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• ANNALES CRYPTOGAMICI et PHYTOPATHOLOGICI •

Volume IV

The CEREAL RUSTS

ANNALES CRYPTOGAMICI

et PHYTOPATHOLOGICI

(incorporating Annales Bryologici)

edited by

FRANS VERDOORN, Ph.D.

Managing Editor of Chronica Botanica 'A New Series of Plant Science Books', etc., Bibliographer, Arnold Arboretum of Harvard University, Bot. Adviser, Board for the Neth. Indies, Hon. Sec., Bot. Section, Intern. Union of Biological Sciences etc.

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Antoni van Leeuwenhoek

1946

WALTHAM, MASS., U.S.A.

Published by the Chronica Botanica Company

The Nature and Prevention *of the* CEREAL RUSTS *as exemplified in the* LEAF RUST of WHEAT

by

K. STARR CHESTER, Ph.D.

Head, Department of Botany and Plant Pathology
Oklahoma Agricultural and Mechanical College

1946

WALTHAM, MASS., U.S.A.

Published by the Chronica Botanica Company

CHECKED 1998

First published MCMXLVI
By the Chronica Botanica Company
of Waltham, Mass., U. S. A.

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244 Flood Building.

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115, Sparks Street.

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Sydney: ANGUS AND ROBERTSON, LTD.,
89, Castlereagh Street.

Melbourne, C. 1: N. H. SEWARD, PTY., LTD.,
457, Bourke Street.

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DEDICAVIT

AVCTOR

"Indeed there are few diseases of plants so obscure as this, and its difficulties, instead of diminishing, appear to increase with each succeeding advance of knowledge."

— E. J. BUTLER AND J. M. HAYMAN, 1906.

"Aspera Robigo, parcas cerialibus herbis,
Et tremat in summa leve cacumen humo.
Tu sata sidcribus caeli nutrita secundi
Crescere, dum fiant falcibus apta, sinas . . .
Parce, precor, scabrasque manus a messibus aufer,
Neve noce cultis: posse nocere sat est, . . ."

— PRAYER AT THE ROBIGALIA, OVID.

"If the stalk and the leaves are attacked by this terrible malady, the best set (of kernels), promising a heavy yield, is reduced to nothing or almost nothing because such a great number of the greedy and gluttonous plants absorb nearly all the nutritive humor of the grain, causing it to become wasted and consumed because of the loss of the nourishing chyle"

— F. FONTANA, 1767.

"Rostpilz und Wirtspflanze sind auf Gedeih und Verderb miteinander verbunden."

— STEINER, 1933.

"Mind and imagination are captivated by the small and great alike, for in each, nature is infinite."

— J. C. FABRICIUS, 1774.

"Wheat-rust may be compared to one of those transcendent actors whose genius delights the world No sooner does the public come to appreciate him in a certain part, and delude itself into thinking that it now comprehends the extent of his abilities, than he suddenly appears in a new creation, so different that it is with difficulty we believe it the work of the same artist. So with wheat-rust: no sooner do we comprehend one phase of its existence than it adopts another, and then another -each time appearing under a new mask, so deceptive that nothing short of the sharpest scrutiny convinces us that it is in reality the same fungus in a new guise."

— N A. COBB, 1890-1894.

"Systematik wird und muss naturgemäss immer bleiben ein von menschlichen Geiste über die Natur ausgebreitetes Schema zur Ordnung der Mannigfaltigkeit der Erscheinungen. Das namlich gilt ceteris paribus auch fur die Rostbiotypen."

— A. SCHEIBE, 1930.

"If we had sufficient accurate knowledge of the causes of the rust we should probably succeed in finding more easily protective agents against this disease, but, meanwhile, it is very profitable to assemble all the observations made on this disease by the lovers of Agriculture."

— DUHAMEL, 1764.

"It is obvious, then, that the red spores may be blown for great distances and that wind currents probably account for the wide general distribution of spores of rust, allowing a rust epidemic of one section of the country to furnish spores for other distant regions in which the crop is less mature."

— H. L. BOLLEY, 1906.

"One says that soaking the seed in such and such a solution prevents rust. Another has, or claims to have, some other preventive. A third says rust is caused by an insect. A fourth states that it is of no avail to sow wheat when the moon is full, for if sown at that time the wheat is sure to rust. Unfortunately, none of these statements is true, and they show us that in the case of rust, we are dealing with something whose nature we do not understand. We are experimenting in the dark. Of course many discoveries have been stumbled upon by this process. There is no denying that. Even a blind hen finds a kernel now and then. We may therefore by groping in the dark some day find the panacea. Let us therefore grope in the dark! Let us soak and manure and poison and rope, - - let us in short diligently try everything that inspires the vaguest hope of lessening the rust evil."

— N. A. COBB, 1890-1894.

"Die Rostfrage ist also in Zukunft eine Züchtungsfrage."

— P. SORAUER, 1909.

FOREWORD

This moment of writing is one of worldwide thanksgiving. Under the hot, brilliant June sun a vast battalion of combines, binders, threshers, and harvest workers is cutting a swath of ripened wheat six hundred miles wide, from Texas into Oklahoma, that will continue through Kansas and Nebraska, through the spring wheat fields of the Dakotas, Manitoba, and Saskatchewan, for eighteen hundred miles northward. From those combines and threshers is beginning to pour, in ever increasing volume, the golden stream of grain that means life to millions of starving victims of war in Europe and Asia.

Nature has been lenient with the wheat farmers of America and the hungry hordes this year. Harvest expectations run high. Rust, the constant menace to production, thus far has shown indications of taking no more than its average annual tribute from the American wheat crop,—a few millions of bushels. The human lives which this will cost are tragic losses, but they are only a small part of those that might have perished had rust in 1946 devastated the Great Plains with one of its periodic outbursts. But in the fields far to the north the wheat is still green, succulent, still not out of danger.

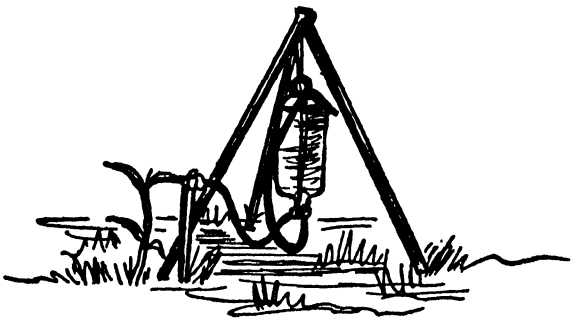
Whatever the loss in wheat,— and lives—, that rust may cause in 1946, it will be but a fraction of the loss which would have ensued had it not been for the rising acreage of rust-resistant wheat, the development of which has been one of the greatest contributions to mankind of modern agricultural science. But the rust problem is far from solved. New rust-resistant crop varieties must be bred to withstand the continual variation of the rust fungi. We still see as through a glass darkly the complex relationship of rust and its host plant and the delicate adjustments of this relationship to the fluctuating environment. This book can, at most, no more than recount the progress which has been made in understanding and preventing rust, and, by summarizing and interpreting past researches in this field, serve as a useful aid to those dedicating their investigations to future efforts at solution of the rust problem. If the book accomplishes these ends, its purpose will have been fulfilled.

Rust research in America has been an outstanding example of teamwork, many workers of the United States Department of Agriculture, the State agricultural experiment station, colleges and universities, and men of the grain industry, combining their efforts toward solution of a major problem. Each investigator is obligated to many others of the team, and the success thus far in rust research is due, in great measure, to this unselfish cooperation which underlies much of the work reported here.

For aid in preparation of the book I am indebted to Mr. D. A. PRESTON *who critically read the entire manuscript, to Mr.* PHILIP A. WILBER, *Miss* MARTHA LOU WILBER, *and Miss* VIRGINIA VANDEGRIFT *who prepared the illustrations, and to Dr.* FRANS VERDOORN *for encouragement and many helpful suggestions on editorial matters. To each of these I wish to express my appreciation.*

The references, except where indicated as abstracts, have all been consulted in the original. Most of the Russian works cited have been translated in full, and copies of these translations are available to fellow workers in the libraries of the United States Department of Agriculture, the Division of Plant Pathology and Botany of the University of Minnesota, the Dominion Rust Research Laboratory in Canada, and of the author.

K. STARR CHESTER



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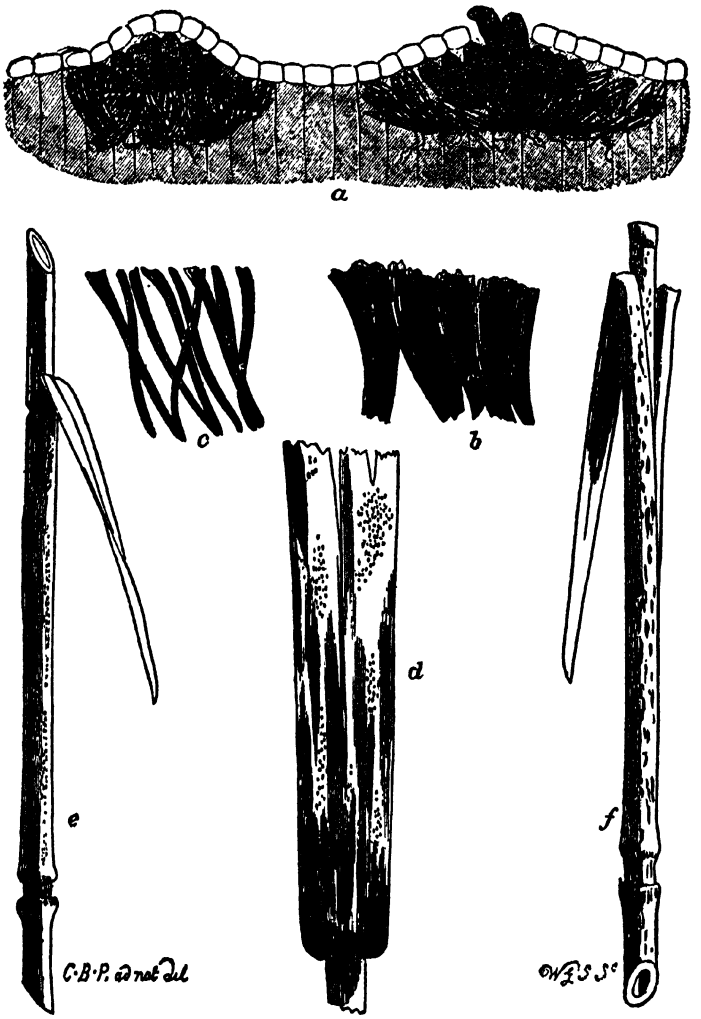

FIG. 53.—PUCCINIA RUBIGO VERA.

Two pustules, showing the subepidermal nature of the fungus, and bed of paraphyses; *b*, Group of paraphyses; *c*, Separate paraphyses; *d*, Part of a blade of Wheat with the Puccinia rubigo vera upon it; *e*, A piece of straw with the same; *f*, A piece of straw affected with Puccinia graminis, for comparison.

(*One of the earliest detailed drawings of wheat leaf rust, by* C. B. PLOWRIGHT, *1882*).

The vignette on page x and 256 shows an early field moist chamber for rust inoculation. It has been redrawn from figure 24 of N. A. COBB's classic "Contribution to an Economic Knowledge of Australian Rusts" (1890/94). The vignette on p. xiv has been based on COBB's figure 108 ("Threshing and winnowing small lots of experimental wheat"), on p. 236 on COBB's figure 25 ("Use of the microscope in the field"), on p. 260 on COBB's figure 14 ("Germinating uredospore of *Puccinia rubigo-vera*"), and on p. 269 on COBB's figure 107 ("Method of harvesting experimental wheat"). — The vignette on page 270 has been made after a drawing of leaf rust on the leaf sheath, in ERIKSSON's "Zur Charakteristik des Weizenbraunrostes" (1897).

Chapter I

INTRODUCTION; NAMES AND HISTORY OF THE DISEASE

Nature and purpose of the present work: —No other class of crops equals the cereals in contributing to man's welfare, and no type of plant disease causes economic loss comparable to that resulting from the rusts of cereals. This group of plant diseases has been the subject of monographic treatments in the past, but none within recent years with the exception of NAUMOV's book on cereal rusts in Russia in 1939.

Researches of the past quarter century have added much to our knowledge of the nature and prevention of the cereal rusts, which indicates the need for a comprehensive treatment of them. In the present work, it was decided to organize the subject matter about the leaf rust of wheat. This course was followed for a number of reasons: the unity resulting from basing the treatment on a single representative of the group of rusts; the fact that this rust exhibits all of the major features of the cereal rusts; that it has been studied sufficiently to permit extended exposition of each of these features; the surpassing economic importance of the rust from a world point of view, which has not been generally recognized; the lack of any monographic treatment of this important disease; and the fact that the writer can discuss this rust, in its various aspects, with more familiarity, it having been the subject of personal research during recent years.

Status of leaf rust: — More than four hundred million acres of the world's crop land are devoted to the production of its most important food crop,—wheat. On a major part of this acreage, in the vast wheat areas of Russia, Poland, Argentina, and the southern Great Plains of North America, and to a great extent in the wheat-producing acreages of India, China, and Australia, the most destructive disease of wheat is its orange or brown leaf rust.

Even more destructive in the northern United States and Canada is the black stem rust of wheat. That the economic significance of stem rust has been generally recognized by scientists and laymen while that of leaf rust has not, is due to several circumstances: the concentration of wheat rust research in the northern Great Plains of North America and comparative absence of it in other lands in which stem rust has a more minor rôle; the surpassing scientific interest in the species of rust fungus that served as the subject of the classic studies of DE BARY on heteroecism, STAKMAN on physiologic specialization, and CRAIGIE on sex in the rusts; the dramatic character of sudden, ruinous visitations of stem rust in comparison with the less spectacular, more gradual wastage of the wheat plant as its vitality is progressively drained away by leaf rust; the lateness of stem rust in comparison with leaf rust, such that stem rust is often present at the time of harvest and hence accused of causing the disappointing yields

revealed by thresher or combine, although it may have been a late comer and minor contributor to the harm; the confusion of the three wheat rusts, coupled with the greater publicity on stem rust, such that farmers and often crop scientists have mistakenly assumed that destructive rust must necessarily be stem rust; and finally the publicity resulting from the dramatic, clear-cut relationship between stem rust and the barberry, recognized for centuries in legislation and governmental expenditures, as compared with the less well-known developmental cycle of leaf rust.

The overwhelming psychological influence of this combination of considerations was such that, until the last two decades, the agricultural significance of wheat leaf rust was entirely obscure; little or no effort was made to understand the disease and develop means for its prevention. It was not until MAINS, JOHNSTON, CALDWELL, and numerous others substituted experiments for opinions and proved that the destructiveness of leaf rust is far greater than had been suspected, not until the Russian pathologists and agronomists, unaffected by the American emphasis on stem rust, began their exhaustive efforts to solve their major wheat disease problem, leaf rust, and not until the disastrous epiphytotic of 1938 destroyed more than one hundred million bushels of the United States wheat crop, that leaf rust emerged from its obscurity and was revealed in its true proportions among the major destroyers of the world's food grain.

Names of the disease: — In early references, from Bible times to the latter part of the 19th century, the various species of rust attacking wheat were not distinguished, but were combined under collective terms. This applies to the Hebrew term "yeraqon" (yellowing) of the Bible, which has been rendered "mildew" in English and "Rost" in German and Swedish. By some early British writers the terms "mildew" and "rust" have been used interchangeably (*e.g.* PLOWRIGHT in 1882 and BARCLAY in 1892). Others such as LITTLE in 1883, restricted "mildew" to stem rust while leaf rust was referred to as "spring rust", or merely "rust". It is fortunate that the term "mildew", as applying to rust diseases, is now archaic, because of possible confusion with the true powdery and downy mildews of cereals. In India, CUNNINGHAM and PRAIN (1896) often referred to wheat rust as "blight".

Except for purely native names, the disease caused by *Puccinia triticina* is known throughout the world by equivalents of the terms: brown, orange, or red (leaf) rust, spring, winter, or early rust, or spotting rust of wheat, or some combination of these terms. In English-speaking lands, "leaf rust" or "orange leaf rust", first used by CARLETON in 1899, are preferred, although some present day British workers apply the term "brown rust", while among farmers, "red rust" is common. PAMMEL (1892*a*) appears to have proposed the name "covered wheat rust" (referring to the subcuticular position of the teliospores), but this name has not been generally adopted. "Brown rust" or its equivalent in other languages, is preferred in Continental Europe.

In Australia the preferred term is "spring rust", in contrast to stem or "summer" rust. "Orange leaf rust" and "spotting rust" are sometimes used. In India the local names vary, but are usually some variant of "rolla"

("rori", "roli", "rora", "rola", etc.), "gerhivi" ("perhivi", "gerhiva", etc.), or "khungi" ("kungi"). While these are often used loosely to refer to rust in general, BARCLAY (1892) was of the opinion that the feminine form ("roli", etc.) was used by natives to refer to stem rust, and the masculine form ("rola", etc.) to leaf rust. The Egyptian term for rusts in general is "hamra".

"Rust" and "mildew" in ancient times: — The leaf rust of wheat was recognized as a species distinct from the other cereal rusts in 1815; prior to this, and even for many years after, the three wheat rusts were commonly looked upon as a single disease, and accordingly the early history of wheat leaf rust is so blended with that of the other cereal rusts that it is difficult or impossible to attribute responsibility for destructiveness to one or another of these species.

LEVINE (1919) gives the following account of rust as mentioned in the Bible:

"It is interesting to know that while still in the desert of Sinai, some thirty-five centuries ago, Moses had warned the people of Israel that if they failed to observe the commandments of Jehovah, the Lord would punish them by destroying their field crops 'with smut and with rust' (Deut. 28: 22). About 1000 B.C. King Solomon prayed to God for clemency, 'If there be in the land famine, if there be pestilence, smut, rust . . . .' (I Kings 8: 37; II Chron. 6: 28). Amos, the peasant-prophet and contemporary of Isaiah, about 750 B.C. reproved the Samaritans for oppressing the poor and crushing the needy. For this God has smitten them 'with smut and with rust' (Amos 4: 9). About 500 B.C. the prophet Haggai reminded the Judeans of the desolation of the Temple, and told them that their neglect had brought failure of crops and scarcity. 'I smote you with smut and with rust and with hail in the labors of your hands, yet ye turned not to me' (Haggai 2: 17), admonished the prophet. As a result of the reprimand and in order to allay the wrath of the Lord, the people lent a hand to complete the construction of the Temple."

ERIKSSON and HENNING in "Die Getreideroste" (1896) give a fairly extensive account of rust in ancient times, which is the basis of the following digest:

ARISTOTLE (384-322 B.C.) noted that rust was more severe in some years than in others; he attributed it to warmth and moisture.

THEOPHRASTUS ERESIUS (371-286 B.C.), a student of ARISTOTLE's, left notes on the particular susceptibility of cereals to rust, especially if they were in valleys or sheltered places. Rust was considered a process brought about by sunshine following dew, especially when favored by the warmth of the moon.

STRABON (66 B.C.-24 A.D.) told of farmers in the Greek islands of Rhodes and Cyprus praying to Apollo to diminish the rust.

VARRO (26 B.C.) included among the protecting gods of farmers, Robigus, the god of rust, and mentioned feasts in his honor, named Robigalia.

COLUMELLA (50 B.C.) proposed gathering piles of chaff in the winter

and burning them on the approach of frost, to avoid both frost and rust injury.

OVID (43 B.C.-17 A.D.) is a source of folklore regarding the origin of rust. According to the account a poor farm couple in the Latin state of Carseoli had a wilful son who caught a fox plundering his chicken yard. The boy wrapped the fox with straw and hay, set this on fire, and turned the fox loose, and as punishment for this sin, the gods visited mankind with rust.

NUMA POMPILIUS (715-672 B.C.) related the origin of the Robigalia, about 700 B.C., to propitiate the rust gods by prayer and sacrifice. According to PLINY's account of this, the feasts took place between the grain festival (Cerealia, Apr. 12-19) and the blossom festival (Floralia, Apr. 28), at the time of the dogstar, Sirius, at which time the appearance of rust was particularly feared. OVID once, early in the morning, met a white-clothed festival throng on the road from Nomentum to Rome. They proceeded to a grove frequented by the rust gods, Robigus and Robigo, on the hill of gardens, near the fifth milestone of the Claudian way. After the procession, preceded by a torch, reached its destination, the priest offered a rather long prayer in which he praised the great might of the gods and petitioned them to deflect the rust from the growing fields. (Prayer in OVID, "Fastorum," Liber IV, v. 911-932). Thereupon sacrifices were made: first were bestown sweet-smelling incense and wine, then they offered the gods the entrails of the animals which had been brought along, usually those of young red dogs, but sometimes of sheep or young calves. Finally there were certain games.

Also at the Cerealia, especially on the last and most important day, April 19, steps were taken to avert rust, including a fox hunt in the Circus in which burning torches were tied to the foxes' tails, symbolic of the rust which would occur if, at the time of the dogstar, hot days followed cold, dewy nights.

Such feasts continued for many centuries, and were part of the state religion (CONSTANTINE). By 323 A.D. they had evidently become blended with the feast of Mark, the Evangelist, on April 25.

PLINY II (23-79 A.D.) emphasized the greater destructiveness of rust in valleys and dewy fields and on certain varieties of cereals. He insisted that the sun was not responsible, and suggested rust prevention by sticking laurel branches in the earth, over which the rust would pass.

During the Middle Ages there were few reports of rust, but there were rare notes that it was present.

Rust from the Renaissance to the period of de Bary: — From the year 1600 onward there were numerous references to rust, although in these earlier years little was known of its nature. SHAKESPEARE in "King Lear" (III, i) notes that among the other acts of deviltry perpetrated by the "foul fiend Flibbertigibbet" he "mildews the white wheat". (We recall that "mildew" is a long-established British term for rust).

During this period there were occasional years of great rust destructiveness, as reported, for example, by HARTLIB (1655) and by ÖRSTED who attributed the crop failures of 1660-62 and 1696-99 in Denmark in part to

rust. THEAL ("History of South Africa," *1*:299) indicates that rust was unknown in South Africa until 1727 when it was so destructive that crops were almost a complete failure, but G. W. THOMPSON in his "Travels and Adventures in South Africa" (*in* POLE EVANS, 1911-12) relates that the wheat was severely attacked by rust in South Africa in 1708-1710. JETHRO TULL called 1725 "a rust year such as man has never seen and hopes never to see again". TULL, in his "Horsehoeing Husbandry" (1733), conceived of rust as the attacks of small insects, "brought, some think, by the East wind, which feed upon the wheat, leaving their excreta as black spots upon the straw, as shown by the microscope" (MCALPINE, 1906). According to CLAS BJERKANDER, a student of LINNAEUS, 1794 was a severe rust year in Sweden; the disease was probably stripe rust. In England, 1804 was a year of severe rust and agricultural circulars on the disease were issued.

Meanwhile the nature of rust and the relationship of stem rust to its alternate host, the barberry, were gradually becoming defined. FELICE FONTANA in 1767 published the first figures of cereal rust following a severe outbreak in Italy in 1766. He was apparently the first to recognize rust as a fungus, parasitic on the cereal plant.

