Filipendula hexapetala*). ×*ca.* ½. BELOW. Blue Field Sage (*Salvia pratensis*) a rosette perennial. ×*ca.* ⅙.

SPRING FELWORT, *Gentiana anglica* (*praecox*). Gentianaceae.

Rather like a small edition of the Felwort with flowers that commonly have four petals and which bloom in early summer instead of the autumn. A local plant of chalk pastures, especially erosion slopes. Whereas *G. amarella* is a summer annual, the Spring Felwort is a winter annual the seeds of which germinate in autumn.

FIELD GENTIAN, *Gentiana campestris*. Gentianaceae.

A biennial with stalked broadly lanceolate leaves and a stiff-branched stem from 4–12 ins. high (10–30 cms.) bearing tubular lilac-coloured flowers. The calyx consists of two broad outer sepals that overlap the two narrow inner ones. The capsule is almost without any stalk and splits longitudinally to release about sixty seeds which are brown, almost spherical with a pit on one side. They are very variable in size and measure from 0·5 to 0·9 mm. and have an average weight of about 0·0002 gm.

A continental-northern type that in Britain is diminishing.

G. baltica is a smaller plant and a winter annual which retains its basal leaves and cotyledons. The capsules contain the same average number of seeds, but only between five and six fruits are formed compared with an average of nine for *G. campestris*, which may, however, sometimes produce nearly sixty capsules.

GREATER FELWORT, *Gentiana germanica*. Gentianaceae. (Pl. III)

A local biennial species with broader leaves and much larger flowers than the Felwort, passing the first season as a rosette and in the following summer producing a flowering stem that may attain over a foot in height. The root system is shallow (*ca.* 6 ins., 15 cms.). The capsules, usually numbering about eight per plant, contain some seventy seeds. These are oval, slightly flattened, brown in colour, with a depression on one of the flat sides and finely dotted. The seeds are very variable in size (0·4–0·8 mm.), sometimes markedly so. Under artificial conditions germination is often very poor and may be long delayed. Seeds freshly harvested and immediately sown in 1948 did not germinate for two years. The populations of this species exhibit great fluctuations.

This is a continental type which in Britain is almost confined to the south-east (cf. map, Fig. 13, p. 39).

SWEET-SCENTED ORCHIS, *Gymnadenia conopsea*. Orchidaceae. 2n=20, 40. (Pl. XVI)

This, perhaps the commonest of the chalk Orchids, has strongly scented pale-purple flowers, but despite its popular designation, this scent has for those with a keen sense of smell, an unpleasant skatological undercurrent. It is easily recognised by the elongated flower spike and the very long and slender spur, which is strikingly curved. The strap-shaped leaves form a rosette which develops in September and is of a bright green colour. They are developed at the apex of a root tuber that is lobed below and somewhat resembles the palm of a hand. This orchid sets seed freely and flowers at the age of three to four years but is perhaps short-lived.

There are apparently both 2n and 4n (=80 chromosomes) strains, of which the tetraploid appears to be the typical plant of the chalk.

ROCK ROSE, *Helianthemum nummularium*. Cistaceae. 2n=32. (Pl. IX and Fig. 20)

A prostrate shrub with rather wiry stems bearing opposite pairs of hairy oblong leaves and easily recognisable by the large yellow flowers of five delicate, often slightly crumpled, petals and the green calyx with three of the sepals so much larger than the other two that these latter can be easily overlooked. The central mop of numerous stamens is also characteristic and the flowers are in fact visited by insects for the sake of their abundant pollen. The stamens respond to the stimulus of touch by moving away from the style, and thereby cross-pollination is promoted.

Fruits are freely produced and each is a capsule splitting into three valves and containing several dark brown or blackish seeds *ca.* 0·0012 gms. in weight, and as they have been found in the nests of harvester ants these are probably one agency of seed dispersal.

The maximum rooting depths observed by the author ranged from 20–30 ins. (50–75 cms.), but Anderson (*loc. cit.*) recorded a maximum depth of only 10½ ins. (26 cms.) and an

average depth of 5 ins. (12·5 cms.). The Rock Rose is winter-green, new leaves being formed chiefly in March and April. The upper epidermis bears some 120 stomata per square millimetre with about 260 to the sq. mm. on the lower. H. Heilig (*Zeit. f. Bot.*, pp. 225–79, 1931) has recorded osmotic pressures in this species of from 20 to 37 atmospheres. Except in the severest winters, foliage is retained throughout.

Musk Orchis, *Herminium monorchis*. Orchidaceae. 2n=40.

A small green-flowered perennial orchid with a small round tuber from which arise two or three leaves and a stem usually about 3–6 ins. (7·5–15 cms.) high, of which the upper inch or two (2–5 cms.) is clothed with numerous small bell-shaped flowers that have a rather honey-like scent. Pollination is effected by minute flies and hymenoptera. Whilst the outer segments of the flower are green and thin the inner are yellow and almost fleshy. Seed appears to be freely set, but vegetative propagation also occurs. The new tuber, or tubers, are found at a short distance from the old, since each is developed at the end of an underground shoot growing horizontally. Of such stolons up to five may be produced and these can attain as much as 4 ins. (10 cms.) in length.

The species is apt to be erratic in its incidence, being present in one year in large numbers and almost absent the next, so that frequently it may perhaps die after fruiting, or at least is short-lived.

The species is a northern-continental one, ranging from Scandinavia and Siberia to the Caucasus and Himalayas. In Britain it is confined to the southern and eastern counties, and does not occur in either Scotland or Ireland.

Lizard Orchis, *Himantoglossum hircinum*. Orchidaceae. (Pl. X)

An unmistakable species because of the exceptionally long lip (*ca.* 4 cms.) to the flowers, which in the early stage is coiled like a spring. The stem is sometimes over 18 ins. long (45 cms.) and bears numerous flowers. The four to six leaves are oblong and the tubers oval. The new leaves are formed in the autumn. Seed is freely set, but the plant is monocarpic, which probably explains its rarity and erratic occurrence. It is a continental-southern type and has only been recorded for Britain as far north as Lincolnshire (cf. map, Fig. 13, p. 39). The increased

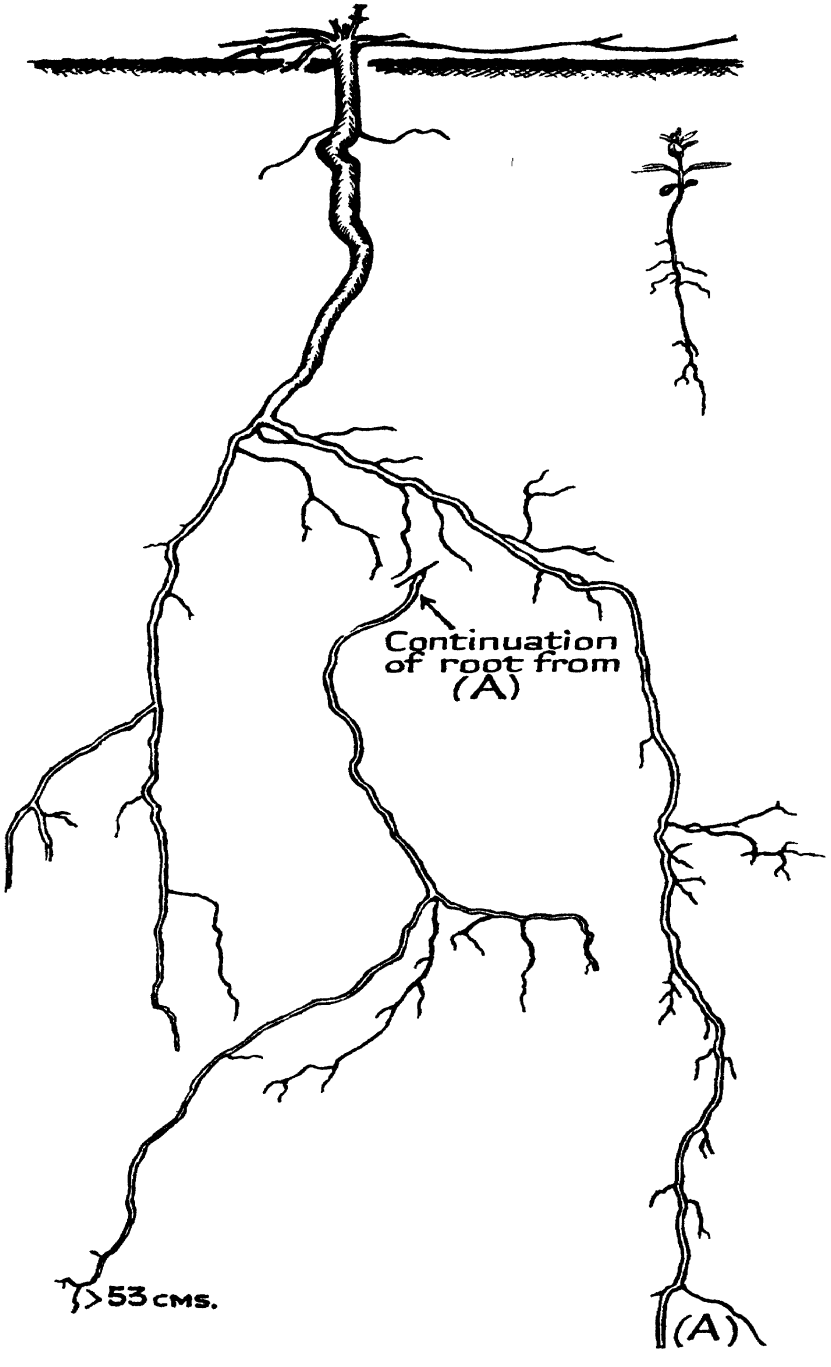


FIG 20. Rock Rose (*Helianthemum nummularium*) showing root system penetrating to over 21 in. (>53 cm.) and a seedling at the six-leaf stage.

area of its occurrence is perhaps due to the fact that numbers of plants were imported into England from the Continent, in the period preceding World War II, for growing in gardens. Since the seeds, like those of other orchids, are wind-borne, their culture in gardens may easily have led to plants appearing in the open country. Of the terrestrial orchids offered for sale this and to a much smaller extent *O. militaris* were the two most frequently purchased. *O. militaris*, which was believed to be extinct, has been again recorded, perhaps as a result of such introduction. This importation has not been so far renewed and no fresh stations appear to have been observed since 1939.

HORSESHOE VETCH, *Hippocrepis comosa*. Leguminosae. 2n=28. (Fig. 10, Pl. IX)

A prostrate perennial forming mats of foliage with pinnate leaves up to 6 ins. long composed of four to eight pairs of leaflets and thus easily distinguished from the Bird's-foot Trefoil, which the flower heads rather resemble, although the individual flowers are smaller and pale yellow. Its most striking feature is the sinuous pods (cf. Fig. 10) which break up transversely into three to six horseshoe-shaped one-seeded segments. The seeds themselves are yellow and weigh about 0·003 gm. Some seeds ('soft' seeds) germinate almost at once, whereas others ('hard' seeds) remain dormant for a short or long period. Germination mostly occurs in spring.

The average depth of penetration of the root observed on shallow chalk soils by Anderson was 8 ins. (20 cms.), but where the soil is deeper or the subsoil much broken, the roots of old plants may reach to over 3 ft. (90 cms.).

The winter-green condition of the prostrate shoots is seen in Fig. 10, which portrays a branch taken from a plant in early January. The manner in which the leaves and axillary branches all come to occupy the horizontal plane can be clearly seen. The winter state is therefore a low mat resting on the soil surface.

P.L. Lohr in a dissertation at Gronigen in 1919 records that leaves from plants of *Hippocrepis* growing at 450 m. had 176 and 128 stomata per square millimetre in the upper and lower epidermis respectively, whereas the comparable figures for plants growing at an altitude of 2,300 m. were 227 and 157.

Chiefly southern in distribution it is found over a large area of south-west Europe. In Britain its northern limit is in Banff

but its main area is south of Westmorland and Durham (cf. map, Fig. 13, p. 39).

CAT'S-EAR, *Hypochoeris maculata*. Compositae. 2n=10. (Fig. 7, p. 19)

A rather rare perennial with a rosette 2–8 ins. (5–20 cms.) across of oval, slightly sinuate, leaves which though frequently spotted with dark purple are sometimes quite plain. The inflorescence is usually branched and bears a small number of yellow flower-heads about 1 in. (2·5 cms.) across. The fruits, which are dispersed by wind, weigh about 0·0015 gm. The tap-root is a fleshy one and penetrates about 12 ins. (30 cms.). In Finland depths of penetration from 8 to 80 cms. have been observed. A species that only attains any appreciable abundance in highly calcareous situations, as for example locally in N. Hertfordshire on the chalk and on the mountain limestone of North Wales, but it may also occur less frequently on base-rich soil, derived from other types of rock or due to drainage (e.g. Kynance Cove, Cornwall).

Koeleria gracilis (=*K. cristata*). Gramineae. 2n=28.

A tufted perennial grass with rather glaucous hairy foliage and a panicle that is interrupted at the base and of a glistening greyish-green colour. A more or less self-incompatible species. The grains exhibit from 50% to 70% germination.

GRASS-LEAVED VETCH, *Lathyrus nissolia*. Leguminosae. 2n=14. (Pl. XII and Fig. 12, p. 36)

This annual Vetch so closely resembles grass, even as to the leaf arrangement in two rows, that its abundance is often overlooked except when the solitary pink flowers, or the pods darkening as they ripen, betray its presence amongst the surrounding sward. The apparent leaves are in fact flattened leaf stalks with a pair of minute stipules at the base of each. Though found on other soils, the Grass Vetch attains its maximum frequency on the chalk. The flowers are self-pollinated and often do not open. The pods normally contain nine seeds (*ca.* 0·009 gms.) and germination, which is usually 40% to 50%, takes place in the autumn.

Not native in Britain north of S.E. Yorkshire. It is absent also from Ireland and the greater part of Wales.

WILD FLAX, *Linum alpinum* v. *anglicum*. Linaceae. 2n=18.

A winter-green perennial which forms a low hummock of prostrate shoots in the vegetative condition, from which several or many ascendent stems arise bearing large pale blue flowers (*ca.* 2·5 cms. across) in the summer. The capsules contain from six to ten flattened seeds that exhibit about 75% germination.

This particular variety, which is locally common on the Gogmagog Hills in Cambridgeshire, may be endemic to Britain.

PURGING FLAX, *Linum catharticum*. Linaceae. 2n=16.

An annual with glaucous oblong leaves in opposite pairs on the lower part of the stem, which grows to a height of from 2–12 ins. (5–30 cms.) and is repeatedly forked below each terminal flower. The buds are characteristically pendant and the flowers are white and about 6 mm. in diameter. The capsules normally contain five seeds weighing about 0·00017 gm. Germination mostly in spring but also in autumn.

The root-system is usually shallow, about 3–4 ins. (7·5–10 cms.). Mycorrhiza have been observed in the root. Germination (*ca.* 70%) normally occurs in the spring.

WILD SANFOIN, *Onobrychis viciaefolia*. Leguminosae. 2n=28.

A long-lived perennial with deep roots and pinnate leaves. The leaflets are narrowly elliptical and number usually from eleven to fifteen, with hairs on the edge. The cultivated plant (*O. sativa*), which occurs as an escape has a coarser growth with much broader leaflets and is normally biennial or at most a short-lived perennial. The elongated inflorescence has deep rose flowers in the wild species, whilst those of the cultivated plants are paler. Hybrids between the two species are not uncommon and the true *O. viciaefolia* appears to be now infrequent and local. The pods are short, dark brown in colour and exhibit a network of ridges bearing small spine-like projections. Each contains a single seed shaped like a tiny Runner-bean seed and weighs about 0·015 gm. Germination averages about 30%. The wild species forms a low mat of foliage, except at the flowering stage when the red stems rise obliquely to a height of 9–18 ins. (20–45 cms.). Except in severe weather the plant retains its foliage throughout the winter.

REST HARROW, *Ononis spinosa*. Leguminosae. 2n=32.

An erect spiny shrub without the unpleasant odour of *O. repens* and devoid of stolons. The pods are normally as long as the surrounding calyx and the seeds weigh about 0·005 gm.

Although occurring on other stiff soils, this species is particularly characteristic of the chalk pastures and similar habitats rich in bases.

Anderson recorded an average rooting depth of 18–28 ins. (45–70 cms.) and a maximum observed of 37 ins. (92 cms.). The shoots disappear during the winter and the dormant buds which are below the surface develop in April.

BEE ORCHID, *Ophrys apifera*. Orchidaceae. 2n=36. (Pl. II)

Easily recognised by the bee-like appearance of the flowers, which usually number from two to eight. A rosette perennial with a summer resting period. New rosettes are formed in September. The root is shallow, usually about 3 ins. (7·5 cms.), and consists of three to five fleshy roots spreading above the round tuber. Wilting coefficient 3–5% (cf. Anderson, *loc. cit.*, p. 95).

Pollination may occur through visits of hymenoptera, but self-pollination is the rule and one to three capsules are commonly produced containing frequently about 10,000 seeds. The plants usually die after seeding, but non-seeding specimens can survive for several years.

This is a continental-southern type which is found in Ireland and extends as far north as Lanark.

SPIDER ORCHID, *Ophrys aranifera* (=*O. sphegodes*). Orchidaceae.

Usually a low-growing orchid about 4–7 ins. high (10–20 cms.), bearing from two to five spaced flowers of a tawny-purple colour with an H-shaped dark marking on the lip.

A southern-continental species confined in Britain to the south-eastern counties from Dorset to Kent (cf. map, Fig. 13, p. 39).

The Late Spider Orchid (*O. arachnites*) is confined to Kent and is a southern-continental type.

MONKEY ORCHID, *Orchis simia*. Orchidaceae. 2n=42.

This orchid formerly occurred in Oxfordshire, Berkshire and Kent. The only remaining station was recently ploughed up. There are usually three or four leaves and an inflorescence about 8 ins. high with pale flowers faintly tinged with violet

and a lip with four very slender lobes, two on either side, and a short tail-like lobe with purple papillae in between the lower pair. Fruiting appears to be infrequent.

It is a Southern European species.

BURNT ORCHIS, *Orchis ustulata*. Orchidaceae. 2n=42.

Rather suggesting a diminutive *Orchis purpurea*, this species is usually not more than 4–6 ins. high (10–15 cms.). At the base is a rosette of grey-green leaves arising from the oval tubers, and the crowded spike consists of very small flowers with a hood-like perianth which in bud is brownish-purple, becoming paler with age. There is a white three-lobed lip, with a very short spur. The flowers emit a scent suggesting Heliotrope and are probably pollinated by diptera.

For the first ten or more years after germination this dwarf orchid produces no leaves and lives as a saprophyte on the organic material in the soil. It flowers in about thirteen or fourteen years after germination.

A markedly continental type, this species extends to Scandinavia and is absent from Scotland and Wales. Very local in its occurrence, this orchid is particularly associated with well-drained situations and would appear to have appreciably diminished both in frequency and abundance within the last half-century.

RAMPION, *Phyteuma tenerum*. Campanulaceae. (Fig. 19, p. 49, Pl. VIII)

A very characteristic species with its almost spherical deep blue heads of flowers, from which the long curved cylindrical styles project and constitute its most conspicuous feature.

The leaves, which have long stalks, are produced in rosettes from the ends of the woody rootstock, which in older plants is branched near the surface. The form of the leaves varies with the age of the individual and their position on the plant. Those on quite young plants are heart-shaped, but by the second or third year before the plant is about to flower the upper leaves develop an elongated oval blade with a crenate margin, and on the flower stalk itself they are almost lanceolate and sessile. When broken, the stem and leaves exude a slightly milky white juice.

After flowering, the head elongates and becomes oval, whilst the calyces of the individual flowers persist and envelop

the small capsules. There may be from 8 to 47 of such capsules in a head, each containing from one to 16 of the shining brown seeds. The latter germinate in spring.

This species was formerly known as *Phyteuma orbiculare*, which is a central European species, whereas *P. tenerum* is a west European species of S.W. France, Spain, S.W. Germany and the Juras, associated with a southern oceanic climate. In this country *P. tenerum* has a peculiarly local distribution (cf. map, Fig. 13, p. 39), and may be quite common on the chalk of one area, as, for instance, the downs of central Sussex, whereas it is local on the downs of Surrey and rare on those of Kent, whilst on the chalk of Hampshire it is even rarer.

The plant is a deeply-rooting (over 30 cms.) summer-green perennial herb, that produces its new leaves from February to April according to the weather conditions. The dormant buds are situated in the surface soil and are normally protected by surrounding turf.

HAWKWEED, *Picris hieracioides*. Compositae. 2n=10.

This very hispid perennial bears numerous hairs, some of which bear a double hook. The stem is often freely branched and bears leaves that half clasp it and yellow flower-heads about 1 in. in diameter (2·5 cms.). The fruits bear a snow-white parachute of hairs and weigh nearly 0·0006 gm.

BURNET SAXIFRAGE, *Pimpinella saxifraga*. Umbelliferae. 2n=18, 36. (Fig. 17, p. 45)

A perennial herb forming rosettes of pinnate leaves of two types (cf. Fig. 17). Those plants in which the leaflets are oval and deeply toothed, somewhat resemble *Poterium sanguisorba*, hence both species are popularly known as Burnets. In the second type the leaflets are pinnatifid. The wiry stems are from 6–30 ins. in height and the flat-topped umbels bear their white flowers in July and August. Like other Umbelliferae, the plant has a definite odour when crushed. The smooth oval fruits are about 3 mm. in length and weigh *ca.* 0·0017 gm.

The rooting depth is variable, but often over 12 ins. (30 cms.). K. Linkola and A. Turikka (*Ann. Bot. Soc. Zool-Bot. Fennicae Vanamo T. 6 no. 6*, pp. 1–207, 1936) provide data from three types of habitat for this species, showing a range of rooting depth in Finland of from 28–100 cms.

HOARY PLANTAIN, *Plantago media*. Plantaginaceae. 2n=24.

Although a widespread plant in short turf on basic soils, it is especially common on the chalk, where its flat rosettes attaining up to 18 ins. in diameter (45 cms.) and, pressed close to the surface, are normally effective in preventing the growth of competitor seedlings beneath them. The spike of flowers is unlike any other Plantain with its pinkish-grey colour and faintly almond-like scent. Each capsule contains from 1–7 seeds (av. 3, cf. R. Dowling *Journ. Linn. Soc.* (*Bot.*), L, p. 329, 1935), often dissimilar in size and shape. Each spike will produce about 80 capsules. The stalks of the stamens are white on some plants and pink on others. The width of the leaves is also subject to considerable variation.

CHALK MILKWORT, *Polygala calcarea*. Polygalaceae. (Fig. 11, p. 31)

A prostrate woody perennial with rosettes of rounded spathulate leaves at the base of the flowering shoots, a feature most easily seen in spring, since the leaves of the rosette tend to be separated somewhat by growth of the axis later on. The prostrate branches spread and root. The flowers are usually a vivid blue. The sepals of the flower are broader than the heart-shaped capsule. This species has a low average output of seeds (about 280 per plant).

The Chalk Milkwort is a southern-continental type and in Britain occurs only in the south-east from Kent and Berkshire to Gloucestershire and Wiltshire (cf. Fig. 11, p. 31).

The plant forms a winter-green mat with the resting buds almost at soil level. It is not a deeply-rooting type.

A very rare Milkwort *Polygala austriaca* is confined to the chalk downs of Kent and Surrey. It is a small plant closely related to *Polygala amara* which occurs in Yorkshire.

SALAD BURNET, *Poterium sanguisorba*. Rosaceae. 2n=28. (Fig. 21, Pl. IX)

The young plant forms a rosette up to 2 ft. (60 cms.) in diameter, and older plants, through branching, clusters of rosettes. These consist of pinnate leaves, which are deep green and slightly glaucous in appearance. The leaflets, about 11 to 21 in number, are rounded or oval, clearly toothed at the edge, dull and smooth above but hairy on the veins below.

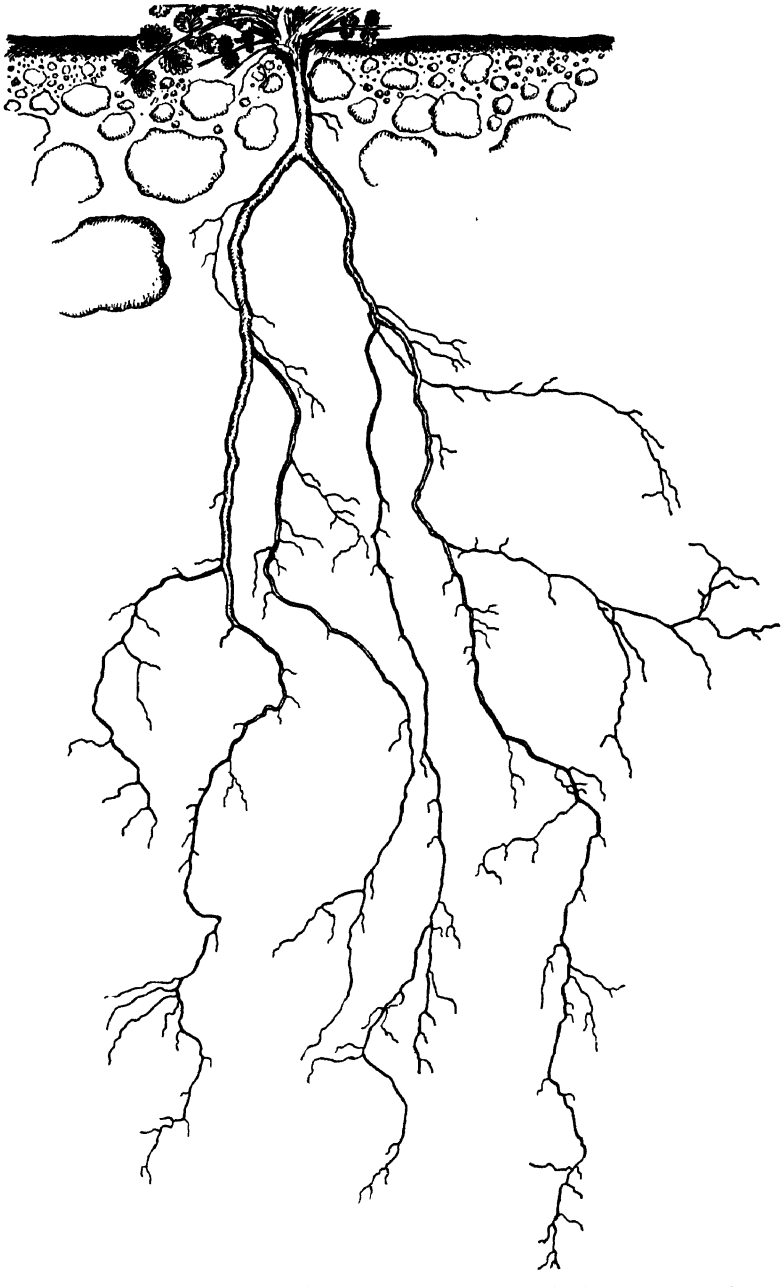


FIG 21. Salad Burnet (*Poterium sanguisorba*), half-natural size, showing both tap-root and laterals penetrating to depths of 12–14 in. (31–37 cm.).

The leaves taste and smell of cucumber and their former use in salads gave origin to the vernacular name. The leaflets are sometimes attacked by a mite *Eriophyes sanguisorbae* which causes them to become swollen and thickly covered with woolly hairs.

The rounded greenish heads of nectarless flowers are borne on branched stems about 6–18 ins. (15–45 cms.) high, arising from the central region of the rosettes. The individual flowers are without petals and small. Each has a calyx of four lobes and those at the top of the head are female with two styles each ending in a crimson tuft of stigmas. The male flowers are toward the base and from each of these there are produced between 10 and 30 stamens with long, pendulous filaments.. Hermaphrodite flowers containing both ovary and one to four stamens are also often present in the middle region. The flowers in the head open from below-upwards and are pollinated by wind. The dark ribbed seeds which are small (*ca.* 0·009 gm.) are shed enclosed in the withered calyx. Dispersal of the fruits is largely by wind, but also by passage through birds. Germination occurs in the autumn. The cotyledons are oval, about 5 mm. in length, with a cordate base. The first foliage leaves are trifoliate.

The species is widely distributed throughout Europe and is tolerant of very severe frost, whilst its deep-rooted character (30–40 ins.=75–100 cms.) enables it to survive prolonged drought. It over-winters as a dome-shaped rosette of old and new leaves. The roots were found by Stahl to contain an endotrophic mycorrhiza.

COWSLIP, *Primula veris*. Primulaceae. 2n=22.

A rosette perennial with umbels of small fragrant deep-yellow flowers much more prevalent in pastures on calcareous soils than elsewhere.

The Oxlip, *P. elatior*, is easily distinguished by its larger pale-yellow flowers without the characteristic perfume of the cowslip, and the throat of the corolla is not puckered. It is confined to East Anglia and is a woodland species.

PASQUE FLOWER, DANE'S BLOOD, *Pulsatilla vulgaris* (=*Anemone pulsatilla*). Ranunculaceae. 2n=32. (Pl. VI)

This typical chalk plant is a dwarf rosette perennial with rich purple flowers that are at first erect, later slightly inclined

and which close up at night. The stem is usually from 4–8 ins. high (10–20 cms.). The flowers are pollinated by bees. The outermost of the mass of yellow stamens are sterile and function as nectaries.

In cultivation a number of flowers may be produced, but in the wild state usually only from one to five are produced on a plant. The fruits number from 24 to 150 per fruit head and bear feathery styles that facilitate wind dispersal, and this is also promoted by the elongation of the fruit stalk after fertilisation.

The rooting depth is usually shallow, penetrating only 3 or 4 ins. (7·5–10 cms.), with a small spread.

A continental species not to be confused with the taller *P. pratensis*, often grown in gardens as *Pulsatilla vulgaris*, which has drooping dull purple flowers. *P. vulgaris* in England occurs southwards from Yorkshire and Gloucestershire (cf. map, Fig. 13, p. 39).

The dormant buds are situated just above the surface, protected by last year's leaf-bases and more especially by the surrounding turf.

FIELD SAGE, *Salvia pratensis*. Labiatae. 2n=18. (Pl. VIII)

A rare rosette plant of the chalk with dark green conspicuously wrinkled leaves which are oblong with a heart-shaped base and have long stalks. The inflorescences bear bright blue flowers and attain a height of from 2–3 ft. (60 to 90 cms.). The flowers are of two kinds: some are female, and others which are larger contain both stamens and ovary. These latter exhibit the highly specialised pollination mechanism familiar in the genus. One lobe of each of the two stamens is sterile and constitutes a lever which when pushed aside by a visiting insect, usually a bee, brings the fertile lobe down on to the insect's back. Fruit is freely produced and germination of the ripe black fruit segments, schizachenes, saved from wild British plants, is usually good (*ca.* 60%). When moistened these schizachenes swell, the outer layer becomes mucilaginous, and in consequence dispersal on the feet of birds probably occurs.

The Field Sage over-winters as a slightly winter-green rosette in which both old and immature foliage is present; these with the branched endings of the rootstock form a low,

dome-shaped aggregate. It is a continental-southern type which is confined in Britain to the south-eastern counties and extremely local.

CHALK SCABIOUS, *Scabiosa columbaria*. Dipsaceae. 2n=16. (Fig. 16, p. 45, Pl. I)

The rosette leaves of this perennial species are often entire, whereas the stem leaves are pinnatifid with narrow segments. Anderson observed an average rooting depth of from 7–17 ins. (17·5–42·5 cms.), with a maximum of 23 ins. (58 cms.), and abundant root-hairs. The flat lavender-coloured heads containing from 70 to 80 flowers are about 1½ ins. across (3·5 cms.) and have large irregular marginal flowers. The heads terminate the branched stem, commonly about 18 ins. (45 cms.) high. The number of fertile fruits per head is usually about 40.

A southern-continental type that does not occur in western Scotland and is commonest in the south-east of England. The leaves wither in late autumn and are renewed in March or early April. The dormant buds are located at ground level.

FIELD FLEABANE, *Senecio integrifolius* (=*S. campestris*). Compositae. 2n=48, 90. (Fig. 4, p. 15)

In the non-flowering stage this appears as a close-pressed rosette of several elliptical leaves which are obscurely toothed, slightly cottony above and definitely so beneath.

Plants flower in their second or third year, or later where competition is severe, when a single stem arises from the centre of the rosette. This is erect, unbranched below, and bears several small elliptical leaves which are green above and white with hairs beneath. At the summit are produced from one to seven (usually 3–4) flower heads in an umbel. Each flower-like head contains a large number of florets, about 10 to 15 oval ray florets and up to ninety or more tubular florets forming the disk. Some seventy fruits usually mature from each head and these develop a silky but small parachute of hairs, by which

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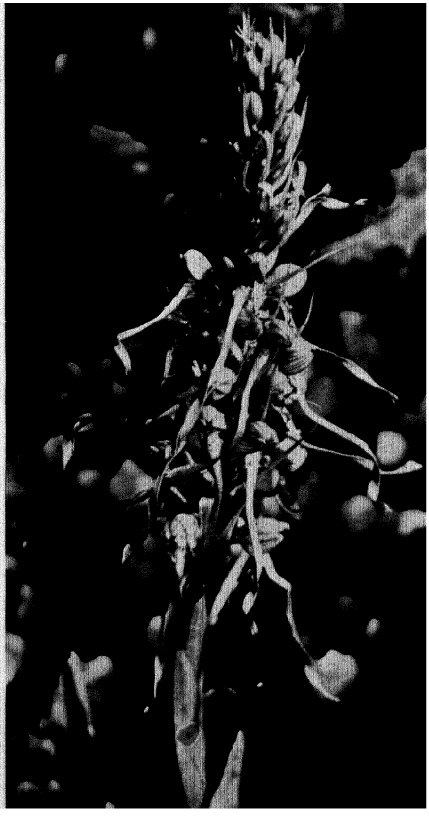
PLATE IX. ABOVE. The Salad Burnet (*Poterium sanguisorba*) and tufts of the Sheep's Fescue (*Festuca ovina*) colonising bare chalk. BELOW. Chalk down with Rock Rose (*Helianthemum nummularium*) on the left and Horseshoe Vetch (*Hippocrepis comosa*) on the right. In the mid-foreground can be seen a single inflorescence of the Kidney Vetch (*Anthyllis vulneraria*). Both ×*ca.* ⅛.











their dispersal by the wind is facilitated. Germination in the laboratory is good (70–80%), but in the natural conditions the species is erratic in its occurrence and most variable as to its abundance. It is certainly a short-lived perennial and plants appear often to die after only fruiting once, but the long period of years that may elapse between two years of abundance in the same locality suggests erratic germination as well as a short span of life.

New leaves are normally formed in the autumn, but in a severe winter these may be killed and fresh leaves develop in March or April. The dormant buds are situated at ground level.

This is a markedly continental type absent from Ireland, and apart from its occurrence in Anglesey confined to the south-eastern counties (cf. map, Fig. 13, p. 39).

Seseli libanotis. Umbelliferae. 2n=22. (Pl. III)

A biennial or perennial rosette plant with doubly-pinnate leaves and pinnately lobed leaflets. The flowering stems rise to a height of from 12–30 ins. (30–75 cms.) and bear rounded umbels of small creamy-white flowers. When the stems die down, the basal fibro-vascular bundles often persist and serve to protect the apex of the rootstock, whilst the dormant buds are located at ground level. The root is branched and fleshy and penetrates to a depth of about 8–12 ins. (20–30 cms.).

A markedly continental type which in Britain is very rare and only found in a few isolated localities in Cambridgeshire, Hertfordshire and Sussex.

LADY'S TRESSES, *Spiranthes spiralis* (=*S. autumnalis*). Orchidaceae. 2n=30. (Pl. XXXI)

An unmistakable plant in bloom, with its spiral of small white almond-scented flowers. The root bears normally two tapering oval tubers, and at the side of the flower stalk with withered flowers, at its base, can be seen the rosette of four or five new leaves which persist through the winter and wither with the approach of flowering the next summer.

* * *

PLATE X. Chalk flora. ABOVE. Wild Chicory (*Cichorium intybus*). × *ca.* $\frac{1}{5}$. BOTTOM LEFT. Wood Barley (*Hordeum sylvaticum*). × *ca.* $\frac{1}{10}$. BOTTOM RIGHT. Lizard Orchid (*Himantoglossum hircinum*). About life-size.

The flowers are visited by bees and seeds are set freely. A capsule contains about 1,300 seeds, and as young plants can often be found in numbers germination is probably good. No leaves are produced until about eight years after germination during which period the nutrition is saprophytic. The plants can flower year after year so that the great fluctuations in number of visible leaves may indicate intermittent resumption of the saprophytic habit.

A southern-continental species extending from Denmark and central Russia to North Africa and Asia Minor, which in the British Isles is absent from Scotland.

BASTARD TOADFLAX, *Thesium humifusum*. Santalaceae. (Pl. VI)

A woody perennial which parasitises the roots of various kinds of plants. It varies markedly in apparent abundance from year to year. This, if not due to inconspicuity in some seasons, would suggest a short life-span. The prostrate shoots bear rather yellow-green linear leaves and inconspicuous whitish flowers.

An oceanic species confined to southern England, eastwards of the line Lincoln to Devon (cf. map, Fig. 13, p. 39).

THYME, *Thymus serpyllum*. Labiatae. 2n=24.

A deeply-rooted, mat-forming, evergreen perennial with small firm aromatic leaves that are only shed in severe winters. H. Heilig has recorded an osmotic pressure of 18 atmospheres for this species and a rooting depth of 14 cms. (*ca.* 5½ ins.). Anderson recorded a maximum depth of 70 cms. (28 ins.) and noted the numerous shallow roots that occur to an average depth of about 4 ins. (10 cms.) and the deeply penetrating roots commonly extending to from 12–20 ins. (30–50 cms.). Actually the Thyme stands up well to drought conditions. The flowers are of two types, the larger male and smaller flowers which are bisexual.

HOP TREFOIL, *Trifolium campestre* (= *T. procumbens*). Leguminosae. 2n=14.

A winter-annual clover with an erect main stem and more or less prostrate lateral branches all bearing small hairs. The pale oval yellow heads are 12–18 mm. long and densely

flowered. They produce a cluster of, normally, one-seeded pods. The seeds weigh approximately 0·00033 gm.

Most abundant on calcareous soils, the Hop Trefoil also occurs in other dry habitats that are basic in reaction.

SPIKED SPEEDWELL, *Veronica spicata*. Scrophulariaceae. 2n=34.

A low-growing evergreen perennial of mat-like habit with prostrate stems that bear small hairy leaves only about 1½–2 ins. above the soil. The inflorescences attain a height of normally not more than 4–10 ins. (10–25 cms.) and bear dense spikes of bright blue flowers with purple stamens.

The seeds are small, brown, *ca.* 0·00013 gm. and are perhaps mainly dispersed by wind.

This species is a characteristic plant of the very continental conditions of central Europe and in Britain is restricted to the calcareous heaths of the Breckland area, where it is very rare and diminishing. The continental *V. spicata* is clearly very closely allied to the larger oceanic *V. hybrida* (Pl. XVIII), and when the two species are grown side by side all doubts as to their distinctness are dissipated, whatever views one may hold as to the taxonomic status they should be given (cf. map, Fig. 15, p. 43).

V

BEECHWOODS

BEECHWOODS are the characteristic woodlands of the chalk hills, and the Beech hangers, made famous by the writings of Gilbert White, possess a unique charm that owes much to the topography of the ground, but even more to the Beech trees themselves. The Beech has sometimes been regarded as an introduced tree, perhaps because undue importance was attached to a statement by Caesar; but in fact there is definite evidence that this tree was present in Britain in the early Bronze Age period, and Beech pollen from the peat of Wales, found by Dr. Hyde, suggests that Beechwoods may have had a more extended distribution in sub-boreal times than now. In common with most other types of natural woodland in Britain a single kind of tree in these hangers shows a marked preponderance over all its companions. This dominance of the Beech coupled with the paucity, or even complete absence, of a shrub layer confers a structure on the Beechwood that is not only distinctive but by reason of the extent of the woodland vistas enhances the rather cathedral-like effect produced by the aisles of the smooth columnar trunks (Pls. XIII and XIV, pp. 112–13).

One of the outstanding features of the structure of the semi-natural Beechwoods is the discontinuity in the ages of the trees and saplings. It is soon realised that these comprise groups belonging to definite age classes, often separated by a period approximating to seven or fourteen years. The reason for this is that a heavy crop of Beech seeds is usually achieved once about every seven years. It is only when such a 'mast year' occurs that there are enough seedlings produced to meet the normal depredations of field-mice in particular and of other animals, as well as the losses consequent upon fungal attack, and still leave a surplus which can grow beyond the stage when the seedlings normally suffer these depredations. In the intervening less productive years the seedlings do not germinate in adequate quantities to survive this heavy infant mortality. Hence the structure of the mature Beechwood reflects these gaps

in the process of regeneration. The frequent absence of any shrubs whatever is mainly a consequence of the very low light intensity in summer and the poor illumination even in spring as compared for instance with that of an oakwood of similar density. The shallow root-system of the Beech has, moreover, the effect of intensifying the competition of the trees with the shallow-rooted shrubs. However, where the woodland margin is not artificially controlled we shall commonly find a varied assembly of shrubs that bear witness to the suitability of the soil conditions for their growth, provided the situation is such that the amount of light is appreciably greater in summer and root competition, at least on the outer side, is of little significance.

Associated trees are chiefly the Oak and the Ash. The former especially occurs on the deeper soils, whilst the Ash is more especially found where the Beech canopy is rather sparse, sometimes because the Beechwood has not yet matured and the Ash, which is an early coloniser, has not yet been suppressed by the superior height and greater shade cast by the Beech, sometimes on soils that, because of their shallowness or wetness, are less favourable to the Beech than the tolerant Ash, which latter, not being checked to the same degree as the Beech, manages to survive. In this connection the experiments carried out some twenty-five years ago by Munch and Dieterich are significant. They showed that there are diverse physiological races of Ash tree. Those that flourish on dry calcareous slopes are inherently different from the marshland Ash trees that flourish on moist soils.

The Beech is a tree that is peculiarly intolerant of waterlogged soils and especially susceptible to a high water content in the soil when this is accompanied by poor aeration.

The only really characteristic deciduous tree met with in company with the Beech is the White Beam (*Sorbus aria*); the appositeness of its name is obvious when the wind displays the white undersides of the leaves. But this tree, like the other associates of the Beech, is to be found more particularly towards the margin or where the canopy of the interior is rather sparse. Not infrequently Yew trees occur in the Beechwoods and these evergreens on the steeper slopes, as at Box Hill in Surrey and Kingley Vale in Sussex, may even become dominant. Usually where the Yew is frequent it forms a second story beneath the Beech (Pl. XIII), and being evergreen it is able to take advantage

of the much higher light intensity before the leaves of the Beech unfold. This is true of the only characteristic shrub which grows in the real beech shade—namely, the evergreen Spurge Laurel (*Daphne laureola*) (Pl. XV) with yellowish-green faintly scented flowers produced in early spring. The other *Daphne* that formerly grew wild in several Beechwoods in England is almost extinct, due to the vandalism of those who removed plants for their gardens or for sale. *Daphne mezereum* though it produces its fragrant purple flowers in March or early April is deciduous and cannot endure so dense a shade as its congener.

Other frequently occurring shrubs or small trees found near the margin, or elsewhere if the shade be mitigated by a gap in the canopy of foliage, perhaps most commonly represent persistent members of the chalk scrub. Such are the Maple (*Acer campestris*), the Elder (*Sambuca nigra*), the Dogwood (*Cornus sanguinea*), the Wayfaring tree (*Viburnum lantana*), the Buckthorn (*Rhamnus catharticus*) and the Spindle (*Euonymus europaeus*), the last three especially characteristic of calcareous soils. The Hazel (*Corylus avellana*) and Hawthorn (*Crataegus monogyna*) are both frequent but, like the Elder, flourish almost equally on a variety of other soils and in many other habitats. The fruits of all these shrubs, except those of the Maple, which are carried by the wind, are dispersed by animals. The Box (*Buxus sempervirens*), a continental-southern shrub, which is also met with in Beechwoods, is marginal and very local, though, as at Box and Box Hill, sometimes common. It has been suggested that the Box is an introduction, but its continental distribution and the fact that it fruits and regenerates freely is consistent with the possibility of its being native. However this may be, some were certainly planted to augment the existing supply of boxwood when the demand for the making of wood blocks for printing increased.

Where Beechwoods have been felled brambles and Willow-herb often colonise at an early stage and may dominate the soil to such an extent as to prevent other vegetation developing.

The soil of the Beechwood is often quite shallow, sometimes only about 4 ins. (10 cms.) in depth and rarely more than 15 ins. (37 cms.) except on the level summits. Thus the root systems of the common species are often shallow too (Figs. 22–25). This soil usually contains not more than 10% organic matter and there is frequently only 5% or even less. On the steeper slopes

the leached particles of soil tend to be carried downwards by rain-wash and such continual erosion often ensures the maintenance of shallow soil in which the organic content is quite low and the reaction remains alkaline (pH 7 to 8·5), but where the slope is more gentle the leached particles accumulate and a soil gradually develops, hence on the level summits soils over 18 ins.

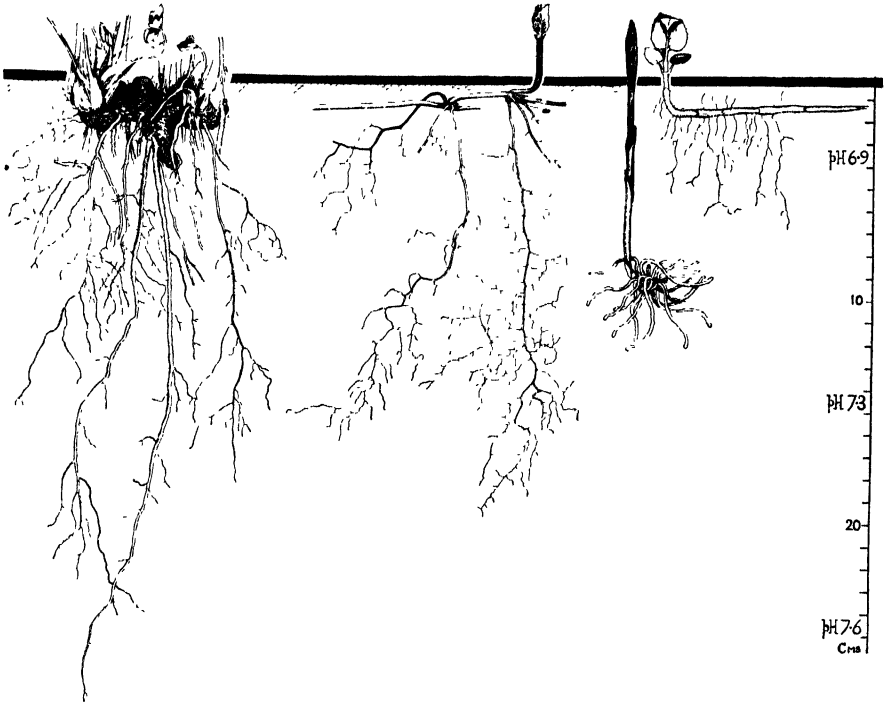


FIG 22 FIG 23 FIG 24 FIG 25

FIGS 22–25. Root systems of plants in dry Beechwood. FIG 22. Wood Sanicle (*Sanicula europea*). FIG 23. Dog's Mercury (*Mercurialis perennis*). FIG 24. White Helleborine (*Cephalanthera damasonium*). FIG 25. Enchanter's Nightshade (*Circaea lutetiana*). Note the slightly acid reaction above and alkaline reaction below.

deep are sometimes found with 15% of organic material in the surface layer and a covering of raw humus and leaf litter of appreciable thickness is not infrequent. In such situations the surface soil may be actually acid, sometimes between pH 4 and 5, becoming less acid with increasing depth till the alkaline subsoil rich in carbonates is reached. These deeper soils showing such a definite gradient in soil structure can retain

considerable moisture even in summer and a water content representing a 25% addition to the dry weight has been recorded at this season after rain.

In those parts where the organic material in the woodland soil, through drainage from above and shelter, remains damp the film of moisture covering the particles of humus to some extent protects them from exposure to the air and the process of oxidation is slower than where the soil is drier. This in part explains why the dry parts of the Beechwood are usually those with the shallowest soils and the thinnest covering of surface humus, whereas the wetter areas often exhibit an appreciable depth of soil and a thick organic covering. These trends are further accentuated by the fact that the dry areas are often subject to removal by erosion and the damp areas are often those of accumulation.

Woodland felling by removing shelter and admitting light leads to more rapid oxidation of the surface humus. Where the original soil is deep and the humus layer thick there would probably be an acid surface layer, but the rapid oxidation after felling is in a minor degree comparable to burning and results in an enrichment of the surface in the nutrient bases that the organic material contained, so that the soil becomes less acid and more fertile. The rich growth that often follows the felling of a Beechwood bears witness to the intrinsic fertility of the soil, and the frequent abundance of the Rosebay Willowherb, which from its occurrence on burnt areas is also called fire-weed, is associated with this change. For this Willowherb is a plant greedy for nitrates, which are deficient on acid soils but abundantly found where bases are plentiful.

Most of us have at some time or another stood entranced by the extreme beauty of the freshly expanding leaves of the Beech trees with their pale green loveliness and silken fringes. But few pause to think of the change in light climate that is thereby being wrought. During the winter months the spreading tracery of twigs and buds, partly because of their orientation, cast a greater shade than the winter framework of the Oak, but nevertheless some 17% of the early spring sunlight reaches the ground level, even in a dense Beechwood, whilst where the canopy is less dense the light intensity in March and April may be as much as 70% that in the open. Thus where the trees are not too crowded there may be sufficient light, whenever the

temperature is warm enough in autumn and winter, for herbaceous plants to manufacture food actively; but with the opening of the leaf buds the shade increases rapidly and from late April till towards the end of November, when the leaves again fall, the light at ground level often does not exceed 2%–4% of that in the open, except for light patches where the sun penetrates the canopy. Indeed, in the shadiest parts, the light on a sunny summer's day may be only 0·4% of that in the open. So whereas during what can be called the 'light phase' lasting only 4¾ months there is ample light in most parts of the Beechwood for herbs growing on the ground to manufacture food faster than they must use it, the conditions for the remaining 7¼ months are very different, for during this latter period most parts of a Beechwood are too shady to admit of the plants of the herb layer living within their income. In summer the speckled but changing pattern of the sun-flecked soil—now illumined now in shade—provides the familiar subdued Beechwood twilight that is more suited to the toadstool and the saprophytic orchid than to furnishing solar energy for the green-leaved plant.

To such straightened circumstances in respect to light must be added that over much of the woodland, as already noted, the soil is shallow and dry in summer, only locally being deep and moist. Even under these latter more favourable conditions in respect to water supply the surface of the soil is apt to be covered with the closely packed flat leaves of the previous season, thus presenting an impediment to circulation of the atmospheric air into the soil and of soil air into the atmosphere. Hence the heavy carbon dioxide gas produced during the respiration of the roots of the trees, by the teeming population of soil bacteria and by the protozoa that feed upon them, tends to accumulate and thus poor soil aeration is added to the other conditions adverse to plant growth. Erbermeyer recorded no less than 0·14% CO_2 in the humus layer of a Beechwood, or nearly six times as much as in the atmospheric air.

Taking all these features into account, it is not surprising to find that the ground flora of a Beechwood is often extremely patchy, sometimes confined to 'light chimneys,' whilst large areas are often entirely bare of vegetation though in such situations, if there is plenty of decaying material in the soil, the

saprophytic Bird's-nest Orchid (*Neottia nidus-avis*) (Pl. XVI) and the Bird's nest (*Monotropa hypopitys*) (Pl. XIV) may, in favourable seasons, be quite common. Another saprophytic orchid, the extremely rare *Epipogium aphyllum* has been most frequently recorded from beechwoods on chalk but has also been found in Oakwoods on acid soil. Its chief interest is that it probably survives for long periods without appearing above ground and even on the Continent it would appear to seed sparingly and to spread mainly by slender underground shoots. The rhizome bears absorptive hairs. Since all these plants have no green leaves but depend for their sustenance on the products of decaying organic material present in the soil they are of course independent of light and the limitations imposed by shade. This is true also of the numerous fungi, both saprophytic and parasitic, which often abound in the Beechwood in a moist, warm autumn. Here on the woodland floor we shall probably find the common *Russula aurata* and *Russula lepida*, perhaps *Marasmius globularis* and *Clitocybe inornata*, both characteristic of Beechwoods, or *Polyporus adustus*, whilst on the decaying Beech trees themselves occur the black gelatinous fruit bodies of *Bulgaria inquinans* and the shining white caps of *Armillaria mucida*. There is indeed a distinctive fungal flora.

Even where the summer shade is not so low as to inhibit an herbaceous covering on the floor of the Beechwood there is great variation with the depth of soil and degree of moisture. Where the soil is shallow and dry we shall probably find the Wood Sanicle (*Sanicula europea*) prevalent and some of the more definitely chalk-loving species such as the Nettle-leaved Bell Flower or Canterbury Bell (*Campanula trachelium*) (Pl. V), the White Helleborine (*Cephalanthera damasonium*, Fig. 24), the Wood Barley (*Hordeum sylvaticum*) (Pls. XIII and X) and the drooping Woodrush (*Luzula forsteri*). Where the soil is somewhat deeper and moister the Dog's Mercury (*Mercurialis perennis*) often forms dense sheets, and locally it may be accompanied by the wild Solomon's Seal (*Polygonatum odoratum = P. officinale*) and the Lily of the Valley (*Convallaria majalis*). The Coral Root (*Dentaria bulbifera*) is of very local occurrence, but quite abundant in some of the Beechwoods of Buckinghamshire. The last, although producing pink flowers, rather like a stock, does not set seed but reproduces by dark purple bulbils produced in the axils of the leaves. The Melic Grass (*Melica uniflora*), though common

in other types of woodland, here sometimes attains an abundance that is quite impressive, whilst the Wood Sorrel (*Oxalis acetosella*), a shade-tolerant species, is sometimes also quite common. The clearings and edges of Beechwoods are often the especial home of the Wall Lettuce (*Lactuca muralis*), which, though found on other types of well-drained soil, on the chalk often attains a high frequency. It is in the Beechwood clearings that the Wild Columbine (*Aquilegia vulgaris*) has its particular home.

Where the soil is deep and moist and the canopy open, a rich growth of herbs develops which comprises a number of species that can be found in most non-acid woodlands, but special mention must be made of the evergreen Woodruff (*Asperula odorata*), the winter-green Wild Strawberry (*Fragaria vesca*) and the Wood Violet (*Viola sylvestris*). All these, by reason of their possession of expanded leaves during the spring months, before the 'shade phase' begins, can to some extent evade the limitations imposed on species such as the Enchanter's Nightshade (*Circaea lutetiana*), which because of the late development of its shoots is more limited to the brighter areas.

The frequent abundance of species with burr fruits in the less shaded areas is sometimes obvious after walking through a Beechwood in the autumn when one's clothes are covered with the fruits of the Wood Sanicle, the Enchanter's Nightshade, the Woodruff and the Burdock. Dispersal, other than by man, is effected by the smaller mammals, and here as in other types of woodland the high proportion of species whose fruits or seeds are dispersed by animal agency is significant.

It is noteworthy that many of the species that are quite common in the woodlands on the chalk escarpments, such as the Dog's Mercury, the Enchanter's Nightshade, the Wild Strawberry, the Wood Sanicle, to mention but a few, may also be encountered in the flushes and along the drainage channels of woods located on so-called non-calcareous soils. Such situations are of course constantly receiving a supply of bases leached out from the higher ground above, and so these flushes, though they may be totally devoid of free carbonates, are often amply supplied with exchangeable bases, hence the apparent anomaly is in fact not inconsistent.

It is noteworthy that the shade plants of the Beechwood include a number of white or pale-flowered species, mostly

strongly scented, which are pollinated by nocturnal species of insects. Examples are furnished by the Solomon's Seal (*Polygonatum odoratum*), the Lily of the Valley (*Convallaria majalis*), the Butterfly Orchis (*Platanthera chlorantha*, Pl. XVI), the White Helleborine (*Cephalanthera damasonium=C. pallens*) and one may add the very local but probably native shrub the Fly Honeysuckle (*Lonicera xylostemum*). The Butterfly Orchis does not in fact emit any appreciable scent until evening, when its odour can be almost overpowering. The Beechwood is also the particular home of the green-flowered members of our flora. To this category belong the Dog's Mercury, the Setterwort (*Helleborus foetidus*), the local Herb Paris (*Paris quadrifolia*), the Broad-leaved Helleborine (*Epipactis helleborine=E. latifolia*), the Moschatel (*Adoxa moschatellina*) and the Spurge Laurel (*Daphne laureola*) (Pl. XV). Some of these are commoner in the Ashwoods on the limestone than in the Beechwoods on the chalk.

The Beechwoods upon the chalk are the classical home of the snail *Helicodonta obvoluta* and here too occurs *Ena montana* both perhaps associated with ancient woodlands and this appears to be true also for the Slug *Limax cinereoniger*, which is more especially found in Beechwoods. *Limax arborum* also associated with ancient woodlands is less restricted to beechwoods. The subterranean *Caecilioides acicula* here finds its chief home as also the small *Pupa secale*. In the damp calcareous woods on the chalk of the south *Clausilia rolphii* is sometimes locally frequent and almost as characteristic there as *C. cravenensis* on the limestones of Westmorland and Yorkshire. The chalk scrub is the especial home of the strongly keeled snail *Helicigona lapicida*.

VI

BIOLOGICAL NOTES ON PLANTS OF THE BEECHWOOD

Fagus sylvatica	Beech
Monotropa hypopitys	Bird's-nest (Pl. XIV)
Neottia nidus-avis	Bird's-nest Orchid (Pl. XVI)
Lithospermum purpureo-coeruleum	Blue Gromwell (Map, Fig. 15, p. 43, Pl. XXI)
Epipactis helleborine	Broad-leaved Helleborine
Platanthera chlorantha	Butterfly Orchis (Pl. XVI)
Dentaria bulbifera	Coral Root (Map, Fig. 15, p. 43)
Mercurialis perennis	Dog's Mercury
Luzula forsteri	Drooping Rush (Map, Fig. 15, p. 43)
Paris quadrifolia	Herb Paris
Daphne mezereum	Mezereum (Map, Fig. 14, p. 41)
Allium ursinum	Ramsons
Helleborus foetidus	Setterwort (Pl. XV)
Polygonatum odoratum (officinale)	Solomon's Seal (Map, Fig. 42, p. 147)
Daphne laureola	Spurge Laurel (Pl. XV)
Lactuca muralis	Wall Lettuce
Sorbus aria	White Beam
Cephalanthera damasonium	White Helleborine
Hordeum sylvaticum	Wood Barley (Pl. X)
Sanicula europea	Wood Sanicle
Oxalis acetosella	Wood Sorrel
Asperula odorata	Woodruff
Taxus baccata	Yew (Pl. XIII)

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RAMSONS, *Allium ursinum*. Liliaceae. 2n = 14.

This garlic has a short, erect underground stem, and the bulb consists of a single fleshy scale. The bulb is situated only a short distance below the surface. The few fleshy roots penetrate to some 4–6 ins. (10–15 cms.). The umbel of star-like white flowers is borne on a triangular stalk and flowering takes place from April to May, when the flowers are visited by various insects for the nectar they secrete. Each three-lobed capsule commonly contains from three to six rounded black seeds (*ca.* 0·0065 gm.) that are shed in late June or July and germinate freely (*ca.* 70%) in April, sometimes more than a year after being shed.

The dark green broadly lanceolate leaves exhibit a torsion of the stalk owing to which the blade is completely inverted.

Common in damp woodlands, especially those of Ash, on calcareous soils and also in limestone pavements this species is sometimes abundant also in the flushes and at the foot of slopes in woodlands on so-called 'non-calcareous' soils.

WOODRUFF, *Asperula odorata.* Rubiaceae. 2n=44.

An evergreen perennial spreading by means of shallow stolons, often forming extensive colonies. 'Leaves' in whorls of usually six to nine of which two only, the true leaves, have axillary buds. The white slightly fragrant flowers, about 5 mm. in diameter, contain nectar.

Two glucosides are present of which one, on hydrolysis, yields coumarin (cf. *Bull. Soc. Chem. Biol.*, 1,009, 1925) which gives the plant the characteristic smell of 'new-mown-hay' when it is dried.

The fruits are beset with hooked bristles and by this means are dispersed on the fur of animals and the clothes of man. Germination occurs in Spring.

WHITE HELLEBORINE, *Cephalanthera damasonium* (=*C. pallens* Rich). Orchidaceae. 2n=36.

A perennial herb with a short woody rhizome and deeply penetrating roots. The erect stem, which is usually from 6–18 ins. high (15–45 cms.) and angled, bears several smooth leaves, the lowest ovate and becoming narrower towards the top, where they are lanceolate with prominent parallel veins and of a greyish-green colour. The large flowers, usually numbering from three to eight, are creamy-white and scentless. Normally self-pollinated, it sets fruit freely and a single capsule may contain many thousand seeds but vegetative multiplication by root-buds also occurs.

Its continental distribution is from southern Sweden to North Africa and Asia Minor, and in conformity with its southern-continental character it does not extend north of Cumberland in Britain. A plant of wood margins where the soil is shallow.

SPURGE LAUREL, *Daphne laureola.* Thymeliaceae. (Pl. XV)

An evergreen shrub with leathery leaves about 3 ft. high (92 cms.) that grows in shadier situations than its deciduous relative, doubtless because its evergreen habit enables it to benefit by the high light intensity between the time of shedding of the tree

leaves in autumn and the expansion of the Beech buds in spring, whenever the temperature of the air is adequate for photosynthesis. The faintly scented flowers, which are green, are of two kinds, some being male and others hermaphrodite. The latter give place to black fruits which are very poisonous as they contain, together with the foliage, a toxic glucoside. Each fruit contains a single hard seed. Germination is normally rather poor.

The Spurge Laurel is a southern-continental type which is absent as a native plant from both Scotland and Ireland.

MEZEREUM, *Daphne mezereum*. Thymeliaceae. 2n = 18.

A deciduous shrub attaining to a height of about 5 ft. (1·5 m.) and producing its pale purple, sweetly-scented flowers before the new leaves expand in March or early April. The flower rudiments destined to mature the following February are already differentiated by June. The red berries which ripen in July are highly poisonous, they contain a single seed, and germination, which is good, begins to take place in the spring of the year following that in which they are shed, and subsequent germinations may spread over two years. The young shrub flowers in about its fifth year. H. Heilig (*Zeit. f. Bot.*, pp. 225–79, 1931) records osmotic pressures for this species of from 10 to 11 atmospheres, and rooting depths of from 30–35 cms. (12–14 ins.). It is very intolerant of injury to its root system. The present rarity of this species as a wild plant in Beechwoods is largely due to vandalism, but it once occurred in fourteen counties or vice-counties (cf. map, p. 41).

CORAL ROOT, *Dentaria bulbifera*. Cruciferae. 2n = 96.

A perennial with pinnate basal leaves and an inflorescence, about 12–18 ins. (30–45 cms.) high, bearing pale lilac flowers and a few stem leaves in the axils of which are produced dark-purple, almost black, bulbils by means of which the plant reproduces itself. Although the flowers sometimes form pods any seeds they may contain are normally sterile, moreover, early removal of the bulbils appears to have no effect on seed production. The horizontal white underground stem is situated at about 7–8 cms. depth and bears small, fleshy, trilobed leaves and simple roots, the annual increments of the shoot are from 2–25 cms. (*ca.* 1–10 ins.)

A species of central Europe confined in Britain to the south-east. See map, p. 43. Its most westerly occurrences are in Staffordshire and south Devon.

BROAD-LEAVED HELLEBORINE, *Epipactis helleborine=E. latifolia.* Orchidaceae. 2n=38.

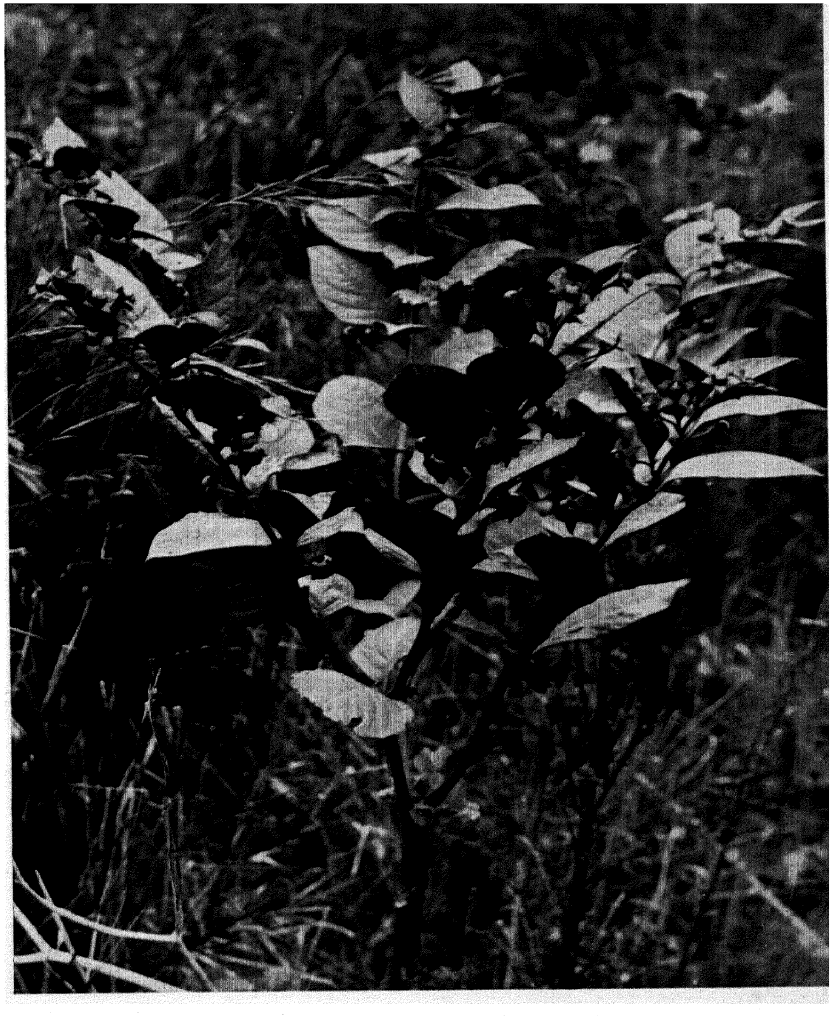
An orchid with a short thick rootstock and numerous fleshy roots and bearing one, or sometimes more, flowering stems about 1 to 2 ft. (30-60 cms.) in height with several broadly oval dull green leaves below and a number of usually reddish-green flowers above. The ovary is asymmetrically pear-shaped and pollination is effected by wasps. Plants flower at the age of from eight to nine years. Though not confined to chalky soil this orchid is commoner in the beechwoods than elsewhere.

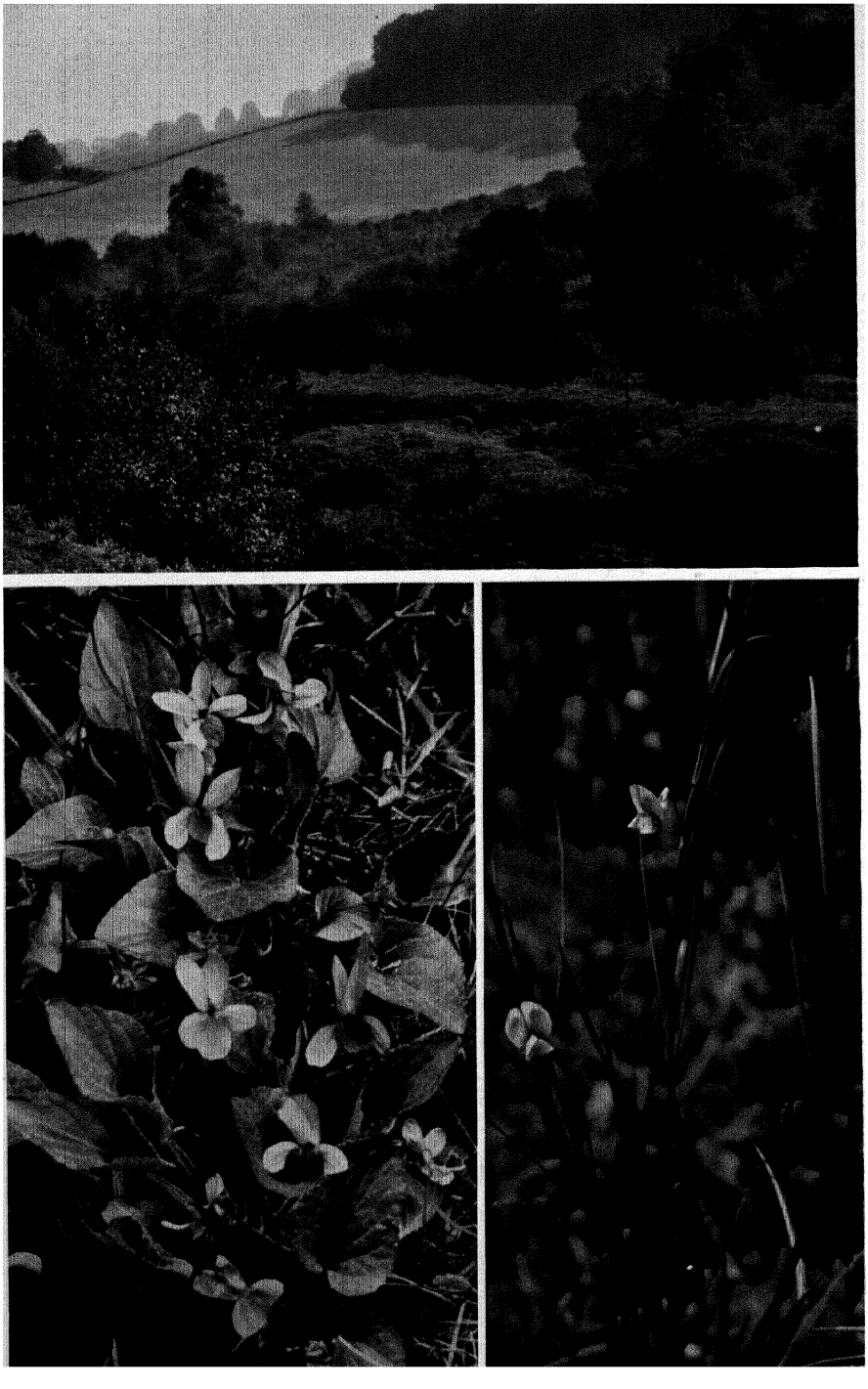
BEECH, *Fagus sylvatica.* Fagaceae. 2n=24.

A deciduous tree that can attain to over 100 ft. (30 m.) and normally lives to about 200 years. The oval leaves are bordered with silky hairs when they first expand. Their arrangement either radially, as on the erect shoots, or more or less in one plane, as on the lateral shade shoots, is largely dependent upon the stimulus of gravity (cf. Lundegardh, *Svensk. Bot. Tid.*, 438, 1916). Young trees and coppiced shoots frequently retain their dead leaves until leaf expansion in spring and such often produce early autumn shoots ('Lammas shoots') after about three weeks' rest in summer. The winter buds are protected by stipular bud-scales. The horizontal disposition of the buds on the lateral shade shoots is responsible for the deep shade cast by the twigs in winter and the completeness of the leaf mosaic in summer. Riegler found that of the rain that falls upon the Beech foliage about 22% was evaporated from the leaves and some 13% reached the soil by running down the branches and trunk. The root-system is shallow. The triangular nuts weigh about 0·23–0·26 gm. They contain about 14% by weight of oil. Germination (*ca.* 50%) is intermittent in spring and the seedling is characterised by the two broad, leathery

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PLATE XI. Deadly Nightshade (*Atropa belladonna*) in fruit. The inflorescences on the left are those of the coarse grass (*Brachypodium pinnatum*). Chalk scrub, Winchcombe. ×*ca.* $\frac{1}{5}$.





cotyledons that persist for some months, and the succeeding two foliage leaves are paired. Those formed subsequently occur singly. The dead leaves lose about half their nitrogen before being shed, but contain a considerable proportion of calcium, so that the annual surface dressing of leaves tends to retard the leaching process of the soil.

SETTERWORT, *Helleborus foetidus*. Ranunculaceae. 2n=32. (Pl. XV)

A short-lived perennial about 2 ft. (60 cms.) high with characteristic foliage which emits a foetid smell when crushed, is rather leathery and persists till the new leaves are formed in March and April. The evergreen character permits full advantage to be taken of warm conditions throughout the period (light phase) when the Beechwoods and Ash woods, where *H. foetidus* occurs, are devoid of leaves. Despite its woodland habitat, *H. foetidus* can apparently develop very high suction forces. F. J. Molz records a range of from 6 to 66 atmospheres for this species (*Amer. Journ. Bot.*, XIII, p. 456, 1926).