But many years before this, the intuition of farmers had led them to believe that there was a necessary relationship between the barberry and cereal rust, as evidenced by the law in Rouen, France, of 1660 requiring the destruction of barberries near grain fields. Some of the high lights of the subsequent activity on stem rust and barberry were: the Connecticut barberry law of 1726 and subsequent barberry laws in other states and countries; destruction of barberries with hot water in England (HORNEMAN, 1820); the controversy among European scientists as to the rôle of barberry in wheat rust; complete proof of the heteroecism and demonstration of the successive spore stages of *Puccinia graminis* by DE BARY (1864-1865) after he, at the age of 22, had declared in an otherwise useful paper (1853) that barberry had no relation to cereal rusts and that the *Uredo* and the *Puccinia* on cereals were two different fungi, and after an accumulation of evidence by other workers (MARSHALL, 1781-84; KNIGHT, 1806; SCHÜLER and TOMMESEN, 1813-1817; BÖNNINGHAUSEN, 1817-1818) of the relation of barberry to cereal stem rust.

Wheat leaf rust had been recognized as a "botanical curiosity" in England in 1718. In 1815, DE CANDOLLE described it as *Uredo rubigo-vera*, a species distinct from PERSOON's *Puccinia graminis*. Strangely, LINNAEUS, as late as the third edition of his "Species Plantarum" in 1864, listed only a single rust (*Lycoperdon epiphyllum* = *Puccinia poarum*) as a living plant, avoiding all reference to the cereal rusts.

The late 18th and early 19th centuries were also marked by occasional great destructiveness of the wheat rusts. "Mildew" was very severe in England in the 1820's and again in 1881 and 1882. The year 1820 was also a notorious rust year in South Africa. There was such immense loss from what was evidently leaf rust in India in 1827 and 1839 that in some districts the harvest did not equal the seed that had been planted (BARCLAY, 1892). Rust was first recognized in Australia and Chile at the end of the 17th century.

From 1880 to 1900: — In the last part of the 19th century the various rust species became generally recognized as distinct. Destructive outbreaks of rust continued to afflict wheat culture throughout the world, and in some cases the increasing economic importance of the cereal rusts led to organized research in an endeavor to prevent the losses caused by them.

ERIKSSON and HENNING (1896) gave a table of the "rust years" throughout the world from 1660-62 to 1892. In Sweden, oat rust was so destructive in 1889 that the royal government granted 10,000 kronen for research on rust prevention. ERIKSSON was appointed to this task, and, with the assistance of HENNING, began his extensive researches which culminated in the publication of "Die Getreideroste" in 1896, and laid the foundations for work on rust specialization which was to follow.

In Australia the destructiveness of "rust-in-wheat" led to the Intercolonial Rust-in-Wheat Conferences in 1890, 1891, 1892, and 1896 and to the fundamental mycological and pathological studies on cereal rusts by COBB, MCALPINE, and PRAIN, and application of Mendelian principles in the production of rust-resistant wheats by FARRER, as BIFFEN was doing in England.

In Germany organized work on cereal rusts was beginning to take form and KLEBAHN was busy with his long series of infection experiments working out the developmental cycles of rusts. PLOWRIGHT in England and MCALPINE in Australia published their monographs of rusts in 1889 and 1906 respectively.

America also was not behindhand in its activity on the cereal rusts. In Kansas, KELLERMAN (1891), HITCHCOCK and CARLETON (1893), and GALLOWAY (1893) undertook extensive experiments on the control of these diseases by various agronomic practices including the use of fungicides. Similar work was in progress in Iowa, (PAMMEL, 1892b), and in Indiana (BOLLEY, 1891).

This might be designated as a formative period; on a broad front endeavors were proceeding to elucidate the rust problem from all conceivable points of view. Could rust be prevented by spraying and dusting; are seed treatments or seed selection of value; how is rust influenced by planting date and rate, weather, location, soil and fertilization, and crop sequence; do varieties differ in rust susceptibility; is early harvesting of a rusted crop a means of reducing losses; does burning rusted crop residue lessen rust; is rust carried in the seed; will the use of seed from heavily rusted crops tend to reduce rust through the operation of natural selection? These and many kindred questions were explored and this exploration served the dual purpose of providing some measure of aid in rust prevention and of defining the problems requiring more intensive study.

From 1900 to 1930: — From its small and obscure beginnings, with ever accelerating pace, the study of cereal rusts reached new heights in the first three decades of the present century, and wheat leaf rust emerged as a pathological problem in its own right. The contributions of the period were numerous and of great importance. The first decade gave little foreshadowing of what was to follow in 1910 to 1930. In Germany, SORAUER in 1909 advanced his proposal for an "International Statistik" of cereal

rusts, a clearing house for all detailed information in this field, from which, by statistical analysis, were to be derived basic principles. Theoretically the proposal had its attractive features; however, it did not gain a foothold with rust workers of other countries. A more significant event of the decade was the three-year sojourn of GASSNER in Uruguay (1907-1910) followed by the extensive studies of his school from 1915 to 1938 with their many important contributions which will be considered in full detail in their appropriate contexts. YACHEVSKI in 1909 published his "Rusts of Grains in Russia", forerunner of the subsequent extensive Russian researches. This was followed by VAVILOV's classic studies on varietal resistance to rusts and the nature of rust resistance in cereals, laying the foundation for Russia's program of breeding for disease resistance.

During the period American work on cereal rusts dominated the scene. STAKMAN'S researches on host specialization in *Puccinia graminis* in 1914 paved the way for worldwide activity on specialization of this and other rusts. The ability of *Thalictrum* species to act as alternate hosts of *P. triticina* was discovered by JACKSON and MAINS in 1921. CRAIGIE in Canada (1927) determined the function of pycnia of rusts, and this fundamental discovery of sex in rusts opened the way for an understanding of variation in rust fungi with its many important theoretical and practical aspects. ALLEN, through her intensive studies of the cytology of rust infested plants, shed valuable light on the relationships between the rust and its host plant, and on the nature of rust-resistance. The epiphytology of cereal rusts, a field in which KLEBAHN had pioneered, became a subject of extensive experimentation by STAKMAN and his co-workers, and gradually there was shaped an understanding of the aerial migration of rusts; TEHON in 1924-28 also made contributions in this increasingly important field of rust epiphytology, and on the methods of appraising rust intensity and rust damage.

In addition to these studies of the fundamentals of the rust problem, great strides were made in America, during this period, toward the control of cereal rusts. Efforts to develop rust resistance in wheat varieties were initiated in Kansas in 1911, in Indiana in 1916, and since in numerous other States. HAYES, MAINS, and others were providing the basis for intelligent breeding for rust resistance through their studies of the manner of inheritance of resistance. The many tangible and valuable results of this research will be dealt with subsequently. MCFADDEN in South Dakota produced the wheat, Hope, which has contributed blood to many present-day rust-resistant varieties. Meanwhile GREANEY in Canada began in 1925 his series of experiments on determination of rust losses and the control of cereal rusts by sulphur dusting which have continued until the present.

Abroad there was also considerable activity in this field. Intensive breeding for rust resistance was begun at Halle in Germany about 1920 and has continued since. RUSAKOV'S school of workers in Russia have made many contributions, particularly to the epiphytology and means of appraising damage from wheat leaf rust, beginning about 1924; NAUMOV in Russia also has been an important contributor to the latter field. At the International Phytopathological Congress in Holland in 1923, proposals were made for internationally coordinated rust work; this was followed by many survey

reports, especially by French workers, but the interest in this direction later flagged.

Important advances in the pure mycology of rusts were being made during this period by ARTHUR and JACKSON in the United States, DIETEL in Germany, and E. FISCHER in Switzerland.

From 1930 to the present: — The past 15 years have been marked by a rising appreciation of the economic importance of wheat leaf rust. KIGHTLINGER and WHETZEL initiated this with their studies of the effect of leaf rust on wheat yields (1926), and this was followed in rapid succession by similar studies of MAINS (1927*a, b,* 1930), C. O. JOHNSTON (1931), NEILL (1931), CALDWELL *et al.* (1932), JOHNSTON and MILLER (1933-1934), WALDRON (1936), and many Russian workers in the 1930's. All came to the conclusion that leaf rust is a disease of serious economic importance, far more destructive than had formerly been believed. This fact was driven home, even to those who still were inclined to regard wheat leaf rust as a minor ailment, by the epiphytotic of 1938, in which an estimated hundred million bushels of the United States wheat crop were destroyed by this disease.

Throughout the world, there was a crescendo of work on wheat leaf rust. In the United States, JOHNSTON in Kansas, CALDWELL in Indiana, and CHESTER in Oklahoma directed attention particularly to physiologic specialization of *Puccinia triticina,* breeding wheat for leaf rust resistance, and the epiphytology of the disease. Uniform Cereal Rust Nurseries were annually grown at many points in the United States with the U. S. Department of Agriculture and the various states cooperating, and these served to control efforts at breeding for rust resistance and to aid studies on the specialization of the leaf rust fungus. Many timely notes in the Plant Disease Reporter, the Cereal Courier, and cereal trade journals provided a day-to-day picture of the annual activities of leaf rust. Commercial interests furthered education and research on the cereal rusts, as witnessed by the annual survey of air migration of rust spores conducted by the Cargill Laboratories in Minnesota, with many collaborators throughout the Great Plains, and by the surveying and educational work of the Conference for the Prevention of Grain Rust. New wheat varieties carrying some degree of leaf rust resistance were developed and introduced.

In Canada, MARGARET NEWTON and her associates developed a program of important researches on specialization of the cereal rusts, the nature of rust resistance, the relationship of environment to rust activity, and breeding for rust resistance. Wheat leaf rust was given due consideration in this program.

The leading foreign contributors to our knowledge of leaf rust during this period were GASSNER and his associates, FRANKE, GOEZE, HASSEBRAUK, KIRCHHOFF, PIESCHEL, and STRAIB, as well as SCHEIBE and SCHILCHER in Germany; RUSAKOV, NAUMOV, BRIZGALOVA, YARKINA, SHITIKOVA-RUSAKOVA, BUCHHEIM and LISSITZINA, RASHEVSKAYA and BARMENKOV and numerous others in Russia; ROBERTS in England; WELLENSIEK in Holland; STEINER in Austria; DODOV in Bulgaria; SĂVULESCU and RĂDULESCU in Rumania; MONTEMARTINI, PETRI, and SIBILIA in Italy; WATERHOUSE

in Australia; MEHTA in India; VERWOERD in South Africa; ASUYAMA in Japan; and RUDORF and VALLEGA in Argentina. The contributions of each of these, in their studies of the rust from various points of view, will be discussed subsequently.

Among the outstanding developments of the period, from our point of view, should be mentioned (*a*) the discovery of *Isopyrum* as a functioning alternate host of *P. triticina* in Siberia (BRIZGALOVA, 1935, 1937*a*), (*b*) extensive studies on the epiphytology and annual cycle of wheat leaf rust in Russia (SHITIKOVA-RUSAKOVA, BRIZGALOVA, STEPANOV, and other workers), in India (MEHTA), and in the United States, and (*c*) the breeding of leaf-rust resistant wheat varieties. In the United States this last activity included workers in the U. S. Department of Agriculture and in the State experiment stations of Kansas, Indiana, Oklahoma, North Dakota, Nebraska, Minnesota, Texas, Georgia, and North Carolina. Abroad, special mention should be made of the Russian work, under the general direction of the All-Russian Institute of Plant Protection at Leningrad, with many testing stations throughout the Union, with its highly systematized program of rust research, breeding, and testing of new strains, the latter being derived by selection and hybridization from the great "world collection" of wheats, assembled in Russia about 1930. In Chapter XV are given details of the programs of breeding for resistance to the rust, in these and other countries.

Chapter II

ORIGIN, DISTRIBUTION, AND ECONOMIC IMPORTANCE

Origin of leaf rust; occupation of other areas of the world:— *Puccinia triticina* is highly specialized to wheat which implies a long-standing association of parasite and host, and as wheat has comparatively recently spread out from its native home and occupied the world, the origin of leaf rust must be sought in the native home of wheat itself.

Authorities agree that wheat is of Eurasian origin. BAILEY'S "Cyclopedia of Horticulture" and "Hortus" indicate that it originated in the region of the Mediterranean and western Asia. Similarly KÖRNICKE and WERNER (1885) place its probable origin in the Mediterranean-West Asia area bounded by the Caspian Sea, the Caucasus, the Mediterranean and Aegean Seas, and the Persian Gulf. From this region, according to KÖRNICKE and WERNER, it spread northward, coming to Germany via Rome, and to Norway in the 12th century. In 1528 a slave found 3 grains of wheat in a shipment of rice from Spain to "New Spain", and these represent the first introduction of wheat into the New World. Wheat invaded the territory that is now the United States in 1602 and the Mississippi Valley in 1718.

Since wheat has been recently introduced into the New World, we must regard its leaf rust as not native to the Americas. ARTHUR, in his list of "Rusts introduced into North America" (1929), includes "*P. rubigo-vera tritici* (Eurasia)."

Although *P. triticina* now largely dispenses with use of an intermediate host, its exhibition, under some conditions, of functioning heteroecism indicates that earlier in its evolution the heteroecism was ingrained in the developmental cycle of the rust. With this the case, the native homes of its alternate hosts should shed light on the native home of the rust. The native habitats of susceptible species of these hosts, *Thalictrum* and *Isopyrum,* indicate that this is some part of Asia. JACKSON and MAINS (1921*b*) found that American species of *Thalictrum* were resistant to *P. triticina,* while the two most susceptible species, *T. flavum* and *T. delavayi,* are native, in the first case to Europe, Western Asia, and Asia Minor, and in the second to Western China (probably the mountains of Tibet and Chinese Turkestan). If the origin of leaf rust is the area at which the distributions of these two species overlap, this would indicate southwestern Asia as the original home of *P. triticina* and this in turn coincides with the native home of wheat.

The evidence from *Isopyrum fumarioides,* the only naturally infected alternate host of leaf rust, indicates central Asia, habitat of *I. fumarioides,* rather than southwestern Asia, as the point of origin of leaf rust. As with *Thalictrum,* American relatives of *I. fumarioides* are resistant to *P. triticina.*

SCHEIBE (1930*b*), on rather questionable evidence, concluded that *P. triticina* is native to eastern continental Europe. He based this on leaf

rust race determinations which led him to consider this area as one in which the races were more aggressive, however, subsequent analyses of the leaf rust race constitution of Europe by others failed to confirm SCHEIBE's view of an eastern group of races more aggressive than those in western Europe. Moreover his theory does not agree with the evidence derived from the original habitats of either aecial or telial hosts of this fungus.

TABLE 1: *World wheat acreages and importance attributed to leaf rust:* —

REGION	WHEAT ACREAGE[1]	IMPORTANCE OF LEAF RUST	AUTHORITY
NORTH AMERICA			
United States.....	54.2	(*See separate table*)	
Canada	25.7	Throughout; often very important but much less so than stem rust	GREANEY, 1936, NEWTON, 1938, and many others
SOUTH AMERICA			
Argentina	17.7	Much the commonest of the 3 wheat rusts; wheat attacked with extreme violence	HAUMAN-MERCK, 1915
		The most damaging wheat rust	HAUMAN & PARODI, 1921
		Usually the most damaging rust	Min. Agr. Nac. Buenos Aires, 1925
		Not so destructive as stripe rust, but very serious	RUDORF *et al.*, 1933
Chile	1.8	Important; grave damage	WUNDER, 1929
		Leaf and stem rusts often very damaging	VALLEGA, 1942*a*
Uruguay	1.1	The most damaging rust	GASSNER *in* HAUMAN & PARODI, 1921
Brazil	.4	Very important; a limiting factor in wheat production	GASSNER, 1915*a*
Bolivia	.1	Present	GASSNER, 1931
Paraguay	..	Present	GASSNER, 1931
Guatemala	..	Present	GASSNER, 1931
EUROPE			
General	..	The most dangerous wheat rust	SCHEIBE, 1930*b*
United Kingdom..	1.5	Considered unimportant in comparison with stripe rust, although common and crops may be damaged with this the only species present	PLOWRIGHT, 1882; LITTLE, 1883; BIFFEN & ENGLEDOW, 1926; ROBERTS, 1936; KALE, 1938; etc.
Poland	4.3	Most common and destructive rust; very dangerous	RALSKI, 1936, 1939
		Most important rust	KALE, 1938.
Sweden	.7	Relatively unimportant; not important because it attacks only leaves	ERIKSSON, 1894; ERIKS. & HENNING, 1896
		Less important than stripe rust	CARLETON, 1899

[1] In millions of acres, 1930-1934 (U. S. Dept. of Agr., "Crop Statistics"); where acreages are very small they are omitted.

TABLE 1. (Continued)

REGION	WHEAT ACREAGE[1]	IMPORTANCE OF LEAF RUST	AUTHORITY
EUROPE (cont.)			
Denmark	.3	Present	
Norway	.03	Present	
Finland	.07	The most important rust	KALE, 1938
Holland	.3	Less important than stripe rust, but sometimes serious	KALE, 1938
France	13.3	Usually of only moderate importance, but sometimes seriously affects yields	DE CANDOLLE, 1815; CRÉPIN, 1923; DUCOMET & FOËX, 1925; MATTRAS, 1932
Germany	5.3	Less important than stripe rust, but sometimes serious	VON KIRCHNER, 1916; KALE, 1938
Rumania	7.7	Of minor importance,—less than stem rust	KALE, 1938
		All 3 wheat rusts are more important than generally recognized	SAVULESCU, 1938*b*
Balkans (gen'l) ..	..	Quite important	SCHEIBE, 1930*b*
Yugoslavia	5.1	Very injurious almost every year	SCHEIBE, 1930*b*
		Less important than stem rust	KALE, 1938
Czechoslovakia ..	2.1	The most serious wheat rust	ŠINDELÁŘ, 1922
Bulgaria	3.0	Great injury every year	DASKALOV, 1930; SAVULESCU, 1933
Austria	.5	Less important than stripe rust but more so than stem rust	HECKE, 1918
		Causes little damage	DREGER, 1923
Spain	11.2	Very common	GONZALES-FRAGOSO, 1926
Portugal	1.3	The least injurious rust	BENSAUDE, 1929
Italy	12.2	Common; often confused with stripe rust	PETRI, 1927
		Less important than stripe rust	MENCACCI, 1929; KALE, 1938
		Aways serious	SĂVULESCU, 1933
Greece	1.6	Of minor importance compared with stripe rust	KALE, 1938
RUSSIA	85.8	*Puccinia triticina* is the most important rust throughout Russia except sometimes in a few localities in which *P. graminis* or *P. glumarum* may be more damaging	NAUMOV, 1939; LITVINOV, 1912; RUSAKOV, 1929*a*; SCHEIBE, 1930*b*
European Russia..	..	Very destructive in No. Caucasus and regions of Eysk, Voluiskie, Kursk, S. W. Russia, Saratov	LUKYANENKO, 1934; SHEKHURDIN, 1936; FRIEDRICHSON, 1937

From its home in Asia, leaf rust has evidently followed the migrations of wheat in comparatively recent times. MCALPINE (1906) regards it as having been introduced into Australia, probably with seed, about 1825, and NAUMOV (1939) considers that it entered America within recent times.

TABLE 1. (Continued)

REGION	WHEAT ACREAGE[1]	IMPORTANCE OF LEAF RUST	AUTHORITY
Asiatic Russia....	..	Very destructive	ESTIFEEV, 1925
		The only rust of importance in E. Siberia	BRIZGALOVA, 1935
		Destroys from 10 to 20% of the crop annually, and in years in which it develops strongly and early it may wipe out the crop. (Wheat stem rust is omitted from the list of important cereal rusts of this area)	RUSAKOV and SHITIKOVA, 1929
		The most damaging rust of West Siberia	MURASHKINSKI *et al.*, 1938
ASIA			
Turkey	7.0	Abundant every year	SCHEIBE, 1930*b*
		Relatively harmless compared with stem and stripe rust	KALE, 1938
Iraq	1.5	Among the most important diseases in 1920	Adm. Rep. Dept. Agr. Mesopot. 1921
Coast, Asia Minor	..	Present	SCHEIBE, 1930*b*
India	33.3	The most damaging rust in Bengal; second to stripe or stem rusts in Central Provinces	BUTLER, E. J., 1918
		Principal damage is from leaf and stripe rusts; stem rust is usually too late to be injurious	PAL, 1936
		Crops frequently devastated by leaf rust	WATERHOUSE, 1939
China	49.1	Rusts are serious on wheat with leaf and stripe rusts the worst	WANG, 1942
Japan	1.3	By far the commonest wheat rust	BARCLAY, 1890
		Annual loss 20%	BARCLAY, 1892
		Much worse than the other rusts	TOCHINAI and KIHARA, 1927
		A great menace	ITO, 1934
AFRICA			
Ethiopia	.02	Everywhere, but not destructive	CASTELLANI, 1938
Belgian Congo....	.01	Present	MARCHAL and STEYAERT, 1929
Kenya Colony	.04	Present	BURTON, 1931*a*

Occurrence and relative importance of wheat leaf rust throughout the world: — Wheat leaf rust occurs wherever wheat is grown; it is the commonest, most widely distributed of all cereal rusts. It appears to be equally well adapted in the coldest climates in which wheat can be grown, as in Siberia, and Canada on the one hand, and in subtropical regions

TABLE 1. (Continued)

REGION	WHEAT ACREAGE[1]	IMPORTANCE OF LEAF RUST	AUTHORITY
East Africa	..	Causes much damage	Rept. Dept. Agr., Uganda, 1921
		Late; less serious than in other areas	DOWSON, 1921
South Africa.....	1.5	Less important than stem rust	POLE EVANS, 1911/12
Madagascar	..	Some years "rust" is very serious	BOURIQUET, 1934
AUSTRALIA			
Australia and New Zealand...	15.5	Present in all Australian provinces, Tasmania, and New Zealand; relatively harmless; less important than stem rust	McALPINE, 1894, 1906; FARRER, 1898; DARNELL-SMITH & MacKINNON, 1915; WATERHOUSE, 1923; MacINDOE, 1933
		The most damaging rust	DOWSON, 1921
		Worse than usually recognized; often confused with stem rust, which is blamed for damage due to leaf rust	WATERHOUSE, 1929/30
		Losses heavier than generally supposed.	WATERHOUSE, 1939

(India, Belgian Congo, Ethiopia) on the other. GASSNER found it 100 km. north of Patagonia, practically at the southernmost limit of wheat culture, while BURTON reported it as occurring up to 11,000 ft. altitude in Kenya Colony. TABLES 1, 2, and 3 indicate the distribution of leaf rust and the relative importance attributed to it in the various wheat-producing parts of the world.

The tables are based on the most authoritative estimates of experienced phytopathologists available. If they fail to any important extent in bringing out the true relative importance of the wheat rusts, such deviation is on the side of minimizing the importance of leaf rust rather than exaggerating it, due to lack of experimental evidence, until recently, of the destructiveness of leaf rust, to failure to discriminate between the three wheat rusts, and to such disproportionate emphasis on stem rust in the literature that less experienced workers tacitly assumed that if there is rust damage to wheat, it must necessarily be stem rust damage. The case of Australia in particular exemplifies the reversal of point of view, from almost complete disregard of the disease in the 1890's to recognition of leaf rust by recent, more critical, and better informed workers, as a disease of major importance in Australia.

The development of understanding of the proportionate rôle of leaf rust in the United States exemplifies the same point. PAMMEL in 1892 wrote: "The destructive wheat pest in the United States appears to be *Puccinia rubigo-vera*", and cited ARTHUR as being of the same opinion. However, CARLETON, who strongly influenced the thought with regard to cereal rusts at that time took the opposite point of view. He not only held that leaf rust caused very little damage in the United States, but even believed that at

TABLE 2: *United States wheat acreage and relative importance of leaf and stem rusts: —*

STATES IN WHICH STATED DISEASE WAS MOST DESTRUCTIVE, 1930–1939, WITH ACREAGES[1]

STEM RUST MOST DESTRUCTIVE	ACREAGE	LEAF RUST MOST DESTRUCTIVE	ACREAGE
Michigan	.83	Pennsylvania	.99
Wisconsin	.11	Ohio	2.0
Minnesota	1.7	Indiana	1.7
Missouri	1.9	Illinois	1.1
No. Dakota	7.8	Iowa	.43
So. Dakota	2.5	S. E. States: Del., Md., Va., W. Va., N. C., S. C., Ga., Ky., Tenn., Ala	2.75
Nebraska	3.3	Arkansas	.06
Montana	3.3	Oklahoma	4.0
Idaho	1.1	Texas	3.2
Wyoming	.25	Kansas	11.1
Washington	2.2	Oregon	.97
Total acreage	24.99	Total acreage	28.30

[1] Based on crop loss estimates from U. S. Dept. Agr., "Plant Disease Reporter" for 1930-39; acreages from 1929-1938, in millions, from U. S. Dept. Agr., "Crop Statistics."

times it was *beneficial,* preventing foliage development of the wheat plant in place of grain (1899). Nor was his influence limited to the United States. FARRER in Australia wrote in 1898: "In the past I have been wasting much time attending to the spotting rust [leaf rust] . . . . and in making varieties to resist it, for I am now convinced that, at Lambrigg at any rate, it does little or no harm, and for that reason I shall cease for the future in marking [selections] for that rust at all." But FARRER indicates that his opinion was much influenced by correspondence with CARLETON, which he quotes, in part, as follows (letter, CARLETON to FARRER, 1895): "I am now fully convinced that *P. rubigo-vera* never does serious damage to wheat, — at least in this country. . . . I have never yet heard of a single instance of severe rust damage in which *P. rubigo-vera* could be traced as the cause."

For the next 20 years or more this disregard of leaf rust persisted. Even as late as 1932 the question was raised in Kansas, "But do they [leaf rust and septoriose of wheat] occur with sufficient frequency and virulence to justify expensive attempts to produce resistant varieties at the sacrifice of more important work?" Yet it is now evident that leaf rust is the most destructive wheat disease in Kansas. The Plant Disease Reporter estimates of wheat losses for Kansas from 1918 to 1939, although admittedly grossly underestimated for leaf rust, show a total of percentage losses from leaf rust that is substantially higher than those for any other wheat disease in that State.

With regard to these estimates, the editor of the Plant Disease Reporter (Suppl. 87: 1. 1935) states: "In general, it is probable the estimates are too low. This has been proved to be decidedly so in the case of wheat leaf rust . . . . They [CALDWELL *et al.*] conclude that leaf rust is a very important factor affecting the yield of winter wheats in the United States." TABLE 2 is based on the evaluations of contributors to the Plant Disease

TABLE 3: *Summary of world acreages on which each of the three wheat rusts is regarded by authorities as most destructive: —*

MOST DESTRUCTIVE RUST. BASED ON THE TWO PRECEDING TABLES. FRACTION AFTER NAME OF COUNTRY INDICATES THE PROPORTION OF DIVISION OF IMPORTANCE OF TWO OR THREE RUSTS ACCORDING TO PRECEDING TABLES. ACREAGES IN MILLIONS.

LEAF RUST	ACREAGE	STEM RUST	ACREAGE	STRIPE RUST	ACREAGE	INDEFINITE	ACREAGE
Argentina	17.7	Canada	25.7	United Kingdom	1.5	France	13.3
Uruguay	1.1	U. S. A. (½).	27.1	Sweden	.7	Portugal	1.3
Brazil	.4	Yugoslavia ...	5.1	China (½) ...	24.5	Bolivia	.1
Poland	4.3	Rumania	7.7	Holland	.3	Denmark	.3
Finland	.07	Greece	1.6	Germany	.3	Norway	.03
Czechoslovakia	2.1	So. Africa ...	1.5	Austria	.5	Belgium	.4
Japan	1.3	Chile (½)....	.9	Italy	12.2	Spain	11.2
Russia	85.8	India (¼)....	8.3	India (¼)....	8.3	Iraq	1.5
U. S. A. (½).	27.1	Australia (½)	7.7	Turkey (½)..	3.5	Ethiopia	.02
China (½) ...	24.5					Belgian Congo	.01
Chile (½)....	.9					Kenya Colony	.04
India (½)....	16.6						
Australia (½)	7.7						
Total 189.57			85.6		51.8		28.2

Reporter. It shows that on more than half the wheat acreage of the United States, leaf rust is the more destructive disease. However, for the purposes of the table, leaf and stem rusts are conservatively considered to have equal destructiveness in the United States.

Turning now to TABLE 3 which summarizes the world situation with respect to the three wheat rusts, we find that on more than half the wheat acreage of the world leaf rust is considered by authorities to be the most destructive of the three diseases, the remaining world acreage being divided between areas where stem rust is predominant, where stripe rust leads, or where no reliable information is available on the relative importance of the three rusts. In the cases of the countries with the largest acreages reporting leaf rust as the most destructive disease, reference to TABLE 1 shows that these reports are from reliable sources; particularly is this true for Russia, with the greatest acreage of all. Many additional references might be made to Russian workers who are unanimous in this regard.

Wheat is the world's greatest single source of food. All workers agree that the rusts are the most destructive diseases of wheat. The foregoing analysis indicates that leaf rust leads the list of rusts in its toll of wheat; *i.e. Puccinia triticina* occupies the notorious position of being the foremost pathogen of the world's foremost food crop.

Official estimates of losses due to leaf rust: — In 1896, ERIKSSON and HENNING published many figures on estimated losses from cereal rusts in various countries. They, as most workers, did not distinguish between the rust species involved, and it is impossible to know (although one can surmise by comparing such figures with our TABLE 1) the extent to which wheat leaf rust was the cause of such losses. The figures, however, are

sufficiently imposing to bring out the enormous economic importance of these diseases. PAMMEL in 1892 furnished similar estimates for America and Australia. Much later, WATERHOUSE (1936) summarized such estimates for the main cereal-growing areas of the world. By way of illustration some of his figures are of interest: total annual loss from cereal rusts in the world, — $500,000,000; average annual loss from cereal rusts in Canada, — more than $40,000,000; in India, — $15,000,000; in Russia, 1932, — $150,000,000; in Germany, 1926, — RM 418,000,000; in New So. Wales, 1916, — $10,000,000; and in Argentina, 1925, — 191,000,000 bu. In India, E. J. BUTLER and HAYMAN (1906) estimated the annual loss in wheat from rusts at Rs. 40,000,000 ($15,000,000); while for Australia, COBB (1890-1894) gave the loss figure for 1890 as $15,000,000. In Siberia, RUSAKOV and SHITIKOVA report (1929) annual losses from leaf rust of 10 to 20% of the crop, with total loss in years in which the rust develops early and strongly.

The estimated losses in the wheat crop due to leaf rust for the United States, 1918-1939, are given in the "Plant Disease Reporter." That these, for the most part, are grossly underestimated, is generally acknowledged. For example, the estimated loss from leaf rust in Maryland in 1922 was 5%. However the "Plant Disease Reporter" (6:24) states that "all leaves were killed by the milk stage," and reference to FIG. 2 shows that the true loss in this case was not 5 but 18.7%. Kansas in 1938 estimated loss from leaf rust at 12% (pointing out however that this was probably an underestimate). According to the "Plant Disease Reporter" (22:243) in Kansas that year "the leaves have been killed very early in most fields so that the plants are coming into head with little foliage remaining." The rust-loss relationships shown in FIG. 2 indicate that the true loss that year in Kansas was nearer 34% than 12%. As a third illustration, K. D. BUTLER (1940*b*) computed from his sulphur dusting experiments that the loss from leaf rust in New York State during 1937-1939 varied from 20 to 25% (2 to 3 million bushels per year). Yet in the years 1919-1927 the "Plant Disease Reporter" estimates of losses in New York from this disease averaged only 1.4% and from 1928-1936 only 3%. He could only conclude that the disease had been greatly underestimated in the years prior to 1937.

Yet in spite of this underestimation, the estimates still point to the heavy annual drain on the wheat crop caused by leaf rust, one that is far out of proportion to the attention and research that has been directed at this disease; especially is this true if we refer to the estimated total annual losses expressed in bushels, reaching its climax with a loss greater than 100,000,000 bushels in 1938.

Socio-economic effects of leaf rust: — The wheat farmer does not ordinarily operate on a wide margin of profit. Average yields in the leading wheat States vary from 8-12 bu. per acre in the Great Plains to 16-20 in the Corn Belt, and with wheat at .50 to $1.00 per bushel, wheat culture is clearly an industry from which a plant disease as destructive as leaf rust can frequently wipe out the profit, or in which its control could go far to assure a margin of profit in an otherwise less certain venture.

Countless examples could be cited of losses due to leaf rust that have

resulted in profitless labor on the part of wheat farmers in various parts of the world. A few of these will suffice to illustrate this point.

The severe epiphytotic in Ohio in 1921 reduced yields to 3-10 bu. per acre (Pl. Dis. Rep. Suppl. 21); in Virginia in 1935, a number of cases of reduction from 30 to 6-8 bu. per acre were noted (*ibid.* Suppl. 96); in 1934 some wheat barely headed in Texas (*ibid.* 18: 150); in 1935 the average loss in Georgia, according to farmers' reports was 50%, and in 1937 the State loss was 30% with some fields total losses (*ibid.* 19: 223, 224; 21: 342); the 1916 attack was clearly shown to have caused a loss of 38% in one wheat variety in Kansas (MELCHERS, 1917); in the 1938 epiphytotic Turkey types of wheat barely headed, with 2/3 loss in Texas (Pl. Dis. Rep. 22:157), and production was reduced 29% in Oklahoma with farmers near Enid, in the heart of the State's wheat belt, harvesting as little as 3 bushels per acre from fields that had given promise of 30-bushel yields (CHESTER, 1939*c*).

Abroad the story is the same, as witnessed by the figures from Russia, ranging up to 71% loss in Asiatic Russia in 1921, as summarized by CHESTER (1944*a*).

CALDWELL (1934) has pointed out the importance of lowered grade of leaf-rusted wheat in areas in which yields are normally low, but where this is to some extent offset by the high protein content which creates a demand and premium price for such wheat to be used in blending with the more starchy softer wheats. In this case the lowering of grade may constitute a major loss factor.

The extreme of destructiveness by leaf rust is seen in fields in which the yield is so low that it will not meet the cost of harvesting the crop, and the crop is plowed up or abandoned. While leaf rust is not often as destructive as this, there are occasional records of such total loss. We have the reports, for example, from Arkansas in 1921 (Pl. Dis. Rep. 5: 24), Oregon in 1934 (*ibid.* 18: 89), and Oklahoma in 1938 (CHESTER, 1939*c*) of numerous fields being totally destroyed and turned under, and many years ago BOLLEY and PRITCHARD (1906) mentioned seeing many sections of wheat practically destroyed, all as a result of the particularly savage attack of this disease. Such total losses from leaf rust also occur in other parts of the world, for example, in Siberia (RUSAKOV and SHITIKOVA, 1929).

It is usual to think of crop geography purely in terms of the adaptation of crops to certain climates and soils. But, whether recognized or not, whenever a disease of a grain crop is regularly so destructive as to prevent profitable culture in certain areas, the culture of that crop will be given up, and other crops will be cultivated in its place.

There are many indications that the destructiveness of leaf rust is a principal reason, perhaps the principal one, why wheat is not grown to any appreciable extent from Arkansas and Louisiana to Georgia. Where it is attempted in Georgia, we have seen that the depredations of leaf rust are very great. The "Plant Disease Reporter" mentions abandonment of wheat culture in a part of North Carolina for this cause (Suppl. 71, 1928), and several writers have suggested leaf rust as the cause of absence of wheat culture in this area. The rusts are also recognized as the principal reason for the absence of small grains in the entire Gulf Coastal Prairie, the

southern Blacklands, and much of the central Blacklands of Texas, and the introduction of rust resistant varieties is expected to open up this great area for cereal culture. RUSAKOV (1927*c*) cites figures of wheat acreages in Siberia that indicate a marked drop in acreage from 1923 to 1926 in the province of Primorsk (from 75,000 to 52,000 dessyatina) while in the same period the wheat acreage in Za-Baikal province rose from 62,000 to 75,000 des. Primorsk province suffers severely from rust (principally leaf rust according to various Russian workers) while there is ordinarily little rust damage in Za-Baikal, and RUSAKOV points out: "It goes without saying that the reduction in wheat acreage is explained not only by factors of a purely economic nature, but also by natural factors, and of these last, rust is one of the most, if not the most important."

It is also clear that additional hardship is sustained by the farmer who is forced to change his type of farming, change the type of his farm equipment, and undertake the culture of crops with which he is less experienced and which may be less profitable than wheat, were it not for the regularity with which wheat suffers from disease.

Leaf rust, while it does at times cause violent yield fluctuation from one year to another, is less characterized by this than stem rust and some other plant diseases. It is more often regarded as producing a fairly regular drain on wheat yields, with only occasional exceptions of rust-free or epiphytotic seasons. Factors which act in this way are sometimes even more dangerous than those that are characterized by their sporadic violence. The latter are so obvious and compel such attention that the grower is conscious of them and usually takes measures to avert them, while he may suffer many times greater damage from less obvious but regularly-present sources of crop loss, such as leaf rust. It is the summation of these more insidious factors which subtly drain away the profits of agriculture that, to great extent, lies at the root of unprofitable farming and it is through their elimination, rather than through governmental subsidies or artificial manipulation of costs and prices, that the farmer's condition, relative to that of workers in other occupations, must ultimately be improved.

Methods of determining leaf rust intensity and destructiveness: — It has been pointed out that the damage caused by wheat leaf rust was grossly underestimated in the "Plant Disease Reporter" from 1918 to 1930 or later. Psychological reasons for this have already been mentioned, but there are other factors that make it difficult to obtain a clear picture of the amount of destruction caused by this disease.

One of these is the complex effect of the rust on yield, which is discussed fully on pages 28-39. It is sufficient here to point out that vigor of wheat growth, water economy, amount of yield, and quality of harvested crop are all involved, and in diseases of this type it is far more difficult to estimate loss than in diseases such as the smuts or fruit rots, where there is a clear-cut proportionality between degree of infection and amount of loss.

The relation of weather to rust and to wheat growth also tends to distort the estimates. Rust is most destructive in seasons in which moisture is abundant, and, hence, in areas in which water deficiency is often a limiting factor, the increased productivity of wheat due to adequate water supply

may obscure the loss caused to the potentially greater crop by rust. For example, in Oklahoma in 1938, when the crop was estimated to have suffered a 29% loss from leaf rust, the average yield per acre was 11.0 bu. per acre as compared with 11.2 bushels for the preceding 10-year average, *which was in a cycle of drought.* The difference between 11.0 and 11.2 bushels per acre was hardly noticeable, and there were many who considered the rust-ridden crop of 1938 as "normal", failing to appreciate the potentialities of the well-watered 1938 crop had not leaf rust stepped in to duplicate the crop-depressing effects of Oklahoma's chief wheat enemy, drought, which is the main reason why Oklahoma's "normal" yields are so much lower than those of meteorologically more favored States. The same thing has been noticed in other States. From Kansas, JOHNSTON wrote in 1938 (Pl. Dis. Rep. 22: 180): "The leaf rust damage will probably be underestimated because of ample rains which will raise the general yield level," and the same point is brought out by TEHON (1939) for Illinois in that year.

The 1938 leaf rust epiphytotic also illustrates a third difficulty in estimating leaf rust damage, namely the fact that it is often only one of several injurious factors affecting the crop in a given season. In that year in Oklahoma, observers cited leaf rust, stem rust, excessive moisture, late harvest, insects, hail, and late freezing injury as affecting the wheat harvest. HUMPHREY indicated difficulty in distinguishing the effects of leaf and stem rusts in Michigan the same year (Pl. Dis. Rep. 22: 369). Considering the tendency to underestimate the damage due to leaf rust and the obvious character of some of these other types of injury, it is easy to understand the difficulty in attributing to leaf rust its proper share in the destruction of the crop, if we lack controlled experiments and accurate measurements.

The "Plant Disease Reporter" in 1937 (Suppl. 110: 187) lists additional reasons for lack of accuracy in estimating leaf rust damage: "In areas where leaf rust is most important it occurs practically every year to a greater or less extent with the result that its effect on yield is apt to be overlooked except in epidemic outbreaks, and even then, for lack of a disease-free standard, the loss may largely be underestimated: because it occurs to some extent every year, it does not focus the attention by a spectacular outbreak as does stem rust; in contrast to the apparent suddenness with which stem rust often attacks, leaf rust is apt to appear early and to develop steadily throughout the season; since it does not cause shrivelling of the grain as stem rust does, its effects are much less conspicuous. Possibly this contrast with stem rust is a chief factor responsible for minimizing leaf rust as a cause of loss. Even in epidemic years, damage is likely to be overshadowed by or confused with that due to stem rust, since, in general, conditions favorable for one rust are also favorable for the other.

"It is probable that if the loss from stem rust were spread over a period of years instead of being concentrated in destructive outbreaks, the disease would attract much less attention than it does. Suppose, for example, that the loss in Minnesota instead of varying from a trace to 57% had been 11% annually, which is the present average and the highest for any State, would it not be considered a routine loss subject to the 'familiarity that breeds contempt', rather than as a calamity to be feared?"

Finally, errors in rust damage estimation have resulted in some cases

from a failure to discriminate or properly identify the species of rust associated with crop destruction. WATERHOUSE has pointed out that this was undoubtedly true of some of the early Australian work; it probably also involves some of the reports from southern Europe and other parts of the world.

The foregoing discussion brings out the reasons for the distorted conclusions that have often been reached in the past because of lack of precise measurements of leaf rust damage, and clearly points to the necessity for such measurements in exact and productive work on this disease.

In order to designate intensity of rust development and have a basis for comparing rust intensities in different wheat varieties and environments, it is clearly necessary to have some standard or scale as a measure of rust intensity. This has long been recognized and led to the use of a number of such scales.

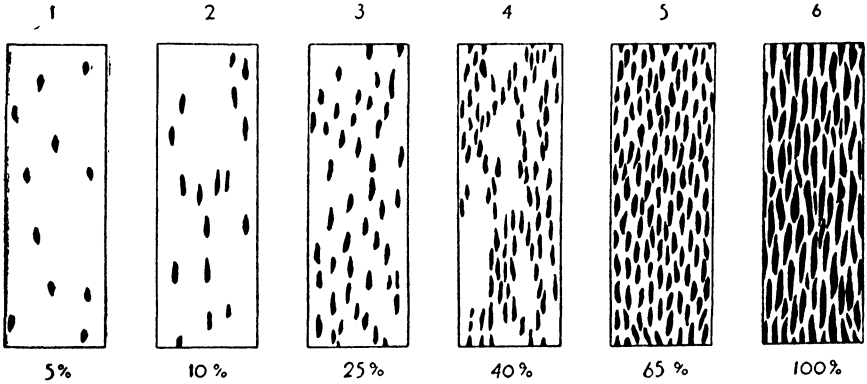

FIGURE 1. — Modified COBB scale for determining rust intensity, in common use in the United States. (After MELCHERS and PARKER).

The first of these, published by COBB in 1892, adopted by the U. S. Department of Agriculture in 1917 with the addition of one degree of rustiness (65%), and published by MELCHERS and PARKER in 1922 is reproduced as FIG. 1.

Other rust scales, diagrammatic or based on descriptive terms, were used by ERICKSSON and HENNING (1896), BUTLER and HAYMAN (1906), YACHEVSKI (1909), NILSSON-EHLE (1911), LITVINOV (1912), VAVILOV (1913, 1919), GASSNER (1915a), RUDORF *et al.* (1933), and RUSAKOV (1927, 1929*c*). RUSAKOV's scale, which is commonly used in Russia, is based on 9 degrees of rustiness, increasing in logarithmic progression, and designated from 0 to 4 "balla" or "Russian units" of rustiness, including 3 degrees of rust intensity in the low range, that have no counterpart on the other scales.

The rust intensity of a field is appraised by random sampling and indicating the average degree of rustiness according to one or another of the rust scales. In Russia it is recommended that this be repeated 6-7 times during the growing season in order to determine the tempo of rust development and the behavior of rust in relation to the vegetative stage of the wheat plant (RUSAKOV 1927*a*, 1929*c*).

When rust is present in extremely small amounts, it is customary to indicate its amount in percentage of leaves affected or number of minutes or hours required to find a few rust pustules. While this is very time consuming it yields valuable information on the extremely important early cycles of infection.

By calculation it becomes possible to express the average rust intensity of small or large groups of fields, and methods for doing this have been proposed by TEHON (1927) and NAUMOV (1924).

In the United States, in tests of varietal resistance to rusts, the customary practice is to multiply the "prevalence" by the "severity" of the rust (0-100% according to the modified COBB scale) and this by the "response" (type of lesion, from susceptible, 1.0 to resistant, 0.0) for each variety in each test, giving the "coefficient" which is taken as a single figure characterizing the reaction of this variety to leaf rust under the given conditions.

The methods for determining rust destructiveness consist of comparing yields of: greenhouse-grown plants subjected to different rust intensities; plants from which different amounts of foliage have been artificially removed to imitate destruction of the leaves by rust; crops grown in years of different rust severity; resistant and susceptible varieties; selections from varieties or groups of lines from segregating hybrid families, showing different rust reactions; field plots protected from rust with fungicides as compared with those exposed to rust; individual plants showing different degrees of rust attack in otherwise uniform fields; and combinations of these. Some information on rust destructiveness is also gained by comparing anticipated with actual yields, the use of questionnaires addressed to farmers, and comparisons of weather and the price levels of grain crops.

No method has yet been proposed for direct translation of rust intensity into crop loss. Sufficient data correlating these two magnitudes have now accumulated to make this possible. This correlation is fully discussed in Chapter III, and with it as a basis the following method is suggested.

Average rust intensity for the field is determined by use of the modified COBB scale. Theoretically only one such determination need be made, although in practice it might often be desirable to repeat the appraisal at later stages of rust and crop development. The best time for appraisal will vary with the season; in general it will be from heading stage onward except in years of severe epiphytotics, when it may be earlier.

Estimated crop loss from leaf rust is directly obtained from TABLE 4, which is based on data from pages 28-33.

Estimated crop loss for localities, counties, states, etc. can be obtained by averaging losses from sample fields, after weighting them for extent of the fields.

While this method meets present needs in surveying for leaf rust and determining more accurately the losses it causes, it could bear improvement when additional experimental data permit. For one thing, it expresses crop losses only in decreased bushel yields, and does not include the accompanying important loss that results from lowered quality of the harvested grain. Secondly, it assumes an arbitrary, steady increase in rust intensity which usually, but not always characterizes leaf rust development as the

TABLE 4: *Relation between wheat leaf rust intensity, wheat growth stage, and yield reduction: —*

RUST INTENSITY (%) AT GIVEN STAGE OF CROP DEVELOPMENT						APPROXIMATE % LOSS FROM LEAF RUST
SEEDLING-TILLERING	JOINTING	BOOT TO HEADING	BLOSSOM	MILK	DOUGH OR WAX	
...	...	tr.	10	25	40	1
...	tr.	10	25	40	65	3
tr.	10	25	40	65	100	10
10	25	40	65	100	100	20
25	40	65	100	100	100	35
40	65	100	100	100	100	50
65	100	100	100	100	100	70
100	100	100	100	100	100	95

season advances. In the third place, it is based on the modified COBB scale and its manner of use in America, because most of the data now available have been gathered by the customary methods of using this scale. The inadequacies of such a procedure have been pointed out by RUSAKOV and it is to be hoped for the future that experimental determinations of crop loss from leaf rust by methods analogous to the more exact ones of RUSAKOV will make possible further refinement of the proposed method.