The green flowers flushed with purple are scented and attract insects by the nectar secreted in the tubular petals. This secretion acts as an osmotic pump and by removal of water from the adjacent stamens can bring about dehiscence of the anthers even in a saturated atmosphere.

Seeds (*ca.* 0·009 gm.) are copiously produced and germinate freely in spring. The contents of each follicle is shed as a single elongate mass. The seeds are dispersed by ants (cf. T. A. Dymes, *Journ. Linn. Soc.* (*Bot.*), XLIII, p. 435, 1916).

A southern species on the Continent, it is in Britain confined to the south-eastern counties except as an escape.

The whole plant is poisonous, chiefly due to the glucoside, helleborin.

The Green Hellebore, *H. viridis*, also occurs in Beechwoods and in Ashwoods on limestone, but attains its greatest abundance in Oakwoods on heavy basic soils.

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PLATE XII. ABOVE. Three stages in plant succession on the chalk. In the foreground chalk pasture; in the middle distance chalk scrub; Beech hangers on the brow of the slope. BELOW. Two Chalk-scrub species. The Hairy Violet (*Viola hirta*) on the left and, on the right, the Grass-leaved Vetch (*Lathyrus nissolia*). Both nearly life-size.

WOOD BARLEY, *Hordeum sylvaticum*. Gramineae. 2n=28. (Pl. XIII)

An erect perennial and tufted grass with broad flat, vivid green leaves and a very short rim-like ligule The sheaths of the lower leaves have backwardly directed hairs whilst the upper sheaths are smooth. The green awned spike is 2 to 4 ins. in length (5–10 cms.) borne on stems up to 3 ft. tall (90 cms.) and consisting of two rows of three-flowered spikelets the lateral members of which are bisexual and the median flowers male. The grains weigh from 0·004–0·007 gm. and a single spike produces from 40–60.

Frequent in better-lighted parts of Beechwoods on the chalk of the Chilterns and the limestone of the Cotswolds, as also the Ashwoods of the northern limestones, this grass seems, like the mollusc *Ena montana*, to be associated with Beechwoods that are lineal descendants of primitive forest.

WALL LETTUCE, *Lactuca muralis*. Compositae. 2n=18.

Commonly biennial, but sometimes perennial, as is shown by the bases of flowering shoots of former seasons on some large plants. The smooth leaves, glaucous and sometimes purplish on the underside, with their triangular terminal lobes as well as the tall inflorescence (up to 3 ft.=90 cms.) of slender, spreading branches bearing small yellow flower heads, are characteristic features. Each head produces an average of five black ribbed fruits (up to fourteen).

A species of well-drained habitats which attains to greatest abundance in clearings and near the edges of calcareous woodlands.

BLUE GROMWELL, *Lithospermum purpureo-coeruleum*. Boraginaceae. 2n=16. (Pl. XXI)

A perennial with narrowly lanceolate hairy leaves about 2 ins. (5 cms.) long, growing about 1 ft. high and spreading by means of barren arched shoots up to about seven in number, which may attain to over 32 ins. (80 cms.) in a season. These runners root at the tip and subsequently give rise to erect flowering shoots from the base of which new barren 'runners' are developed in the autumn. The flowers are a brilliant blue-purple in colour about 18 mm. in diameter. Usually not more

than one or perhaps two nutlets are formed from a flower. These are almost spherical, hard, highly polished and of a milky-white colour. New leaves are formed at the end of March or early April.

Germination which is intermittent occurs in autumn and spring and may even extend over several years. This is a continental-southern species which reaches as far north as Belgium, and in Britain is found locally from South Wales to Kent, being most frequent in the scrub of woodland margins on the limestone (cf. map, p. 43).

DROOPING RUSH, *Luzula forsteri*. Juncaceae. 2n=24.

A perennial with a tufted evergreen habit distinguished from the common Woodrush (*L. pilosa*) by the drooping inflorescence and the absence in fruit of the reflexed branches that characterise *L. pilosa*. Also distinguished by the tapering apex of the capsule which is broad and blunt in *L. pilosa*.

L. forsteri is an oceanic species of the European flora which is confined to the southern part of England and Wales (cf. map, p. 43) and is generally commoner on the limestones of the west than on the chalk of the eastern counties. The black seeds (0·001–0·003 gm.) bear a short arillar appendage that renders them attractive to ants, which assist in their dispersal.

DOG'S MERCURY, *Mercurialis perennis*. Euphorbiaceae. 2n=64. (Fig. 23, p. 87)

A summer-green perennial with branching rhizomes at a shallow depth bearing roots that usually penetrate to 10–15 cms. (4–6 ins.), sometimes to 30 cms. The leaves will expand in mid-January if the season be mild and may remain till November, so that a considerable part of the 'light phase' may be utilised for food synthesis. Male and female flowers occur on separate plants. Fruiting is sparse. The seeds which ripen in May (*ca.* 0·008 gm.) are dispersed by the explosive rupture of the fruits to a distance of from 3–4 m. (*ca.* 10–13 ft.). Many seeds are not viable, the germination ranging from 1–10% (av. 5%). Seedlings, which are usually hypogeal, appear from February to April. Extension is normally by growth of the rhizomes with an average annual rate of spread of 4–6 ins. (10–15 cms.), which gives rise to the extensive stretches of this social

species that is more abundant in calcareous woodlands than elsewhere (cf. S. K. Mukerji, *Journ. Ecology*, XXIV, pp. 38–81, 1936). The shoots contain a chromogen which can by oxidation produce a permanent blue pigment or a fugitive blue passing to permanent yellow (cf. Haas, and Hill, *Biochemical Journal*, p. 233, 1925). The young shoots emerge as bent structures that on reaching the light are stimulated to straighten out.

BIRD'S-NEST, *Monotropa hypopitys*. Ericaceae. 2n=16, 48. (Pl. XIV)

A fleshy, cream-coloured saprophyte with numerous roots and a stout stem bearing oblong scale leaves below and a bent inflorescence above of usually a small number of pendant flowers which are visited by insects for the nectar. M. Mobius (*Flora*, p. 399, 1918) showed that the orientation of the shoot was largely a response to the stimulus of gravity.

After fertilisation the response to gravity changes and the fruit stalks become erect. Each capsule splits open longitudinally along the five chambers. The numerous seeds, about 2,000 or more, in each capsule, are quite small with a central body and a loose net-like testa at both ends.

The plant contains an endotrophic mycorrhiza. From investigations carried out by H. L. Francke (*Flora*, 129, 1, 1935) he concluded that this association of the flowering plant and fungus is an essential one. Sterile seeds failed to germinate but in the presence of the fungus germination occurred, albeit a low proportion (0·3–0·5%). The development of haustoria in the host is greatest when the Bird's-nest is growing most vigorously—namely, September and October. The fungus is probably a *Boletus* and appears to grow most readily at a reaction of pH 5.

The seeds of *Monotropa*, which weigh only 0·003 mgms., contain an endosperm of only nine cells and an undifferentiated embryo of only three cells.

The species is widely distributed in the north temperate regions of both hemispheres.

BIRD'S-NEST ORCHID, *Neottia nidus-avis*. Orchidaceae. 2n=36. (Pl. XVI)

A brown-flowered saprophyte which occasionally in clearings will produce chlorophyll in its leaves. Normally it is a

deep-shade species occurring where there is ample pabulum of dead leaves. There is a very short rhizome bearing numerous fleshy roots which contain persisting mycorrhizal hyphae in the middle cortex. The plant is perennial, one or sometimes two buds being formed at the base of the flowering stem. Vegetative multiplication can take place by means of adventitious buds upon the roots. The honey-scented flowers are visited by flies, and fruits are freely produced.

The species occurs on the Continent from Scandinavia and mid-Russia to Spain and the Urals. It occurs through the British Isles, except in the extreme north of Scotland. Bernard (*Rev. Gen. Bot.*, 1902) states that plants flower in from seven to eleven years after germination.

Wood Sorrel, *Oxalis acetosella*. Oxalidaceae. 2n=22.

Although common in other types of woodlands, the Wood Sorrel is particularly characteristic of certain types of shady Beechwoods owing to its great tolerance of low light intensity, growing freely where the illumination is only 1/300 of that in the open.

The slender, shallow rhizome exhibits regions of elongation, alternating with regions of slow growth. The latter are associated with the formation of foliage leaves and flowers. The leaves consist of three leaflets that move together at night. The surplus food they form is stored in the swollen leaf base from which the leaf stalk is subsequently shed. Thus the portions of rhizomes which have short internodes exhibit crowded leaf bases that collectively provide a store of food at the expense of which new growth is made in spring. The beautiful white flowers with purple veins of early spring are followed by inconspicuous flowers that do not open, but produce seeds by self-fertilisation. The fruit stalk at first bends down but straightens towards maturity. Three days before the seed is ripe there is a rapid swelling of the fruit stalk as a result of a localised conversion of starch to sugar, and the content of water is doubled. (cf. Troll, *Flora*, p. 344, 1924). This in turn leads to a swelling of the soft covering (aril) of the seed and when the fruit splits the turgor of the aril causes it to turn inside out, ejecting the seeds, which weigh 0·0024 gm., with violence.

The vegetative extension by rhizome growth averages about 7 cms. per annum.

HERB PARIS, *Paris quadrifolia*. Liliaceae. 2n=20. (Fig. 35, p. 135)

A perennial herb with a shallow (7–10 cms.) horizontal underground stem. From this arise the upright shoots, each bearing a whorl of normally four (rarely three to six) oval leaves of a dark green colour with five prominent veins, parallel to the entire margin, and net-veined between. The epidermal cells in outline, and the stomata in arrangement, are irregular, thus resembling a Dicotyledonous plant. The epidermal cells contain chloroplasts. The solitary green flowers usually have parts in fours and the four-celled ovary develops at maturity into a bluish-purple berry containing numerous (about 28) rather kidney-shaped seeds about 2·5×1·5 mm. and weighing approximately 0·004 gm., but like many other woodland species, fruiting is infrequent. The seeds are distributed by birds, but are also alleged to be dispersed by ants.

The roots contain an endotrophic mycorrhiza.

BUTTERFLY ORCHIS, *Platanthera chlorantha*. Orchidaceae. 2n=42. (Pl. XVI)

An unmistakable rather tall orchid of the moister situations in partial shade in Beechwoods. Commonly between 9 and 18 ins. tall (22–45 cms.) with two to three oblong leaves at the base; these arise from a pair of unlobed tubers. The inflorescence is a lax spike of from ten to twenty greenish-white flowers that emit a strong sweet scent, especially at night, and bear long spurs (*ca.* 3 cms.) which from their frequently horizontal orientation give a characteristic appearance to the inflorescence. The flowers are pollinated by moths and fruiting is common.

SOLOMON'S SEAL, *Polygonatum odoratum* (*officinale*). Liliaceae. 2n=20.

A perennial with a fleshy sympodial rhizome producing arched and *angled* stems from 6–12 ins. high (15–30 cms.) bearing two rows of oblong, pointed rather leathery leaves and firm, pendent greenish-white flowers, most often solitary but rarely two or three together. Flowering is not infrequently sparse. The berries are blue-black when ripe and contain from two to seven seeds (*ca.* 0·04 gm.), though large patches of

this plant are often sterile. Germination is hypogeal. Apart from its doubtful occurrence in Kent, its distribution in Britain is in the higher rainfall areas (cf. map, p. 147).

The much larger *P. multiflorum* (Pl. VII) has *round* stems and the pendent flowers are normally in groups two to five in number. The chromosome number of this species is apparently very variable, as 2n=18, 20, 28 and 30 have all been recorded. The leaflets of both species have a large apical water-pore.

SANICLE, *Sanicula europea*. Umbelliferae. 2n=16. (Fig. 22, p. 87)

A winter-green perennial with simple lobed leaves and simple umbels of small flowers. Roots to depths of over 11 cms. Osmotic pressures of 6·8–7·7 atmospheres were recorded by Heilig.

The fruits bear hooked bristles and are dispersed on the coats of animals and often on the clothes of man. Germination occurs in spring.

WHITE BEAM, *Sorbus aria*. Rosaceae. 2n=34.

A deciduous tree that may attain to 40 ft. (12·3 m.) or more, with oval leaves which have a doubly serrate margin and are white underneath. The flowers are in creamy-white clusters and give place to oval bright red fruits about ½ in. (1·25 cms.) long which contain two or three, rarely up to six, seeds each weighing about 0·03 gm. The buds are protected by stipular bud scales.

The White Beam is a tree with deeply penetrating and widely spreading roots from which shoots may arise. Apomictic strains are known.

YEW, *Taxus baccata*. Taxaceae. 2n=24. (Pl. XIII)

An evergreen tree of slow growth attaining about 15 ft. (4·5 m.) in twenty years and 30–40 ft. (9–12 m.) or more at maturity. Root shoots commonly develop around the main trunk with which they may fuse and this 'clustered-column' effect has resulted in exaggerated estimates of the ages of old trees. The male and female flowers are normally borne on separate trees. The seed is surrounded by an aril which is pink, mucilaginous and sweet and when ripe the fruits are largely disseminated by birds. Germination occurs in part in the

spring after the fruits are shed but mostly in the second year or sometimes even in the year following.

The foliage of the yew is poisonous due to an alkaloid taxine, but some of the fatalities from the eating of yew by cattle and horses appear to be associated with the consumption of withered foliage and are alleged to be due to perforation from the needle-like apices of the withered leaves.

The Yew can attain a great age, probably 800 years or more and thus outlives the Beech with which it is associated. Osmotic pressures of the sap of as much as 32 atmospheres have been recorded. It is resistant to frost except when accompanied by sunshine as it is susceptible to winter drought. The terminal buds of the Yew are frequently galled by the larvae of *Cecidomyia taxi* which produce the cone-shaped structures at first that later become the familiar rosette-like terminations to the affected shoots.

VII

SCRUB AND CORNFIELDS OF THE CHALK

COLONISATION AND SUCCESSION ON THE CHALK

THE pioneer plants on bare chalk vary in no small degree with the facilities of colonisation depending on the proximity of seeding vegetation. But apart from such accidental circumstances the first plants to appear are often non-flowering plants, such as mosses. Of these the minute *Seligeria calcarea*, only 1–3 mm. in height, is sometimes common on bare chalk in the southern and eastern counties, often covering extensive patches on the vertical face of chalk cliffs, where its dwarf shoots of deep green leaves occupy small pits in the surface, doubtless the outcome of the solvent action of the H_2CO_3 resulting from the respiration of the moss. Other and much larger pioneer mosses are the yellowish green *Camptothecium lutescens* and *Hypnum molluscum*, whilst at a somewhat later stage the beautiful *Neckera crispa* is characteristic, though rather local and *Hypnum swarzii* and *H. chrysophyllum* are frequent.

The jelly-like lumps of a greenish hue often conspicuous on chalk slopes as well as in the early stages of colonisation of level ground is the blue-green alga *Nostoc*, which under the microscope is seen to consist of necklace-like contorted chains of blue green round cells embedded in the jelly-like matrix.

The pioneer grasses are often of tufted habit, especially the Sheep's Fescue (*Festuca ovina*) and the annual *Scleropoa rigida* (*Festuca rigida*). The Quaking Grass (*Briza media*) and *Koeleria gracilis* both of tufted habit, often appear quite early in the process of colonisation although more characteristic of the later phases.

In the succession of plants, which appear with the passage of time, several of rapidly spreading habit often play a conspicuous part. Of these the most important are the Bent Grass (*Agrostis stolonifera*), which roots freely at the joints of its prostrate branches, the Glaucous Sedge (*Carex flacca*) that extends beneath the surface in a similar manner, the Red Fescue (*Festuca rubra*) and such quickly colonising plants as the Colt's-foot

(*Tussilago farfara*), the Bird's-foot Trefoil (*Lotus corniculatus*) and the Wild Strawberry (*Fragaria vesca*). With the continued leaching of the soil, the prevalence of Sheep's Fescue usually gives place to a dominance of the Red Fescue and the erstwhile open community becomes a closed turf. It is usually at this later stage when a definite soil has been formed that the Chalk Brome (*Bromus erectus*) and the False Brome (*Brachypodium pinnatum*) appear, their success depending on the intensity of grazing. If the latter be slight these coarser grasses flourish and the advent of seedling shrubs and trees is not precluded. The rapid spread of the latter grass during the last twenty-five years is especially due to the diminished grazing by sheep.

The development of seedling shrubs, particularly Hawthorn (*Crataegus monogyna*), which is the commonest pioneer, initiates and leads to the establishment of chalk scrub (Pl. XII). This scrub at first consists of scattered shrubs with open herbage between, but with the lapse of years, especially with the advent of Brambles and Roses, such as the Sweet Briar, *Rosa rubiginosa*, which is the most characteristic rose, may pass into an almost closed thicket. Apart from the almost ubiquitous Hawthorns, the most frequent shrubs include the Hazel (*Corylus avellana*), the Elder (*Sambucus nigra*), the Dogwood (*Cornus sanguinea*) and in some areas the Juniper (*Juniperus communis*) none of which are confined to the chalk, though commoner there than elsewhere. All but the Hazel, be it noted, have fleshy fruits and their dispersal is dependent upon animals.

More characteristic but often less common are several shrubs whose conspicuous fruits provide a brilliant spectacle against the background of their autumn tints. The Spindle (*Euonymus europaeus*) with its beautiful pink fruits splitting open to expose the seeds surrounded by their golden arils; the black-fruited Privet (*Ligustrum vulgare*), a far more attractive shrub than the cultivated species; the Wayfaring Tree (*Viburnum lantana*) with its scarlet fruits and the orange and yellow of the foliage that earlier in the year was green in colour and mealy in texture, providing a vivid contrast to the clustered black berries of the Purging Buckthorn (*Rhamnus catharticus*), the food plant of the larvae of the beautiful Brimstone butterfly that gladdens our eyes in spring. The White Beam (*Sorbus aria*) is also a characteristic feature, but usually appears at a late stage, when the scrub is passing into woodland; and this is true also of the

Maple (*Acer campestris*) and the Gean (*Prunus avium*). So too the very local Box (*Buxus sempervirens*), which gives its name to Box in Wiltshire and Box Hill in Surrey as well as Boxmoor in Hertfordshire, is perhaps to be regarded more as a member of the shrub layer of the Beechwood, which indeed is its more usual continental status, than as a constituent of the scrub. The great demand for boxwood by the blockmakers of the past when woodcuts were the vogue may perhaps account in part for the very limited survival of the Box at the present time.

The Juniper tends to be abundant on shallower drier soils and more exposed situations than where Hawthorn predominates, and can ultimately produce more sheltered conditions because of its evergreen habit, and in its shelter the Yew (*Taxus baccata*) may colonise; but some of the dense Yewwoods that still remain may perhaps represent survival of the second layer of Beechwood from which the Beech trees have perished.

It is worthy of note that most of these shrubs have fleshy fruits, and distribution of the seeds by birds plays a not inconsiderable part in effective colonisation. The stage at which seedling trees such as Ash, Oak and Beech appear is largely determined by the intensity of grazing and depth of soil. Where the grazing of old chalk downs was intense, young Oak seedlings could often be seen which had been prevented from developing by the feeding of the sheep and rabbits.

The passing from grassland to scrub is naturally encouraged by a favourable water supply as well as by a low intensity of grazing. Thus on many downs we can see scrub to have developed in the valley bottoms and on the valley slopes because here there is drainage water from above, a considerable degree of shelter from drying winds and, owing to the angle of slope, the amount of grazing is less. But as the scrub grows in height and density it creates more shelter at the periphery and so creeps upwards till, if unhindered, the open down will itself revert to the condition of woodland that obtained in prehistoric times. Indeed, when exposed downs have been enclosed by wire netting to exclude the ubiquitous rabbit, the absence of the browsing animal and the partial shelter, which even wire netting provides in a degree much greater than one might suppose, combine to enable scrub to develop quite rapidly. The depth of penetration of the fractured chalk by the roots of the shrubs and the CO_2 which these produce whilst

alive, the humus which they form when they decay, assist in accelerating the increasing depth and rapidity of soil formation.

Amongst the characteristic herbaceous species of the chalk scrub is one that attains the dimensions of a shrub—namely, the Dwale or Deadly Nightshade (*Atropa belladonna*), a handsome plant conspicuous alike when in flower, bearing its dull purple and green bells, and even more when these give place to the bright black luscious-looking but poisonous berries (Pl. XI). It owes its poisonous properties to the presence of the alkaloid atropine ($C_{17}H_{23}O_3N$), which occurs throughout the plant, but does not in fact protect it from browsing rabbits, which appear to eat its young shoots with impunity. The large size of the annual growth of this herb is rendered possible by reason of the bulk of food reserves stored up in the fleshy branched tap-root. This is true also of the White Bryony (*Bryonia dioica*) the bulky, often forked, root of which was once sold as a substitute for Mandrake. Two frequent climbers of the chalk scrub, are herbaceous, the White Bryony, a member of the Cucumber family, which its leaves resemble, and the Black Bryony, which is the sole European representative of the essentially tropical Yam family. Others are woody, such as the Honeysuckle (*Lonicera periclymenum*), the Bitter Sweet (*Solanum dulcamara*), with flowers like those of the potato, and the Wild Clematis or Old Man's Beard (*Clematis vitalba*), all, however, occur in other types of scrub on diverse types of soil, but especially on such as are well supplied with bases; and it is noteworthy that in soils poor in bases the Bitter Sweet tends to occur in the hollows, or even in water, where the soil is enriched by the bases leached from the higher ground.

Most of the more characteristic herbaceous species here, as in chalk grassland, are of restricted distribution. For instance, the Gromwell (*Lithospermum officinale*), with its greenish flowers and shining hard white fruits, due to the presence of calcium in the seed coat, the Wild Liquorice (*Astragalus glycyphyllos*), with its curious greenish-white pea-like flowers, the Wild Columbine (*Aquilegia vulgaris*), the dainty Meadow Rue (*Thalictrum collinum*) and the beautiful semi-parasitic Red Cow-wheat (*Melampyrum cristatum*), with its crested bracts and yellow and red flowers—all these are local, whilst the last-named is quite erratic in its occurrence; though not exclusively found on the chalk, they appear to be normally restricted to lime-rich soils.

Some very rare species are only to be found in chalk scrub, such, for example, as the Lady Orchid (*Orchis purpurea*). On the other hand, plants that we shall almost always find in the chalk scrub, such as Ploughman's Spikenard (*Inula conyza*), the Hairy St. John's Wort (*Hypericum hirsutum*), the aromatic Marjoram (*Origanum vulgare*), the Black Mullein (*Verbascum nigrum*), the Nettle-leaved Bell-flower (*Campanula trachelium*) (Pl. V), the Crosswort (*Galium cruciatum*), the Cranesbill (*Geranium columbinum*) and the Spotted Orchis (*Orchis fuchsii=maculata*), though commoner here than elsewhere, are none of them confined to this habitat.

In time of scarcity, as during the great wars, the shallow soils overlying the chalk have been ploughed up sometimes to yield so poor a cereal crop that they have very soon been permitted to revert once more to the untended state. Such circumstances obtained during the Napoleonic Wars and again under the stimulus of grain shortage during the two world wars. One such area which was ploughed up by an optimist, without the stimulus of abnormal prices, about 1900, has remained derelict ever since and furnished an admirable example of the succession of phases in the colonisation of chalk soil. At first the erstwhile arable became colonised with grasses, and Wild Strawberries were abundant, though cornfield weeds persisted in the more open vegetation for some years. Soon, however, young Hawthorns, Dog Roses, Dogwood, Spindle and other shrubs appeared, constituting a very open scrub, and the shelter thus established as well as the protection from browsing created a favourable environment for the species characteristic of wood margins and hedgerows, so that some thirty-five years after cultivation had ceased no less than 125 different kinds of flowering plants were found by the author growing on this area. After the lapse of fifty years much of the area had almost attained the status of woodland, with a marked increase of the more shade-loving species and a diminution over most of the area of the light-demanding species, now driven to the better illuminated periphery of the sides of trackways. But though the succession has proceeded full circle in the sense that the area long since open has gone back to the phase we term 'woodland,' a type of plant community it no doubt bore in prehistoric times, it is a very different woodland from those we regard as lineal descendents of primitive forest, quite apart from the absence of

ancient trees. How long a period of years must elapse for the processes of soil development and maturation of the community of plants and animals to reach that state of fluctuating equilibrium with the physical environment that we term the 'climax community' is unknown. Certain it is, however, that even after the lapse of centuries the artificial Beech plantation, though superficially resembling a semi-natural Beechwood, is in some respects distinguishable from the latter, particularly in the absence of certain species of animals such as the slugs *Limax cinereo-niger* and *Limax arborum* and local plants, such as the Solomon's Seal and Wood Barley, despite the apparently favourable facilities for colonisation by such.

WEEDS OF THE CHALK AND OTHER CALCAREOUS SOILS

The plants that spontaneously appear on the cultivated calcareous soils, be it of gardens or of arable fields, often include those we find as pioneers in the early stages of colonisation of bare untilled soils. Both situations alike have this in common, that the degree of shading of one plant by another is slight and in other respects there is but little competition. Whereas, however, a garden or arable field on chalk or limestone usually has a fair depth of soil, this, in early stages of colonisation, is initially quite shallow. On the other hand, the later stages of the succession, when a soil has developed, usually exhibit a stratification that may be advantageous (cf. p. 18), whereas the homogeneity of the tilled soil sometimes leads to nutrient deficiencies.

If we go into a cornfield on the chalk we shall most likely find a common and characteristic yellow-flowered weed, the White Mustard (*Sinapis alba*), easily recognised by the distinctive pod, beset with spreading, bristly hairs and with a flattened beak almost as long as the portion that contains the seeds. Probably too we shall see the Wild Mignonette (*Reseda lutea*) with flower-heads similar to those of the garden Mignonette, but without its sweet scent. Equally a feature of these soils but less frequent are the pretty little purple-flowered Venus' Looking-glass (*Legousia hybrida*=*Specularia hybrida*), the Chalk Lamb's Lettuce (*Valerianella dentata*), the large-flowered Mouse-ear Chickweed (*Cerastium arvense*), the narrow-leaved Hemp Nettle (*Galeopsis angustifolia*), a yellow Pansy (*Viola anglica*) and locally the Cornfield Caraway (*Carum segetum*, Fig. 28).

The Wild Carrot (*Daucus carota*) is another frequent plant of chalky fields, but less restricted to them. Of common weeds that are often found on other soils, but are usually far more abundant on the chalk than elsewhere, mention must be made of the Field Scabious (*Knautia arvensis*), the Bladder Campion (*Silene inflata*), others of the yellow Pansies (*Viola agrestis* and *Viola variata*, to mention only the two commonest), the Shepherd's Needle (*Scandix pecten-veneris*), the small Toadflax (*Linaria minor*), and the Scarlet Pimpernel (*Anagallis arvensis*).

A weed of gardens in the same category is the little shining-leaved Cranesbill (*Geranium lucidum*). The Common Fumitory (*Fumaria officinalis*) and *Fumaria micrantha* are commoner on the chalk than elsewhere, but two of the small-flowered British species of this genus are practically confined to calcareous soils—namely, *F. parviflora* and *F. vaillantii*. Both are found mainly in the south-eastern counties, the latter with a more restricted distribution than the former, and both alike absent from Ireland. The most characteristic species of chalky cornfields are again rare or very local: such, for example, as the Red Chamomile (*Adonis annua=A. autumnalis*), once so common in the cornfields of Sussex and Surrey as to have been collected and sold in Covent Garden Market, but now a very local rarity. So too the Thorow Wax (*Bupleurum rotundifolium*)



FIG 27

FIG 26

FIG 26. Thorow Wax (*Bupleurum rotundifolium*) from a chalky cornfield (×½) showing seedling with root to depth of 9 in. (23 cm.). FIG 27. Flowering shoot showing the perfoliate leaves.

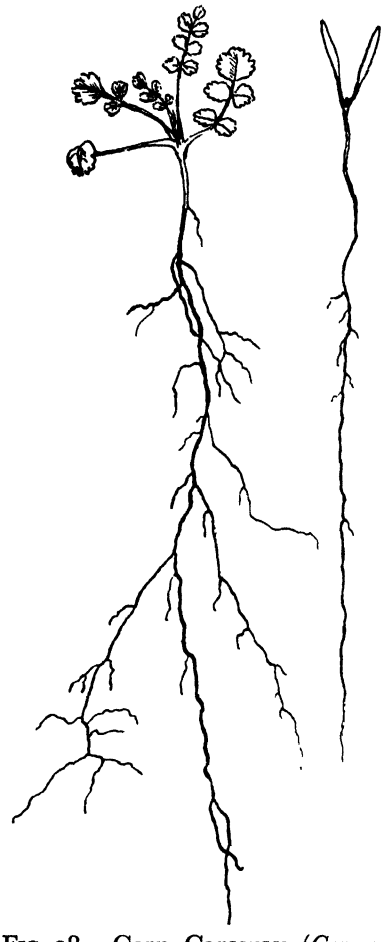


FIG 28. Corn Caraway (*Carum segetum*). Seedlings of two ages (×½). Note the early development and depth of the tap-root.

(Fig. 26), as its possession of a genuine vernacular name attests, was a not uncommon plant of the chalk, but now only to be relied upon to appear annually in a few localities. Again, the Earthnut (*Bunium bulbocastanum*, Fig. 43, p. 158), which is restricted to a few localities in four of our southern counties, is confined to calcareous cornfields. The annual Larkspur *Delphinium gayanum*, once a feature of the chalky fields of E. Anglia, is now a rarity.

The Night Catchfly (*Silene noctiflora*), looking rather like a white Campion with, however, yellowish flowers and sticky stems, is also a local plant that occurs on other types of dry soils. The Pawnbroker's Plant (*Galium tricorne*) is a rather local plant on calcareous soils and resembles a Goosegrass, with fruits commonly in groups of three, though these do not bear the hooked bristles of its congener. The Fluellen (*Linaria spuria*) and the Rough-headed Poppy (*Papaver hybridum*), though not confined to calcareous soils in the more strict sense, are probably always associated with soils that are well-drained and basic. Lastly we may mention the very rare *Teucrium botrys*, which is found on calcareous soils only (Pl. I).

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PLATE XIII. Beechwoods. BELOW. Beechwood with open canopy near Stroud, Gloucestershire, shewing herbaceous vegetation and trees of different age classes. The pale patches on the largest tree-trunks are the lichen *Parmelia caperata*. The grass in the foreground on the right is the Wood Barley (*Hordeum sylvaticum*). ABOVE. Beechwood on steep chalk slope in Kent showing Yew trees (*Taxus baccata*) forming a second tree layer. Associated with the low illumination there is almost no herb layer.









The Wild Candytuft (*Iberis amara*) and the Ground Pine (*Ajuga chamaepitys*, map, Fig. 13, p. 39, and Pl. I) sometimes grow in profusion in chalky cornfields, though the natural home of the former is probably the woodland margin and of the latter the early phase of colonisation. Mention should also be made of the semi-parasitic Cow-wheat (*Melampyrum arvense*), which formerly occurred in several areas on the chalk, but has become extremely rare. The Candytuft has white flat flower-heads similar to those of the garden annual and is not infrequent on the disturbed soil around rabbit burrows on the open down, but, in common with other pioneer annuals, it finds a congenial home in the artificially disturbed soil of the cornfield, the adverse period of cultivation being evaded in the seed stage. The Ground Pine, which is a yellow-flowered relative of the blue-flowered Bugle of our woodlands, is normally biennial and so more liable to destruction by winter cultivations.

* * *

PLATE XIV. The Beechwood flora. BELOW. Close canopy beechwood in Buckinghamshire in late spring showing absence of ground flora, and trees of definite age classes. ABOVE. Bird's nest (*Monotropa hypopitys*), a saprophyte of shady woods, Tring, Herts. × *ca.* ⅓.

GEOGRAPHICAL ELEMENTS OF THE SUCCESSION

	Pioneers (and Arable on Chalk)	Chalk Grassland	Chalk and Limestone Scrub	Chalk and Limestone Woodland
Oceanic	*Carum segetum*			
Southern oceanic		*Blackstonia perfoliata* *Helianthemum polifolium* *Phyteuma tenerum* *Polygala calcarea* *Thesium humifusum*	*Rubia peregrina*	*Iris foetidissima*
Northern oceanic		*Centaurium capitata*		
Southern continental	*Adonis annua* *Ajuga chamaepitys* *Aster linosyris* *Bunium bulbocastanum* *Bupleurum rotundifolium* *Galeopsis angustifolia* *Galium anglicum* *Legousia ybridah* *Papaver hybridum* *Teucrium botrys*	*Aceras anthopophora* *Althaea hirsuta* *Anacamptis pyramidalis* *Asperula cynanchica* *Briza media* *Hippocrepis comosa* *Himantoglossum hircinum* *Onobrychis viciaefolia* *Ophrys apifera* *Ophrys arachnites* *Ophrys aranifera* *Orchis simia* *Prunella laciniata* *Salvia pratensis* *Spiranthes spiralis* *Trinia glauca*	*Atropa belladonna* *Iberis amara* *Lithospermum purpureo-coeruleum* *Orchis purpurea* *Orobanche elatior*	*Buxus sempervirens* *Cephalanthera damasonium (pallens)* *Clematis vitalba* *Daphne laureola* *Tilia platyphyllos* *Viburnum lantana*
Continental	*Melampyrum arvense*	*Anemone pulsatilla* *Gentiana germanica* *Hypericum montanum* *Orchis ustulata* *Senecio integrifolius* *Seseli libanotis*	*Astragalus glycyphyllos* *Cynoglossum montana* *Orchis militaris* *Orobanche major*	*Dentaria bulbifera* *Fagus sylvatica* *Phyteuma spicata*
Northern continental		*Astragalus danicus* *Gentiana amarella* *Gentiana campestris* *Herminium monorchis*	*Hypericum hirsutum* *Melampyrum cristatum*	*Actaea spicata*

VIII

BIOLOGICAL NOTES ON CHALK SCRUB PLANTS

Rhamnus catharticus	Purging Buckthorn (Map, Fig. 15, p. 43)
Campanula trachelium	Canterbury Bell
Melampyrum cristatum	Crested Cow-wheat
Atropa belladonna	Deadly Nightshade (Map, Fig. 15, p. 43)
Stachys germanica	Downy Woundwort (Map, Fig. 15, p. 43)
Ophrys muscifera	Fly Orchis
Lithospermum officinale	Gromwell
Hypericum hirsutum	Hairy St. John's Wort
Viola hirta	Hairy Violet
Juniperus communis	Juniper
Orchis purpurea	Lady Orchid
Origanum vulgare	Marjoram
Inula conyza	Ploughman's Spikenard
Ligustrum vulgare	Privet
Euonymus europaeus	Spindle
Clematis vitalba	Traveller's Joy
Viburnum lantana	Wayfaring Tree
Astragalus glycyphyllos	Wild Liquorice

☆

WILD LIQUORICE, *Astragalus glycyphyllos*. Leguminosae. 2n=16.

A prostrate herbaceous perennial of wood margins and scrub on calcareous soils, where it has apparently decreased in frequency. The greenish yellow flowers are inconspicuous.

The root is stout and deeply penetrating (over 30 ins.=75 cms.) and the winter buds are situated on, or in, the surface layer. New leaves are usually fully expanded by the end of February. The seeds weigh *ca.* 0·0045 gm.

Though a continental type, it prefers moist conditions and except on the calcareous boulder clay of the eastern counties is most frequent in the limestone woods of the west and north.

DWALE or DEADLY NIGHTSHADE, *Atropa belladonna*. Solanaceae. 2n=72. (Pl. XI)

A tall perennial herb that attains to from 2–6 ft. (60–180 cms.). It dies down completely in winter and has a large, branched fleshy root from the summit of which the shoots arise about the end of March or early April. The massive dormant buds are situated in the soil with their tips at or just below the surface.

The downy leaves are located in pairs of unequal size. The whole plant is highly poisonous owing to the presence of the alkaloid atropine. This has apparently little or no effect on rabbits, which are a cause of the rarity of this plant in some areas. The flowers are bell-shaped, about 1 in. long, yellowish-green near the stalk, shading into dull purple. The fruit is a two-lobed shining black berry about the size of a small cherry. It contains from 70 to over 200 seeds and from 40 to over 500 fruits may be produced by a single plant. The average output of a plant is over 6,500 seeds, with a fairly high germination. Distribution is mainly through bird droppings and subsequent rainwash. It is perhaps significant that in the U.S.A. the seeds are often treated with strong acid for forty-five minutes before sowing, which suggests that the germination in nature may be accelerated by passage through a digestive tract. Adams (*Amer. Journ. Bot.*, p. 415, 1927) records that germination took place after about ten months.

This is a southern-continental type, and in Europe the Dwale reaches its northern limit in Poland, and B. Pater records that in Klausenburg, Transylvania, and Czechoslovakia it is confined to woods where the Beech is the dominant tree, and there *A. belladonna* is, as with us, characteristic of the clearings. It is absent from both Scotland and Ireland (cf. map, p. 43).

CANTERBURY BELL or NETTLE-LEAVED BELLFLOWER, *Campanula trachelium*. Campanulaceae. 2n=34. (Pl. V)

The basal leaves of this perennial are heart-shaped with long stalks and coarsely toothed margins. The stem is strongly ribbed and bears bristly hairs directed downwards. In the chalk scrub and the Beechwood clearings, which this species frequents, the stem reaches a height of 2–3 ft. (60–90 cms.) and bears blue flowers about 2 cms. in length.

The capsules are bent downwards and the seeds escape from three pores near the stalk, through which they are jerked by the wind.

Germination takes place mostly in the autumn, but some seeds do not germinate till the spring. Germination has been observed up to eighteen months after shedding of the seeds.

A species widely distributed in Europe.

TRAVELLER'S JOY, *Clematis vitalba*. Ranunculaceae. 2n=16.

A woody climber that can attain a considerable size and age (over forty years). The plumed fruits to which the popular name of Old Man's Beard is due are in part dispersed by the winds of autumn, but many of them remain attached till the spring. Mostly germination takes place in April and May, and T. A. Dymes stated that those shed in the autumn were the earliest to germinate. The embryo is undeveloped at shedding and takes some seventeen days to mature. The flowers do not secrete nectar, but are visited by flies and by bees for their pollen. Like many other woody climbers, the vessels of the spring wood are large. The stalks of the pinnate leaves are sensitive to the stimulus of contact and act as tendrils. The first-formed leaves of the seedling are simple.

SPINDLE, *Euonymus europaeus*. Celastraceae. 2n=64.

A bushy shrub or tree often 10 ft. or more in height, with green four-angled twigs and paired leaves with short stalks and with blades tapering to an acute tip. The small greenish-white flowers, each with four petals, are either male, female or bisexual on different trees and freely visited in May or June by flies that seek the nectar. The fruits are four-lobed pink capsules, each lobe containing one or two seeds, each surrounded by a bright orange wrinkled covering. The seed weighs about 0·016 gm. and contains an embryo which is already green. Dispersal is by birds. Germination takes place one or two years after shedding.

Vegetative propagation takes place by adventitious shoots from the roots. The Spindle is the winter host of the Black Bean aphid, *Aphis fabiae*.

Common on calcareous soils in England, especially the south. It is rare in the north and in Scotland and sparsely distributed in Ireland.

HAIRY ST. JOHN'S WORT, *Hypericum hirsutum*. Hypericaceae.

An erect perennial with leaves containing glands that appear as translucent spots when held against the light, and the only British St. John's Wort, except the aquatic species, with hairy leaves. The stems, which may be up to 3 ft. in height (90 cms.), are usually tufted. The root-system is much branched and reaches to over 12 ins. (30 cms.). The flowers are small

and pale yellow and contrast with the black glands which edge the sepals. The capsule contains some 70 seeds, which are oval and weigh about 0·00009 gm. They are dispersed by wind and rainwash and although most germinate quickly, some may not do so till the lapse of nearly a year.

A widely distributed continental type which is very rare in Ireland, but in Scotland extends northward as far as Ross. It may, however, be indicative of climatic preferences that whereas the number of seeds per capsule yielded an average of 72·3 from plants growing in southern England, the average for fifty capsules from plants growing in Northumberland was only 51·6—a difference between the averages of 20·7 seeds with a standard error of difference of only 2·07.

PLOUGHMAN'S SPIKENARD, *Inula conyza.* Compositae. 2n=32.

A biennial species with a rosette of long, oval tapering leaves that are netted above and hairy beneath. When crushed, the leaves emit a pleasing aromatic scent. From the rosette in the second year arise one or few stems 2–4 ft. high (60–120 cms.), each branching into a crowded inflorescence of inconspicuous yellow flower heads. The fruits bear a shining red parachute of hairs and weigh about 0·0001 gm. The root is fibrous and rather shallow, the rooting depth being usually about 12 ins. (30 cms.).

JUNIPER, *Juniperus communis.* Coniferae. 2n=22.

Although by no means confined to calcareous soils, the Juniper is a characteristic shrub on some chalk downs, where, as in areas of Buckinghamshire and Wiltshire, the ranks of its fastigiate bushes, up to 4 ft. in height, may look like regiments of soldiers. The needle-like leaves are in whorls of three. The cone ripens into a blue-black berry about 8 mm. in diameter in the second year, and contains from 1 to 8 seeds.

PRIVET, *Ligustrum vulgare.* Oleaceae. 2n=46.

A narrower-leaved and far more attractive shrub than the privet of our gardens. The leaves are lanceolate with an acute tip. It forms bushes up to 10 ft. (3 m.) high, alike in the chalk scrub in Ashwoods and on calcareous dunes. It is partially evergreen. The black berries contain 2–4 seeds which weigh nearly 0·008 gm.

GROMWELL, *Lithospermum officinale.* Boraginaceae. 2n=28.

A perennial herb with hispid leaves half clasping the stems. These latter are stiff, tufted and branched above bearing small greenish-white flowers (*ca.* 7 mm.), which produce fruits that most commonly occur singly (*ca.* 0·01 gm.) and are hard polished white and tapering. They germinate intermittently, usually about 70–80% in the first year. Frequently in the wood margin or scrub or on limestone in the south, more rarely on calcareous dunes.

CRESTED COW-WHEAT, *Melampyrum cristatum.* Scrophulariaceae. 2n=18.

An annual semi-parasite 5 to 20 ins. (12-50 cms.) high bearing four-angled dense heads of yellow flowers tipped with purple arising from the four rows of finely toothed bracts. The yellowish-brown seeds are about 5 mm. in length and weigh from 0·007 to 0·01 gm. They frequently exhibit delayed germination and the appearance of the plant is often erratic.

FLY ORCHIS, *Ophrys muscifera.* Orchidaceae. 2n=36.

There are two almost globular tubers bearing lanceolate blue-green leaves and a stem about 12–15 ins. high (30–38 cms.), usually carrying about three to eight flowers, widely spaced, that resemble an insect and which are stated to be pollinated as the result of visits by male insects deluded into believing the flower to be a female.

Fruit production is often absent, but the occurrence of the plant is erratic. It grows in the semi-shade of scrub and in the better lighted and moister parts of Beechwoods, also in other types of woodland on moist calcareous soil such as Ashwoods.

Individuals live for a number of years.

LADY ORCHID, *Orchis purpurea.* Orchidaceae. 2n=42.

A tall plant, with ovoid tubers and from three to five oblong usually greyish-green leaves, growing to a height of some 15 ins. (*ca.* 38 cms.). It bears a dense spike of flowers each with the upper perianth segments forming a dark reddish-purple hood contrasting strongly with the very pale three-lobed lip spotted with purple. The new leaves are formed in early February.

A plant of the chalk scrub which was once so abundant in

Kent as to have been commercially exploited, but during the last seventy-five years this species has disappeared from Berkshire, Middlesex, Surrey and Sussex and become a rarity even in Kent.

Darwin recorded that only eleven capsules were set on ten spikes of this species, but as the number of seeds is large the diminution of the species is more likely to be due to artificial restriction than to natural inadequacy of reproduction.

MARJORAM, *Origanum vulgare*. Labiatae. 2n=30.

A tufted perennial with aromatic hairy foliage. The cluster of stems increases in size through the peripheral production of new shoots at the end of short stolons. Most of the roots are shallow, 2–8 ins. (5–20 cms.), but numerous. The stems, which are from 10–30 ins. high (25–75 cms.), bear corymbs of flowers of two types: male, with stamens only, which are smaller and pale, or bisexual flowers, which are larger and purple. Osmotic pressures of from 18–20 atmospheres have been recorded for this species, which retains its foliage throughout the winter.

BUCKTHORN, *Rhamnus catharticus*. Rhamnaceae. 2n=24.

A spinous bushy shrub with a dark bark commonly attaining about 10–12 ft. in height (3–3·6 m.). The oval leaves are serrated along the margin and clusters of small yellow green unisexual flowers are produced in May. The fruits are almost spherical in shape, black in colour and contain four stones, each with one curved seed. The flesh of the fruit contains purgative glucosides formerly used in medicine. The seeds are distributed in the droppings of birds, and germinate freely (up to 90%). The cotyledons come above ground, are thin and large, and thus contrast with those of *Frangula alnus*, where they are hypogeal, small and fleshy. (For distribution see map, p. 43.)

DOWNY WOUNDWORT, *Stachys germanica*. Labiatae. 2n=30.

A plant of wood margins and hedge banks on dry calcareous soil, now perhaps confined to Oxfordshire oolite, but formerly found in Hampshire, West Kent, Buckinghamshire, Northamptonshire, Lincolnshire and Denbigh (see map, p. 43).

It was first recorded in 1663, and there is no reason to believe that its occurrence is due to human introduction, though the

destruction of natural marginal scrub is probably the cause of its diminution.

A biennial spreading by stolons and growing from 1–3 ft. high (30–90 cms.) with wrinkled heart-shaped rosette leaves covered with silky hairs.

The small pale rose-purple flowers are produced in dense whorls separated from one another. The nutlets are oval brown, very slightly rugose and about 1·5–2 mm. Their average weight is 0·002237 gm.

WAYFARING TREE, *Viburnum lantana.* Caprifoliaceae. 2n=18.

A deciduous bushy shrub with opposite leaves usually from 3–9ft. (*ca.* 1–3 m.) in height. The leaves are protected during the winter by a covering of mealy hairs and there are no bud scales. The dome-shaped inflorescences are already formed by the winter and mature in April. The flowers are devoid of nectar and visited by bees for their pollen. The fruit, which ripens in September, is a one-seeded oval berry about 7 mm. long, red at first and finally blue-black. The stone is rather flattened, with grooves on one side, and weighs about 0·04 gms. Dispersal chiefly depends on birds. Germination mostly occurs in May, but dormancy into the second year sometimes obtains.

The Wayfaring Tree is a southern-continental species found in both hemispheres, and in Britain does not occur as a native north of Yorkshire.

HAIRY VIOLET, *Viola hirta.* Violaceae. 2n=20. (Pl. XII)

A perennial with a short stem bearing very hairy heart-shaped leaves and inodorous dull blue flowers with a hooked spur. Extension sometimes takes place by means of short runners. A shallow-rooting species of the chalk scrub, where the depth of penetration is often only 4–6 ins. (10–15 cms.), but in the easily penetrated drier soils of the sand dune the depth may be much greater (cf. Fig. 59, p. 203).

The oval brown seeds are probably distributed by ants, and germinate in spring.

The leaves of plants growing in scrub often exhibit marked increase in size after flowering at the beginning of the 'shade phase.' They wither away in summer and are replaced in autumn. Fleshy pink flowers, which are self-fertilised and do not open (cleistogamous flowers), are formed in the latter part

of the flowering period. The species is apparently unaffected in its flowering by the length of the daily period of illumination. Not infrequently incipient spurs are present on the other petals (cf. Britton, *Journ. of Botany*, p. 141, 1904). *Viola calcarea* which is closely allied to *V. hirta* has narrow petals and a small spur whilst the orientation of the petals is such that they approximate to a St. Andrew's Cross both in form and colour.

IX

BIOLOGICAL NOTES ON SOME CHARACTERISTIC WEEDS OF THE CHALK

Scleropoa rigida	Chalk Fescue
Bunium bulbocastanum	Earth Nut
Lithospermum arvense	Gromwell
Ajuga chamaepitys	Ground Pine (Map, Fig. 13, p. 39)
Galeopsis angustifolia	Hemp Nettle
Linaria spuria	Male Fluellen
Galium tricorne	Pawnbroker's Plant (Map, Fig. 14, p. 41)
Melampyrum arvense	Purple Cow-wheat
Adonis annua	Red Chamomile
Papaver hybridum	Rough-headed Poppy
Valerianella dentata	Slender Corn Salad
Bupleurum rotundifolium	Thorow Wax
Legousia hybrida	Venus' Looking-glass (Map, Fig. 14, p. 41)
Sinapis alba	White Mustard
Iberis amara	Wild Candytuft (Map, Fig. 15, p. 43)
Reseda lutea	Wild Mignonette
Lathyrus aphaca	Yellow Vetchling
Teucrium botrys	

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RED CHAMOMILE, *Adonis annua* (=*A. autumnalis*). Ranunculaceae. 2n=32.

A rare agricultural weed formerly common in the chalky cornfields of the south-east; now, except as a casual, almost confined to a few areas in Sussex and Wiltshire.

Its finely-cut foliage and red flowers, like a miniature anemone, witness to the aptness of the country name. The flower axis bearing a central cluster of carpels elongates after fertilisation, so that the fruit-head becomes a cylindrical group of achenes which are dark when ripe and ridged in a net-like manner.

Germination is periodic. Of fruits from a single head, some may exhibit a marked dormancy, germination taking place mostly in spring, but sometimes in autumn, one, two or even three years after sowing.

A. annua is a southern-continental species which, often flowering and fruiting late in the year, is more dependent than many species on a fine autumn.

For distribution map, cf. Salisbury, E. J. 'Ecological Aspects of Meterology' (*Journ. Roy. Met. Soc.*, pp. 337–58, LXV, 1939).

GROUND PINE, *Ajuga chamaepitys*. Labiatae. 2n=28.

Normally a winter annual, but sometimes behaving as a summer annual, with a shallow root-system penetrating some 2–4 ins. (5–10 cms.). At first forming a rosette, of simple leaves with little or no lobing, close-pressed to the soil. When the stem, which is commonly branched from the base, develops this bears rather crowded hairy leaves with three narrowly linear lobes, so that the whole plant has somewhat the appearance of a dwarf conifer and is seldom more than 4–5 ins. (10–12·5 cms.) high. The flowers are clear yellow in colour with small red spots on the lip, and occur singly in the axils of the leaves. The nutlets are deeply pitted and brown, about 0·00116 gm. in weight, and mostly germinate in the autumn, sometimes in the spring. Germination is continuous and over 50% has been observed. Seedlings were found to survive a temperature of 22° F. (—5·5° C.), but succumbed at temperatures of 13° F. (—10·5° C.).

The species is a southern-continental type, in England confined to the south-east from Cambridge and Hampshire to Kent (see map, p. 39).

THOROW WAX, *Bupleurum rotundifolium*. Umbelliferae. 2n=16. (Figs. 26 and 27, p. 111)

A summer annual, germinating in the spring, that, except as a casual, is only found as a cornfield weed upon the chalk. It grows to a height of 12–24 ins. (30–50 cms.) and has smooth round stems which in the young plant bear elliptical leaves (cf. Fig. 26). But those formed later completely surround the stem as though this had grown through the leaves, which are of a glaucous green from the presence of a superficial waxy bloom. The yellow flowers are in compound umbels, the smaller umbels being each surrounded by a whorl of three to five pointed and rather yellowish-green leaves.

The plant is a member of the southern-continental element of our flora, and is in Britain confined to a few localities in the south and south-eastern counties, where it can be relied on to appear season after season, though as a casual it has been recorded as far north as Kircudbright. Its comparative rarity to-day in contrast to its former frequency on the southern and eastern chalk is probably accounted for by the improved methods of screening agricultural seeds from abroad.

For map of recorded occurrences, see E. J. Salisbury, *The East Anglian Flora*, Map 22 (Norwich, 1932).

EARTH NUT, *Bunium bulbocastanum*. Umbelliferae. 2n=22.

The thrice pinnate leaves and slender leaflets of this species and indeed the whole habit greatly resembles the Common Pignut (*Conopodium denudatum*). The white umbels of flowers are borne on stems up to 30 ins. in height (75 cms.), which together with the leaves die away completely in winter, and the plant persists by means of an underground corm that is black in colour and from 1–2 ins. in diameter (2·5–5 cms.). The fruits germinate freely in spring and the seedlings are noteworthy for their monocotyledonous character (cf. Fig. 43, p. 158).

A southern-continental type that extends as far north as Belgium. This species in Britain is very local in calcareous fields of Hertfordshire, Buckinghamshire, Bedfordshire and Cambridge, usually amongst corn, but also in the semi-open vegetation of early phases of the chalk succession.

HEMP NETTLE, *Galeopsis angustifolia*. Labiatae. 2n=16.

A narrow-leaved annual bearing numerous small hairs which give the plant a slightly greyish-green appearance. It bears rather crowded rose-coloured flowers, which appear large for the size of the plant, at the end of the main stem and its branches.

A summer annual, the seeds of which germinate in May.

A southern-continental species, absent from the west of Ireland and from N.W. Scotland.

THE PAWNBROKER'S PLANT, *Galium tricorne*. Rubiaceae. 2n=44.

An annual, climbing by means of its unbranched stem, which bears recurved hooks. Similar to the common Goose Grass, but a much smaller plant, and distinctive by its characteristic fruits grouped usually in threes, each covered with granular protuberances and attached to inwardly curved stalks. Each weighs about 0·0115 gm. Germination occurs in autumn.

A southern-continental species not native north of Holland. In Britain it occurs from Northumberland southwards, being most frequent in the south-eastern counties on calcareous soils. It is absent from Ireland. (Fig. 14, p. 41.)

WILD CANDYTUFT, *Iberis amara*. Cruciferae. 2n=14; 16.

An annual of disturbed calcareous soil, frequent at the edge of rabbit burrows, with toothed or pinnatifid leaves and a branched stem from 6–12 ins. high (15–30 cms.) bearing inflorescences that are at first flattened, with white flowers, the outermost ones with larger marginal petals. The inflorescence elongates as the orbicular fruits ripen. Each fruit contains several yellow flattened seeds (av. 0·0025 gm.).

The plant is very bitter to the taste.

This species occurs mostly south-east of the line from the Bristol Channel to the Wash (cf. map, p. 43).

YELLOW VETCHLING, *Lathyrus aphaca*. Leguminosae. 2n=14.

In this species, as in the Grass Vetch, a true leaf blade is absent, here represented by an unbranched tendril. In the seedling, however, the first leaves have, in place of their tendril, a small blade of two or three leaflets. The solitary yellow flowers, simple tendrils and large glaucous arrow-head-shaped stipules are characteristic.

The seeds (av. 0·021 gm.), numbering two to seven in a pod, germinate in the autumn. This species has occurred as a casual weed in many parts of southern England, but is only found regularly on the calcareous soils of the south (e.g. Dorset, Sussex), where perhaps alone this winter-annual can normally survive hard winters. It is widespread in France, where too it is particularly a feature of calcareous fields.

VENUS' LOOKING-GLASS, *Legousia hybrida*. Campanulaceae. 2n=20.

This cornfield annual has oblong leaves beset with bristly hairs and with a wavy margin. The flowers, which have petals that appear blue-purple when open and lilac-purple when closed, possess calyx lobes that are narrow and project beyond the petals.

The capsule, which varies from 1 to 1½ ins. long (2·5–3·7 cms.), contains a large number of seeds, about sixty, which escape through three openings at the side near the top. The seeds are elliptical, dark brown, and shining. They weigh about 0·00032 gm. Germination is mostly in the autumn, but some seeds have a natural dormancy of several years.

A southern-continental species mainly found in the south-

eastern counties of England, except as a casual. Its continental character is reflected in its absence from Ireland and most of Wales (cf. map, p. 41).

MALE FLUELLEN, *Linaria spuria*. Scrophulariaceae. 2n=14.

A prostrate summer annual with rounded or oval leaves that are covered with hairs, some of which are glandular. The snapdragon-shaped flowers have a short spur and are clear yellow with a purple throat. The fruits, which are almost globular, open by pores through which the pitted seeds escape. Each fruit contains from 10 to 38 seeds which have an average weight of 0·0004 gm. Germination which is somewhat erratic takes place in the late spring or early summer, usually in May or June.

It is a southern-continental species found as far north as Holland, and in Britain occurs in the southern portion of England only, from Lincolnshire and South Wales to Kent, and is particularly associated with chalky fields. It occurs on sand also, but more particularly when the latter is basic; however, its association with calcareous soils is perhaps an outcome more of their physical than of their chemical characteristics.

GROMWELL or WHITE FORGET-ME-NOT, *Lithospermum arvense*. Boraginaceae. 2n=28.

A hispid annual with a simple, or but sparingly branched stem, bearing a forked inflorescence of creamy-white small flowers about 8 mm. in diameter. The tapering stony nutlets are of a shining-grey colour slightly wrinkled and number four or fewer per flower. They weigh usually about 0·006 gm. but vary considerably in size. Germination which is intermittent can attain over 80% and may be spread over two years.

The cotyledons and the stem just beneath them are alike hairy.

PURPLE COW-WHEAT, *Melampyrum arvense*. Scrophulariaceae. 2n=18.

A semi-parasitic annual now extremely rare, but formerly less so, and though recorded as a casual on various types of soil, only exhibiting persistence in calcareous areas. The seeds are smooth, brown, slightly curved and wedge-shaped, about 4–5·5 mm. in length by about 2–2·5 mm. broad at the widest

part. Their average weight is approximately 0·159 gm. Owing to the size and weight of the seeds approximating to those of wheat grains they were, prior to the use of modern screening methods, sometimes introduced with corn 'seed' from the Continent.

ROUGH-HEADED POPPY, *Papaver hybridum*. Papaveraceae. 2n=14.

An annual poppy easily distinguished from the common field poppy by the oval fruit beset with bristles and, when in flower, by the inner pair of petals being similar in size to the outer and by the club-shaped stalks of the stamens. (In the Common Poppy (*P. rhoeas*), the filaments are not dilated above and the inner petals are appreciably smaller than the outer.) The flowers are visited by insects for their pollen and a single flower may contain from 60 to 150 stamens. The seeds weigh about 0·00016 gm. and mostly germinate in September and October, though some may germinate in spring, and these last alone survive after severe winters.

This winter-annual is a southern type and in Britain is found only in the area south-east from Wales and Durham.

WILD MIGNONETTE, *Reseda lutea*. Resedaceae. 2n=48.

Commonly a biennial, though sometimes perennial, with pinnately lobed leaves. The spikes are densely-flowered with a conical apex and consist of pale yellow flowers each producing from sixteen to twenty stamens.

The capsules contain about fourteen shining black seeds that weigh about 0·0008 gm. They are largely dispersed by birds, and germinate in the spring. Probably only a casual north of Durham.

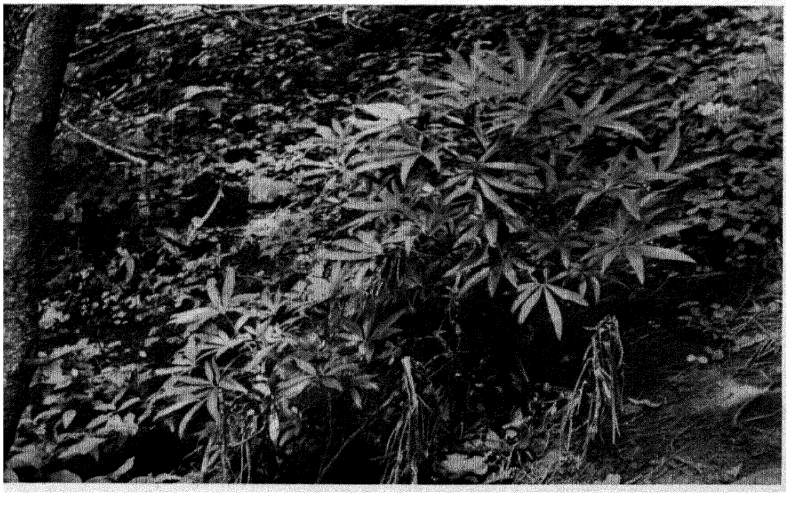
CHALK FESCUE, *Scleropoa rigida*. Gramineae. 2n=14.

A stiff annual grass that has narrow leaves with incurved edges and an ascending rosette-like habit when large. Small plants are, however, usually erect and on dunes may be depauperate, with the inflorescence reduced to a few flowers. The branches of the panicles spread out in a rigid manner and

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PLATE XV. Beechwood species. ABOVE. The evergreen shrub Spurge Laurel (*Daphne laureola*) in flower in April. × *ca.* $\frac{1}{6}$. BELOW. The winter-green Setterwort (*Helleborus foetidus*). × *ca.* $\frac{1}{12}$.







are in two rows. The grains are very small and have an average weight of 0·0002 gm.

Of widespread occurrence through Great Britain and Ireland.

WHITE MUSTARD, *Sinapis alba*. Cruciferae. 2n=24.

A large plant, rather like a Charlock, but with pinnately lobed leaves, attaining a height of up to 36 ins. (90 cms.). The pods are very hispid, with spreading bristles and a flattened beak as long as the lower seeded portion. The more or less spherical seeds are usually pale-coloured and weigh about 0·00625 gm. Each pod produces from six to eight seeds. Although widely distributed and occurring on a variety of soils, it is only on the calcareous soils that it is very abundant and attains the status of a pest.

Teucrium botrys. Labiatae. 2n=10.

A bushy, freely branched, biennial or annual with pinnatifid hairy leaves and not usually attaining more than 8 ins. (20 cms.) in height. It bears pale reddish-purple flowers with a swollen sac-like calyx. The flowers are grouped three to four in the axil of each bract.

The seeds are brown with numerous pits and weigh *ca.* 0·001 gm. They germinate in the autumn. Plants produce from 240 to 1,000 nutlets.

The species is a southern-continental one, in Britain confined to Surrey.

SLENDER CORN SALAD, *Valerianella dentata*. Valerianaceae. 2n=14.

Suggests a slender version of the Common Corn Salad with spreading branches and flesh-coloured flowers, whereas *V. locusta* has pale blue flowers which tend to be aggregated.

A species that is far commoner as a cornfield weed on chalk than on any other type of soil. An average plant will produce about 260 fruits.

* * *

PLATE XVI. Beechwood orchids. AT LEFT. Fly Orchis (*Ophrys muscifera*). CENTRE. The saprophytic Bird's-nest Orchid (*Neottia nidus-avis*). RIGHT. Butterfly Orchis (*Platanthera* (*Habenaria*) *chlorantha*). All about life-size.

X

GARDENING ON CALCAREOUS SOILS

FROM the specialised nature of the chemical and physical conditions of calcareous soils, it is natural that the number of exotic species which can be cultivated with success upon chalk is far more restricted than on soils of a less extreme character. But in fact since all plants require calcium in some degree it is not surprising that they exhibit almost every gradation of tolerance from species which, like most Rhododendrons and Heaths, cannot endure free calcium carbonate but must obtain their requirements of calcium in the form of exchangeable ions, to such as *Spartium junceum* and even some Heaths (e.g. *Erica carnea*), which will flourish in soil that consists mostly of broken chalk. The changing relation of many wild species to chalk tolerance as we pass from the southern to the northern limits of their geographical range emphasises for us the importance of the physical conditions of moisture content, warmth and aeration, all of which affect the success of plants that can be cultivated on chalk. Not a few failures on this type of soil are attributable as much to lack of adequate root development, through insufficient soil moisture and shallow root run, as to actual excess of lime. Indeed, the exotic flora of the chalk can be developed in far greater variety than many horticulturists imagine, and though we must, in the shrubberies, forgo our choice Azaleas, Styrax and *Eucryphia glutinosa*, the selection available is both numerous and attractive.

Most coniferous trees grow but poorly on chalk, but there are a few exceptions, notably the attractive Bottle-brush Fir (*Abies pinsapo*) and the Grecian Fir (*Abies cephalonica*) which flourish under such conditions. For our shelter belts we can employ *Pinus insignis*, *P. laricio*, *Cupressus macrocarpa*, *Cedrus atlantica glauca*, *Quercus ilex* and in more sheltered spots *Phyllyrea*, all of which are evergreen trees that tolerate a high proportion of lime in the soil.

Of exotic deciduous trees nearly all the species of *Acer*, apart from the Japanese Maples, will grow well, but some of the most satisfactory are the Chinese species, *Acer ginnala*, *A. Henryi*

and *A. griseum*, which alike assume a beautiful red coloration in autumn whilst the last-named is also peculiarly attractive for its bark. Most of the Crabs and Cherries grow well if the unbroken rock is not at too shallow a depth. *Malus baccata* with its cherry-like fruit, *Malus floribunda* with its exquisite pink buds, *Malus* John Downie and *M. spectabilis* are all to be recommended for their blossom alone, but the fruits and autumn coloration in addition yield the gardener a prolonged dividend of beauty.

Of the Cherries, *Prunus sargentii*, *P. serrulata* and *P. yedoensis* are especially attractive, the last-named, planted against the dark background of *Pinus insignis*, providing a fairy-like wealth of blossom that is of surpassing loveliness. Species of *Amelanchier* and *Exochorda* also provide an aesthetic feast albeit a somewhat ephemeral one. More lasting are the Hawthorns, most of which grow well on chalk, and of these *Crataegus punctata*, *C. coccinia*, *C. cordata* and *C. mollis* are well worthy of culture.

Of the less familiar trees, *Davidia vilmoriniana*, *Hoheria lyallii*, *Pittosporum tobira*, *Abutilon vitifolium*, *Eleagnus campanulatus*, *Cornus mas* and *Catalpa bignonoides* will all tolerate chalk, although a surface dressing of non-chalky soil (p. 17) may help greatly. Of the flowering shrubs the Syringas and Mock Oranges (*Philadelphus*) the Deutzias and Weigelias do well. The leguminous shrubs are well represented in the chalk-tolerant class, and of these *Spartium junceum*, *Genista hispanica*, *G. aetnensis*, *Cytisus nigricans*, *C. praecos* and *C. virgata* are all well worth growing. Buddleias, Viburnums, Euonymus *spp.*, Cotoneasters, Escallonias, Olearis and Forsythias can be relied on to vary the texture and prolong the floral season, whilst climbers such as Honeysuckles and Clematis in variety flourish too. Of undershrubs the Helianthemums prefer chalk and Sarcococcas flourish upon it.

Though a large number of the shrubs mentioned bear white or yellow flowers, *Ceanothus thyrsiflorus* and *Ceratostigma wilmottianum* can be relied on to develop an intensity of blue rarely seen when growing on other types of soil.

Herbaceous planting on the chalk is not unduly restricted, for the species of *Dianthus* flourish, so also do Paeonies, Hellebores, many Labiatae, and amongst the monocotyledons, Solomon's Seals and *Eremurus*. Indeed, it would be easier to compile a list of those garden plants that abhor chalk than of those which appear to like it.

XI

THE LIMESTONE VEGETATION

NEARLY all the other types of habitat not derived from the chalk that are definitely calcareous are situated on the limestones, if we except most sand dunes which are here considered separately. This fact brings with it two chief implications. Firstly, the chalk, we have seen, is almost pure calcium carbonate and only leaves a very small residue when leaching is complete, whereas the limestones are very impure carbonates with varying chemical composition which leave a large residue when leached that varies both in amount and character according to the particular stratum of limestone from which the soil has been derived. The limestone soils are thus in general deeper and more retentive of moisture than the chalk soils. Secondly, most of the limestones in this country are situated in the west and north, in regions, that is, of higher rainfall as compared with the chalk of the south and east. Soil and climate combine therefore to produce a moister calcareous environment enhanced, it may be, on the one hand, by a surface which is nearly level or, on the other, diminished by a steep topography that ensures complete drainage and, by erosion, prevents accumulation of any appreciable depth of the impure residues already referred to.

Limestones not only contain normally a higher proportion of insoluble residue than the chalk, but the range of variation in this respect is very considerable. The Geological Survey memoir on *The Limestones of Scotland* (1949) includes a large amount of analytical data which show that, for example, the carboniferous limestones, which are the most important in Britain in respect to vegetation, may contain from as little as 0·5% insoluble residue to as much as 58% whilst the average is over 11%; furthermore nearly a quarter of the samples had over 20%. The proportion of magnesium carbonate ranged from just over 1% to nearly 6%, whilst in the dolomitic limestones the proportion of this ingredient may be from 26% to 43%. It is therefore obvious that soils of similar maturity derived from limestones are likely to be deeper and moister than

those derived, under similar conditions of time and topography, from the chalk and they are, moreover, likely to exhibit a far greater range of texture. ($CaCO_3$ in Ashwoods examined 0·01–68%.)

The vegetation reflects these differences from the chalk. If for instance we take a walk over the Cotswold hills formed by the oolitic limestones we shall find a flora very similar superficially to that of the downs of Sussex or Kent. But we shall soon realise that the definitely continental-southern types are sometimes absent or far more local. The Ground Pine (*Ajuga chamaepitys*) does not, for example, extend westwards beyond Hampshire. If we wish to see here the blue pageant of the Chalk Milkwort (*Polygala calcarea*) we have to seek it on the steep south-facing slopes of Rodborough. Similarly, the Pasque Flower, which is locally common on the chalk of the east, finds its western limit in the Cotswolds, where not only is it also confined to the steep southern slopes, but even there is rare. Moreover, if our walk be in the late spring, we shall note that the Cotswold turf is dotted with numerous spires of the Early Purple Orchis (*Orchis mascula*), a flower which in the east of England we associate with damp woods on calcareous, or at the least basic, soils, and only rarely do we find it there in the open in exceptionally damp chalk pastures. Yet here on the limestone pastures in the moister climate of the west the Purple Orchis is a common plant outside the woodland shelter.

Another feature that will soon arrest our attention is the prevalence in the Cotswolds of the Great Cotton Thistles (*Cirsium eriophorum var. britannica* (Pl. XIX and map, Fig. 15, p. 43). This we may find as a scarce plant on the chalk of Hertfordshire, Kent and Sussex, but never in the profusion that it can be seen in Gloucestershire, starring the rough pastures with its giant rosettes in the neighbourhood of Sapperton and in summer rearing its large handsome purple heads some 6 or 7 ft. into the air. The type *C. eriophorum* is a continental species favoured by the climatic conditions that obtain in central Europe, but it has produced this variety which is suited to the more humid conditions of an oceanic climate and flourishes on the limestone soils of the west and north, with a higher rainfall, just as it does in the old damp trenches of Vimy Ridge, although so sparse on the drier soils and under the less humid conditions of south-eastern England. The oolitic pastures of the west are

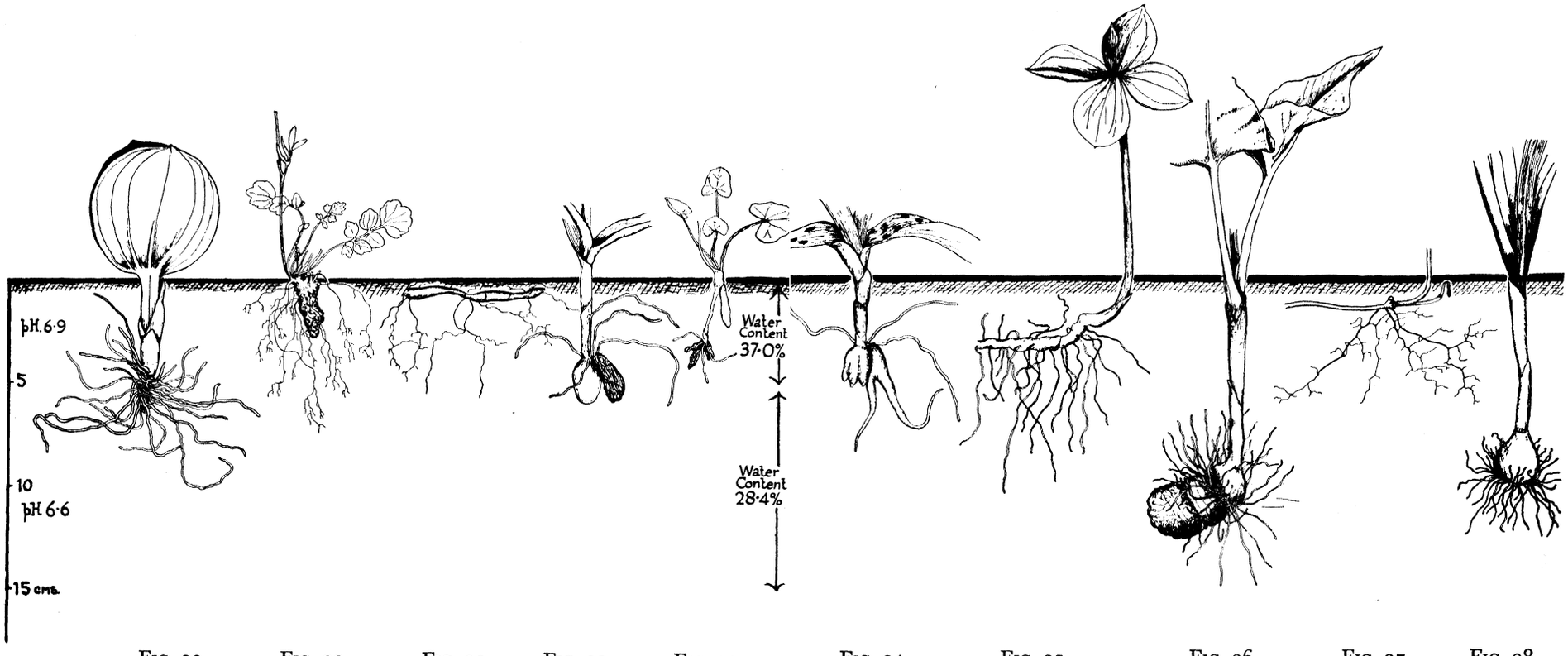


Fig 29 Fig 30 Fig 31 Fig 32 Fig 33 . . Fig 34 Fig 35 Fig 36 Fig 37 Fig 38

Figs 29–38. Plants of Damp Ashwood with high water content and shallow root systems.

Fig 29. Twayblade (*Listera ovata*). Fig 30. Lady's Smock (*Cardamine pratensis*). Fig 31. Wood Anemone (*Anemone nemorosa*). Fig 32. Early Purple Orchis (*Orchis mascula*). Fig 33. Lesser Celandine (*Ficaria verna*). Fig 34. Common Spotted Orchis (*Orchis fuchsii*). Fig 35. Herb Paris (*Paris quadrifolia*). Fig 36. Cuckoo-pint (*Arum maculatum*). Fig 37. Dog's Mercury (*Mercurialis perennis*). Fig 38. Wild Hyacinth (*Scilla nutans*), Note the reaction near the surface of the calcareous clay is almost alkaline (pH 6·9), whereas below the soil is more acid (pH 6·6).

also the particular home of a rare cress (*Thlaspi perfoliatum*).

In the woods too we find those plants that like moist calcareous soils have become commoner than on the chalk. On the edges of some of the Ashwoods that occupy the limestone valleys of the Mendips we can see the blue-purple Gromwell (*Lithospermum purpureo-coeruleum*) growing in some profusion whereas, in the east it is a rarity of the chalky boulder clay (map, Fig. 15, p. 43, and Pl. XXI). (Cf. J. W. White, *Journ. Bot.*, XX, 74, 1884). In the Cotswold woods we can see drifts of Lily of the Valley (*Convallaria majalis*), the very name of which emphasises its association with the moist hollows rather than the drier slopes. The wild Solomon's Seals (*Polygonatum odoratum=officinale* (map, Fig. 42, p. 147) and *P. multiflorum* (Pl. VII) flourish here as nowhere else and Herb Paris (*Paris quadrifolia*) is as abundant as in the damp coppices of Kent, where the Cuckoo-flowers spread their lavender-tinted carpet in April.

The damp woods of the Cotswolds are the particular home of two local plants, the yellow Gagea (*Gagea lutea*), an inconspicuous bulbous species with tiny yellow flowers that blossoms in spring, and the rarer kind of Yellow Saxifrage (*Chrysosplenium alternifolium*), both also to be found in the limestone woods of the north.

The Cotswold woods are the sole home in Britain for the Red Helleborine (*Cephalanthera rubra*). We have already

referred to the frequency of *Lithospermum purpureo-coeruleum* in the Mendip woodlands, and here in the pastures the Spring Potentilla (*P. verna*) is commoner than in most other areas. The limestone cliffs of the Cheddar Gorge are well known as the sole locality in Britain for the Cheddar Pink, and further west the cliffs of Bristol provide the chief stations for a rare crucifer, *Arabis stricta*. The White Rock Rose (*Helianthemum polifolium*) is one of the glories of the Somersetshire limestone and though very local has been known there since Dr. Plukenet first recorded it in the 17th century. The limestone gorge of the Wye Valley presents a calcicole flora in which the abundance of the Nodding Melic Grass (*Melica nutans*, map, Fig. 42, p. 147) is a conspicuous feature, and the Beechwoods which clothe the valley sides exhibit such calcicole trees as *Sorbus latifolia*, closely related to the White Beam, and the large-leaved Lime Tree (*Tilia platyphyllos*) that is easily distinguished from the other Lime Trees by the large, strongly ribbed fruit. This latter tree is a southern-continental type that occurs as far north in Europe as Denmark and exhibits natural regeneration from seeds in Britain, so that its distribution and behaviour, as well as its mode of occurrence on the limestone in the woods of Herefordshire and Monmouth, is not inconsistent with its being a native tree. Moreover, the occurrence of pollen of *Tilia platyphyllos* in mesolithic peat in Kent (Burchill, J. P. T. and Erdtman, G., *Nature*, Vol. 165, p. 411, 1950) indicates that this species was in England long before any deliberate introduction by man can be held to have been probable. In woods on limestone Wych Elm (*Ulmus glabra= montana*) is often frequent and the Lime (*Tilia cordata*) occasional whilst Privet may be common. Mostly the differences from Beechwoods are those of abundance rather than of kind.

Farther west on the limestone of Bere Head grows that interesting Umbellifer *Trinia glauca*, whilst in the Gower Peninsular we find *Draba aizoides* and on Worm's Head a pasture reminiscent of the downs, but with fewer species, though one notable addition is the Hoary Rock Rose (*Helianthemum canum*, map, Fig. 14, p. 41). The limestone headlands of the Great and Little Orme that stand on either side of Llandudno exhibit several interesting features. The abundance of the lesser Meadow Rue (*Thalictrum minus*), of the Lady's Tresses Orchid (*Spiranthes spiralis*, Pl. XXXI) and of the Spring Sandwort (*Arenaria verna*, Pl. XVIII) is the culmination of a tendency that

is general as we pass from east to west. But here too we shall find a generally impoverished calcareous flora, enriched, however, by certain noteworthy additions. This is the chief locality for the Wild Cotoneaster (*C. integerrima*, Pl. XX) and that curious Aster the Goldilocks (*Aster linosyris*). The former, according to early accounts, was once common on these hills, but now unhappily is almost extinct, whilst the latter species is much diminished also. On the Little Orme can be found the tall Speedwell, *Veronica hybrida* (Pl. XVIII), an oceanic relative of the closely allied continental *Veronica spicata* that is confined to dry calcareous heaths in Breckland (cf. map, p. 43). Here too the annual Gentian (*Gentiana baltica*), a close ally of the biennial Field Gentian (*Gentiana campestris*), sometimes accompanies the Lady's Tresses Orchid in its abundance.

If we pass to the limestone of North West Yorkshire, we shall note again a diminution, or complete absence, of some of the members of the chalk flora, but in compensation we find abundance of a Bedstraw (*Galium pumilum*) in the turf and this is sometimes dotted with the yellow pansy (*Viola lutea*, map, Fig. 42, p. 147). The moist meadows in late spring are pink with the blooms of the Bird's-eye Primrose (*Primula farinosa*). Here too we can see abundant *Cystopteris fragilis*, whilst two other Limestone Ferns, *Dryopteris villarsii* and *Asplenium viride*, together with the grass *Sesleria varia* are almost as characteristic of these Craven limestones as the snail *Clausilia cravenensis*.

A walk over the limestone pastures of, for example, the Ingleborough district of Yorkshire will at once show how much these have in common with the vegetation of the chalk downs. Here, as there, we can see several of the downland orchids, the Bee Orchis, the Frog Orchis, the Sweet-scented Orchis, the Pyramidal Orchis, quite common on the permian limestone, and even the Dwarf Orchis, a continental type is locally not infrequent. It is not surprising that some of the more southern types, such as the Spider Orchis and the Man Orchis, are absent, but there is one northern type of orchid that is very rare in the south—namely, *Leucorchis albida*—whilst the presence of the Hoary Rock Rose (*Helianthemum canum*, map, p. 14) and the Spring Sandwort (*Arenaria verna*, Pl. XVIII) introduces elements that are only found on the chalk in the higher humidity of the west.

These limestone pastures of the north-west yield the familiar

Salad Burnet, the Rock Rose, the Dropwort, Squinancy-wort, Yellow Centaury, Horseshoe Vetch, Kidney Vetch, Felwort, Field Gentian, Chalk Scabious, the Chalk Brome, the clustered Bell Flower, Carline Thistle, Marjoram and even the continental Pasque Flower. But whereas in the chalk pastures of the south these species are generally distributed and common, on the limestones of N.W. Yorkshire some are rare and often far more restricted with respect to habitat conditions. For example, the Yellow Centuary (*Blackstonia perfoliata*) is uncommon, the Squinancy-wort (*Asperula cynanchica*) is a rarity, and so too is the Dwarf Thistle (*Cirsium acaulos*). The Kidney Vetch (*Anthyllis vulneraria*) is not common, the Rock Rose (*Helianthemum nummularium*) is very rare and the Horseshoe vetch (*Hippocrepis comosa*) is very local, whilst all three exhibit a marked restriction to ledges, banks and similar situations where topography ameliorates the effects of higher rainfall.

In the limestone woods we can find the Spurge Laurel, the Deadly Nightshade, Solomon's Seal, Lily of the Valley, Fly Orchis and Wood Barley. In the limestone scrub, Purging Buckthorn, Spindle and Wayfaring Tree with Old-man's Beard and bushes of Elder constitute a plant community very similar to the scrub of the chalk.

Some of the additional calcicoles in this area we have already noted, others are *Dryas octopetala*, *Saxifraga oppositifolia*, *Draba incana* and *Draba muralis*.

The particular structure of these mountain limestones, with beds of varying thickness interspersed with non-calcareous and therefore relatively insoluble strata, has resulted in those remarkable natural rock gardens termed 'limestone pavements' that suggest 'crazy paving' on a gigantic scale (Pl. XVII). Here the often shallow but broad fissures are colonised by many species including Lilies of the Valley (*Convallaria majalis*), Melancholy Thistle (*Cirsium heterophyllum*), the Limestone Fern (*Gymnocarpium robertianum*), Bell-flower (*Campanula latifolia*), with a variety of other commoner species, such as Dog's Mercury, Broad-leaved Garlic and Wood Sorrel, that in the height of the season provide a spectacle at once beautiful and unique. On the cliffs here one can encounter *Draba incana* with its twisted pods more frequently than on the calcareous dunes of the Gower Peninsula.

The colonisation of these limestone pavements consists at

first of perennial herbs, such as those just mentioned, but sooner or later shrubs and trees appear. Of these the true Bird Cherry (*Prunus padus*) is both the most characteristic and beautiful with its pendent racemes of shining white flowers (Pl. XVII). It often occurs as a shrub, but may assume the habit and dimensions of a tree. Of the larger trees the commonest is the Ash (*Fraxinus excelsior*), and some of the limestone pavements that have been longest exposed bear Ash-Hazel woods in which the conspicuous species include the Limestone Fern (*Gymnocarpium robertianum*), the Green Spleenwort (*Asplenium viride*) and the Touch-me-not Cress (*Cardamine impatiens*). Here too we may find a beautiful dark red-flowered Helleborine *Epipactis atrorubens*.

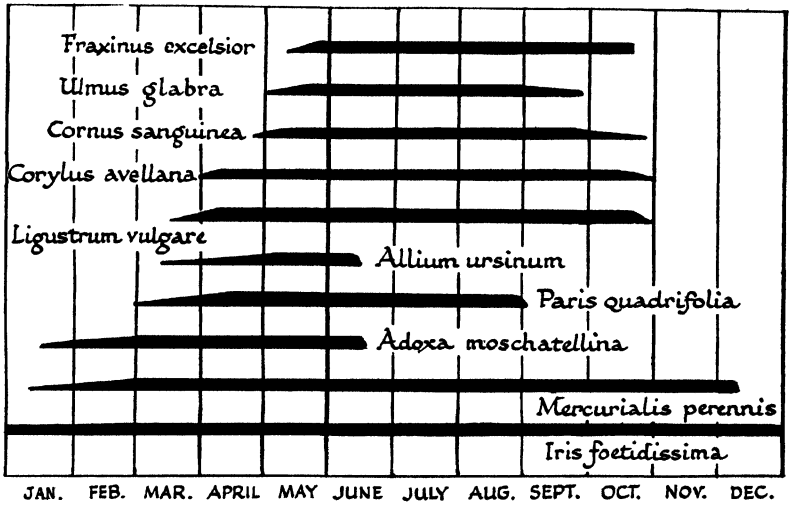


FIG 39. Diagram showing duration of foliage for typical plants of the Ashwood.

The limestone soils of Britain are especially characterised by the presence of woods dominated by the Ash tree (*Fraxinus excelsior*), a species which, in contrast to the Beech, is very tolerant of a high water content in the soil, although capable of enduring the dry conditions of shallow soils. Whereas the typical Beechwood with a continuous canopy exhibits a low light intensity at ground-level even in spring and deep shade in the summer, the illumination in an Ashwood is relatively high, alike in the 'light phase' and the 'shade phase,' due both to the type of branch system and the translucency of the canopy formed by the pinnate foliage of the Ash tree. Thus the

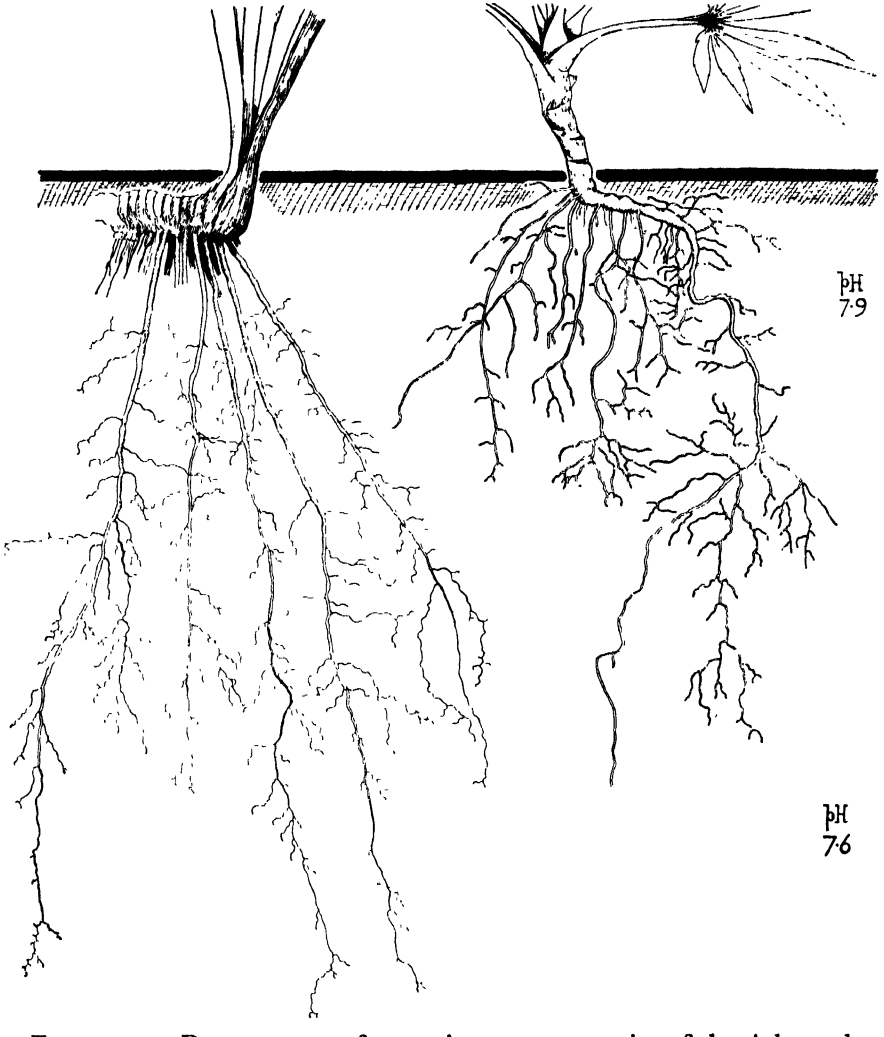
illumination under Ash trees in full leaf may often be as much as 17% of that in the open. A frequent consequence of this is that the shrub layer, which is sparse or even absent in the dull light of the Beechwood, is well developed and dense in the better lighted Ashwoods, though at ground level the illumination in the latter may be no greater than in a Beechwood owing to the double screen provided by the canopy of the Ash above and the foliage of the shrubs below. The well-developed shrub layer or herbaceous layer, or even both, in the Ashwood is facilitated by the late development of the leaves of the Ash tree compared with the Beech, or even the Oak, as the following data (cf. E. J. Salisbury, 'Phenology and Habitat,' *Q. J. R. Met. Soc.*, 251–63, 1921) show. It will be seen that on the average the interior of an Ashwood enjoys fifty-three more days free from appreciable shade than a Beechwood and, of these, fifteen days at least are of great significance in respect of the manufacture of food by the plant.

	Av. date of		*Length of*
	leaf expansion	*leaf fall*	*shade phase*
Beech (*Fagus sylvatica*)	115 (April 25th)	327 (Nov. 22nd)	212
Oak (*Quercus robur*)	125 (May 5th)	319 (Nov. 15th)	194
Ash (*Fraxinus excelsior*)	130 (May 10th)	289 (Oct. 16th)	159

Very common features of these Ashwoods are the green 'flushes' along the lines of drainage where the Dog's Mercury (*Mercurialis perennis*), Moschatel (*Adoxa moschatellina*), Cuckoo Pint (*Arum maculatum*), Herb Paris (*Paris quadrifolia*), Broad-leaved Garlic (*Allium ursinum*) and Meadow Saffron (*Colchicum autumnale*) furnish an emerald carpet in spring and the last-named produces bands of pink blossoms in autumn. The starry white sheets of the Broad-leaved Garlic when in full bloom in April often cover the flushes and lower slopes, as this species may do also in some Oakwoods of the west where, although the soils are not such as we normally designate calcareous, the flush water provides a copious and constant supply of exchangeable bases leached from the higher ground above and so ensures conditions favourable to many calcicole species.

As a tree the Ash occurs commonly in this country in two quite distinct types of habitat, viz. on upland calcareous soils in regions of considerable precipitation and on soils where the water content is high and sometimes not obviously calcareous. Woodlands in which the Ash is the dominant tree are found on

the limestones of the north and west of England up to an altitude of 1,000 ft., and on the chalk and calcareous greensand in the Isle of Wight, Dorset and Devon. It is to be noted that



FIGS 40–41. Root systems of two winter-green species of the Ashwood (about one-third actual size). FIG 40. Stinking Iris (*Iris foetidissima*) rooting depth 12 in. (30 cm.). FIG 41. Setterwort (*Helleborus foetidus*) rooting depth approximately 9 in. (23 cm.).

Fraxinus does not form woods upon the drier calcareous soils of the S.E. though occasionally present in small numbers or as a local dominant in clearings. The Ash is, however, an abundant constituent of the woods on calcareous marshes and

boulder-clays with high water content, where, as in Somerset and Cambridge, it is co-dominant with the Common Oak (*Quercus robur*) (cf. C. E. Moss, *Vegetation of Somerset*, p. 41, London, 1907, and R. S. Adamson, *Journ. Linn. Soc.* (*Bot.*), p. 348, 1912).

In the Fenwood or Carr fed by alkaline waters this tree is often abundant and on siliceous soils is common in the Alder-Willow association. It is clear then that damp calcareous soils favour the Ash to such an extent that under these conditions it can compete with trees casting a much deeper shade, and this probably to a large extent explains the distribution of the Ash and Beech. Both species flourish on soils containing a high percentage of lime, but whereas a dry soil favours the Beech a damp one favours the Ash. So that the present distribution of the two types, coinciding as it does with a difference in rainfall, probably represents the position of equilibrium. At their western limit on the Cotswolds are found woods which are transitional from Beech to Ash (Tansley and Adamson, *Journ. of Ecology*, Vol. I, p. 81, 1915). The occurrence of Ashwoods on very shallow dry red marls may be an outcome of sylvicultural treatment, but it would appear that certain types of dry calcareous shallow soils, especially of a dolomitic character, are favourable to the Ash.

The Ashwoods of the northern limestone have three interesting species not met with elsewhere: the Baneberry (*Actaea spicata*), a large summer-green herb tolerant of appreciable shade; the wild Jacob's Ladder (*Polemonium coeruleum*), that the study of sub-fossil pollen-grains in post-glacial peats suggests may formerly have been more widely distributed than at present; and the Lady's Slipper Orchid (*Cypripedium calceolus*), that has an extremely restricted distribution and is one of the rarest members of our flora, comparable to *Cotoneaster integerrima* confined to the limestone of N. Wales, and now almost extinct (Pl. XX).

In Northumberland the high rainfall area of Teesdale contains the sugar limestone band to which are restricted the Spring Gentian (*Gentiana verna*), a Dog Violet with hairy capsules (*Viola rupestris*), a rare Sedge (*Carex digitata*) and an even rarer Milkwort (*Polygala amara*), this localisation being doubtless due to the peculiar physical and chemical nature of the substratum. Another such restriction is shown by the Oxlip (*Primula elatior*), a continental species that gives a yellow colour

to the woodlands around Saffron Walden in May. It is a feature of the chalky boulder clay, but the ease with which it can be grown on moist soils which are not appreciably calcareous suggests that for this species the physical rather than the chemical conditions may be paramount.

The flora of Ireland comprises less than two-thirds the number of species that occur in Great Britain, although possessing perhaps some thirty species which do not occur in the latter area. The general floristic impoverishment of the Irish flora is reflected in the calcicole flora. Notable absentees from Ireland include the Field Oat Grass (*Helictotrichon pratensis*), the Greater Felwort (*Gentiana germanica*), the Horseshoe Vetch (*Hippocrepis comosa*), Spiny Rest Harrow (*Ononis spinosa*) and Bastard Toadflax (*Thesium humifusum*) amongst the pasture plants, whilst amongst the woodland and scrub species may be cited *Astragalus glycyphyllos*, the woodland Everlasting Pea (*Lathyrus sylvestris*), the Lily of the Valley (*Convallaria majalis*) and Herb Paris (*Paris quadrifolia*). We have already called attention to the fact that some plants that grow on calcareous soils do so mainly because of the physical conditions that obtain there, and so we can understand that in a wetter or colder climate a species may be associated with calcareous soils which in more genial conditions might show no such preference. It is for this reason that the proportion of species which tend to be associated with calcareous soils augments as we pass, for example, from the south to the north of Finland. It is doubtless for a similar reason that we find in the more humid climate of Ireland certain species are regarded as calcicole which show no such marked soil preference in southern and eastern Britain. Such, for instance, are *Hypericum perforatum* and *Trisetum flavescens*.

The Irish flora includes several species that do not occur in Britain and which exhibit a marked preference for calcareous soils. Such are the Sandwort *Arenaria ciliata*, the Hairy Cress *Arabis brownii* that occurs in sandy places on the west coast, the saxifrages *Saxifraga sternbergii* and *S. hirta* both features of the limestone pavements in company with the orchid *Neotinea intacta*. Two other calcicoles that are very rare and local in England are locally common in Ireland. The shrubby cinquefoil *Potentilla fruticosa* that is confined to a small area in Teesdale is abundant on the limestone from N. Clare to E. Mayo.

The Eyebright, *Euphrasia salisburgensis*, is common on the limestones of Ireland but has only been found as a great rarity in Yorkshire. The Strawberry tree, *Arbutus unedo*, and the heath *Erica mediterranea*, neither of which are found in Britain, occur according to Praeger in siliceous as well as calcareous habitats. (*The Botanist in Ireland*, 1934.)

The very local *Draba muralis* is a feature of the English limestone, but is more common on old walls, where the mortar joints provide the calcareous conditions which promote its success. In Ireland it is regarded by Lloyd Praeger as an introduction that is spreading (cf. *The Botanist in Ireland*, p. 72, 1934). Similarly, though the Rue Saxifrage (*Saxifraga tridactylites*) is common on the more stable phases of dune development where the sand is calcareous, this species is even more familiar as a plant of the old mortar joints of walls. Thus these latter provide an artificial extension of the natural habitats similar to that provided by hedgerows for the natural flora of the wood margin and scrub.

Such extensions, unless their significance be fully apprehended, may easily lead to misconceptions as to the requirements of a species. For example, the occurrence of the Bloody Crane's-bill (*Geranium sanguineum*) not far from Dowel's Brook in the Wyre Forest, which occupies in the main very acidic soils derived from the siliceous millstone grits, poor in bases, might suggest an indifference to the presence of calcium carbonate did one fail to appreciate that a curved band of Spirorbis limestone is situated in rocks above where this species occurs.

It is worth noting that the Cat's-foot (*Antennaria dioica*), which we commonly associate with the humid conditions of mountains, was at one time to be found at low altitudes in various localities on the chalk downs. For instance, this plant formerly grew on the Dunstable Downs, and I remember seeing two plants still there some twenty-five years ago. On Royston Heath it no longer flourishes except, possibly, as a great rarity. It is possible that the lowering of the permanent water

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PLATE XVII. ABOVE. The Fragrant Orchis (*Gymnadenia conopsea*) in turf of Red Fescue. ×⅔. BELOW. Limestone terraces and pavements near Ingleborough. The wood in the foreground is mainly Ash whilst the trees in the middle distance, colonising the limestone pavements are Ash and Bird Cherry (*Prunus padus*). The pasture below is the habitat of *Primula farinosa*.



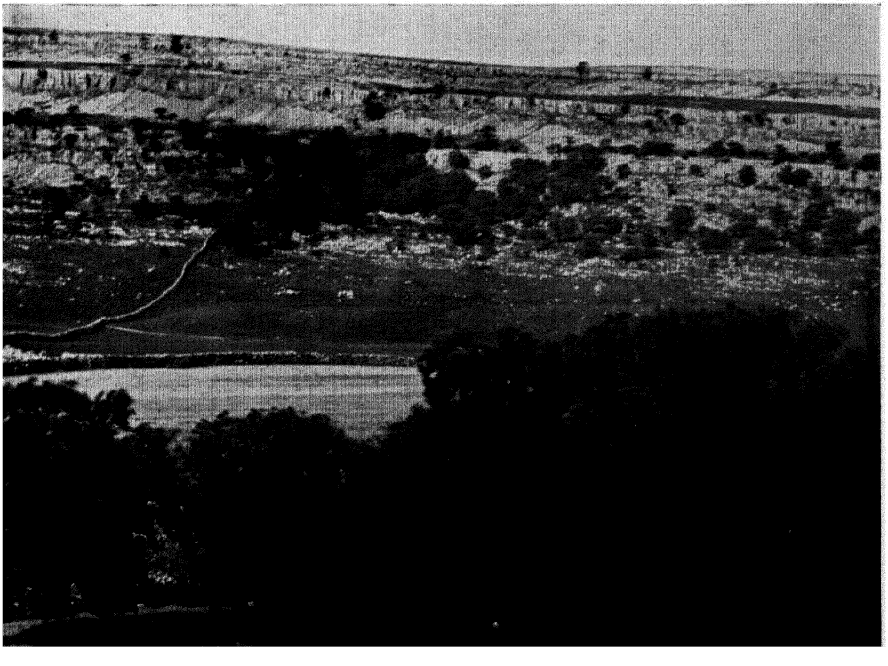






table during the last few centuries, of which there is some evidence, may have been responsible for the diminution of this species, as also of the Club Moss (*Lycopodium clavatum*), which was formerly present, though a great rarity, on the Bedfordshire chalk downs, despite its usual association with acidic soils.

There are an appreciable number of species of flowering plants that we may find growing abundantly on calcareous soils which also occur on non-calcareous soils provided these are well drained, such as, for instance, may be provided by sands and grits. It seems probable that for these species the physical conditions of good drainage, soil temperature, etc., are the more significant factors. Amongst such *Calamintha acinos* and the Viper's Bugloss (*Echium vulgare*) are striking examples. They are both particularly frequent on the chalk, but the abundance they can exhibit on areas of derelict cultivation in Breckland, even where these have no calcium in the soil other than as exchangeable bases, suggest no appreciable demand for this element, although it must not be forgotten that under such conditions the pressure of competition is not severe.

Having regard to the multiplicity of the conditions that combine to determine the success or failure of a species in competition with its neighbours, of which soil and climate are but two, however important, it would be surprising if we did not occasionally find species that normally are associated with calcareous soil sometimes growing where there are no free carbonates and where perhaps the amount of exchangeable bases is not high. Nevertheless, one must avoid attaching undue significance to such apparent exceptions, and indeed the importance of calcareous conditions in affecting the nature of vegetation is nowhere better demonstrated than in areas where calcareous and non-calcareous soils are in abrupt juxtaposition. These provide us with nature's demonstrations of the effect of soil distinctions over long periods of time which the effects of an artificial experiment carried out for a period of years, in place of centuries or even millennia, may fail to evoke.

Such an one could be seen, and still may for all I know, in Dinmore Wood, Herefordshire, which was a wooded hill of

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PLATE XVIII. The Limestone flora. ABOVE. The western spiked Speedwell (*Veronica hybrida*), $\times\frac{2}{3}$, North Wales. BELOW. Spring Sandwort (*Arenaria verna*), Great Orme, Carnarvonshire. Life-size.

non-calcareous Old-Red Sandstone, but a band of highly calcareous cornstone passed vertically up the hill, more or less parallel with the railway tunnel beneath. As one traversed the wood in spring one saw the dead bracken fronds and other dark remains of the characteristic vegetation of siliceous soils, when suddenly, on approaching the band of cornstone, there appeared a belt of vivid green where the young shoots of Dog's Mercury, Herb Paris, Cuckoo Pint and Moschatel formed a home for the chalk-loving snail, *Cyclostoma elegans*, whilst down below the Spurge Laurel (*Daphne laureola*) and the Canterbury Bell (*Campanula trachelium*) were flourishing. None of these species was present except where the cornstone had provided a suitable soil, and the transition on either side of the narrow calcareous band was quite abrupt. Again, in Haugh Wood, south of Hereford, we can see soil derived from the highly calcareous 'Ledbury marble' occupied by a part of the wood in immediate juxtaposition to the much larger area that rests on the siliceous Mayhill Sandstone. The latter is occupied by an Oakwood of *Quercus petraea* (*Q. sessiliflora*) with a ground flora of Whortleberry (*Vaccinium myrtillus*), Heather (*Calluna vulgaris*) and Bracken. Then as we step over on to the Wenlock limestone the trees are *Quercus robur* mixed with Ash, and in place of the Whortleberry and Bracken we find such plants as Dog's Mercury, Cuckoo Pint and the calcicolous Wood Vetch (*Vicia sylvatica*) (Pl. XXI).

Similarly, we can find abrupt transitions in the vertical direction, particularly where there is a high rainfall and a relatively impermeable calcareous substratum. Thus on the Wenlock limestone at Conygree Wood, Ledbury, you can see a carpet of Whortleberry and Heather growing in a leached and humus-rich soil that rests, with but a very rapid transition, upon the limestone beneath (cf. E. J. Salisbury and A. G. Tansley, *Journ. Ecology*, IX, pp. 19–38, 1921), or again in the north, near Ingleborough, one can see Heather, Whortleberry and Crowberry (*Empetrum nigrum*), established, no doubt in the first instance as seedlings, in a completely leached bed of acidic soil, with roots passing down into the crevices of the mountain limestone beneath. Since these so-called calcifuge species looked remarkably vigorous and healthy, it is possible that we have here the counterpart of the experiment described previously with stratified soil, but concerning calcifuge instead of calcicole plants.

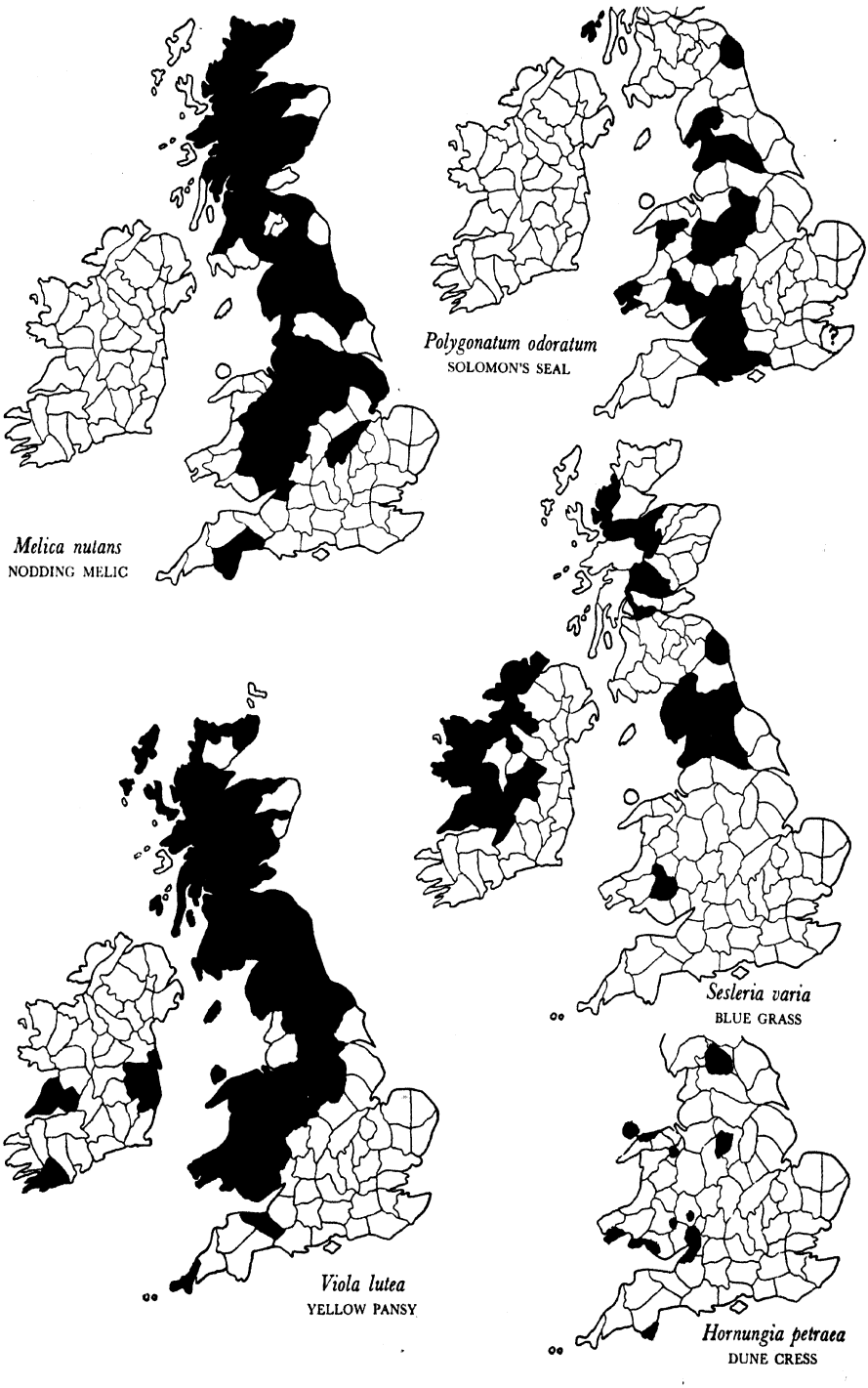


FIG 42. Distribution maps of limestone and dune species. Oceanic types.

XII

BIOLOGICAL NOTES ON SOME CHARACTERISTIC LIMESTONE SPECIES

Actaea spicata	Baneberry
Primula farinosa	Bird's-eye Primrose
Geranium sanguineum	Bloody Crane's-bill
Sesleria varia	Blue Moor Grass (Map, Fig. 42)
Dianthus caesius	Cheddar Pink
Cirsium eriophorum v. *britannicum*	Cotton Thistle (Map, Fig. 15, p. 43, Pl. XIX)
Aster linosyris	Goldilocks
Helianthemum canum	Hoary Rock Rose
Galium pumilum (*G. sylvestre*)	Limestone Bedstraw
Gymnocarpium robertianum	Limestone Polypody
Colchicum autumnale	Meadow Saffron
Polygala amara	Milkwort
Dryas octopetala	Mountain Avens
Hypericum montanum	Mountain St. John's Wort (Pl. XIX)
Melica nutans	Nodding Melic Grass (Map, Fig. 42)
Dryopteris villarsii	Rigid Buckler Fern
Cardamine impatiens	Touch-me-not Cress
Helianthemum polifolium	White Rock Rose
Vicia sylvatica	Wood Vetch (Pl. XXI)
Lathyrus sylvestris	Woodland Everlasting Pea
Viola lutea	Yellow Pansy (Map, Fig. 42)
Chrysosplenium alternifolium	Yellow Saxifrage
Gagea lutea	Yellow Star-of-Bethlehem
Carex digitata	
Koeleria vallesiana	
Neotinea intacta	
Trinia glauca	

BANEBERRY, *Actaea spicata*. Ranunculaceae. 2n=16.

This herbaceous perennial is a special feature of the Ash-woods of the northern limestone. It has rather firm foliage. New leaves are formed in late February or early March. The black berry contains several seeds (5–12) and dispersal is by birds. Germination takes place more readily in darkness than in light (Kinzel). The seeds weigh about 0·006 gm. The plant possesses a mass of roots about 12–14 ins. deep (30–35 cms.) and Heilig records an osmotic pressure of 10 atmospheres.

A northern species confined in Britain to Yorkshire, Lancashire and Westmorland.

GOLDILOCKS, *Aster linosyris*. Compositae. 2n=18.

This beautiful Aster easily recognised by its finely divided leaves and lack of ray florets is a perennial tufted herb, with dormant buds close to the soil surface. The new leaves develop in February.

It is a southern-continental type that has a very restricted distribution in Britain on the mountain limestone of Devon and Somerset, the Gower Peninsular of South Wales and on the isolated Humphrey Head in Lancashire.

TOUCH-ME-NOT CRESS, *Cardamine impatiens*. Cruciferae. 2n=16.

A cress of calcareous woodlands sometimes over a foot high. The pinnate leaves have numerous stalked leaflets which are deeply toothed. The small white flowers (*ca.* 6 mm.) are sometimes without petals. The slender pods split open in an explosive manner, distributing the small seeds to an appreciable distance. Germination occurs in spring.

Carex digitata. Cyperaceae. 2n=52.

A tufted sedge with soft broad flat leaves and slender spikelets all diverging from the subtending bracts. A northern-continental type, confined in England to woods on limestone from Yorkshire and Derbyshire to Herefordshire and Devon.

YELLOW SAXIFRAGE, *Chrysosplenium alternifolium*. Saxifragaceae. 2n=48.

A rather succulent winter-green perennial with alternate leaves, the basal ones kidney-shaped and beautifully crenate; easily distinguished from the common Yellow Saxifrage (*C. oppositifolium*) until the flowering period, when their similarity increases. This is a northern-continental type chiefly associated with partial shade in woods on the limestone of the west and north, where alone does it attain any appreciable frequency.

COTTON THISTLE, *Cirsium eriophorum* v. *britannicum*. Compositae. 2n=34. (Pl. XIX)

A biennial plant with handsome spinous pinnate leaves which in the first year form a rosette that may attain nearly 4 ft. in diameter (1·2 m.). The stem is up to 6 ft. in height (1·8 m.) and bears large purple flower heads surrounded by an involucre of woolly bracts. The polished mottled fruits

number from about 100–300 per head, but many are eaten by beetle larvae.

This is an oceanic variety of the continental species and is commonest on the limestones of the Cotswolds (cf. map, p. 43).

MEADOW SAFFRON, *Colchicum autumnale*. Liliaceae. 2n=38; 42.

A southern perennial herb with a deeply seated corm usually 4–8 ins. (10–20 cms.) beneath the surface and producing its broad leaves, three to five in number and from 6–12 ins. (15–30 cms.) in length, in spring. The foliage withers in late summer and the two or three flowers are produced in late September. The capsules which mature about June, contain a number of small seeds (*ca.* 0·0044 gm.), which are probably distributed mainly by rain-wash.

The corm contains a considerable amount of starch and the poisonous colchicine. Characteristic of the flushes in woodlands, it occurs abundantly in some damp limestone meadows that may have once been woodland.

CHEDDAR PINK, *Dianthus caesius*. Caryophyllaceae. 2n=60; 90.

An evergreen perennial pink with glaucous foliage and leaves that are rough along the edges, forming a mat-like group of rosettes arising from the woody branched rootstock.

The fragrant pink blooms are about 1 in. across (2·5 cms.) and usually solitary, either hermaphrodite or female.

It is a Mediterranean-type extending on the Continent as far north as Belgium and only wild in Britain on the limestone cliffs of Cheddar, where it attains its northern and western limit. The seeds germinate in the autumn. Recorded from German dunes.

RIGID BUCKLER FERN, *Dryopteris villarsii* (*Lastrea rigida*). Polypodiaceae.

A stiffly growing tufted fern characteristic of limestone clefts and found in Flintshire and Snowdonia, but only frequent in the limestone pavements of the north. The firm dull green fronds are 1–2 ft. high (30–60 cms.) and bear numerous glandular hairs when young that produce a glaucous effect and a slight fragrance.

MOUNTAIN 'AVENS, *Dryas octopetala*. Rosaceae. 2n=18.

An arctic-alpine woody evergreen mat-plant, mostly on limestone rocks, which occurs near sea-level in Ireland, but

ascends to 2,700 ft. (830 m.). The oval crenate leaves are dark green and polished above but hoary beneath. The white flowers usually have eight or nine petals, but vary greatly in size. Mostly they are from 25 to 40 mm. in diameter, with stamens and carpels functional. Male flowers may be produced on the side branches which do not attain so large a size (25–30 mm.), whilst female flowers can also occur with very short functionless stamens and these are from 20 to 30 mm. in diameter (cf. H. Harms, *Ber. Deut. Bot. Ges.*, 16, p. 292, 1918). The flowers are visited by insects for the nectar and pollen. The awned fruits are dispersed by wind. Endotrophic mycorrhiza occurs in the root.

YELLOW STAR-OF-BETHLEHEM, *Gagea lutea*. Liliaceae. 2n=72.

A bulbous perennial with small yellow flowers about 18 mm. in diameter when wide open, but which close about midday. There is a single basal leaf. The capsule may contain up to eighteen seeds or more, but in Britain these are rarely produced, and reproduction is mostly vegetative by means of up to twelve or fifteen bulbils arising from the base of the small rounded bulb. White in *The Bristol Flora* (p. 589, 1912) refers to the great uncertainty in the flowering of this plant and suggests that it seldom or never sets seed.

G. lutea is a continental species that in Britain mostly occurs in the woods on limestone.

LIMESTONE BEDSTRAW, *Galium pumilum* (*G. sylvestre*). Rubiaceae. 2n=44.

A prostrate perennial evergreen species similar to, though less tufted than, the common Heath Bedstraw (*Galium saxatile*) and with six to eight leaves in a whorl in place of the six of *G. saxatile* and with narrow lanceolate leaves bearing marginal hairs backwardly directed.

BLOODY CRANE'S-BILL, *Geranium sanguineum*. Geraniaceae. 2n=84.

An herbaceous perennial with a robust branched root-stock, which bears the dormant shoots a short distance above the surface. The large solitary flowers, over 1 in. across (2·5–4 cms.), vary from pink to purple, more rarely white. The seeds which are wrinkled weigh about 0·011 gm. and are

forcibly ejected from the fruit to a distance of as much as 13 ft. (4·5 m.) from the parent plant.

It occurs on limestone and calcareous dunes from Ross southwards and occasionally in Ireland. Although the flowers are far from being blood-coloured, the deeply cut leaves not infrequently assume a dark red autumnal coloration.

LIMESTONE POLYPODY, *Gymnocarpium robertianum* (*Polypodium robertianum*). Polypodiaceae.

A fern with a scaly creeping stem by means of which it spreads and sometimes forms large patches as on limestone screes in the Cotswolds. The fronds are triangular and similar to those of the Oak Fern, but stiff in texture and bearing glandular hairs. A characteristic fern of the limestone from Perthshire southwards, its intolerance of poor drainage may be the major factor in its restriction.

HOARY ROCK ROSE, *Helianthemum canum*. Cistaceae. 2n=22.

A prostrate shrub with small grey leaves forming a low dome or mat of crowded foliage. The yellow flowers are small compared with the common Rock Rose, usually about 7–18 mm. in diameter. The seeds have an average weight of 0·00074 gm.

In Britain it is confined to N.W. England, N. and S. Wales and the W. of Ireland (see map, p. 41). In the last-named area it occurs as a variety with the upper surface of the leaves devoid of the covering of grey hairs.

WHITE ROCK ROSE, *Helianthemum polifolium*. Cistaceae. 2n=20.

A low growing shrub similar to the common Rock Rose but with grey foliage and white flowers. The stamens are sensitive and when touched move from the erect to the horizontal position and return in about fifteen seconds. The seeds which ripen in July exhibit intermittent germination from mid August to mid May. Young plants usually flower in the third year. The species is a southern-oceanic one.

MOUNTAIN ST. JOHN'S WORT, *Hypericum montanum*. Hypericaceae. 2n=16. (Pl. XIX)

A tufted perennial with short, prostrate winter-green shoots and stiff, erect inflorescences. The oblong or oval leaves are

smooth above, with marginal black glands, and with short hairs beneath. The rigid stems which are only branched above produce a rather dense inflorescence of pale yellow slightly fragrant flowers, giving place to crowded capsules, each containing an average of 120 small seeds (the seed weighs about 60 mgms.). They are dispersed by wind and usually exhibit from 70–80% germination, which in nature normally occurs towards the end of March. New shoots begin to develop from mid-March to early April.

A continental species most frequent on the limestones of the west, but not extending into Ireland and, except in Kirkcudbright, absent from Scotland.

Koeleria vallesiana. Gramineae. 2n=42.

A rare tufted perennial grass of the limestone of Somerset with much less hairy leaves and an inflorescence that resembles a small foxtail and is not interrupted like that of *K. gracilis.*

A southern-oceanic type.

Woodland Everlasting Pea, *Lathyrus sylvestris.* Leguminosae. 2n=14.

A coarse perennial with winged stems arising from a creeping rootstock and leaves consisting of a pair of stipules, one pair of large sword-shaped leaflets and a branched tendril.

The pod contains 10 to 14 seeds. The seeds may take a year to germinate. Occurs from mid-Scotland southwards; absent from Ireland.

Nodding Melic, *Melica nutans.* Gramineae. 2n=18.

A perennial grass spreading by means of stolons with flat slightly hairy green leaves which have a very short rim-like ligule extended, on the side away from the leaf-blade, into an awn-like outgrowth. The arched inflorescences bear pendent oval spikelets purple and green in colour, all drooping to the lower side. More or less confined to calcareous woods in the areas of higher rainfall. Occurs N.W. of the line from Dorest to the Wash; absent from Ireland. The grains weigh *ca.* 0·0026 gm.

The spikelets contain two fertile flowers followed by a series of abortive flowers each more reduced than the preceeding one (cf. A. Arber, *The Gramineae*, p. 176, 1934).

Neotinea intacta. Orchidaceae.

A perennial with a rosette of oblong spotted leaves with a dense and often spirally twisted inflorescence up to about 10 ins. high (25 cms.) of small (*ca.* 4 mm.) pale purple flowers. It is confined to the limestone pastures of Galway and Mayo and is a member of the southern-oceanic element of the European flora

Polygala amara and *P. austriaca.* Polygalaceae.

Both these Milkworts are small dwarf perennials with rosettes of leaves similar to *P. calcarea.* *P. amara* usually has pale reddish flowers and the flowering shoot attains some 3–4 cm., producing flowers that are only about 4·5 mm. long with capsules which are shorter than the sepals, which latter bear a network of branched veins. The seeds are about 1·5 mm. in length.

This is a northern-continental species confined in Britain to the porous sugar-limestone soils of Teesdale.

The closely allied *P. austriaca* has even smaller flowers, about 2·5 mm. long, with narrow sepals of which the veins are unbranched, and smaller seeds, *ca.* 1·2 mm. It is a continental type confined in Britain to the Kentish chalk.

Bird's-eye Primrose, *Primula farinosa.* Primulaceae. 2n=18.

Rather like a miniature lilac-coloured Auricula with a yellow eye, the heads of flowers are borne on bare stems usually 2–6 ins. (5–15 cms.) high arising from a rosette of rather narrow leaves which are smooth above and covered with a waxy powder beneath that is either white or yellow. As in the Primrose, the flowers are of two types on different plants, either with the stigma at the top of the tube and the stamens lower down (Pin-eyed) or these positions reversed (Thrum-eyed). Although self-fertilisation is possible, the number of seeds produced is then small. Normally the two types of flower ensure cross-pollination and the average number of seeds produced per capsule is about fifty. The average number of capsules produced by a plant is four or five, so that the seed production is of the order of 200 to 250 in a season. The flowers are freely visited by both bees and butterflies.

Blue Moor Grass, *Sesleria varia.* Gramineae. 2n=28.

A perennial creeping tufted grass with narrow, flat glaucous leaves. The stems from 6–18 ins. high (15–45 cms.) have oval heads of flowers of a somewhat blue-grey colour.

A species especially of central and western Europe, most frequent in Britain on the limestones of the N.W. and of local occurrence in Ireland. *S. coerulea* is an east European and Scandinavian type with which the British plant was confused.

Trinia glauca. Umbelliferae. 2n=18.

A biennial or perennial herb with pale bluish-green bipinnate foliage and a fleshy tap-root. The male and female flowers are normally borne on separate plants. The male plants are quite small (6–7 ins.=15–17·5 cms.) whilst the female plants are about 1 ft. high (30 cms.) with larger leaves. The winter state is marked by the fibrous remains of the leaf-bases. The smooth, ovoid mericarps weigh about 0·0016 gm. and germination is intermittent.

The species is a southern-continental type found in Britain only on the limestones of the Bristol area and in Devon on Berry Head.

Wood Vetch, *Vicia sylvatica.* Leguminosae. 2n=14. (Pl. XXI)

A climbing perennial with pinnate leaves ending in much-branched tendrils and producing one-sided clusters of white flowers veined with blue. The pods contain three to four seeds.

A northern-continental species which is here chiefly to be found on the limestones of the north and west. For distribution map, cf. E. J. Salisbury, *The East Anglian Flora*, Map 4 (Norwich, 1932).

Yellow Pansy, *Viola lutea.* Violaceae. 2n=48.

A perennial very closely allied to *V. curtisii* with normally larger flowers (*ca.* 2 cms.) which are either yellow, purple, or with upper petals blue and lower yellow. The slender rhizomes branch freely just beneath the surface and produce leafy shoots which are only slightly hairy and bear solitary flowers.

XIII

THE DUNELAND HABITAT

THE coasts of the British Isles are in a perpetual process of change. Here the change is secular and so imperceptible as to pass unnoticed, there rapid so that some parts suffer obvious loss, through erosion by the waves, whilst in yet others there are equally manifest gains, where the additions to the land surface take the form of either salt-marshes, sand dunes, or shingle beaches, their character depending mainly on the degree of fineness or coarseness of the material of which they are composed and their location dependent upon the local topography and degree of water movement.

If, in imagination, we take a walk along the fourteen miles of the Chesil Bank we should note, as we leave the Isle of Portland and progress towards Burton Bradstock, that the shingle changes from the large pebbles several inches across at the Weymouth end, gradually becoming smaller and smaller till, by the time we reach Abbotsbury, the material has become fine shingle, whilst towards Burton Bradstock the beach consists of almost coarse sand; and the fact that the local fishermen are alleged to be able to recognise their position on the beach at night by merely taking up a handful of the shingle is a tribute to the precision of this gradation. The efficient sifting action of the current to which this progressive change of structure bears witness is an outcome of the relation which obtains between the carrying capacity of the sea-water and its rate of movement.

It is only in the relatively quiet waters that fine sand and mud can be deposited, for with quicker flow these particles would be carried further on. So it is in the comparatively sheltered stretches of an advancing coast line, or what had once been such, that sand has been deposited upon the sloping shore. When at low tide this becomes exposed the on-shore winds carry the dry sand grains to higher levels beyond tidal action and thus provide the material for dune formation. The deposition of sand upon the zone between tidal lines implies a current

adequate for sand-grain carriage from a source of erosion elsewhere with a slowing down that permitted the water-borne sand-grains to have been shed. Such slowing down often occurs in protected bays and near the mouths of estuaries and it is in such situations that dune systems are most frequently encountered.

Sand dunes occupy extensive areas along our coasts and have been the playgrounds of man for centuries. In Scotland they are commonly termed 'links' which name to-day suggests their frequent use for golf rather than their pristine condition of rough ground. In East Anglia the name 'meals' or 'meols' (*melr*, old Norse for sandbanks) is commonly in use, and it is interesting to note that this was the name of the old village of Meols, now a part of Southport, located on the dunes of the Lancashire coast. In the West country the term 'burrows' (*beorg*, O.E. hill) is employed (e.g. Braunton Burrows, Devon, Kenfig Burrows, Glam.) and 'towans' is a name used in Cornwall. The name dune, like down, is derived from the Old English *dun* and emphasises the hilly character of the topography, just as the local appellation 'dene' (*denu*, O.E. valley) emphasises the undulating character.

In Scotland dunes border the coasts of Caithness at Freswick and Reay, where the abundance of the Meadow Rue (*Thalictrum minus* v. *dunensis*) is a conspicuous feature, whilst the links of Keiss and Dunnet in the same county show various stages of dune development with extended areas of the more mature flattened condition. Further south a large dune system borders the Moray Firth and constitutes the Culbin sands, notable for their mobile condition and spreading over some 18 sq. miles, whilst similarly on the southern shore of the Firth of Tay are the Tentsmuir sands. The fixed dunes in both these areas have been extensively planted in recent years by the Forestry Commission and the former mobility of the Culbin sands has thereby been largely stabilised. South of the border the chief dunes in Northumberland are at Holy Island and in Lincolnshire at Mablethorpe. Dunes occur in Yorkshire at Spurn Head. South of the Wash the dune systems at Scolt Head and Blakeney Point are of especial interest as having been developed on shingle spits and, together with those of Hunstanton, they have been the subjects of detailed study. In Suffolk there is an appreciable area of dunes at Kessingland.

South of the Thames there are no important dune systems on the Kent, Sussex and Hampshire coasts, although mention may be made of the dunes at Deal, Hythe, Rye and St. Helens in the Isle of Wight, which were formerly localities for interesting dune species. The dunes at Studland in Dorset not only occupy an appreciable area, but are comparable to those of Culbin

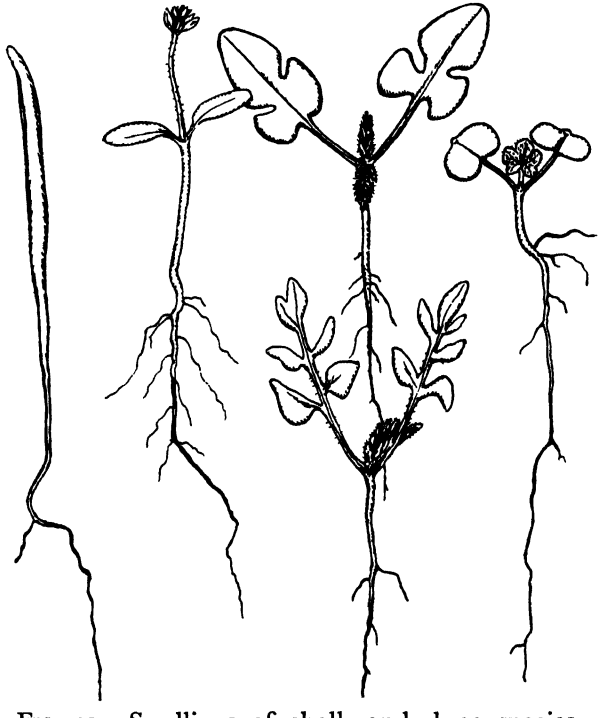


FIG 43. Seedlings of chalk and dune species. From left to right. Earth-nut (*Bunium bulbocastaneum*) showing the single cotyledon; Cross-wort (*Galium cruciatum*); Stork's-bill (*Erodium neglectum*) with three-lobed cotyledons above, and Scented Stork's-bill (*Erodium moschatum*) below; Dove's foot Crane's-bill (*Geranium molle*).

sands with respect to their low content of calcium. South Devon now has no appreciable area of dunes, but those at Dawlish Warren were once much more extensive and like the dunes at Slapton Sands are interesting plant habitats. The north Cornish coast has dunes of some significance near Hayle, extending almost to Godrevy Point. The dunes at Holywell, at Perran Bays and near the mouth of the Camel Estuary, as well as those at Bude, are all rich in calcium. Passing into the

Bristol Channel, the north Devon coast has a number of dune areas of which the more noteworthy are those at Westward Ho, Braunton Burrows and Woolacombe. The dunes at Braunton are not only extensive (Pl. XXVI) with a flora and fauna of particular interest, but present a valuable series of stages in dune development and many large 'slacks' between the ridges.

The coast of Somerset exhibits a small dune area at Minehead and a large one at Burnham and Berrow, but on the other side dune systems are numerous all along the South Wales coastline. The most interesting of these are Merthyr-Mawr Warren, Porthcawl, Kenfig, Aberavon, Crymlyn, Penard, Oxwich Burrows, Whitford Burrows, Towyn, Pembry Burrows and Laugharne Burrows. Of these, the dune system at Kenfig shows instructive developmental stages, and the dunes at Tenby are especially interesting, if of small area, as the home of the introduced snail *Helicella pisana*, from Natal, which occurs there in great abundance (Pl. XXIII). Further west come the dunes of Freshwater West Bay near Milford Haven and the Burrows near St. Davids. In mid-Wales dune systems occur at Morfa Dyffryn, Morfa Harlech and Morfa Bychan, the first-named being noteworthy for its dune 'slacks.' On the Lleyn Peninsula there are attractive dunes at Abersoch, whilst in Anglesey there are extensive dunes at Newborough Warren and Cymmeran, both about three square miles in area.

On the North Welsh coast the dunes at Llandudno are small, but those at Rhyl are extensive. The dunes of the Wirral at Hoylake, West Kirby and Wallasey have been largely converted to golf links; but the extensive dunes of the Lancashire coast at Formby, Ainsdale and Southport, occupying some twenty-two square miles and bordering some sixteen miles of coast, often from one to three miles wide, still retain large unspoilt areas and exhibit in a striking manner the formation of parallel dune ridges where the sequence in space accords with their sequence in time and thus show clearly the stages of development of dune soils and their changing flora, whilst the slacks which separate the ridges are characterised by a rich vegetation. At St. Anne's golf has again largely claimed the sand hills, but further north interesting dune areas are to be seen at Walney and near Ravenglass, Fothergill, Maryport, Allonby Bay and between Beckfoot and Silloth. In the South Hebrides highly calcareous dunes occur with sands containing as much as 70% $CaCO_3$.

In Ireland dune systems are not infrequent, and we shall have occasion to refer to those at Waterford and on the north Irish coast.

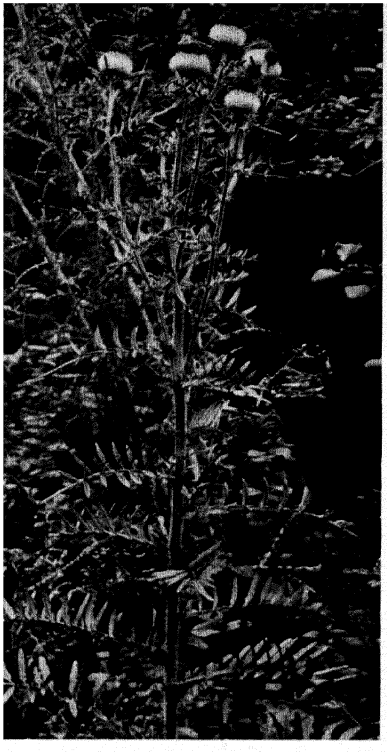
It will be evident from this brief enumeration of only a selection of the dune areas fringing our shores that though much more frequent and extensive in some regions than others they are sufficiently distributed throughout to permit the dune flora as a whole to include members of most of the more specialised geographical elements of our flora. Thus in the dune slacks of Caithness we can find the northern species *Primula scotica*, looking like an Auricula in miniature, whilst in the slacks at Braunton occurs the Mediterranean Ball Rush (*Scirpus holoschoenus*, Pl. XXVI). The total area of coastal sand dunes is by no means inconsiderable, and hence their economic exploitation not uncommonly conflicts with their preservation for amenities. Their recreational value is great and as the sequel will show they provide the home for a number of native plants of supreme interest, not only for their own sake but because dunes illustrate in a spectacular way the phenomenon of soil formation and the part which vegetation plays in this process.

DUNE SOILS

When dunes are first formed they can scarcely be said to provide a soil, for they consist almost entirely of sand grains and shell fragments with a limited admixture of organic material blown up from the dried drift lines of the sea shore. Occasionally this source of enrichment may be very considerable. Thus the drift line at Scolt Head, on the coast of Norfolk, one April consisted of countless millions of the carapaces of small crabs about 3–4 mm. in diameter, mostly empty but, from the powerful odour, evidently by no means exclusively so. Where salt-marshes adjoin a dune system, drift lines after a storm may present vast multitudes of the small mollusc *Paludestrina stagnalis* and in one year at Blakeney Point the drift of these extended for many yards and was in places more than 6 ins. deep and

* * *

PLATE XIX. Limestone flora. TOP LEFT. Cotton Thistle (*Cirsium eriophorum var. britannicum*), $\times \frac{1}{12}$, Winchcombe, Gloucestershire. TOP RIGHT. St. John's Wort (*Hypericum montanum*), Little Orme, Carnarvonshire. BELOW. Bird Cherry (*Prunus padus*) on Limestone Pavement at Ingleborough. $\times \frac{1}{4}$.











over 1 ft. in width! The shells of mollusca and the carapaces of crabs are chiefly significant as a source of carbonates, but the organic material in their composition, although only containing about a tenth of its weight of nitrogen and in the snails representing but a small fraction of the whole, may nevertheless not be negligible as a source of this element. In this connection it must also be remembered that the inter-tidal zone from which dune sand originally comes has a rich fauna, the dead bodies of which must be a contributory source of nitrogen. Professor Herdman, for example, estimated that in the intertidal zone along one stretch of coast the population of lugworms in a length of one mile was of the order of between three and four millions. Moreover the presence of carbonates in the younger dune soils favours the activity of nitrogen-fixing organisms whether free living or in the roots of leguminous plants. It is noteworthy that the root systems of the Clovers and Vetches that frequent fixed dunes are usually amply supplied with root nodules sometimes highly pigmented with haemoglobin, suggesting a high level of efficiency.

The details of change with respect to soil characters can be more appropriately dealt with in relation to dune development and succession, since these changes are of a regular character correlated with the period that has elapsed since the dune was formed; but it will be convenient here to note the more salient characteristics of dune soils which change in degree and even in kind with the passage of time.

The high degree of mobility is, at the outset, the feature which is most significant in relation to vegetation, and with this is linked the very poor capacity of dune soils for retaining water, both of which features are associated with the large size of the sand grains compared with the particles that mostly comprise normal soils. This mobility is sometimes manifest in removal by wind, at others in rapid addition, so that both a rise and a fall in the sand surface may alike occur, and this at a rapid rate that inhibits the growth of any but highly specialised types. Moreover, although the dunes begin to be formed above tidal level the youngest stages are liable to inundation

* * *

PLATE XX. Limestone flora. ABOVE. Limestone Cliffs near Clapham showing colonisation by Ash, Ivy and Elder. BELOW. The wild Coton-easter (*C. integerrima*) confined to Mountain Limestone of North Wales.

by exceptionally high tides and, since the newest dunes are nearest the sea, the pioneer plants, even if not occasionally covered by sea-water in storms, are inevitably subject to wind-blown spray. The first plants to arrive must in consequence be able not merely to withstand the vagaries of a shifting and arid medium but a measure of temporary and sometimes marked salinity.

The sources of supply from which dunes are built up are the sandy expanses exposed at low water, especially during the spring tides. More particularly, when landward gales prevail, the exposed sand surfaces dry out and as this takes place the sand particles become mobile. The amount of wind which is necessary to start the sand grains into action depends upon their size, or we can regard this from the aspect of the outcome, which is that the average size of the sand that forms any dune is, stated in general terms, related to the average strength of the prevailing on-shore winds. Thus, to quote extreme examples, the dunes on the Portuguese coast, exposed to the full force of the Atlantic gales, are made up of coarse grains with an appreciable percentage over a millimeter in diameter,[1] whereas those at Southport on the Lancashire coast, where the normal wind velocity is much less, have a lower proportion of coarse grains and a higher proportion of small ones, whilst the dunes of the Norfolk coast, where high on-shore winds are even less prevalent, consist of sand grains whose average size is even smaller, and very large grains over 1 mm. in diameter are absent (cf. Table I).

TABLE I. SAND-GRAIN SIZE IN SURFACE SAND OF DUNES (DEPTH 0–6 ins.)

Diameter of grains	*Comporta Portugal*	*Southport Lancashire*	*Blakeney Norfolk*
Over 1 mm.	8·1%	1·2%	0·0%
0·3–1 mm.	89·8%	90·5%	17·9%
0·25–0·3 mm.	2·0%	3·0%	68·9%
0·2–0·25 mm.	—	3·0%	8·9%
Less than 0·2 mm.	—	2·0%	4·1%

Usually a wind velocity of about one mile an hour is necessary to make grains of 0·25 mm. (*ca.* 0·0097 in.) diameter begin to move along the surface, and higher speeds are requisite to lift them. As R. A. Bagnold has shown the medium sized

[1] J. S. Westgate (*U.S. Dept. Agric. Bull. Plant Industry*, 65, 1904) records for the Cape Cod dunes 77% of grains 0·5–1mm. in diameter and on the windward face nearly 65% of sand grains 2–6 mm. associated with frequent winds of fifty to sixty miles per hour.

grains of wind-borne sand build up their numbers by the grains first started into movement falling back to the surface and so impinging on others, which are thus initiated in their flight, and these in turn strike still other grains—a process of multiplication of mobile sand (termed saltation) that increases till so many grains are air-borne that the air may become saturated with the smaller grains and we experience the stinging bombardment that is sensational evidence of the multitude of grains which the wind is hurrying landwards. It is, however, the lighter grains, usually under half a millimeter in diameter, and commonly under 0·3 mm., which travel in the air whilst the heavier grains are rolled by the wind along the surface and the finest dust is blown inland and lost to the dune system. Incidentally the diverse size of the sand grains is responsible for the surface eddies of the wind that create the sand ripples that give the remarkable texture to dune slopes.

Since the sand only becomes mobile when it is dry it is apparent that the length of time for which the foreshore—the source of supply—is exposed and the nature of the weather at low tide, whether hot and windy or cold and wet, will to a great extent determine the amount of sand that is contributed towards dune formation at any one period between tides; and as the exposure is more prolonged and complete during the spring tides than during the neaps, it is obvious that the former periods are more favourable for the supply of sand and that this supply is likely to fluctuate markedly in amount both according to the weather conditions and the state of the tide.

Furthermore, since the strength of the wind determines the size of the air-borne grains and the wind often tends to be more boisterous nearer the shore than further inland, it is not surprising that in general the finest or lightest sand is carried furthest landwards and the coarsest and heaviest grains tend to be shed nearer the sea. This sifting activity by the wind is particularly important in that sand is not entirely uniform in composition and shell fragments, consisting of a mixture of chitin and calcium carbonate, provide particles that are lighter for their size than the grains of quartz that make up so large a proportion of dune sand. As a consequence, the fore-dunes, although often rich in shell particles, frequently exhibit a lower proportion than the dune ridges a short distance further in, but this only applies to the surface layers, since these inner dune

ridges were each in turn themselves once the fore-dunes of the system.

Not infrequently the empty and almost intact shells of the land and marine mollusca are winnowed out by the wind in this way and collect in drifts, where they become buried under sand to constitute local accumulations of calcium carbonate (Pl. XXVIII). Sometimes such shell drifts are carried into parts of a dune system where the sand is otherwise almost or completely devoid of carbonates, and thus such areas present a juxtaposition of contrasting soil conditions and of vegetation which these adjacent conditions support. This has in the past misled botanists as to the soil preferences of the plants observed, because the remarkable lack of uniformity was not realised.

As we shall see later, the dune soils undergo changes with time, of which depletion of carbonates is one of the most marked, especially near the surface; but the shell fragments in the wind-borne sand tend to mask this process and it will be evident from what has already been stated that such retardation of the normal course of soil maturation in this respect will tend to be greatest where the parent material is richest in carbonates and where the prevailing winds are strongest. Indeed, on the Portuguese dunes already referred to only the oldest dunes far inland exhibit the changes noted above, whereas they are very pronounced on the Norfolk coast and on the relatively sheltered dune system at Southport.

The wind which has brought the harvest of sand may likewise remove it, and this is especially liable to occur when the wind blows for some time from a different quarter of the compass than the direction normally prevailing. Only when circumstances bring about a local check to the wind velocity that is a continuing condition, due perhaps to a change in topography or very commonly the presence of a dead or living obstacle, does dune formation begin, and its further progress depends upon colonisation by plants that will provide protection and stabilisation of the rising surface and thus ensure that the rate at which sand grains are added at least exceeds the rate of their removal. Such conditions of greater stability will moreover be enhanced by any circumstances that help the sand to retain moisture after rain and retard its drying in fine weather, since so long as the surface sand grains remain moist they are comparatively immobile.

Sand dunes are to be regarded as temperate deserts the arid condition of which is conditioned not by climatic circumstances as obtain in true deserts but by the lack of capacity of the dune soil to retain water. The sand dune is therefore what is technically known as an edaphic desert (i.e. a desert due to soil conditions), and the degree to which it is entitled to be regarded as such will depend mainly upon two features. Firstly, the coarse texture of the sand, since the larger the soil particles the smaller will be their collective surface in a given volume of soil and it is this total surface that determines how much water can be retained by the mineral particles of the dune. As we have seen, the size of the sand grains is in large part determined by the average wind velocity, so that, other conditions remaining the same, the dunes on coasts with high winds will not only lose more water by evaporation, but there will be less water that can be held by the soil to meet this loss. On the other hand, when the dunes are formed by light winds on a protected shore the grains of sand will have a smaller average size and their total surface for a given volume will be greater whilst the loss by evaporation will be lower. Thus we see that the more windy a coast-line the less favourable the conditions are for plant growth. Secondly, the retention of water by the surfaces of the mineral particles is relatively unimportant compared with the capacity for water retention by any organic material, and hence the sources of addition of organic matter to the dune sand are of the greatest significance in determining the degree of suitability of the dune for plant life. Initially the organic content of dunes depends on the supply from drift and the additions provided by the dead remains of the pioneer species. The latter factor augments with the increasing size of the dune, an aspect to which we shall return when dealing with the changes that dunes undergo with the passage of time, technically known as 'dune succession.' Such succession changes are a feature of all natural habitats and plant communities, but the dune systems are almost unique in that the stages in their development exhibit a sequence in time that corresponds to their sequence in space, so it is possible to study such changes with a degree of certainty that is unattainable in most other plant communities.

Dune sand, as we have noted, normally originates on the foreshore and is blown by onshore winds, when the sand is exposed at low tide, to levels above the range of high tides. It

is important to recognise that the movement of sand particles is essentially a surface phenomenon, so that it is the circumstances obtaining at the level where air and sand meet that are most significant in this connection. Since the agent of transport is air movement the capacity to cause the sand grains to pass from a state of rest is a function of the velocity of wind action at this particular level. Anything which tends to diminish wind velocity will reduce the size of the sand particles which the wind is capable of bringing into motion, and any obstacle which causes what may be termed a 'wind shadow' will, on the lee side, bring about a shedding of all air-borne particles above the size and weight which the diminished rate of air movement in this relatively calm area is now capable of carrying as its burden. As movement is inimical to the growth of plants, it would seem natural to expect that the coarser-grained dunes might be more readily colonised by vegetation than those which are of fine texture, but though this, in a measure, is true, two facts militate against such a consummation: firstly, the coarser the texture the smaller the aggregate surface of the sand grains per unit volume, and, secondly, coarse-grained sands imply the prevalence of high velocity winds during dune building and therefore the probability of a corresponding capacity for sand removal.