The method is suggested for use in determining crop losses in commercial acreages, and may be applied by workers with a minimum of pathological training. For pathologists and breeders, who are interested in obtaining more precise measurements of rust intensity and its results, some combination of the methods enumerated above will be more suitable.

Chapter III

EFFECT OF THE RUST ON THE HOST PLANT AND ITS YIELDS

Effect on the physiology and development of the host plant: — As early as 1899, CARLETON noted excessive transpiration associated with leaf rust. WEAVER (1916) cites some apparently unpublished data from the University of Minnesota in 1904, in which wheat plants, with and without leaf rust, were enclosed in paraffin-covered baskets, so sealed that all water loss was by transpiration. Although only 1% of the leaf area of the infected plants was occupied by rust pustules, weighings showed that these lost 38% more water than the normal plants, and it was felt that all of this loss could not be accounted for by escape of water through the torn leaf epidermis.

An extensive series of experiments on water economy of leaf-rusted wheat plants was carried out by JOHNSTON and MILLER in Kansas from 1933 to 1940. Plants were grown in glazed stone jars with the soil surface sealed against evaporation by a coating of beeswax or paraffin. They determined that infected wheat lost much more water than uninfected wheat, the excess in transpiration varying from 31.7 to 104% depending on the duration of infection. The results were similar in 2 years of experimentation.

Continuing their researches, JOHNSTON and MILLER found that a susceptible wheat variety heavily inoculated at anthesis transpired 17% more than uninfected wheat, while a resistant variety, that showed only necrotic flecking as a result of inoculation, transpired only 3.1% more than the checks. At night the heavily rusted variety lost 78% more water than the checks, but in the daytime the difference was much less. Their results indicate that the excessive transpiration is primarily due to loss of water through the ruptured cuticle, and that during the day this effect is masked by the higher stomatal transpiration of normal plants, than in rusted plants, many of the stomata of which were obstructed by rust appressoria.

In later experiments, moderately rusted plants were found to transpire 83.41% (1935) and 89.62% (1936) more than unrusted plants at night, and there was indication that part of this excessive loss of water was due to respiration of the fungus itself.

The abnormal water loss resulting from leaf rust infection has also been noted by MAINS in Indiana (1930), by PAL in India (1936), by MACINDOE in Australia (1933), and by SUKHORUKOV (1938) and YARKINA (1940) in Russia. SUKHORUKOV considers this to be the most harmful effect of the rust, and YARKINA reports that weakly rusted plants transpired 20-60% and severely infected plants 200-300% more than healthy plants. WEISS (1924), on the other hand, did not find a significant difference between the

water requirements per gram of vegetative mass or grain produced in weakly (10%) infected wheat.

A physiological factor associated with heightened water loss in rusted plants, is the increased permeability of the cells of rusted leaves noted by SUKHORUKOV. ALLEN (1926) reports increased osmotic pressure in cells of leaf-rust-infected tissues, but she bases this conclusion on the fact that killing agents that plasmolyze normal cells fail to plasmolyze infected ones. The phenomenon observed could be better explained as a result of increased permeability of the diseased cells, in agreement with SUKHORUKOV, than as due to increased osmotic pressure of which there is no conclusive proof.

The extravagant use of water by rusted plants quite naturally represents a grave handicap or danger to the wheat plant when, as is so often the case, the crop is growing under conditions of limited water supply or even drought.

That leaf rust leads to the premature death of wheat leaves is a matter of common observation. In severe epiphytotics all the wheat foliage may be destroyed before or a few days after heading. Many observers have noted that this is accompanied by decreased yields and considering the function of leaves in the manufacture of food for storage in the seeds, it is only natural to conclude that reduction of photosynthetic tissues necessarily is followed by reduction of stored food.

When this loss of foliage occurs long before normal death of the leaves and ripening of the plant, at heading time or before, the loss of photosynthetic tissue is particularly injurious. For the remainder of its life the plant is forced to depend on the limited amount of chlorophyll in leaf sheaths (if these, too, have not been destroyed by rust), culms, glumes, and awns. We cannot disregard the importance of the photosynthetic activity of these latter organs, however, as is well brought out by the fact that wheat which has lost all of its leaves in the post-heading stage, still manages to produce some grain. Likewise the relationship between time at which the foliage is lost and extent of decrease in the yield has been repeatedly noted.

Even in resistant varieties of wheat which react to leaf rust by the formation of small necrotic flecks, the loss of photosynthetic tissue represented by these flecks, if the latter are numerous, is reflected in the decreased yields, as has been shown by WALDRON (1936).

But this is only one aspect of the effect of leaf rust on photosynthesis, — its reduction through the reduction of available green leaf tissues. YARKINA (1940, 1941*b*) has also investigated the *energy* of photosynthesis in rust-infected wheat leaves. She finds that this is stimulated by weak rust but retarded by strong rust. In her experiments the energy of photosynthesis was increased 281% in irrigated and 430% in non-irrigated wheat under the influence of weak leaf rust, while severe rust infection lowered the energy of photosynthesis to 81% and 87% of that of healthy plants under irrigated and non-irrigated conditions respectively. When this reduced rate and amount of photosynthesis, expressed in a lowered ability to assimilate CO_2, is combined with an accelerated respiration and transpiration, there results a rapid exhaustion of the plant.

ALLEN's experiments (1926, 1927) indicate that leaf rust interferes with the translocation of carbohydrates. Tissues of a susceptible wheat

variety infected with 6-17 day old mycelium showed excessive starch accumulation. This effect was seen only under field conditions in clear, dry weather, not in wet seasons with intermittent dark days. As the infections became older, starch again became scarce, which she suggests may be due to the use of starch by the fungus. No such starch accumulation accompanied infection of a resistant wheat variety.

The digestion of starch by amylase (diastase) has been studied by YARKINA (1941*b*). She found that amylase activity is increased in leaves that are weakly infected with leaf rust (1 Russian unit), but that this drops back to the level of amylase activity of the healthy plant or below it when the plants are strongly infected (3-4 Russian units).

MALCHENKO-DYAKONOVA (1936) in preliminary tests reported a striking increase in respiratory activity in leaf-rusted wheat plants. Her experiments are not clear cut, unfortunately, because her plants were also accidentally infected with stripe rust and powdery mildew. She also demonstrated an increase in catalase activity in weakly (5%) rusted plants, as compared with healthy controls, but this difference was less striking as rust intensity was increased. YARKINA likewise found some increase in catalase activity in leaf rusted wheat plants, but she considers that this may be an increase in catalase activity of the fungus, rather than of the host plant.

The disruption of normal physiological processes brought out in the preceding subsections results in markedly altered plant growth.

Many workers have observed the reduction in size of the various organs of the wheat plant as a result of leaf rust. In severe epiphytotics the plant as a whole may be reduced to ½ its normal size; and in particular the heads are short and small. JOHNSTON and MILLER (1934) and MAINS (1930) illustrate this reduction in plant and head size. According to NAUMOV (1939), leaf rust shortened heads, in one case, from 5.5 cm. to 4.1 cm. He reported that length of culms was reduced from 40 cm. to 36.7 cm. and other workers have made similar observations. The top internode is said to suffer most.

JOHNSTON and MILLER (1933, 1934) and PAL (1936) have called attention to the serious deterioration of the root system as a result of leaf rust attack, as shown by a decrease in the number of fibrous roots, discoloration of the roots, and lowered dry weight of the root system.

RUSAKOV and SHITIKOVA (*in* NAUMOV, 1939) report a reduction in the number of tillers of 20-45%, as a result of leaf rust attack, and LUKYANENKO (1934) also noted a marked reduction in tillering capacity of leaf rusted wheat. JOHNSTON and MILLER (1934) and MAINS (1930) find, however, that wheat that has been heavily rusted for a long period of time may produce many new tillers at heading time. The writer has noted the same, but the tillers were very short and not fruitful, as was also noted by MAINS.

Lodging is usually more commonly associated with stem rust than with leaf rust. TEHON (1924) states that lodging can result in extreme cases of leaf rust, and CALDWELL and COMPTON speak of much fallen straw in leaf rusted plots. In the 1938 epiphytotic, lodging was common in Oklahoma and Kansas, and while it was complicated with other factors, in addition to

leaf rust, workers in both States were of the opinion that leaf rust was the chief cause of the lodging.

Various workers are in agreement that rust infection in the fall predisposes winter wheat to winter killing. In 1882 PLOWRIGHT pointed this out, and considered it advantageous in destroying overwintering rust. A few years later, BOLLEY (1889*b*) noted that fall-rusted leaves "because of their reduced vitality were unable to resist the cold and died back from the tips". MAINS (1930) has confirmed these observations and illustrated the winter-killed rust-infected leaves. SALMON and LAUDE (1932) have published statements and a photograph showing that Kawvale wheat, which is relatively rust resistant, survived the winter of 1929-1930 much better than Fulcaster wheat which is very rust-susceptible. No attempt was made, in this case, to correlate fall rust and winter survival; it does raise the question, however, as to the extent to which rust resistance is a factor in Kawvale's winter hardiness.

We have seen that leaf rust results in increased transpiration, and it follows that rusted plants are more susceptible than normal ones to damage from heat or hot, dry winds. This would be particularly true of winter wheat if maturity was delayed by rust attack, as is claimed by several workers. Heavy rust postponed maturity as much as 3 weeks in the experiments of JOHNSTON and MILLER (1934). HAYES *et al.* (1927) found a high correlation between leaf rust and lateness of heading date. BOLLEY and PRITCHARD reported (1906) that in 1888 leaf rust so delayed maturity of the spring wheat crop that it was nearly all ruined by a fall freeze. On the other hand K. D. BUTLER (1940*b*), PETURSON and NEWTON (1939), and writers of several notes in the "Plant Disease Reporter" associate hastened maturity, and consequently reduced yields, with leaf rust. There are also reports of fields almost or entirely failing to mature as a result of heavy leaf rust infestation. JOHNSTON and MILLER (1934) found it difficult to tell when rusted plants were mature, as the glumes remained abnormally green when they should have lost this color.

Leaf rust may also be a factor in increasing injury from insects. This was particularly noticeable in Oklahoma in 1938 when army worms attacked the wheat after the last green foliage had been destroyed by leaf rust. The worms, having no leaves to feed on, attacked the heads directly, thus greatly increasing the damage.

We must bear in mind that the various detrimental effects indicated above, are operating together and often aggravating one another. For example increased water loss could be borne more easily by a normal plant than one in which the root system is underdeveloped as a result of insufficient photosynthetic energy and amount of photosynthetic tissue. Similarly the effect of reduced photosynthesis is increased by its association with accelerated rate of respiration: *i.e.* the plant not only makes less food, but at the same time it squanders what it has. Meanwhile, the economical utilization of the products of photosynthesis is impaired by the disruption of normal translocation and amylase activity.

The wheat plant reacts with increased physiological activity when attacked by a small amount of rust, it shows an increase in photosynthetic energy and amylase activity, comparable to the stimulation of slight mechan-

ical injury, but as the amount of rust increases there is a rapid exhaustion of the entire plant, all major physiological processes are disrupted, and dwarfing or killing of the plant parts results as an outward manifestation of the disease. We will now see in what manner this altered metabolism and development affect the quantity and quality of the crop.

Effect on grain yields: Quantitative aspects: — Severe leaf rust may either reduce the tillering capacity of wheat or result in the production of new, small, non-fruitful tillers at heading time. This can be reflected in the number of fruitful heads produced.

MAINS (1930) did not note much difference in the numbers of heads produced per plant, leaf rusted and healthy, and JOHNSTON (1931) observed only a minor difference in this respect in his greenhouse experiments. PAL (1936), however, reports that leaf rust reduced the number of heads, and NAUMOV (1939) cites work of RUSAKOV and SHITIKOVA showing as much as 20-29% reduction in the number of wheat heads as a result of early leaf rust.

The data relative to the effect of leaf rust on the number and fertility of spikelets produced per head, are somewhat at variance. In Russia, BRIZGALOVA (1935) and LUKYANENKO (1934) found no great correlation between leaf rust and the number of spikelets produced, whether fertile or sterile; however RUSAKOV (1929*e*) reported 40% fewer spikelets per head as a result of heavy leaf rust. MAINS (1930) found that strong rust resulted in an abnormally high percentage of sterile spikelets at the tops and bottoms of heads; *i.e.* the spikelets that blossom last.

In 1911, E. C. JOHNSON noted extensive floret sterility in the southern Great Plains which he associated with the work of thrips and especially with "rusts". (His work was concentrated on stem rust, but his use of the plural implicates leaf rust, the only other wheat rust in that area). He concluded that "undoubtedly the most important agents causing floret sterility [in wheat] at San Antonio and vicinity are rusts." The insect appeared to be secondary, completing the destruction initiated by the rusts. It is noteworthy that the years 1908 and 1909 in which he noted the highest percentages of floret sterility were years of abundant, early leaf rust in Texas.

Nearly all who have investigated the subject agree that a very important manifestation of reduced productivity of leaf rusted wheat is the reduction in the number of kernels produced, and their total weight per head. We find numerous statements in the "Plant Disease Reporter" associating heavy leaf rust with "poor fill" of the heads and with production of only one kernel at each node. In the words of one farmer in the 1938 epiphytotic, "Some heads were empty at the top, others at the bottom, and some had no grain at all."

This effect of leaf rust was studied in detail by MAINS (1930), CALDWELL and his associates (1932, 1934), JOHNSTON and MILLER (1931, 1933, 1934), and several workers abroad. CALDWELL *et al.* found that lowered yields were due primarily to fewer kernels per head, and to a less extent to lighter kernels; this was also the experience of JOHNSTON and MILLER. MAINS, who published excellent photographs illustrating this fact, found

that in cases of early infection, the principal loss factor was fewer kernels per head, while with later attacks the weight of the grain was more impor-

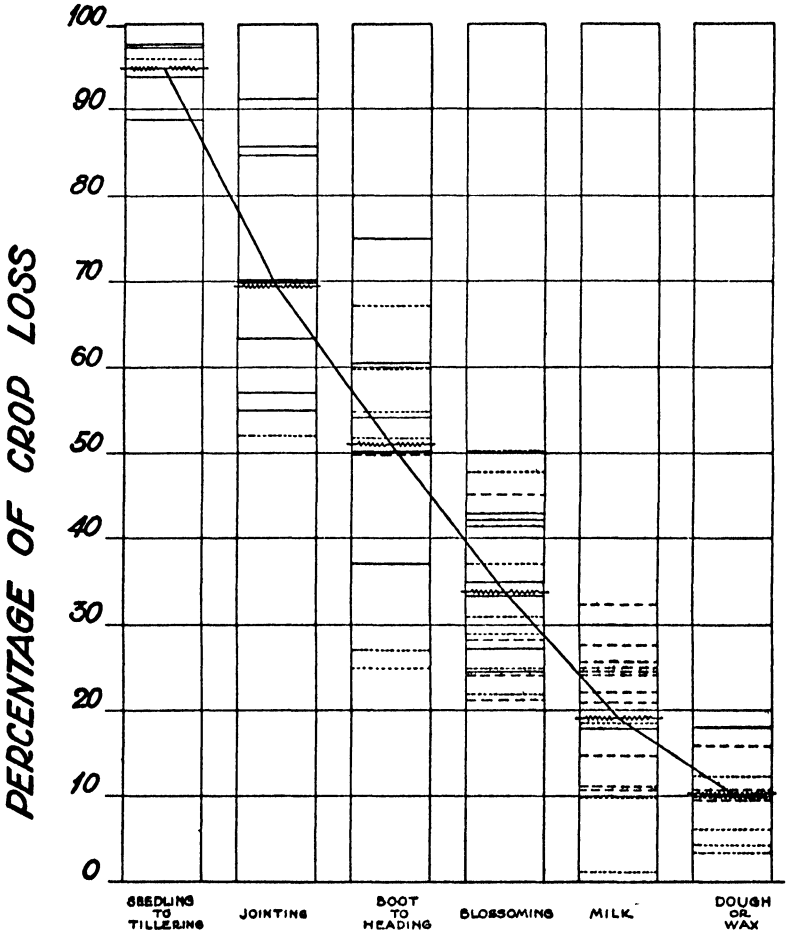

FIGURE 2. — Wheat yield reductions due to total defoliation at the indicated developmental stages. Each horizontal line represents the results of a separate test, by the method of greenhouse epiphytotics (———), sulphur dusting experiments (- - - -), or leaf-clipping experiments (.....). The broken line connects the average yield reductions (*Based on the experiments of* Anon., 1935, BRIZGALOVA, 1935, ÇALDWELL *et al.*, 1934, EIDELMAN, 1933 *a, b,* GROOSHEVOI and MAKLAKOVA, 1934, JOHNSTON, 1931, JOHNSTON and MILLER, 1934, KIESSELBACH, 1925, LUKYANENKO, 1933, MAINS, 1927 *a, b,* 1930, PAL, 1936, PESOLA, 1927, ROEBUCK and BROWN, 1923, RUDORF *et al.*, 1933, RUSAKOV, 1929 *a, c, e, cited by* LUKYANENKO, 1934, RUSAKOV and SHITIKOVA, 1932, *cited by* NAUMOV, 1939, SHEVCHENKO, 1933, and TELECHKO and SIRYACHENKO, 1933).

tant. This appears reasonable, as the number of kernels would depend on the fertility of the spikelets which in turn would be affected by pre-blossoming, but not by post-blossoming devitalization from rust, and this also

evidently accounts for such apparent contradictions in the literature as the assertions of NEILL (1931), BRIZGALOVA (1935), and LUKYANENKO (1934) that losses are due principally to lowered grain weight, and to a much less extent to reduced number of grains, in contrast to the reports mentioned above, which are also confirmed by PETURSON and NEWTON (1939), RUDORF and JOB (1934), PAL (1936), RUSAKOV (1929*e*), WATERHOUSE (1939), and SHEVCHENKO (*in* NAUMOV, 1939). Loss in kernel weight is often considerable. WALDRON's summary of American data on this point (1936, p. 400) includes the results of 21 experiments revealing losses in kernel weight of 1.5% to 27.6%, averaging 12.9%, while Russian workers report losses in kernel weight, resulting from leaf rust, of 17.1%, 21%, and 24%.

The most obvious and inclusive expression of the influence of leaf rust is that of reduced grain yields. The literature contains many references to this, based either on threshing returns or on experimental studies.

The four experimental approaches to this question which have yielded most exact results are greenhouse infection experiments in which wheat at definite stages of its development, and subjected to definite intensities of rust, is compared with uninfected wheat; field tests in which wheat that has been protected from rust infection by fungicides is compared with unprotected, rusted wheat; experiments in which the effect of leaf rust is simulated by mechanical removal of leaves, in which the yields of plants so treated are compared with those of untreated plants; and comparisons of yields of strains of wheat differing in rust susceptibility but otherwise similar.

The graph of FIG. 2 is based on 68 experiments of the first three of these types, performed by many experimenters in America and abroad, and includes all such experiments that have been reported in sufficient detail to permit their use in preparation of the graph. The types of experiment and sources of the data are indicated.

Study of the graph brings out a number of interesting points. First we note that the data are consistent and without any greater variation than might well be expected, considering that they were obtained by different workers, under different experimental conditions, and by three distinct experimental approaches. The graph brings out clearly and forcibly the relationship between developmental stage of the wheat at the time of defoliation and extent of the grain loss resulting, the loss ranging from about 10% if maximum defoliation occurs in the dough stage to 95% if this occurs before the jointing stage, with proportionate losses from defoliation at intermediate growth stages.

Considering the extent of the data upon which the graph is based, their homogeneity, and the consistency of the trend as indicated by the curve connecting average losses for wheat defoliated at successive stages of development, it is believed that the graph faithfully presents the amount of loss sustained by wheat if defoliated at the indicated growth stages. If this is true, then we have in the relationships shown by the graph a most useful tool to serve in accurate loss estimates in the future, and to correct and interpret loss estimates of past years.

The faithfulness of the graph in delineating leaf rust losses is also

TABLE 5: *Additional records of relationship between rust intensity and percentage yield reduction: —*

RUST %	PERCENTAGE YIELD REDUCTION IN SPECIFIED TYPE OF TEST		
	GREENHOUSE TEST	SULPHUR DUSTING TEST	RESIST. VS. SUSCEPT. VARIETIES
1-10	22.3(k), 0-20.5(l)	4.4-5.6(a), 18.0(i)	12.3(e), 15.50(j), 0(m)
10-20	14.5(n)	7.2(b)	16.5(m)
20-30		9.7(d), 30.0(o)	
25-40			19(j)
30-40		30(p), 16(q), 18(h), 19.6(w), 30(p)	
40-50		18.5(w), 84.4(r), 6.9(o)	14.8(f)
50-60		6.9, 22.1(o)	12.3(f)
60-70	55.7(k)	51(p), 22.1(o), 7.7(k)	35.6(f), 28(g)
70-80		37(p), 50(c), 8.1(k)	20, 34(f), 3.2, 45(g)
65-100			26.7(j)
80-90		12, 14.5(s)	22.7(f)
75-100		10.9, 24.3(t)	
90-100		27(v)	31.8(f), 39.5(u)

References: (a), SHEVCHENKO, 1925, *in* NAUMOV, 1939; (b), RUSAKOV, 1931, *in* do.; (c), PRONICHEVA, 1935, *in* do.; (d), BRIZGALOVA, 1933, *in* do.; (e), SHEVCHENKO, 1926, *in* do.; (f), LUKYANENKO and PRONICHEVA, 1926, *in* do.; (g), STARKOV, 1936, *in* do.; (h), GREANEY, without date, *in* NEWTON, 1938; (i), RUSAKOV, 1929*a*; (j), LUKYANENKO, 1934; (k), JOHNSTON, 1931; (l), JOHNSTON and MILLER, 1934; (m), WALDRON, 1936; (n), WEISS, 1924; (o), BRIZGALOVA, 1935; (p), PETURSON and NEWTON, 1939; (q), RUSAKOV, 1927*a*; (r), KIKOINA, 1935; (s), PHIPPS, 1938; (t), MAINS, 1927*b*; (u), RUSAKOV, 1937, *in* NAUMOV, 1939; (v), BROADFOOT, 1931; (w), KIGHTLINGER and WHETZEL, 1926.

brought out by supporting facts from other sources. A single example will suffice here; others are apparent in the discussion to follow. Following the 1938 leaf rust epiphytotic in Oklahoma a questionnaire was sent to leading farmers requesting, among other information, data on wheat yields per acre in 1938 and in the rust free year 1937. When these reports were tabulated (CHESTER, 1939*c*) and averaged (omitting reports for the partially rust-resistant wheat variety Tenmarq) we find that the 32 reporting farmers indicated average yields of 14.7 bu. per acre in 1938 and 23.3 bu. per acre in 1937. This is a loss of 34% in 1938 as compared with rust-free 1937. In 1938 the wheat was defoliated by rust approximately at the blossoming stage, and according to the graph this would indicate a loss of 34.3% as compared with the loss of 34% actually observed. It is recognized that there were other differences in these two seasons besides the difference in leaf rust intensity, and this case is cited merely to bring out the fact that in 1938, when leaf rust was the dominant factor depressing yields, the yield depression was of the same order of magnitude as that resulting from accurate experimentation and indicated in the graph.