Thus it is that when sand accumulates around any dead obstacle this can only lead to dune building if there be colonisation by a perennial species that by its growth and production of organic material effectively and continuously diminishes the risks of removal of the sand grains by wind action below that of the rate of accumulation. At least in the earliest phases, there is always the risk of a deficit in this balance-sheet of sand addition and sand removal. However, under conditions of normal dune development, the credit balance increases with age although the sand income exhibits a contemporaneous decrease. The fall in rate of removal is the outcome of two circumstances: one slow but very important—namely, the gradual change in the dune surface owing mainly to the addition of organic material. This renders the sand less liable to extreme desiccation and in other respects causes the sand grains in the surface to become less mobile. The second factor, which is relatively rapid in its operation, is an outcome of the growth of the plants themselves—namely, the shelter to

the surface which they afford. It is too often forgotten in this connection that the removal of the grains by wind is a sort of paring off of successive layers from the surface and that therefore an extensive root system *beneath* the surface has *no direct protective effect* whatever. But the permeable screen which is presented by the shoot system and foliage of the pioneer plants has a much greater sheltering effect than one might suppose, partly no doubt because the intricate deflections of the air currents passing through the maze of foliage are to some extent mutually arresting.

An important feature to bear in mind is that, owing to the frictional resistance of the surface of the dune and the irregularities of topography, the wind movement is least just above the sand and there is always a gradient of increasing wind velocity from below upwards. Therefore the surface grains are not subject to such strong wind forces as those that are encountered at higher levels. The accompanying data which illustrate this feature were obtained on the Braunton Dunes in April by means of a specially sensitive cup anemometer, for the loan of which I was indebted to Dr. Sheppard, then of H.M. Meteorological Office. The wind velocities here recorded represent the averages of a number of determinations at each height, but, as the records at each level were made with the same instrument and so are comparable in that respect, they suffer from the fact that the determinations were not made

TABLE II. WIND VELOCITIES MILES PER HOUR ON DUNES

Height above surface	*Bare dune*		*Dune with sparse Marram Grass*	
	Range	*Av. v.*	*Range*	*Av. v.*
24 ins. (60 cms.)	10·3–20·36	14·7	7·4 –10·2	8·5
18 ins. (45 cms.)	11·78–15·48	13·2	8·1 – 9·1	8·6
12 ins. (30 cms.)	11·76–12·7	12·2	3·5 – 7·3	5·3
9 ins. (22·5 cms.)	11·0 –13·5	12·4	4·0 – 5·3	4·7
2 ins. (5 cms.)	7·3 – 9·6	8·3	1·34– 2·5	1·7

simultaneously at the different levels. To meet the difficulty of the varying wind velocity, especially at the maximum height, successive determinations were made in ascending and descending sequence. The general trend from below upwards would appear to warrant the validity of the results for comparative purposes. They show that even on the bare dune the velocity of the wind 2 ins. above the surface was diminished to almost

half that which obtained at 2 ft. above ground-level, whilst on the dune clothed with sparse Marram Grass the corresponding reduction is to less than one quarter. The wind force was also measured just above the surface (5 cms. = 2 ins.) both in front of and behind an isolated Marram Grass tuft that represented the beginning of a new dune. These determinations were made with a view to estimating the extent of the shelter effect which such a pioneer plant afforded to the sand behind it and thus also its influence in causing sand-laden breezes to shed their burden.

It was found that at this level (5 cms.) when the force of the wind was from 4·8 to 5·9 miles per hour in front of the Marram Grass, the wind force behind the grass was reduced to from 1·6 to 4 miles per hour, the respective means being 4·4 miles per hour ±0·6 and 2·3 miles per hour ±0·3.

The effect of a wind of over 20 miles per hour velocity was also determined on a dune front facing the direction of the wind. The wind force was determined at three different levels on the flat in front of the dune, at the same three levels halfway up the slope and on the dune crest, 20 ft. above the flat sand in front of the dune.

TABLE III. WIND VELOCITY ON DUNE SLOPES FACING WIND

Height above surface	*Top of dune (20 ft.)*	*Halfway down slope*	*Foot of slope*
18 ins.	19·3 miles/hr.	13·6 m/hr.	11·2 m/hr.
9 ins.	17·3 ,,	10·8 ,,	6·6 ,,
2 ins.	11·8 ,,	—	8·3 ,,

On the windward face of another dune 10 ft. high, the mean velocity at the crest at all levels was 16·3 miles per hour compared with 9·6 miles per hour at the foot of the slope. The presence of the dune ridge behind thus affords a measure of protection to its shoreward face, but implicit in this is a more rapid accretion amongst the grass upon the ridge than amongst that upon its face so that the fore-dune grows in height with increasing wind exposure until the forces of accretion are just balanced by those of wind erosion. At what altitude this balance is achieved will depend on such factors as the kind of plants concerned in affording protection and the favourability of the conditions for their growth. Where onshore winds are normally high (so ensuring maintenance of supplies of sand) and

there is maintained a high and evenly distributed rainfall the optimum conditions are likely to be achieved, provided the nature of the sand remains the same. It is therefore noteworthy in this connection that the highest dune ridges on our shores are usually to be found on the west coast where such conditions obtain.

The first salient feature of dune soils is therefore their diminishing mobility and, the second, the slowly but gradually augmented internal surface that a given volume of sand presents for water retention; both features which are brought about by the pioneers and which ameliorate their environment.

THE WATER RELATIONS OF DUNE SOILS

The features of dune soils already described emphasise the great importance of the water supply as affecting not only their capacity to support vegetation but also the relative permanence of the dune itself. Comparison of rainfall on coastal as compared with inland situations of the same altitude suggests that dune systems receive similar amounts of precipitation to other

RAINFALL INLAND AND COASTAL

	Inland, 1921	*Inland, 1930*	*Coastal, 1921*	*Coastal, 1930*
Av. number of days with more than 0·01 in. of rain	130	180	143	199
Av. total rainfall in year	18·41	32	21·157	35 ins.
Av. fall per day	0·141	0·177	0·148	0·176 ins.

Data for twenty-two inland stations and twenty-four coastal stations of between 23 and 27 ft. altitude showing that the latter tend to have a more distributed rainfall.

lowland areas. In Fig. 44 the total rainfall for both a dry year (1921) and a wet year (1930) has been plotted against the number of rainy days for a series of both inland and coastal stations between 23 ft. and 27 ft. in altitude, and this shows a slight tendency for the coastal stations to be the wetter if the difference has significance. It is clear then that the dryness of dune soils is almost wholly consequent upon their low capacity for water retention and an environment favourable to rapid evaporation, so that to assess the status of the water supply available for their flora we must determine the actual amount of water present in the sand both after rain and in periods of

drought. This has been done at various periods of the year in a number of British dune systems and the following account is based on the data thus obtained.

In assessing the water contents of sand dunes, it must be recognised that the great majority of dunes do not rise more than about 60 ft. (18·4 m.) above mean sea-level and although

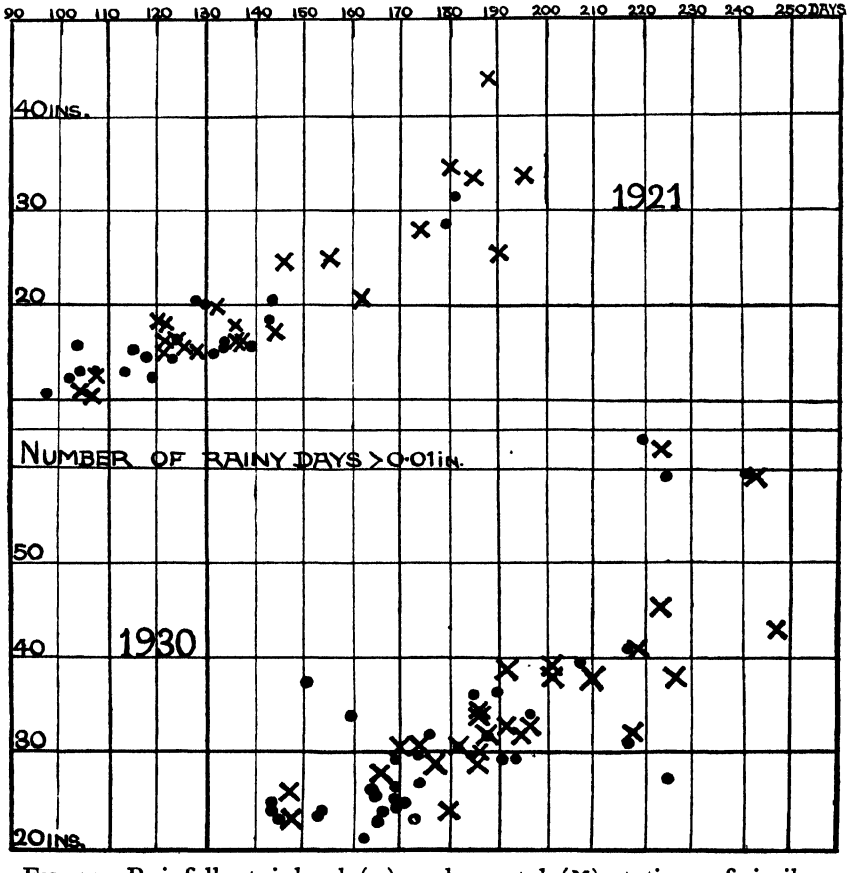


FIG 44. Rainfall at inland (•) and coastal (×) stations of similar altitude in a wet and a dry year in relation to the number of 'rain days.' Locations 23–27 ft.

exceptional elevations are sometimes attained, as, for instance, in Gascony, where the dunes reach to over 250 ft. (cf. A. E. Carey and F. W. Oliver, *Tidal Lands*, p. 58, London, 1918), such high dunes usually are only met with on the main seaward ridge. Except for the early stages of the yellow dune, where the pioneer grasses are the chief constituents of the vegetation,

the elevations in Britain are in general low. Thus the dune surface is often not many feet above the permanent salt-water table. This latter unlike the water-table inland undergoes a marked rise and fall with the tides and the lighter fresh water of the dune soil, which floats on the heavier salt water below, exhibits fluctuations of level in correspondence with those of the tide. This has been demonstrated by Hanley and Hill (T. G. Hill and J. A. Hanley, 'The Structure and water content of shingle beaches,' *Journ. Ecology*, Vol. II, 1914), who have shown that there is little mixing of the salt and fresh water despite these vertical movements; there is, however, a definite lag of some forty-eight hours in the rise and fall within the dune compared with the tidal rise and fall. Clearly in so porous a medium the level of the water-table will affect the rate of drainage from the surface sand after rain and, as a consequence of the changing gradient, the effect of a given amount of precipitation upon the water content of a particular soil horizon will be liable to vary with the state of the tides. Since capillary rise in sand is rapid, although the maximum vertical rise is much less than in finer texture soils, it is evident that in low level dunes and more especially in and near dune slacks the pushing up of the fresh water table by the underlying salt water may bring the former within reach of root systems by capillary action, so that we must recognise the possibility of periodic enrichment of the water supply and, perhaps more significantly, a much reduced rate of downward seepage, whereby the effective water supply for the deeper-rooted species is enhanced.

Data from a number of dune systems obtained, both in spring and in summer, in periods of rain and during or after spells of drought, enable us to form a fairly clear picture of the water supply available to the dune vegetation throughout the year (Figs. 46, 47). For this purpose the percentage *volume* of water in the soil is, however, far more informative than the percentage weight, which latter for different parts of a dune system may be completely misleading since the weight of comparable volumes of a young dune soil and an old one, especially near the surface, may be entirely different, and it is the volume of soil that the root system exploits and not the weight of soil that is biologically significant. This can best be illustrated by reference to actual soil samples taken to a depth of 6 ins. both from the young yellow dunes at Dawlish Warren and from the

old dunes, rich in organic material, in the same dune system. There is evidence to support the assumption that, apart from the disappearance of carbonates, the sand in the old dune is, for the purposes of our present consideration, essentially the same as that from the young dune. Nevertheless, owing to the organic material present, the sand grains are fewer in an

TABLE IV. WATER CONTENTS AND LOSS ON IGNITION OF DUNE SOILS

W =water content % by weight *L*=loss on ignition % by weight
WV=water content % by volume

1. BRAUNTON, DEVON, AFTER DRY SPELL

		Yellow dunes Locs. E, F and G			*Fixed dunes Locs. S, T and Z*			*Old dunes Locs. M and N*			
Depth	*Loc.*	*W*	*L*	*W/L*	*W*	*L*	*W/L*	*W*	*L*	*W/L*	*Av. L.*
0–6 ins. (0–15 cms.)	F	0·28	1·76	0·15	1·72	3·59	0·49	7·93	3·79	2·09	2·92
	E	0·46	1·91	0·24	2·90	2·73	1·06	5·40	2·90	1·86	
	G	3·11	2·57	1·21	2·5	4·12	0·60				
Av. 0–15 cms.		*WV* 1·92			*WV* 3·16			*WV* 5·55			
6–12 ins. (15–30 cms.)	F	3·72	3·54	1·05	0·57	2·7	0·21	5·92	1·74	3·40	2·56
	E	4·42	2·00	2·21	1·76	3·66	0·48	5·72	1·71	3·34	
Av. 15–30 cms.		*WV* 6·07			*WV* 1·62			*WV* 7·56			
12–18 ins. (30–45 cms.)	F	4·40	3·39	1·30	4·09	1·27	3·22	4·34	1·82	2·38	2·33
	E	4·75	1·69	2·81							
	G	3·44	3·50	0·98							
18–24 ins. (45–60 cms.)	G	3·65	1·60	2·28	4·17	2·06	2·02	4·40	1·80	2·44	1·82
24–30 ins. (60–75 cms.)	F	4·70	2·22	2·11	4·19	1·82	2·30	4·92	2·76	1·78	2·37
	E	4·02	2·67	1·50							
48 ins. (120 cms.)					4·88	1·4	3·48				
		WV	*L*	*W/L*	*WV*	*L*	*W/L*	*WV*	*L*	*W/L*	*Av. L.*
Mean all depths		5·07	2·44	1·38	4·4	2·59	1·10	7·3	2·36	2·33	2·49

2. DYFFRYN-ON-SEA, MERIONETH, OLD DUNE

Depth in inches	*W*	*L*	*W/L*
0–2	4·3	1·34	3·20
6	5·7	2·10	2·71
12	4·2	1·39	3·02
18	2·4	1·02	2·35

equivalent volume of the old dune soil and this organic matter is very light in comparison with the quartz that comprises most of the sand grains.

As a result 100 c.c. of the yellow dune soil weighed 153·4 gms. whereas precisely the same volume of soil from the old dune weighed only 81·2 gms.

Water contents, expressed in the normal way as percentages of the dry weights of these soils, would thus not be comparable since the figure for the old dune soils would represent the water retained in a volume of soil nearly double that represented by the same weight from the yellow dune. Moreover, such differences as may be exhibited by the extent of the root systems of particular species when growing in dunes of different ages might even exaggerate the discrepancy.

TABLE IVa. WATER CONTENTS AND LOSS ON IGNITION OF DUNE SOILS

3. RYE, SUSSEX, AFTER RAIN

	Medium-aged dune				*Old dune*			
Depth	*WV*	*W*	*L*	*W/L*	*WV*	*W*	*L*	*W/L*
0–2 ins.	7·0	3·6	1·69	2·1	16·6	13·0	5·49	2·4
6	6·9	5·1	2·34	2·1	6·1	5·2	2·39	2·1
12					7·4	5·1	2·34	2·1
24	7·7	5·2	2·34	2·2	6·6	4·6	2·10	2·2
36					8·2	5·7	2·59	2·2
	Av.*L.* 2.12				Av.*L.* 2.98			

4. PORTHCAWL DUNES, GLAMORGAN, AFTER RAIN

	Yellow dune				*Fixed dune*		
Depth	*WV*	*W*	*L*	*W/L*	*W*	*L*	*W/L*
0–2 ins.	8·4–13·4	6·1–8·7	2·48–3·84	2·3	6·1–11·5	2·72–4·94	2·2
12	8·9– 9·2	5·7–6·6	2·59–2·99	2·2	6·6– 8·0	2·99–3·54	2·2
18	7·0– 8·7	4·7–5·6	2·14–2·54	2·2	4·7– 5·5	2·14–2·49	2·2
	Av. *WV* 9·2				Av. *WV* 9·8		

5. KENFIG BURROWS, GLAMORGAN

	L		*WV after rain and W/L ratio*				
Depth	*Medium-aged fixed dune*	*Grey dune*	*Medium-aged dune*		*Grey dune*		*Old dune*
			WV	*W/L*	*WV*	*W/L*	*WV*
0–2 ins.	4·14	4·7–5·4	13·1	2·3	14·3–17·2	2·3	25·4–33·1
6	3·79	2·54	12·0	2·3	8·3	2·2	24·6–25·3
12	2·99	2·76–2·79	11·9	2·2	9·1	2·2	17·6
18	2·49	—	8·1	2·2	—		—
42	1·74	—	5·9	2·2	—		—

6. OXWICH YOUNG DUNES, GLAMORGAN, DRY WEATHER

Depth in inches	*L*	*W*	*WV*	*W/L*
0–2	0·44	0·92	1·4	2·1
6	0·74	1·6	2·4	2·1
12	1·34	2·8	4·4	2·1

Young dunes at Porthcawl in a period of rainy weather had water contents in the first 5 cms. amounting approximately to from 8–13% by volume (i.e. 8–13 c.c. of water in each 100 c.c. of sand). These dunes supported a flora of dune annuals with shallow roots that chiefly exploit the first few centimetres of the dune sand. Again at Rye in Sussex, following showery damp weather, water contents were recorded in the spring, in a vegetation of dune annuals, ranging from 5–10% by volume.

On the other hand, during a long spell of dry weather at Braunton some dune annuals were growing in sand with only from 0·72 to 1·61 c.c. of water per 100 c.c. of dune soil. Large numbers of determinations of the natural water contents on the dune soils of Blakeney Point show that here too the springtime water supply is of the order of 4%, but in late spring and summer it is often under 1%. Since the non-available water in a dune soil is commonly of the order of 0·5% it is mainfest that most of the moisture in the sand can be utilised by the plant, but how far this is adequate can only be ascertained by consideration of the volume of soil exploited by the root systems of different species, a subject to be dealt with later. But it is important to recognise that in general the amount of water available in the soil increases with the age of the dune and still more that the water content usually augments with depth and is, as we should anticipate, far more constant in amount at the deeper levels. This higher and less fluctuating supply is of great significance for the deeper-rooted perennials which, unlike the annuals that perish with the advent of the summer drought, persist in a normally active condition throughout the year. Thus in a late phase of a yellow dune, supporting plants of the Portland Spurge (*Euphorbia portlandica*, see Fig. 45), the water contents during a long spell of very dry weather were as follows:

ca. 0–15 cms. (0–6 ins.) 5·61% by volume.
ca. 37 cms. (15 ins.) 12·54% ,,
ca. 1 metre (40 ins.) 16·32% ,,

Where, as in old dunes, the vegetation has built up a high organic content towards the surface, this absorbs a considerable

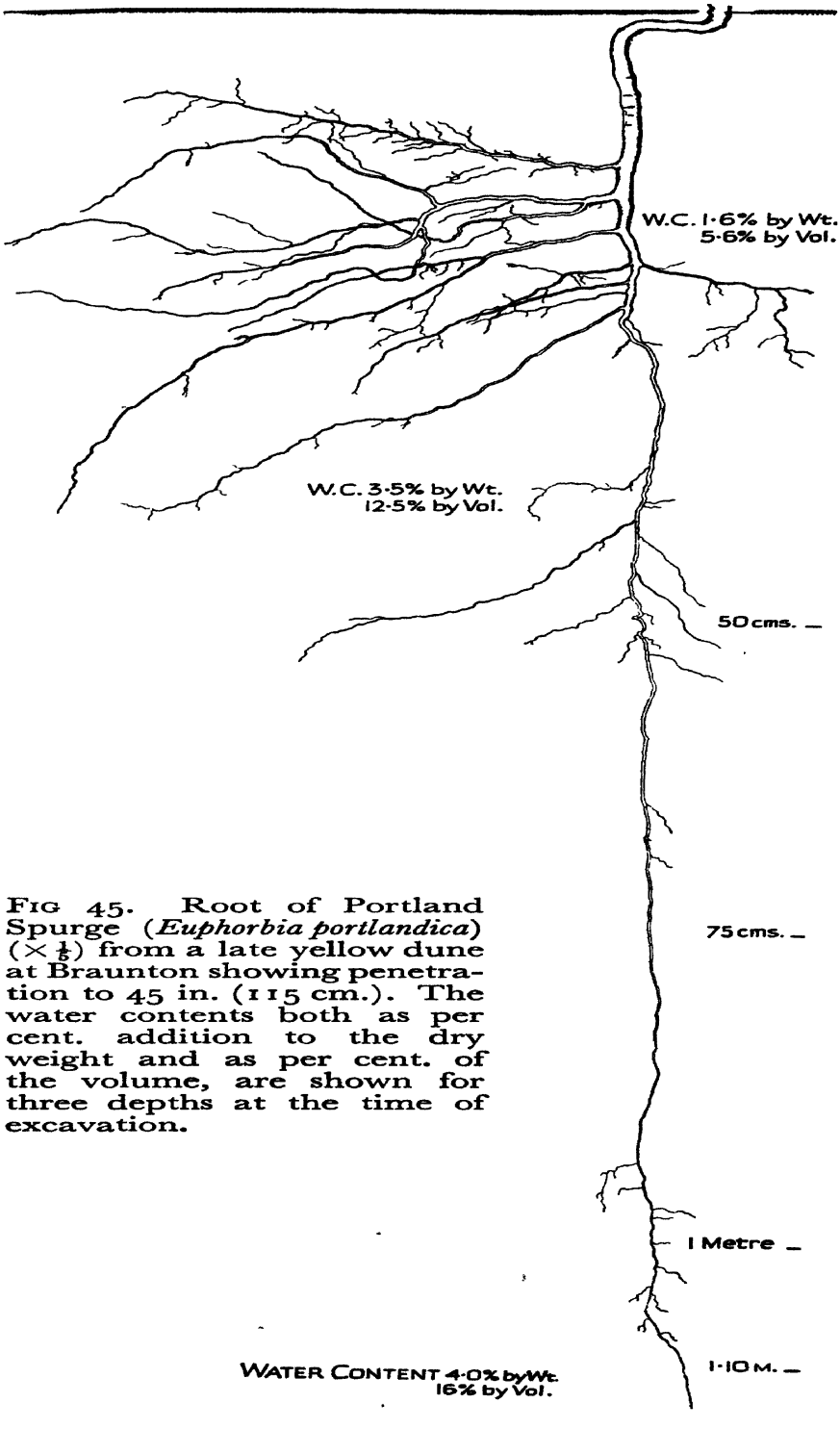


FIG 45. Root of Portland Spurge (*Euphorbia portlandica*) ($\times \frac{1}{5}$) from a late yellow dune at Braunton showing penetration to 45 in. (115 cm.). The water contents both as per cent. addition to the dry weight and as per cent. of the volume, are shown for three depths at the time of excavation.

proportion of the less heavy falls of rain, so that in a sense the upper layers may deprive the lower of supplies of moisture. Partly in consequence of this, and partly because the fall in organic content from above downwards implies a decreasing capacity for water retention, there frequently obtains in very old dunes a water gradient that after rain has its maximum near the surface, as is shown by an example from an old dune bearing Privet scrub and Bracken for which the data are given below:

		Loc. A	*Loc. B.*
0–15 cms. (0–6 ins.)	% volume of water	28·3	21
15–30 cms. (6–12 ins.)	,,	19·7	20
30–45 cms. (12–18 ins.)	,,	14·2	
60–75 cms. (24–30 ins.)	,,	14·4	15

The data given in Tables IV and IVa from dune systems in various parts of Britain show the water contents at various

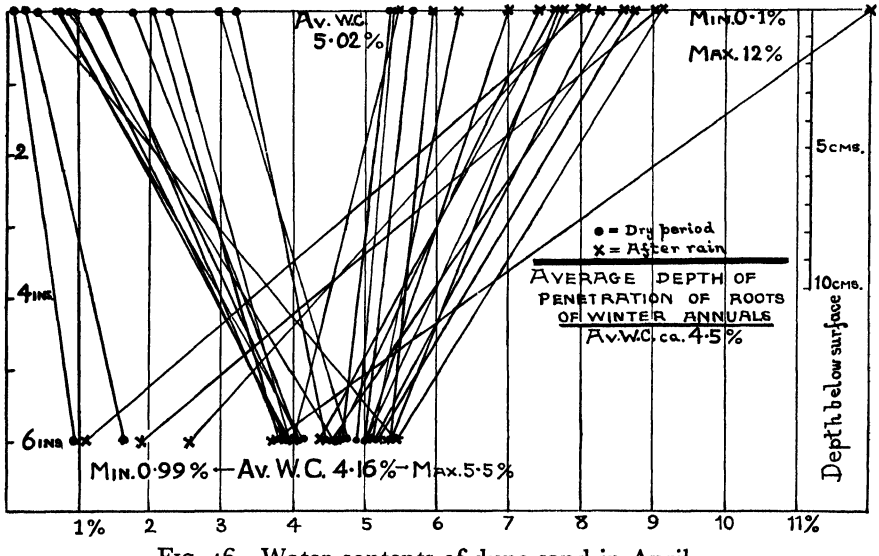


FIG 46. Water contents of dune sand in April.

depths for dry periods and soon after rain both in the customary form, as a percentage addition to the dry weight, and for most locations, also in the more informative presentation as a

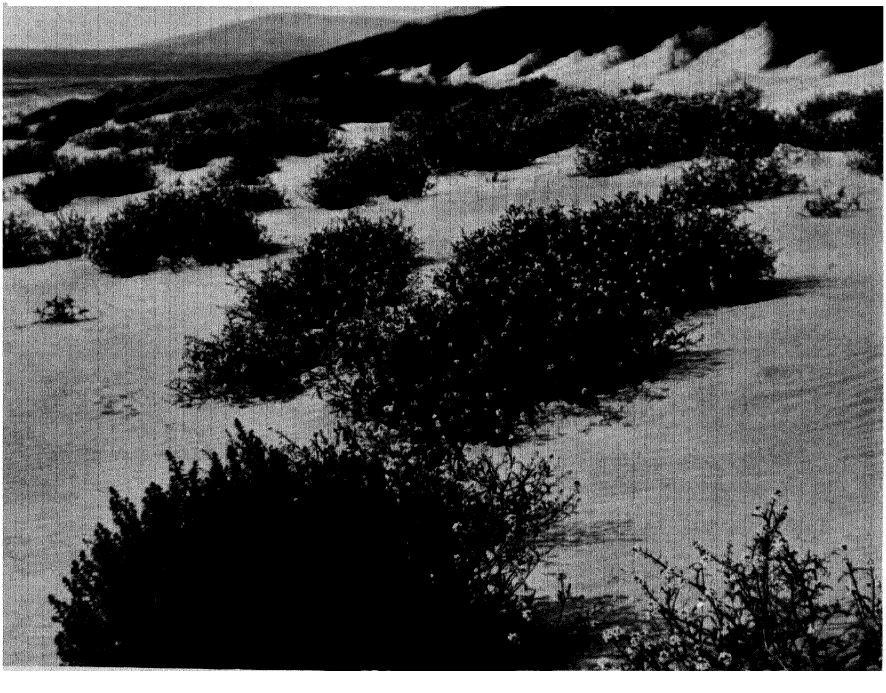
* * *

PLATE XXI. Plants of the limestone woodland. ABOVE. The Wood Vetch (*Vicia sylvatica*), Ross on Wye. × ½. BELOW. Blue Gromwell (*Lithospermum purpureo-coeruleum*), the other foliage is that of Herb Bennett. Cheddar, Somerset. Life-size.









percentage of the volume. The water content as a percentage of the dry weight is given for comparison with the % loss of weight on ignition corrected for loss of CO_2 from carbonates. These data provide the ratio of percentage water content by

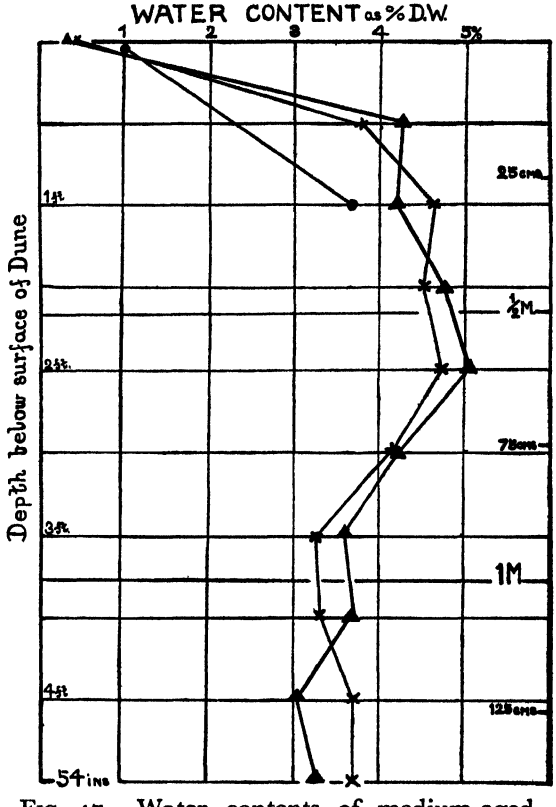


FIG 47. Water contents of medium-aged dunes in summer.

weight to percentage loss on ignition. It will be noted that this ratio, although it may be very low on young yellow dunes (possibly because organic material in young dunes may be

* * *

PLATE XXII. Embryo dunes. ABOVE. Embryo dunes at Harlech (following a former drift zone) created around plants of Sea Rocket (*Cakile maritima*) and Prickly Saltwort (*Salsola kali*). Three seedling Marram Grass plants have colonised the rear of the embryo dunes. The main dune ridge to the right is clothed with Marram Grass. Two drift lines parallel to the fore dunes are seen beyond. BELOW. Detail of above showing Sea Rocket in full bloom and a plant of Prickly Saltwort in front to left.

non-colloidal, derived from the drift line), is generally remarkably constant despite wide variations in the amount of organic matter present, and this bears witness to the predominant part played by the organic matter in determining the water retention of dunes. Examples of the water contents of dune soils from both yellow and grey dunes after a dry spell and after rain are shown in Figs. 48 and 50.

The change of water retention by the dune surface with increasing age is well illustrated by the data from Rye dunes. Comparing the young yellow dunes with 7% by volume of water and the old dunes with 16·6%; or again, Kenfig Burrows, where the medium aged yellow dune yielded 13% of water by volume, the grey dunes from 14% to 17% and the old dunes from 25 to 33%, we see that the old dunes retain about twice the amount of water compared with young dunes for equal volumes of sand. (See also Table V below.)

In general, the augmentation of organic content with increasing age is obvious and especially marked at Blakeney

TABLE V. WATER CONTENTS, APRIL

	I. DYFFRYN-ON-SEA, WALES						BORTH-Y-GEST, WALES		
Depth	*Young dune*		*Medium-aged dune*		*Old dune*		*Young dune*		*Av.*
	W	*WV*	*W*	*WV*	*W*	*WV*	*W*	*WV*	*WV.*
0–2 ins. (0–5 cms.)	2·8	4·2	2·0	3·2	4·3	6·4	2·9	4·2	4·5
6 ins. (15 cms.)					5·7	8·3			
12 ins. (30 cms.)			4·1	7·3	4·2	6·4			6·8
18 ins. (45 cms.)	2·1	3·2			2·4	3·7			3·4
24 ins. (60 cms.)			5·4	7·7					
36 ins. (90 cms.)			5·8	9·0			5·8	8·5	8·7
48 ins. (120 cms.)			6·2	9·2					
60 ins. (150 cms.)			5·9	9·1			7·1	10·7	9·9
Mean *WV* 0–18 ins. (0–45 cms.)		3·7		5·2		6·2			

Mean *WV* of all depths at both locations was 6·74 ± 0·4

2. TALWN-BACH DUNES, WALES HARLECH, WALES

Depth ins.	*Depth* cms.	*Medium-aged yellow dune* W	*Medium-aged yellow dune* WV	*Older fixed dune* W	*Older fixed dune* WV	*Semi-fixed dune* W	*Semi-fixed dune* WV	*Av.* WV
0–2	0–5	3·5	5·6	5·6	7·9	3·2	4·6	6·0
5–6	13–15	8·2	12·5	5·7	7·4	3·6	5·3	8·4
8–9	20–23			7·3	9·8			
12	30	3·7	5·9	5·8	8·0	4·1	5·9	6·6
18	45	3·8	6·0			4·2	6·3	6·1
24	60	4·7	7·2			4·5	6·6	6·9
36	90	4·3	6·5			4·2	6·1	6·3
						Mean WV all samples		7·0 ±0·2

and Southport, where the changes with time are not seriously complicated by any considerable landward travel of windborn grains continually bringing raw sand from the fore-dunes to cover the maturing surface of the old. To such sand movement is probably to be attributed the somewhat equivocal figures cited for Braunton dunes, although even there, in fact, the lower figures for loss on ignition were from young yellow dunes and the highest from the old dunes covered with scrub.

Just as the organic matter tends to augment with age so does the reaction of the soil tend to alter. Usually alkaline at first, markedly so in highly calcareous dunes such as those at Padstow (pH 8·5), the older dunes become gradually more acid as leaching proceeds and hydrogen ions replace the bases (cf. Table VI).

TABLE VI. SOIL REACTION OF DUNES

Dune system	*Young dunes* pH	*Old dunes* pH
Burnham (Somerset)	7·9	6·2
St. Cyrus (Kincardine) (Gimingham's data)	7·8–8·0	6·6–7·8
Southport (Lancs)	7·4–8·2	5·5–6·8
Blakeney (Norfolk)	7·2–7·4	5·5–7·0
Braunton (N. Devon) (calcareous)	*ca* 8	
Padstow (Cornwall) (highly calcareous) (Hepburn's data)	8–8·5	
Culbin Sands (Moray) (non-calcareous)	5·0	5
Tenby (Pembrokeshire)	7·2	6·5
Newborough (Anglesey)	7·4–8·5	6·6–6·8
Walney Island (Lancashire) (Pearsall's data)	7·0–7·5	4·8–5·5
Isle of Man (Moore's data)	7·6	5·8–6·4

(The pH figures are negative logarithms, e.g. pH 5·5 is 10 times more acid than pH 6·5. The neutral point is pH 7.)

It will be apparent that, especially in more mature dunes, the organic content tends to decrease with depth, though, as the Oxwich data show, the reverse may obtain in young dunes and even in old dunes where the accretion of sand during exceptional gales may lead to a surface layer poor in organic material as well as to marked fluctuations in the vertical distribution of the organic content, a feature to which buried accumulations of rabbit droppings sometimes contribute markedly. A striking example of alternation between layers of sand poor in organic material and layers of sand with appreciable amounts of organic matter is shown by the section of an old dune in Fig. 51 (p. 190).

It will be observed that the ratio of natural water content of dune soils expressed as weight per 100 gms. dry soil to loss on ignition tends to a value that may be as high as 3 or over after rain on old dunes, but is more commonly 2·2 to 2·3. In young dunes, however, this value even after rain may be quite low and suggests that the organic material in the earliest stages of dune formation may be of a nature that adds little to the absorptive capacity of the soil.

Data obtained at Blakeney in Norfolk by the writer showed that the first 7 cms. of a dune soil contained between 1,184 and 8,032 rabbit droppings per square meter, but in fact, although this appears large, it only represents an annual addition of about 0·18% by weight to the soil. More significant is the fact that these rabbit droppings decay very slowly and represent localised centres of high water-retaining capacity into which the roots penetrate and are especially exploited by them.

THE WATER CONSUMPTIONS OF DUNE PLANTS

The actual water losses which dune plants exhibit are naturally, in respect to their absolute values, dependent upon the size of the plants, but fortunately for the purpose of obtaining a balanced picture of the water losses in relation to water income it is the relative magnitude that is significant, so that it is possible to utilise small species and individuals as indicative of the conditions obtaining with respect to the larger. For this purpose dune plants were grown in their native sand in glass containers and the whole weighed periodically to assess the rate of water loss. Actually precautions were taken against loss from the sand surface itself because this might well have

been abnormal under the experimental conditions; but, since in nature water loss from the sand surface must occur, it will be realised that the data obtained represent an under-estimate of the actual water consumption in the field. Wilting occurs when the water content is about 0·5%.

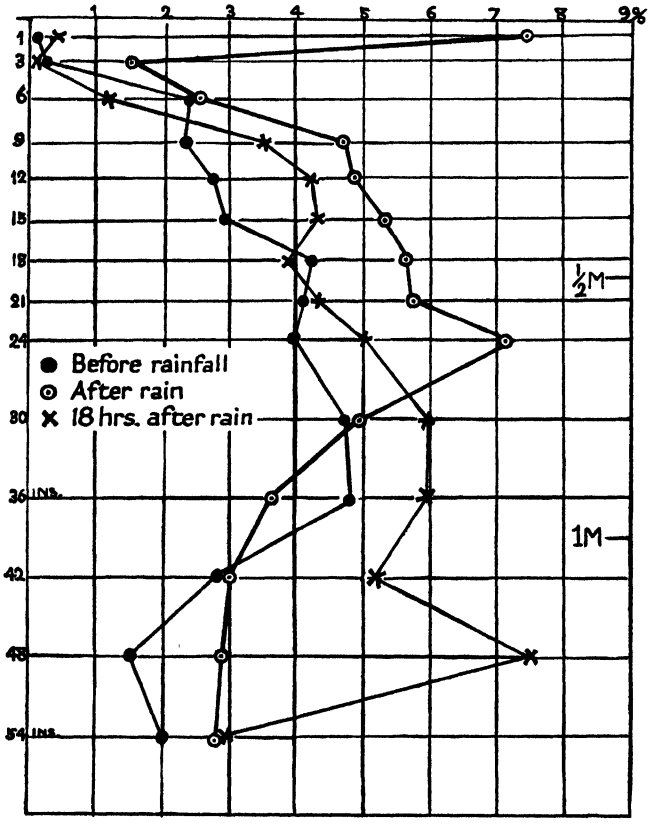


FIG 48. Water contents of yellow dunes before and after rain in summer, Blakeney Point, Norfolk. The surface water contents are here represented as such, but in fact are averages for the top inch of sand.

The species chiefly experimented with were the dune annuals, since these could be grown in relatively small volumes of dune soil and thus permitted more accurate determination. The extent of the root systems of each of the plants employed and the volume of dune soil exploited was estimated so as to compare the rate of loss with the probable water income.

The following transpiration rates expressed in grams per square centimetre per hour represent averages over several days with varying temperature conditions.

TABLE VII. TRANSPIRATION RATES AS LOSS/SQ.CM./HR.

	gm.
Stellaria apetala Plant A	0·010
Stellaria apetala, Plant B	0·014
Cerastium semidecandrum, Plant A	0·016
Cerastium semidecandrum, Plant B	0·018
Cerastium semidecandrum, Plant C	0·032
Cerastium tetrandrum	0·011
Erophila verna	0·015
Medicago minima	0·008
Trifolium arvense	0·006
Erodium maritimum	0·014
Phleum arenarium	0·005

Mean of 8 spp. 0·013 gm./sq.cm./hr.

The results are all of the same order of magnitude with a mean value of 0·013 grams. of water lost for every square centimetre of leaf surface in one hour. But in sunny weather the values would attain the maxima observed, which were from three to five times these mean values.

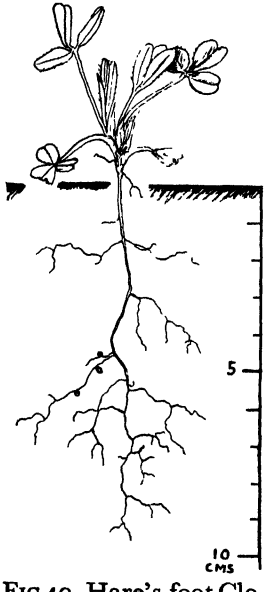


FIG 49. Hare's-foot Clover (*Trifolium arvense*), showing the root system with three root nodules.

Nevertheless, rates of loss per unit area of leaf surface are of less significance for our present purpose than the loss of water per plant in relation to the volume of soil that its roots can draw upon for their supplies. These data were obtained for a series of plants of which the first example we may cite is a young plant of the annual Hare's-foot Clover (*Trifolium arvense*). The total leaf area of the eighteen rosette leaves was 10·57 sq. cms. whilst the root system exploited a volume of certainly not more than 95 c.c. of dune sand. The loss of water amounted to approximately a cubic centimetre per day and the water content of the dune soil would normally be about 4% by volume, so that the available water supply in a dry period would be exhausted in less than four days. Actually I have seen plants of this and the

other annuals we shall mention apparently unharmed after a period of six weeks without rain.

The second example we will cite is the small Medick (*Medicago minima*). There were eight leaves and the water loss in sunny weather would probably be about ⅛ c.c. per day. Assuming exploitation of the sand to a distance of 0·5 cm. from the root this would furnish 33 c.c. which would provide about 1·0 c.c. of available water, a supply that could suffice the plant for some five days, if there were no loss direct from the sand surface to the air.

Let us apply the same line of thought to a young perennial species. The plant selected was a small Portland Spurge with a root extending to a depth of 14 cms. and exploiting a volume of approximately 42 c.c. The leaf area was just under 29 sq. cms. and the water loss about 0·7 c.c. in a day. On the basis of the water content of the dune soil from which the plant was obtained wilting might be expected to occur in from two to three days if there were no rainfall. Calculations based on other species yielded similar conclusions, namely that wilting, under the conditions of water supply that usually obtain in dry periods, should supervene in from one to four days. Actually no such catastrophe occurs and indeed, as already stated, at Braunton in April, 1938 the dune plants withstood over six weeks without rain.

The answer to the riddle is almost certainly the internal formation of dew within the sand dune soil itself, the warm moisture-laden air from above the adjacent sea, after sunny days, being drawn into the pore spaces of the soil as a concomitant of the upward convection currents maintained especially on the southern face and crest of the dune after dusk. The warm moist air impinges on to the cold grains of the dune's interior and there dew is deposited. It is because of this phenomenon that the sand a few inches below the surface of a dune during a dry spell may be found to be moistest following upon the hottest days. In a very hot spell of weather in June the internal temperature of a dune was determined from the side of a 4-ft. pit throughout the night and it was found that the temperature within the dune fell below the dew point between 11.30 p.m. and 12.30 a.m. and did not rise above it till 5.30 a.m. The minimum temperature was reached at 1.30 p.m. when it was 1·5° C. below the dew-point (see Fig. 52, p. 195). But

far more important than the mere fact of such internal dew formation is the amount of moisture that accrues. An estimate of this was obtained by two methods. Firstly, in dry weather by determining the water content of samples from the side of pits before and after conditions favourable to dew formation.

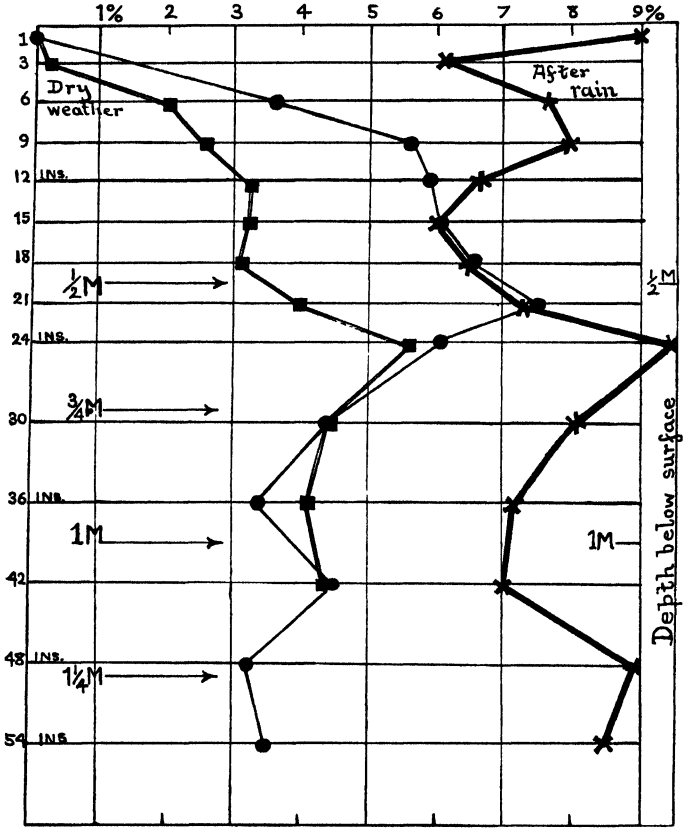


FIG 50. Water contents of grey dunes before and after rain. Early phase of grey dune in summer, Blakeney Point, Norfolk. Compare with Fig. 48.

Secondly, by numerous composite samples from the surface of dunes. Both methods showed increases of water content during the hours of darkness.

Composite soil samples were taken at depths of 3 ins. and 12 ins. respectively from a number of loci on a medium-aged dune bearing Marram Grass, mosses and lichens. The first series of samples were taken *during a spell of hot sunny weather* about 11 a.m. and the second series of samples was taken very

late the same day when the sky was clear and the conditions during darkness had, apart from the presence of wind, been moderately favourable for dew formation.

Water content			
morning		*night*	*Difference p.m.-a.m.*
0·53% by wt.	3 ins.	0·71%	+0·18%
1·18% by wt.	12 ins.	1·31%	+0·13%

During the same period samples were taken from the side of a pit dug in the same dune ridge to a depth of 4 ft. So as to diminish the evaporation effect on the open hole, the first few inches of the samples were discarded, but the fact that the water contents were lower than for comparable samples taken at similar depths from undisturbed parts of the dune indicates that this factor introduces an appreciable error, so that the absolute values here obtained are too low and only their relative values are significant. It should be emphasised that this fact stresses the appreciable thickness of sand through which evaporation takes place, a freedom of gaseous movement that is of no little importance for internal dew formation.

TABLE VIII. WATER CONTENTS OF SAMPLES FROM SIDE OF PIT IN MEDIUM-AGED DUNE

	Water content	
Depth	*freshly dug*	*10·45 a.m.*
	25/VII/38	*27/VII/38*
3 ins.	0·43%	0·18%
6 ins.	0·47%	
12 ins.	0·71%	0·35%
24 ins.	2·0%	
36 ins.	5·0%	1·94%

It will be noted that even at a depth of 3 ft. the water content after the pit had been opened two days was less than half that when freshly dug, but the increases in water content at all the three depths shown in the late evening of 27th, as compared with the late morning of the same day were much greater than those shown by the equivalent samples from the undisturbed dune, due perhaps to 'cold air drainage' (cf. Table X). The increases shown by the pit samples may indeed be taken as indicative of the increases that might have been observed in the undisturbed dune at an early hour in the morning.

A series of samples was obtained from a deeper pit immediately after digging, which gives an idea of prevailing water

contents obtaining in a medium aged dune during a severe drought (Table IX).

TABLE IX. WATER CONTENTS AT SIDE OF PIT IN DUNE

Depth	*Water content*
3 ins.	0·63%
6 ins.	0·81%
12 ins.	2·06%
24 ins.	4·30%
36 ins.	4·9%
48 ins.	5·1%
63 ins.	4·8%
66 ins.	3·3%

The optimum water content at 4 ft. from the surface and the decrease in water content at a depth of 66 ins., which was confirmed by replicate samples, is instructive. If the capillary water played any considerable part in yielding liquid or vapour towards the maintenance of the moisture supply in the upper layers of the dune we should anticipate an increasing water content as we pass from above downwards, but the fact that a maximum moisture can obtain above the deeper levels may be taken as indicative of the preponderant part played in the water supply of the dune by condensation from the vapour supplied by the external rather than the internal sources. It is precisely when the water table is lowest during very dry spells that an increase and subsequent decrease with depth has been observed both at Blakeney Point and elsewhere.

TABLE X. WATER CONTENTS BY WEIGHT OF SAND AFTER AND BEFORE DEW-FORMATION, BLAKENEY POINT

Depth		*Samples*	*27/VII/38 Night samples*	*27/VII/38 Day samples*	*Gain night–day*
3 ins.	*Three*	1A	0·59%	0·18%	+·41%
12 ins.	*depths*	1B	0·99%	0·35%	+·64%
36 ins.	*in pit*	1C	3·80%	1·94%	+1·86%
Composite sample at 3 ins.		1D	0·71%	0·53%	+0·18%
Composite sample at 12 ins.		1E	1·31%	1·18%	+0·13%

The next series of samples were collected on a very hot sunny day after several hours during which conditions were obviously highly favourable both for evaporation from the soil and for transpiration from the vegetation. It may obviously be assumed

that the water contents here recorded for the day samples were not the minimum water contents, since for several hours subsequent to sampling climatic conditions were all favourable to continued water loss. It will be realised that at all three depths in the dune ridge and in both the composite samples, representing the average for a number of areas on the same ridge, the water contents of samples taken at night are consistently higher; and this increase having regard to the circumstances obtaining can only be attributed to a gain in water content resulting from *condensation on or in the soil, and the maximum gain at 36 ins. indicates the latter.* Thus we have here definite evidence for the supply of water to the dune plants by internal dew formation. The increases cited are in percentage weight, but in volume they represent an average increment of about 0·9 c.c. of water per 100 c.c. of soil which if of daily occurrence would, as we have seen, probably meet the plants' requirements. Owing to the low water contents obtaining we can regard downward movement of water as negligible, especially having regard to the short time-interval involved. Clearly the gains at 3 ins. and 12 ins. are of the same order, but the data from the 3-ft. depth indicate that internal dew formation is of more importance than surface deposition.

PORE SPACE

Calculations show that if all the soil particles were spherical, of the same size and packed as tightly as possible, then the total air space between them would vary from 26%–47% of the soil volume, according as the spheres were staggered or superposed in successive layers. Measurements on a mobile dune soil at Braunton Burrows, N. Devon, indicated a pore space of

TABLE XI. PORE SPACE IN SEMI-FIXED DUNES, HARLECH

Depth of sample	*Pore space per 100 c.c. of dune soil*	
0–2 ins. (0–5 cms.)	42·4%	
6 „ (15 cms.)	46·0%	
12 „ (30 cms.)	44·7%	mean 44·4%
18 „ (45 cms.)	43·0%	
24 „ (60 cms.)	46·0%	

between 40% and 41% whilst a series of determinations at successive depths from semi-fixed dunes at Harlech showed the pore space to be of a similar order of magnitude.

The addition of organic material may augment the pore space by preventing such close packing of the mineral particles, but, on the other hand, it provides very fine material that fills in the interstices between the sand grains and thus diminishes the volume available for the soil atmosphere.

Nevertheless, it will be apparent that dune soils are very porous and readily permeable. The carbon dioxide content of the soil atmosphere is low and often comparable to that of the atmospheric air. This is doubtless due in the main to two causes. Firstly, owing to the comparatively low rate of CO_2 production by the soil organisms, except in the later phases of dune development where the organic pabulum is appreciably augmented, and secondly through the ready ventilation by atmospheric air which is facilitated in two ways; namely by convection currents set up at the surface on sunny days and by the rise and fall of the water table corresponding with the tidal rhythm.

CHLORIDES

It is a not uncommon belief that sand dunes are a saline habitat and that the plants which grow there must be salt-tolerant; but actually this is far from the truth, for though, of course, wind-borne spray ensures a certain supply of salt to the dune system, the actual amounts present, especially in the older dunes, would appear surprisingly small unless we recall that except in dry weather there is little opportunity for any accumulation from this source of supply, since in so porous a medium the sodium chloride received by the surface is soon washed down by rain and diluted in summer by dew formation. The following data obtained during a spell of dry weather from a fixed dune on the Norfolk coast sufficiently emphasise the

Depth	*%Chlorides*
Surface	0·00–0·01
6–12 ins.	0·01–0·014
12–18 ins.	0·005–0·198

normally low content of chlorides even in conditions which might be expected to favour their presence. I am indebted to Lord Robinson for the information that the chloride content of the dunes at Newborough amounts to 0·023–0·026%. In the dunes of the Gulf of Lyons the content of sodium chloride is

even lower, only, according to Kuhnholtz-Lordat,[1] amounting, to 0·0002%. So it may be assumed that dune soils are normally not saline despite their proximity to the sea. It must, however, be stressed that in shallow dune systems where the surface of the salt water table may come up to or near the floor of the 'lows' between the dune ridges high salinities may obtain there, especially during periods of drought. In such situations from 3–5% of chlorides may occur and up to 1% is not uncommon. Thus it is in these saline 'lows' that such salt-tolerant species as the Sea Milkwort (*Glaux maritima*), one of the Sea Lavenders (*Statice reticulata*) and the Sea Heath (*Frankenia laevis*) are especially characteristic. The last two are Mediterranean species that in Britain find their chief home on our south-western coasts.

Though the soil solution in the dune has not then any appreciably augmented osmotic value due to sea salt, its frequent paucity may demand a rather high suction force to render it available. So it is pertinent to note that characteristic sand dune species have been shown capable of developing fairly high osmotic pressures and therefore suction forces of comparable magnitude. Thus for a typical dune perennial, the Sea Holly (*Eryngium*), Killian has recorded from 9 to 14·3 atmospheres and over eleven atmospheres has been found in the Sea Convolvulus (*Calystegia*). For a typical sand dune annual, *Cerastium semidecandrum*, Volk has recorded from 9·5 to 14·3 atmospheres.

DUNE TRAVEL AND FORM

The rate of advance of dune systems is naturally very varied. On the Atlantic seaboard of France an average of about 30 ft. a year has been observed with local advances of up to 80 ft., but on the coast of Lancashire near Great Crosby the average rate of advance based on observations by T. M. Reade over a period of forty years was 3 ft. 6 ins. per annum (1·05 m.), whilst in the region of Freshfield the average rate of advance over a period of some 15 years ranged from 18–24 ft. (=5·4–7·2 m.) per annum. On parts of the Norfolk coast the extension over a period of years was of the order of 5 ft. (1·5 m.) per annum. These rates of advances are means inclusive both of

[1] *Les dunes du Golfe du Lion*, Theals, Montpellier, 1923. Max Onno in the dunes of Holstein recorded from 0·003–0·05% chlorine.

ridges and of the intervening 'slacks.' As a new series of embryo dunes grow and coalesce the grains which go to build them are so many less available for the growth of the other dunes on the landward side. So as the new ridge develops it increasingly diminishes the supply of sand to the older part of the system

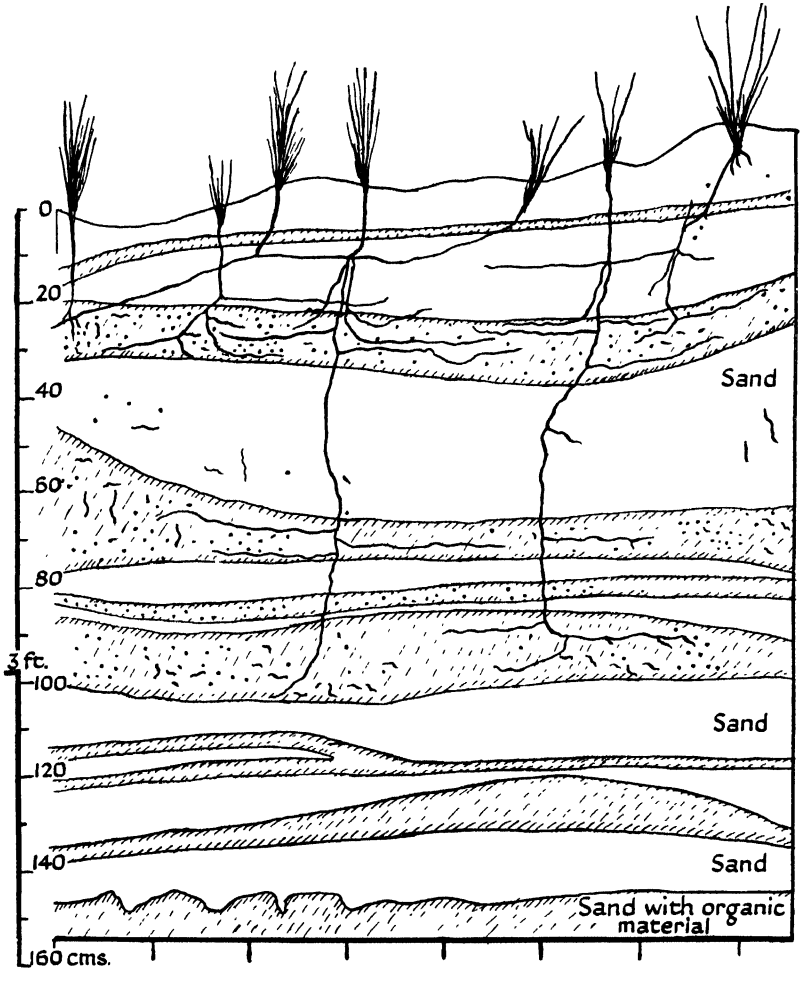


FIG 51. Semi-diagrammatic representation to scale of the root system of the Marram Grass (*Ammophila arenaria*) in the vertical section of a dune on the Norfolk coast about 25 sq. ft. in extent (*ca.* 2·5 sq. m.). Yellow sand is shown white and layers of dark sand, containing considerable organic material, by diagonal shading. Roots, shown as black lines or as black dots where cut across, are seen to be most numerous in the organically enriched and therefore moister strata. (This is at variance with what W. G. Waterman (*Bot. Gazette*, 1919) inferred from cultures.)

which eventually comes to lose more than it gains. This increasing shelter of the inner dunes by the outer in a growing system is one of the contributing causes to the lower height of the old dunes compared with the younger. The other and more important one is that the soil from the ridges which have initially steep slopes gradually becomes eroded by rain and washed down into the 'slacks' between so that an old dune system usually presents its greatest elevation at the second or third ridges whilst the oldest portions have a flattened-out meadow-like appearance and at this phase they are commonly appropriated to the purposes of recreation or agriculture.

Since, as we have seen, the growth and development of the dune is dependent on the increasing stability and protection of the surface resulting from the covering of vegetation it is not a matter for surprise that any destruction of the protective carpet of plants by, for example, rabbit burrows or the wearing through of the plant mat by continued use of a trackway, will provide the starting point of dune degeneration and destruction. From such beginnings 'blow-outs' develop which may extend further and further till widespread removal takes place and so-called wandering dunes replace the stable ones (Pl. XXVII).

The methods of arrest commonly employed consist of introducing some obstacle, not only to check further movement but around which sand will collect. The use of brushwood or even netting on a dune may be effectively employed to prevent the surface mobility that initiates radical change. Ultimately, however, success depends upon the use of living material that can by its growth keep pace with the altering conditions. For this Marram Grass is most commonly utilised (see foreground in Pl. XXVI), planted in the wetter months in such a way as to form squares of about 2 m. in width with a series of short rows of marram cuttings in each square.

XIV

THE TEMPERATURES OF DUNE SOILS

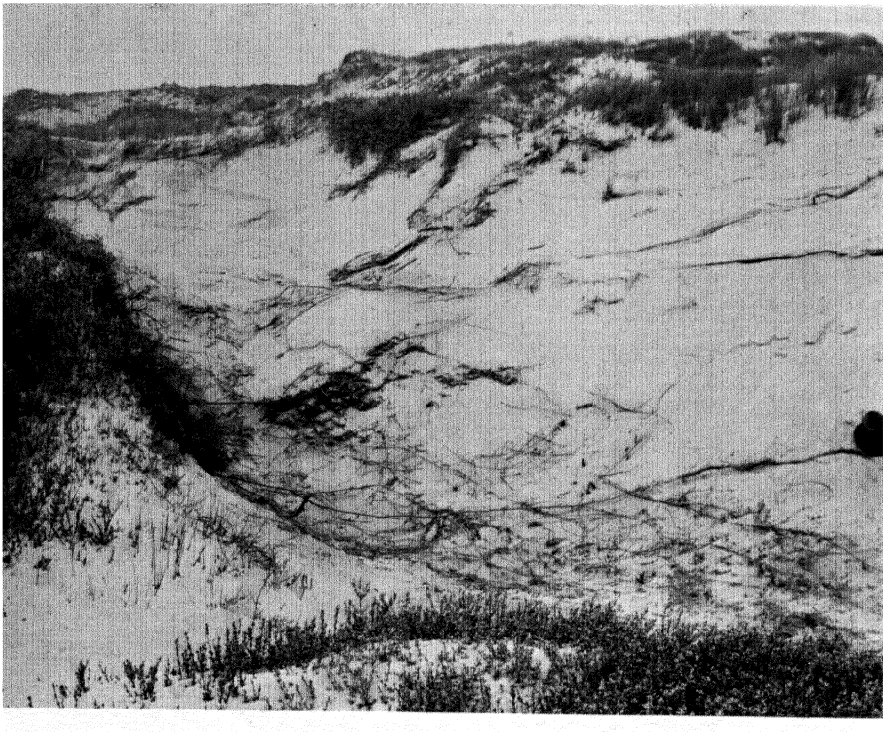
THE arid conditions on dune systems are accentuated by the high daytime temperatures that can be attained on sunny days. We have already emphasised the low content of water in the surface soil of dunes and the large proportion of pore space they contain. These features, which are most marked in the youngest stages and less so in the oldest, combine to render the sand a very poor conductor of heat. So, when the sun's rays beat down upon the surface, the superficial sand grains attain a high temperature because, in contrast to moister and denser types of soil, no appreciable proportion of the radiant heat derived from the sun is transferred to the deeper layers, which, in fact, remain cool. The surface sand on a hot summer's day may attain to over 60° C. (=140° F.) and temperatures taken simultaneously in the surface sand and at a depth of 5 cms. (*ca.* 2 ins.) in spring showed that whereas the temperature at the former depth was over 40° C. (=104° F.) that at the latter was only 31°–32° C. (*ca.* 89° F.). Temperatures taken in the yellow surface sand at fifty-six localities showed a mean temperature of just over 22·13° C. compared with 20·3° C. at 5 cms. In older dunes the additional organic matter in the surface increases the power of the soil to conduct heat in two ways—namely, by its capacity to retain moisture and by filling the interstices between the sand particles, so that the contrast in sunshine between the surface temperature and that of the sand a little lower is less marked.

The importance of this retention of heat near the surface for the vegetation is a twofold one. Firstly, the roots are embedded in cool sand even on the hottest days and this contrast between

* * *

PLATE XXIII. BELOW. Marram Grass flowering on the main ridge of the dune system at Blakeney Point, Norfolk. To left, fore dunes which have formed round young plants of Marram Grass. ABOVE. Seaside Radish (*Raphanus maritimus*), showing flowers and fruits, on Tenby Dunes and bearing numerous specimens of the introduced snail (*Helicella pisana*).







the hot sand grains above and the cool particles below establish just those relations that promote upward currents of hot air and the inflow of the saturated warm air that leads to dew formation in the cool interior of the dune. Secondly the layer of air immediately above the surface on a sunny day in spring is quite commonly 2°–3° C. warmer than the air generally (cf. E. J. Salisbury, 'On the Day Temperatures of Sand Dunes,' *Trans. Norfolk and Norwich Nat. Soc.*, pp. 333–55, XIII, 1932–3), so that even when the air temperature on bright days in winter is so low as to be unfavourable for the manufacture of sugars by the green leaves of plants generally, at more than a very slow rate, the foliage of the dune annuals, which is situated close to the soil may, when the sun is shining, be surrounded by warm air that is favourable to fairly rapid photosynthesis. Actually, temperatures taken on sunny days in April when the air temperature generally was 9° C. (48° F.) have shown that the leaves of the annual dune species were surrounded by air which was from 7·5° to 11·5° C. higher. Such conditions must often enable these winter annuals of the sand dune actively to manufacture food material when the physiological processes of species of other more normal habitats are almost at a standstill owing to the low temperatures of the air by which the foliage is surrounded. The inflow of moist air into the dune and internal dew formation naturally lead to a lowering of the surface temperature of the dune, and to this may be probably attributed the, by no means infrequent, occurrence of air temperatures just above the dune which are actually in excess of the temperatures of the surface sand with which the air is in contact (cf. Salisbury, *loc. cit.*, p. 347). The phenomenon is more frequent on the younger dunes than on the older and on the seaward faces than on the landward, precisely those topographical features to which moisture-laden air has the readiest access.

The shading effect of the leaves of the Marram Grass when the temperature of bare sand in spring is about 30° C. (86° F.)

* * *

PLATE XXIV. Dune flora. ABOVE. Eroded dunes, Southport, showing extensive roots of dune Willow (*Salix repens*). The hat, on the right, marks the tip of the root which arises from the Willow tuft 37 ft. away on the extreme left. BELOW. Dune 'slack,' Talwn-Bach, with numerous tussocks of Spike Rush (*Juncus acutus*). To the right in standing water occur *Equisetum limosum, Baldellia ranunculoides, Hypericum elodes et alia.*

may bring about a lowering of the soil temperature by 6° C., but under mosses and lichens in bright sunshine the surface temperatures of the sand are often appreciably higher than in adjacent bare areas, a fact that can only be attributed to the dark colour of these plants as a result of which they reflect far less sunlight than the bare sand and absorb an appreciably higher proportion of the radiant energy that they receive (e.g. 1 cm. depth in bare sand 41°–42·2° C.; under the lichen *Cladonia furcata* 41·1° to 47·7° C.). It is in harmony with this that there is a tendency for soil temperatures to augment slightly with dune age, as the following averages of a large mass of data would indicate.

	Ridge I (youngest)	*Ridge II*	*Ridge III (oldest)*
Spring	12·4° C.	12·6° C.	12·9° C.
Summer	25·0° C.	26·7° C.	26·7° C.

The daily fluctuations of temperature, especially near the surface, are very marked, and these are shown graphically in Fig. 52 which illustrates the temperature changes at three different depths in both a yellow dune and a grey dune over a period of two days in August, except for a six hours' interval from 11 p.m. to 5 a.m. (G.M.T.) during which no readings were taken. It will be seen that for some nine hours in the yellow dune the temperature of the sand immediately below the surface fell appreciably below the dew-point and may possibly have done so to a greater depth at a later period during the night. In the grey dune the surface temperature fell below the dew point for a shorter period, whereas for the yellow dune the range observed near the surface was 30° C. (=54° F.), at a depth of 15 cms. (=6 ins.) the range was only 4·5° C., whilst at 30 cms. (1 ft.) the lowest temperature recorded was less than 4° C. below the maximum. The temperatures in the grey dune exhibit far less pronounced daily fluctuations at the surface and fluctuations of a similar order of magnitude at the lower levels. The much lower maximum and the much flatter 'curve' for the older dune surface is an accompaniment of the much better heat conduction of the more mature soil.

From such facts it will be obvious that the conditions for the underground parts of the deeply-rooted perennials are comparatively uniform, in this as in other respects, whereas the dune annuals with their shallow roots systems must endure fluctuations of a very marked character that augment the

specialised nature of the environment and thus reduce the number of species which can flourish here.

For some observations on the temperatures in dunes during the severe weather in January, 1940, I am indebted to Dr. W. O. Howarth, who recorded the conditions in the yellow Marram Grass dunes at Southport. The soil was frozen solid

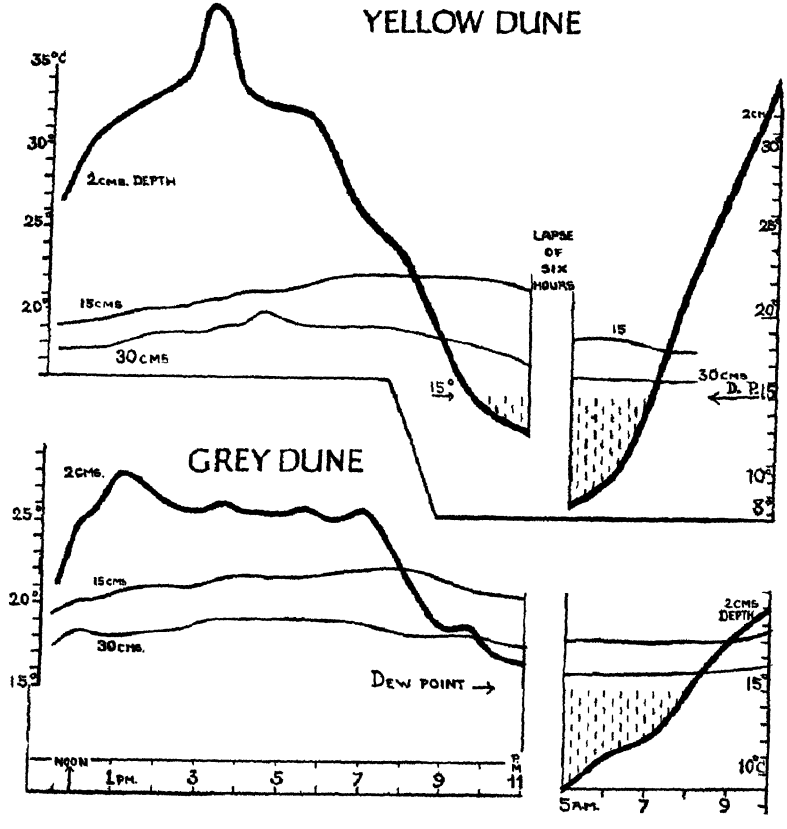


FIG 52. Dune temperatures showing daily rhythm. Note the fall below the dew-point in the surface temperature at night and the more marked extremes in the yellow dune than in the maturer soil of the grey dune.

to a depth of 6 ins. The lowest temperature was —4·5° C. at the surface (*ca.* 24° F.) and it was not till a depth of 24 ins. (60 cms.) was reached that the temperature rose above the freezing-point. It is obvious therefore that even the perennials in the younger dune phases must endure considerable seasonal fluctuations in temperature between summer and winter.

XV

THE ROOT SYSTEMS OF DUNE PLANTS

THE account already given of the water supply in dunes has shown us that, in broad outline, there is at depths of between 2 and 3 ft. a more or less constant if moderate supply of moisture, adequate however to maintain vegetation even during periods of summer drought. At shallower depths the available water diminishes and, especially in the yellow dunes, the surface layers during the season of low rainfall have

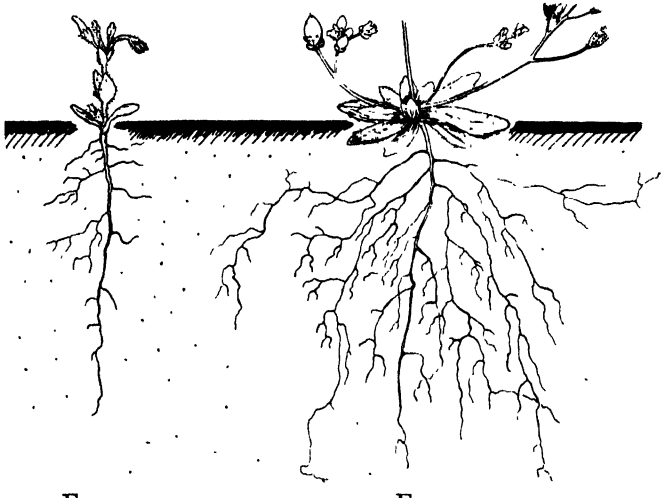


FIG 53 FIG 54

FIGS 53–54. Dune annuals. FIG 53. Mouse-ear Chickweed (*Cerastium semidecandrum*). FIG 54. Whitlow Grass (*Erophila verna*). Llanbedr, April. Two-thirds actual size.

the lowest content of moisture. During the winter months and early spring, however, the water supply in the surface sand is renewed frequently by precipitation, and with the addition of organic material, which with increasing age of the dune is mainly near the surface, the power of water retention increases. Hence during the wetter season the first few centimetres normally also furnish an adequate supply of moisture. The normal situation is thus a permanently sufficient water supply below and a reasonably sufficient but seasonal supply above.

It is in conformity with these generalisations that the root systems of dune species are found to comprise two categories, namely the shallow systems of the winter annuals that mostly germinate about September and persist till the following summer, and the deeply penetrating root systems of the biennials and perennials.

The following table of rooting depths of eighteen common dune annuals based on examination, for most species, of a number of individuals shows that these are mostly quite shallow. The range of rooting depth is sometimes appreciable and especially marked in the specimens examined of the Dove's-foot Crane's-bill (*Geranium molle*). Indeed, exceptionally deep-rooted specimens of any of the annuals are likely to be found where organic material occurs at a greater depth from the surface and, for instance, buried rabbit droppings penetrated by fine roots are often met with. Such organic enrichments will necessarily imply an increased capacity for water retention, and roots have been shown experimentally to follow in their growth a gradient of increasing moisture when this is not too high or too low and there is good aeration, conditions that are here fulfilled. Thus the extent and distribution of the root system is naturally greatly influenced by the distribution of water-retaining material, a feature well shown in the diagrammatic representation of the root distribution of Marram Grass (Fig. 51) where the particular association of the roots with the organically rich layers of sand is clearly manifest.