There are, in the literature, records of many other determinations of yield losses in relation to leaf rust that could not be used in the construction of the graph because of insufficient data, particularly with reference to stage of development of the crop at the time at which a given rust intensity was reached. These records are indicated in TABLE 5, and they introduce a fourth type of evidence, namely that from comparisons of rust resistant and susceptible genetic families of breeding wheats. Their chief importance is,

first, in giving abundant confirmation to the preceding graph in the sense that the recorded losses are considerable, even when the plants are only partially defoliated, and, second, in bringing out the importance of reporting such data in full detail. For example, in the figure we see that different workers have found that rust intensity of 70 to 80% resulted in measured crop losses that ranged from 3.2% to 50%. This is entirely conceivable if the worker who reported 3.2% loss was recording the maximum of rust in the submature stage of wheat development, while the 50% loss was associated with 70-80% rust in a much earlier stage of plant growth.

The literature also contains many data on the yield-depressing effect of leaf rust combined with other diseases, or with unfavorable environments for best wheat yields. Thus, in nearly all of GREANEY's extensive work on sulphur dusting for rust control in Canada, his crops were affected by both leaf and stem rusts, and the marked yield increases following dusting must be attributed to control of both diseases, but principally of stem rust. The same applies to part of JOHNSTON's work (1938*a*), and to some of the reports of the very destructive effects of epiphytotics of the two diseases (*e.g.* Pl. Dis. Rep. 21:274, 1937, DODOV's report (1933) of 30,000,000 RM. loss in wheat in the Danube valley in 1932, and that of RUSAKOV (1926*c*) of 75% destruction of the wheat crop over a vast area of Siberia and Manchuria in 1923). The reports leave it clear that in cases of leaf rust combined with stem rust, *Septoria* diseases (SALMON and LAUDE, 1932), heat (WALDRON, 1936) and other detrimental influences, an important share in the responsibility for the ensuant destruction must be attributed to the leaf rust component.

The bushel weight of wheat is a function of size and weight of individual grains, which will be considered below. Its practical importance as a yield factor lies in the fact that grain of low bushel or test weight is penalized in price.

Low test-weight is commonly associated with leaf rust epiphytotics and has also been determined experimentally to be the result of severe leaf rust infestation.

Conditions of experiments and data obtained have been so variable that we cannot generalize here as has been done for yields of grain. In 16 tests, performed by various workers using the sulphur dusting method and that of comparing yields of resistant and susceptible lines of wheat, the depression in test weight due to severe leaf rust (averaging 75%) was an average of 1.57 lbs. per bushel. In one case it was given as high as 3 lbs. and the low extreme was .3 lbs. In addition to the lowered quality that this represents, it also means a yield reduction in weight per bushel of 2.5% which must be combined with the loss in yield in bushels per acre to give the full extent of the loss in grain yields. In severe epiphytotics of leaf rust, the reduction in test weight has been reported as much greater than 1.57 lbs. per bushel. For example in Indiana, during the epiphytotic of 1935, test weights were lowered 2.6 lbs. per bu., (Anon., 1936), while in Oklahoma, questionnaire data from 31 farmers and millers indicated average test weights of 57.2 lbs. for the epiphytotic year 1938 as compared with an average of 60.4 lbs. for the rust-free year 1937, a difference of 3.2 lbs. per bushel (CHESTER, 1939*c*).

Reduction in the size of the kernels is considered to be a major factor in the reduction of wheat yields by leaf rust. This is well shown in MAINS' illustration of the grain from rusted and normal wheat plants (1930).

Kernel weight is usually expressed as weight per 1000 kernels, and is found to be definitely lowered as a result of leaf rust attack. Long ago, BARCLAY (1892) in India observed that it took 60 grains from heavily rusted wheat to equal the weight of 10 kernels of normal wheat. Although some workers, *e.g.* JOHNSTON and MILLER, CALDWELL and his associates, and PAL, consider the reduction in kernel weight to be of less importance as a yield factor than reduction in their number, others, as NEILL, attach much significance to this phase of leaf rust effect, and, in fact, the absolute values for reduction in 1000-kernel weight are often considerable (PETURSON and NEWTON, 1939: 16-27%; PHIPPS, 1938: 8%; CALDWELL *et al.*, 1932: up to 12.1%; LUKYANENKO, 1934: up to 17.1%; JOHNSTON, 1938a: 10.1 and 28.3%; WALDRON, 1936: from 30.4 to 23.7 gm. weight per 1000 kernels; RUSAKOV, *in* NAUMOV, 1939: reduction from 30 to 25 gm. weight per 1000 kernels; and BRIZGALOVA, 1935: reduction from 26.39 to 20.71 gm. per 1000 kernels.)

LUKYANENKO (1934) reports that an effect of heavy leaf rust is to lower the ratio of dry weight of grain to dry weight of the total plant bulk. Susceptible varieties of wheat showed only 59 to 77% of dry weight of grain as compared with resistant varieties.

Effect on grain yields: Qualitative aspects: — The nitrogen or protein content is so important a characteristic of wheat grain that it markedly influences its price, and in certain dry regions, *e.g.* the drier parts of the southern Great Plains, the high protein content of the grain that is characteristic of wheat grown in those areas is an advantage that tends to offset the low or uncertain yields.

Many workers have found that increasing leaf rust is correlated with a decrease of protein or nitrogen in the grain. CALDWELL and COMPTON (1938) found leaf rust associated with protein reductions up to 11.5%, JOHNSTON (1938*a*) up to 13.1%, and PHIPPS (1938) about 8%. LUKYANENKO (1934), in comparing the rust resistant Hybrid 622 with the susceptible variety Ukrainka, when both were subjected to leaf rust, found the protein content reduced from 15.50% to 14.31% in the latter. The reduction in protein has been found to affect not only the whole grain but also the bran, middlings, and flour (ANON., 1933). GREANEY *et al.* (1941) have published many data on low protein in wheat grain associated with rust, but considered stem rust to be more responsible than leaf rust in this. BRIZGALOVA (1935*a*) reported an increase in the protein content of wheat grain correlated with increase in leaf rust. It is difficult to interpret the contradiction between her data and those of all other investigators, though it might be pointed out that her comparisons were not between heavily and lightly or non-rusted grain, but between two degrees of rustiness, both of which were relatively severe. The same applies to the results of BROADFOOT (1931). Leaf rust increased the grain protein in some of the experiments of PETURSON, NEWTON, and WHITESIDE (1945) and decreased it in others.

Few data are available on the effect of rust on fat content of grain, BRIZGALOVA (1935), whose results are subject to criticism made in the preceding paragraph, found more rust correlated with less fat in the grain from early and medium plantings, and the reverse in grain from late plantings. There is as yet no evidence that leaf rust exerts any practically significant effect on the fat content of the grain.

With the reduction in protein content of wheat grain as an effect of leaf rust, there is a corresponding increase in the proportion of carbohydrates (starch and sugars). The absolute amount of carbohydrates in the grain is reduced, however. With greater relative starchiness and softness of the grain there is often associated light color and the condition known as "yellow berry", a factor which lowers the market grade and price of the grain, and is a serious defect, especially in those areas that normally secure a premium for high protein wheat. As high as 300% increase in yellow berry has been noted as a result of leaf rust. This transformation from a hard, vitreous, protein-rich grain to a soft, yellow, starchy one, is regarded by some workers as one of the most serious effects of leaf rust.

CALDWELL *et al.* (1934) found that phosphorus and ash in the wheat grain were unaffected by leaf rust.

There is disagreement in the literature as to whether leaf rust causes shrivelling of the grain, a serious degrading factor that is a common result of stem rust. BOLLEY AND PRITCHARD represent one extreme view when they state (1906) that any rust which kills the foliage by the dough stage will cause shrivelled grain under ordinary soil and weather conditions. BARCLAY made similar observations (1892) and TEHON (1924) also states that leaf rust sometimes badly shrivels grain. At the other extreme we have numerous assertions by JOHNSTON, HUMPHREY, HAYES, CALDWELL, and others that leaf rust does not normally cause the grain to shrivel.

Epiphytotic leaf rust is usually followed by the harvesting of more or less shrivelled grain. On the other hand, little shrivelling is seen in greenhouse infection experiments. MAINS gives a clue to the situation when he points out (1930) that leaf rust combined with dry weather results in shrivelled grain. It may be that wheat growing under ideal conditions except for leaf rust infection is capable of producing plump grain, but such ideal conditions rarely occur outside the greenhouse, and one can well understand how wheat under the strain of heavy leaf rust infection, with excessive water loss and reduced photosynthesis, could be quite unable to produce plump grains when to this strain are added the rigors and hazards of nature. Although leaf rust alone may not cause shrivelling, it is certainly one of the leading factors which combine to produce this effect.

The official grading of wheat grain for quality includes consideration of a number of the points discussed above: protein content, color, presence of yellow berry or of shrivelling, test weight, and general appearance of the grain. Since leaf rust is detrimental to each of these factors, the market grade is an over-all expression of the effect of leaf rust on grain quality.

PETURSON and NEWTON (1939) in sulphur dusting experiments with two wheat varieties that are resistant to stem rust but not to leaf rust, in which the comparison was between two degrees of leaf rust intensity, found that the protected wheat (with 13 to 32 % leaf rust) in all cases was placed

one grade higher than the unprotected wheat (with 33 to 77% leaf rust). GREANEY has also recorded extensive data on the market grades of dusted and undusted wheat, but in general it is not possible to determine to what extent leaf rust, rather than stem rust, was responsible for the lowered grades regularly received by the more heavily rusted, unprotected wheat.

The flour and its bread-making qualities can be adversely affected by leaf rust. PHIPPS (1938) found that the volume of loaf produced was reduced from 578 to 510 cc. (standard bake) and from 708 to 640 c.c. (bake with Nymalt improver) when the flour was from leaf rusted wheat; his photographs illustrate these differences. Such flour also made dough that was slightly less firm to handle and developed faster than normal. Dough of flour from non-rusted wheat showed lack of gassing with long fermentation but still gave the best loaf. Indiana workers have also reported reduction of loaf and cake volume and time-test value with flour from leaf rusted wheat. In Canada, PETURSON and NEWTON (1939), who were comparing wheat with two intensities of leaf rust, and not rusted with non-rusted wheat, found that the flour from the more heavily rusted wheat, besides being lower in protein, had a higher carotene value (which imparts an undesirable color to the flour), but under the conditions of their tests they did not observe any great differences in loaf form and volume or dough strength using the flours from the wheats with two rust intensities. LUKYANENKO (1934) found the milling and baking quality, expressed numerically, dropped from 88.8 to 80.0 in the flour from leaf rusted wheat Ukrainka as compared with that from the resistant Hybrid 622. GREANEY *et al.* (1941) have furnished many data on the lowered milling and baking qualities of flour from rusted wheat, but it is difficult to distinguish the effects of leaf and stem rusts in these data.

Many years ago, BOLLEY found that the light, small seed from a rusted wheat crop, when planted, produced seedlings that were thin-stalked, narrow-leaved, with weak vitality and poor power of stooling, and which were likely to die if the soil was poorly drained, heavy and cold, or dry after germination. Farmers' experiences also seem to bear this out, as seen by their disinclination to use the small, light grain as seed. Following the 1938 leaf rust epiphytotic many Oklahoma farmers considered the harvested grain unfit for seed, and resorted to use of the 1937 crop or to importation of seed wheat for planting the 1939 crop. RUSAKOV (1925) observed a similar situation following the epiphytotic of 1923 in Russia.

This represents a twofold loss to the farmer. First there is the loss in cash value of wheat that is unfit for seed and must be marketed for milling at a low price or even be used as a low grade stock feed. This loss is especially marked when the crop had been planned for production of certified seed. A second loss is represented by the necessity of importing seed at a higher price than the home-grown product and which sometimes, as was the case in Russia in 1923, is of varieties or strains unadapted to local growing conditions. Even if seed of the preceding crop is used, there is a loss represented by the cost of an additional year of storage of the seed.

Additional confirmatory data on the quantitative and qualitative effects of leaf rust are to be found in the paper by PETURSON, NEWTON, and WHITESIDE (1945), received after the foregoing sections had been printed.

Effect on fodder yields: — In addition to reduction of grain yields, leaf rust often causes a notable loss in the mass of vegetative parts, and whether these have cash or feeding value or are returned to the soil to increase its humus content, this form of loss must be added to our account with *Puccinia triticina.*

In some areas, *e.g.* southern Texas and Australian coastal areas, wheat is regularly grown exclusively for hay or grazing, and in winter wheat regions an important return from the crop is the winter pasture it affords. Even in leading wheat regions, farmers often look upon the pasturage as the principal form of harvest from the wheat crop. Moreover the straw has many valuable uses. Leaf rust may markedly reduce the yield of the vegetative parts of the wheat plant, as can be seen from the following examples.

CALDWELL and his coworkers (1932, 1934, 1938) in several experiments found straw yields reduced from 10 to 18% by moderate to heavy rust attacks. JOHNSTON and MILLER (1934) reported that if plants were heavily rusted from the seedling stage to maturity, straw yields were reduced as much as 33%. In MAINS' experiments (1930) the loss in straw as a result of leaf rust varied from 11 to 70%. Combining and averaging the figures from these last mentioned workers, we find that heavy rust from the seedling to tillering stage onward resulted in 44.9% loss in straw yield, from the jointing stage onward, 40% loss, from the boot stage onward, 23.2% loss, and from the blossoming stage onward, 10.8% straw loss. Comparable losses were observed by PETURSON, NEWTON, and WHITESIDE (1945). Much smaller losses were reported when the rust intensities were lower or the stage at which rust developed was later, as seen in sulphur dusting tests (CALDWELL *et al.* 1934) and comparisons of resistant and susceptible genetic families (LUKYANENKO 1934) as well as in artificial inoculation experiments (JOHNSTON and MILLER, 1934).

In Russia, LUKYANENKO found that 65-100% of leaf rust reduced wheat straw yields 12-20%, and 25-40% of rust reduced them by 4-18%. Thus, on the average, the straw losses are significantly high, although less than half as great as the grain losses for the same rust intensity at any given stage of host development.

Leaf rust can cause a serious, though, as yet, unmeasured loss, in winter wheat pasture in the southern Great Plains, as in 1940, 1942, and 1944 when pastures in Kansas and Oklahoma were noticeably yellowed and dried. In western Siberia, rust in the fall may reach an intensity of 40%, and there are similar reports from Australia .

It has been pointed out that leaf rust causes a very considerable reduction in the yield of the vegetative parts of the wheat plant. We also find that these parts are chemically altered as a result of the disease.

In the normal wheat plant there is a progressive decrease of sugars in the leaves, stems, and chaff as the plant approaches maturity (Anon., 1937). However, in the leaf-rusted plant there is a greater loss in reducing sugars, sucrose, and starch than in the normal plant, proportionate to the degree of rust intensity. CALDWELL and COMPTON (1938), MAINS (1930), and JOHNSTON and MILLER (1934) call attention to color changes in the straw, and to the leaf-rust-induced inhibition of the red color of the

straw that is normal in some wheat varieties, which also is indicative of carbohydrate shortage.

While this abnormal decrease in carbohydrates appears to be primarily due to the decreased amount and energy of photosynthesis in leaf-rusted plants, ALLEN's histological studies (1927) indicate that there can be modifications of the carbohydrates in infected plants related to the enzymatic activity of the leaf rust fungus. She finds, in plants that are incompatible with the fungus, that there is induced a decomposition of the cell walls beyond the seat of infection, with the production of pectin which gelatinizes, swelling the cell walls, and she considers that this is probably due to pectinase activity on the part of the fungus, breaking down the middle lamella.

Accompanying the decrease in carbohydrates, many workers have noted an increase in the proteins and other nitrogen-containing substances of leaf-rusted vegetative parts. BOLLEY and PRITCHARD (1906) cite Canadian tests in which rusted wheat straw was found to contain 7.64% of protein as compared with 2.44% in normal straw and SUKHORUKOV (1938) found that rusted wheat leaves contained more urea and ammonia than healthy ones. The most extensive study of the nitrogen content of leaf-rusted wheat is that of GASSNER and FRANKE (1938). These workers determined that in the healthy wheat plant, as the leaves grow older, the ratio of protein N to soluble N decreases, the soluble N remaining constant while the amount of protein N falls. In leaf-rusted plants there was little nitrogen difference from healthy plants for the first two weeks after inoculation but very great differences were noted beginning 21 days after ioculation. There was 21 times as much protein N, 10 times as much soluble N, and 16 times as much total N in the rusted plants.

These results were obtained with a highly susceptible variety. When the experiment was repeated with a resistant variety, differences of the same type, but much less striking, were noted. Similar but even more striking results were obtained when the experiment was performed with plants grown in sand culture in nutrient solutions of different nitrogen levels.

Nor was this nitrogen increase merely relative, proportionate to the decrease in carbohydrates. GASSNER and FRANKE determined that there was more nitrogen in absolute amounts in rusted than in healthy leaves.

There are several possible ways of accounting for this excess of nitrogen in the rusted plant, none of which has been satisfactorily proven. GASSNER and FRANKE consider that it could not be due to the nitrogen of the rust mycelium because the mass of the latter is far too small to account for the absolute increases in nitrogen. These workers attribute the nitrogen excess to the failure of inoculated plants to lose nitrogen as healthy plants do with advancing age.

But there is another, particularly interesting possibility. D'OLIVEIRA in Portugal (1939, 1940*a*) grew wheat and barley plants in water or nitrogen-free media with and without rust infection. He confined his experiments to work with *Puccinia glumarum, P. anomala,* and *P. graminis,* and we can only apply them to *P. triticina* by analogy. Gravimetric analysis of the seedlings showed that those which were rust-infected con-

tained considerably more absolute nitrogen than the normal plants, and the longer the plants had been rusted the greater was this difference. It cannot be concluded that the difference was due to the loss of nitrogen contained in the seed by the healthy seedlings, and inhibition of this loss in the rusted plants, because the nitrogen determinations for the healthy plants were practically invariable over the period of the experiment, while those for the rusted plants steadily rose, well above the original N content of the healthy plants. This leads to the intriguing conclusion that the rusts are able to fix atmospheric nitrogen, and if this is borne out by future experiments, it will serve to explain, in part at least, the high N content of rusted plants in comparison with healthy ones. D'OLIVEIRA also considers that this may explain the long-retained greenness of leaf tissues about rust lesions (*see* page 48) when uninfected leaf tissues have become fully yellowed.

At the Oklahoma Agricultural Experiment Station there is a plot of land that has been cropped continuously with wheat for 53 years. Part of this plot has been unfertilized, and part manured. The unfertilized part still yields an average of 12 bu. per acre (the average for wheat production in Oklahoma). Nitrogen fixation by the rust may explain the otherwise almost unaccountable source of nitrogen to permit such yields after 53 years of cropping without fertilization. A comparable and even more striking case in point is that of the famous Broadbalk wheat plots of the Rothamsted Experimental Station, which in 1943 bore their 100th successive crop of wheat.

Many years ago it was commonly believed by farmers that the feeding to livestock of rusted hay could result in such symptoms of poisoning as colic, bloody urine, and intestinal disturbances, and some maintained that these symptoms ceased when the rusty hay was removed. ERIKSSON and HENNING (1896), opposing this view, pointed out that in the rust epiphytotic year 1889 in Sweden (when stripe rust was probably the dominant disease) there was not reported a single case of cattle poisoning associated with feeding of rusty straw, and believed that the poisoning previously reported was due to some other property of the feed than its rustiness.

In America, BOLLEY and PRITCHARD (1906) found that a similar view was held by farmers, but they contended that there is much evidence against the toxicity of rusty hay or straw, and indicated that cattle eat it with great relish, when it is properly cured, and without signs of poisoning. They suggested that the poisoning suspected of being due to rust was actually the result of eating water hemlock which is common on undrained fields. ARTHUR (1929), without specifically mentioning wheat leaf rust, states: "It is probable that no member of the rust family, when eaten, possesses toxic properties injurious to animals or man." Despite the great amount of wheat that was abandoned for grain in Oklahoma in the 1938 leaf rust epiphytotic, and in many cases used for hay or forage, no case of resultant toxicity has come to the writer's attention, although he was in the logical position to receive such reports and Oklahoma farmers are alert to report livestock poisoning from various poisonous plants.

On the other hand, we have ARTHUR'S authority (1929) that anaphy-

lactic reactions in man may be due to various rusts. He cites a letter from Mr. F. T. CADHAM advising that cutaneous reactions of two patients suffering from asthma were equally pronounced with uredospores of wheat leaf rust and stem rust, and since there have not been observed serological differences between any of the grain rusts tested for anaphylactic reaction, ARTHUR concludes: "Doubtless the spores of any of the grain rusts are likely to be pathogenic to susceptible persons. As the air is often laden with urediniospores in the vicinity of grain fields, especially at harvest time, such a source of infection [*i.e.* sensitization] is highly probable."

Possible benefits of the rust: — CARLETON, who, we will recall, considered leaf rust as practically non-injurious to wheat, went so far as to consider it beneficial at times, by preventing too much top growth at the expense of grain, and he mentions observations in which the worst rusted plants produced the best grain (1899). He cites a statement of LITTLE (1883) to the effect that in the English fens, leaf rust is beneficial by reducing excessive luxuriance of the wheat. The lack of experimental verification of this notion and the very extensive data on the destructiveness of leaf rust reported in this chapter do not justify further consideration of this alleged benefit of leaf rust.

There is, however, one way in which wheat leaf rust may possibly be of limited benefit. It has been pointed out that rusted wheat hay contains much more protein than healthy wheat hay. Considering the high value and cost of protein in livestock feed, it is conceivable that under conditions of light or moderate leaf rust, where the crop is used for hay or forage, the increased amount of protein might represent greater feeding value than the accompanying loss in carbohydrate and dry weight, and in times of severe leaf rust epiphytotics, where potential grain yields are low, the use of the crop as a protein-rich source of feed might be a valuable means of salvaging some of the loss otherwise sustained from the rust. This is a point well worth experimental study.

The "benefit" of rust or any other crop calamity in averting the unsettling effects of crop surpluses is a controversial matter in the field of economics, and need not be discussed here.

Chapter IV

SUSCEPTS

From the practical point of view, *Puccinia triticina* is purely a pathogen of wheat. No other crop of economic importance is subject to the attack of this fungus to more than an inconsequential degree. The uredinial and telial (orange and black rust) stages, however, may occur on a few related members of the *Gramineae,* while the alternate pycnial and aecial stages, although absent in nature throughout most of the world, have been shown experimentally to be capable of infecting species of *Thalictrum,* the meadow rue, and have been found naturally on *Isopyrum* (*Leptopyrum*) *fumarioides,* the basilisk, in Siberia, these alternate hosts both being members of the crowfoot family, the *Ranunculaceae.*

Species of grains and grasses: — With one or two very minor exceptions, susceptibility to the uredinial-telial stage of wheat leaf rust is confined to but one of the numerous tribes of the *Gramineae,* namely the *Hordeae,* the tribe which includes the cultivated cereals, wheat, barley, and rye, and a few closely related wild relatives of these.

The wheats are the natural hosts of *Puccinia triticina* and among them we find the highest degree of susceptibility to this rust. Yet this susceptibility is by no means universal in the genus *Triticum,* in which there are displayed all degrees of susceptibility and resistance from the one extreme represented by *T. aestivum* var. Cheyenne which is highly susceptible to all races of leaf rust with which it has been tested, to *T. timopheevi* at the opposite extreme, which appears to be very nearly immune from leaf rust.

There is an interesting correlation between chromosome number and leaf rust reaction among the species of *Triticum.* A high degree of susceptibility is characteristic of all the species with the haploid number of 21 chromosomes (*T. civerstormum, compactum, macha, spelta, sphaerococcum, vavilovi,* and *aestivum*). The 7-chromosome wheat, *T. monococcum* is characterized, on the other hand, by a very high degree of resistance to leaf rust. The 14-chromosome group, while in general characterized by moderate to high resistance to leaf rust (*e.g.* in *T. dicoccoides, dicoccum, durum, polonicum,* and *timopheevi*), includes species which are predominantly resistant but contain varieties that under some circumstances show a moderate degree of susceptibility (*T. orientale, persicum, pyramidale,* and *turgidum*). The 14-chromosome wheats, as a group, are thus intermediate in reaction between the highly susceptible 21-chromosome group and the highly resistant 7-chromosome *T. monococcum,* though behaving more nearly like the latter.

Although given species are characterized as very susceptible (*e.g. T. aestivum*) or resistant (*e.g. T. dicoccum*), such species are not necessarily

homogeneous in rust reaction but contain varieties that under some conditions display rust reactions that are atypical for the species as a whole.

The goatgrasses are so closely related to the wheats, that some authorities, such as ENGLER-PRANTL and the Index Kewensis, list *Aegilops* under *Triticum*. It is not surprising, then, to find a number of *Aegilops* species which are moderately or even very susceptible to races of leaf rust that are important on wheat. Likewise the wheatgrasses (*Agropyron*), which bear close relationship to wheat, are in some cases susceptible to leaf rust. WATERHOUSE (1936) has found race 26 of *P. triticina* occurring naturally on *Agropyron scabrum* in Australia. The majority of species of both *Aegilops* and *Agropyron,* however, are resistant to or immune from *Puccinia triticina.* The wild ryes, species of *Elymus,* for the most part are resistant or immune, but are variable with a slight to moderate degree of resistance being shown in a few cases.

The cultivated and wild barleys (*Hordeum* spp.) in general are resistant to wheat leaf rust, although, as is true of the other grains and grasses, they have their own leaf rusts to contend with. Those who have obtained infections on barley inoculated with wheat leaf rust spores report that the infections are less indicative of susceptibility than in wheat; the rust pustules are smaller with a greater tendency for them to be surrounded by the chlorotic zones that characterize uncongeniality between host plant tissues and rust fungus. NEWTON and BROWN obtained susceptible-type infections of barley by hypodermic inoculation of embryonic tissues with wheat leaf rust spores; however, as soon as the tissues passed beyond the embryonic stage they became very resistant. *P. triticina* does at times infect barley in nature, but apparently with only a low grade type of infection, and not on a broad scale. The resistance of barley to wheat leaf rust coupled with its susceptibility to wheat stem rust, has made barley useful in stem rust studies, in that mixtures of the two rusts can usually be freed of the *P. triticina* component by a passage through barley. Sometimes, however, the leaf rust persists through such a passage (JOHNSTON, 1936).

Commercial rye shows a still higher degree of resistance to wheat leaf rust, and the genus *Secale* as a whole is resistant or immune with the exception of occasional cases in which a moderate or uncongenial type of susceptibility is expressed.

The remaining members of the *Hordeae,* grasses of the genera *Haynaldia, Hystrix, Lolium,* and *Nardus,* are all reported to be resistant to wheat leaf rust in greater or less degree. Some 250 species of more than 70 genera of grasses in the other tribes of the *Gramineae* have all been found to be highly resistant to or immune from the wheat leaf rust with two doubtful exceptions, so that we may conclude that for all practical purposes susceptibility to *Puccinia triticina* is confined to certain genera of the *Hordeae.*

Intergeneric hybrids of the Hordeae: — So far as rusts are concerned, in the numerous wheat-rye hybrids which have been obtained and tested, the hybrids partake of the wheat parent's reactions: susceptibility to wheat leaf rust and resistance to rye leaf rust, *Puccinia dispersa.* Natural *Aegilops-Triticum* hybrids are also very susceptible to *P. triticina,* but Michel's grass, which may be a hybrid between wheat and *Elymus condensa-*

tus but which has the general characteristics of rye, is reported as practically immune from wheat leaf rust. JOHNSTON (1940) explains the susceptibility of wheat-rye hybrids on the basis of the genetics involved. Since rye has only 7 chromosomes and common wheats have 21, hybrids are highly sterile; fertility has been established by repeated back-crossing with wheat, which has given the progeny a preponderance of wheat characters.

Resistance or immunity of wheat to the leaf rusts of other grains and grasses: — Just as most other *Gramineae* are resistant to wheat leaf rust, so is wheat, in general, resistant to or immune from the morphologically similar forms of leaf rust that have as their principal hosts other *Gramineae*. Numerous investigators have failed in attempts to transfer rye leaf rust (*P. dispersa*) to wheat by use of either aeciospores or uredospores. A number of species of grass leaf rusts have aecial stages on the meadow rue, *Thalictrum* spp., which also is infected with *P. triticina*. MAINS (1932) has shown, however, that aeciospores from *Thalictrum* will infect wheat only if they are of the wheat leaf rust, and not if they are of leaf rusts of other *Gramineae*.

Reactions of wheat varieties of commercial importance: — It is not the purpose of the present work to give a detailed account of the rust reactions of the large number of wheat varieties grown commercially, but rather to make such generalizations as are warranted, to point out some noteworthy individual cases of rust reactions, and to indicate the sources of data on leaf rust reactions in the different wheat-growing areas of the world.

Until recently no wheat with adequate resistance to leaf rust has been grown comercially in America. In discussing the results of breeding for leaf rust resistance in Chapter XV, there is given a list of the new, leaf rust resistant American wheat varieties, with some of their other characteristics (TABLE 19). Without important exception, it can be said that all other commercial American common and club wheats are susceptible to leaf rust to an undesirable extent. The durums, as a class, are resistant.

Many workers agree that on the average the hard wheats are less susceptible to leaf rust than the soft wheats. No such generalization can be made in comparing the winter with the spring wheats; some investigators consider that the winter wheats as a group are more resistant than the spring wheats and some claim the reverse. In each of the main classes of common wheats, — hard and soft red winter, white winter, and red and white spring, — there are a few varieties with greater or less resistance to leaf rust, although in each class the majority of varieties are susceptible.

The principal sources of data on the reactions of North American wheat varieties are: mimeographed annual reports of variety trials by the U. S. Department of Agriculture and the State Experiment Stations, and a mimeographed summary, "Reaction of wheat varieties to the major diseases and Hessian fly", in which the leaf rust data are compiled by JOHNSTON, CALDWELL, COMPTON, and HUMPHREY; a similar list by CARTWRIGHT and SHANDS (1944); many records in the "Plant Disease Reporter" and the annual summaries of plant diseases of the Canada Department of Agriculture; reports of the State Agricultural Experiment stations, particularly

those of Indiana, Kansas, Georgia, and North Carolina; articles on registration of new wheat varieties in the Journal of the American Society of Agronomy; CLARK and BAYLE'S "Classification of wheat varieties grown in the United States in 1939" (U. S. Dept. Agr. Tech. Bull. 795. 1942); the "Handbook of Canadian spring wheat varieties" of NEWMAN, FRASER, and WHITESIDE (Can. Dept. Agr., Farm. Bull. 18. 1937); and the publications of CALDWELL, CARLETON, JOHNSTON, MAINS, MELCHERS, NEWTON and her associates, SCHAAL, WOODS, and others.

Principal sources of the leaf rust reactions of foreign wheat varieties are: — Argentina: RUDORF and JOB (1934), RUDORF *et al.* (1933), VALLEGA (1942*b*, 1944); Australia: COBB (1890-1894), MCALPINE (1896), MACINDOE (1933), WATERHOUSE (1938); Austria: SCHILCHER (1935*b*); Bulgaria: DODOV (1931*a*); Chile: VALLEGA (1942*a*); China: WANG (1942); France: BEAUVERIE (1923), FOËX (1924), GUYOT (1924), FOËX *et al.* (1924), MOREAU (1925), JOESSEL (1926), Anon. (1931), RIVIER (1932), Anon. (1934); Germany: KÖRNICKE and WERNER (1885), SORAUER (1909), VON KIRCHNER (1916), RUDORF (1927), SCHEIBE (1928, 1930*a*, 1930*b*), HUBERT (1932), CÂLNICEANU (1934), VOHL (1938), HASSEBRAUK (1940*c*); Holland: WELLENSIEK (1930); India: HOWARD *et al.* (1922), MEHTA (1940); Italy: PETRI (1927), RIVERA and CORNELI (1929), SIBILIA (1935b), MONTEMARTINI (1939); Japan: ASUYAMA (1936); Poland: RALSKI (1936, 1938, 1939); Rumania: SĂVULESCU *et al.* (1937), RĂDULESCU (1939/40); Russia: LITVINOV (1912), VAVILOV (1913, 1919), RUSAKOV and POKROVSKI (1928), FOMIN (1935), STEFANOVSKII (1936, 1937), GORLENKO (1936*a*), BARMENKOV (1939), NAUMOV (1939), BROYAKOVSKI (1940); Sweden: ERIKSSON (1896, 1897); Uruguay: GASSNER (1919, 1932), SPANGENBERG (1932).

Noteworthy cases of individual variety reactions: — Certain varieties of wheat are so highly susceptible to most or all of the known physiologic races of leaf rust that they are useful in "spreader rows" to increase inoculum potential in variety testing plots, as well as for culturing mixed populations of leaf rust in the greenhouse. These include Cheyenne and Little Club which are susceptible to all physiologic races of leaf rust against which they have been tested. Other varieties which have been used abroad for this purpose are: Strubes Dickkopf, Michigan Bronze, Ukrainka, Vbirali, Hohenheimer, Wilhelmina, Quax, and Agra local.

Due probably to a gradual change in the race composition of leaf rust in North America, certain varieties that were formerly regarded as resistant are now classified as susceptible. This applies to such well-known commercial varieties as Kanred, Marquis, and Mediterranean, and is particularly well illustrated by Turkey. In the U. S. Department of Agriculture Yearbook of Agriculture for 1898, Turkey was listed as leaf rust resistant, and in 1899 it led the list of varieties recommended for leaf rust resistance by CARLETON. In various records in the "Plant Disease Reporter" from 1919 to 1924, it was sometimes listed as resistant, sometimes as susceptible. Since that time, Turkey has been reported as susceptible, and in the 1938 epiphytotic it was one of the most heavily rusted commercial varieties in Oklahoma and Kansas.

In Chapter XV, in connection with breeding for rust resistance, are mentioned the principal leaf-rust-resistant wheat varieties abroad.

Aecial stage on Thalictrum (Meadow rue): — Prior to 1919 many fruitless attempts had been made by various workers to determine the occurrence of the O-I stage in the developmental cycle of *Puccinia triticina* by inoculating various species with basidiospores of the rust. The chief investigators concerned were ERIKSSON (1899) and KLEBAHN (1900, 1904), and to their negative results may be added the subsequent ones of JACKSON and MAINS (1921*b*), and D'OLIVEIRA (1940*b*). Their materials included 52 species of 19 plant families, with particular attention directed at families known to contain aecial hosts of closely related rusts (*Puccinia rubigo-vera* in the sense of MAINS, 1932). None of these, including the alternate hosts of the leaf rusts of rye, barley, and oats, proved susceptible to *P. triticina.*

In 1919 JACKSON and MAINS undertook a series of infection experiments in which they succeeded in producing pycnia and aecia on species of *Thalictrum,* the meadow rue, but on none of the many other genera tested. The work was continued in 1920 and published in 1921. Proof of this heteroecism was completed when aeciospores from species of *Thalictrum* were sown on wheat and produced typical uredinia and telia of *Puccinia triticina.* Strong infection with production of numerous aecia occurred only on 4 exotic species, two of them, *T. delavayi* and *T. flavum,* of Asiatic origin, and two others unnamed. Tests on several other species of *Thalictrum,* indicated more or less uncongeniality with *P. triticina,* and this includes the two American species used, *T. dioicum* and *T. polygamum.*

In later years other investigators extended our knowledge of the capability of *Thalictrum* species to act as intermediate hosts of *P. triticina,* particularly EREMEEVA in Russia, MEHTA in India, ITO in Japan, WATERHOUSE in Australia, and D'OLIVEIRA in Portugal. This work has shown that on the whole the degree of susceptibility of the genus *Thalictrum* to *P. triticina* is not high. Of about 30 species tested, only 5 have been reported as showing strong susceptibility, and there are conflicting reports for 3 of these. A number of the species are highly resistant or immune. There is no good correlation between susceptibility and geographic home of the species; those five which are susceptible are native, respectively, to China, Europe and Asia, the Himalaya region of India, Europe, and, in the case of *T. minus,* Europe, Asia, and Africa.

Following JACKSON and MAINS (1921*b*), the completion of the demonstration of *Thalictrum* as intermediate host of *P. triticina* by carrying the infection from *Thalictrum* back to wheat has been confirmed by EREMEEVA (1926), DUCOMET and SCHAD (*in* DUCOMET and FOËX, 1925), ALABOUVETTE and MENERET (1927), and ITO (1934).

A complicating feature of the relationship of *Puccinia triticina* to *Thalictrum* lies in the fact that species of *Thalictrum* are susceptible to a number of other rusts which have evidently been frequently confused with *P. triticina.* None of these species or races on *Thalictrum* except *P. triticina* attacks wheat, yet they may be very similar morphologically to *P. triticina,* and in such cases infection tests on *Gramineae* are necessary to determine their identity.

Aecial stage on Isopyrum (Leptopyrum): — Fruitless efforts to demonstrate the inclusion of *Thalictrum* species in the developmental cycle of *Puccinia triticina* in eastern Siberia (Lake Baikal region), combined with the logical necessity for functioning of an intermediate host of this rust in that area, led BRIZGALOVA into a search for some other aecial host of this rust. An obvious suspect was the perennial Ranunculaceous weed, *Isopyrum* (*Leptopyrum*) *fumarioides*, the "basilisk", which is very commonly found heavily infected with aecia on wheat fields in this area. In 1935, BRIZGALOVA inoculated wheat with these aeciospores and produced typical *P. triticina*. Later (1937*a*) she was successful in the reverse experiment of infecting *Isopyrum* with basidiospores of *P. triticina* from wheat.

Isopyrum or *Leptopyrum* species, although they occur elsewhere in the world, including North America, have not been reported as suscepts of *P. triticina* except in Siberia. The only rust described on the American species *I. biternatum* is *Puccinia rubigo-vera agropyrina* which has grasses but not wheat as uredial-telial hosts. *I. biternatum* is the only species of *Isopyrum* in the wheat belt of the United States; 3 or 4 additional species occur on the Pacific slope but these have not been reported as hosts of any rust species. MAINS (1932) was unable to infect *I. biternatum* with basidiospores of *Puccinia triticina* from wheat.

Chapter V

SYMPTOMATOLOGY

Gross signs and symptoms on wheat: —As the name "leaf rust" suggests, the uredinia and telia are predominantly on the leaves; however they are not restricted to these, but are frequently found on the leaf sheaths and occasionally on the culms, just below the heads. They also may occur on the glumes and awns, but probably not on the kernel itself, as sometimes happens in the case of stem rust. While culm infection is reported as rare, MELCHERS (1917) has found as much as 10-25% infection on culms. ERIKSSON, who first described infection of the sheaths (1897) noted that with equal leaf infection some varieties had sheath infection while others did not.

The uredinia, while occurring on both sides of the leaf, are commonest on the upper surface, and the reverse is true of the telia. As the mycelium extends through the entire thickness of the leaf, it is common to find a pustule on the upper surface with a later-formed one directly under it on the lower surface. Both types of pustules are scattered at random over the surfaces of the leaves, which led ERIKSSON to apply the name *"dispersa"*, in contrast to the grouping of pustules in rows or in limited areas of the leaf, as in stripe rust. Eventually the whole leaf may be uniformly covered with pustules, at a concentration as high as 200 per sq. cm., but even in this case the pustules, in general, remain distinct, not becoming confluent. The telial pustules, when they occur on the culms, tend to be arranged lengthwise of the culm in rows. They are often confluent.

When uredinia are few, and not crowded, it is customary to find, 10 days to 2 weeks after the appearance of a uredinium, that this is surrounded by a complete (or partial, if abutting on a vein) circle of smaller uredinia. This has been illustrated by ARTHUR (1929), DODOV (1931*b*), and ALLEN (1926). Sometimes there may be 2 or 3 such circles of secondary uredinia about a primary one.

The characteristics of uredinial lesions in wheat varieties with varying degrees of resistance to leaf rust will be considered in another connection (pages 74-75).

The uredinia are quite variable in size and form. They are smaller than those of stem rust, measuring .5 — 2 or even 3 mm. × .5 — .8 mm. or less, and are roundish to elongate or elliptical; with increasing intensity of infection the pustules are smaller than when they are few in number. At first they are subepidermal, but soon the epidermis ruptures with a longitudinal slit, exposing the powdery masses of spores, and leaving an inconspicuous white collar of epidermis surrounding the pustule.

The color of the spore masses has been variously described as red, orange, yellow, orange-red, orange-yellow, orange-brown, rust-brown, cinnamon-brown, ferrugineous, brown-ocher, reddish brown, and "terra

sienna". Part of this variability is due to the fact that the color of the spore masses changes as they vary from moist to dry conditions. SCHAFFNIT (1909) attributes the color to a lipochrom (xanthin), the molecules of which become more thickly layered as the spores lose water or as they become more mature, producing a progressive darkening of them.

The better published illustrations of this stage include the excellent colored plates of ERIKSSON and HENNING (1896) and MCALPINE (1906), and figures in the works of BOEWE (1939), MAINS (1930), MAINS and JACKSON (1926), MAINS *et al.* (1926), BOLLEY (1889*a*), BOLLEY and PRITCHARD (1906), E. J. BUTLER (1918), DODOV (1931*b*), NAUMOV (1939), PETRI (1927), PLOWRIGHT (1882), and CHESTER (1942*b*).

Many observers have noted that the huge quantity of uredospores floating in the air during epiphytotics may be such as to stain clothes and other exposed objects with brownish masses of spores. SĂVULESCU reported that during a rust epiphytotic in Rumania in 1932, the leaves of books in his laboratory were entirely covered with air-borne uredospores. In the 1938 epiphytotic the writer (1939*c*) received a number of wheat samples from mill operators and farmers who inquired about the red discoloration of the brush ends of wheat kernels. This proved to be due merely to large numbers of air-borne spores entangled in the brush. RUSAKOV (1927*c*), in reply to a questionnaire regarding rusts in Russia, received comments mentioning "fogs and rains like blood", "yellow dews", "yellow coating of vegetation", "yellow fog", "red dews observed almost every day", in all cases associated with rust epiphytotics.

In recounting the signs of leaf rust one cannot disregard the organisms often associated with it. One of these is the hyperparasitic fungus *Darluca filum,* the shiny, dark, globose pycnidia of which may be so numerous in parasitized leaf rust uredinia as to give them a distinctly blackish cast. Uredinial pustules under very moist conditions sometimes become overrun with species of *Fusarium,* so as to give the uredinium a cottony, pinkish or white appearance. In fields in which the rust is abundant, the writer has often seen large numbers of the small, black Phalacrid beetle, *Phalacrus politus,* feeding on leaf rust spores, and there are other insects and fungi associated with the rust (*see* page 177) which are to be included as signs of the disease.

The telia are oblong, rarely linear in shape, sometimes arranged in lines. They remain long covered by the epidermis, not bursting forth in powdery masses as do the uredinia. In color they are described as lead-gray, "atrofusca", blackish-brown, black to dark brown, dull black, or blackish. Above them the epidermis bulges out slightly, but is unbroken. They are usually found on tissues that are dying, yellowed or brownish, and shrivelled.

When uredinia first appear there is usually little or no discoloration of the surrounding leaf tissues, but as the infection proceeds and especially when the lesions are numerous, the leaf becomes partially or completely yellowed and then dies. The yellowing of the foliage is such a regular and important symptom of leaf rust, that in cases of severe attack it imparts a characteristic color to fields when viewed from a distance. This was described in detail in the 1938 epiphytotic in the Southwestern Great Plains (CHESTER, 1939*c*): "When the wheat was only 9 inches high the fields

looked yellowed and scorched, and just before heading, as the uppermost leaf (the color of which imparts a prevailing color to the field) became yellow and dry, the fields took on the false appearance of ripened grain. One seasoned crop scout described this as 'death pallor' ". Later the fields again appeared green from a distance, due to the color of the emerging heads, although no green foliage remained, but as the crop approached maturity it did not have the golden color of normal grain, but was described by MELCHERS and JOHNSTON (1939) as ashy or scalded and not normal yellow.

A striking manifestation of the adaptation of leaf rust to its host plant is seen in the abnormal retention of chlorophyll in a zone surrounding a rust pustule, long after the adjacent leaf tissues have become yellowed or even dead. These "green islands" are associated with numerous other rust and powdery mildew diseases. They may be regarded as evidence of a tendency toward symbiosis in the rust-host relationship (VON TUBEUF, 1897), as a result of nitrogen fixation by the rust (D'OLIVEIRA, 1939, 1940*a*; *see* page 38), or as the climax of a long association of host and parasite in which the ability to derive nourishment from more distant tissues while preserving the vitality of its immediate site of infection is an exquisite adaptation permitting the obligate parasite to survive to the latest possible moment. Even in old, dried leaves, long since dead, one can sometimes find definite traces of the "green islands".

A usual symptom of leaf rust in resistant varieties of wheat, is the spotting or flecking of the leaves with tiny yellowed or necrotic spots which may bear no uredinia, or only minute, depauperate ones. During leaf rust epiphytotics this condition may become so noticeable as to attract the attention of casual observers. It appears to have been first described by MELCHERS and PARKER (1920).

Flecking and other types of reaction of resistant varieties, are discussed in connection with their experimental production in rust race identification (page 74 *ff.*). It should be mentioned, however, that the appearance of flecks is also sometimes associated with natural infection of susceptible varieties. For example, flecks without uredinia were observed in Kansas in the fall of 1928 and these, surviving the winter, produced uredinia in the spring (Pl. Dis. Rep. 13:23. 1929). In this case they were symptoms of dormant infection. Another such expression was seen in the epiphytotic of 1938. Examination of wheat fields just before the height of the epiphytotic, revealed great numbers of tiny chlorotic flecks on the upper leaves, which as yet bore no uredinia. Some wheat workers who observed these suspected that they were due to *Septoria tritici*. Instead they were incipient lesions of leaf rust, and with the passage of a few days these flecked leaves were all but covered with myriads of uredinia, breaking forth from the flecks. The uncommon feature of this natural step in the development of leaf rust infections lay in the great numbers of the flecks, due to the intensity of the attack, such that the leaves were well toward being yellowed by leaf rust even before the pustules appeared.

Following the display of yellowing, the leaf and sheath tissues soon die, until, in cases of severe attack, little or no living foliage may be left at

stages of wheat development in which healthy plants should have 4 or 5 normal leaves.