TABLE I. ROOTING DEPTHS OF DUNE ANNUALS

			Observed range in cms.	*Number measured*	*Average in cms.*
1	*Erophila verna*	Whitlow Grass	2·6–7	20	4·9 ±0·2
2	*Vicia lathyroides*	Spring Vetch	4–10	8	6·2 ±0·4
3	*Valerianella locusta*	Lamb's Lettuce	3·5–10·5	4	6·2 ±0·8
4	*Cerastium semidecandrum*	Mouse-ear Chickweed	3–16	51	6·7 ±0·2
5	*Veronica arvensis f. minor*	Field Speedwell	3–9·5	8	7·1 ±0·4
6	*Aira praecox*	Spring Silver Grass	4–15·5	34	7·4 ±0·3
7	*Myosotis collina*	Dwarf Forget-me-not	3–15·5	29	7·4 ±0·4
8	*Scleropoa rigida*	Rigid Fescue	5–10·5	14	7·5 ±0·3
9	*Alchemilla arvensis*	Parsley Piert	3–19·5	75	8·4 ±0·02
10	*Cerastium tetrandrum*	Mouse-ear Chickweed	4·5–22	50	9·1 ±0·36
11	*Trifolium arvense*	Hare's-foot Clover	7·5–10·5	5	9·2 ±1·2
12	*Geranium molle*	Dove's-foot Crane's-bill	4–44	50	9·9 ±0·8
13	*Phleum arenarium*	Sand Cat's-tail Grass	5–14·5	60	10·0 ±0·2
14	*Poa annua*	Annual Grass	6–19·5	18	10·1 ±0·5
15	*Arenaria serpyllifolia*	Sandwort	4·5–21·5	50	11·5 ±0·3
16	*Stellaria apetala*	Dune Chickweed	5·5–25	8	15·1 ±1·7
17	*Erodium cicutarium*	Stork's-bill	5·5–36	58	15·9 ±0·6
18	*Anagallis arvensis*	Pimpernel	7·5–32·6	17	19·6 +1·1

The probable degree of error of the means is shown in the last column, and except where the number of specimens examined was few this figure is seen to be quite small. If we consider the total of 559 root systems measured, as a whole, the average rooting depth is 9·8 cms. or not quite 4 ins. and of the five species most characteristic of dunes (viz. 2, 4, 10, 13 and 16) all but *Stellaria apetala* (Pl. XXVII) exhibit rooting depths of about or less than this figure. Amongst the rarer, but characteristic, dune species the same feature is observed. Thus specimens of the Dune Centaury (*Centaurium littorale*, Fig. 55)

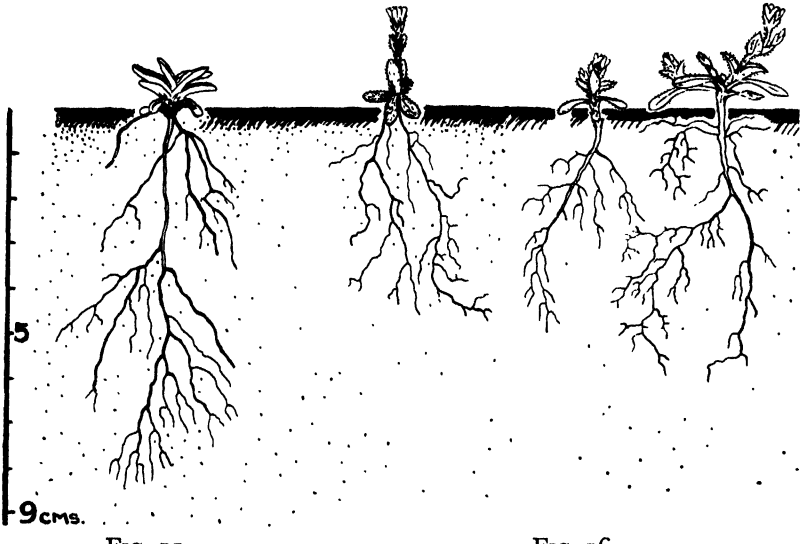


FIG 55 FIG 56

FIGS 55–56. Dune annuals, Llanbedr. April. FIG 55. Dune Centaury (*Centaurium littorale*). FIG 56. Three plants of a Mouse-ear Chickweed (*Cerastium tetrandrum*).

had rooting depths of about 8·5 cms. whilst the roots of *Hornungia petraea* (Fig. 81, p. 240) were also quite shallow. Judging from the data provided by O. H. Volk (*Zeit. f. Bot.*, p. 81, XXIV, 1931) for some of these sand-loving species, the osmotic suctions they are capable of developing though appreciable are not very high. Thus for *Cerastium semi-decandrum* he records osmotic pressures of from 9·5 to 14·3 atmospheres; for *Saxifraga tridactylites*, with rooting depths of 4 to 10 cms. in the sandy areas he investigated, osmotic pressures of 5·7 to 11·9 atmospheres were attained and for *Sedum acre* 6·6 to 10·7 atmospheres (rooting depths 8-12 cms.).

The accurate drawings, to scale, of typical specimens of dune annuals (Figs. 53–6 and 71–81) illustrate the form of their root systems better than measurements and show that there is, as might be expected, a marked tendency to lateral spread very well exhibited by a specimen of the dune Chickweed (*Stellaria apetala*) where the roots penetrated to a depth of only 9 cms., but spread to a breadth of 25 cms. (Fig. 72, p. 237.)

The perennial and biennial dune plants offer a very striking contrast in respect to their roots, although the time occupied in the excavation of their entire underground parts precludes the provision of statistical data on a comparable scale. A good example is the Spurge (*Euphorbia portlandica*, Fig. 45, p. 175), of which sixteen specimens were excavated. The depth of penetration ranged from 21 to 129 cms. (8 to 50 ins.) and the average was $61{\cdot}5 \pm 4{\cdot}4$ cms. or about 24 ins. Its congener, the Sand Spurge (*Euphorbia paralias*) (Pl. XXXI), which tolerates more mobile conditions and thus younger dune stages, may have roots reaching to greater depths, and since it occurs where the surface is subject to considerable accretion, the depth of penetration may be appreciably augmented. Thus in the specimen figured (Fig. 64, p. 218) the root extended to 130 cms. below the original dune surface on which the seed germinated and through 'flotation' the subsequent surface from which the shoots projected was another 14 cms. higher, so that the plant was obtaining water from a depth of about 4 ft. 8 ins.

Owing to their brittle character, it is almost impossible to excavate the roots of the Sea Holly (*Eryngium maritimum*) (Fig. 63) intact and so the extent of the finer roots is apt to be underestimated. But four specimens which were obtained almost in their entirety penetrated to depths of from more than 130 cms. to 171·5 cms. (4 ft. 3 ins. to 5 ft. 7 ins.) and we can assume that the mean rooting depth is in excess of the average of these data (151 cms.).

Another common plant of the early stages of which several root systems were investigated was the Rest Harrow (*Ononis repens*, Fig. 66). Here again of the eight plants several were not followed to the extremities so that the average here is too low a figure but, even so, the depth in half the plants examined was over 140 cms. (over 4 ft. 6 ins.). For the entire thirteen perennial species whose rooting depths were measured the average is 85 cms. (2 ft. 9 ins.) and it is noteworthy that the two of these

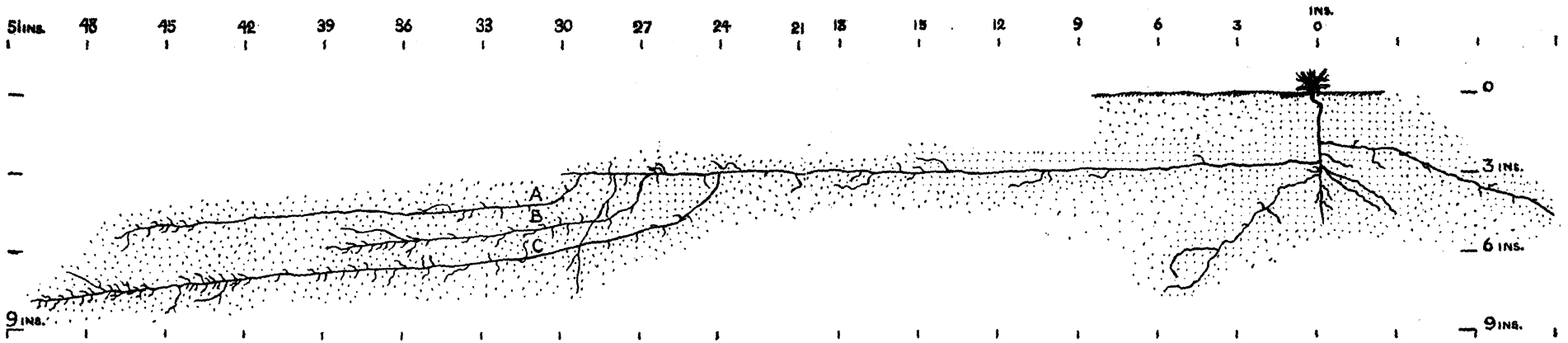


FIG 57. Root system of young plant of Prickly Saltwort (*Salsola kali*) with lateral roots extending horizontally to a distance of 49 in. (125 cm.). The roots A, B and C occupied approximately similar horizontal courses, but for clarity have been represented as vertically separated.

which are most characteristic of sand dunes have the deepest root systems. Moreover, those with the shallower roots are plants of the later yellow dune phases and are more associated with the fixed condition where the vegetation completely clothes the surface and the water content is higher. In this connection it must be noted that the shallower-rooted specimens of the Portland Spurge came from fixed dunes and the deeper root systems from late yellow dunes. The Sea Stork's-bill (*Erodium maritimum*), a species with beautiful rosettes close-pressed to the soil (Pl. XXIX), is a perennial or biennial species that is characteristic of the older dunes with an almost closed turf. It has a shallow root system with an average depth of 8·5±0·3 cms. and a range in the twenty-two specimens examined from 5 cms. to 11·5 cms.

TABLE II. ROOTING DEPTHS OF DUNE PERENNIALS OF YELLOW AND FIXED DUNES

		Observed range in cms.	*Number of Specimens*	*Average in cms.*
Taraxacum laevigatum	Sand Dandelion	38–41 (Fig. 61)	5	39·5 ±0·4
Polygala oxyptera	Dune Milkwort	>40 (Fig. 70)	1	40+
Thymus serpyllum	Thyme	60 (Fig. 87)	1	60
Euphorbia portlandica	Portland Spurge	21–129 (Fig. 45)	16	61·5 ±4·4
Viola canina v. *ericetorum*	Dog Violet	33–110 (Fig. 60)	7	71·3 ±6·9
Salvia horminoides	Clary	>70 (Fig. 69)	1	70+
Hypochoeris radicata	Cat's-ear	60–114 (Fig. 88)	4	74 ±7
Diplotaxis tenuifolia		>76 (Fig. 68)	1	76+
Lotus corniculatus	Bird's-foot Trefoil	>83 (Fig. 100)	1	83+
Ononis repens	Rest-harrow	>92–184 (Fig. 66)	8	125·6 ±7·6
Galium verum	Lady's Bedstraw	124–135	2	129·5
Euphorbia paralias	Sand Spurge	130 (Fig. 64)	1	130
Eryngium maritimum	Sea Holly	>120–171·5 (Fig. 63)	4	151 ±5

When we come to study the roots of the perennials of the dune slacks we find that, corresponding to the damp character and often high organic content of the soils here, the root systems are shallow also, as shown by the characteristic form of the Stag's-horn Plantain that here abounds (*Plantago coronopus f. pygmea*) (Pl. XXIX). The very shallow-rooting Waterblinks (*Montia minor*), which only persists so long as the soil remains moist, is an extreme example with roots only 2–3 cms. deep (cf. Fig. 75, p. 237).

TABLE III. VARIATION IN DEPTH OF ROOTS OF STAG'S-HORN PLANTAIN (PLANTAGO CORONOPUS)

Depth in cms.	*No. of plants*	*Depth in cms.*	*No. of plants*
2–4	1	10–12	8
4–6	6	12–14	12
6–8	8	14–16	8
8–10	12	16–18	2

Average of 57 plants, 10·2 ± 0·1 cms. (*ca.* 4 ins.)

This tendency for roots to become shallower as the moisture increases and the degree of soil aeration diminishes is not only exhibited by species of the different dune habitats, but even by the same species when growing under different conditions in these respects. The two specimens of Hairy Violet (*Viola hirta*), one from a fixed dune and the other from the damp margin of a dune slack, sufficiently illustrate this feature (Figs. 58 and 59). The root of the specimen from the drier habitat extended to a depth of 50 cms., whereas that from the damper only penetrated to a depth of 27 cms. But the roots

of the plants of slacks may be quite extensive when the species concerned is tolerant of poor aeration, as is shown by the root system of the dwarf form of one of the Sea Lavenders (*Statice binervosa*, Fig. 90, p. 270) which occurs in the brackish lows of some dune systems. The specimen illustrated despite the small size of the overground parts had a root depth of 59 cms. (23 ins.) and a spread of 77 cms. (30 ins.).

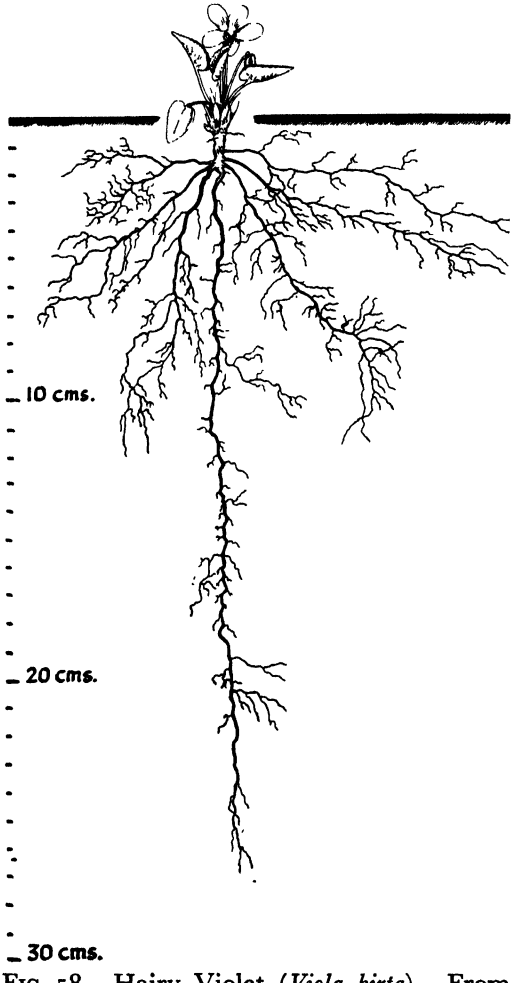


FIG 58. Hairy Violet (*Viola hirta*). From moist margin of dune-slack, old dunes, Kenfig Burrows, showing relatively shallow root system with copious lateral development near surface (compare with Fig. 59). About one-third actual size.

The biennials of the yellow dunes, such as the Hound's-tongue (*Cynoglossum vulgare*) and the biennial type of Henbane (*Hyoscyamus niger*) have deep roots and this character is shared by the Ragwort, which, though abundant on dunes, is common in other light-soil habitats. The root system of *Cynoglossum* illustrated (Fig. 67, p. 231) shows the leaf bases where five changes in level of the surface of the dune have occurred, but apart from these the rooting depth is nearly 50 cms. and even a one-year plant can have a root 34 cms. long, whilst that of a two weeks' old seedling had already attained 7 cms.

The extent of the root system in relation to the total size of the overground parts which we have had occasion to note, as exemplified by *Statice binervosa*, is also shown in a striking manner by the

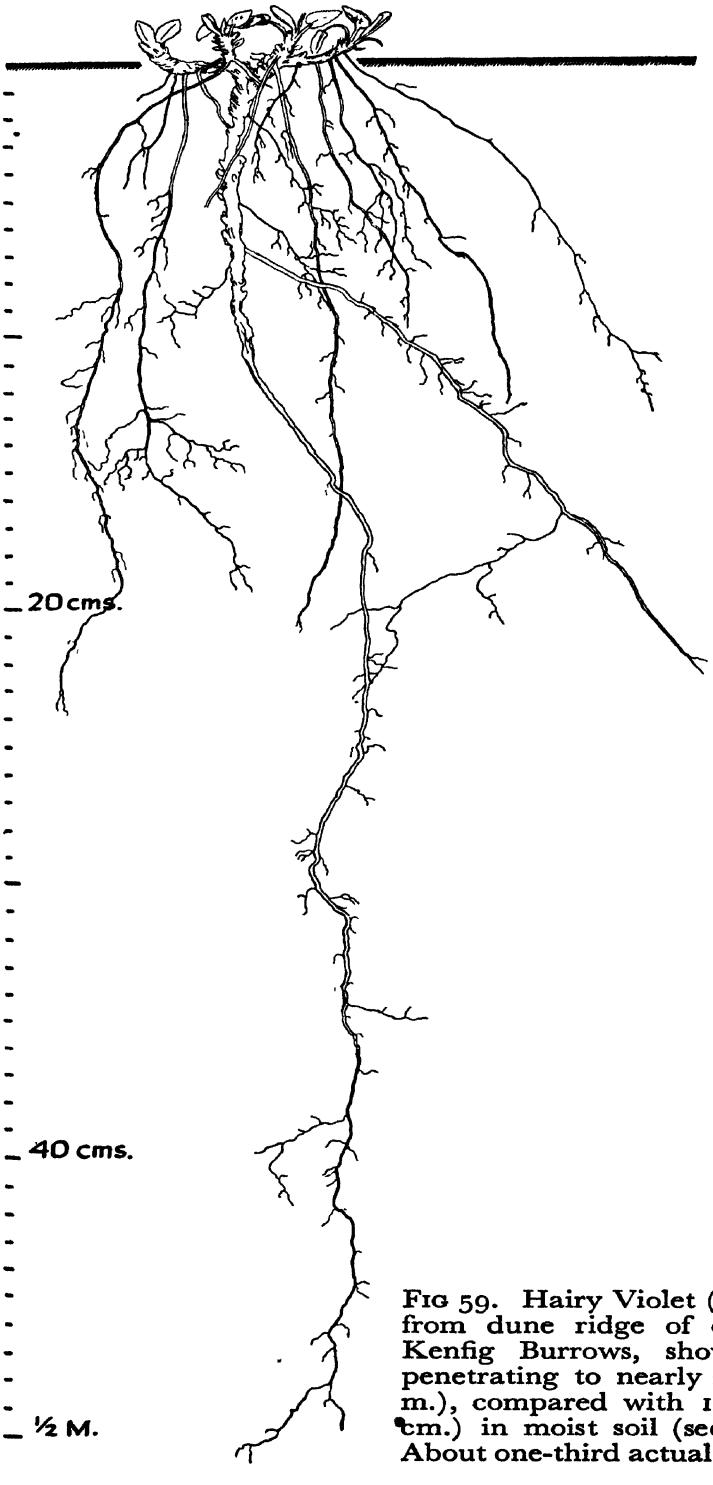


FIG 59. Hairy Violet (*Viola hirta*) from dune ridge of old dunes, Kenfig Burrows, showing root penetrating to nearly 20 in. ($> \frac{1}{2}$ m.), compared with $10\frac{3}{4}$ in. (27 cm.) in moist soil (see Fig. 58). About one-third actual size.

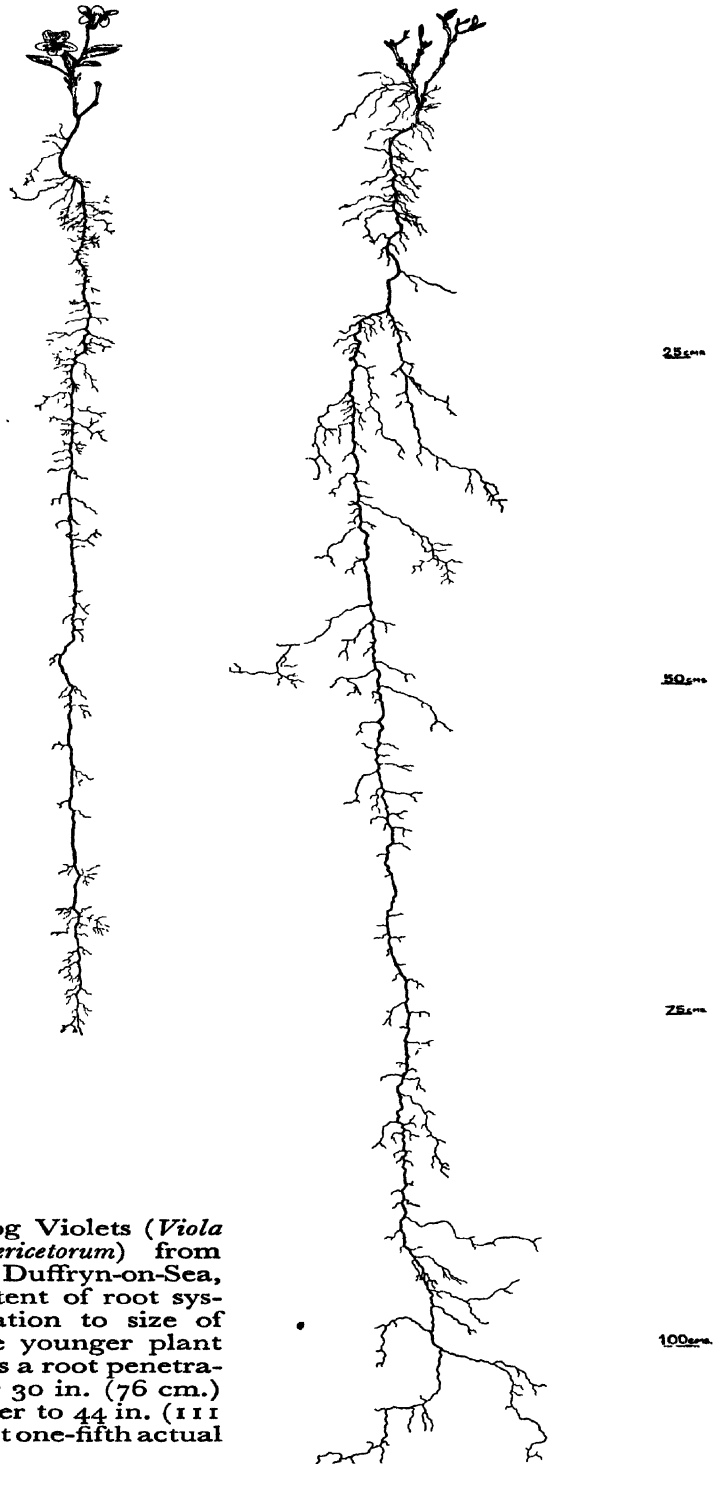


FIG 60. Dog Violets (*Viola canina* v. *ericetorum*) from fixed dunes, Duffryn-on-Sea, showing extent of root system in relation to size of plant. The younger plant in flower has a root penetrating to over 30 in. (76 cm.) and the older to 44 in. (111 cm.). About one-fifth actual size.

root system of the Dog Violet (*Viola canina* v. *ericetorum*) which may attain a depth of over 1 m. when the shoot system is but a few inches in height (cf. Fig. 60). This is doubtless connected with the favourable conditions for root growth that obtain in the dune soil whence the specimens figured were excavated—namely, good soil aeration and ample carbonates. Even more spectacular is the extensive root system of the Creeping Willow the roots of which may radiate for great distances (cf. Pl. XXIV).

The fleshy roots of several of the perennial species portrayed exhibit by their transverse striation the periodic longitudinal contractions that they have undergone and by means of which the rosettes of leaves produced at successively higher levels on the plant are repeatedly pulled down into close contact with the soil. A good example of this is seen in the Dandelion (*Taraxacum laevigatum*) (cf. Fig. 61).

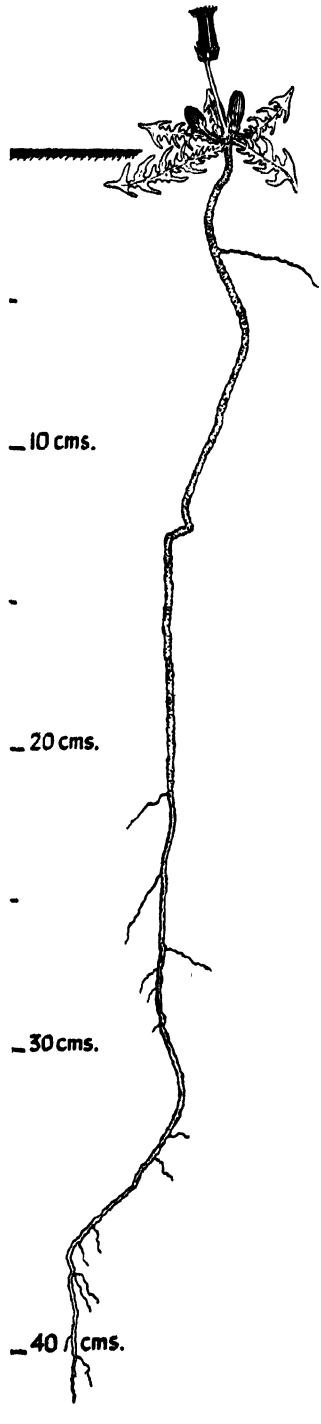


FIG 61. Dune Dandelion (*Taraxacum laevigatum*) from fixed dune. The horizontal wrinklings of the tap-root are due to the longitudinal contractions that maintain the leaf-rosette at ground level.

XVI

THE DRIFT LINE AND DUNE FACE

LET us imagine we are on a sandy foreshore in summer. Turning our backs upon the sea and walking directly landwards, we note at once a yellow dune ridge facing us clothed with the bluish-green leaves of the Marram Grass waving in the wind (Pl. XXIII). But between us and this high ridge there are usually low hummocky fore dunes, likewise clothed with plants, and often in addition, corresponding to the position of the highest drift lines formed during the autumn gales, a discontinuous belt of plants which for purposes of description can be termed the drift line or dune face vegetation, though in reality these plants are frequently the pioneers of dune formation. But the description will serve, since these same plants may be found providing the seaward fringe of green even where dune growth is in abeyance.

Because the plants of the dune face are mainly distributed by the tides, although dispersal by wind may also participate, they are especially associated with the uppermost drift lines. Their dispersal may be by seeds as with the Sea Orache (*Atriplex hastata*), by fruits as, for example, those of the Sea Rocket (*Cakile maritima*), or even by fruit clusters, such as those of the Wild Beetroot (*Beta maritima*); but they all alike are found mingled with the drift and so the plants to which these sea-spread propagules give birth tend to form a belt or, less commonly, successive belts following one or more contours of the sloping shores. But just as the sand, exposed at low tide, dries out in the wind and is blown landwards, so too, these propagules in the drift may be bowled along the sands and wafted hither and thither. In this manner the regular arrangement along contours is masked or sometimes even obliterated. If the seed-containing tidal drift is buried by sand, before its constituents dry out and are further disseminated by wind, the contoured distribution remains well defined, whilst a prevalence of fine weather at the season when the seeds are shed will facilitate a more scattered and irregular occurrence.

Because tidal carriage plays a major rôle in the dispersal of these plants, it is important to appreciate that these drift lines along which they grow represent extreme wave limits under exceptional conditions only attained during the highest tides and storms of autumn or early winter. For though the kinds of plants commonly found here are in some degree what are termed 'halophytes,' with a considerable tolerance for sodium chloride, the species concerned cannot usually endure prolonged immersion in sea water and this is especially true of the Sea Rocket (*Cakile maritima*, Pl. XXII).

The dispersal of fruits and seeds with the drift has the particular significance that normally when germination takes place the seedlings and young plants are assured of a supply of decaying organic material such as is provided by seaweeds and zoophytes and a varied assortment of flotsam and jetsam from the marine forms of plant and animal life. This not only supplies nutrients[1] and especially nitrates, but also adds greatly to the water-retaining capacity of the immediate surroundings of the roots of the plants of the dune-face after a fall of rain. When there are well developed dune-face species which do not appear to be associated with drift it will usually be found on digging the plants up that they are in fact rooted in drift that has been buried under blown sand. Nevertheless, this habitat is manifestly one that becomes very arid in spells of dry summer weather and the salinity of the soil solution increases the difficulty of an adequate supply of water to these plants. It is therefore noteworthy that the most successful plants here are species with fleshy leaves in which water is stored up and which thus have a reserve within their tissues that serves to prevent complete desiccation when water absorption by the roots is either negligible or impossible. The Prickly Saltwort (*Salsola kali*, Fig. 57 and Pl. XXII) stores up water not only in its fleshy spinous leaves but in the stems also; yet this does not obviate the necessity of a root-system that is remarkably extensive for the size of the over-ground shoots and one which moreover develops rapidly and at an early stage. (The specimen figured exhibited a root spread of 59 ins.)

The Sea Rocket has very fleshy leaves and likewise an extensive root system, whilst the species of Orache (*Atriplex*

[1] Analysis of the soil of one such drift line showed a high content of calcium (4·9%) and potash (2·04% K_2O) and an appreciable amount of phosphorus (0·39% P_2O_5). The chloride content was low—namely 0·16%—doubtless due to leaching by rain.

littoralis, *A. hastata*, *A. laciniata*) all store water in the foliage and in addition, in varying degrees according to the species, bear upon the leaves hairs with swollen tips containing watery fluid so that after rain they glisten with these minute globe-like reservoirs.

Determinations by Lundegardh and Killian of the osmotic pressure of the cell sap of some of these drift-line species is instructive as showing the high osmotic suctions they are capable of exerting and also as some indication of the salinities they would be likely to endure.

Arenaria peploides	16·5–18·5	atmospheres
Atriplex littoralis	over 37	,,
Euphorbia peplis	9–20	,,
Glaux maritima	20–29·3	,,
Salsola kali	11·1–30·6	,,

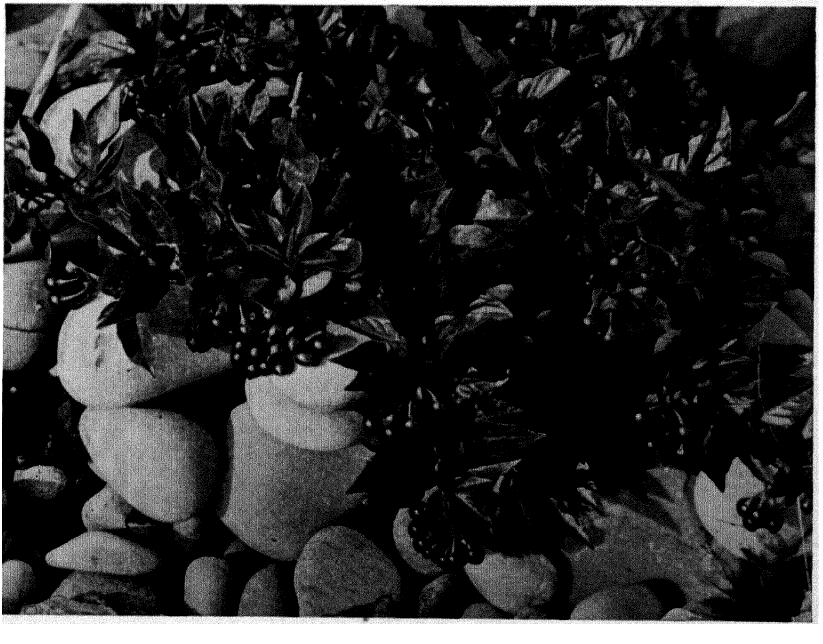
Since one atmosphere of osmotic pressure represents a potential suction force of 14·7 lb. per square inch, we realise from these data that a Prickly Saltwort plant is potentially capable of sucking in water with a force equivalent to 450 lb. per square inch and *Atriplex littoralis* with a suction equivalent to over 540 lb. per square inch. As the osmotic pressure of sea water is about 22·4 atmospheres, it will be appreciated that such littoral plants might even obtain water from sand that had been saturated by a wave and subjected to a measure of concentration by the heat of the sun's rays. But under such conditions the growth would naturally be very stunted, yet such facts enable us to understand how it is that quite healthy roots of the Saltwort may be found extending some distance seawards from plants in drift lines only slightly above normal high-tide level.

The commonest and most characteristic plants of the dune face drift line are annual species—namely, the Prickly Saltwort (*Salsola kali*), two species of Orache (*Atriplex hastata* and *A. littoralis*) and the Sea Rocket (*Cakile maritima*). The first three have inconspicuous flowers, but the last-named, when abundant and luxuriant, can provide a display that is quite magnificent

* * *

PLATE XXV. ABOVE. A very rare species of fixed sand dunes, *Romulea columnae*, with flowers open to the sunshine, the small fleshy leaved plants are the Stonecrop, *Sedum anglicum*. About twice life-size. (Reproduced by the courtesy of Dr. P. D. Wilson.) BELOW. Characteristic plant of the strand flora, the Maritime Woody Nightshade (*Solanum dulcamara var. maritima*). $\times \frac{1}{8}$.









(cf. *Cakile* zone at Harlech, Pl. XXII). Unlike the Saltwort, which in arid areas such as parts of Australia can become an inland pest, the Sea Rocket is an oceanic species that ranges from Spitzbergen to N. Africa and the Persian Gulf. Another member of the same family as the Sea Rocket is the Sea Radish (*Raphanus maritimus*, Pl. XXIII) particularly a feature of the dune face in the south-west. Locally the Marguerite-like *Matricaria maritima* with its finely-cut fleshy leaves, against the dark background of which the white flower-like inflorescences form a striking contrast, is common. The little annual Spurge (*Euphorbia peplis*) is now extremely rare, as also the maritime species of Ironweed (*Polygonum maritimum*) with its silvery-white stipules; but the near ally of this latter, *Polygonum raii*, is still of frequent occurrence and the protruding fruits render it easily distinguishable from the familiar Ironweeds of waste places and arable fields. There is only one perennial that occurs with any frequency—namely, the Wild Beetroot (*Beta maritima*), but the maritime variety of the Woody Nightshade (*Solanum dulcamara* v. *maritima*) is locally to be met with and distinguished from the type of the species found in our woodlands by its frequently unlobed fleshy leaves and prostrate habit (Pl. XXV). Another perennial is the Sea Kale (*Crambe maritima*) which, however, is really a shingle species found locally in the drift line of dunes where these rest on a shingle beach, a feature exhibited also by the Sea Sandwort (*Arenaria peploides*). This would appear to be true also of the Shingle Dock (*Rumex crispus* v. *trigranulatus*), a biennial closely related to the common Crisped Dock of inland habitats, and the Scurvy Grass (*Cochlearia danica*), but whether the same normally applies to the local and beautiful Frosted Orache (*Atriplex laciniata*) is less certain since, though mostly a shingle species, it does occur on the drift lines of dunes, where shingle is absent. In the north the fleshy-leaved *Mertensia maritima*

* * *

PLATE XXVI. BELOW. General view of the Dune system of Braunton Burrows with mobile yellow dunes in the foreground of which a small area on the right has been artificially planted with rows of Marram Grass to arrest sand movement. In the middle distance are fixed dunes and dune 'slacks.' Note isolated clusters of Marram Grass on the younger dunes and their increasing coalescence in the older stages. ABOVE. Inflorescences of the Ball rush (*Scirpus holoschoenus*) which occurs in some of the old 'slacks' on the Burrows. $\times \frac{1}{2}$.

may occur on the dune drift line, but this too is characteristically a shingle plant.

Sometimes the perennial grasses *Agropyron junceum* and *A. pungens* accompany the other plants of the drift line, and then they are often the initiators of a dune. Any of the species mentioned, whether annual or perennial, by providing a check to wind movement may effectively cause the deposition of airborne sand grains and thus initiate a dune, but with the annual plants, such as the Saltwort and Sea Rocket, this can be only temporary. With the withering of the foliage and the death of the plant the obstacle becomes progressively less effective and the accumulated sand soon becomes redistributed, and only the advent of some pioneer perennial, usually a grass, can enable these dunes around the annuals to make more than an evanescent contribution to the dune system.

DUNE FACE AND DRIFT LINE PLANTS

A=annual; *B*=biennial; *P*=perennial
c=common, f=frequent, o=occasional, r.r.=rather rare,
r=rare, v.r.=very rare, l=local

P.	*Agropyron junceum* (pioneer) c. . .	Sea Wheat Grass
P.	*Arenaria peploides* (pioneer) c. . .	Sea Sandwort
A.	*Atriplex hastata* L. c. . . .	Orache
A.	*Atriplex laciniata* L. r. . . .	Frosted Orache
A.	*Atriplex littoralis* L. c. . . .	
A.	*Atriplex patula* L. f.	
P.	*Beta maritima* L. o.	Wild Beetroot
A.	*Cakile maritima* Scop. c. . . .	Sea Rocket
P.	*Crambe maritima* L.	Sea Kale
A.	*Euphorbia peplis* L. (v.r. mostly extinct) .	Spurge
A.	*Matricaria maritima* f. . . .	Seaside Chamomile
P.	*Plantago maritima* f.	Sea Plantain
P.	*Polygonum maritimum* L. (v.r. mostly extinct)	
B.	*Polygonum raii* Bab. f. . . .	Seaside Ironweed
B.	*Raphanus maritimus* l. . . .	Sea Radish
A.	*Salsola kali* L. c.	Prickly Saltwort
P.	*Silene maritima* (Hornem.) With. o. (pioneer)	Sea Campion
P.	*Solanum dulcamara* v. *maritima* r.r. .	Seaside Woody Nightshade

XVII

THE YOUNG DUNES

OF the smallest dunes that we shall find those which are destined in the years to come to develop into a part of the dune system are as yet but isolated hummocks of sand, only a few inches high, that have collected, usually, around grass seedlings. Similar sand hummocks can be seen to have formed around annuals of the drift zone or even dead obstacles, but unless these come to be colonised by perennial plants they have no continuing significance in dune formation. Two kinds of perennial grass seedlings are commonly met with forming such embryo dunes. One of these, the Sea Wheat Grass (*Agropyron junceum*) is extremely tolerant of sea water. It can grow quite well with as much as 1·5% of salt in the sand and will tolerate up to 6%. Moreover, it will endure quite prolonged inundation by a high tide. As a consequence this grass can form dunes at a lower level on the shore than most other plants, even within reach of the highest spring tides. It has, however, a rather drooping habit of low growth and is therefore not a very efficient collector of sand; its extension is far more horizontal than vertical, so that by itself the Wheat Grass forms dunes that do not attain a height of more than 3 or 4 ft. Its tolerance of salt water, however, renders it a valuable precursor to other species, its habit affords good protection to the surface from wind, and so locally it may provide the dominant vegetation of the fore dunes, as one sees between Ainsdale and Birkdale on the Lancashire coast.

The second perennial grass, and by far the most important pioneer dune plant on British coasts, is the Marram Grass (*Ammophila arenaria*=*Psamma arenaria*, Pl. XXIII). This species is much less tolerant of salt and can only endure about 2% in the soil compared with the 6% that the Sea Wheat can survive. The Marram Grass, moreover, suffers appreciably from salt water spray in storms and any prolonged immersion in sea water will kill it, so that its rôle as a coloniser is at a higher level than that possible for the Wheat Grass. Compared with the latter, the

Marram Grass has a stiffer, more erect habit and the tufts of its long leaves, which appear almost cylindrical in dry weather, may project from 2 to 3 ft. above the dune surface and, as the data on p. 167 show, are efficient in diminishing the force of the wind and so bringing about the deposition of more sand. The embryo dunes formed around the grass seedlings are usually kite-shaped, with the direction of the 'tail' indicative of the prevailing wind. The extent to which this direction changes when the wind has veered to another quarter is a measure of the degree of stabilisation that the vegetation has produced, and such change is often noticeably greater where the embryo dune is 'still-born' by having collected around a dead object.

Another perennial species of the foreshore must be referred to as a pioneer dune-builder—namely, the Sea Sandwort (*Arenaria peploides*). This never forms very large dunes except in association with the perennial grasses, and is to be regarded as a drift line and foreshore plant of shingle rather than of sand. It becomes a dune-builder rather by accident than because the dune is particularly its home. This plant withstands the arid conditions of the habitat partly by reason of its extensive underground stems and root system, partly because any temporary deficiency in water supply can be met by the copious store of water in its succulent leaves, which are well protected by a thick-walled epidermis that itself constitutes an effective water jacket surrounding the internal tissues.

EARLY YELLOW DUNE

c=common, f=frequent, o=occasional, v.r.=very rare

P.	*Agropyron junceum* (L.) Beauv. c. . .	Sea Wheat Grass
P.	*Agropyron pungens* (Pers.) Roem. & Schult. c.	Spiked Couch Grass
P.	*Ammophila arenaria* ab.	Marram Grass
P.	*Arenaria peploides* L. o.-c.	Sea Sandwort
P.	*Calystegia soldanella* (L.) R.Br. (med.) (17) .	Sea Convolvulus
P.	*Diotis candidissima* (L.) Sm.=*Otanthus maritimus* (L.) Hoffmgg. & Link. v.r. . .	Cotton Weed
P.	*Elymus arenarius* L. f.	Lyme Grass
P.	*Eryngium maritimum* L. c.	Sea Holly
P.	*Euphorbia paralias* f.	Sand Spurge
P.	*Festuca arenaria* c.	Sand Fescue

Both the Marram Grass and the Sea Wheat Grass exhibit a feature that they share with other pioneer dune plants and which the Marram Grass exhibits in a striking degree, namely

that when the shoots become buried by sand this stimulates their further growth. We are all familiar with the effect of darkness or dull light in bringing about an elongation of the internodes of stems and reduction of leaf development of many species, and this response of dune plants is to be regarded as a specialised example of such etiolation. But any growth is only possible at the expense of food material and such is furnished in these grasses by the copious food reserves that are stored up in the extensively branched underground stems.

During a period of high winds successive layers of sand are added so that the foliage of the pioneers may become completely buried and the dune is raised until the level is such that sand is removed as rapidly as it is added. During the building period the grass grows through to the new surfaces, often branching in the process and producing a new crop of foliage at the higher level and so creating conditions favourable to further accretion. Thus there tend to be periods of rapid dune building alternating with periods of apparent quiescence when plant growth is often most active. Because the stimulus to growth furnished by periodical sand burial involves development not only of the terminal buds but commonly of lateral buds also, the outcome is a continually increased branching. Hence, though the extent of the surface of the dune increases as it grows in height, the living protection afforded by the shoots and foliage more than keeps pace. It follows that the risk of erosion does not materially augment despite the increasing wind velocity to which the surface grains are exposed as the elevation of the dune rises.

The seedlings of the Sea Holly, Sand Spurge and other perennial pioneer species often colonise the dune when it is only a few feet in height, but as each successive layer is added the shoots grow to the new surfaces and the foliage becomes separated by an increasing thickness of sand from the level where the seeds germinated, and the effective rooting depths augment. So efficient is the Marram Grass in this respect that it not infrequently brings about a rise of more than 1 ft. (30 cms.) in a year, whilst its spread laterally may exceed 36 sq. ft. (*ca.* 3·4 m.) per annum (see Fig. 62). This spread is effected by means of underground stems from which tufts of leaves appear above the sand at intervals and roots that penetrate into the sand and particularly exploit the layers that contain most organic matter and are therefore richer in water and nutrients (cf. Fig. 50, p. 184).

Measurements of a number of plants over a period of years indicates that both the pioneers *Agropyron junceum* and *Ammophila arenaria* have a remarkable capacity for rapid spread, in their early stages of growth, which must render them peculiarly fitted for the occupation of a mobile habitat. The average areas occupied by twenty plants of Wheat Grass (*Agropyron junceum*) in the

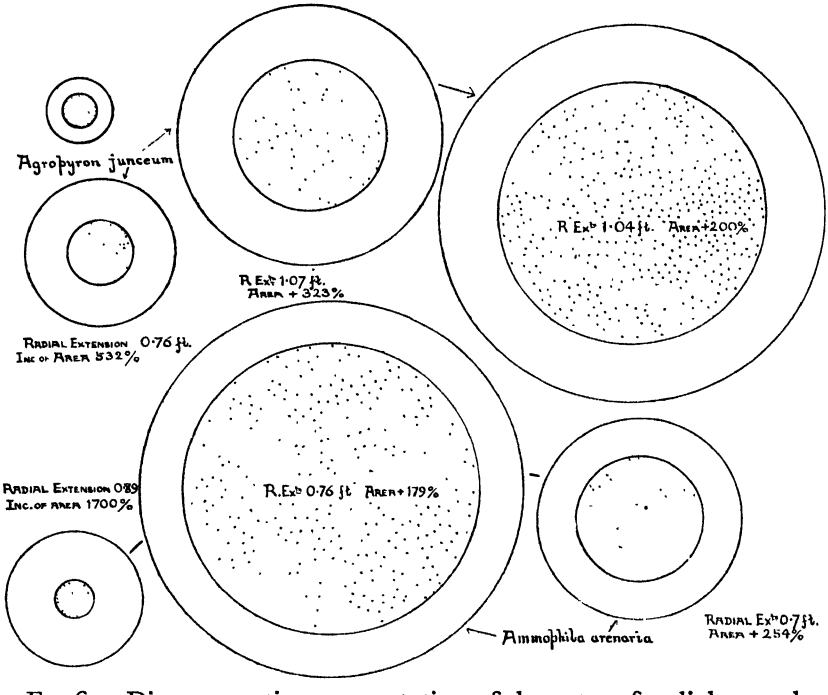


FIG 62. Diagrammatic representation of the rates of radial spread of plants of Sea Couch Grass (*Agropyron junceum*) over a period of four years, and of Marram Grass (*Ammophila arenaria*) over a period of three years. The diagrams represent averages for a number of similar individual plants. The dotted area is the average at the end of the previous season, and the white area the average extension. The arrows serve merely to indicate which diagrams refer to the same species, and the sequence follows the increase in area. (Norfolk coast.)

first few years of their development were: 1 sq. ft., 5·7 sq. ft., 18·4 sq. ft., and 37·4 sq ft., the maximum annual increment, amounting to about 600%, being exhibited during the second year's growth. The rate of radial extension gradually rises during the first three years to about a foot per annum (cf. Fig. 62).

The Marram Grass (*Ammophila arenaria*), though spreading initially at a slightly slower rate—namely, about 0·7 ft. per

year (*ca.* 17 cms.), exhibits a maximum radial extension in the second year of growth which, in the plants studied, amounted to an average increase of area of no less than seventeen times. *Agropyron junceum*, through its greater toleration of sea water, can not only colonise at lower levels, but tends to occupy sand that is normally moister and hence firmer than that higher up, where the Marram Grass is the dominant pioneer. The remarkable capacity for rapid spread of the latter, once the dune has progressed beyond the stage at which salinity might check the growth of the Marram Grass, may, therefore, be of some significance in its more mobile station.

Penetration of the sand by the growing rhizomes is facilitated by the fact that the apex is protected by an ensheathing leaf the tip of which is hard, woody and spine-like, with a sharp point that is not only effective for piercing the dune soil, but capable of withstanding the inevitable abrasion that passage through the sand involves. How sharp the points of these stems are is attested by the not infrequent occurrence of roots of various species, or even rhizomes of the Sand Sedge and the Marram Grass itself, which have become impaled.

Other grasses that can play a similar rôle as pioneers though usually later in their arrival are the Sea Lyme Grass (*Elymus arenarius*) and the Sand Fescue (*Festuca arenaria*). The former is less tolerant of exposure, the latter of salinity.

A feature which, perhaps as much as any other, fits these pioneers for growth on a dune is that they all possess an automatic mechanism that adjusts the water expenditure from their foliage to the water income from their roots. The causal mechanism of this adjustment is well seen in the Marram Grass. On a really wet day the Marram Grass leaves can be observed well-nigh flattened, whereas the condition in which most people see them is as a partially closed cylinder. The upper surface of the leaf is longitudinally ribbed and, at the base of each of the intervening furrows, there extend throughout the entire length of the leaf rows of thin-walled cells. Since the complete surface of the leaves is elsewhere protected against excessive desiccation by the thick outer walls of the epidermis, these lines of thin-walled cells are the first to lose water when a deficiency occurs. The ridges contain hard girder-like strands of tissue that offer considerable resistance to shrinkage of the soft tissues that flank their sides, and especially resist any

longitudinal shrinkage of the leaf. Hence, when the thin-walled cells (termed 'motor cells') lose water their contraction is almost wholly lateral. The ridges are thus brought together, resulting in the leaf curling so that the whole blade assumes a cylindrical form. Since the stomatal apertures through which water vapour escapes are restricted to the sides of the furrows, and the outer surface of the leaf is cuticularised and so relatively impermeable, loss of water vapour is reduced to a minimum when the leaf rolls up, and the extent to which the leaf becomes flattened out and water loss increases is nicely adjusted by the degree of turgidity of the thin-walled motor cells. On a dry, windy day the leaves of the grasses appear like narrow tubes split along one side, and this split widens or narrows in exact relation to the increase or diminution of the ratio between water absorption and water loss. This feature is of most importance when conditions are most extreme, but some idea of the efficiency of the mechanism can be gained from the fact that experiments with *Elymus* have shown that, even under but slight air movement, the rolled leaves transpire only about a tenth of the water lost by the leaves when flat.

The special features referred to, all of which these pioneer grasses possess, are shared, wholly or in part, by other perennial plants though not in combination to such an extent. After the initial stages of dune formation have passed two conditions in particular have become less extreme. The increasing shelter produced by the foliage of the pioneers has substantially reduced mobility, whilst the organic matter derived from decay of leaves, roots and stems has increased the capacity of the dune to retain water, especially at the surface, and this not only ameliorates the conditions for growth but also contributes to stabilisation. Further, the growth in height of the dunes above storm tides has ensured an appreciable depth of sand in which fresh-water conditions are assured and the risk of periodic salinity minimised.

It is therefore not surprising that the stage of fusion of embryo dunes, when the isolated units merge into a young dune ridge, is often marked by the advent of other pioneer plants which exhibit an increase in variety of species and numbers of individuals as the conditions become progressively improved.

The rapid lateral extension of the embryo dunes quickly results in their mutual fusion so that a new ridge is established

parallel to that which preceded it.

The Sea Lyme Grass (*Elymus arenarius*) is a pioneer that is only less specialised in this rôle than the other perennial grasses just considered. From its large size (it can attain a height of up to 5 ft.), its long and numerous rhizomes and its robust foliage, this grass is well equipped as a dune-builder and is often planted for that purpose. But though the Lyme Grass will tolerate up to 12% of salt it is very sensitive to wind and thus tends to colonise the later phases except where the fore dunes are particularly sheltered.

Another perennial grass which may appear at this stage is a second species of Wheat Grass (*Agropyron pungens*). Like the Sand Fescue, it is not very tolerant of saline conditions, but can make an appreciable contribution to the stabilising of the dune.

Conspicuous among the early arrivals of plants other than these grasses are the Sea Holly (*Eryngium maritimum*) and the Sea Spurge (*Euphorbia paralias*); both show the capacity to grow up to a new surface when covered by sand in a marked degree (so-called 'flotation'), as is illustrated in the drawings of plants excavated from large dunes which show the successive levels of foliage production corresponding to the repeated increments to the dune surface (see Figs. 63 and 64). Both are possessed of leathery leaves with thick cuticles and are very resistant to desiccation. Moreover, the thick fleshy root of the Sea Holly, which in

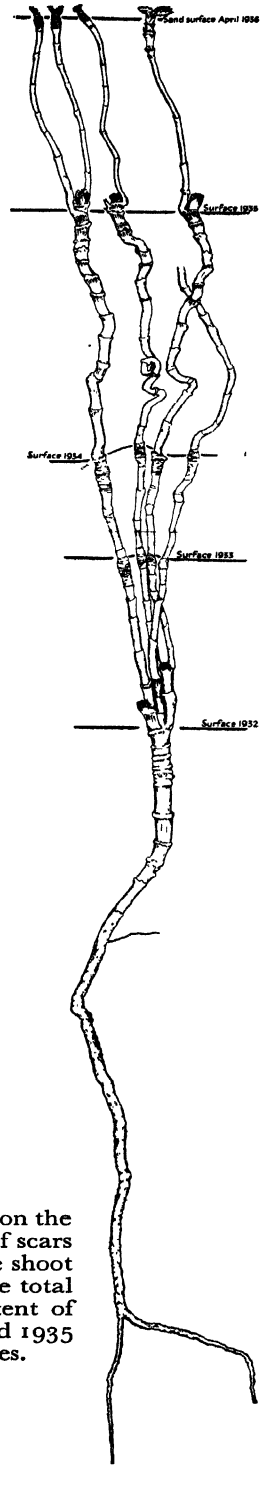
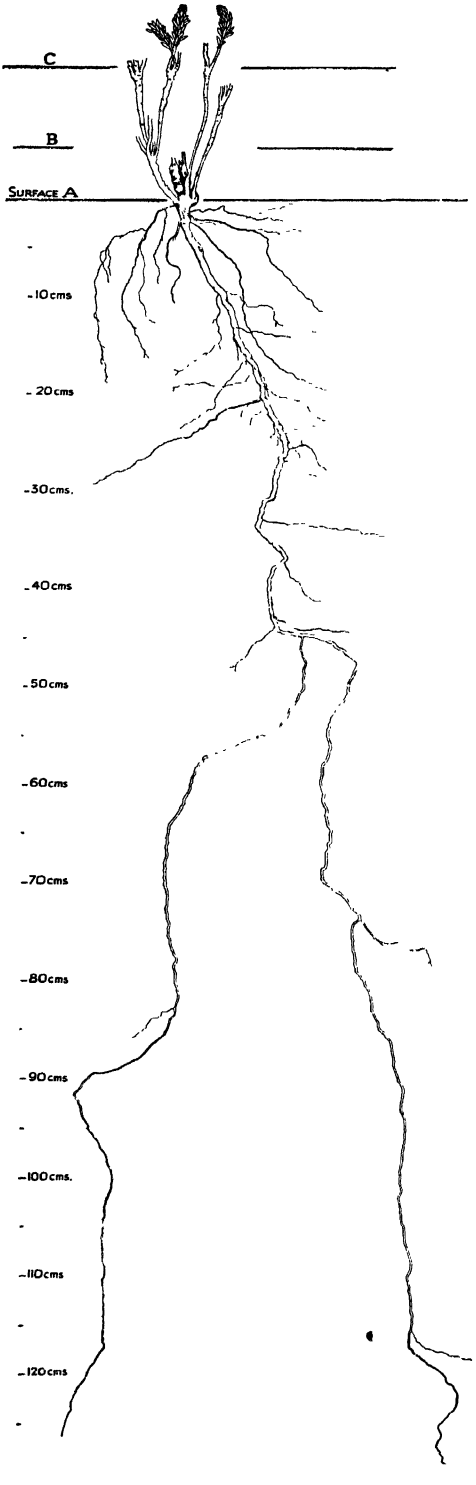


FIG 63. Sea Holly (*Eryngium maritimum*) from a dune on the Welsh coast (scale one-eighth actual size). The leaf scars indicate the five successive dune surfaces to which the shoot system had been stimulated to grow ('flotation'). The total depth is over 5 ft. 7 in. (172 cm.), but the full extent of the root is not shown. The dark scars at the 1932 and 1935 surfaces indicate the former positions of flowering axes.



Elizabethan times was candied to produce a comfit, acts in part as a water reservoir. Although, according to Killian, it is capable of developing an osmotic pressure of 9–14 atmospheres, it is not very tolerant of sea water. However, the fruits which are often dispersed by the tides can germinate after forty-five days' immersion and float for an appreciable period. Its spread is also facilitated by the production of buds from portions of the roots as well as from the underground stems. The latter were found by J. Turmel (*Bull Soc. Bot. Fr.*, 94, p. 138, 1947) to exhibit marked polarity, inverted fragments still producing shoots from the now lower, but morphologically upper, end and similarly roots from the morphologically lower surface although now uppermost. The Sea Holly figured was excavated from a yellow dune on the Welsh coast and shows the positions of five successive dune surfaces. The first of these represents the summer level of 1932, and it will be noted

FIG 64. Sand Spurge (*Euphorbia paralias*) showing 'flotation' in relation to three changes in dune level at Llanbedr. Owing to the increments in level the root tip is situated about 55 in. (140 cm.) from the surface of the dune.

that the root extends to a depth of probably at least 1 m. (39 ins.), having regard to the thickness of the root where it was broken off. Above the level of the first dune surface a series of leaf scars indicate the new dune level some 18 cms. (*ca.* 7 ins.) higher. The third series of leaf scars indicate a rise of another 12 cms. (*ca.* 4½ inches) to the summer level of 1934. Probably the winds of the winter months ensuing were unusually strong, bearing an extra burden of sand, since the surface of 1935 is 26 cms. (*ca.* 10 ins.) above that of the previous season. In the year following a further accretion of 21 cms. (*ca.* 8 ins.) occurred, so that the total rise amounted to 77 cms., or approximately 29½ ins., and the depth from the surface to which the roots penetrate was increased to above 1¾ m., or nearly 5 ft. 9 ins. (cf. Fig. 63).

The Sand Spurge (*Euphorbia paralias*) shows a similarly marked capacity for keeping pace with the changing levels. In the specimen drawn to scale (in Fig. 64) it will be noted that three successively higher dune surfaces have led to branching and new shoot production, the three levels collectively representing a rise in the dune of 14 cms., whilst the roots penetrate a further 130 cms.

These two examples exemplify sufficiently the changes in level which the pioneers must be able to tolerate, and it is therefore obvious that species in which the capacity for what we have termed 'flotation' is not marked will by force of circumstances be relegated to the older and more stable phases of dunes where the reduced changes in level impose a less severe handicap. Since, however, different dune systems and even sometimes different parts of the same system of comparable age differ in their rates of accretion, the stage at which the less adaptable plants arrive may at one place be later or at another earlier in dune development.

The particular qualities of grass roots that make them so valuable an asset in soil improvement by means of temporary leys in agricultural practice are no less important in dune-building. The annual production and decay of grass roots, their copious development and intensive ramification through the sand mass which they exploit, achieves an intimate mingling of organic material with the mineral matrix that, at one and the same time, raises the capacity for retention of rain water and helps to bind together the discrete particles of sand. Thus it is that with the advent of the perennial grasses the young dune may be said to have reached the first stage in the process of contributing to an addition to the mainland of a more or less permanent nature.

XVIII

BIOLOGICAL NOTES ON PLANTS OF YELLOW DUNES

Otanthus maritimus (*Diotis candidissima*)	Cotton Weed (Map, p. 293)
Glaucium flavum	Horned Poppy
Elymus arenarius	Lyme Grass (Map, p. 293)
Ammophila arenaria (*Psamma arenaria*)	Marram Grass
Salsola kali	Prickly Saltwort
Ononis repens	Rest-harrow
Carex arenaria	Sand Sedge
Euphorbia paralias	Sand Spurge (Map, p. 289)
Calystegia soldanella	Sea Convolvulus
Agropyron junceum and *A. pungens*	Sea Wheat and Couch Grass (Map, p. 289)
Eryngium maritimum	Sea Holly
Cakile maritima	Sea Rocket
Raphanus maritimus	Seaside Radish (Map, p. 289)
Carex incurva	Dune Sedge

*

SEA WHEAT GRASS, *Agropyron junceum*. Gramineae. 2n=28.

A perennial grass spreading by its underground stems and producing rather untidy masses of glaucous foliage the blades of which became rolled under drought conditions. The edge of the leaf is smooth. The rather lax spike is 3–4 ins. in length (5–10 cms.), with smooth and shining spikelets widely spaced.

Both the adult plants and seedlings can tolerate a high concentration of salt (up to 6%) and prolonged inundation by sea water.

The species is a southern-oceanic one which occurs in America as well as Europe.

A. pungens is a larger and more erect grass with more rigid rolled leaves. The edge of the leaf is toothed and the spikelets are rough instead of being smooth and shiny and are crowded in a dense spike. It is far less tolerant of salt water. For distribution in Britain see map, page 289. Both species are known as Sea Couch Grass.

MARRAM GRASS, *Ammophila arenaria*. (*Psamma*) Gramineae. 2n=14 or 28. (Pls. XXIII and XXXI)

A creeping perennial grass with leaves that have somewhat the appearance of tufts of slightly curved rushes in dry weather,

but in damp conditions are seen to be rich green and smooth on the outer or lower face and whitish-green and ribbed on the inner or upper face. The flowering stems which are from 2–3 ft. (60–90 cms.) high bear cylindrical heads 4–5 ins. in length. Flowering specimens are usually found only on the mobile dunes and are often confined to the fore dunes on the seaward side of the main dune ridge. Dispersal is probably by wind. A clump derived from a single plant can produce over 30,000 'seeds.' Germination occurs chiefly in spring.

Ostenfeldt, in *The Botany of the Faroes* (Copenhagen, 1910), states that in the Faroe Islands neither *Ammophila arenaria* nor *Agropyron junceum* appear to fruit readily if at all, and their continued existence depends on vegetative propagation. The cells of the piliferous layer may secrete mucilage that binds together the adjacent sand particles and produces a caddis-worm case structure, that may have some protective value, as in other desert plants. This feature is seen also in *Statice binervosa* (cf. Fig. 90, p. 270).

SEA ROCKET, *Cakile maritima* Scop. Cruciferae. 2n=18.

An annual plant the adults of which may attain to any size from 1 ft. to 1 yd. (30–90 cms.) across. It is freely branched in a somewhat zigzag manner and bears fleshy leaves containing storage water that are often pinnately lobed, although the lobing may be obscure. The pale lilac flowers exhibit four rounded petals and are about 1 cm. in diameter. They are sweetly scented and attractive to a variety of insects which seek the nectar. The chief feature of interest is the fruit, which is a constricted pod that does not open to set free the seeds, but separates into its two portions, which are dispersed by the tides entire. There are two seeds in the fruit, one in the upper portion above the constriction and one in the lower. Moreover, the two seeds often differ in size and weight, the upper being the heavier. The half-fruits become buried in the sand with other drift and germination takes place in spring and averages over 60%. The cotyledons are fleshy and strap-shaped.

The species is found on coasts from Spitzbergen to N. Africa and the Persian Gulf. Large plants, such as those shown at Harlech (Pl. XXII), would produce some 10,000 fruits or nearly twice that number of propagules. Roots can extend over 39 ins. (> 1 m.). Dr. P. Olsan-Seffer in an unpublished paper

recorded experiments which showed that in clay soil the growth of *Cakile* was only about a quarter that of its growth in sand.

SEA CONVOLVULUS, *Calystegia soldanella*. Convolvulaceae. 2n=22.

This is perhaps the most conspicuous of the dune perennials when in full bloom, since its pink trumpet-shaped flowers with rose-coloured stripes are nearly 2 ins. across. The smooth fleshy leaves are dark green, kidney-shaped in outline and stalked, arising, like the solitary blooms, from the creeping underground stems. The stomatal index ranges from about 15% to 18%.

The seeds are round, black and weigh about 0·057 gm. and vary in number from one to four in the capsule although fruit production is often meagre, but vegetative spread rapid (from 0·5 m. to 1 m. per annum). The flowers are often eaten by rabbits. Germination is epigeal. The cotyledons are oblong-cordate with notched apices. Osmotic pressures of 9 to 11·4 atmospheres have been recorded.

A species of wide distribution that occurs all round the coasts of Britain except in the extreme north.

SAND SEDGE, *Carex arenaria*. Cyperaceae. (Pl. XXXI)

The extensive rhizomes of this perennial which are situated normally at a depth of about 6 ins. (15 cms.) have a slightly aromatic odour when crushed. Rhizomes bear short roots (40–60 cms.) and long roots that may penetrate over three meters. The rate of spread may be over 12 ft. (3·6 m.) per annum. The tufts of evergreen leaves that arise at intervals from the underground stems attain about 8–12 ins. (20–35 cms.). There are no stomata in the upper epidermis and about 120 to the square millimeter in the lower. The shoots viewed from above show the leaves in three vertical series.

It can occur inland on sandy heaths as on the Breckland sands of Suffolk where it is abundant.

Generally distributed throughout the coasts of Europe (except in the Arctic) Siberia and North America.

Fruit oval, yellowish brown. Germination in spring *ca.* 75%.

DUNE SEDGE, *Carex incurva*. Cyperaceae.

A dwarf perennial, the leaves with involute margins and recurved and with very long creeping stems. An arctic type, in Britain confined to sandy shores of Scotland.

LYME GRASS, *Elymus arenarius*. Gramineae. 2n=56.

A perennial grass growing up to 6 ft. (1·8 m.) in height, spreading rapidly by underground stems the annual increments of which may exceed a metre. In wet weather the leaves are seen to be about 8–16 mm. wide with parallel, flat-topped ridges on the upper surface. The stomata are at the sides and the thin-walled motor cells at the base of the grooves. In dry weather the glaucous leaves are rolled. The long flower-spikes (4–10 ins.=10–25 cms.), although somewhat flattened, are less so than in the Couch Grasses, where the spikelets are solitary. The grains are some 14 mm. in length and weigh about 0·0077 gms. They germinate in an intermittent manner. Since the foliage of this grass dies away in autumn it affords little protection to the surface during winter storms.

The Lyme Grass is widely distributed on dunes in north temperate regions and occurs around the whole of the British Isles with the exception of the west of Ireland (cf. map, p. 293).

SEA HOLLY, *Eryngium maritimum*. Umbelliferae. 2n=16. (Fig. 63)

A deeply rooting herbaceous perennial with leathery, smooth leaves that have pale veins and thickened margins, bearing spines at the ends of the leaf teeth. The basal leaves are rounded in outline and three-lobed. The glaucous bloom is due to minute particles of wax. Stomata occur almost equally in the epidermis of both surfaces; 60 to 74 per square millimeter were counted on the upper and 52 to 66 in the lower. It is quite unlike most members of its family both in the undivided leaves and the curious oval head of blue flowers. This inflorescence is set in a cup of five spiny leaves and below each flower of the head is a narrow bract ending in three spines. The entire structure is essentially similar to that of normal members of the carrot tribe if we assume suppression of the stalks of the main umbel and the reduction of the secondary umbels, that such stalks normally bear, to a solitary flower. Pollination is effected by small insects. The fruits are rather corky in texture and float readily. They are dispersed by tide and wind.

The plant is distributed round the Atlantic and Mediterranean coasts and throughout the dunes of the British Isles.

SAND SPURGE, *Euphorbia paralias* L. Euphorbiaceae. 2n=16.

As with other members of this genus, all parts of the plant if broken exude a milky juice. The yellowish-green leaves are without stalks, narrow and rather crowded with so leathery a texture as to be relatively stiff and the resistance to loss of water which their thick cuticle offers is realised from the length of time that detached shoots require before showing any signs of wilting. The upper leaves on the flowering branches are oval, and the female flowers situated in their axils consist of a single three-lobed and wrinkled green ovary bearing at its summit three stigmas. Around this will be seen what appear to be five stamens, but each is actually an entire male flower reduced to its simplest term. The stems, which are often reddish in colour, are from 6–18 ins. high (15–45 cms.) and form a bushy cluster. The seeds weigh about 0·0047 gm. are of oval form and of a grey colour minutely dotted with white. Seedlings are to be found in the spring. (Pls. XXVII and XXXI).

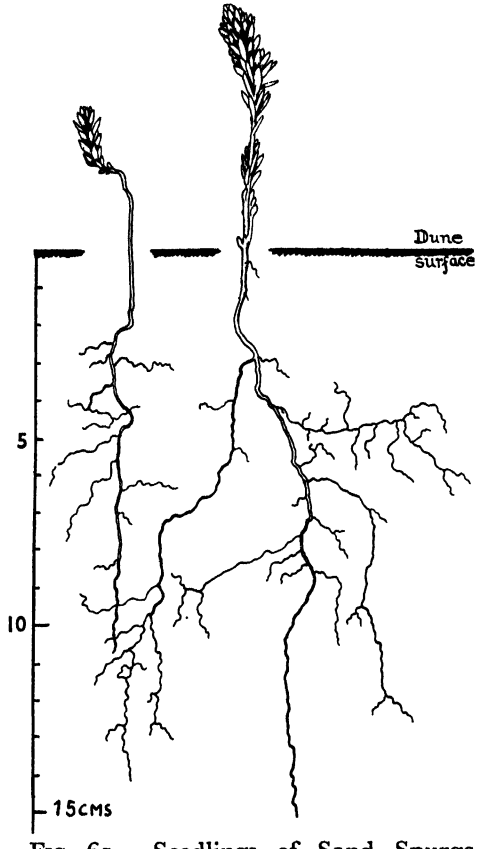
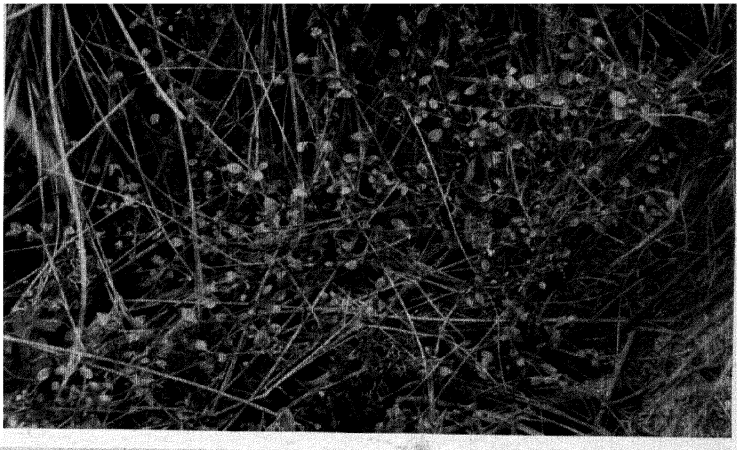


FIG 65. Seedlings of Sand Spurge (*Euphorbia paralias*) in September, about two months old. Note the imbrication of the foliage and the extent of the roots in relation to the size of the plants.

* * *

PLATE XXVII. Sand dune flora. TOP. The Dune Chickweed (*Stellaria apetala*=(*boraeana*) growing on a fixed dune, in the foreground is seen one of the dune lichens. MIDDLE. Recently formed mobile dune overwhelming a dune slack. Note the rejuvenated character of the Marram Grass which has been reached by the mobile sands compared with plants in the foreground growing in old stabilised sand. BELOW. Dune erosion with colonisation of the floor by Prickly Saltworts and seedlings of Sand Spurge.













This species belongs to the southern-oceanic element in the European flora. Its range does not extend northwards of Belgium, and in the British Isles it occurs at intervals from Norfolk all round the south and west coasts to Wigtown and around the Irish coast, but is almost absent from Scottish dunes, as we might expect from the continental distribution.

HORNED POPPY, *Glaucium flavum*. Papaveraceae. 2n=12.

A biennial, or short-lived perennial, with glaucous, rather hispid fleshy foliage forming a rosette and bearing large yellow flowers 2–4 ins. (5–10 cms.) in diameter. The pods are long and curved, sometimes attaining about 30 cms. in length and containing numerous (up to about 500) black seeds that are kidney-shaped, shining and reticulately pitted. A single plant can produce up to 60,000 seeds. Seedlings can be found in both autumn and spring, especially the former.

Osmotic pressures from 6–19 atmospheres have been recorded, and the stomatal indices observed are fairly high (17–22%).

The whole plant contains a yellow latex.

A species with a definite southern trend that does not occur in Scotland north of Kincardine and Argyll or in Ireland from Mayo to Antrim, although present in most of the coastal counties southwards.

REST-HARROW, *Ononis repens*. Leguminosae. 2n=32.

A long-lived perennial without spines and with leaves that have sticky glandular hairs emitting a slightly unpleasant aromatic scent. The prostrate shoots produce stolons freely and rapidly respond to burial by renewed growth. The pink flowers, which are without nectar and visited for pollen, are succeeded by pods which are shorter than the protecting calyx and contain one to four seeds. The seeds are about 3 mm. in

* * *

PLATE XXVIII. Sand dune flora. ABOVE. The Musk Stork's-bill, (*Erodium moschatum*) on fixed dunes, Somerset. MIDDLE. An exposed accumulation of snail shells on Braunton Dunes in the foreground, to the right, mostly the moss *Tortula* and to the left Creeping Willow (*Salix repens* agg.). BOTTOM. Silverweed (*Potentilla anserina* var. *sericea*) colonising the young dune; the small rosettes of narrow pointed leaves are those of the Sand Sedge (*Carex arenaria*).

length, oval and covered with small tubercles. They weigh about 0·006 gm. The plant has very tough stems, that are responsible for the popular name, and roots that penetrate the soil to considerable depths.

COTTON WEED, *Otanthus maritima* (=*Diotis candidissima*). Compositae.

The history of this sand-dune species in Britain is interesting for whereas it was formerly to be met with locally from the coasts of Suffolk around the southern seaboard to Anglesey (see map, p. 293), to-day it is confined to the Scilly Isles. It is a perennial herb almost woody below, bearing well-nigh white leaves felted with abundant hairs and small yellowish heads of florets. The fruits have no parachute and are dispersed by wind and tide.

The species is a Mediterranean dune plant that with us rarely attains more than 12 ins. (30 cms.).

The seeds germinate both in spring and autumn.

SEASIDE RADISH, *Raphanus maritimus*. Cruciferae. 2n=18.

A biennial, very hispid plant that frequents rocks as much as sand dunes. It attains a height of about 2 ft. (60 cms.) in the year of flowering and is freely branched and bushy. The leaves are rather fleshy, with about 360 stomata per square millimeter and a high stomatal index (*ca.* 30%). The pod has a slender short beak with two to four segments, and deep constrictions between them each containing a single seed. These one-seeded segments break apart at the constrictions and by virtue of their corky walls and the contained air float readily. They are dispersed by the tide.

The species is a markedly oceanic one found on the Atlantic seaboard of Europe from Holland to Spain, and on the coasts of Britain except northern Scotland and rarely in the east (see map, p. 289) (Pl. XXIII).

PRICKLY SALTWORT, *Salsola kali* L. Chenopodiaceae. 2n=36. (Pl. XXII)

A much-branched annual with ribbed green stems and succulent cylindrical leaves each ending in a spine. The whole plant is covered with minute down-like hairs. The root-system is shallow but wide-spreading, frequently radiating

more than 2 ft. (>60 cms.) from the axis. The stomata are transversely orientated and the stomatal index is high (*ca.* 21%–25%).

The flowers are minute with five chaffy sepals, no petals and three to five pendulous stamens. Pollination is by the wind.

The fruit is dispersed by the tides, still enclosed in the five-lobed calyx which has become enlarged. The fruit contains a single seed in which there is a greenish embryo beautifully coiled in a spiral manner.

This species has a wide distribution and has become a pest in the sandy areas of Australia. W. H. Volk records osmotic pressures in this species of from 11–15·4 atmospheres and rooting depths of from 15–22 cms. The pH of the soil ranged from 7·4 to 8·3 (*Zeit. f. Bot.*, pp. 81–185, XXIV, 1931).

XIX

THE LATER YELLOW DUNE PHASES

THE main ridge of a dune system, like the embryo dunes from which it was once derived, still presents a considerable surface of bare sand that implies mobility both in the vertical and horizontal directions. Nevertheless, the numerous tufts of Marram Grass provide such degree of protection, compared with the earliest stages, that an appreciably greater variety of plants can now survive. All must still be able to endure the accretion of fresh sand, but any rise in level is now much slower so that a reduced growth rate can suffice. Moreover, the risks of any appreciable salinity are normally negligible. So the flora of the main ridges though still essentially a community of perennials, that are readily stimulated into new growth, includes also some biennials, such as the common Ragwort (*Senecio jacobaea*), and even sparsely scattered annuals that are chiefly to be seen on the lee side of the Marram tufts, where stability is most assured.

The height of the main ridge of a dune system is dependent on a number of variable circumstances, such as the height and frequency of the tides, the amount of sand available on the foreshore, the average strength of the 'on-shore' winds, the amount and seasonal distribution of rainfall and not least, though in large measure determined by the foregoing, the nature of the colonising plants. Marram Grass can build up dunes that normally attain a height of from 30–60 ft. The main ridge of the East Coast dune systems is usually 30–50 ft., whilst on the north Devon and the North Wales coast the ridges rise to heights of up to 100 ft., as at Braunton and Prestatyn.

The slopes of the main ridges often attain 30°, the usual angle of rest of dune sand, but may even exceed this on the seaward face, where the coarser sand tends to be deposited and the network of roots and stems permit of a higher angle of equilibrium when wind erosion has removed sand from the seaward slope.

The Marram Grass is by far the most abundant species on

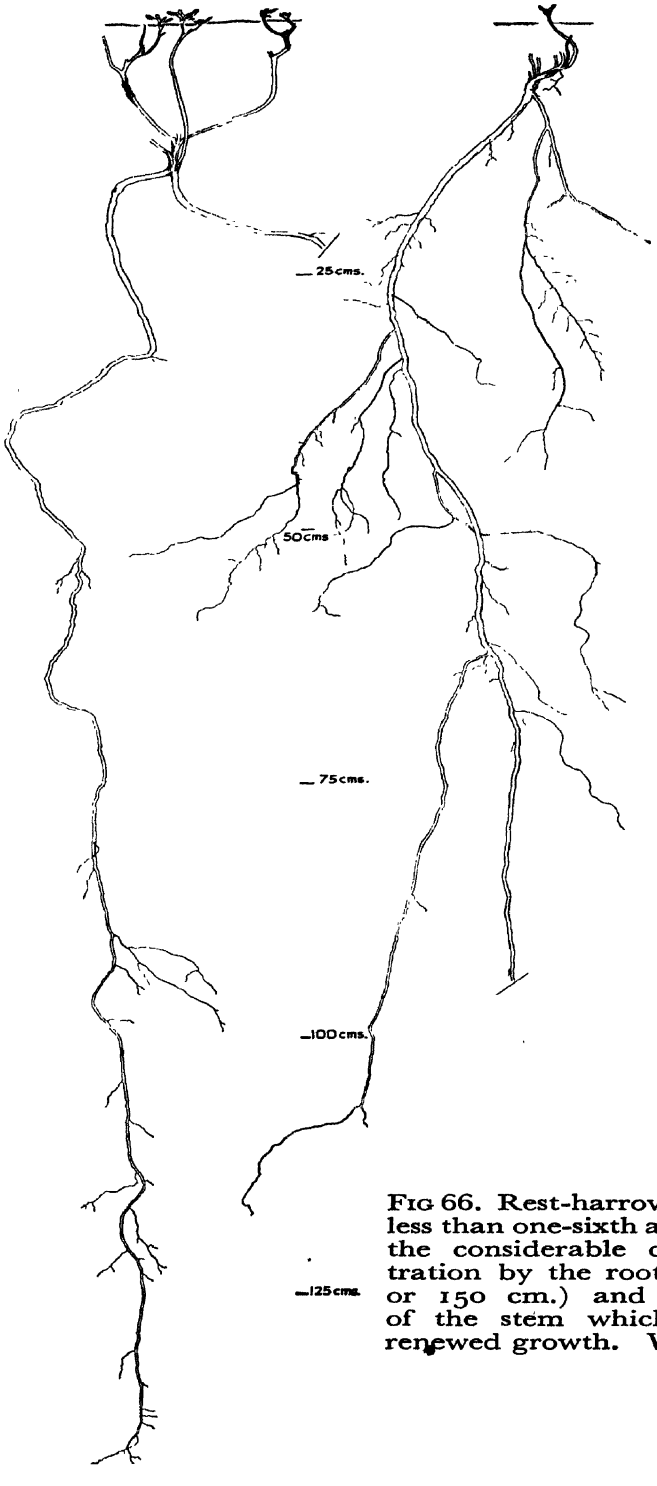


FIG 66. Rest-harrow (*Ononis repens*), less than one-sixth actual size. Note the considerable depth of penetration by the root (about 58 in., or 150 cm.) and the branching of the stem which accompanied renewed growth. Welsh coast.

the main ridge, but is often accompanied by the Sand Fescue and sometimes in more sheltered situations by the Lyme Grass. How far these are accompanied by other species is much influenced by the extent and number of the fore-dune ridges, since these affect the degree of stability and accretion of the main ridge. Of the perennials other than grasses which share the capacity of rapid growth to a new surface the Sea Spurge and Sea Holly have already been referred to. Not so efficient in vertical extension but with a marked capacity for rapid lateral spread is the Sea Convulvulus (*Calystegia soldanella*) with large trumpet-shaped pink flowers and kidney-shaped, dark green fleshy leaves that rest close to the ground. It sends fleshy stems obliquely through the dune, the tips of which bear a leaf bent back in such a manner that the undeveloped juvenile blade is drawn through the sand and the brunt of the friction is borne by its bent stalk. On reaching the light the stalk straightens and the blade enlarges. The annual increments may be from 5–7 ft. in length and a patch can more than double its area in a single season. The rosette-like arrangement of the leaves gives considerable protection from the wind to the sand surface beneath. The spread of the Sea Convolvulus is mainly vegetative, the more so that on rabbit-infested dunes the flowers are eaten in preference to the leaves. The seeds are large and weigh about 0·06 gm. This appreciable food supply thus provided enables the seedling to establish a root, deeply in proportion to its size, at an early stage in development.

Another perennial that often arrives at an early stage is the dune form of the Rest-harrow (*Ononis repens*). This has a great capacity for evading burial and its habit of frequent branching as it grows commonly results in its sticky glandular leaves forming a turf-like covering over the dune surface, constituting a most efficient wind shield. When such emergent shoots flower they sometimes present the appearance of a green mat bearing numerous crimson pea-like blooms almost resting on the sand. Actually, these leaves and flowers represent the terminations of a shoot system which may extend downwards through over 4½ ft. (140 cms.) of sand (cf. Fig. 66) that is the outcome of years of accretion, and in which the repeated branching bears visible witness to the dune surfaces of bygone seasons.

The striking testimony to past rises in level shown by the Sea Holly and the Sand Spurge have already been described,

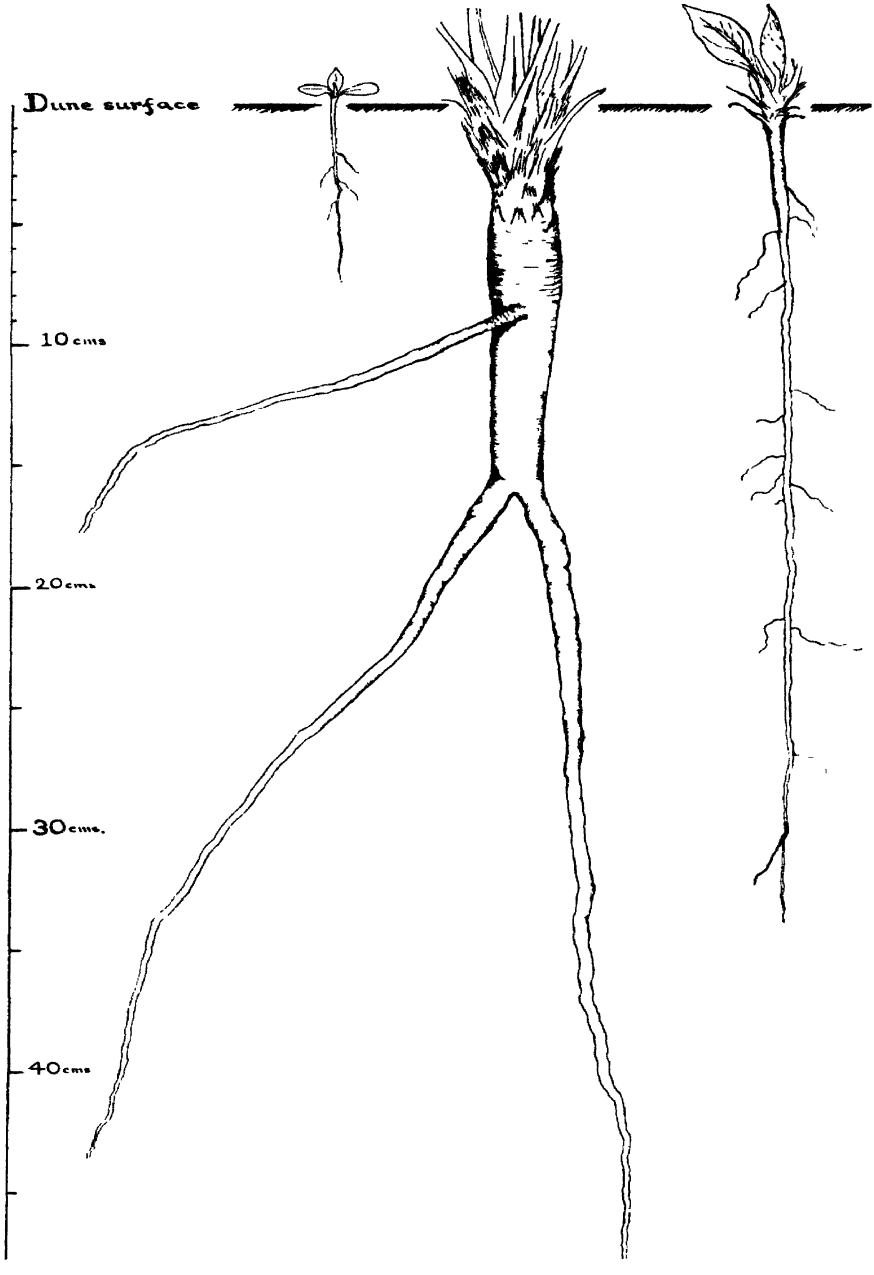


FIG 67. Root of the biennial Hound's-tongue (*Cynoglossum officinale*) showing (i) seedling, (ii) young plant several weeks old with long tap-root, (iii) plant in second season before flowering showing horizontal contraction marks on the fleshy tap-root, about two-thirds actual size. Llanbedr.

but by contrast with the last-named the Portland Spurge shows this feature to a far less marked degree; but as this species occurs normally on older yellow dunes (Fig. 89, p. 261), which are less mobile than those where the Sand Spurge is common, it is a moot point whether this is indicative of lack of capacity for 'flotation' or merely lack of opportunity. From the old example shown in (Fig. 45, p. 175) it will be noted that the roots extend to a depth of over 1 m. (*ca.* 40 ins.), but no evidence of 'flotation' is manifest. In the later states of yellow dune development the Sand Sedge (*Carex arenaria*) is often abundant. It is particularly effective as a check to surface wind action and notable for the rapidity of its horizontal spread. The underground stems possess hard, sharp-pointed tips which pierce the sand as growth pushes them forwards. An annual increment may be yards in length, producing tufts of leaves at intervals which are thus arranged in linear series radiating from the parent plant. Next season each of these tufts may be the point of origin of one or more radiating branches again bearing tufts of foliage at intervals emerging above the sand and exhibiting, as is usual with sedges, three vertical series of leaves, best seen if viewed from above. Thus in a few years the dune crust is occupied with a network of rhizomes and the groups of leaves arising from them constitute an interlacing series of discontinuous hedges that effectively check wind action.

A biennial which may arrive early is the Ragwort (*Senecio jacobaea*), but only if the rate of accretion is slow, since the rosettes which the seedlings form in the first winter are readily susceptible to burial, otherwise the rapidity with which the seedlings develop an extensive root-system during the wetter months fits this species for enduring the dry conditions of the early dune phases. The Hound's-tongue (*Cynoglossum officinale*, Fig. 67) is a biennial which also rapidly forms a deep root that can attain 34 cms. (*ca.* 13 ins.) in the first year, whilst an old plant has a thick, fleshy tap-root that may penetrate to over ½m. (20 ins.). The specimen illustrated shows the remains of old leaf bases indicative of five successive levels of the dune surface, but collectively these only amount to a rise of 5 cms. (about 2 ins.), and indeed this perhaps represents the approximate degree of instability that the Hound's-tongue will normally tolerate. So too a number of other perennials, not especially dune species, which can form deep root systems are to be

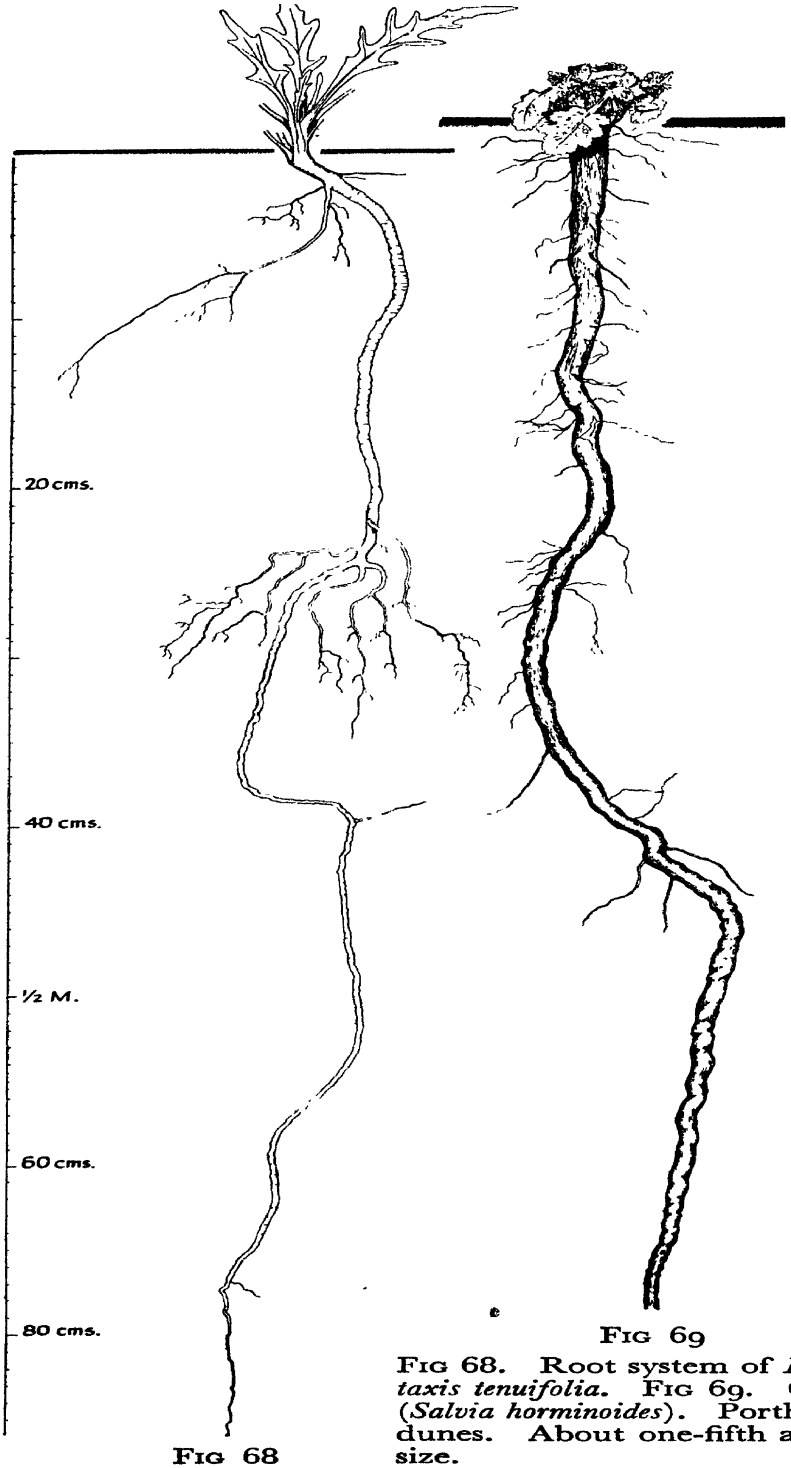


Fig 68

Fig 69

Fig 68. Root system of *Diplotaxis tenuifolia.* Fig 69. Clary (*Salvia horminoides*). Porthcawl dunes. About one-fifth actual size.

met with in these early phases when the changes of level are comparatively slight—such as, for example, the Common Cat's-ear (*Hypochoeris radicata*). As shown (in Fig. 88, p. 247) the first-year plant may have a root almost as deeply penetrating as that of an individual which is several years old, but whereas the root of the former is unbranched that of the latter showed a far more extended exploitation of the sandy soil. The Clary (*Salvia horminoides*) and the *Diplotaxis tenuifolia* (see Figs. 68 and 69) are both species of dry habitats that are met with on yellow dunes, but exhibit little evidence of capacity for 'flotation' and are confined to areas of relative vertical stability.

Two perennial species with a limited power of 'flotation' and which are more or less restricted to dunes are found especially on the later yellow phases. These are the dune variety of the Lesser Meadow Rue (*Thalictrum minus v. dunensis*) and the Dune Milkwort (*Polygala oxyptera*, Fig. 70). The first is particularly a feature of the more calcareous type of dune, especially in the north, whilst the Milkwort is a local plant of dune systems with a southern trend.

In addition to the perennials, the more stable yellow dunes come to support a large number of annuals, numerous as to individuals and representing a considerable variety of species. These annuals become more and more abundant as the dune surface gains in stability whether this be the outcome of intrinsic qualities such as increasing content of humus and moisture, or of extrinsic ones such as increasing shelter. It may be said that the perennials provide the framework of the dune and its grosser protection, whilst the annuals provide a carpet that completes the wind shelter during the season when the dune surface is usually exposed to the severest gales but when it is also frequently wet and therefore least mobile.

Most of the dune annuals may be termed 'winter annuals,' since they germinate normally in the early autumn and flower the following spring or summer. Thus in September one can find on the older dunes large numbers of seedlings of the Mouse-ear Chickweeds (*Cerastium* spp., Figs. 53 and 56), Parsley-Piert (*Alchemilla arvensis*), Corn Salad (*Valerianella locusta*, Fig. 80), Stork's-bill (*Erodium neglectum*), Wall Saxifrage (*Saxifraga tridactylites*), Dove's-foot Crane's-bill (*Geranium molle*), Forget-me-not (*Myosotis collina*), Dune Chickweed (*Stellaria apetala*) and Sand Cat's-tail Grass (*Phleum arenarium*), although

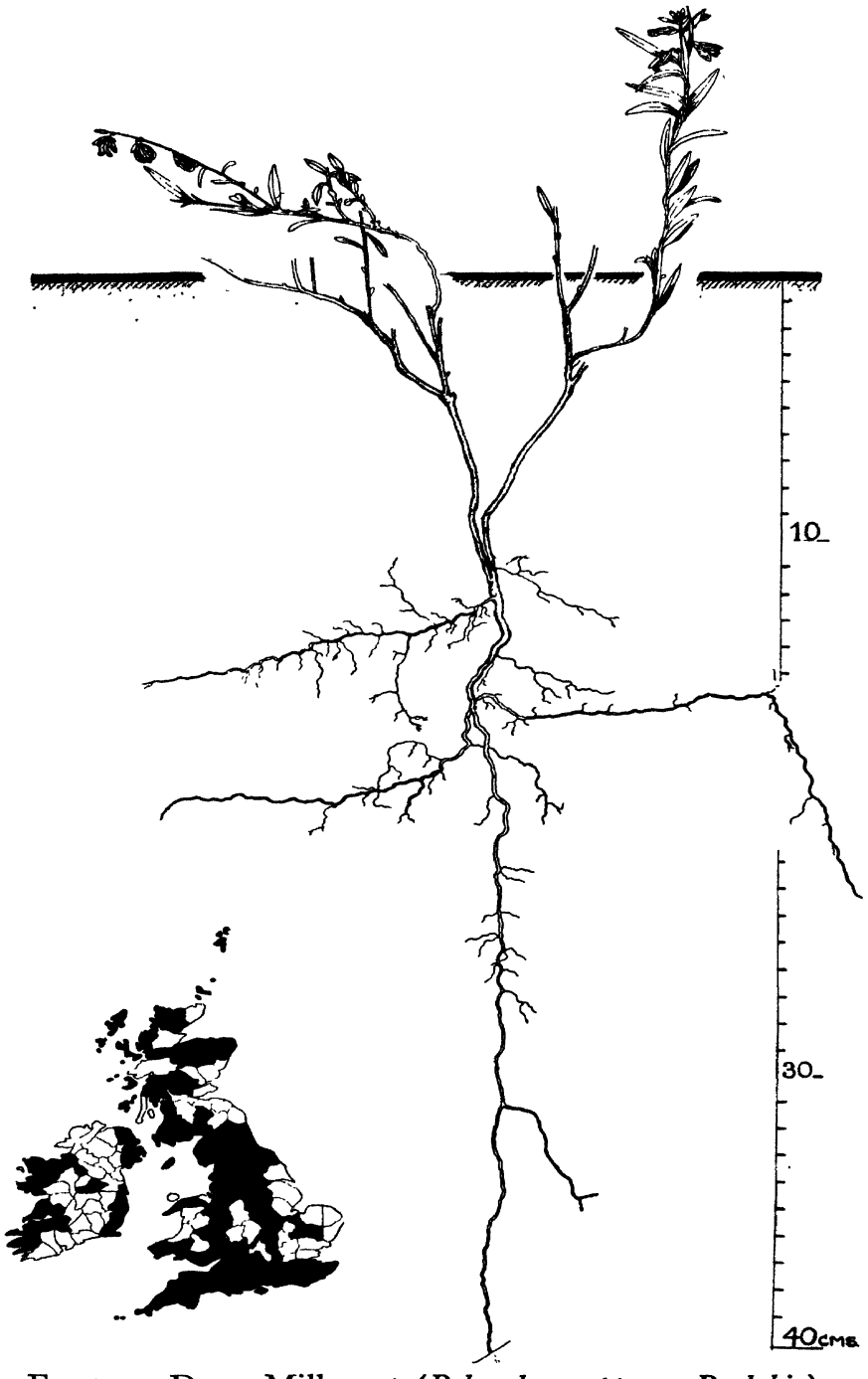


FIG 70. Dune Milkwort (*Polygala oxyptera*=*P. dubia*) showing flowers, fruit, root system, one-third actual size, and geographical distribution. Rye dunes.

the seeds of nearly all of these may germinate in the spring also, and this is especially true of the last three named. Thus the active period of all these plants coincides with the damper months when the surface sand of these older dunes is normally at its moistest, whilst most of these plants have flowered and fruited before the hot, dry days of summer may render the conditions too arid for their support. Most of these annuals are common in other sandy habitats as well as dunes, but the Chickweed (*Stellaria apetala*, Pl. XXVII and Fig. 72) and the Cat's-tail Grass, *Phleum arenarium* (Fig. 73) are characteristic and rarely occur inland except in the sandy Breck country. The local *Hornungia petraea* is also a characteristic winter annual of the calcareous dunes of the south-west (Fig. 81, p. 240). That this prevailing type of life-history is no mere accident is indicated by the fact that the characteristic annuals of the salt marshes are summer annuals germinating about April and, in the dune communities, this is the prevailing season for the germination of the drift-line plants, the Sea Stock, the Prickly Saltwort and the Orache.

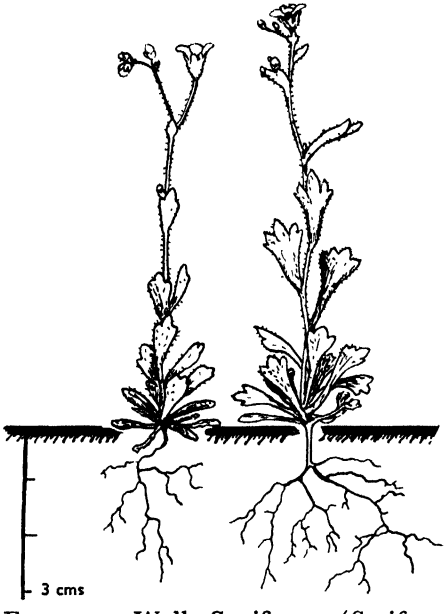


FIG 71. Wall Saxifrage (*Saxifraga tridactylites*), two-thirds actual size.

The seedlings of the dune perennials and biennials are commonly to be met with in spring; but it is a noteworthy feature that the comparatively large food reserves of such seeds as those of the Sand Spurge (*Euphorbia paralias*), the Sea Purslane (*Arenaria peploides*) and the Hound's-tongue (*Cynoglossum*) are, like those of the Sea Convolvulus already referred to, mainly utilised in root production, so that at an early stage of development and long before the wetter period of the year has passed their roots have penetrated to a depth in the sand where the moisture content is not only higher but subject to far less frequent or pronounced fluctuation.

In addition to the annuals already referred to there are others which, though common on dunes, may be equally frequent or even more so in other habitats. For instance, the Whitlow Grass (*Erophila praecox*, Fig. 54, p. 196), the Hare's-foot

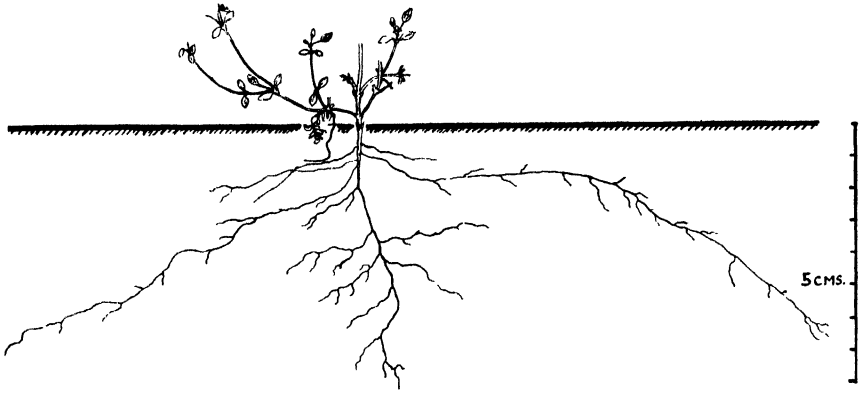


FIG 72. Dune Chickweed (*Stellaria apetala*), about half actual size.

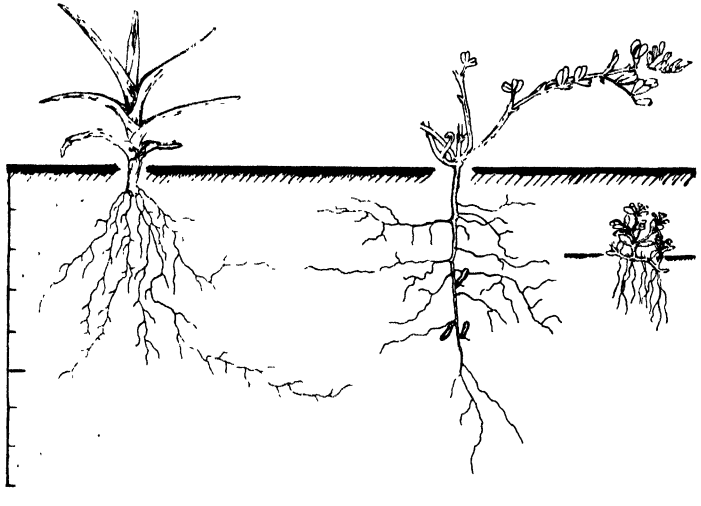


FIG 73 FIG 74 FIG 75

FIGS 73–75. Dune annuals in April, Braunton, about half actual size. FIG 73. Sand Cat's-tail Grass (*Phleum arenarium*). FIG 74. Spring Vetch (*Vicia lathyroides*) showing three root nodules. FIG 75. Waterblinks (*Montia verna*).

Clover (*Trifolium arvense*, Fig. 49, p. 182), the Scarlet Pimpernel (*Anagallis arvensis*, Fig. 76), and the Hairy Cress (*Cardamine hirsuta*). The last two are best known as weeds of cultivated

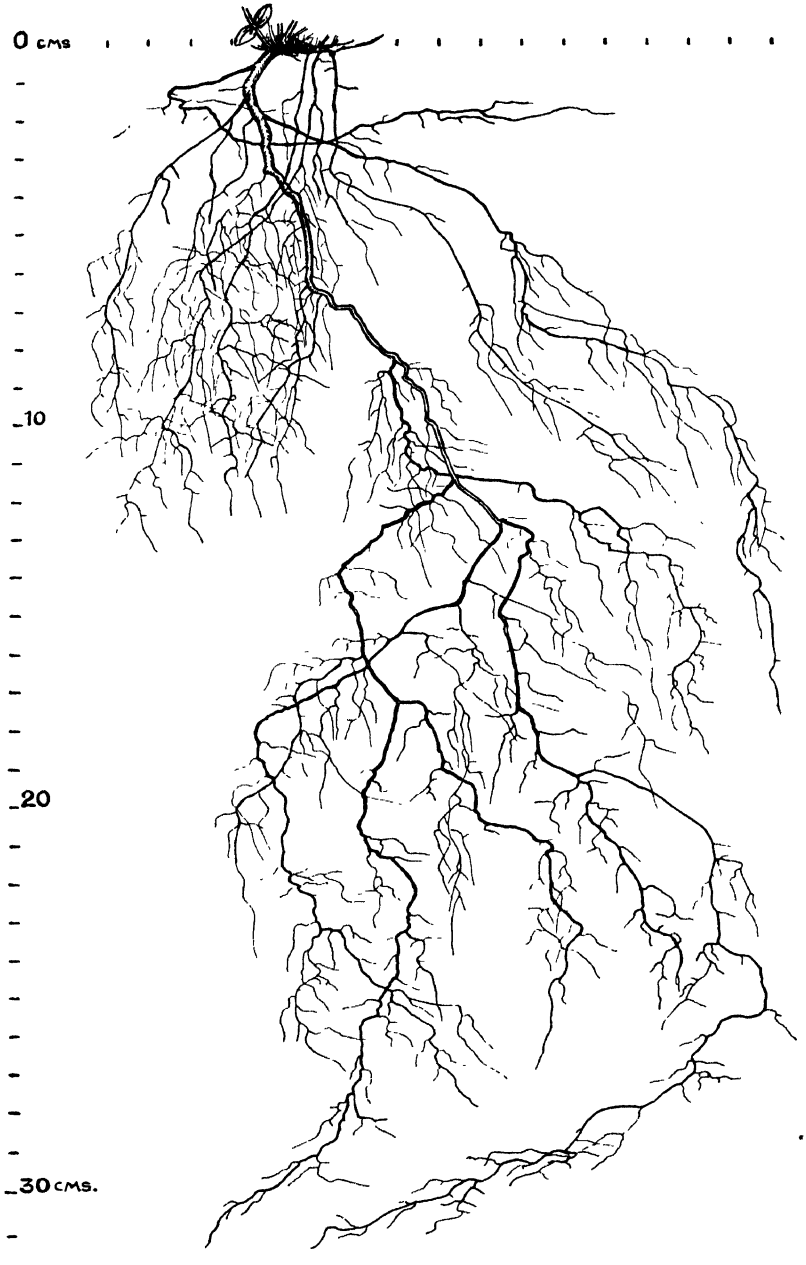
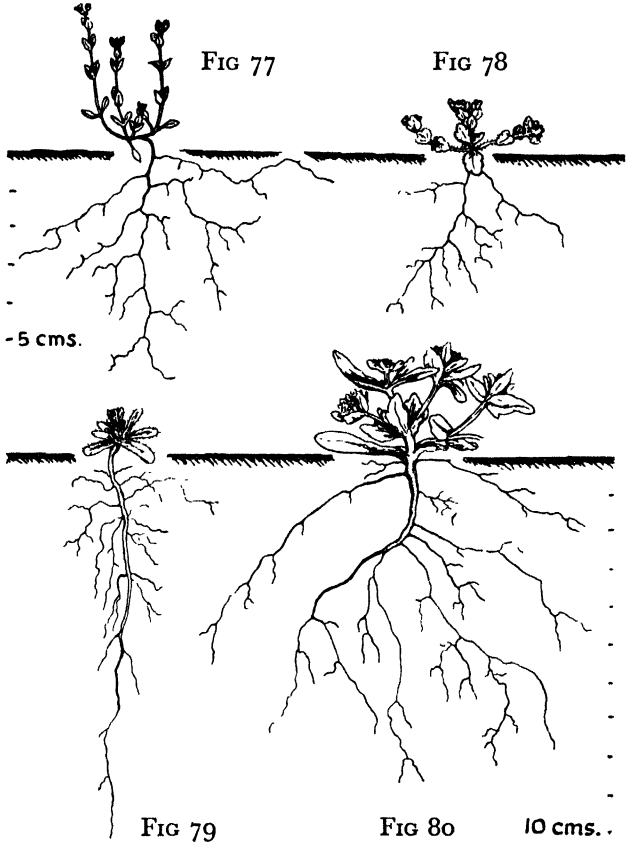


FIG 76. Biennial plant of Scarlet Pimpernel (*Anagallis arvensis*) showing extensive root development in dune soil exploiting a volume of approximately 1,000 cu. in. of sand (16·2 cubic decimetres). Blakeney Point, Norfolk. Scale half actual size.

and other artificially disturbed ground, but the sand dune may well be a natural habitat for these species. The Spring Vetch (*Vicia lathyroides*, Fig. 74), easily distinguished from other Vetches by its small, solitary, stalkless flowers and the two or three pairs of leaflets that comprise the leaf, forms prostrate



FIGS 77–80. Dune annuals, Braunton, April, about half actual size. FIG 77. Sandwort (*Arenaria leptoclados*). FIG 78. Field Speedwell (*Veronica arvensis v. nana*). FIG 79. Sheep's Bit (*Jasione montana*). FIG 80. Corn Salad (*Valerianella locusta*).

rosettes close to the surface. Though frequent inland it is probably commoner on dunes than elsewhere.

The Stork's-bill (*Erodium cicutarium*) is common in many dry habitats, but some of the segregates formerly included in this species, such as *E. neglectum* and *E. pimpinellifolia*, are almost confined to dunes. This is true also of the rare and coarser biennial

species, *E. moschatum* (Pl. XXVIII). All these Stork's-bills have seedlings unlike those of most plants in that the two seed leaves instead of being simple are lobed. When the seeds germinate in autumn the cotyledons of *E. neglectum* are seen to be three-lobed whilst those of the Musk-scented Stork's-bill (*E. moschatum*) are even more lobed and might be described as pinnatifid (cf. Fig. 43, p. 158), although the leaflets of the adult foliage of *E. moschatum* are much less deeply indented than those of *E. neglectum*. Despite their occurrence in other habitats, the Mouse-ear Chickweeds (*Cerastium semidecandrum* and *C. tetrandrum*) can be regarded as characteristic. Both are rosette plants during the winter and their hairy leaves bear viscid glands to which sand grains adhere; in summer when flowering they commonly attain only a short height. The small white flowers of the first-named have the parts normally in fives, those of the second in fours; but the most striking distinction is the scale-like character of the leaves, from the axils of which the flowers arise, and the curved tip to the seed-pod of *C. semidecandrum* whereas the bracts of *C. tetandrum* are similar to the other leaves and the capsule is nearly straight.

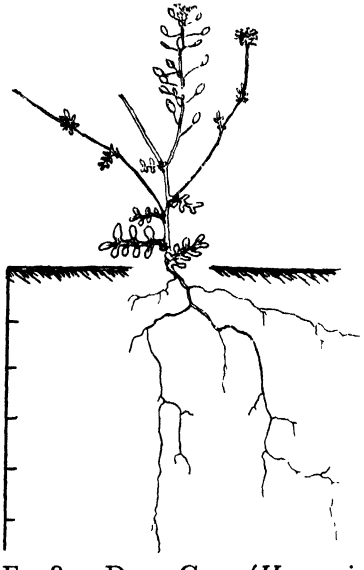
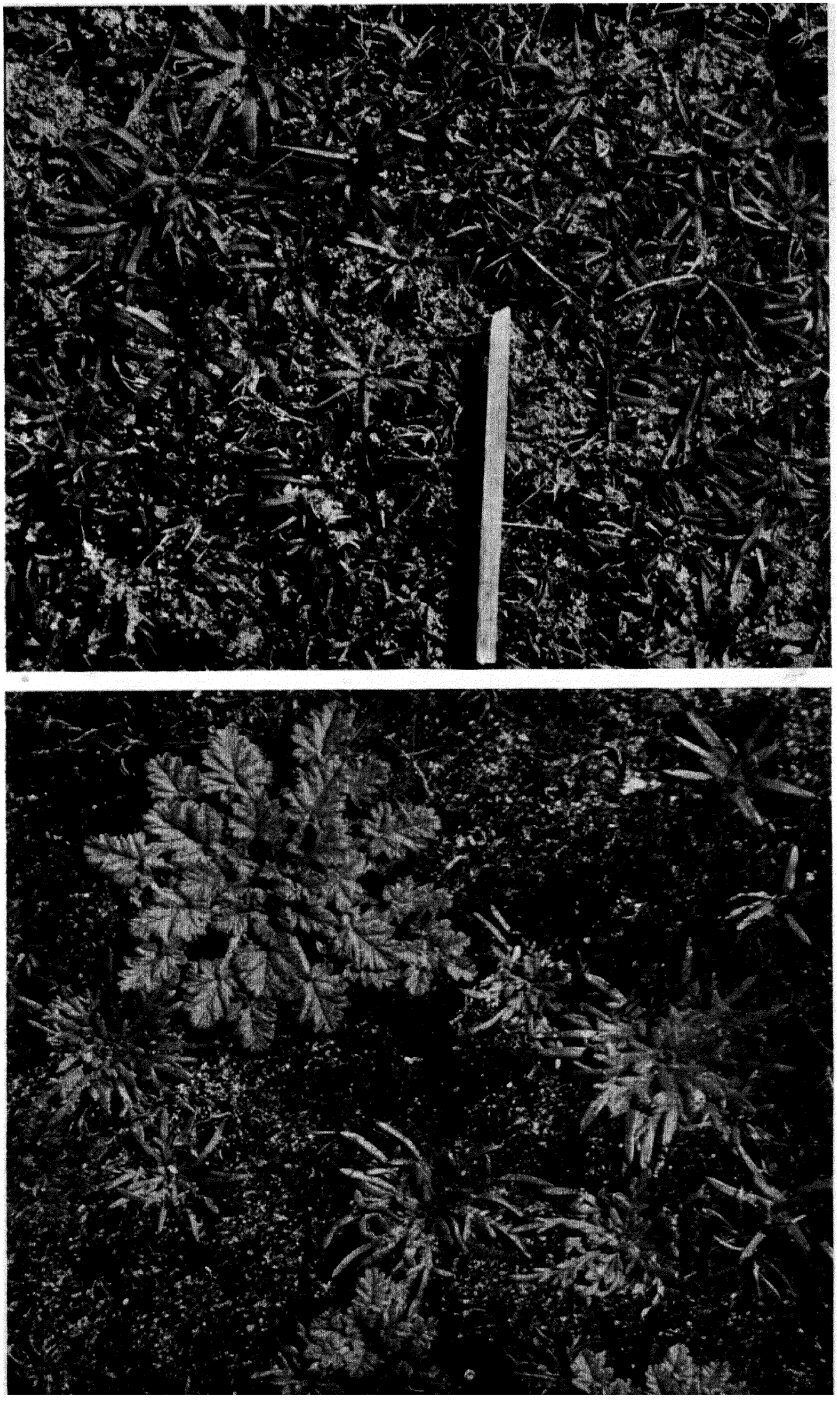


FIG 81. Dune Cress (*Hornungia petraea*). Fixed dune, Abersoch, April. Two-thirds actual size.

The Dune Chickweed (*Stellaria apetala*=*S. boreana*) is easily recognised as differing from the common Chickweed of our gardens by its yellowish-green foliage and the complete absence of petals from the flowers. It is of interest to note that this plant, so characteristic of open situations in the later dune

* * *

PLATE XXIX. BELOW. A fixed dune with a turf of mosses and rosette plants. The largest rosette at the top is that of the Sea Stork's Bill (*Erodium maritimum*) a small plant of which is seen below. The others are those of the Stag's-horn Plantain (*Plantago coronopus*). ABOVE. Stag's-horn Plantains carpeting a dune slack. Note the simple leaves (*P. coronopus forma pygmea*) compared with the lobed leaves of the same species seen in the lower picture.







phases where shading is negligible, has the smallest seeds of any of our British Chickweeds, whereas the Hedge Chickweed (*Stellaria neglecta*), a plant of shady habitats, has the largest (av. width of seed).

Both *Hornungia petraea* and *Teesdalia nudicaulis* are cruciferous annuals that pass the winter as rosettes close-pressed to the soil and alike bear minute flowers that are perhaps normally self-pollinated and in both yield four-seeded pods. Neither are conspicuous enough or sufficiently abundant to have familiar English names. *Teesdalia nudicaulis* is commoner on sandy and gravelly heaths inland than it is on the older dunes, whilst *H. petraea*, though very characteristic and common on the calcareous dunes of South Wales, is also met with less frequently on limestone rocks.

Naturally, the smaller dune annuals tend to be abundant on the latest stages of the yellow dunes where there is the optimum combination of stability and a low level of competition, though some attain their maximum in the later grey dune phase, provided an open area in the plant covering permits them to germinate. The Cudweed (*Filago minima*), Parsley-Piert (*Alchemilla arvensis*) and *Teesdalia nudicaulis* deserve mention in this connection, whilst the small Waterblinks (*Montia verna*) is often present, usually very dwarf, where conditions in winter are damp. Species that may be locally frequent include several annual grasses, such as *Scleropoa rigida*, *Desmazeria loliacea*, *Aira caryophyllea* and *Aira praecox*, which are often present on dunes as dwarf, slightly branched and miniature forms compared with plants of the same kinds of grasses from other habitats.

Among the species that usually appear late and are rather local may be cited the yellow Dune Pansy (*Viola curtisii*) and the Smooth Cat's-ear (*Hypochoeris glabra*, Fig 86, p. 246). They are perhaps both features rather of open communities in the fixed dune phase than of the yellow dunes themselves.

The behaviour of the Pimpernel deserves special mention, since this can sometimes be found flowering a second season on

* * *

PLATE XXX. ABOVE. Grass of Parnassus (*Parnassia palustris*) growing in a dune slack at Southport. The shrub on the left is the Creeping Willow (*Salix repens*). BELOW. Squinancy-wort (*Asperula cynanchica*) on the dunes at Tenby.

dunes. There is some evidence that this biennial condition follows on partial sand burial (cf. Fig. 76) and may be the

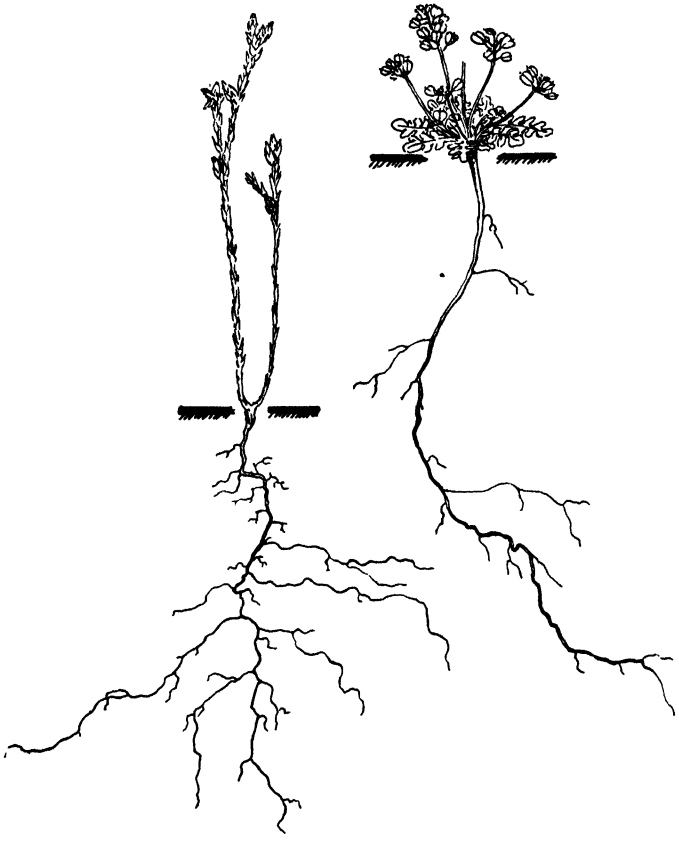


FIG 82 FIG 83

FIGS 82–83. Dune annuals from late fixed dunes, Kenfig Burrows. FIG 82. Small Cudweed (*Filago minima*). FIG 83. *Teesdalia nudicaulis*. Two-thirds actual size. Respective rooting depths approximately 3½ and 4½ in. (9 and 11·5 cm.).

outcome of reproductive suppression in the first year, since it is well known that repeated disbudding of some annuals can induce prolongation of the life-span.

LATE YELLOW DUNE SPECIES

A.=annual; *B.*=biennial; *P.*=perennial; *Ca.*=calcicole

v.c.=very common, c=common, f.c.=fairly common, f=frequent, o=occasional, r.r.=rather rare, r=rare, v.r.=very rare

A	*Alchemilla arvensis* (L.) Scop. c.	Parsley-Piert
P	*Ammophila arenaria* (L.) Link. v.c.	Marram Grass
A	*Anagallis arvensis* L. f.c.	Scarlet Pimpernel
A	*Arabidopsis thaliana* (L.) Heynh. o.	Thale's Cress
A	*Arenaria leptoclados* (Rchb.) Guss. f.	Sandwort
P	*Asparagus maritimus* (L.) Mill. r.	Wild Asparagus
P	*Brassica monensis* (Huds.) (Cumberl. and Lancs.). r.	Isle-of-Man Cabbage
A	*Bromus madritensis* L.	
P	*Calystegia soldanella* (L.) R.Br. c.	Sea Convolvulus
A	*Capsella* spp.	Shepherd's Purse
P	*Carex arenaria* L. c.	Sand Sedge
A or B	*Centaurium littorale* (D. Turner) Gilmour. o	Dune Centaury
A	*Cerastium semidecandrum* L. v.c.	Mouse-ear Chickweed
A	*Cerastium tetrandrum* Curt. v.c.	Mouse-ear Chickweed
A	*Cerastium viscosum* L. o.-f.	Mouse-ear Chickweed
A	*Cirsium vulgare* (Savi) Ten. f.	Spike Thistle
A	*Cochlearia danica* L. f.-c.	Scurvy-Grass
P	*Cynodon dactylon* (L.) Pers. v.r.	Finger Grass
B	*Cynoglossum officinale* L. c.	Hound's-tongue
A	*Datura stramonium* r.	Thorn-apple
B	*Daucus carota* L. r.	Carrot
P	*Daucus gummifer* Lam. r.	Sea Carrot
A	*Desmazeria loliacea* (Huds.) Nym. o.	
A	*Diplotaxis muralis* (L.) DC. o.	Wall Rocket
P	*Diplotaxis tenuifolia* (L.) DC. r.r.	
A	*Erigeron canadensis* L. o.	Canadian Fleabane
A	*Erophila verna* (L.) Chevall. agg. c.	Whitlow Grass
P	*Eryngium maritimum*	Sea Holly
P	*Eupatorium cannabinum* L.	Hemp Agrimony
P	*Euphorbia paralias* L. c.	Sand Spurge
P	*Euphorbia portlandica* L. f.	Portland Spurge
Ca, A	*Galeopsis angustifolia* Hoffm. r.	Hemp Nettle
P	*Hippophae rhamnoides* L. f.	Sea Buckthorn
A	*Hordeum maritimum* With. o.	Seaside Barley
A	*Hypochoeris glabra* L. f.	Smooth Cat's-ear
A	*Lepturus filiformis* (Roth.) Trin. v.r.	
B	*Matthiola sinuata* (L.) R.Br. (? extinct)	Sea Stock
B	*Oenothera biennis* L. o.	Evening Primrose
P	*Ononis repens*	Rest-harrow
A	*Phleum arenarium* L. c.	Sand Cat's-tail Grass
A	*Poa annua* L. f.	Annual Meadow Grass
A	*Polycarpon tetraphyllum* L. v.r.	

LATE YELLOW DUNE SPECIES—*contd.*

P	*Ranunculus repens* L.	Creeping Buttercup
A	*Ranunculus sardous* Crantz. r.	
P	*Rumex rupestris.* r.	Seaside Dock
B	*Senecio jacobea* L. v.c.	Ragwort
A	*Senecio vulgaris* L.	Groundsel
A	*Sonchus arvensis* L.	Creeping Sow-Thistle
P	*Thalictrum dunensis*	
A	*Trifolium arvense* L. f.c. . . .	Hare's-foot Clover
Ca, A	*Trifolium campestre.* o.	Hop Trefoil
A	*Trifolium dubium* Sibth. f. . . .	Lesser Hop Trefoil
P	*Tussilago farfara* L. o.	Colt's-foot

In addition to the above the following species may occur in the late yellow dunes but are even more characteristic of the early fixed stage. They have however been included in the numerical summary: *Aira caryophyllea, Aira praecox, Cardamine hirsuta, Erodium cicutarium* agg., *E. Moschatum, Filago minima, Geranium molle, Hornungia petraea, Hypochoeris radicata, Montia verna, Myosotis collina, Polygala oxyptera, Salvia horminoides, Saxifraga tridactylites, Scleropoa rigida, Stellaria apetala, Teesdalia nudicaulis, Valerianella locusta, Vicia lathyroides, Viola curtisii.*

73 species comprising:

44 annuals	60%
5 biennials	7%
24 perennials	33%

XX

THE FIXED AND GREY DUNE

THE stage of development that can be termed the fixed dune is one when the addition of sand, if still going on, is slow and surface movement of sand grains has become negligible. It is a phase convenient to recognise although it cannot be defined with precision. Topographically the profile is marked by a lowering of level and a general flattening of contours as compared with the main dune ridge; vegetationally the beginning of the phase marks the transition from the open community largely dominated by marram grass with bare patches of sand still visible, that is a feature of the yellow dune phase, to the condition with a more or less continuous carpet of vegetation the density of which depends both upon the age of the dune and the precise floristic composition of the plant covering.

Usually when the fixed dune condition is reached Mosses begin to play a conspicuous rôle in the colonisation of the sand surface, but because Lichens may become prominent at this and later phases of development and impart a grey tint to the plant covering the term 'grey dune' has often been applied. It must, however, be recognised that the extent to which Lichens contribute is materially influenced by climatic and soil conditions, so that the degree of appropriateness of the epithet 'grey dune' is apt to vary from one locality to another. The great resistance of many Lichens and Mosses to severe desiccation renders these cryptogams peculiarly tolerant of the violent fluctuations in water supply which the superficial species of the dune must sometimes endure.

When the fixed dune stage is approached, the dune annuals, as previously indicated, attain their greatest frequency; but so far as the shallower-rooted species are concerned they evade the adverse summer drought by passing this in the, resistant, seed phase. Their vegetative parts have withered and the surface protection they afforded has been very greatly diminished, so the advent of these drought-resistant cryptogams fills the chinks

in the armour of wind protection that permits further progress.

A number of Mosses play a part in bringing about the fixed dune condition, though one in particular is not only often the first to appear and may be present in great abundance, but is highly characteristic in the sense that it is almost confined to dune systems. This Moss is *Tortula ruraliformis* of an erect, unbranched habit which not infrequently occurs as a continuous

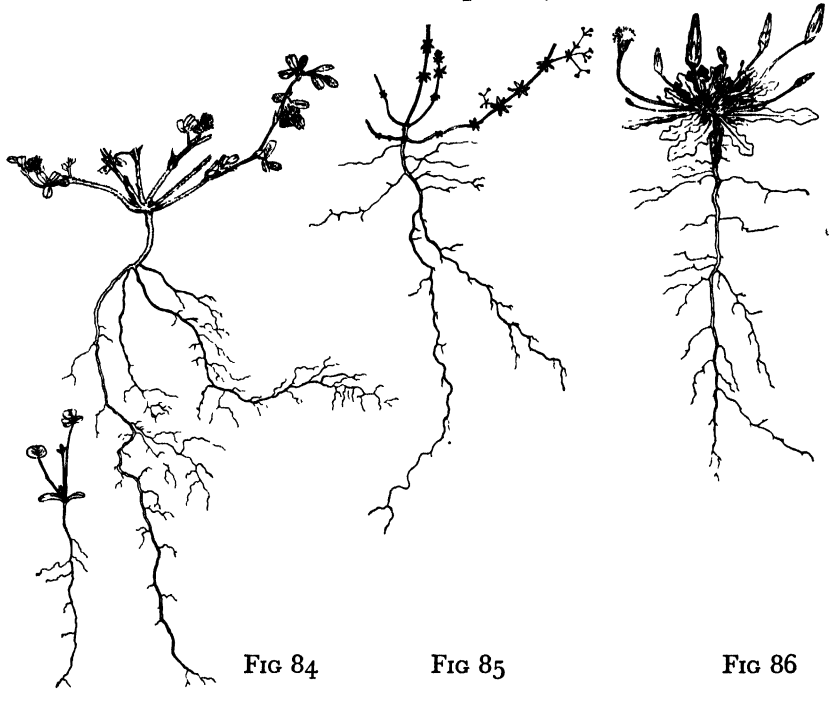


FIG 84 FIG 85 FIG 86

FIGS 84–86. Dune annuals. FIG 84. Seedling and adult plant of the Least Medic (*Medicago minima*). FIG 85. *Galium anglicum*. FIG 86. Smooth Cat's-ear (*Hypochoeris glabra*). All about two-thirds actual size and showing rooting depths of approximately 3 in. (7·5 cm.). Norfolk coast.

carpet over large areas. The other common Mosses on dunes are also met with, often more frequently, in other habitats. Amongst these mention may be made especially of the calcicole Moss *Camptothecium lutescens*, of *Brachythecium albicans*, a Moss common in dry, sandy habitats generally and of *Ceratodon purpureus*, *Hypnum cupressiforme*, *Tortula ruralis*, together with various species of *Bryum*.

The Lichens that fill the chief rôle are species of *Cladonia*, especially such as *Cladonia furcata* and *C. sylvatica*. Species of

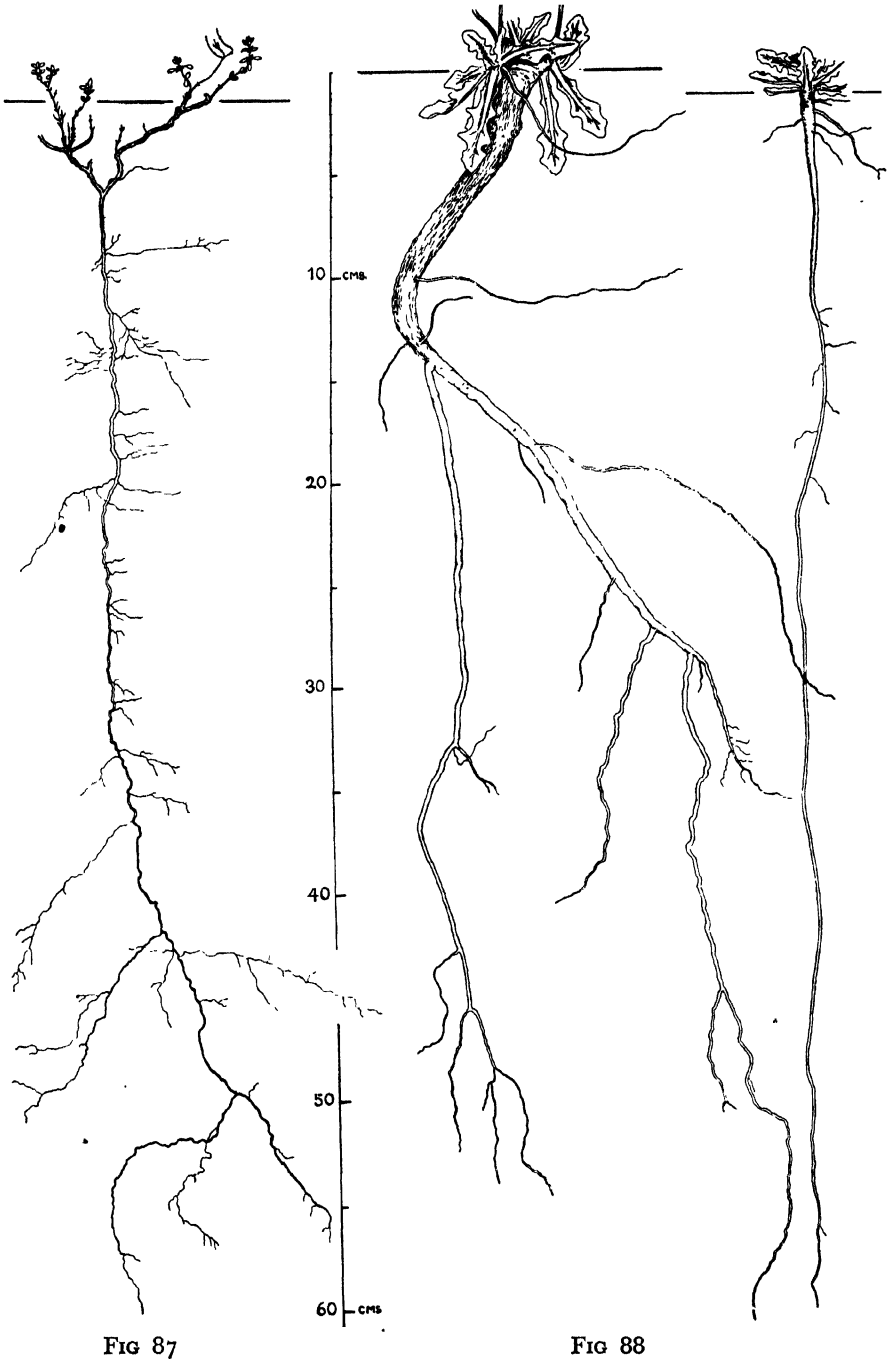


FIG 87 FIG 88

FIG 87. Root system of Thyme (*Thymus serpyllum*). FIG 88. Cat's-ear (*Hypochoeris radicata*) showing adult plant and first-year seedling. Note the attainment of depth by the latter before any appreciable branching occurs. Llanbedr dunes. (About one-quarter actual size.)

Peltigera (e.g. *P. canina* and *P. rufescens*) may be conspicuous, but their flat, spreading growth is less suited to withstand any accretion and it is the very stable late stages with which they are more particularly associated. The erect habit of *C. furcata*, like that of the Moss *T. ruraliformis*, permits and even induces slow accretion. Calcicolous species that are not normally significant, as, for instance, the Moss *Cylindrothecium coccineum* may become abundant on higher calcareous dunes.

The general effect of the continuous carpet that these Mosses and Lichens provide is not only the surface stability but the greatly augmented addition of organic material. Nevertheless, though in these respects the conditions for plant growth are more favourable, the Marram Grass, at this phase, is seen to be losing vigour, as evidenced by its smaller size and absence of flowering. Usually the grey dune phase exhibits increasing senescence of *Ammophila arenaria* (Pl. XXVII) as well as of any other pioneer species that may have survived, possibly due, in part, to increasing acidity of the soil, in part, to the diminishing soil aeration, but in no small degree to the pressure of competition.

It will be apparent from what has been already stated that the highly specialised habitat conditions which characterised the early stages of the yellow dune have been progressively ameliorated, so that more and more kinds of plants may be expected to be able to endure the improved conditions, and so we find that the fixed dune stage is marked by two outstanding floristic features—namely, the greatly augmented number of species present and the disappearance, or marked diminution, of all the more specialised pioneer types. Thus the flora of the dune proper, as distinct from its 'slacks,' becomes richer but less interesting. This does not necessarily mean that there is any diminution in the harmony between the biological types present and the environment that they occupy, but merely perhaps that this is less obvious. It must never be forgotten, if we are to apprehend the relations of organisms to their surroundings, that the so-called adaptation to extreme conditions is but one type of specialisation and that the absence of any such, especially if accompanied by a capacity to respond to varying circumstances, may itself be a specialisation of high survival value. The obvious specialist may represent the biological type that has only survived by reason of its potentialities of developing harmony in one direction forced upon it by an incapacity to

withstand the more severe competitive pressure that obtains in an increasing degree as optimal conditions are approached.

Thus we find that, ignoring casuals, there occur on fixed dunes in Britain some 145 different kinds of flowering plants, compared with 70 species on the late yellow dune phases and only 26 kinds on the early yellow dunes and dune face taken together.

FIXED DUNE SPECIES

More especially found in the earlier phases of fixed dunes

A=annual; *B*=biennial; *P*=perennial; *Sh*=Shrub; *G*=geophyte; *Ca*=calcicole

c=common, f.c.=fairly common, f=frequent, o=occasional, r.r.=rather rare, r=rare, v.r.=very rare

P	*Achillea millefolium* L. o.-c.	Yarrow
P	*Agrimonia eupatorium* L. r.	Agrimony
Ca, P	*Agrimonia odorata* (Gouan) Mill. v.r.	Scented Agrimony
P	*Agropyron repens* o.	Couch Grass
P	*Agrostis stolonifera* L. f.	Bent Grass
A	*Aira caryophyllea* L. f.	Silver Hair Grass
A	*Aira praecox* L. c.	Spring Hair Grass
P	*Allium vineale* L. r.	Crow Garlic
Ca, P	*Anacamptis pyramidalis* (L.) L.C. Rich. o.	Pyramidal Orchis
Ca, B	*Anthyllis vulneraria* L. f.	Kidney Vetch
Ca, B	*Arabis hirsuta* L. o.	Hairy Cress
A	*Arenaria serpyllifolia* L. c.	Pearlwort
Ca, P	*Asperula cynanchica* L. o.	Squinancy-wort
Ca, P	*Astragalus danicus* Retz. (Scot. f.)	Milk Vetch
Ca, P	*Atropa belladonna* L. v.r.	Deadly Nightshade
P	*Ballota nigra* L. r.	Black Horehound
P	*Bellis perennis* L. c.	Daisy
B	*Blackstonia perfoliata* (L.) Huds. o.	Yellow-wort
Ca, P	*Brachypodium pinnatum* (L.) Beauv. r.	False Brome
Ca, P	*Briza media* L. r.	Quaking Grass
Ca, A	*Calamintha acinos* r.	
Ca, P	*Campanula glomerata* r.	Clustered Bell-flower
A	*Cardamine hirsuta* L. f.-c.	Hairy Cress
B	*Carduus tenuiflorus* Curt. f.	Narrow-headed Thistle
Ca, P	*Carex flacca* Schreb.	Glaucous Sedge
B	*Carlina vulgaris* L. c.	Carline Thistle
P	*Centaurea nigra* o.	Hardheads
Ca, A	*Centaurium pulchellum* c.-f.	Small-flowered Centaury
A	*Centaurium umbellatum* Gilib. c.-f.	Pink Centaury
P	*Cerastium vulgatum* L. f.	Mouse-ear Chickweed
Ca, P	*Cichorium intybus* L. r.	Chichory
P	*Cirsium arvense* (L.) Scop. f.	Creeping Thistle

FIXED DUNE SPECIES—*contd.*

Ca, P	*Coeloglossum viride* Hartm. o. . .	Frog Orchis
P	*Corynephorus canescens* (L.) Beauv. (chiefly east coast)	
A	*Crepis capillaris* (L.) Wallr. c. . .	Hawk's-beard
P	*Dactylis glomerata* o. . . .	Cock's-foot Grass
?Ca, B	*Echium vulgare* L. f.c. . . .	Viper's Bugloss
P	*Epilobium parviflorum* Schreb. r. .	Small-flowered Willowherb
?Ca, P	*Epipactis dunensis* Godf. v.r. . .	Dune Helleborine
Ca, P	*Epipactis palustris* (L.) Crantz. f. .	Marsh Helleborine
Ca, A	*Erigeron acris* L. c. . . .	Fleabane
A	*Erodium cicutarium* agg. L'Herit. v.c.	Stork's Bill
B	*Erodium maritimum* (L.) Ait. (f. in W.)	Seaside Stork's-bill
B	*Erodium moschatum* (L.) Ait. r. .	Scented Stork's-bill
P	*Euphorbia portlandica* f. . . .	Portland Spurge
?Ca, A	*Euphrasia officinalis* agg. . . .	Eyebright
Ca, P	*Festuca ovina* L.	Sheep's Fescue
A	*Filago germanica* f. . . .	Cudweed
P	*Foeniculum vulgare* Mill. r. . .	Fennel
Ca, A	*Gentiana amarella* L. c. . . .	Felwort
Ca, A	*Gentiana baltica* Marb. f.	
Ca, B	*Gentiana campestris* L. o. . .	Field Gentian
Ca, P	*Gentiana verna* L. (Ireland) . .	Spring Gentian
A	*Geranium molle* L. v.c. . . .	Dove's-foot Crane's-bill
Ca, P	*Geranium sanguineum* L. (highly calc. dunes only)	Bloody Crane's-bill
Ca, P	*Gymnadenia conopsea* L. (R.Br.) o. .	Scented Orchis
P	*Hieracium murorum* L. r. . .	Wall Hawkweed
Sh	*Hippophae rhamnoides* l.f. . .	Sea Buckthorn
Ca, A	*Hornungia petraea* (L.) Rchb. (calc. dunes o.)	Dune Cress
A or,B	*Hyoscyamus niger* L. f. . . .	Henbane
P	*Hypericum perforatum* L. r. . .	St. John's Wort
P	*Hypochoeris radicata* L. c. . .	Cat's-ear
Ca, B	*Inula conyza* DC. f. . . .	Ploughman's Spikenard
Ca, P	*Iris foetidissima* L. (f. in S.W.) . .	Stinking Iris
B	*Jasione montana* L. o. . . .	Sheep's-bit
A	*Kohlrauschia prolifera* (L.) Kunth. v.r.	
B	*Lactuca virosa* L. o. . . .	Prickly Lettuce
A	*Lagurus ovatus* L. v.r.	
A	*Lamium amplexicaule* L. o. . .	Henbit-deadnettle
P	*Leontodon autumnalis* L. c. . .	Autumn Hawkbit
P	*Leontodon hispidus* L. f. . . .	Bristly Hawkbit
P	*Leontodon nudicaule* f.	
Ca, P	*Linaria repens* (L.) Mill. f. . .	Creeping Toadflax
Ca, A	*Linum catharticum* L. f.c. . .	Purging Flax
P	*Lotus corniculatus* L. c. . . .	Bird's-foot Trefoil
A	*Lycopsis arvensis* L. f. . . .	Bugloss
Ca, P	*Marrubium vulgare* L. o. . .	Horehound

FIXED DUNE SPECIES—*contd.*

A	*Matricaria inodora* L. f. . . .	Mayweed
P	*Medicago lupulina* L. c. . . .	Black Medic
A	*Medicago minima* (L.) Bartol. o. (E. and S. E. only) . . .	Least Medic
A	*Melilotus altissima* Thuill. o. . .	Melilot
A	*Moenchia erecta* (L.) Gaert. v.r.	
A	*Myostis collina* Hoffm. c. . .	Dwarf Forget-me-not
A	*Myosotis versicolor* Sm. f.	
Ca, P	*Ononis repens* L. c. . . .	Rest-harrow
A	*Ononis reclinata* L. v.r. . . .	Annual Rest-harrow
Ca, P	*Ophrys apifera* Huds. . . .	Bee Orchis
Ca, B	*Pastinaca sativa* L. r. . . .	Wild Parsnip
Ca, A	*Picris echioides* L. o. . . .	Ox-tongue
P	*Plantago coronopus* L. c. . .	Stag's-horn Plantain
P	*Plantago lanceolata* L. . . .	Ribwort
P	*Plantago major* L.	Greater Plantain
Ca, P	*Polygala oxyptera* Rchb. f. . .	Dune Milkwort
P	*Potentilla anserina* L. c. (esp. in lows)	Silverweed
P	*Potentilla erecta* (L.) Rausch. f. .	Tormentil
?Ca, P	*Prunella vulgaris* L. c. . . .	Self-heal
A	*Ranunculus parviflorus* L. (S.W. only f.)	Small-flowered Buttercup
Ca, B	*Reseda lutea* L. o.	Wild Mignonette
B	*Reseda luteola* L. f. . . .	Dyer's-weed
P	*Rumex crispus* L. o. . . .	Crisped Dock
P	*Rumex rupestris* Le Gall. r. . .	Sand Dock
A	*Sagina apetala* Ard. f. . . .	Pearl-wort
A	*Sagina procumbens* L. c. . . .	Creeping Pearlwort
Sh	*Salix repens* c.	Creeping Willow
Ca, A	*Saxifraga tridactylites* L. c. . .	Wall Saxifrage
G, P	*Scilla autumnalis* L. r. (S.W.) . .	Autumn Squill
G, P	*Scilla verna Huds.* r. (S.W.) . .	Spring Squill
Ca, A	*Scleropoa rigida* (L.) Griseb. f. .	Rigid Fescue
A	*Senecio sylvaticus* L. v.r. . .	Wood Groundsel
A	*Senecio viscosus* L. v.r. . . .	Sticky Groundsel
A	*Silene anglica* L. v.r. . . .	English Catchfly
A	*Silene conica* L. r.	
P	*Smyrnium olusatrum* L. r. . .	Alexanders
A	*Solanum nigrum* L.	Black Nightshade
A	*Sonchus asper* (L.) Hill. . . .	Prickly Sowthistle
A	*Sonchus oleraceus* L.	Sowthistle
Ca, P	*Spiranthes spiralis* L. f. . . .	Lady's Tresses
A	*Stellaria apetala* Ucria . . .	Dune Chickweed
A	*Stellaria media* (L.) Vill. . . .	Chickweed
P	*Taraxacum laevigatum* (Willd.) D.C. c.	Dune Dandelion
A	*Teesdalia nudicaulis* (L.) R.Br. v.r. .	Shepherd's Cress
Ca, P	*Thalictrum minus* L. v. *dunensis* o.-l.f.	Dune Meadow-rue
P	*Thymus serpyllum* L. f.c. . .	Thyme

FIXED DUNE SPECIES—*contd.*

A	*Trifolium arvense* f.	Hare's-foot Clover
A	*Trifolium glomeratum* L. r.	
A	*Trifolium pratense* L. o.	Crimson Clover
A	*Trifolium scabrum* L. r.	Rough Clover
A	*Trifolium striatum* L. o.	Striated Clover
A	*Trifolium suffocatum* L. r.r.	Buried Clover
A	*Trigonella ornithopedioides* (L.) D.C.	Bird's-foot Clover
A	*Valerianella locusta* L. f.c.	Corn Salad
A	*Verbascum blattaria* L. v.r.	Moth Mullein
Ca, P	*Verbascum nigrum* L. r.	Black Mullein
B	*Verbascum thapsus* L. o.	Mullein
B	*Verbascum virgatum* Stokes v.r.	
A	*Veronica arvensis* L. c.	Field Speedwell
A	*Vicia lathyroides* L. f.c.	Spring Vetch
P	*Viola canina* v. *ericetorum* l.f.	Dog Violet
Ca, P	*Viola curtisii* E. Forst. f.	Dune Pansy
A	*Viola nana* (D.C) Corbiere v.r.	Dwarf Pansy
A	*Vulpia bromoides* (L.) S.F. Gray. o.	
A	*Vulpia membranacea* (L.) Dunn. r.	
A	*Vulpia myurus* (L.) Gmel. o.	Capon's-tail Grass
P	*Botrychium lunaria* (L.) Sw. l.	Moonwort

145 species comprising:

60 annuals	41·6%
18 biennials	12·5%
65 perennials	45·1%
2 shrubs	1·3%

LATE FIXED DUNE SPECIES

More particularly found in the late phases of fixed dunes together with most of the perennial species of the earlier phases of fixed dunes

Tree	*Acer pseudoplatanus*	
P	*Ajuga reptans* L. r.r.	
P	*Antennaria dioica* L. v.r.	Mountain Cudweed
P	*Anthoxanthum odoratum* f.	
B	*Arctium minus* (Hill) Bernh.	Burdock
P	*Arum maculatum* L. o.	Cuckoo-pint
P	*Anchusa sempervirens* L. v.r.	Alkanet
P	*Arrenatherum avenaceum* Beauv.	False-Oat Grass
Tree	*Betula alba*	Birch
P	*Brachypodium sylvaticum* (Huds.) Beauv. f.	
Ca, P	*Bromus erectus*, Huds. v.r.	Chalk Brome
A	*Bromus mollis*, L. o.	Soft Brome
Sh	*Calluna vulgaris* L. l. ab.	Heather
P	*Campanula rotundifolia* f.	Harebell
P	*Carex extensa*, Good. r.	