This loss of foliage, and the altered physiology of the wheat plant that is suffering from leaf rust, lead to marked alterations in the development of the plant as a whole and of its various organs. As these changes have already been described in detail (page 24 *ff.*), they will not be discussed further, beyond pointing out that the complete symptomatology of leaf rust includes the altered metabolism (physiological symptoms) and the developmental changes (dwarfing, abnormal tillering, lodging, accelerated or retarded maturity, and lowered quantity and quality of grain and hay yields) which are characteristic of the leaf-rusted wheat plant.

Gross signs and symptoms on Thalictrum and Isopyrum: — According to ALLEN (1932), the first symptoms on *Thalictrum* are tiny yellow flecks, less than 1 mm. in diameter, appearing 6-7 days after inoculation. These grow, according to the age and vigor of the infected leaf; if many infections are present, each remains small. Hypertrophy is characteristic of this and closely related rusts. If petioles are infected, they become swollen to 3 times their normal diameter, while infected leaf blades become distorted, thickened, and bulging at the areas of infection, until they may be 2-3 times normal thickness. The tissues are tense and spring apart when cut. The younger and more tender the leaf at the time of inoculation, the greater the resulting deformity. The infections are often described as gall-like. Individual lesions on leaves are up to 8-15 mm. in diameter and irregular in outline, limited more or less by the veins, and orange or citron yellow to reddish brown in color. They may be confluent, occupying extensive areas of the host tissue. These symptoms have been illustrated by JACKSON and MAINS (1921*b*), NAUMOV (1939), and BONDARTSEV (1931).

The pycnia occur on both leaf surfaces. They are numerous, crowded, and conspicuous; they are found beneath the epidermis and bulge out as honey-yellow, globoid or subgloboid fructifications, 80-145 μ broad and 80-130 μ high. As they approach maturity the leaf surfaces become yellow with exudation of viscid nectar, which has a delicate odor of hyacinth.

The aecia form principally on the under surface of the leaf, where they are crowded and occupy about half the thickness of the swollen leaf. Occasionally one may be found on the upper surface. They are in the form of cups or short cylinders, .2 to .6 mm. in diameter and up to .5 mm. deep, with a white or yellowish peridium, the margin of which is erose or lacerate, and recurved.

The above description applies to infection in a fully susceptible species of *Thalictrum*. When more or less resistant species are inoculated, infection is weaker and the pycnia and aecia, if formed at all, tend to be small and depauperate. The symptoms and signs have been described entirely from artificially inoculated plants, as natural infection of *Thalictrum* by *Puccinia triticina* is rare in nature if, indeed, it occurs at all.

BRIZGALOVA (1935) who discovered the rôle of *Isopyrum fumarioides* as a natural alternate host of *P. triticina* in Siberia, gives only a scant description, and no figures, of infection on this host. According to her account, the weed, from early spring onward, is very heavily infected.

Seven days after artificial inoculation of *Isopyrum* with basidiospores of *P. triticina,* yellowish spots on leaves and stems indicate sites of infection. Two to 3 days later, on the yellow, now hypertrophied spots, there appear pycnia, and a day or two later, aecia. The latter develop in great numbers on the markedly hypertrophied host tissues.

Complication of symptoms with those of other types of plant injury: — The typical picture of infection of wheat by leaf rust, as set forth in the foregoing paragraphs, may be confused with or modified by the detrimental effects of other diseases or environmental hazards. This was particularly evident during the epiphytotic of 1938, when there were numerous such complicating factors, and when many crop scouts and wheat specialists, imbued with the traditional disregard of leaf rust as a serious yield factor, could not envisage the relative significance of leaf rust in that season, and regarded the effects of leaf rust as expressions of injury from other causes.

We have seen that yellowing of wheat foliage is a principal symptom of leaf rust. Yellowing of wheat may also result from inadequate nitrogen in the soil, which in turn may be due to infertility of the soil or to leaching away of nitrates or microbial action that reduces the amount of available nitrogen, which last are associated with excessive rains. It will be seen in a later section that nitrogen deficiency sufficient to induce yellowing of wheat foliage is incompatible with leaf rust and that even in severe leaf rust epiphytotics, nitrogen-starved plants can be only weakly rusted in comparison with plants having access to adequate nitrogen. When observers associate heavy leaf rust with nitrogen starvation in the wheat plant, as VALLEAU has done (Pl. Dis. Rep. 19: 134. 1935), they are evidently confusing the yellowing caused by leaf rust with that which they attribute to nitrogen starvation.

When leaf rust and stem rust are both present in a crop, the traditional fear of the latter and disregard for the former sometimes results in attributing to stem rust symptoms that in reality are the consequence of leaf rust. We have seen that epiphytotic leaf rust alone can at times result in lodging and shrivelled grain, both of which symptoms are regularly associated with attacks of stem rust, and if both diseases are present, even though the latter is in minor amount, it is often held wholly responsible for these symptoms. In 1938 the widespread lodging of wheat was also variously ascribed to late freeze, foot rots, excessive moisture, and *Septoria* infections of the culms. The poor fill of grain that year was frequently attributed to a late spring freeze. It may be more than a coincidence that late freeze injury and leaf rust severity often seem to occur together, and hence are confused, since mild late-winter weather is both favorable to leaf rust and to late freeze injury, which is most marked on plants that come into spring activity prematurely. A discussion of these and other factors accompanying the 1938 epiphytotic in the Southwest is given in the writer's analysis of that season (1939*c*). In brief, it is evident that the various manifestations of crop injury in that year were primarily the result of the intense leaf rust attack, and not of the various other hazards cited, except locally: the areas most severely affected by the late freeze were outside the area of heavy leaf rust attack, and produced high yields; the distribution of sterility in the heads

was not such as results from freezing injury, but that associated with devitalization of the plant; stem rust injury was authoritatively appraised as very light; where leaf-rust-resistant varieties were grown beside susceptible varieties, the former, although exposed to all the other crop hazards, produced high yields, while the leaf-rust-susceptible varieties yielded poorly; and finally, we have reviewed the demonstrations, under controlled experimental conditions that severe leaf rust produces exactly those symptoms that characterized the 1938 crop in the Southwest, excepting, of course, the effects of such clear-cut additional factors as hail and the attacks of insects.

Microscopic symptoms: — We are particularly indebted to ALLEN (1926, 1927, 1932) for descriptions of the finer details of the symptomatology of leaf rust, and the following account is based mainly on her work. It refers only to the host reactions to *Puccinia triticina,* the behavior of the fungus itself, during the process of infection, being considered in a later section (pp. 55-58). The microscopic symptomatology of leaf rust is also well brought out in ALLEN's numerous published illustrations (*l.c.*) and in those of BOLLEY (1889*a*), HITCHCOCK and CARLETON (1893), and CALDWELL and STONE (1936).

The picture of host reaction in a susceptible wheat is one of tolerance on the part of the wheat cells with a minimum of injury to them until late in the infection period. As ALLEN points out, — "On the whole these infections on Little Club [susceptible] wheat form an excellent picture of congeniality between host and parasite. The rust grows freely, and the host lives on with the least possible disturbance compatible with feeding the parasite." ALLEN's studies were confined to relatively early stages in the infection period; ultimately the infected host tissues, as we have seen, become exhausted, yellowed, and die although some semblance of congeniality between host and fungus persists to the end, as indicated by the "green island" phenomenon (page 48).

Following entry of infection threads and development of mycelium and haustoria in the host tissues, the cells of the host show no injury until the 6th day after inoculation, although there is a movement of the host nuclei toward haustoria without perceptible movement of other cell contents. The host nucleus appears to be powerfully attracted by the haustorium, so that it is often flattened against the latter, or even envelops it. If the host cell has two nuclei, both attach themselves to the haustorium, or if there are two haustoria and a single nucleus, the latter may lie between or be dumbbell-shaped contacting both. The nucleus does not appear to suffer from this relationship.

The point of entry of the fungus is indicated by a discolored stoma; evidently some substance is secreted by the fungus which alters the guard cells, killing them. There is little or no observable effect on the cell walls, although occasionally they may be swollen and disintegrated at certain points. The nuclei of the stomatal accessory cells and adjacent epidermal cells reorient themselves, moving to the cell wall nearest the substomatal vesicle (CALDWELL and STONE, 1936).

A few cells may be killed and a few nuclei die early in infection, but sometimes there are no dead cells even 9 to 12 days after infection and no

more than 1 per cent dead in 16-day old infections. After the haustorium enters a cell it remains normally functional for 6 days or more. Measurements show very little reduction in the size of the plastids, which is a good indication of maintenance of cell health. In some cases there is abnormal retention of starch in the infected tissues, although in old infections starch may again become scarce, due, perhaps, to its utilization by the fungus.

The nuclei of infected tissues become elongate and somewhat pointed, though not greatly increased in volume and unchanged in diameter. (This is in marked contrast with stem rust, in which case they greatly increase in volume, collapse, and die.) Few of the nuclei die, — not more than 2 to 10% in the oldest infections studied by ALLEN.

In those few cells that die, the cell content is dissolved and homogeneous; the cell lobes become strands, and the cell is reduced to a small, irregular mass that stains intensely red with the triple stain. Other cells may be crushed and thus killed by the mycelium of the fungus, or they may be distorted by its pressure, since the older, drained hyphae swell considerably (as from a diameter of 3 μ to 5.6 μ).

In a resistant wheat, in contrast to the case of a susceptible wheat, there is a violent response of the host cells, such as to create conditions in which the fungus is unable to maintain its nutritional economy. As in susceptible wheats, the nuclei of the stomatal accessory cells move over to the side of the cell wall nearest the fungus, but here the wall of the host cell may show evidence of injury, being dark or not reacting to stains, indicating alteration of the cell walls by secretions of the fungus.

The invaded cells are killed, and minute dead seats of infection are common, consisting of a dead appressorium, substomatal vesicle, stoma, and infection hypha, leading to a single dead cell. The adjacent walls of living cells may be greatly swollen (lamellate) with slightly damaged cell contents, but the injury is localized, and nearby surrounding cells are healthy in appearance.

In resistant seedling plants the plastids of newly invaded cells are very small, — 3.1 $\times$ 1.8 μ, while those in cells just beyond the infection are intermediate in size, 3.9 $\times$ 2.5 μ, as compared with the plastids of healthy cells (5.3 $\times$ 2.7 μ). There is no excess of starch around or in the zone of infection. Outside this zone the cells show wart-like wall thickenings, and staining of these with methylene blue or ruthenium red shows that they contain pectin, indicating a decomposition of the walls into pectin which gelatinizes to swell the walls.

In older resistant plants, the plastids of the first-attacked, injured cells are very small and show a slight excess of starch. Outside the zone of infection the cell walls degenerate with warty swellings, pectinization, and gelatinization, apparently due to secretions of the fungus.

If the infection does not die out at once (due to death of the first-invaded cells), it expands slowly but with decreasing violence of host reaction until the mycelial spread may have reached a diameter of .5 mm., followed by weak sporulation. In typical seats of infection, the center cells are dead, and are interspersed with empty, often misshapen fungous hyphae. About this are abnormal cells with pectinized walls and warts, bumps, or intercellular wedges that stain almost black with the triple stain. When a

haustorium penetrates a host cell, the nucleus and cytoplasm of the latter surround or coat the haustorium, but the host nucleus soon dies, sometimes after first swelling; the plastids disintegrate into red-staining smears, and then the cell collapses. Soon the haustoria die, becoming short, thick, and deep staining, or showing concentric layers of different staining properties. In the first 100 μ beyond the mycelium the cells have reduced plastids and cytoplasm, but beyond this they look normal except that the pectin reaction of cell walls may be detected as far as 300 μ from the mycelium. It should be emphasized first, that in a resistant wheat, although the cells attacked react violently, there is comparatively little disturbance to the cells at a short distance from the infection, and second, that the violence of host reaction decreases with the age of the infection and the distance to which the mycelium has succeeded in spreading.

In *Thalictrum,* as in the susceptible wheat, ALLEN's description suggests a marked degree of compatibility between host and fungus. She mentions little direct killing of the host cells by the fungus, or other cell symptoms, except that the first cells invaded by direct penetration may die, and host cells may be crushed as the aecia expand. The primary hypha and later-formed haustoria become coated with a layer staining like the cell walls, which might possibly represent a defensive action on the part of the host cell. Accompanying the massive, subepidermal fungous growths frequently seen, the function of which is unknown, are dark-staining masses of exudate on the leaf surfaces.

The microscopic symptoms of infection in *Isopyrum* have not been described.

Chapter VI

ETIOLOGY

Technical name of the pathogen: — There are 3 concepts of the species of wheat leaf rust. One, *Puccinia triticina* Erikss., limits the species to the leaf rust of wheat (and, to a slight extent, of some closely related grasses) with its alternate stage on *Thalictrum* (experimentally) and *Isopyrum* (naturally). This is the usage followed in 95% of the wheat rust publications, including the works of GASSNER and his school in Germany, RUSAKOV, NAUMOV, and virtually all other Russian workers, CRAIGIE, NEWTON and their associates in Canada, the editors of most publications of the U.S. Dept. of Agriculture as well as STAKMAN, HUMPHREY, JOHNSTON, and CALDWELL in the United States, WATERHOUSE in Australia, KLEBAHN, SACCARDO, SYDOW, DIETEL (*in* ENGLER-PRANTL) E. FISCHER, J. H. MILLER, and many others.

The second concept, *P. elymi* Westd. or *P. clematidis* Lagerh. includes in addition leaf rusts of grasses with aecia on various *Ranunculaceae*. This was the usage of ARTHUR and FROMME in 1920, G. H. CUNNINGHAM in 1932, and KERN in 1929.

The third concept groups rusts of more than 90 species in 16 genera of grasses, with aecial stages on 36 species of plants in 25 genera of 4 unrelated families, into the composite species *P. rubigo-vera* (D.C.) Wint., which has been subdivided by MAINS (1932) into 56 named *formae speciales* one of which is *sp. f. tritici* (Erikss.) Carl., and corresponds to Eriksson's *P. triticina*. This is the usage followed by ARTHUR, MAINS, STEVENSON, G. W. FISCHER, and rarely by occasional foreign workers as ASUYAMA in Japan.

The narrow concept of *P. triticina* is preferred by the writer because (*a*) the rusts grouped in *P. rubigo-vera* in some cases show definite morphological differences (aeciospore width and shape, uredospore size and color, teliospore size, shape, and pedicel length, size of uredial sori), as well as physiological differences (requirement of pre-germination dormancy of the teliospores), because (*b*) the composite species *P. rubigo-vera* is almost without counterpart in the lack of botanical relationship among its aecial hosts, because (*c*) *P. triticina* alone is thoroughly entrenched in the literature, which last is also the sole reason why stem rust is termed *Puccinia graminis* and not *P. lineare* (ARTHUR, 1934), and because (*d*) the stricter definition of the wheat leaf rust avoids confusion in the minds of agronomists and others, since the common name of *P. rubigo-vera*, "leaf rust of grasses," leads to the false conception that the cereal leaf rusts, wheat leaf rust in particular, include infection of wild grasses as an important phase of their life cycles. Convenience is also served in the use of a narrower concept: in a literature search, for example, the student of wheat rust wastes no effort in tracing down references through the use of the key words *"Puccinia triticina,"* whereas if his key must be *"Puccinia rubigo-vera,"* the variety *"tritici"* may be omitted in indexes, thus leading the worker to many references to the grass rusts that bear no relation to the object of his search.

Morphology of the pathogen: — The earliest published technical description of the wheat rust was the brief one of DE CANDOLLE in 1815, under the binomial *Uredo rubigo-vera.* This was expanded, — still with reference to the broad concept which includes many grass rusts —, by WINTER in 1880-1884. His description of *Puccinia rubigo-vera* has been amended by COBB in 1890-1894, JACKSON and MAINS in 1921, and ARTHUR in 1934. ERIKSSON and HENNING in 1894 described their *Puccinia dispersa,* which included leaf rusts of both wheat and rye, and hence their description is a variant of WINTER'S.

ERIKSSON'S original description of *Puccinia triticina* in 1899 is given below.

"II. *Uredo triticina.* — Sori 1-2 mm. longi, .5-.8 mm. lati, ferruginei, per totam paginam folii, imprimis superiorem, sine ordine *subaequaliter dispersi,* interdum *etiam vaginam caulemque* occupantes. Uredosporae globosae-ellipsoideae, aculeatae, 19.2-27.2 μ diam., vulgo *tarde germinantes.*

"III. PUCCINIA TRITICINA. — Sori *oblongi,* atrofusci, *hypophylli, dispersi,* interdum *etiam vaginam caulemque* occupantes, epiderme tecti. Sori majores loculati; loculi paraphysibus brunneolis circumdati. Teleutosporae oblongatae-clavatae, saepe obtusae et obliquae, 30.4-38.4 μ longae, cellula basali 11.2-14.4 μ, terminali 14.4-16.0 μ latis, pedicello brevi, *naturaliter hibernatae vere germinantes.* Promycelium subpallidum."

When the aecial stage of *P. triticina* was produced on *Thalictrum* by JACKSON and MAINS in 1921, they added the following description of this stage:

"Pycnia amphigenous, mostly epiphyllous, numerous, crowded upon more or less swollen, reddish brown to yellowish areas, 2 to 15 mm. in diameter, conspicuous, subepidermal, honey-yellow, globoid or flattened globoid, 80 to 145 μ broad by 80 to 130 μ high; ostiolar filaments 95 to 190 μ long, agglutinated to form a prominent, broad column.

"Aecia hypophyllous, crowded in more or less swollen, gall-like, reddish brown or yellowish areas 2 to 15 mm. in diameter, cupulate or short cylindric, 0.2 to 0.6 mm. in diameter, up to 0.5 mm. high; peridium white or yellowish, the margin erose or somewhat lacerate, recurved; peridial cells oblong or somewhat rhomboidal in longitudinal radial section, 14 to 19 by 18 to 29 μ, abutted or slightly overlapping, the outer wall 6 to 7 μ thick, transversely striate, the inner wall thinner, 2 to 3 μ, very coarsely verrucose; aeciospores angularly globoid or ellipsoid, 16 to 20 by 16 to 26 μ; wall colorless, thin, 1 μ or less, very closely and finely verrucose."

Mycelium; cytology; sexuality: — The following account is based mainly on ALLEN'S well-illustrated study of leaf rust infection in Little Club and Malakof wheat (1926, 1927) and in *Thalictrum* (1931, 1932).

The uredinial germ tube enters the leaf through a stoma. Above the stoma the protoplasm of the germ tube becomes aggregated forming an appressorium, a hemispherical cushion of dense protoplasm overlying the stoma, leaving behind the empty remainder of the germ tube which is separated from the appressorium by a septum. There may be 2 or more appressoria overlying the same stoma, in which case the later ones to form are partly superimposed over the first. Two appressoria may fuse into one. The appressoria figured by ALLEN measure approximately 30 μ in diameter by 15 μ in depth.

From the appressorium an infection thread grows through the end of the stoma to the substomatal cavity where it enlarges to form an ovoid or irregularly ellipsoidal substomatal vesicle. Two such vesicles in a single substomatal cavity may fuse to form one. The cytoplasm from the appressorium

flows into the substomatal cavity leaving behind the empty, collapsed appressorium.

From the substomatal vesicle an infecting hypha grows inward, across the air chamber beneath the stoma, in a direction at right angles to the leaf surface. The protoplasm of the substomatal vesicle flows into this infecting hypha until the vesicle may be nearly or entirely evacuated.

When the infecting hypha comes in contact with a mesophyll cell a septum may develop just back of the hypha tip, forming a haustorium mother cell. This cell usually flattens out against the host cell wall and often becomes shoe-shaped. The contents of the haustorium mother cell then pass through the wall into the host cell through a slender tube or haustorium neck, to form a large cylindrical, worm-shaped, or sometimes irregularly branched haustorium measuring 44 μ or more in length.

Meanwhile the infecting thread becomes branched behind the haustorium mother cell. The branches produce new haustoria in the fashion described above, these branch secondarily and form more haustoria until there is an extensive, branched system of feeding hyphae and haustoria. In seedling leaves the mycelium does not attain a very massive growth or any great diameter, but in older plants the mycelial system is more massive. Here freshly growing hyphae have dense contents and diameters averaging slightly more than 3 μ, while the older hyphae are empty, and average 5-6 μ in diameter. ALLEN ascribes the limited spread of the mycelium to the weak development of hyphae that function as "runners" or "stolons."

As the infection proceeds, hyphae become concentrated at the center of the lesion and extend out under the epidermis as uredospore initials, from each of which a tip cell is set off by a septum, this cell then developing into a uredospore. With the increasing pressure of the young uredospores the epidermis ruptures and the spores are released. As the host plant approaches maturity the spore initials develop into teliospores and paraphyses, rather than uredospores, but the teliospores remain covered by the epidermis.

The uredial generation of rusts is commonly considered sporophytic and composed of binucleate cells; *Puccinia triticina,* however, shows some exceptions to this rule. The young uredospores and their stalk cells have 2 nuclei. The appressorium, when fully formed, has 4 nuclei. The substomatal vesicle commonly has 8 nuclei, although this number may vary somewhat. On the formation of the infecting hypha, one or two nuclei remain back in the substomatal vesicle; the others pass out into the hyphae. Young hyphae usually have 4 nuclei but the number is irregular, and later they appear in fairly regular groups of 3. The later developed hyphae regularly have 3 nuclei. The first haustorium mother cell probably has 2 nuclei and later formed haustorium mother cells have 3. The haustorium itself has 1 nucleus.

The cells around the margin of the developing uredinium are regularly 2-nucleate, and ALLEN suggests ways in which these could have resulted from the 3-nucleate feeding hyphae. In any case, the uredospores, produced from binucleate initial cells are binucleate themselves. This nuclear history is essentially the same in either susceptible or resistant varieties of wheat.

On *Thalictrum* the germinating wheat leaf rust sporidium produces a 4- to 6-celled hypha which penetrates an epidermal cell to form a primary feeding hypha. This soon branches, and secondary and tertiary branches

form, the hyphae growing down between the palisade cells to the more open air spaces below, sending finger- or sack-like or branched, 1- or several-celled haustoria into host cells with which they may come into contact.

After 6-7 days of extended mycelial growth, reproductive activity begins; hyphae grow to upper and lower surfaces of the leaf, producing pycnia and receptive hyphae. Hyphae mass under the epidermis. From the outset the mass shows organization, with the hyphae directed at a common center. Some of these are slender, destined to become paraphyses; others are thick and upright, and will become the buffer cells and lift up the epidermis and resist its pressure. Still others are to be spermatiophores; these are slender, tapering cells that grow in from the base and sides of the developing pycnium. Their entrance causes the young pycnium to expand and arch out into a spherical mass that crushes adjacent host cells. This swelling creates a central cavity in the center of the pycnium. Next the paraphyses pierce the epidermis to form a central outlet, the ostiole, the buffer cells wither and die, and the spermatiophores abjunct large numbers of pycniospores or spermatia which exude through the ostiole in a matrix of viscous, fragrant nectar. The spermatia, judging by ALLEN'S illustrations, are ovoid and about $1.5 \times 3\ \mu$ in size.

Meanwhile other hyphae are growing into stomatal cavities on the lower surface of the leaf. These become the "emergent" or "receptive" hyphae, and they are most numerous in infections with few or no pycnia. Hyphae continue to orient themselves toward the stomatal cavity and grow into it until it is filled with a dense fungous growth. A mass of fungous cells shaped like a biconvex lens, and immediately below the epidermis, now becomes differentiated, the cells being large and nearly empty, and these soon die. This, ALLEN designates as a "space-making" area in which the aeciospores will later arise. Bordering this area the small dense hyphal cells begin to extend down into the cavity to become sporogenous cells. At their tips the rudiments of spores are formed progressively, and as the process continues spore chains extend out into the cavity, crushing the dead cells of the "space-making" area, until ultimately the pressure of the developing aecium causes the spore mass to burst through the host epidermis as an open aecium, surrounded by a vase-shaped peridium, one fungus cell in thickness, the peridium having developed from the outermost basal cells, as the aeciospore chains were developing.