LATE FIXED DUNE SPECIES—*contd.*

P	*Chamaenerion angustifolium* (L.) Scop. r.r.	Rosebay Willowherb
A	*Claytonia perfoliata* Donn. r.	
B	*Conium maculatum* L. r. . .	Hemlock
P	*Conopodium denudatum* Koch r. .	Pig-nut
P	*Dianthus deltoides* L. r. . . .	Meadow Pink
Ca, P	*Draba incana* L. r. calc dunes	
Sh	*Erica cinerea* o.	Heath
Sh	*Erica tetralix* r.	Cross-leaved Heath
P	*Festuca juncifolia* St. Am. v.r.	
P	*Festuca rubra* L. f. . . .	Red Fescue
A	*Filago minima* (Sm.) Pers. c. . .	Small Cudweed
Ca, P	*Galium cruciatum* L. (highly calc. dunes only)	Crosswort
P	*Galium saxatile* L. (leached dunes only)	Heath Bedstraw
Ca, P	*Galium verum* L. f. . . .	Lady's Bedstraw
A	*Gastridium ventricosum* Schinz. and Thell. v.r.	
Ca, P	*Geranium pratense* r. . . .	Meadow Crane's-bill
W, P	*Glechoma hederacea* L. o. . .	Ground Ivy
Ca, P	*Helictotrichon pratense* (L.) Pilger. v.r.	Smooth Oat-grass
Ca, P	*Helictotrichon pubescens* (Huds.) Pilger. (highly calc. dunes only) . .	Hairy Oat Grass
P	*Hieracium pilosella* L. f.c. . .	Mouse-ear Hawkweed
P	*Hieracium umbellatum* L. o. . .	Umbelled Hawkweed
Ca, P	*Hippocrepis comosa* L. r. . .	Horseshoe Vetch
Sh	*Hippophae rhamnoides* o. . . .	Sea Buckthorn
P	*Holcus lanatus* L. (calcareous dunes) f.	Yorkshire Fog
P	*Holcus mollis* L. (non-calc. dunes) r.	Soft Grass
Ca, P	*Hypericum hirsutum* L. v.r. . .	Hairy St. John's Wort
P	*Juncus squarrosus* L. o. . . .	Moor-rush
P	*Koeleria albescens* DC. v.r.	
P	*Koeleria gracilis* Pers. o.	
Ca, P	*Koeleria vallesiana* (calc. dunes) r.	
Ca, Sh	*Ligustrum vulgare* o.-c. . . .	Privet
Ca, P	*Listera ovata* (L.) R.Br. f. . .	Twayblade
Ca, A	*Lithospermum arvense* L. o. . .	Field Gromwell
Ca, P	*Lithospermum officinale* L. (calc. dunes) o.	Perennial Gromwell
P	*Luzula campestris* (L.) D.C. f.c. .	Fieldrush
P	*Luzula multiflora* (Retz.) Lej. o. .	Woodrush
B	*Lychnis alba* Mill. r.r. . . .	White Campion
A	*Montia verna* f.	Waterblinks
A	*Myosotis arvensis* (L.) Hill. r. . .	Forget-me-not
P	*Nardus stricta* (old leached dunes) r.	Moor Grass
Ca, P	*Origanum vulgare* r.	Marjoram
A	*Ornithopus perpusillus* L. o. . .	Bird's-foot
A	*Orobanche apiculata* Wallr. r. . .	Broomrape

LATE FIXED DUNE SPECIES—*contd.*

Ca, P	*Pastinaca sativum* Benth. & Hook. v.r.	Wild Parsnip
P	*Pimpinella major* Huds. v.r. . .	Great Saxifrage
Ca, P	*Pimpinella saxifraga* L. o. . .	Burnet Saxifrage
Ca, P	*Platanthera chlorantha* v.r. . .	Butterfly Orchid
A	*Poa pratensis* L. o. . . .	Meadow Grass
P	*Polygala serpyllacea* Weihe (leached) r.	Thyme-leaved Milkwort
P	*Polygala vulgaris* L. f. (leached) r.	Milkwort
Ca, A	*Polygonatum odoratum* (Mill.) Druce v.r.	Solomon's Seal
P	*Potentilla procumbens* Sibth. r. .	Creeping Tormentil
Ca, P	*Poterium sanguisorba* o. . . .	Salad Burnet
Ca, P	*Primula veris* L. o. . . .	Cowslip
P	*Pyrola media* Sw. r. Northern dunes	Wintergreen
P	*Pyrola minor* L. r. Northern dunes .	Lesser Wintergreen
P	*Pyrola secunda* L. v.r. . . .	Wintergreen
P	*Ranunculus acris* L. . . .	Field Buttercup
P	*Ranunculus bulbosus* L. . . .	Bulbous Buttercup
P	*Ranunculus repens* L. . . .	Creeping Buttercup
Ca, Sh	*Rhamnus catharticus* o.	Purging Buckthorn
P	*Romulea columnae* Set. & Maur. v.r.	
Sh	*Rosa spinosissima* Lat. . . .	Scotch Rose
P	*Rumex acetosa* L. o . . .	Sorrel
P	*Rumex acetosella* L. f. . . .	Sheep's-Sorrel
Sh	*Salix repens* L. ab.	Creeping Willow
P	*Salvia horminoides* Pourr. o. . .	Clary
P	*Saponaria officinalis* L. r. . .	Soapwort
Sh	*Sarothamnus scoparius* f. . . .	Broom
P	*Saxifraga granulata* r. . . .	Meadow Saxifrage
P	*Scrophularia scorodonia* L. (r. S.W. only)	Hairy Figwort
P	*Scrophularia nodoso* r. . . .	Figwort
P	*Sedum acre* L. c.	Stonecrop
A	*Sedum anglicum* Huds. o. . .	White Stonecrop
A	*Sherardia arvensis* L. v.r. . .	Field Madder
P	*Sieglingia procumbens* r.	
Sh	*Solanum dulcamara* f. . . .	Woody Nightshade
P	*Spergularia rubra* L. o. . . .	Red Spurrey
Sh	*Tamarix gallica* o. . . .	Tamarix
P	*Taraxacum officinale* Weber. f.c. .	Dandelion
P	*Teucrium scorodonia* L. f. . .	Wood Sage
B	*Tragopogon minor* Mill. r. . .	Salsify
P	*Trientalis europea* L. (Scot. v.r.)	
Ca, A	*Trifolium campestre*	Hop Trefoil
A	*Trifolium filiforme* L. o. . . .	Least Hop-trefoil
P	*Trifolium repens* L. . . .	White Clover
A	*Trifolium subterraneum* L. . . .	Subterranean Clover
Sh	*Ulex europaens* f.	Gorse
Sh	*Ulex nanus* L.	Petty Whin

LATE FIXED DUNE SPECIES—*contd.*

P	*Urtica dioica* L. o. . . .	Stinging Nettle
Sh	*Vaccinium myrtillus* l.c. (leached) .	Whortleberry
P	*Veronica chamaedrys* L. f.. . .	Germander Speedwell
P	*Veronica officinalis* L. f. . .	Heath Speedwell
P	*Veronica serpyllifolia* L. f. . .	Thyme-leaved Speedwell
A	*Vicia angustifolia* L. o. . . .	Purple Vetch
A	*Vicia hirsuta* S.F. Gray. v.r. . .	Hairy Vetch
P	*Vicia cracca* L. r.	Hedge Vetch
Ca, P	*Viola calcarea* L. v.r. . . .	Chalk Violet
P	*Viola canina* L. v. *ericetorum* f.c. .	Dog Violet
P	*Viola hirta* L. f.	Hairy Violet
P	*Viola riviniana* Rchb. (Culbin) v.r. .	Wood Violet
P	*Athyrium filix-foemina* (L.) Roth. o. .	Lady Fern
P	*Equisetum arvense* L. o. . . .	Field Horsetail
P	*Lycopodium clavatum* L. (Culbin) .	Clubmoss
Ca, P	*Ophioglossum vulgare* r. . . .	Adder's-tongue
P	*Polypodium vulgare* L. v.r. . .	Polypody
P	*Pteridium aquilinum* (L.) Kuhn. c. .	Bracken

161 species comprising:

17 annuals . . .	10·5%
4 biennials . . .	2·5%
86 perennials 38 also present in earlier phase . .	77·5%
16 trees & shrubs . .	10%

DUNE SCRUB SPECIES

This develops at a late phase and exhibits two facies; the more typical scrub develops on dunes which have an initially high carbonate content, whilst where the initial carbonate content is low the scrub is more of the nature of heath with so-called calcifuge species.

	Acer pseudoplatanus L. r. . .	Sycamore
	Arctostaphylos uva-ursi l. . . .	Bear-berry
Ca	*Astragalus glycyphyllos* r. . .	Liquorice Vetch
	Betula alba L. f.	Birch
	Calluna vulgaris Salisb. l.c. . .	Heather
	Chamaenerion angustifolium l.f. .	Rosebay Willowherb
Ca	*Clematis vitalba* L. f. . . .	Old-Man's-beard
Ca	*Corylus avellana* L. c. . . .	Hazel
Ca	*Crataegus monogyna* Jacq. f. . .	Hawthorn
	Empetrum nigrum l.c. . . .	Crowberry
	Erica cinerea L. o. . . .	Heath
	Erica tetralix L. o. . . .	Cross-leaved Heath
Ca	*Euonymus europaeus* L. o. . .	Spindle
Ca	*Fraxinus excelsior* L. f. . . .	Ash

DUNE SCRUB SPECIES—*contd.*

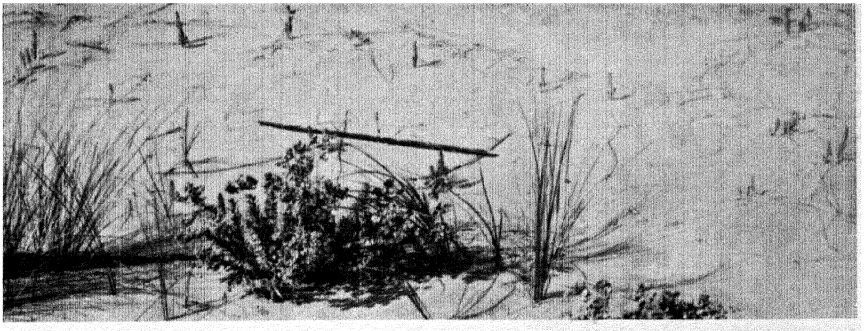
	Hedera helix L. f.c.	Ivy
Ca	*Helianthemum nummularium* r.	Rock rose
	Juniperus communis L. r.	Juniper
Ca	*Ligustrum vulgare* L. f.c.	Privet
Ca	*Mercurialis perennis* L. o.	Dog's Mercury
	Oxalis acetosella L. r.	Wood Sorrel
	Pinus sylvestris L. r.	Scot's Fir
	Populus tremula v. *sericea* r.	Aspen
	Primula acaulis Huds. (f. in W.)	Primrose
	Prunus cerasus L. r.	Cherry
	Prunus spinosa L. f.	Blackthorn
	Quercus robur f.	Oak
Ca	*Rhamnus catharticus* L. f.	Purging Buckthorn
	Rosa arvensis Huds. o.	Field Rose
Ca	*Rosa rubiginosa* L. o.	Sweetbriar
	Rosa spinosissima L. f.c.	Scotch Rose
Ca	*Rubus caesius* L. f.	Dewberry
	Rubus fruticosus L. agg. f.	Blackberry
	Salix arenaria f.	Dune Willow
?*Ca*	*Sambucus nigra* L. f.c.	Elder
	Sarothamnus scoparius	Broom
Ca	*Solanum dulcamara* L. f.	Woody Nightshade
	Sorbus aucuparia o.	Mountain Ash
	Tamarix gallica r.	Tamarix
	Ulex europaeus L. o.	Gorse
	Ulex nanus o.	Petty Whin
	Vaccinium myrtillus L (non calc.)	Whortleberry
	Vaccinium vitis-idaea L. (Culbin)	Cowberry

68 species comprising:

31	perennial herbs (including 26 spp. also in earlier phases)	44·7%
8	trees	12·0%
29	shrubs	43·2%

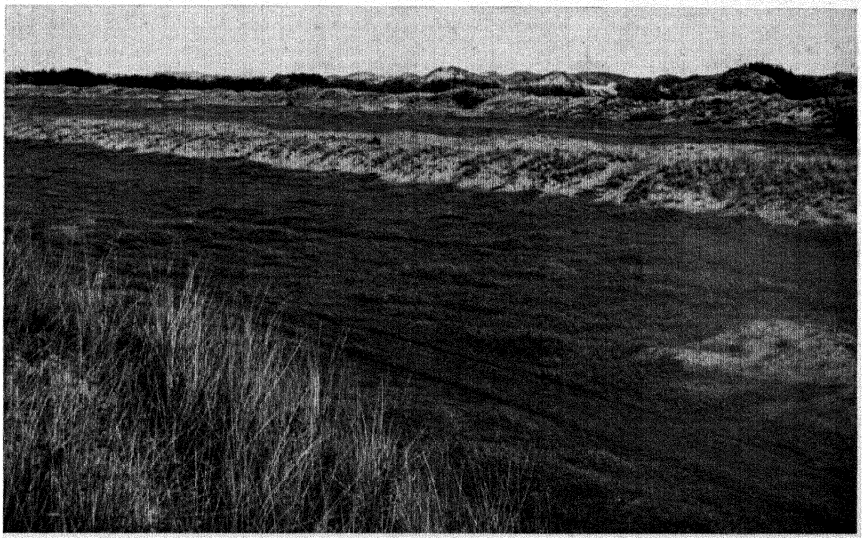
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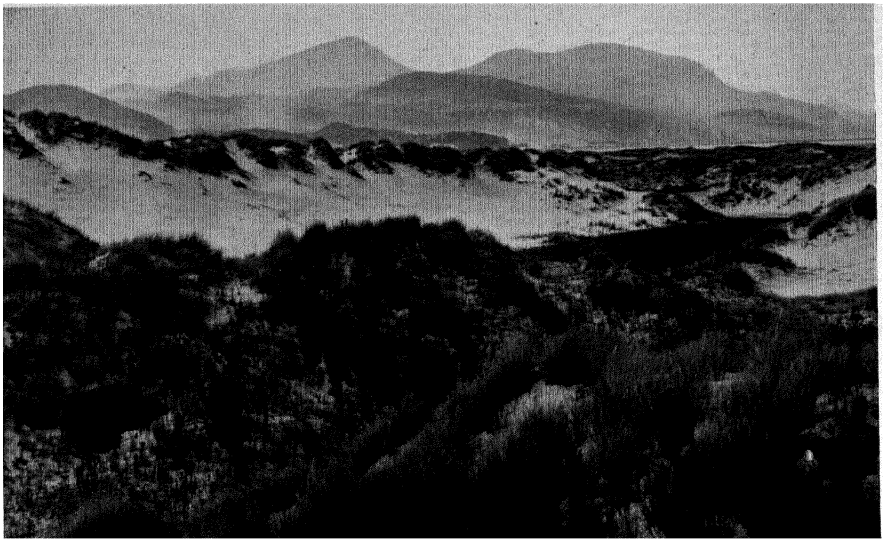
PLATE XXXI. Dune flora. BOTTOM. Southport dunes showing two dune slacks separated by a narrow dune ridge and both occupied by a dense turf of the creeping Willow (*Salix repens* agg.). Two further dune ridges are seen to right (seawards). MID LEFT. Lady's Tresses Orchid (*Spiranthes Spiralis*) growing in dune slack, Talwn-Bach. White flower to right is the Knotted Spurry (*Sagina nodosa*). In front to right, shoot of a Mare's-tail (*Equisetum varigetum*). To the left Purging Flax and the Sedge is *Carex flacca*. MID RIGHT. Dune slack, Braunton, with *Teucrium scordium*, *Equisetum varigetum*, and Sand Sedge. TOP. Sand Spurge (*Euphorbia paralias*) adult plant in foreground with Marram Grass and Spurge seedlings dotted about behind. Duffryn-on-Sea, Wales.

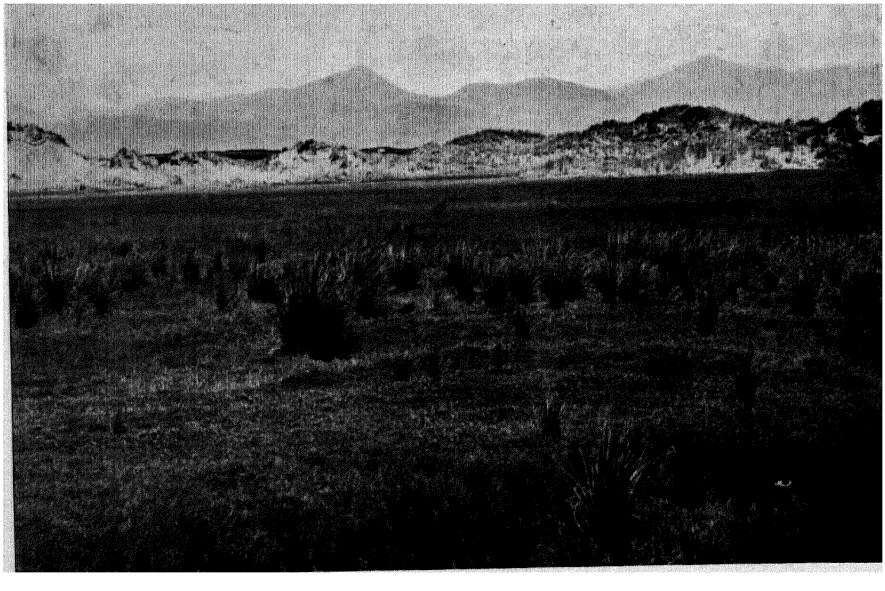












XXI

BIOLOGICAL NOTES ON PLANTS OF OLDER DUNES AND DUNE SCRUB

Ononis reclinata	Annual Rest-harrow
Scilla autumnnalis	Autumn Squill
Trifolium suffocatum	Buried Clover
Rosa spinosissima	Burnet Rose
Stellaria apetala (*S. boraeana*)	Dune Chickweed
Hornungia petraea	Dune Cress
Thalictrum minus v. *dunensis*	Dune Meadow Rue
Polygala oxyptera (*P. dubia*)	Dune Milkwort
Viola curtisii	Dune Pansy
Corynephorus canescens	Hair Grass
Hyoscyamus niger	Henbane
Cynoglossum officinale	Hound's-tongue
Medicago minima	Least Medic
Cerastium semidecandrum	Mouse-ear Chickweed
Cerastium tetrandrum	Mouse-ear Chickweed
Centaurium spp.	Pink Centauries
Euphorbia portlandica	Portland Spurge
Phleum arenarium	Sand Cat's-tail Grass
Hippophae rhamnoides	Sea Buckthorn
Matthiola sinuata	Sea Stock
Hypochoeris glabra	Smooth Cat's-ear
Vicia lathyroides	Spring Vetch
Erodium cicutarium agg.	Stork's-bill
E. maritimum	Sea Stork's-bill
E. moschatum	Musk Stork's-bill
Koeleria albescens	

*

THE PINK CENTAURIES, *Centaurium* spp. (=*Erythraea*). Gentianaceae. 2n=34–56.

There are several pink Centauries native to Britain; all of them behave as winter annuals with a rosette condition. The commonest is *C. umbellatum*, which is probably more abundant in chalk pastures than anywhere else. The flowers of this are

* * *

PLATE XXXII. BELOW. Dune Slack at Talwn-Bach with numerous tussocks of the Spike Rush (*Juncus acutus*) and yellow dunes beyond. ABOVE. Yellow dunes at Talwn-Bach with Marram Grass (*Ammophila arenaria*). The older ridge shows numerous dead stems of Ragwort (*Senecio jacobaea*). The dark patch in the middle on the right is a dune slack with dense Creeping Willow (*Salix repens*). The mountains of Snowdonia form the background to the North.

comparatively large and the rosettes typically consist of oblong leaves that have two to six prominent nerves in addition to the midrib extending from base to tip. *C. pulchellum*, which is frequent on dunes, has smaller rosette leaves and much smaller flowers, whilst *C. littorale*, which is a dune slack plant (cf. map, p. 291), has flowers which are similar in size to those of the common species but the rosette leaves are quite different, having typically inrolled margins. *C. capitatum* is a very rare dwarf oceanic species of dunes and chalk pastures near the sea, which has the flowers normally crowded together in a head and differs from all the others in having the stamens attached to the base of the corolla tube instead of near the throat. It is confined to England from Northumberland southwards. It is an oceanic species which extends to Scandinavia, but despite Matthews' designation of this as a northern-oceanic type it would appear to have a southern trend. The seeds of all species are small and weigh about 0·00004 gm. or less.

MOUSE-EAR CHICKWEED, *Cerastium semidecandrum*. Caryophyllaceae. 2n=36.

A winter annual, usually paler green than *C. tetrandrum* with sticky hairs and from 2–20 cms. in height. The bracts have a broad white membranous margin, and a striking feature is that the flower stalks bend downwards when the flower withers, only becoming erect again when the fruit is ripe. The capsule is slightly curved and contains about twenty-seven pale brown seeds some 0·5 mm. long, weighing between 30 and 60 mgms. The rooting-depth, which is normally about 8 cms., may reach twice that depth. O. H. Volk records osmotic pressures of 9·6 to 14·3 atmospheres and also its occurrence in soils with a reaction ranging from pH 4·9 to pH 8·3. Germination takes place mostly in September.

Generally distributed in suitable stations throughout the British Isles, though less so in Ireland.

MOUSE-EAR CHICKWEED, *Cerastium tetrandrum*. Caryophyllaceae. 2n=36.

A winter annual often less than 1 in. high (*ca.* 2 cms.) and seldom more than 6 ins. (15 cms.) with rather spathulate leaves which, together with the stem, bear sticky glandular hairs to which sand grains adhere. The bracts are leaf-like and the petals and stamens most commonly four, though sometimes

five. The slightly curved capsule usually contains over thirty oval brown seeds about 6 mm. long, each weighing about 70 mgms. They are dispersed by the wind and germinate in the autumn.

A widely distributed plant of western Europe which occurs rarely in inland stations.

HAIR GRASS, *Corynephorus canescens*. Gramineae. 2n=14.

A tufted perennial grass with narrow, stiff blue-green leaves 1–2 ins. (2·5–5 cms.) long forming almost prickly cushions about 4 or 5 ins. high (10–12·5 cms.) with shallow roots penetrating to a depth of only 3 or 4 ins. (7·5–10 cms.). The pyramidal panicles are small (2·5–7·5 cms.) and are produced only in long days. The fruits are small and a single plant will produce from 400 to 3,000 'seeds,' although completely barren plants are frequent.

The species is a markedly continental one confined in Britain to the East Coast dunes, chiefly in Norfolk but also by the Forth estuary. Volk records osmotic pressures of 12·7 atms.

HOUND'S-TONGUE, *Cynoglossum officinale*. Boraginaceae. 2n=24. (Fig. 67)

A hoary-leaved biennial with long-stalked, elliptical basal leaves forming a rosette in the first season which arises from the top of a stout fleshy tap-root. The dull red-purple flowers are produced in the second season, on stems about 12–20 ins. (30–50 cms.) high, and each gives place to four flattened fruits with a thickened border about 6 mm. across with hooked spines that facilitate dispersal by animals and human clothing. The curious mouse-like odour of the plant is unmistakable.

Germination normally takes place in April and the appreciable food reserve in the seed provides the means for rapid elongation of the juvenile tap-root, that at first grows mainly in length and subsequently in thickness. Germination is intermittent and may be spread over a period of eight years.

STORK'S-BILL, *Erodium cicutarium* agg. Geraniaceae. 2n=20 or 40.

An annual or biennial plant which, as it grows on dunes, has the leaves in a rosette, close-pressed to the sand. The littoral segregates of this species have been described by Salmon and Baker (*Journal of Botany*, p. 21, 1920) as follows:

(1) Pit of carpel not surrounded by a furrow.

E. glutinosum Dum. Inflorescence of two to three flowers, anthers pale yellow. Flowers about 6 mm., beak of fruit 15–20 mm.

E. neglectum S. & B. Inflorescence of three to five flowers, anthers claret-coloured. Flowers about 12 mm., beak of fruit 20–22 mm.

(2) Pit of carpel surrounded by a furrow.

E. lebelii Jord. Inflorescence of three to six flowers, anthers pinky-yellow. Flowers about 16 mm., beak of fruit 22 to 24 mm.

These plants all have a definite tap-root, sometimes slightly branched, reaching from 10 to over 34 cms. in depth and frequently with numerous laterals near the surface that spread from 3 to 28 cms. The flowers are slightly protogynous and self-fertile. They open about 7 a.m. and close about midday. The petals are shed between 11 a.m. and 2 p.m. on the third day.

A plant normally produces between 50 and 200 seeds. The seeds are forcibly ejected in the carpel. They normally germinate almost simultaneously from early in August to September and the cotyledons are asymmetrically three-lobed.

SEA STORK'S-BILL, *Erodium maritimum*. Geraniaceae.

A rosette biennial with simple leaves crenately lobed at the margin and with inconspicuous flowers often without any petals. The stout tap-root may penetrate 30 cms. but is often short with prominent surface laterals.

This is an oceanic species of S.W. Europe. In the British Isles it extends to Scotland (see map, p. 289) and though mainly coastal does also occur inland.

MUSK STORK'S-BILL, *Erodium moschatum*. Geraniaceae. 2n=20.

A biennial, far more robust than any of the segregates of *E. cicutarium* agg., and with much less divided leaves. A single plant will produce from 500 to 8,000 seeds. The average weight of a seed is 0·00222 gm. and the seeds germinate more or less simultaneously in autumn (95% has been observed within fifteen days). The cotyledons are pinnate usually of

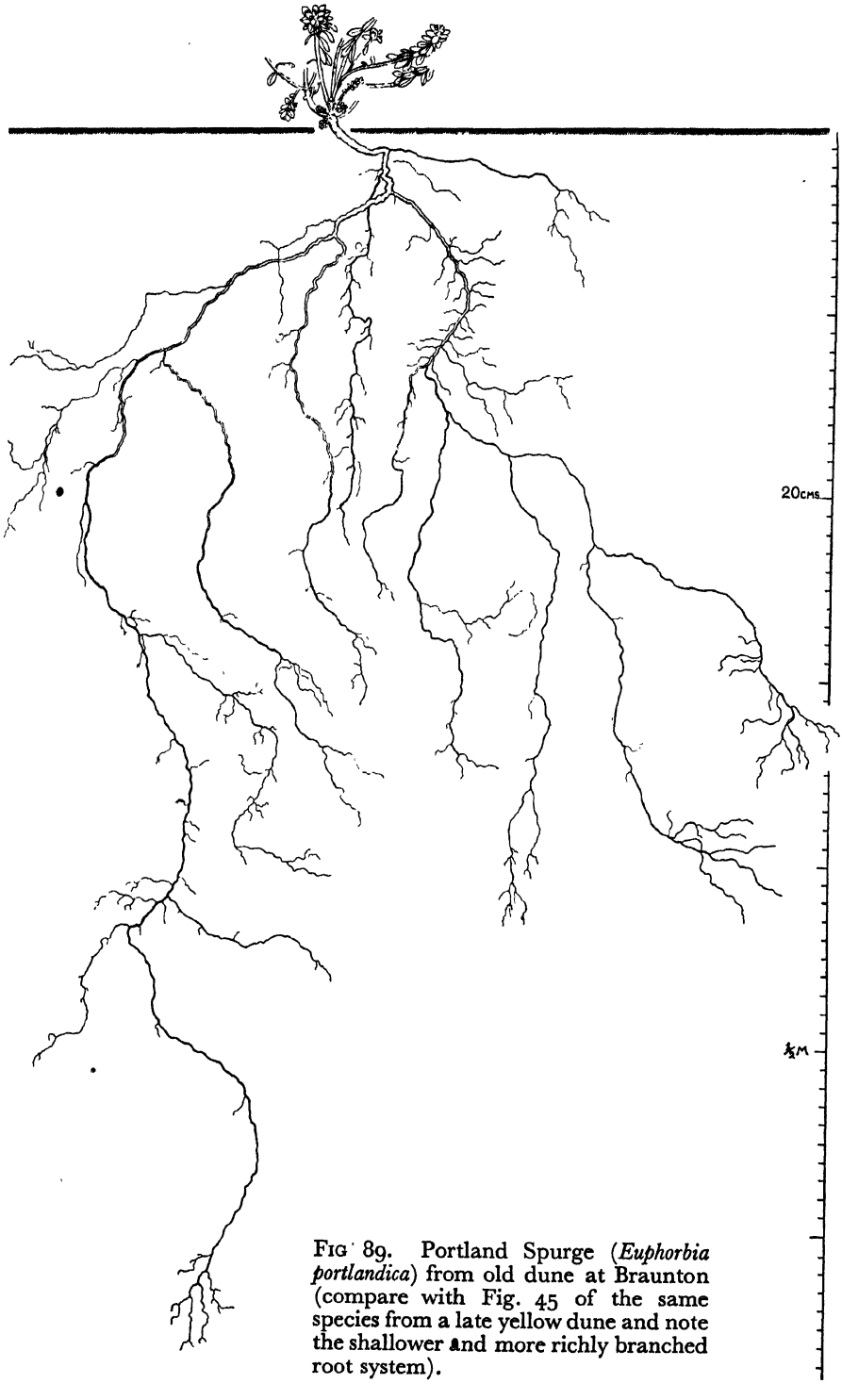


FIG. 89. Portland Spurge (*Euphorbia portlandica*) from old dune at Braunton (compare with Fig. 45 of the same species from a late yellow dune and note the shallower and more richly branched root system).

five or six leaflets or lobes. The seedlings can endure nearly 12° C. of frost (i.e. temperatures down to 20° F.).

For a distribution map of this species, see E. J. Salisbury, 'Ecological Aspects of Meterology' (*Q. J. R. Met. Soc.*, LXV., pp. 337–58, 1939), where the temperature relations of the species are discussed.

PORTLAND SPURGE, *Euphorbia portlandica*. Euphorbiaceae. 2n=16.

A perennial with usually a number of curved stems branched above and bearing numerous crowded leathery leaves. Capable of responding only to a moderate degree of burial, it is restricted to the medium and late stages of dune development.

The seeds are smaller than those of *E. paralias* and have an average weight of 0·0016 gm. The roots penetrate deeply into the sand and seeds on germination, which is intermittent, utilise the food reserves mainly in root growth.

The species is a markedly oceanic one that in Britain attains its greatest abundance on the more sheltered dunes in the S.W. It is found south-westwards from Wigtown to Hampshire and around the Irish coast (see map, p. 291).

SEA BUCKTHORN, *Hippophae rhamnoides* L. Elaeagnaceae. 2n=20–24.

A rather stiff and straggling bushy shrub from 5–10 ft. high. The brown branches end in thorns and bear tufts of leaves each of which is dark green above with a few scattered hairs, whilst below such hairs form a silvery covering. The flowers are quite small and green, but the female give rise to beautiful orange-coloured fleshy fruits, each containing one seed about 8 mm. in diameter, which are produced as a result of the calyx becoming swollen and soft after fertilisation. The fruits are very acid and astringent and rich in vitamins C and A (C=610–821 mg./100 gms.; A=180,000 units, F. Brunke). The flowers are wind-pollinated and the small leaves or bracteoles of the male flowers form a hood-like protection for the pollen in damp weather, but separate and permit the pollen to be blown away when the air is dry. The seeds weigh about 0·014 gm. They are oval, *ca.* 2·5×4 mm., and shining brown with a median groove. Germination (up to 40%) is epigeal. The cotyledons are oblong and fleshy, about 8 mm. in length.

The Sea Buckthorn is widely distributed in the north temperate regions of the Old World. In Britain it is probably native on the East Coast, but in the north and west, as in Ireland, it is probably introduced (see map, p. 293). Whereas it is a coastal species in northern Europe, it is found inland in Southern Europe and central Asia. The roots bear nodules, but whether the organisms they contain are able to fix nitrogen is uncertain. The character of these organisms is in doubt. Thus Arcularius (*Centralbl. f. Bakt. Parasit.*, p. 191, 1928) regarded the organism as a fungus, whereas L. Born (*Bot. Arch.*, p. 441, 1931) stated that the nodules of *Hippophae* contained bacteria. Its association with the later phases of fixed dunes is perhaps explained by Massart's assertion that this shrub can meet a fall in level of the surface, but not a rise. Under dune erosion adventitious shoots arise from the roots (cf. *Esquisse de la Géographie Botanique de la Belgique*, Bruxelles, 1910).

DUNE CRESS, *Hornungia petraea*. Cruciferae. 2n=12.

An annual which germinates in the autumn, perhaps in the spring also, and passes the winter as a rosette plant. The flowers are minute with strap-shaped petals notched at the apex. A single plant produces an average of about 100 pods, each of which contains from two to four pale brown seeds. Very small plants are not uncommon and occasionally very large plants are found which yield over 6,000 seeds. *Hornungia* (*Hutchinsia*) *petraea* is a Mediterranean type probably commonest in this country on calcareous dunes in S. Wales, but it grows also on limestone rocks, both coastal and inland.

HENBANE, *Hyoscyamus niger*. Solanaceae. 2n=34 or 36.

Easily recognised by its sticky, foetid, foliage and sulphur coloured flowers veined with purple, this occurs on dunes as two different varieties. One is annual and the seeds of this normally germinate in early summer or late spring and the plants usually die by September. The other variety is a biennial overwintering as a robust rosette-plant. The characteristic capsules are urn-shaped and open by the detachment of the dome-shaped lid: the numerous seeds, about 330 in a capsule, are dispersed through being jerked out by the wind. The average weight is nearly 0·0008 gm. They often lie

dormant for long periods in the soil and germination is favoured by alteration of low and high temperatures so that buried seeds often fail to receive the requisite stimulus until brought near the surface by rabbits or in other ways. According to W. H. Lee (*Lancs. & Cheshire Naturalist*, Vol. 10, p. 22-26) the flowers are often self-pollinated.

SMOOTH CAT'S-EAR, *Hypochoeris glabra*. Compositae. 2n=10 or 12. (Fig. 86)

An annual forming small rosettes of oblong leaves which are almost devoid of hairs and usually but slightly toothed. The branched flowering stems bear no leaves other than small scales and the Dandelion-like yellow heads are only about half an inch in diameter (10-14 mm.). The fruits are of two types, the inner with beaks and the outer fruits without, although varieties occur in which all the fruits are beaked or all the fruits without beaks. Both types yield a similarly high rate of germination which may occur either in autumn or spring. The species is sometimes badly attacked by the rust *Puccinia hypochoeridis*. It is a member of the central European element in our flora.

Koeleria albescens. Gramineae.

A perennial grass with short creeping stems and rolled leaves. The panicle is shining white.

An oceanic type confined to dunes in Cornwall, Dorset, Anglesey and Forfar.

SEA STOCK, *Matthiola sinuata*. Cruciferae. 2n=14.

A woolly biennial with a number of pinnatifid leaves in the rosette stage. The flowering stems attain about 8–24 ins. (20–60 cms.) and bear purple flowers which are fragrant at night. The seeds are about 3×2 mm., flattened oval in shape with a narrow transparent border. They weigh about 0·00193 gm. and are mainly dispersed by the wind.

A characteristic species of dunes in the Mediterranean now almost extinct in Britain, though at one time it was to be found and was probably native in Sussex, Dorset, Devon, Cornwall and most of the Welsh maritime counties from Flint to Glamorgan (cf. map, p. 291). It is recorded from two areas, Clare and Wexford, in Ireland.

LEAST MEDIC, *Medicago minima*. Leguminosae. 2n=16. (Fig. 84, p. 246)

A prostrate annual of very variable size distinguished by its pods of four to five coils bearing a double row of curved spines and the down of fine hairs upon the leaves and stem. There are two to six seeds in a pod but most commonly four. The pods are dispersed by animals or alternatively the seeds (0·0006 gm.) are shed later and transported by rainwash. The seeds are usually ripe by the end of June and germinate in late August or September but some usually remain dormant and germinate the following spring or in subsequent years. The species is a markedly continental one.

ANNUAL REST-HARROW, *Ononis reclinata*. Leguminosae. 2n=64.

A small summer annual growing from 2–6 ins. high, of a stiff erect habit bearing leaves with sticky hairs.

Although the pod is only about 10 mm. long, it usually contains from 9 to 15 small seeds which weigh 0·0008 gm.—that is, less than a fifth of the average weight of the seeds of *O. spinosa*, a perennial species of the closed community of calcareous pastures. Germination of the seeds of *O. reclinata*, sown simultaneously takes place at intervals over a considerable period.

O. reclinata is a southern species found on dunes in the Channel Islands and formerly also on those of Devon and Cornwall.

SAND CAT'S-TAIL GRASS, *Phleum arenarium*. Gramineae. 2n=14.

Usually from 2–6 ins. high (5–25 cms.), this grass has a rooting-depth that ranges normally from 5–13 cms. Very commonly the plant bears only one inflorescence which will produce from 18 to 150 'seeds,' but large plants may produce as many as ten inflorescences.

The 'seeds' germinate freely (over 90%) almost simultaneously, either in autumn or in spring, and the plants usually wither by July or August.

Distributed all round our coasts southwards of Banff and northern Argyll.

DUNE MILKWORT, *Polygala oxyptera*. (*P. dubia*) Polygalaceae. (Fig. 70, p. 235)

This perennial species is superficially rather similar to the common milkwort, without a basal rosette of leaves, but whereas

in a fruiting plant of the latter the capsules are narrower and hidden by the sepals in the Dune Milkwort the capsules are broader than the sepals. Although commoner on sand-dunes this local species also occurs on chalk downs.

BURNET ROSE, *Rosa spinosissima*. Rosaceae. 2n=28.

A characteristic shrub of dunes, though also found on other dry soils. Very spiny and semi-prostrate, it spreads by suckers and by seed. The latter germinate in from ten months to two years after being shed.

AUTUMN SQUILL, *Scilla autumnalis*. Liliaceae. 2n=28.

This bulbous perennial is a markedly southern-oceanic species. The infloresence of reddish-purple flowers is usually seen in late August or September and the leaves develop towards the end of the flowering period and persist through the winter. The seeds germinate in the autumn. For distribution map see E. J. Salisbury, 'Ecological Aspects of Meteorology,' *Q. J. Roy. Met. Soc.*, LXV, p. 342, 1939.

DUNE CHICKWEED. *Stellaria apetala* (=*S. boraeana*). Caryophyllaceae. 2n=22.

A sprawling yellowish-green annual similar to the common chickweed, but without petals and with smaller seeds. The capsule which usually contains about eleven seeds splits open at the apex into teeth which spread apart in dry weather. The average weight of a seed is about 140 mgms. and germination is mainly in the spring.

A southern-continental type ranging from southern Scandinavia to Asia Minor. In Britain it occurs on dunes in the south from North Wales to Norfolk. It is also found on sandy heaths inland, where it is of a darker green colour and of a more compact habit.

DUNE MEADOW RUE, *Thalictrum minus* v. *dunensis* (=*Thalictrum arenarium*). Ranunculaceae. 2n=42.

This is a perennial which grows to from 12–18 ins. in height (20–45 cms.). It bears many small flowers on a spreading inflorescence of which the stamens are the most conspicuous feature. The achenes are freely produced, three to five from each flower, and apomixis is probably normal. Reproduction

is, however, more often by underground shoots than by seed. The new leaves are formed at the end of February from dormant buds situated in the surface layers of sand.

BURIED CLOVER, *Trifolium suffocatum*. Leguminosae.

A very inconspicuous annual that forms rosettes up to six inches (15 cms.) in diameter the entire plant is often of a yellowish-green colour that enables it to be recognised even when small. The flowers are minute whitish in colour and far less conspicuous than the calyces with their recurved teeth. The flower head is not stalked and almost buried in the sand close to the centre of the rosette, hence the specific epithet. The seeds, which weigh nearly 0·00024 gm., are both 'soft' and 'hard,' the latter exhibiting a dormancy that may be prolonged for years. The species is a southern-oceanic type.

SPRING VETCH, *Vicia lathyroides*. Leguminosae. 2n=10. (Fig. 74, p. 237)

This prostrate annual is very variable in size with small (5-7 mm.), solitary, lilac flowers and leaves consisting of two to three pairs of leaflets. The seeds which weigh nearly 0·0024 gm. usually germinate in the autumn. Depauperate plants which produce but a single pod are not infrequent but large plants may bear more than a hundred. Each pod usually contains about seven seeds.

DUNE PANSY, *Viola curtisii*. Violaceae. 2n=26.

A perennial pansy which responds by renewed growth to moderate burial by sand. The flowers are bright yellow, about 1 cm. in length. Reproduction is by seed and also by short stolons which result in mat-like aggregates of the rosettes of leaves that form prior to the elongation of the stem when flowering occurs.

The foliage is usually very hairy and the somewhat woody underground stems are much branched and from these the flowering shoots emerge.

This pansy is widely distributed on the west coast and around Ireland, but is infrequent in the eastern counties (see map, p. 291).

XXII

THE DUNE 'LOWS' AND 'SLACKS'

WITH the establishment of the successive parallel dune ridges there are created the intervening 'lows' or hollows that necessarily receive and retain more moisture; moreover, as a consequence of the shelter afforded by the bounding ridges these depressions are subject to less severe wind action, hence to reduced evaporation. Furthermore the drainage these hollows receive brings with it the nutrients leached from the surrounding dunes, often the finer grains of sand and also organic particles.

In respect therefore to moisture, stability and nutrition the 'lows' are more favourable habitats than the ridges that bound them. With the passage of time the accumulation of finer material combined with proximity of the floor of the 'low' to the permanent water table often results in the retention of water in the hollows either intermittently, in periods of heavy rainfall, or more or less permanently throughout the year except during abnormally dry seasons. Such wet 'lows' are commonly referred to as 'dune slacks.' But though the hollow between ridges which does not normally contain standing water is conveniently designated a 'low' and the wet type is usefully distinguished as a 'slack' there is every gradation between one and the other so that only the vegetation of the extremes is clearly distinguishable.

Very commonly, as for example on the dunes at Southport (Pl. XXXI), the 'lows' become colonised at an early stage by the Creeping Willow (*Salix repens*), a low growing shrub, with leaves which are silvery beneath, that is admirably fitted for the colonisation of a poor soil by virtue of its extensive roots. One of these that was excavated measured as much as 37 ft. (11·4 m.) from its point of origin and another 21 ft. (6·4 m.) (cf. Plate XXIV). Moreover, since this willow readily spreads by the rooting of its prostrate stems, it soon occupies the entire 'low' and the accumulation of sand amongst its shoots rapidly produces a number of hummocks that may coalesce and lead to almost

complete obliteration of the hollow. In many dune systems where the Creeping Willow is absent or less aggressive, the early stages of colonisation of the 'lows' are marked by the abundance of the Stag's-horn Plantain (*Plantago coronopus*) but assuming a form, imposed by the conditions of growth, that renders it almost unrecognisable to those only familiar with the normal appearance of this species (Pl. XXIX). These conditions in the early stages of a 'low' are not only severe in respect to water supply, but often include an appreciable measure of salinity and the Stag's-horn Plantain can tolerate up to at least 0·5% of Sodium chloride in the soil. The habitat form or 'ecad' of *Plantago coronopus* in these 'lows' has simple or but slightly toothed leaves which may be almost devoid of hairs. Further the spike of flowers, which in this species is normally long and many flowered, is in these plants of the 'lows' quite short and each often bears but two flowers. This 'ecad' has been named variety *pygmaea*, but when the writer grew such plants in normal soil they gradually lost their peculiarities and in two years had become typical Stag's-horn Plantains. This condition is therefore an outcome of nurture and not of nature and is a form not a variety. It is interesting to note that this remarkable 'ecad' bears a rather striking resemblance to another member of the Plantain family, *Litorella uniflora*, which is not uncommon in dune 'slacks,' particularly those of the west.

Since the younger 'lows' are only separated by, at most, a few dune ridges from the sea, they are liable to inundation by exceptionally high tides during storms, when by chance a dune ridge becomes breached. Such circumstances produce brackish 'lows' in which the Sea Milkwort (*Glaux maritima*) which can endure a higher salinity even than the Stag's-horn Plantain, is a characteristic feature although equally at home in 'lows' that are not brackish if competition be not too severe. It is in saline lows that the Sea Heath (*Frankenia laevis*) and the Sea Lavenders (*Statice binervosa* (Fig. 90) and *Statice reticulata*) may occur on the east coast dunes, although the first two at least are really plants of the flanks of old shingle beaches rather than dunes. All three of these plants can tolerate temporary immersion in sea water and the Sea Heath is known to be capable of developing an osmotic suction of up to 83 atmospheres. It is remarkable in possessing a capsule that splits open when wet and not as with most capsules when dry.

Two Rushes are particularly characteristic of the 'lows.' One of these *Juncus acutus* is a southern-oceanic species and has its greatest abundance in the dune hollows of the South-west (Pls. XXIV and XXXII). This Rush forms large tussocks 2–4 ft. in height and as its specific name indicates its green shoots

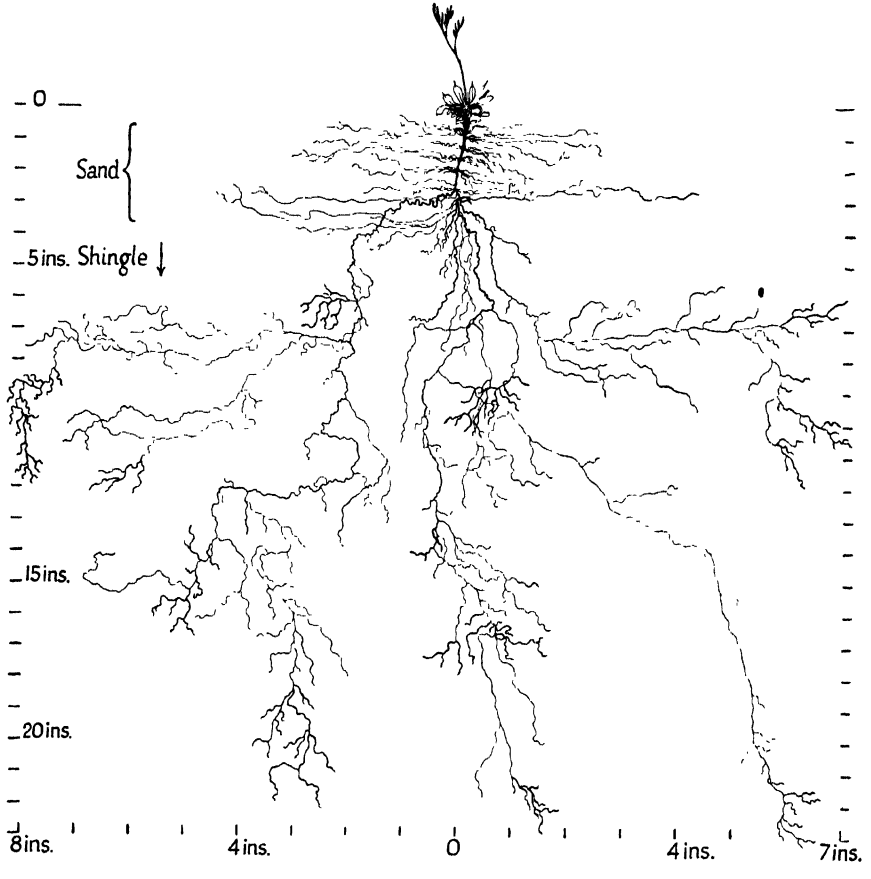


FIG 90. Small specimen of Sea Lavender (*Statice binervosa*) from a dune 'slack,' Norfolk. Note the caddis-like investments of the root tips, the horizontal superficial roots and the copiously branched deeper roots. The root system is very extensive in comparison with the shoot system.

have hard sharp-pointed tips. It is recorded that Arthur Balfour when playing golf once drove a ball that could not be found until it was discovered impaled upon a flowering stem of this Rush. Like many species characteristic of habitats that are intermittently available, *Juncus acutus* has a remarkably large seed production, despite the fact that many of the stems

in a tuft are flowerless. A single flowering stem will produce from 39 to 358 seed capsules (average 145±8·2) each capsule containing from 89 to 173 seeds (average 135±3·5). The number of fruit-clusters on a Rush plant varies greatly, but the average is probably about seventeen, so that a mature tussock of this Rush may normally be expected to produce each year some 327,000 seeds. The seeds themselves are very small and weigh only 0·000082 gm.; they are in consequence readily dispersed by wind.

The second species of Rush characteristic of 'lows' is *Juncus balticus*, a northern type of creeping habit the stems of which grow 1 or 2 ft. in height. Another Rush-like plant of the dune low is the Ball-rush (*Scirpus holoschoenus*) found only at Braunton Burrows (Pl. XXVI). It has characteristic spherical inflorescences and is a southern type which P. A. Burollet mentions as a feature of the 'lows' in Tunis, growing in association with *Juncus acutus* (cf. *Le Sahel de Sousse*, 1927). In 'lows' one finds a close ally of the Felwort—namely, *Gentiana uliginosa*—and one of the less common kinds of Pink Centaury, which is easily recognised by its unmistakable rosette leaves which are narrow and have inrolled margins. In the dune slacks, especially of the west, the Horsetail (*Equisetum variegatum*) is characteristic and often abundant (Pl. XXXI). There occur also in these damper hollows and on the margins of the slacks various Mosses and Liverworts of which the most characteristic is *Petalophyllum ralfsii*, a Liverwort about $\frac{1}{3}$ in. (*ca.* 8 mm.) across and peculiar in bearing on the upper surface of the thallus two rows of erect plates. Another characteristic Liverwort is *Moeckia flotowiana*.

Mostly, however, the plants of the dune slacks are species frequent in other types of damp habitats. Thus a striking feature of the dune 'slacks' on the Lancashire coast is the abundance of the Grass of Parnassus, the cream flowers of which one particularly associates with limestone bogs. The plants of the 'slacks' are often remarkably tussock-like in habit (Pl. XXX), and bear flowers that are exceptionally large and sometimes numerous, although cultivation in normal conditions soon brings a return to average size and habit. The margins of the 'slacks' in Lancashire are often characterised by a rich drift of decaying leaves of the creeping willow, and the organically rich sand that results from these accumulations supports a

characteristic and very beautiful Wintergreen, *Pyrola rotundifolia* v. *arenaria*.

In the damp 'lows,' especially of the west coast dunes, *Selaginella spinosa* is often quite common, although, like the Moonwort (*Botrychium lunaria*), which is locally frequent on dunes, it is more commonly found as a plant of mountain slopes.

But though the plants of dune 'slacks' are mostly those we might find elsewhere, they often present themselves in a strange guise, being extremely depauperate compared with their normal growth. Plants of Pink Centaury and Brookweed (*Samolus valerandi*) can be seen less than $\frac{1}{2}$ in. high bearing but a single flower. Minute tufts of Eyebright (*Euphrasia nemorosa*) and Knotted Spurrey (*Sagina nodosa*) bearing flowers which appear out of all proportion to the size of the plant, together with minute specimens of the Chaffweed (*Centunculus minimus*), Allseed (*Radiola linoides*) and *Tillaea muscosa* which further justify the claim of these species to be the smallest of the seed plants in the British Flora. Very rarely the two diminutive rushes *Juncus pygmaeus* and *J. capitatus* may also occur.

A useful indication of the adequacy of the water supply available to plants in habitats where this is the limiting condition for growth, as in the sand dune, is the degree of expansion of the leaves. Fortunately, there is a means by which this can be conveniently assessed. Of the cells which constitute the epidermis of the leaf a certain proportion are, at a very early stage of development, converted into stomata, and this proportion though, like almost all other features of living organisms, subject to some variation, has a numerical value that is characteristic of the species concerned. So if we know this stomatal index as it is termed $\left[\left(\frac{S}{E+S}\times 100\right)\right.$, where E is the number of epidermal cells per unit area and S the number of stomata in the same area] the number of stomata on a unit area of leaf of any species gives us a measure of the aridity of the habitat, since this will be determined by the amount of growth that the intervening cells have made. If growth of the epidermal cells has been small the stomata will be crowded and the number that can be counted in a unit area will be high, but if the water economy of the plant has been ample the growth of the cells between the stomata will be large and the number of stomata seen in a unit area of the epidermis will be correspondingly small.

Among the marsh plants that are frequent in dune 'slacks' are the Marsh Pennywort (*Hydrocotyle vulgaris*), a creeping member of the Carrot Family (*Umbelliferae*), with round disk-like leaves each borne on a central stalk, and the Brookweed (*Samolus valerandi*) a member of the Primrose Family (*Primulaceae*) whose leaves form a rosette from the centre of which the flowering stem arises. Both species are to be met with in real dune 'slacks' and also in the hollows which occupy an equivocal status in that they can be classed as 'slacks' during the wetter months and as 'lows' during the summer. In such intermittently wet hollows plants of various species including those mentioned may be found growing normally in the moist middle region and also abnormally in the dry margin. The plants occupying the latter are usually depauperate individuals sometimes of extremely small size and bearing perhaps a single flower. On examining their foliage, it was found that the number of stomata in 1 sq. mm. of the epidermis of the leaves of the Marsh Pennywort growing in the moist area varied from 104 to 126, whereas the same area of epidermis from the leaves of plants growing in the dry margin contained from 203 to 302 stomata. Since, however, the proportion of stomata formed is slightly higher for the dry habitat than the wet one (stomatal indices, moist area 22%, dry area 25%), allowance has to be made for this in assessing the significance of the mean values. Making this correction, we find that the stomatal frequencies are in the ratio of 5·2 to 10·3. Leaves from plants of the Brookweed showed from 41 to 54 stomata in a square millimeter of the damp habitat plants and 123 to 224 in the same area of leaves from the dry habitat. Again correcting for the difference in number of stomata formed, the frequencies are in the ratio of 5·3 to 12·6. The two species both furnish a similar assessment—namely, that the conditions of water supply in the moist area are twice as favourable as in the dry area. The effect on size is, however, far greater since the average diameter of the leaves of the depauperate Marsh Pennyworts was 4 mm. whilst those of the damp habitat plants was 35 mm., so that the average leaf areas were in the ratio of approximately 1 to 72. Comparison of Bog Pimpernel leaves from the two areas (av. stomatal frequencies, moist area 47 and dry area 74) and those of *Plantago coronopus* (av. stomatal frequencies, moist area 130 and dry area 452) both in respect to stomatal frequencies and leaf size serve to emphasise

further that any beneficial factor such as water supply has an influence which increases at compound interest to produce its ultimate effect. Thus, as measured by seed output, the annual *Samolus valernadi* in its depauperate condition produces one capsule which may contain perhaps as few as seventeen seeds and certainly not more than forty in comparison with the, by no means optimal, plants of the damp hollow bearing probably twenty or more capsules each containing about seventy seeds, an output of at least thirty-five times that of the depauperate specimens.

A comparison of stomatal frequencies of leaves of the Scarlet Pimpernel from plants growing in dunes and in arable land indicated a difference in water availability of the same order as that just considered, and here too the respective reproductive capacities in the two types of habitat exhibit a cumulative effect during the life-span of this species similar to that shown by the Brookweed.

Some interesting rarities occur locally in dune hollows, as, for instance, the brownish saprophytic Coral-root Orchid *Corallorhiza trifida* and the small Twayblade *Listera cordata* in Scotland, whilst on some of the southern dune systems there occur *Microcala filiformis*, *Orchis incarnata* v. *dunensis*, *Parentucellia* (*Bartsia*) *viscosa* and *Teucrium scordium* (Pl. XXXI).

Again some of the dune hollows in Caithness are to be seen dotted with the exquisite rosettes of *Primula scotica*, a northern relative of the Bird's-eye Primrose that empurples our limestone swards. From these Caithness 'slacks' has been recorded, also a marsh species of increasing rarity, the Small Pepperwort, *Polygonum minus*.

Most of the plants that predominate in the 'slacks' are common or widespread marsh dwellers. Sometimes presented as swards of the smaller types in which the pink-flowered Bog Pimpernel (*Anagallis tenella*), the white-flowered Knotted Spurrey (*Sagina nodosa*), the yellow of the Lesser Spearwort (*Ranunculus flammula*), the blue of the Ivy-leaved Bell-flower and the rich green foliage of the Marsh Pennywort (*Hydrocotyle vulgaris*), are all conspicuous features. Sometimes the vegetation is more luxuriant, with the purple flowers of the Marsh Cinquefoil (*Comarum palustre*), and the three-petalled blooms of *Baldellia ranunculoides* indicating the peaty character of the substratum. Where the standing water is relatively permanent robust aquatic

vegetation may develop with such types as Reed Mace (*Typha latifolia*), Burr Reed (*Sparganium erectum*) and even, very locally, the Greater Spearwort (*Ranunculus lingua*) bearing its handsome yellow flowers, or the beautiful sedge-like Galingale (*Cyperus longus*). Perhaps, however, the most unexpected feature of these 'slacks' is to find in calcareous dune systems, species, that we commonly associate with dry chalky situations, flourishing here in soil that is always moist and often under water. Thus in such situations, one has seen Yellow-wort (*Blackstonia perfoliata*), Felwort (*Gentiana amarella*), Field Gentian (*G. campestris*), Purging Flax (*Linum catharticum*) and Eyebright (*Euphrasia nemorosa*) all growing together as on a chalky downland.

Even more unexpected perhaps is the occasional presence of the Bird's-nest (*Monotropa hypopitys*) which we are accustomed to regard as a plant of the shady Beechwood. All of which occurrences serve to emphasise how much there is in common between the conditions for growth on the sand dune and the chalk.

The soils of these dune 'slacks' merit comment. They are enriched by leaching from the dune ridges on either side (c.f. p. 282). Thus the soil of an old dune 'slack' at Braunton was found to have one and a half times as much carbonates as the adjacent dune and another had slightly less, doubtless due to the greater wind-borne enrichment of the ridge than the hollow by comminuted shells. Old dune 'slacks' at Southport had from 1·4% to 13·9% carbonates (av. 4·0% ± 0·8) with from 5%–9% organic matter. The carbonate content of the corresponding ridges was less than 1%. There is often quite a high organic content as illustrated by a 'slack' at Newborough Warren which yielded 18·7%. Hence when dune 'slacks' partially dry out the exposed floor is often highly fertile as witnessed by the growth of the Liverwort *Riccia crystallina* the rosettes of which are normally about the size of a sixpence (2 cms.) but growing on the floor of a dune 'slack' they attained the size of a half-crown (3 cms.)

XXIII

BIOLOGICAL NOTES ON PLANTS OF DUNE 'SLACKS'

Salix arenaria	Creeping Willow
Rumex cuneifolius	Dock
Rumex rupestris	Dune Dock
Epipactis dunensis	Dune Helleborine
Parnassia palustris	Grass of Parnassus
Gentiana amarella v. *uliginosa*	Marsh Felwort
Epipactis palustris	Marsh Helleborine
Frankenia laevis	Sea Heath
Glaux maritima	Sea Milkwort
Juncus acutus	Spike Rush
Plantago coronopus f. pygmaea	Stag's-horn Plantain
Teucrium scordium	

☆

DUNE HELLEBORINE, *Epipactis dunensis*. Orchidaceae.

This superficially looks like a dwarf form of the common Helleborine (*E. helleborine* = *E. latifolia*) of our woods, which also occurs on dunes, but the leaves of *E. dunensis* are in two ranks instead of all round the stem, the flowers are small green and never open wide and are perhaps always self-fertilised. The roots are slender and wiry, not numerous and fleshy as in *E. latifolia*, and whereas the latter is a shallow-rooting species *E. dunensis* is deeply-rooting. There are also differences in the structure of the flower (a rostellum is normally absent in *E. dunensis*) and in the testa of the seed.

E. cambrensis has been described as a new species by C. Thomas (*Watsonia*, p. 283, 1950) from Kenfig Burrows, who figures a plant having 30 cms. of stem below ground and states that in most specimens this depth is greatly exceeded.

MARSH HELLEBORINE, *Epipactis palustris*. Orchidaceae. 2n=40.

This perennial orchid has whitish-green flowers flushed red and a creeping rhizome from which stolons may be produced. The flowers are pollinated by bees. It is frequent in dune slacks and from there spreads into drier dunes or grows through to the drier sand surface when buried by drifting sand.

SEA HEATH, *Frankenia laevis*. Frankeniaceae.

A prostrate perennial bearing oval leaves about 6 mm. or less in length with the margins bent over, forming large mats

of foliage close to the surface. Roots are freely produced from the prostrate shoots and are mostly shallow (*ca.* 11 cms.). The flowers are pale rose-purple in colour and often sparsely produced. The capsule splits open under moist conditions to release the 4–10 small seeds, which are dispersed by rainwash and germinate in spring. In Britain the production of fertile seeds is poor.

A Mediterranean species confined in Britain to the East Coast (see map, p. 293).

MARSH FELWORT, *Gentiana amarella* (*Axillaris*) v. *uliginosa*. Gentianaceae.

This is an annual of dune slacks in Pembroke, Carmarthen and Glamorgan (cf. J. E. Lousley, *Watsonia*, p. 279, 1950).

SEA MILKWORT, *Glaux maritima*. Primulaceae. 2n = 30.

A pseudo-annual which persists and spreads by means of its fleshy stolons. The individual shoots are annual. The plant is without hairs and the simple opposite leaves are oblong and darker green above, with scattered dots. On the upright shoots the leaves are seen to form four rows, but on the prostrate shoots they all occupy approximately the same plane, due to accommodation in the growth of the internodes and the basal portion of the leaves. Although the flowers have no petals, the pink coloration of the sepals gives the appearance of a corolla, the absence of which brings the five stamens directly opposite the sepals.

Flowering is most profuse in situations, such as on the unshaded edge of a 'slack,' where the soil is moderately dry and the illumination high towards the flowering season. In moist, shady situations the plants may be wholly vegetative.

The fruit is a capsule commonly containing six seeds and splitting open by five valves.

The seeds, which are quite small, were found by Kerner in the mud attached to birds' feet, but as the habitats of the plant are mostly sandy the distance of such dispersal can do little more than ensure colonisation of newly formed 'slacks.' Measurements by W. L. Moss (*Journ. Ecology*, p. 310, 1921) of the rooting-depth ranged from 2–14·5 ins. (5–36 cms.). The salinity of its habitats is normally not high (0·3% NaCl).

Mason (*New Phytologist*, p. 193, 1928) has recorded mycorrhiza in this species. The stomatal index is about 14%.

SPIKE RUSH, *Juncus acutus*. Juncaceae.

A tall perennial tufted Rush forming large clumps from 2–4 ft. in height and characterised by the sharp, hard points of the stems. A large proportion of these latter are often flowerless but those that are fertile produce a massive head of fruits which is chestnut-brown in colour and may consist of from 40 to 350 almost spherical but slightly triangular capsules. Each of these is about 6 mm. in diameter and contains some 135 small seeds which are readily distributed both by wind and upon the feet of birds. The seed output of a fertile clump can be very large and it was estimated that for one large individual the total seeds produced were considerably over a million.

The species is a southern-oceanic one and its distribution is south-western and Mediterranean, but it has become widely established even as far as Australia. In Britain its distribution corresponds to the climatic preferences indicated by its continental range. It is, for instance, abundant in the dune 'slacks' of Devonshire and Wales, whilst it is almost extinct from the dunes of Kent and very rare in its other eastern stations (see map, p. 293).

GRASS OF PARNASSUS, *Parnassia palustris*. Saxifragaceae. 2n=18.

This beautiful herbaceous perennial is a plant of wet flushes on limestone and of dune 'slacks.' The short oblique stem bears the heart-shaped leaves in a rosette, and when these wither the winter bud is situated almost at surface level. The cream cup-shaped flowers with their characteristic branched green staminodes are usually about 1 in. in diameter, but in the rich soil of some dune 'slacks' the flowers may attain an appreciably larger size and the plants become very floriferous. This has been termed v. *condensata*, but plants of this type grown side by side with the normal form in the same soil were in two years' time indistinguishable from one another. The seeds are minute and distributed by wind; they weigh 0·000024 gm. Germination takes place both in the autumn and in the spring. Most plants do not produce more than two or three capsules, but since each of these contains about 750 seeds and germination

can attain 76%, whilst vegetative propagation can also occur, the reproductive capacity is appreciable.

STAG'S-HORN PLANTAIN, *Plantago coronopus f. pygmaea.* Plantaginaceae. 2n=10. (Pl. XXIX)

Comparison of the stomatal indices of giant, well-nourished plants of *P. coronopus* with those of the *forma pygmaea* from the same region showed averages respectively of 23% and 25%, a difference that was not statistically significant; but the number of stomata in a square millimeter of the epidermis of the two forms was strikingly dissimilar, namely for the giant plants 106 to 155 stomata per square millimeter and for *forma pygmaea* 428 to 516. The capsules usually contain five seeds, the lower four larger (av. 1·2 mm. × 0·7 mm.), which are shed in September and germinate in the autumn. The single upper seed is smaller (av. 0·9 mm. × 0·5 mm.), remains in the cap-like upper portion of the capsule and usually germinates in the spring. The larger seeds become markedly mucilaginous when moist and are perhaps distributed by contact, whilst the smaller seeds have little mucilage and are perhaps dispersed in the caps by wind. The seeds endure high salinities and germination will take place in sea-water with an osmotic pressure of about 16 atmospheres (cf. R. Dowling, *Annals of Botany*, XLVII, p. 861, 1933).

DOCK, *Rumex cuneifolius* Campd. Polygonaceae.

A Dock with tough leathery leaves and crisped margins which is a native of maritime dunes in South America. It has become established on the dunes at Phillack (Cornwall); Braunton Burrows, Devon; Kenfig Burrows, Glamorgan; and at Wallasey in Cheshire. It is a perennial with a woody rhizome more than 1 m. in length and over 1 ft. (35 cms.) deep in the sand, sending up shoots at intervals which reach from 15–30 cms. (cf. J. E. Lousley, *Rep. Bot. Soc.* and *Exch. Club*, p. 579, 1944). The fruits are distributed by tidal action, and Lousley (*l.c.*) found that immersion in sea-water did not impair their germination, moreover, that they floated for a period of years. From twenty seeds Lousley obtained fifteen seedlings.

DUNE DOCK, *Rumex rupestris.* Polygonaceae.

A perennial with oblong rather thick undulate leaves. The fruits are distinctive with narrow perianth segments the inner

bearing swellings that obscure all but their tips. The fruits normally germinate about October.

A markedly oceanic species belonging to the Lusitanian element, recorded in Britain from Cornwall, Devon, Glamorgan and the Channel Isles.

CREEPING WILLOW, *Salix arenaria*? Salicaceae. 2n=35?

A low-growing more or less prostrate shrub with small oblong leaves which are silvery beneath. When covered by sand, it responds by growth to the newly raised surface and adventitious roots develop from the buried branches. Conversely, if sand be removed by erosion and the overground parts destroyed the plant is not necessarily killed, since adventitious shoots can develop from the roots, which are both extensive and penetrate to some depth. (Pl. XXIV).

The catkins are produced alike in long-day and short-day conditions. The dune Willows are possibly mostly *S. arenaria* or hybrids of this species with *S. repens*. Many have more or less hairy capsules whereas *S. repens* has smooth capsules and is more of an inland plant.

Teucrium scordium. Labiatae. (Pl. XXXI)

A hairy-leaved pseudo-annual the erect shoots of which die away, persistence being effected by the short stolons which constitute the resting state in winter and produce the next season's flowering stems, terminally, and later the stolons, laterally. The stomatal index, as we should expect in a damp-habitat species, is low, about 4·5–5% and the number of stomata per square millimeter in normal plants is about 200.

The germination is intermittent and in one's own experience low (under 40%).

A northern-continental type of very local occurrence in Britain, the dune 'slacks' of Braunton Burrows being one of its chief stations. (For distribution, cf. E. J. Salisbury, *The East Anglian Flora*, Map 80, Norwich, 1932.)

XXIV

THE CALCICOLE FLORA OF DUNES

ANY observant person walking over the medium-aged dunes of most of our dune systems could scarcely fail to note the number of flowers which one commonly associates in one's mind with the chalk country or other types of calcareous soils. Thus if one is traversing the extensive dune ridges near Freshfield on the Lancashire coast one may come across Bee Orchids (*Ophrys apifera*), Scented Orchids (*Gymnadenia conopsea*) and Pyramidal Orchids (*Anacamptis pyramidalis*), the yellow flowers of the Kidney Vetch embedded in their woolly heads, the curious but attractive everlasting-like inflorescences of the Carline Thistle and the pretty blue flowers of the Felwort, all of which we should normally seek on a chalk down. If we analyse the dune sand from the areas where these plants grow, we should find that the sand usually contains appreciable amounts of calcium carbonate (cf. data in list of calcicole species, Table I, p. 285).

If we were exploring the dunes at Tenby, we should, at least in the past, have found an even more varied selection of chalk plants, with the Squinancy-wort (*Asperula cynanchica*) quite abundant and the Pyramidal Orchids much more common than on the Lancashire dunes—facts not surprising, since the calcium carbonate content of the Tenby fixed dunes is between 12% and 15%. This much higher content of carbonate is due to the calcareous character of the rocks from which the dune sand is derived, and indeed extreme examples are afforded by the dunes in the island of Harris in the Hebrides and at Rock in north Cornwall, with respect to which Gimingham *et al.* have recorded between 45% and 70% carbonates for the former and Hepburn between 52% and 69% for the latter. At the other extreme the young fixed dunes at Studland may have under 0·01% and rarely as much as 0·9%, whilst the Culbin Sands on the Moray Firth have normally no detectable free carbonates and usually all the calcium present is in exchangeable

form. On these two dune systems so-called calcifuge species appear early in the dune succession.

The fact is that, as the appended data respecting carbonate contents of various dune systems show most dune sands contain an appreciable amount since, even if the parent rock from which the mineral particles are derived be non-calcareous, the blown sand almost always contains a certain proportion of comminuted shell fragments derived from marine mollusca. We may note that in areas where actual calcareous rocks are not available calcareous sands are used as a soil amendment, as for instance between Peterhead and Fraserburg in Scotland where the sands were formerly dug for liming the land because of the abundance of shell fragments. It should be noted that the dune plants bring back through their roots some of the calcium washed downwards by the rain and this supplies the wherewithal for the land snails to build their shells. Thus plant and animal combine to restore to the surface a proportion of what would otherwise be lost by leaching. Through the continuing action of rain-water charged with CO_2, the leaching process nevertheless relentlessly goes on, so that the more mature dunes have less and less carbonate as they get older and even dunes which initially were alkaline in the course of many years eventually become acid, both through loss of the neutralising carbonates and the increase of acid organic residues.

The prevalence of these chalk plants in the dune flora may thus be most noticeable in the early phases of the fixed dunes. Sometimes, as on the Southport dune system, where leaching has proceeded some way, it will be noticed that the ridges of the older dunes do not bear any chalk-loving species, but such are found growing in the dune 'slacks' or hollows between the ridges where the soil has been enriched by the leaching from above and has often a high content of exchangeable bases if not actually of carbonates. Here chalk plants that one usually associates with dry calcareous conditions, such as Yellow-wort (*Blackstonia perfoliata*), Field Gentian (*Gentiana campestris*) and Purging Flax (*Linum catharticum*), may be seen growing, perhaps temporarily, in shallow water. More commonly, however, the dunes present the two salient features which are favourable, either separately or in combination, to the growth of the species we regard as characteristic of chalk soils—namely, an adequate supply of calcium, and the physical condition of

high porosity conducive both to good aeration and soil warmth.

No less than seventy-five different kinds of herbaceous plants normally associated with calcareous soils have been recorded from British dunes and in general their abundance and variety on any one dune system is correlated with the amount of carbonate present when this is below about 10%. Above that amount the diversity of species is apparently influenced more

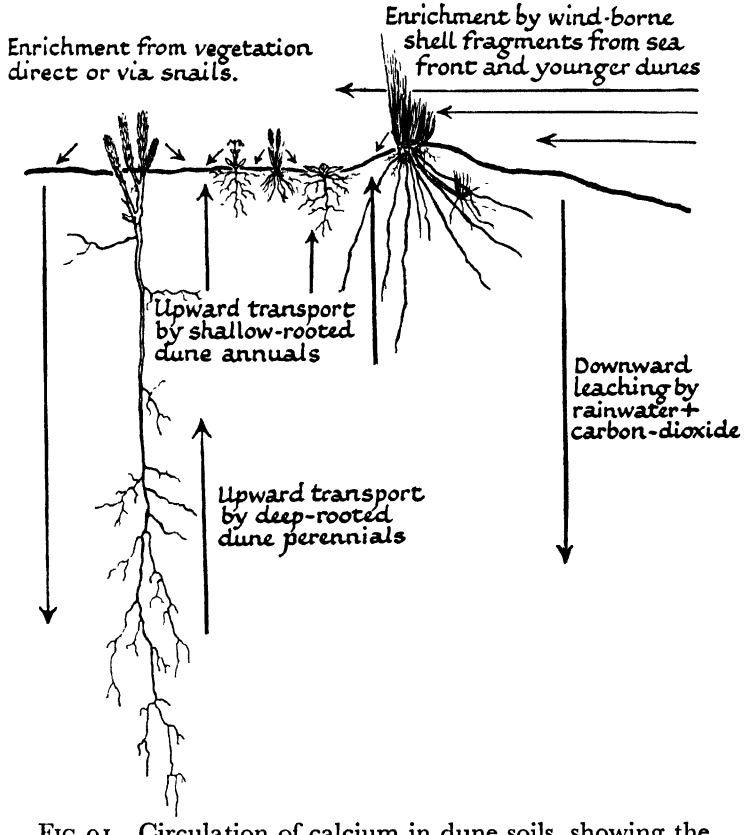


FIG 91. Circulation of calcium in dune soils, showing the chief factors influencing removal from and transport to the surface layers.

by other factors. It must, however, be emphasised that there are various influences that may disturb the regularity of any pattern of vegetation in a particular dune system. Local accumulations of snail shells may produce a highly calcareous soil pocket in an otherwise leached area, and high onshore winds may carry sufficient unleached material from the young

dunes, or even the foreshore, on to the old dunes. Thus stormy weather can lead to a covering of the leached acid surface by calcareous sand and if such a process recurs at intervals, the landward dune ridges may be composed of a succession of leached and unleached layers. Such conditions admit of the close juxtaposition of what are termed 'calcicole' and 'calcifuge' species which may be entirely misleading if the heterogenity of the substratum in which they grow is not apprehended.

The amount of calcium in the Culbin sands as indicated by the graphs of J. D. Ovington is approximately 120 mg. per litre of CaO in the surface of an unplanted dune, which represents about 0·02 gm. of carbonate as $CaCO_3$ per 100 c.c. of sand. His data furnish clear evidence of the surface increase of some nutrients, such as phosphorus, magnesium, manganese and potassium, after the dunes had been planted for 20 years, doubtless as a consequence of release of the elements from the fallen foliage (J. D. Ovington, *Journ. Ecology*, pp. 303–19, 1950). From the graphs of volumetric data the volume of sand appears to be round about 75% at the surface and about 60% in the deeper layers of unplanted dunes. Even in such dunes as those of Culbin the combined accumulative effect of plants and snails may lead to local establishment of conditions of calcium contents much higher than the average. This perhaps explains the occurrence of such species as *Linum catharticum*, *Gentiana campestris* and *Platanthera chlorantha* which Stewart and Patton recorded from the Culbin sands (*Trans. Bot. Soc. Edinburgh*, pp. 27–40, XXIX, 1924) and which are species normally associated with soils having a good supply of bases.

TABLE I. CALCIUM CARBONATE AND ORGANIC CONTENTS AND REACTION OF DUNES

	pH	*Organic* %	*$CaCO_3$* %	*Rain-fall, ins.*	*Authority*
IRELAND					
Bundoran	..	1–4	9·0–20	..	E.J.S.
Tranmore, Waterford	..	..	12–25	..	E.J.S.
Dog's Bay, Galway, Fixed, D.	8·1	..	75	..	A. G. Tansley
Rosapenna, Donegal, Fixed, D.	8·3	..	48·6	..	A. G. Tansley
SCOTLAND					
Tentsmuir	..	..	1·4–0·29	..	G. K. Fraser
Culbin Sands	5	..	Nil as Carb. ca. 0·004	..	G. K. Fraser
Harris, Hebrides	7·2–7·6	..	45–70	47–50	C. Gimingham *et al.*
St. Cyrus, Kincardine	6·6–8	0·14–2·6	1·06–2·6		C. Gimingham *et al.*
ISLE OF MAN	5·8–7·6	0·86–1·24	0·75–3·3	..	E. J. Moore
ENGLAND					
Blakeney, Norfolk	5·5–7·4	0·4–2·7	0·01–6·3 av. 0·3	23	E.J.S.
Rye, Sussex	..	..	1·4–12·2	..	E.J.S.
Studland, Dorset	..	0·0–0·92 av.0·33	0·0–0·5 av. 0·01	32	E.J.S.
Burnham, Somerset	6·2–8·0	1–3·4	0·04–2·5 av.1·1	29	E.J.S.
Slapton, South Devon	..	..	2·2	..	E.J.S.
Dawlish Warren, South Devon	..	0·5–9·0	0·3–0·8	32	E.J.S.
Woolacombe, North Devon	..	..	14·5	..	E.J.S.
Braunton, N. Devon	7·2	1·0–4·9	10·3–24 av. 15·5	32	E.J.S.
Rock, Padstow, N. Cornwall	8–8·5	0·25–0·85	52–69 av. 58	..	Hepburn
Bude, N. Cornwall	..	2·9–10·2	....	33	E.J.S.
Freshfield & Southport, Lancashire	6·8–7·4	0·1–25·7	0·03–6·7 av. 2·0		E.J.S.
Barrow, Walney Is.	4·2–7·5	..	....	32	Pearsall
WALES					
Porthcawl, South Wales	..	..	4·8–7·5 av. 6·7	42	E.J.S.
Kenfig, South Wales	..	1·7–5·4	0·0–2·6 (locally 31) av. 1·0	42	E.J.S.
Whitford Burrows, Gower	..	..	3·2–14 av. 10·5		E.J.S.
Oxwich, Gower	..	..	1·4–2·6	..	E.J.S.
Tenby, Pembroke	6·5–7·2	1·4–2·7	3·6–15·3	41	E.J.S.
Llanbdr, Talwn-Bach and Duffryn, Mid Wales	..	0·02–8·8	0·0–6·3 av. 1·04	..	E.J.S.
Harlech, Mid Wales	..	..	0·7–1·6 av. 1·1	..	E.J.S.
Borth-y-Gest, Mid Wales	..	..	0·3–4·6 av. 1·7	..	E.J.S.
Abersoch, N. Wales	..	..	1·5–5·1 av. 1·6	44	E.J.S.
Newborough, Anglesey	6·6–8·5	0·2–0·5 6·5–18(old)	0·5–2·0	42	Forestry Commission E.J.S.
FRENCH Dunes, Golfe du Lion	..	0·08–0·44	5·5–30·0	..	Kuhnholtz-Lordart
DUTCH Dunes	..	..	0·1–4·0	..	....
Observed Range	4·2–8·5	0·0–25·7	0·0–75	23–50	J. Lebrun

TABLE II. PLANTS OF DUNES COMMONLY ASSOCIATED WITH CALCAREOUS SOILS

The abbreviations, c.=common, f.=frequent, o.=occasional, r.r.=rather rare, r.=rare, v.r.=very rare, all refer to frequencies of occurrence on dunes and not to abundance.

The percentages of carbonates are mostly from the author's own determinations from loci where the species concerned was growing and are only a rough guide to their habitat preferences in this respect since they only represent a selection of the stations for each of the species. But when a calcicole species was found in a situation expected to be poor in carbonates samples were always taken so that low values tend to be better represented than high.

A. HERBACEOUS SPECIES

Agrimonia odorata	Scented Agrimony, v.r. (one det. only 12%)
Anacamptis pyramidalis	Pyramidal Orchid, o.–f., 2–13·5%
Anthyllis vulneraria	Kidney Vetch, f., 1·5–50%
Arabis hirsuta	Hairy Rock Cress, o.–f. (1·5–6%)
Asperula cynanchica	Squinancy-wort, o., 10–50%
Astragalus danicus	Milk Vetch, f. in north, 1·0%
Astragalus glycyphyllos	Wild Liquorice, r., ?
Atropa belladonna	Deadly Nightshade, r. (one det. only 12%)
Blackstonia perfoliata	Yellow-wort, f., 1–50%
Brachypodium pinnatum	r. (one det. only 14%)
Briza media	Quaking Grass, o., 0·03–4%
Bromus erectus	Chalk Brome
Campanula glomerata	Clustered Bell-flower, 1%
Carex flacca	Grey Sedge, o.–f., 2%–48%
Carlina vulgaris	Carline Thistle, f.c., 0·1–50%
Centaurium littorale	Seaside Centaury, r., 0·1–6%
Centaurium pulchellum	Small flowered Centaury, 0·1–50%
Centaurium umbellatum	Pink Centaury, c., 0·1–50%
Chicorium intybus	Chicory, r., ?
Coeloglossum viride	Frog Orchis, r.r., 0·03–54%
Cynoglossum officinale	Hound's-tongue, c., 2–50%
Draba incana	Rock Cress, v.r. (calc. dunes, W. Ross)
Echium vulgare	Viper's Bugloss, c., 0·01–15%
Epipactis helleborine	Hellebore, 1–14%
Erigeron acris	Fleabane, c., 1–50%
Euphrasia officinalis agg.	Eyebright, c., ?
Festuca ovina	Sheep's Fescue, f., 1%
Galium cruciatum	Crosswort, r.r. (1–14%)
Gentiana amarella	Felwort, c., 1–15%
Gentiana baltica	Annual Gentian, f., in west, 1–14%
Gentiana campestris	Field Gentian, r., 0·01–14%
Gentiana verna	Spring Gentian, v.r., ?
Geranium columbinum	r.r., ?
Geranium pratense	Field Crane's-bill, r., 1%

A. HERBACEOUS SPECIES *cont.*

Geranium sanguineum	Bloody Crane's-bill, r., 2–14%
Gymnadenia conopsea	Sweet scented Orchis, o., 1–2%
Helianthemum nummularium	Rock Rose, r., 1%
Helictotrichon pratense	Field Oat-grass, r., 1%
Helictotrichon pubescens	Hairy Oat Grass, r. (1–45%)
Hippocrepis comosa	Horseshoe Vetch, r.r., ?
Hornungia petraea	local, 1·5–2%
Hypericum hirsutum	Hairy St. John's Wort, r.r., 1–1·7%
Inula conyza	Ploughman's Spikenard, f., 0·1–50%
Iris foetidissima	Roast Beef Plant, f. in west, 5–15%
Koeleria gracilis	r., 1–2%
Linaria repens	Creeping Toadflax, r. (one det. only 50%)
Linum catharticum	Purging Flax, f., 0·1–60%
Listera ovata	Twayblade, o., 0·01–6%
Lithospermum officinale	Gromwell, r., 10–15%
Marrubium vulgare	Horehound, r., ?
Monotropa hypopitys	Bird's nest, v.r., 0·1–2%
Ononis repens	Rest-harrow, c., 0·3–50%
Ophrys apifera	Bee Orchis, f., 1–10%
Origanum vulgare	Marjoram, r., 1%
Parnassia palustris	Grass of Parnassus, r. (one det. only 2·5%)
Picris echioides	Ox-tongue, o. (one det. only 10%)
Pimpinella saxifraga	Burnet, o., 1%
Polygala oxyptera	Milkwort, f., 0·01–13%
Polygonatum odoratum	Solomon's Seal, v.r.
Poterium sanguisorba	Salad Burnet, c., 0·05%
Primula veris	Cowslip, (1–10%)
Reseda lutea	Wild Mignonette, o., ?
Scleropoa rigida	c. (one det. only 12%)
Spiranthes spiralis	Lady's Tresses, f., 0·3%–10%
Thalictrum minus agg.	Meadow Rue, o., 1–61%
Thymus serpyllum	Thyme, c., 0·1–48%
Trifolium campestre	Hop Trefoil, f., 1–10%
Verbascum nigrum	Black Mullein, r.r. (one det. only 7%)
Viola calcarea	Chalk violet, v.r.
Viola hirta	Hairy violet, o., 6–10%

B. SHRUBS AND TREES

Ligustrum vulgare	Privet, o., 2–50%
Rhamnus catharticum	Purging Buckthorn, r.r.
Rubus caesius	Dewberry, o.
Sambucus nigra	Elder, f.
Viburnum lantana	Wayfaring Tree, r.r.

*

XXV

THE DUNE FLORA AND ITS GEOGRAPHICAL RELATIONS

THE British Dune flora is made up of some 400 different kinds of vascular plants, in addition to which there are a number of mosses and lichens, a few liverworts and numerous fungi, together with slime fungi (Myxomycetes), bacteria and algae.

The flowering plants are predominantly perennial herbs, such constituting 53% of the total. Next in order of numerical importance are the annuals, constituting 28%. Biennials contribute 7% and species with resting bulbs or corms 4%, whilst the woody plants contribute 6·5% of shrubs and about 1% of trees.

All of these, however, are not equally characteristic, and if we only consider those species for which our sand dunes are the chief or only habitat, then the total is reduced to little over 60 species, with again a preponderance of perennials (50%) and a large proportion of annuals (37%), with but one woody plant—namely, the Sea Buckthorn (*Hippophae rhamnoides*). Chief amongst the characteristic species are the perennial dune grasses and a sedge, the Marram (*Ammophila arenaria*), the coastal Couch Grasses, *Agropyron junceum* and *A. pungens*, the Lyme Grass (*Elymus europaeus*), the Sand Fescue (*Festuca arenaria*) and the Sand Sedge (*Carex arenaria*). The Sea Convolvulus (*Calystegia soldanella*, Convolvulaceae), the Sand Spurge (*Euphorbia paralias*, Euphorbiaceae), the Sea Holly (*Eryngium maritimum*, Umbelliferae), and the seaside Meadow rue (*Thalictrum dunense*, Ranunculaceae), are, all four, plants with smooth leathery leaves easily stimulated to renewed growth by sand burial and capable of withstanding considerable dessication. It is noteworthy that each is a representative of a different family. The now almost extinct *Otanthus maritimus* (=*Diotis maritima*), which belongs to still another family, the Compositae, is a hairy-leaved Mediterranean perennial that is

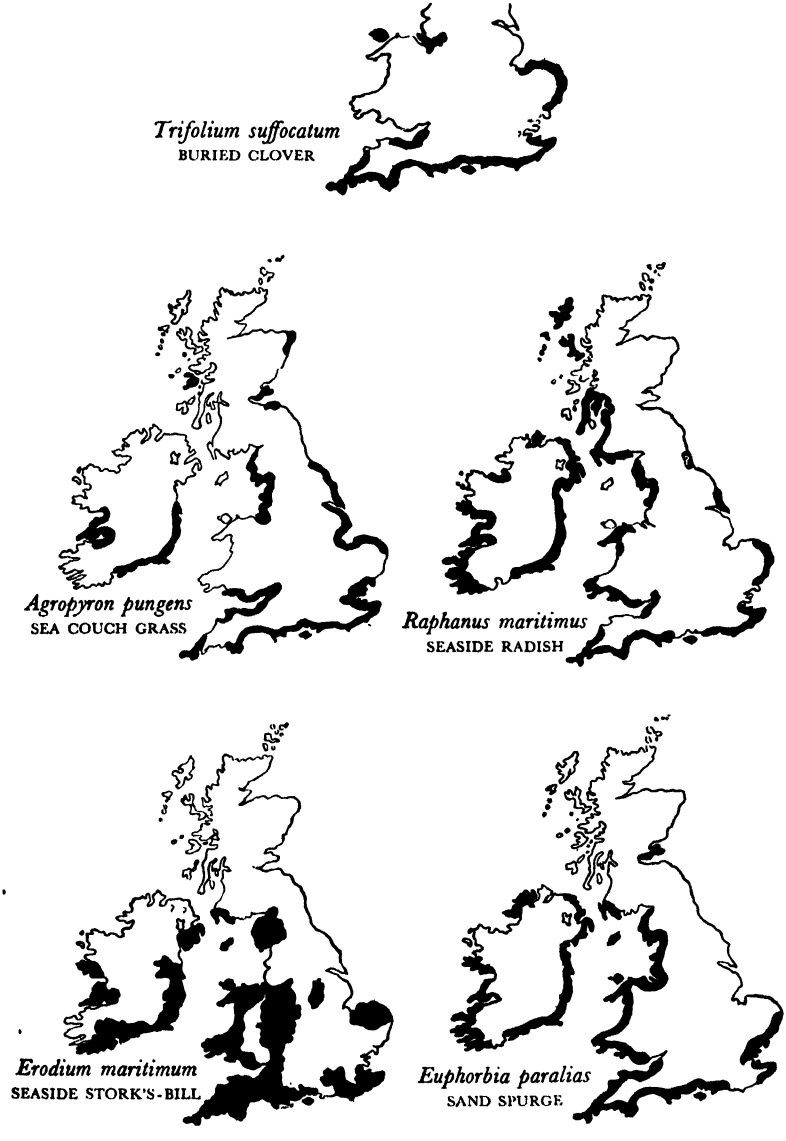


FIG 92. Distribution maps of dune species.

a feature of the dunes in the Gulf of Lyons and was formerly to be met with on several dune systems on our southern shores.

Common and characteristic annuals are the Mouse-ear Chickweeds (*Cerastium semidecandrum* and *C. tetrandrum*), a yellowish-green Chickweed without petals (*Stellaria apetala*=*S. boreana*) and the sand Cat's-tail Grass (*Phleum arenarium*); but these also occur, though less commonly, inland on sandy soil, as, for example, in Breckland. It is amongst the comparative rarities that the species which grow almost exclusively on sand dunes are chiefly to be found, although the dune-face annuals—namely, the Prickly Saltwort (*Salsola kali*) and the Sea Rocket (*Cakile maritima*), are exceptions to this generalisation since they are alike characteristic and common. Some of the most exclusively dune species are amongst our rarest British plants, as, for example, the Wild Asparagus (*Asparagus maritimus*, Liliaceae), the Ball Rush (*Scirpus holoschoenus*, Cyperaceae), and the crocus-like *Romulea columnae* (Iridaceae) (Pl. XXV), whilst others almost confined to dunes are very local in their occurrence, as, for instance, *Hornungia petraea*, Fig. 81, p. 240 (Cruciferae), chiefly on the calcareous dunes of S. Wales, the Autumn Squill (*Scilla autumnalis*), a markedly oceanic species, an inconspicuous Clover (*Trifolium suffocatum*, see map, p. 289), and the Maritime Centaury (*Centaurium littorale*, Fig. 55, p. 198).

The dune flora comprises various geographical elements; some of the more typical species have a wide distribution, as, for example, the Marram Grass itself, which is found throughout Europe and North America. The Sea Holly (*Eryngium maritimum*) has a wide distribution over Europe, Asia Minor and Northern Africa. Amongst the annual species *Cerastium semidecandrum* occurs on dunes in North America as well as over Europe. *Hornungia petraea* occurs throughout Europe and extends to western Asia and North Africa. But apart from these more widely ranging plants certain geographical components are conspicuous. Of these the best represented is the Oceanic component. This comprises a Western element of which the most characteristic members are the Sand Sedge (*Carex arenaria*), the Portland Spurge (*Euphorbia portlandica*), the Maritime Stork's-bill (*Erodium maritimum*), the yellow Dune Pansy (*Viola curtisii*) and the rare Sand-dune Dock (*Rumex rupestris*). The seaside Radish (*Raphanus maritimus*), the Sea Kale (*Crambe maritima*), the White Stonecrop (*Sedum anglicum*)

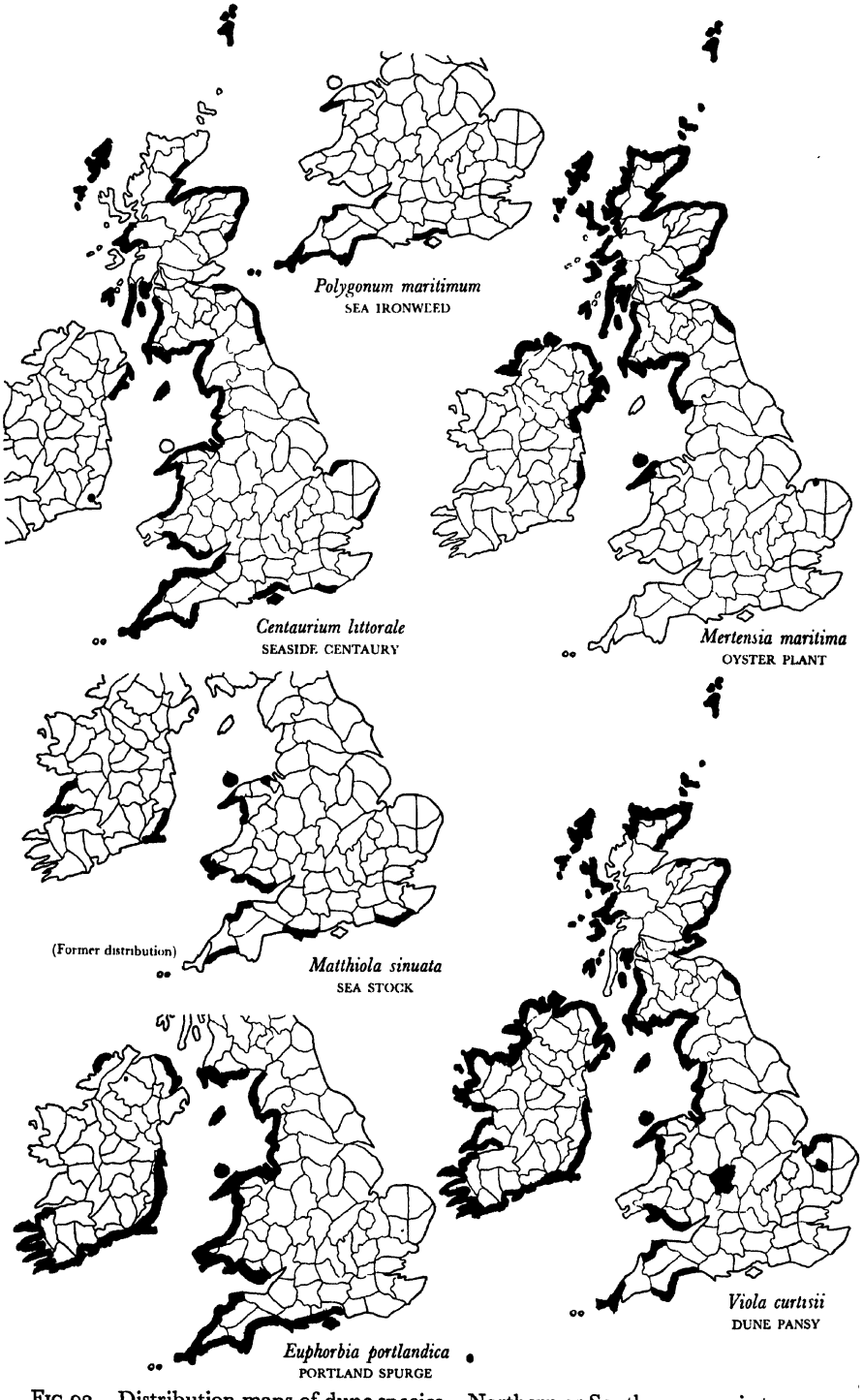


FIG 93. Distribution maps of dune species. Northern or Southern oceanic types.

and the Spring Squill (*Scilla verna*) are also definitely western in their distribution obviously favoured by oceanic conditions, but are not especially dune plants although sometimes inhabiting these. Mention should be made here of the annual *Cerastium tetrandrum*, which shows a western trend in its European distribution. (See Figs. 92–3.)

The oceanic component also comprises elements which though clearly favoured by the relatively equable and humid conditions that obtain in western areas exhibit either a northern or southern preference. The southern-oceanic element is a relatively large one and includes some seventeen species that occur on dune systems, and of these the more characteristic are cited below.

SOUTHERN-OCEANIC DUNE SPECIES

Agropyrum junceum
Agropyrum pungens (Fig. 92)
Euphorbia paralias (Fig. 92)
Juncus acutus (Fig. 94)
Ononis reclinata
Phleum arenarium
Polygonum raii
Romulea columnae
Scilla autumnalis
Trifolium suffocatum

The oceanic species with a northern trend include the Sea Purslane (*Arenaria peploides*), the Sea Orache (*Atriplex maritima*), two Pink Centauries (*Centaurium capitatum* and *C. littorale*) and a Rush, *Juncus balticus*.

The Mediterranean element embraces several characteristic dune plants, mostly however rare, such as the Wild Asparagus (*Asparagus maritimus*), the almost extinct *Otanthus* (*Diotis*) *maritima*, *Euphorbia peplis*, *Polygonum maritimum* and the Sea Stock (*Mathiola sinuata*). It is human interference that has no doubt been responsible for the disappearance of these species from localities where they formerly grew, though the fact that they are near their climatic limit in southern or western England accounts for their susceptibility to such interference. (Fig. 94.)

That our sandy shores should provide a suitable habitat for species of western Europe is to be expected, and indeed some of those cited such as *Euphorbia portlandica* and *Rumex rupestris* are members of the group of markedly south-western oceanic species that are sometimes referred to as the 'Atlantic' or 'Lusitanian' element. On the other hand, considered superficially it would seem unlikely that the continental component of the European flora would be a feature of our maritime dunes,

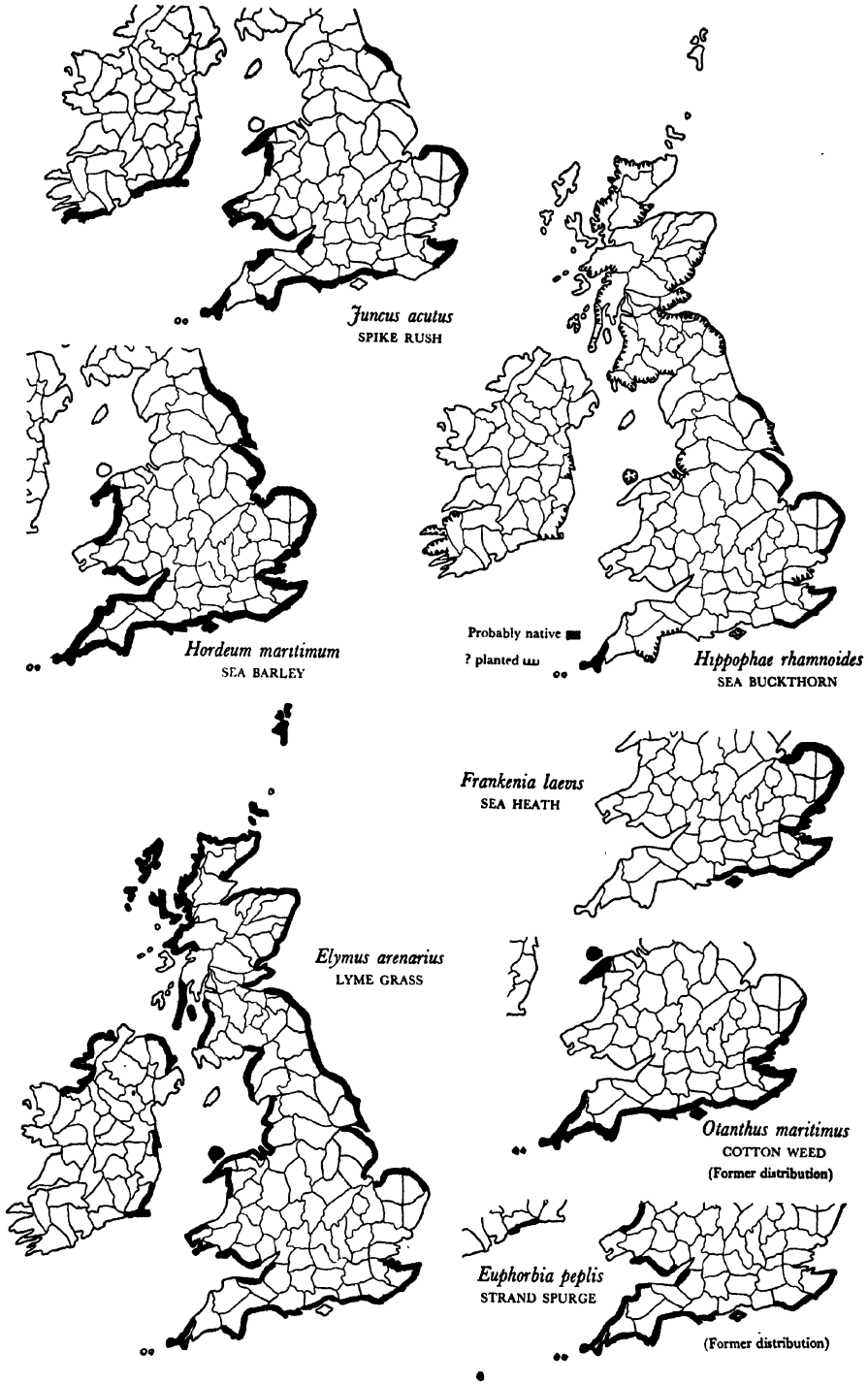


FIG 94. Distribution maps of dune species.

but in fact the nature of the soil accentuates the differences between winter and summer and thus enables certain members of this component to maintain themselves. The grass *Corynephorus canescens* and the Burnet Rose (*Rosa spinossissima*) are continental perennials, whilst species of short duration are represented by the Medic (*Medicago minima*), the Catchfly (*Silene conica*) and the Small Cat's-ear (*Hypochoeris glabra*); only the two perennial species cited above are, however, in any appreciable degree dune species. Of northern-continental plants the Annual Gentian (*Gentiana baltica*) is the most characteristic, but several species which are more or less characteristic of dune 'slacks' belong to this category—namely, the dune Wintergreen (*Pyrola rotundifolia*, v. *arenaria*), the Saprophytic Orchid (*Corallorhiza trifida*), the Marsh Sage (*Teucrium scordium*) and the Knotted Spurge (*Sagina nodosa*). To this geographical group also belongs the chalk-loving Milk Vetch (*Astragalus danicus*), which occurs especially on Scottish dune systems. The Grass of Parnassus (*Parnassia palustris*) found in the dune slacks of the north is a northern calcicole. Southern-continental types include no very characteristic species. *Anacamptis pyramidalis*, *Diplotaxis tenuifolia*, *Dianthus prolifer*, *Erodium moschatum*, *Plantago coronopus*, *Silene anglica*, *Spiranthis spiralis* and *Trifolium scabrum*, all of which belong to this group, are met with on dunes.

The dune habitat has, as we have seen, a characteristic flora of flowering plants and the Cryptogamic vegetation is scarcely less distinctive. Some of the Mosses and Liverworts of the dunes have already been named. W. Watson cites the following as the most abundant: *Tortula ruraliformis*, *Camptothecium lutescens*, and *Brachythecium albicans*, with species of *Hypnum* and *Bryum* in the 'slacks' and 'lows.' For full lists his papers should be consulted but it should be noted that amongst these he calls attention to calciphilous types such as *Barbula tophacea*, *Trichostomum crispulum*, and the Liverworts *Pellia fabbroniana*, *Preissia quadrata*, *Lophozia badensis*, and *Scapania aspera*. So too we may emphasise that the dunes have also their characteristic Lichens such as the Cladonias and Peltigeras and distinctive Fungi of which *Psalliota arenicola*, *Psilocybe ammophila* and *Clitopileus popinaiis* may serve as examples. The last named occurs on downs also (cf. Wakefield E. M. & Dennis R. W. G. *Common British Fungi*, London, 1951.)

XXVI

THE SAND-DUNE FAUNA

APART from the introduced *Helicella pisana* to which reference has already been made, the mollusca of dunes are mostly those to be found in other calcareous habitats. *Helicella virgata* is sometimes quite common and so too is *H. nemoralis*. The only species which can be regarded as coastal is *Bulimus acutus*.

The animal life of dunes includes several night-flying moths the larvae of which depend upon dune plants for their food. Thus the Shore Wainscot Moth (*Leucania littoralis*), with narrow brown fore-wings each bearing a median white line, has larvae which feed on the Marram Grass, whilst another brownish moth, *Arenostola elymi*, has larvae which feed exclusively on the Lyme Grass (*Elymus arenarius*). The Salt Wort, Sea Holly and Sea Rocket will equally serve as food for the larvae of the Sand Dart (*Agrotis ripae*), but another sand-dune species of the same sub-family, the Coast Dart (*Euxoa cursoria*), has larvae that feed on diverse grasses, whilst those of a third species (*Astebia praecox*) have even more catholic tastes; but both these moths are, nevertheless, essentially sand-dune Lepidoptera. In this habitat occur particularly the Grass Eggar Moth (*Lasiocampa trifolii*), and rarely the Bedstraw Hawk moth (*Celerio galii*). The Spurge Hawk moth (*Celerio euphorbiae*) is restricted to dunes since the food plant is the Sand Spurge (*Euphorbia paralias*), but it is now nearly a century and a half since larvae of this species were found at Braunton Burrows, where they were then frequent.

Since the members of the Class Arachnida are mostly carnivorous with a wide range of diet their restriction to particular habitat conditions is not often marked, but mention may be made of one sand-dune spider, *Philodromus fallax*, which, when its legs are withdrawn, resembles a large sand grain both in form and colour. The False Scorpion (*Chelifer latereillei*) is also more especially a dune species.

There are likewise sand-dune beetles, such as the brownish-yellow *Calathus mollis*, the purplish Tiger Beetle (*Cicindela hybrida*), *Anomala oenea* and the Black Weevil (*Otiorrhynchus atroapterus*) besides a number of smaller species. The only known British localities for the beetle *Aegialia rufa* are the sandhills of the Cheshire coast and Sharp *et al.* (c.f. *Merseyside*, Liverpool, 1923) cite a number of species of Coleoptera which are a feature of the sandhills in that area. So too the dunes yield characteristic Hymenoptera such as the large Solitary Bee (*Colletes cunicularia*), the Digger Wasp (*Oxybelus argentatus*), and plant Bugs, for example *Therapha hyoscyami*. The Marram Grass bears galls consisting of short imbricated leaves caused by the larvae of *Eurytoma hyalipennis* which live in the haulm and from which the insects emerge in June, whilst the fiery red swellings of the stem and leaves of the Burnet Rose are caused by the Hymenopteran *Rhodites spinosissimae*.

The foregoing examples serve to show that the dunes present a characteristic fauna as well as a distinctive flora and emphasise the integration of the biological community as a whole with the physical complex which we collectively term the dune habitat.

XXVII

THE CHANGES OF DUNES WITH INCREASING AGE

WE have repeatedly had occasion to refer to the gradual changes that dunes exhibit with the passage of time, and the different character of the vegetation on dune ridges of increasing age and stability has already been described. There is in fact an ordered sequence in the passage from raw sand to mature soil and from the sparse pioneers of the youngest dunes to the complete carpet of plants which clothes the oldest. Thus we can recognise a definite succession of changes in the soil and of phases in the vegetation. Because the distribution of dunes in space normally corresponds to their order in time we are enabled to study such phases with a degree of certainty as to their sequence that is unparalleled in most other types of plant community. Just because these changes may occupy centuries it is impossible for any one person actually to observe more than a brief part of any plant succession, so that for most types of vegetation we can only infer the different phases, whereas in dune systems the successive stages are commonly arranged in order with the youngest nearest the sea and the oldest furthest from the shore. Occasionally the orderly arrangement is disturbed by redistribution of the material of old dunes and rejuvenation occurs through accretion of fresh sand. Such irregularities are usually easily recognised and comparison of different parts of the same dune system or of one series of dunes with another provides sufficient safeguard against mistaking an abnormal phase for a normal one.

Of the soil changes that accompany the passage of time the most pronounced are (i) decreased mobility, (ii) increase of organic content, (iii) increase of water-retaining capacity, (iv) leaching out of carbonates, (v) change of soil reaction. Of these the first, though obvious, is not usually capable of exact assessment, being dependent on a number of variables including the local climatic complex. In any system it is obvious that the oldest dunes are in general far less subject to erosion by wind

than the younger phases, but the degree of mobility at any one stage of development is determined alike by the precise floristic composition of the plant covering, the nature of the dune soil and its moisture content at the period under consideration.

The water content naturally varies with the weather con-

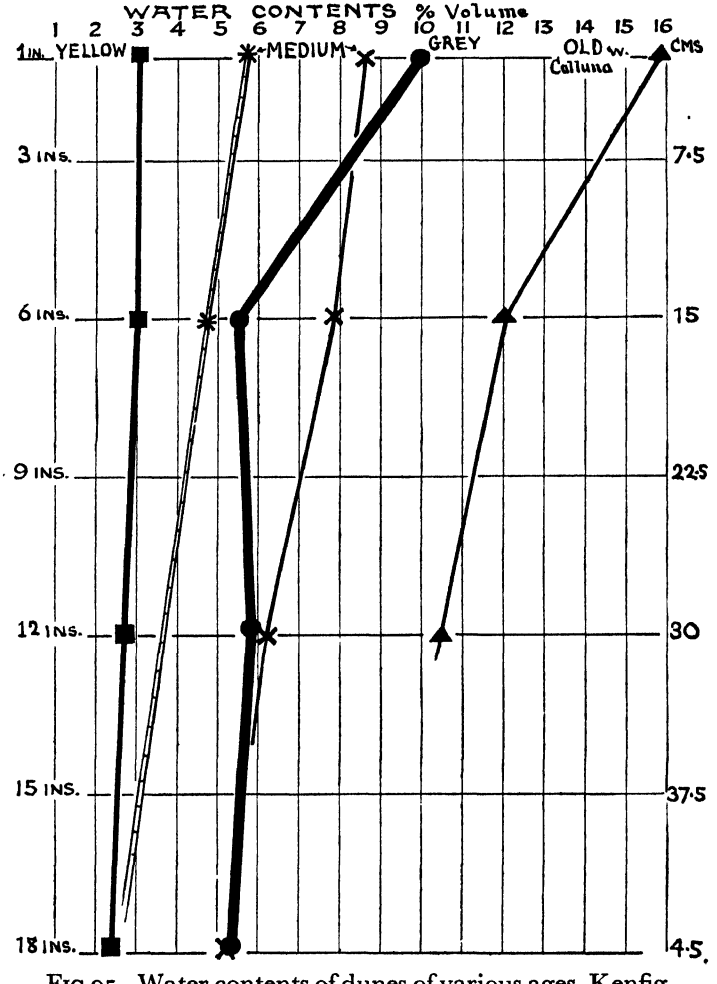


FIG 95. Water contents of dunes of various ages, Kenfig dunes, after rain, April 1937.

ditions, but the data already furnished show that contemporary determinations in the successive stages of dune development normally exhibit an augmentation with age that corresponds with the increasing organic content. The accompanying diagram (Fig. 95) showing the natural water contents of the

soils of dunes of different ages at Kenfig Burrows soon after rain, when the amount retained was probably not far from its maximum brings this feature out strikingly. The loss on ignition corrected for the loss of CO_2 from the carbonates enables us to estimate with sufficient accuracy the change in this soil constituent; and the data obtained from a large number of soil samples from the dune systems at Blakeney Point on the Norfolk Coast and at Southport, where the dune ridges can be dated with some approach to accuracy, show that the rate of increase of organic material augments slowly at first, but is appreciably greater after the lapse of about two centuries than in the earlier periods. Moreover, it will be apparent that in the drier climate of the east coast with a rainfall of about 25 ins. (641 mm.) the growth rate of the vegetation, on such an edaphic desert as a sand dune, will be slower than on the west coast with a mean annual rainfall of about 32 ins. (813 mm.) and hence we might expect, what in fact obtains—namely, a higher rate of increment of organic material in the sand at Southport than at Blakeney (cf. Fig. 96).

At Blakeney the youngest dunes contain in the surface sand under 0·5% of organic material rising to from 3% to 6% in the oldest dunes. At Southport the youngest dunes contain an average of from 0·5% to 0·7% of organic material, older dunes have 3% to 4% whilst the oldest Heather-clad dunes have from 4% to 15%.

In the Braunton Burrows of north Devon the yellow dunes have about 1·8% and the fixed dunes, possibly 200 years older, nearly 4%. Yellow dunes at Bude, N. Cornwall, contained 2·9% and old fixed dunes 10·2%. Similarly at Kenfig on the S. Wales coast, the young yellow dunes contained under 2% of organic matter and grey dunes from 3% to 5%, whilst still older Heather-clad dunes yielded from 9% to 13%. Old dunes at Llanbedr about 200 years old contained about 8%. It is apparent therefore that the increase of organic content with age is a general feature of dune systems. The rate of increase, however, varies with the climate and vegetation as well as with the character of the sand. Thus, largely owing to the slower rate of bacterial decomposition, the accumulation of dead leaves, roots and other organic material is favoured by acid conditions, whereas a high carbonate content with the accompanying alkaline reaction promotes rapid decay. For example

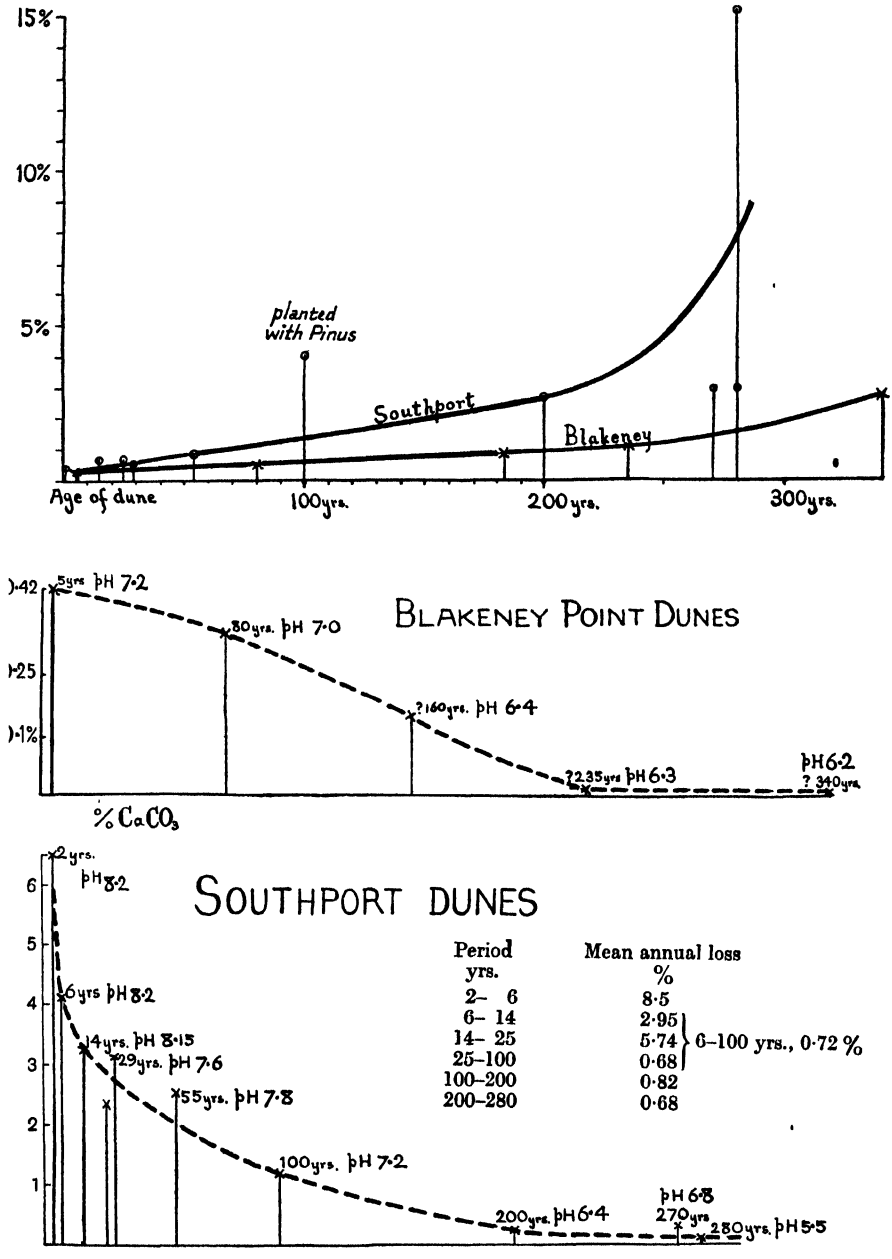


FIG 96. Changes in dune soils with time at Blakeney Point, Norfolk, and at Southport, Lancashire. The uppermost diagram shows the increase of organic material with increasing age, and the two lower the decrease in content of calcium carbonate and the changes in reaction. (From E. J. Salisbury, *Journ. Ecology*, XIII, 1925.)

old dunes at Braunton which have a high content of carbonates (14–16% $CaCO_3$) have only 2% more organic material than the young dunes in the same system, whereas the dunes of Southport, with a much lower initial content of carbonates, have accumulated a high content of organic material in a period of similar duration.

The advent of the Heather (*Calluna vulgaris*) no doubt normally accelerates the production of humus and is itself a sign of soil conditions unfavourable to rapid decomposition; but the phase at which the Heather arrives is dependent upon the nature of the sand originally and so we find, for instance, that on the dunes at Studland the Heather is present on ridges that are only about eighty years of age, a fact that harmonises with the very low initial content of carbonates (0·00–0·2% $CaCO_3$). Samples from areas of these dunes probably about 150 years old only contained a small proportion of organic material (0·2–0·6%) whilst even from areas over 200 years old the surface sand might still contain under 1%. Here the sluggish rate of production has been perhaps due to the slow growth of vegetation in a dune sand exceptionally poor in nutrients from the outset, and to an annual rainfall that is not far above the lower limit in which Heather flourishes, especially on so porous a soil and in an area of such low humidity.

Initially the calcium carbonate of dune sands is usually appreciable and often high, though those of the Culbin Sands on the Moray Firth furnish an example where little or no free carbonates are normally present. In those dunes, however, where the original content of calcium carbonate is significant, the successively older phases commonly exhibit a progressive leaching which would always lead to complete removal of free carbonates from the surface layers in a few hundred years were it not that this consummation may be delayed, or even temporarily prevented, by two main influences both operating the more effectively the higher the content of carbonates in the original foreshore sand and young dunes. These factors are, firstly, the wind transport of carbonates, particularly as shell fragments, from the younger dunes to the older; and, secondly, the return of carbonates to the surface by the action of the vegetation in which the deep-rooted perennials play a major rôle, the enrichment of the surface taking place directly by the decay of their overground parts or indirectly through animals

such as snails which feed upon the plants. Other causes of retardation of the edaphic succession, of a similar nature, which may operate in a lesser degree are the action of earthworms, which neutralise the acid surface soil by means of their calciferous glands that are renewed from below (cf. E. J. Salisbury, *Journ. Linnean Soc.*, XLVI, pp. 415–425, 1924), and capillary rise and concentration of the soil solution at the surface that may occur in hot weather, following rainfall sufficient to saturate the soil. (Fig. 91, p. 283.)

The rate of the removal, or leaching, will tend to be faster where the average rainfall is high, for though this will lead to a more luxuriant vegetation and a consequent increase in the pumping action of the deeply-rooted perennials just referred to, the augmented CO_2 in the soil atmosphere, resulting from a copious vegetation, will ensure the conversion of the relatively insoluble carbonate into the far more soluble bicarbonate and saturation by this gas of the percolating rainwater, so that it becomes the effective solvent H_2CO_3.

TABLE I. CARBONATES IN DUNES, BRAUNTON BURROWS

(Av. for all samples 15·5%)

Depth		*Yellow mobile dune*		*Fixed dunes*		*Old dunes*	
Ins.	*Cms.*	*Range* %	*Mean* %	*Range* %	*Mean* %	*Range* %	*Mean* %
0–6	0–15	24·0–13·44	18·05	17·6–9·6	14·5	14·9–10·3	12·21
6–12	15–30	19·8–14·8	16·81	16·5–14·8	15·8	14·7–12·7	13·8
12–18	30–45	16·8–16·7	16·8			19·3–14·5	16·4
18–24	45–60	21·5–17	18·65	20·4–16·9	18·6	15·4–14·2	14·7
24–30	60–75	18·3–16·6	17·51	18·6–16·8	17·1	18·5–14·9	16·1
Av. per 100 gms. dry soil 0–30 cms.		17·8±0·3 gms.		15·1±0·2 gms.		13·6±0·27 gms.	
Av. wt. per 100 c.c. of soil 0–30 cms.		25·44 gms.		21·96 gms.		20·7 gms.	

In the diagrams for the Blakeney and Southport dune systems the rate of leaching with age is clearly shown (cf. Fig. 96) and the carbonate contents from both young and old dunes in various dune systems illustrate the same feature (cf. Fig. 98). The combined effects of the diminishing amount of basic material and increasing organic content with the accompanying organic acids is the change from an originally alkaline to an acid reaction, and so we find that whereas the yellow dunes of

most systems have a reaction between pH 7 and pH 8·5 the old dunes are commonly appreciably acid with a reaction between pH 5 and pH 6, whilst heather-covered dunes may have a still higher acidity.

This change of soil reaction, with increasing age, was shown by the author to obtain in the two dune systems just referred to and has since been observed in dune areas of South Wales and Devon. Similarly Prof. Pearsall found that the yellow dunes of Walney Island had a reaction of pH 7·5 to 7 and the old dunes a reaction of 4·8 to 4·5. Again Dr. Moore in the Isle of Man found that the young dunes were appreciably alkaline with a reaction of pH 7·6 whilst the old dunes were acid with a reaction ranging from pH 6·4 to 5·8. The dunes at St. Cyrus, Kincardineshire, are in the young stages markedly alkaline (pH 8), whereas the old fixed dunes are only less so (pH 7·8), but the dune pasture is definitely acid (pH 6·6) (cf. C. H. Gimingham *et al.*, *Trans. Bot. Soc., Edinburgh*, pp. 387–411, 1951).

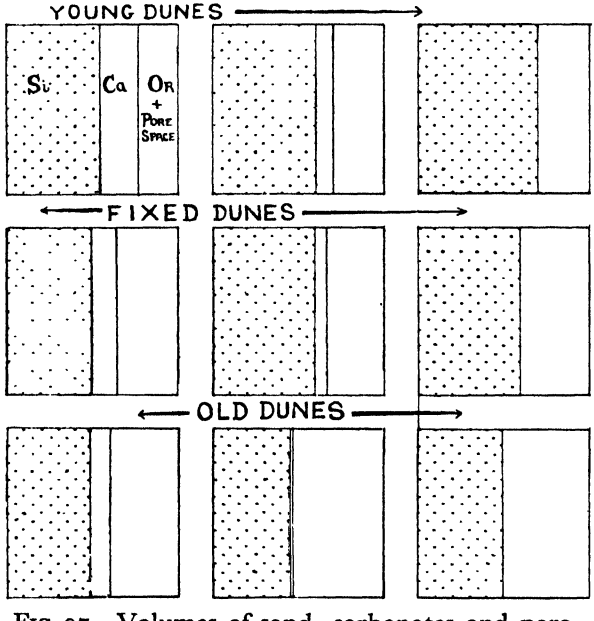


FIG 97. Volumes of sand, carbonates and pore-space in dune soils of different ages. The vertical series at left are based on calcareous dunes, that on right on siliceous dunes.

So it would appear justifiable to assume that temperate dune systems in general exhibit this trend from the alkaline

to the acid condition, although the actual rate of leaching and age at which an acid reaction is attained will depend both on the chemical nature of the original dune sand and the climatic conditions of the area concerned.

Certain soil trends are graphically represented in the diagram (Fig. 97) in which the volume occupied by the siliceous and calcareous constituents of the total volume of the soil is shown to scale based on determinations made both from dune systems that are markedly calcareous and others predominantly siliceous. The remaining volume of the soil consists almost entirely of pore space and organic matter. As the volume of this latter changes markedly with the water content of the soil it has not been separately portrayed, as such presentation would have been unrealistic. These diagrams do clearly show how the major constituents, that chiefly determine the weight of a dune soil, diminish with age and thus how misleading a picture of the availability of nutrients would be presented by data relating to the amount per unit weight. An equal volume of an old dune soil containing an appreciable amount of organic matter may be only about half the weight of the dune sand from a young dune; moreover since the root systems of a particular species may be, and often are, smaller in the older dune soil than the younger, both by reason of the higher moisture content and the greatly increased root competition, it follows that far from compensating for the soil change this difference in root growth actually accentuates the comparative availability of nutrient supplies.

Local circumstances of dune systems or its several parts may obscure the trend of leaching, but they cannot hide the essential fact, though a few isolated samples may not appear to bear out this generalisation. If, however, we set forth graphically the carbonate contents of a number of samples from dune ridges of different ages, although there will be found appreciable overlap, nevertheless, the modal values are quite distinct, as shown in the data presented for the young and old dunes at Braunton (cf. Fig. 98).

One further soil change must be referred to—namely, the less efficient aeration with the passage of time, the soil atmosphere of the older dunes being usually richer in CO_2 and poorer in oxygen than that of the younger phases. In most respects, however, the soil conditions may be said to be ameliorated with the passing of the years, and we not only find that the sparse

vegetation of the pioneers gives place to a closed community of herbaceous vegetation, but this in turn passes into dune scrub in which such shrubby species as Privet and Elder that have a preference for calcareous conditions are often common on the more calcareous dune systems, sending their roots down well

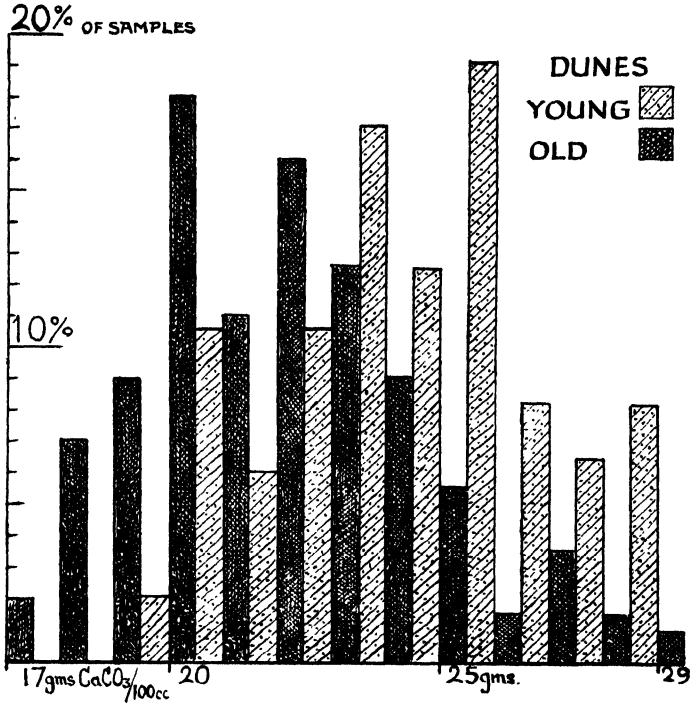


FIG 98. Diagram showing variation of carbonates in numerous samples from young and old dunes in the Braunton Burrows. The heights of the columns are proportional to the numbers of samples, and the position of the column on the horizontal scale indicates the number of grams of calcium carbonate in 100 cc. of the dune soil. Mode for young dunes 25 grams., for old 20 grams.

below the superficially leached layers. On the dunes with an initially low carbonate content the shrubby vegetation often develops as dune heath, with Heather (*Calluna vulgaris*) as the most conspicuous member. Finally, if the dune vegetation is not interfered with by man, a condition that rarely obtains, a woodland with trees may become established. Thus on the calcareous sands of Braunton Burrows woodland with Oak

trees (*Quercus robur*) and such shrubs as Hazel (*Corylus avellana*), Hawthorn (*Crataegus oxycantha*) and Blackthorn (*Prunus spinosa*) has developed. In the shade of the trees or shrubs woodland herbs are encountered, whilst on the non-calcareous sands of the Moray Firth Pine trees colonise amongst the Heather, and the Pine plantations established here and elsewhere by the Forestry Commission are as it were only an anticipation of the natural trend of events. (For Dune-Scrub species see p. 255.)

These changed conditions from the youngest to the oldest phases epitomise the trend of natural forces to change extreme conditions in the direction of the mean. For similarly the aquatic conditions of the dune 'slack' tend to become silted up by the action both of physical forces and the plants which live there and so exhibit a trend likewise to ultimate woodland. Further we note that, reflecting the extreme initial conditions, the dune is at first occupied by specialists of the plant kingdom and the number of kinds involved is naturally small. Gradually the variety of species augments till a peak is attained when the habitat conditions represent for a majority a compromise that is adequate. For most of the original pioneer species the conditions of the older fixed dunes have already become insupportable, whilst for the somewhat later arrivals the conditions of life are still tolerable, though far less favourable than in the yellow dune stages. When the shrubs and trees form a closed canopy their effect is such that conditions have again become highly specialised and the capacity to endure, this time shade, once more effects a selection of the plant population, just as capacity to endure the aridity and mobility of the soil effected a selection of other species at the outset. These trends are reflected in the numbers and types of species that we find in the successive dune phases as set forth in the accompanying Table II in which is a summary of the totals obtained from the author's examination of most of the important dune systems in Great Britain together with such published records as have served to supplement this.

Since the transition from one stage to the next is a process and not an event, the line of demarcation must be an arbitrary one so that the stragglers that persist from the previous phase, or precocious members of the succeeding one, tend to blur the picture. Nevertheless the general features that emerge are independent of minor numerical adjustments that a different

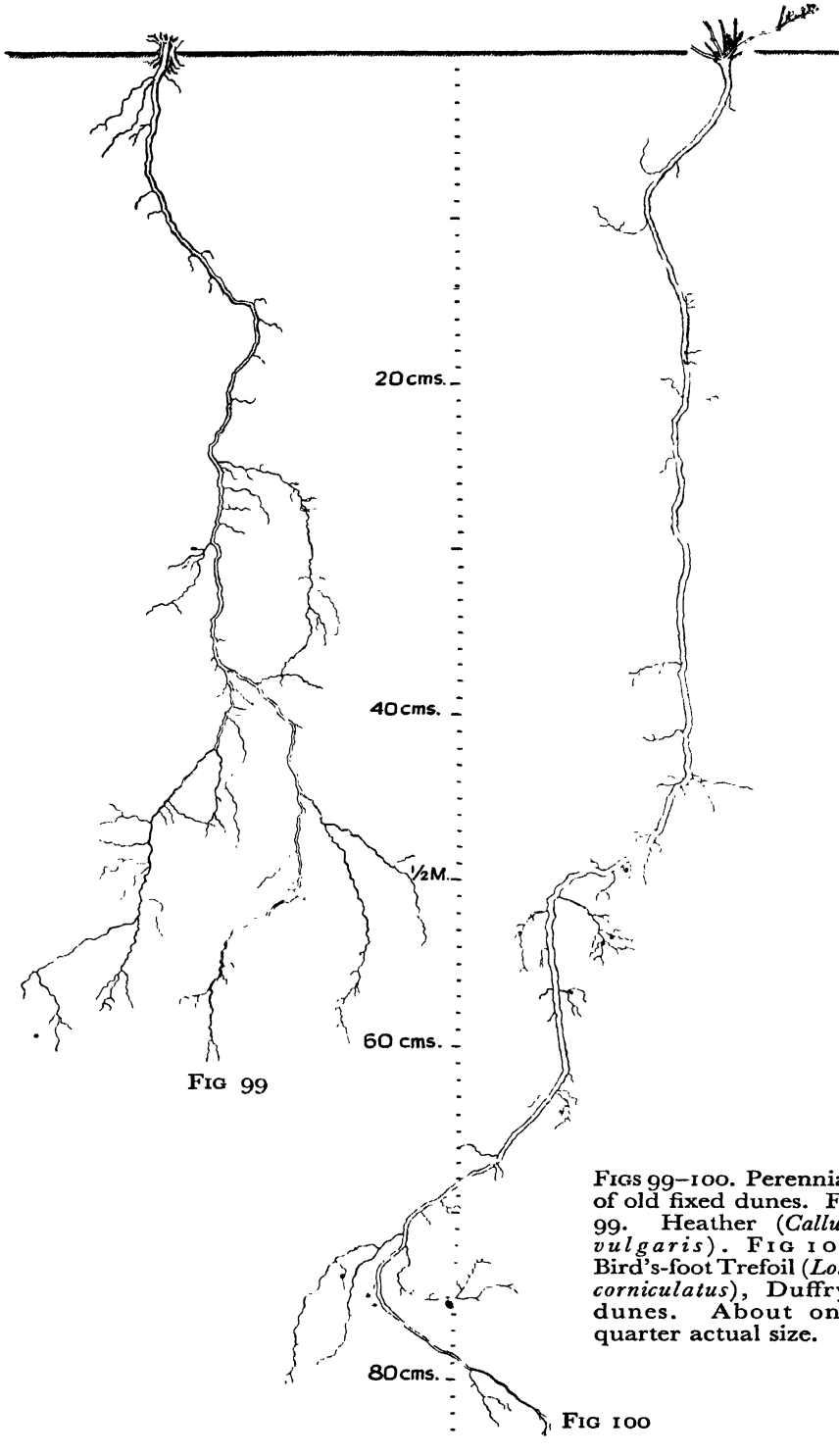


FIG 99

FIG 100

FIGS 99–100. Perennials of old fixed dunes. FIG 99. Heather (*Calluna vulgaris*). FIG 100. Bird's-foot Trefoil (*Lotus corniculatus*), Duffryn dunes. About one-quarter actual size.

TABLE II. NUMBERS OF SPECIES IN PHASES OF DUNE VEGETATION

	Embryo dunes	*Yellow dunes*	*Fixed dunes*	*Late fixed dunes*	*Dune scrub*
Perennials (herbaceous)	7 (38·9%)	24 (33%)	65 (44·8%)	124 (77·5%)	68 (44·7%)
Biennials	2 (11·1%)	5 (7%)	18 (12·4%)	4 (2·5%)	—
Annuals	9 (50%)	44 (60%)	60 (41·3%)	17 (10·0%)	—
Total non-woody spp.	18	73	143	145	68
Shrubs	—	—	2 (1·3%)	14 (8·7%)	29 (43·2%)
Trees	—	—	—	2 (1·2%)	8 (12%)
Total herbs, shrubs and trees	18	73	145	161	105

*Mostly in the transition phase to scrub.

judgment in this respect would entail. The marked rise and decline in the absolute numbers of annual species is unequivocal whilst the high proportion of these therophytes, in the earlier as compared with the later phases, is in accord with their prevalence in climatic deserts all the world over and emphasises the justice of describing the sand dune in its beginnings as an edaphic desert. So too from the first stage onwards there is a steadily augmented proportion of perennials and both these trends gain in significance if the woody species of the last two phases be taken into account, though it must be emphasised that the shrubs and trees of the later phases of fixed dunes are, more than most species, suspect as indicators that a transitional stage has been attained beyond what can be properly regarded as mature fixed dune.

In the earliest stages the effective changes are brought about by flowering plants, and though these continue their importance the advent of Mosses and Lichens accompanies and is a most significant factor in the progress to the fixed dune and the grey dune phases. Whether the ultimate goal will be dune heath or woodland is to a considerable degree dependent on climatic conditions. Where the rainfall is adequate to permit, and neither the prevalence of high winds, low temperatures, nor even excessive rabbit population, prevents, scrub or woodland is the climax. Under low rainfall, or other inhibitors of tree growth and the larger shrubs, a dune heath develops with such plants as Heather (*Calluna*), Heath (*Erica cinerea*), Crowberry (*Empetrum nigrum*), Whortleberry (*Vaccinium myrtillus*) and Bearberry (*Arctostaphylos uva-ursi*). Thus we find a trend towards woodland on the dunes of the south-west where the shelter is adequate (e.g. Braunton) and towards dune heath on the east

coast and in the north. In general too, the grey dune phase with an abundance of lichens is more pronounced where the trend is towards heath and less marked where the rainfall is higher and the trend is towards woodland.

The dune flora thus exhibits in a particularly striking degree the development of a plant community adjusted throughout to the environmental circumstances and passing from a highly specialised state though conditions of increasing amerlioration to a wholly different habitat largely as a consequence of the activities of the organisms it supports. These activities of the plants and their dependents which affect the habitat, termed the biotic factors, are here conspicuously significant and in few communities can the interaction of soil, climate, and the plant covering, be so clearly seen. The pioneer specialists that render the habitat suitable for their successors bring about their own extinction and the final outcome makes possible the establishment of a community of an entirely different character.

KEY TO

THE COUNTIES AND VICE-COUNTIES OF THE BRITISH ISLES

ENGLAND & WALES

0 Channel Isles

PENINSULA

1 Cornwall W.
2 Cornwall E.
3 Devon S.
4 Devon N.
5 Somerset S.
6 Somerset N.

CHANNEL

7 Wilts N.
8 Wilts S.
9 Dorset
10 Isle of Wight
11 Hants S.
12 Hants N.
13 Sussex S.
14 Sussex E.

THAMES

15 Kent E.
16 Kent W.
17 Surrey
18 Essex S.

THAMES *contd.*

19 Essex N.
20 Herts
21 Middlesex
22 Berks
23 Oxford
24 Bucks

ANGLIA

25 Suffolk E.
26 Suffolk W.
27 Norfolk E.
28 Norfolk W.
29 Cambridge
30 Bedford
31 Hunts
32 Northampton

SEVERN

33 Gloucester E.
34 Gloucester W.
35 Monmouth
36 Hereford
37 Worcester

SEVERN *contd.*

38 Warwick
39 Stafford
40 Salop

SOUTH WALES

41 Glamorgan
42 Brecon
43 Radnor
44 Carmarthen
45 Pembroke
46 Cardigan

NORTH WALES

47 Montgomery
48 Merioneth
49 Carnarvon
50 Denbigh
51 Flint
52 Anglesey

TRENT

53 Lincoln S.
54 Lincoln N.
55 Leic. & Rutld.

TRENT *contd.*

56 Notts
57 Derby

MERSEY

58 Cheshire
59 Lancashire S.
60 Lancashire Mid.

HUMBER

61 S.E. York
62 N.E. York
63 S.W. York
64 Mid.W. York
65 N.W. York

TYNE

66 Durham
67 Northumb. S.
68 Cheviotland

LAKES

69 Westmorland and N. Lancs.
70 Cumberland
71 Isle of Man

SCOTLAND

W. LOWLANDS

72 Dumfries
73 Kirkcudbright
74 Wigtown
75 Ayr
76 Renfrew
77 Lanark

E. LOWLANDS

78 Peebles
79 Selkirk
80 Roxburgh
81 Berwick
82 Haddington

E. LOWLANDS *contd.*

83 Edinburgh
84 Linlithgow

E. HIGHLANDS

85 Fife & Kinross
86 Stirling
87 Pth. S. & Clkn.
88 Mid. Perth
89 Perth N. (or E.)
90 Forfar
91 Kincardine
92 Aberdeen S.
93 Aberdeen N.

E. HIGHLANDS *contd.*

94 Banff
95 Elgin
96 Easterness

W. HIGHLANDS

97 Westerness
98 Main Argyll
99 Dumbarton
100 Clyde Isles
101 Cantire
102 Ebudes S.
103 Ebudes Mid.
104 Ebudes N.

N. HIGHLANDS

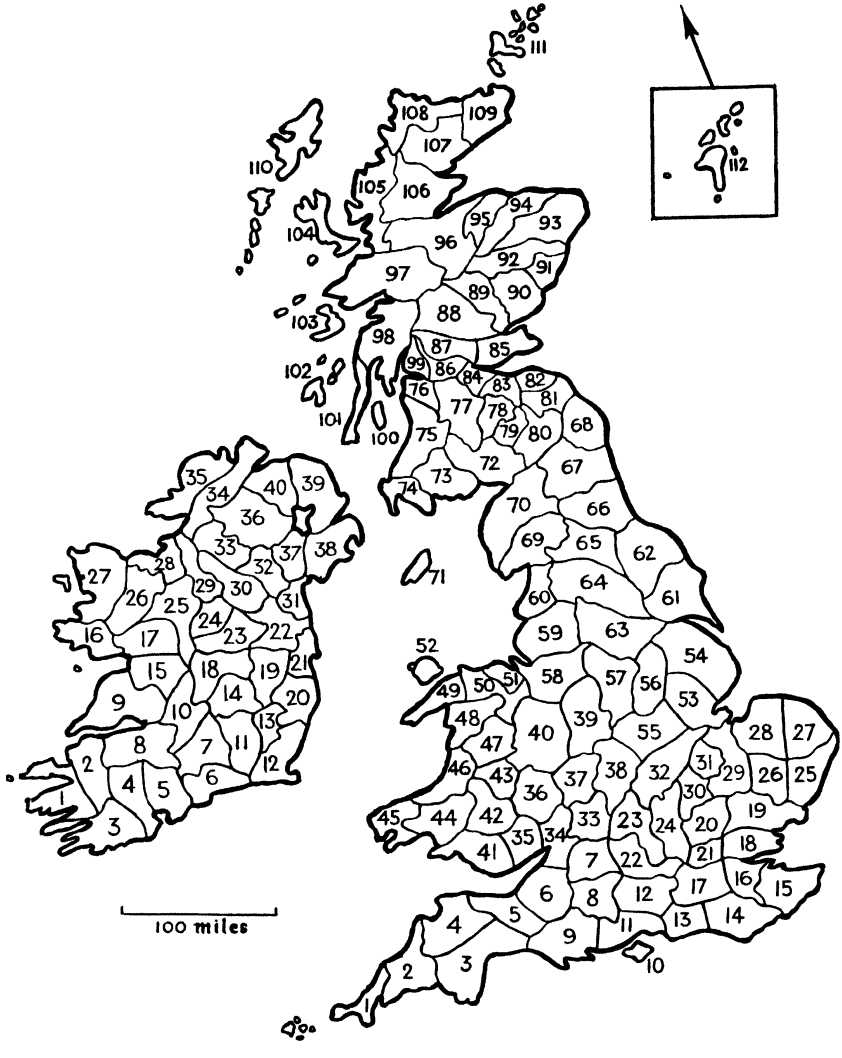
105 Ross W.
106 Ross E.
107 Sutherland E.
108 Sutherland W.
109 Caithness

NORTH ISLES

110 Hebrides
111 Orkneys
112 Shetlands

IRELAND

1 Kerry S.
2 Kerry N.
3 Cork W.
4 Cork Mid.
5 Cork E.
6 Waterford
7 Tipperary S.
8 Limerick
9 Clare
10 Tipperary N.
11 Kilkenny
12 Wexford
13 Carlow
14 Queen's Co.
15 Galway S.E.
16 Galway W.
17 Galway N.E.
18 King's Co.
19 Kildare
20 Wicklow
21 Dublin
22 Meath
23 Westmeath
24 Longford
25 Roscommon
26 Mayo E.
27 Mayo W.
28 Sligo
29 Leitrim
30 Cavan
31 Louth
32 Monaghan
33 Fermanagh
34 Donegal E. (or S.)
35 Donegal W. (or N.)
36 Tyrone
37 Armagh
38 Down
39 Antrim
40 Derry


100 miles

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