ALLEN gives the following account of sexuality and nuclear phenomena in the processes described above. The sporidium is haploid, + or —. On germinating it forms a 4-6 celled hypha in an epidermal cell which branches and develops to form a haploid mycelial system of uninucleate cells. The cells of the spermagonium and the spermatia are uninucleate, as are also the receptive hyphae.

The fungus is heterothallic, and without fertilization of this haploid mycelial system by another of the opposite sex, the system will remain haploid and no aeciospores will be formed, although sterile aecia may be formed. A haploid infection is self-sterile although it produces both spermatia and receptive hyphae.

After fertilization of the receptive hyphae by spermatia of another haploid mycelial system, the sporophytic or diploid mycelium becomes multinucleate, and this multinucleate condition advances progressively from the

receptive hyphae to remote parts of the infection. The fertilized receptive hyphae contain several nuclei, 2 to 11 or more, evidently due to multiple fertilization, not to nuclear divisions. At first the female nucleus can be recognized as larger than those introduced (male) but in later cell divisions this difference is lost and the two sexes cannot be distinguished. Fertilization usually takes place at the lower leaf surface; no pore is seen in the receptive hypha after fertilization. The change of mycelium from haploid to diploid is due either to growth of new diploid hyphae to replace the haploid ones, or to progressive "diploidization" from the receptive hypha back through the haploid mycelium already extant, — probably the former.

The multinucleate condition appears to extend continuously from the fertilized receptive hypha to the cells of the developing aecium, which contain from 2 to 12 nuclei. As the aecium matures the binucleate condition becomes established and regular. It is believed that each cell and each aeciospore then contains one nucleus of male and one of female origin as is true of other fungi, but there is no evidence concerning the process producing this condition. Young basal cells have 2 to 8 nuclei, usually an even number, but the nuclei are not paired. The extra nuclei are distributed to the young cells of the spore chain, the process soon ending in a binucleate condition. In other fungi the 2-legged appearance of the basal cells suggests, or is taken as evidence of, cell fusion, but in the case of *P. triticina* ALLEN has fully established the fact that cell fusion, resulting in the diploid condition, takes place long before the basal cells are formed.

Chemistry and physiology of the pathogen: — Very few data have been published relative to the chemical composition of *Puccinia triticina;* these concern only the content of nitrogen and coloring matter in the spores. GASSNER and FRANKE's analyses of the spores (1938) indicate that 26.75% of their dry weight is protein nitrogen and 4.42% soluble nitrogen giving a total of 31.17% nitrogen, the ratio of protein N to soluble N being 6.05. We see that these spores have an exceedingly high nitrogen content as compared with more familiar plant tissues. We recall in this connection D'OLIVEIRA's suggestion that rust may be able to fix atmospheric nitrogen (page 38) which could conceivably be related to these high nitrogen values for the fungus.

SCHAFFNIT (1909) noted the darker color of desiccated spores, which he attributed partly to a concentration of the molecules acompanying water loss and partly to internal changes incident to maturation of the spores. The coloring matter is a lipochrom (xanthin) which, on ether-alcohol extraction gives an amorphous, oily-resinous residue. There also appears to be present a crystalline, non-lipochromatic coloring substance. This is very susceptible to light, quickly losing its color on exposure to light. Simultaneously in ether-alcohol extraction there are obtained odoriferous substances, probably terpenes, but it is not known whether these are identical with colorless, prismatic needles found in the residue after evaporation. Various species of insects feed on rust spores (*see* page 177), and from the bodies of certain of these, dipterous larvae, the lipochrom has been extracted with ether-alcohol.

The osmotic value of *Puccinia triticina* uredospores and germ tubes has been investigated by STEINER (1930), STOCK (1931), HASSEBRAUK

(1932*a*), and RONSDORF (1934). In STEINER'S experiments, uredospores were placed in hanging drops of sugar solutions and examined for subsequent germination. He found that the highest sugar concentrations at which 50% of the spores germinated, had osmotic values of 8.129 to 11.112 atmospheres, while the upper limit at which any spores would germinate was 15.993 to 17.772 atm. HASSEBRAUK repeated STEINER'S experiments and found these values to be 10-13 atm. and 19.6 atm., respectively. The variation in the results of the two sets of experiments may be due to the fact that HASSEBRAUK'S spores were fresh and uniform while STEINER'S were old and of different ages and sources.

STOCK and RONSDORF carried out experiments in which germ tubes of uredospores which had been germinated in water were transferred to sugar solutions of various molarities. STOCK'S work would seem to indicate rather high osmotic values for the germ tubes, as these, unless empty, were not plasmolyzed by 2 and 3 molar solutions, although empty parts of germ tubes or ungerminated spores in 3 to 5 molar solutions showed collapse of walls or protoplasm. Spores and germ tubes plasmolyzed for 24 hours and 2 hours, respectively, in 5 molar glycerine, germinated and developed normally on return to water, but this did not follow if pure glycerine was used. RONSDORF, using younger germ tubes than STOCK, found these more susceptible to plasmolysis, which usually began at a concentration of .5 mol. $CaCl_2$ (34.9 atm.) and was very marked at .6 to .7 mol. (43.4 to 52.4 atm.). At times stronger solutions were required but the reason for this was not apparent. Germ tubes thus plasmolyzed, if returned to water, resumed growth. Spores were plasmolyzed by 1.5 to 2 molar sucrose solutions, with their contents shrunken from the spore wall and starlike, but they recovered when placed in water. If spores were kept 5 days in .65 mol. $CaCl_2$ and then placed in water, half of them germinated, and a smaller percentage germinated if a .8 molar solution was used. In general, germ tube growth was retarded in the sugar and salt solutions. A variation in temperature from 10° to 22° C. did not influence plasmolysis.

The high osmotic values of *P. triticina* may be a factor in "the astonishing drought resistance" of the fungus, mentioned by RUSAKOV (1929*d*). SCHAFFNIT (1909) found that after drying for 3 days at 26° C., 1.021 gm. of spores had their weight reduced to .92 gm., with 10% water loss, but in moist air the spores quickly became turgescent again, with increased volume and brighter color.

STOCK (1931) germinated uredospores of *P. triticina* on buffered agar titrated with N/10 HCl or KOH to various *p*H levels with the following results:

*p*H of substrate:	3.1	3.8	4.6	6.0	7.2	8.0	8.5	9.0
Germination %:	1.8	38.8	99.3	100	88.4	74.1	68.3	60.5

Thus the optimum *p*H for spore germination is 4.5-6.5 which is similar to that for other rusts. The range is so broad that it is doubtful that *p*H of the leaf surface in nature plays any essential rôle in determining leaf rust infection. STOCK observed that at *p*H 9.0 the germ tubes were very short and flattened at the ends, as also is true of germ tubes at high temperatures. The rate of growth and ultimate length of the germ tubes were quite dependent on *p*H, both being greatest at *p*H 4.6 and progressively less at *p*H

6.0, 7.2 (or 3.8), 8.0, and 8.5. In this respect the OH^- ions are evidently more injurious than the H^+ ions.

A number of workers have tested the effect of metal salts and various other chemicals on spore germination. This work was directly related to efforts at controlling the rust by spraying and dusting, and accordingly these results will be considered in Chapter XIII in connection with this means of rust control.

Teliospore production in *P. triticina* is a response to certain modifications in the metabolism of the host plant, and this subject is consequently treated in Chapter X in connection with the nutrition of wheat as affected by the rust.

STOCK (1931) used 22 stains, classified by RUHLAND as acid or basic "vital stains," on ungerminated spores and germ tubes of *Puccinia triticina,* in concentrations of 1:10,000 to 1:1,000,000. He obtained no clear-cut case of vital staining without killing or injuring spores or germ tubes. There was some "vital staining" of old germ tubes but these were already reaching their limits of life. Germ tubes that were treated with stains and then transferred to water as soon as the first coloring appeared, were plainly injured.

We have only fragments of information, little more than conjectures, on the nature and action of secretions of the leaf rust fungus, an undiscovered key to its remarkable manner of life. YARKINA (1941*b*), finding an increase in catalase activity in leaf rusted wheat plants as compared with healthy plants, interpreted this as due to catalytic action of the fungus. We recall, in this connection, the well-known, highly developed enzymatic systems of those fungi which can be studied in artificial cultures, *e.g.,* the wood-decay fungi. Inability to culture rust fungi except in the living plant prevents studies of this question by the techniques used with other fungi.

ALLEN (1926) suggested that the heightened osmotic values of rust-infected tissues, as shown by the plasmolytic effects of killing and fixing agents on healthy, but not on infected tissues, may be due to secretions of the fungus, to altered host cell activity, or to both. In explanation of the gradually increased tolerance of the fungus by a resistant host plant with increasing age of infections, she states (1927) that "the chemical interplay of fungous secretions and host secretions becomes regulated or adjusted in some fashion, so that the rust thrives to a greater degree." The nature of this adjustment is not known but ALLEN offers two theories: (*a*) that the first formed haustoria secrete substances toxic to the attacked cells, but that this secretion gradually diminishes, or (*b*) that the first toxic secretion may diffuse out to nearby cells, there inducing a defensive reaction on the part of these cells, analogous to antibody formation, so that later they can tolerate the fungus, this defensive reaction enabling the fungus to survive.

Obligate parasitism of the rust: — There is hardly a question in phytopathology so absorbing yet so elusive as the obligate parasitism of the rust fungi. Many investigators have sought in vain the philosopher's stone underlying the problem: a means of culturing rusts on nutrient media other than the living plant. With *Puccinia triticina,* STOCK (1931) carried out an extensive series of such trials. He attempted to culture the rust on 1% agar with addition of nutrient salts, carbohydrates, nitrogen compounds, carbohydrate-nitrogen combinations, and host autolysate and expressed sap. The materials included glucose, saccharose, mannite, glycerine, Knopf solu-

tion, glycocoll, asparagin, peptone, and combinations of these, with or without the addition of hydrogen peroxide, but all gave negative results. Eight-day-old autolysate reduced the spore germination percentage, but had no effect on growth of germ tubes. Two-day-old autolysate had no effect. Expressed juice of wheat plants whether unsterilized, heat-sterilized, or bacto-filtered had no effect unless microorganisms developed, which hindered germination. He concludes from his experiments, that *Puccinia triticina* at least in the diploid stage, is an entirely obligate parasite, and that, considering his other results on plasmolysis and vital staining (pages 59 and 60), the germ tubes are unable to take up substances in solution.

The relationship between host plant and rust fungus has more in common with symbiosis than the host-parasite relationships of many other fungi, *e.g.*, the violently destructive attack of *Sclerotinia fructicola* on stone fruits. GÄUMANN aptly termed it "parasitism with the brakes on." MARSHALL WARD'S impression of early stages of rust infection was "that the rust is not destroying the leaf, but slowly occupying its host, and even stimulating its cells to more intense activity." We have already had instances of this stimulatory effect of the leaf rust fungus (pages 25-28). VON TUBEUF, referring to the green islands, caused by various rusts and powdery mildews (*see* page 48), remarks "one can even believe that these green islands, so long as inorganic substances and water are supplied to them, live with the fungus as lichens, especially those lichens whose algae obtain water and inorganic material direct, not through the fungal hyphae." RAINES (1922), citing this viewpoint of VON TUBEUF, and referring to rusts in general, points out that the parasite does not attack the living substance of the host protoplast, but confines itself to a relationship in which it shares the available food resources of the cell. The rust haustorium is not an implement for mechanical destruction but more like the placenta of the mammalian foetus for establishing physiological communication with the host's food resources. This is correlated with the fact that increase in host vigor leads to increased susceptibility of the host.

This mutualistic relationship may not mark all stages of rust-host association. At some stages the rust may be more truly parasitic, and to the extent that mutualism is not established, to that same extent is the host resistant to rust injury in the ordinary sense. If, as in many resistant wheat varieties, the first cells attacked are destroyed and a mutualistic state does not ensue, the rust mycelium soon dies and the plant as a whole does not suffer.

In the nutrition of the rust fungus, then, lies the secret of many basic problems: the obligate parasitism of the rusts, their alternation of hosts, their narrow host ranges, their physiologic specialization, their dependence on photosynthetic activity and vigor of the host plant, and the mechanisms for resistance of host to rust. We have little inkling of the nature of this nutritional regime, but what little we do have indicates that the nutritional relationship is closely akin to symbiosis, the fungus being exquisitely adapted to deriving its substance from the host cells with the least possible and longest delayed injury to the latter. It is even possible that the fungus, in return for its support, may make some small contribution to the economy of the host plant, through stimulating it to a higher level of photosynthetic

efficiency in early stages of infection, or even, perhaps, through furnishing the host with nitrogen which the fungus has fixed from the atmosphere (see pages 37-38).

Main features of the life cycle: — At this point we will briefly consider the succession of stages in the developmental cycle of *Puccinia triticina,* reserving the details of each stage for later treatment.

The susceptible wheat plant may be attacked at any period in its development in which living, green tissues are present, and environment is suitable. The infection commonly results from uredospores, produced on other wheat plants; in eastern Siberia it may result naturally from aeciospores produced on *Isopyrum fumarioides,* and it may be artificially produced by aeciospores from species of *Thalictrum.* In any of these cases, the result is essentially the same. The germ tube of a spore enters a stoma of the wheat plant, grows down until it comes in contact with parenchyma cells, establishes a nutritional relationship by producing haustoria within these cells, and continues development in this fashion until there results an elaborate mycelial system. In 6 to 10 days, more or less, depending upon environmental conditions, a pale spot above the mycelium marks a developing uredinium, which, within a day or two, ruptures the wheat epidermis exposing a powdery mass of uredospores. These readily detach, under the influence of their own weight or light currents of air, and may fall to the ground or be borne away by air currents. In a well developed uredinium some 2000 or more spores may be produced and liberated each day for as much as two weeks or more, and the number is increased by the formation of one or more circles of smaller uredinia which in time develop about the primary uredinium.

Should any of these spores come to rest on uninfected green wheat tissues, with favorable conditions of temperature and moisture a new infection can result, and the process of such repeated uredinial generations may continue indefinitely, so long as there are available infection courts and suitable environment. If infection is followed by low temperatures, the mycelium may lie dormant until the return of warmth permits uredinial development.

As the wheat plant approaches maturity, the production of uredinia diminishes and in their stead, but principally on the under sides of leaves and on leaf sheaths, the mycelium produces telial sori. The teliospores within these remain covered by the host epidermis until this weathers or decays away.

The teliospores, on formation, are unable to germinate; they require a period of maturation, often several months or more. At the expiration of this time, under favorable conditions of temperature and moisture, each teliospore in the sori of rusted wheat debris may germinate to produce, from each cell, a 4-celled promycelium, each cell of which discharges its contents into a basidiospore that, by analogy with other rusts, is presumably shot off forcibly into the air where it may be carried up and away by convection and other air currents.

In nature the production of infections by these basidiospores is extremely rare or absent, with the exception of eastern Siberia, where the spores regularly and heavily infect the weed *Isopyrum.* With this exception the

teliospore-basidiospore stage is almost entirely a blind alley in the developmental cycle of wheat leaf rust.

In the average case, in which a stage on an alternate host is not involved, the life of the fungus is maintained by a perpetual series of uredinial generations. The gap between harvest of a rusted crop and first infection of the succeeding crop is bridged by various means, depending largely on the climate and the manner of culture of wheat. In lands such as Uruguay and parts of Australia, wheat is in the vegetative state the year round, and perpetuation of the rust is a simple matter of continuous passage of uredospore infections from older to younger wheat. In many winter wheat areas the fungus survives the winter as inactive mycelium within the tissues of dormant winter wheat, producing uredinia and spores on the resumption of warmer spring weather, or its inactivity may be varied by occasional generations of uredinial reproduction during mild periods in late fall, winter, or early spring. In still other cases uredospores produced in the fall and deposited on suitable courts may remain ungerminated for much of the winter, due to low temperatures or dry weather or both, still retaining their viability and initiating infection on the advent of warmer moist weather.

In areas with rigorous, open winters, and where winter wheat is not grown or is winterkilled, the fungus cannot overwinter locally, and infection in the spring, except in those rare cases involving an intermediate host, is due to uredospores brought in by the winds from distant areas in which the rust has succeeded in overwintering on wheat. This applies, for example, in parts of Siberia.

Oversummering of the rust is in a state of active reproduction, with repeated uredinial generations in spring wheat areas. Where winter wheat is grown, if the summers are not too hot, the uredospores formed prior to harvest of the crop may infect volunteer wheat and live on this in the uredinial stage until the rust can pass back to young wheat seedlings in the fall. If, however, the summers are hot and dry, little or no living wheat may be found during several months, and in this case the infection of the winter wheat in the fall must be by means of uredospores brought in by winds from cooler areas where wheat is vegetating and the rust is actively reproducing during the summer. In the southern Great Plains of North America the rust thus returns from the northern Great Plains in the fall, and in India it oversummers in the cooler foothills of the Himalaya Mountains from which it returns to the Plains in the fall.

We have seen that, to a very limited degree, a few species of grass may support the uredinial stage of wheat leaf rust; the rust reactions on these, however, are usually of a low grade and there is no recorded case in which they play any significant part in the epiphytology of the rust, their rôle being merely to supplement, slightly, the uredinial reproduction on wheat.

We can comprehend the course of events in infection of the alternate host, *Isopyrum,* only by analogy with other rusts and with the behavior of *Puccinia triticina* when artificially inoculated on *Thalictrum,* since the *Isopyrum* stage has not been described in full detail. The rust overwinters in the form of dormant, maturing teliospores in the debris of wheat fields. In early spring these germinate and the basidiospores may be borne to nearby plants of the alternate host and there initiate infections, which, in the case

of *Isopyrum,* is favored by the fact that the plant is a common wheatfield weed.

In *Thalictrum,* artificially introduced infection by the basidiospores results in development of feeding mycelium in the aecial host, followed by the appearance of pycnia shortly thereafter. Pycniospores are discharged in droplets of nectar and insects are attracted by the nectar and in feeding upon it transfer the pycniospores to receptive hyphae, resulting in fertilization of the latter. Diploid mycelium (*see* page 57) then develops and aecia are formed from which aeciospores are discharged, probably forcibly. In eastern Siberia the aeciospores from *Isopyrum* are carried by air currents to nearby wheat plants and if the environment is favorable, the latter become infected, in a week or ten days producing uredinia to initiate a series of uredinial generations, and the cycle is complete.

These then are the principal features of the developmental cycle of *Puccinia triticina.* Following sections will deal in more detail with the sequence of activities of the fungus, and after a detailed study of the effects of environment on these developmental processes, we will consider the developmental cycle of the fungus in various selected areas of the world as it is modified and conditioned by the climates, geography, and cultural practices of these areas.

Proof of heteroecism in Puccinia triticina: — JACKSON and MAINS in 1921 were the first to demonstrate heteroecism in wheat leaf rust by inoculating certain *Thalictrum* species with basidiospores of *P. triticina* and on them producing aecia and aeciospores that resulted in typical uredinia and telia of wheat leaf rust when the aeciospores were transferred back to wheat. This was subsequently confirmed by many other workers.

In 1935, BRIZGALOVA in Siberia succeeded in infecting wheat with aeciospores naturally occurring on *Isopyrum fumarioides,* and in 1937 she reported completion of the demonstration of heteroecism by returning the infection to *Isopyrum* through inoculations of the aecial host with *Puccinia triticina* basidiospores. She demonstrated that the wheat-*Isopyrum* cycle occurs in nature, and is, indeed, of great importance in perpetuation of the rust in eastern Siberia, and not a botanical curiosity without a counterpart in nature, as is the case with the wheat-*Thalictrum* cycle.

Rôle of alternate hosts in nature: — The statement has been made that the meadow rue, species of *Thalictrum,* is of little importance in the life cycle of *Puccinia triticina* under natural conditions. Let us now examine the data on which this statement is based.

So far as North America is concerned, ARTHUR (1934) stated that "The full rôle of the aecial stage for *P. rubigo-vera tritici* is unknown, as it has not yet been recognized in nature." In Illinois, where leaf rust is abundant, TEHON (1924) searched in vain for the fungus on the common *Thalictrum dioicum* which is somewhat susceptible. Nor does ARTHUR'S rust manual (1934) list any rust on *Leptopyrum* or *Isopyrum* in the United States and Canada, other than *Puccinia rubigo-vera agropyri* and *agropyrina* which do not infect wheat. These negative results have some significance when we recall the great extent of rust research in North America.

In South America the story is the same. Although *Thalictrum* species

occur there they have not been found to function as alternate hosts of wheat leaf rust (GASSNER, 1915*a*, 1932; RUDORF *et al.*, 1933, 1934). This applies also to other parts of the Southern Hemisphere. MEHTA devoted much attention to this in India (1929, 1931*a*, 1931*b*, 1934, 1940). After 16 years of search he could only say that *Thalictrum* has never been found in India infected with a rust proven to be *Puccinia triticina*. *Thalictrum* is rare in the Indian plains where 95% of the wheat is grown; the more susceptible species of *Thalictrum* do not occur in that country; the teliospore stage of the rust is also very rare in India; and the few aecia collected on *Thalictrum* in the Indian hills have been proven to be of another rust species, unable to infect wheat. In Belgian Congo, although leaf rust occurs, *Thalictrum* is absent according to MARCHAL and STEYAERT (1929).

HEMMI in Japan (1935) thinks that *T. minus* var. *elatum* may function in spreading wheat leaf rust in northern Japan, but offers no proof of this.

In eastern Siberia, RUSAKOV (1925, 1927*b*) states that *Thalictrum* is very rare. In early reports SHITIKOVA-RUSAKOVA found aecia on *Thalictrum* which she attributed to *P. triticina*, although, as they appeared only after leaf rust had developed on the wheat, she felt that their sole significance was in increasing the rust, the primary source of which was attributed to south winds from northern Manchuria. Later, however, BRIZGALOVA (1935, 1937*a*) showed that the aeciospores on *Thalictrum* in eastern Siberia belong to *Puccinia persistens* and that they are incapable of infecting wheat.

From European Russia there came early reports that *Thalictrum flavum* is fairly prevalent and strongly attacked by *Puccinia triticina* (BONDARTSEV, 1931) which serves as a source of windborne inoculum from Poland (KALE, 1938, 1939). RUSAKOV (1929*a*) found no relation between *Thalictrum* and wheat leaf rust in European Russia, and in his recent and authoritative book (1939) NAUMOV states that apart from the case of *Isopyrum* in eastern Siberia, alternate hosts have minimal or no function in Russia, including the Far East and most of Siberia. Not a single proven aecium of *P. triticina* has been found in this vast area, and the aecia found on *Thalictrum* are not of *P. triticina*. This is particularly significant in view of the very extensive search for this stage that has been made by Russian workers in the past 2 decades.

Turning lastly to Europe we again find, in general, a similar situation. DUCOMET and FOËX (1925) recorded the presence in Europe of 11 species of *Thalictrum*. The most widespread of these are *T. minus* and *T. flavum*, both of which are susceptible to *Puccinia triticina*. Yet, they ask, "Are their frequence and the abundance of aecia on them sufficient to give us the right to consider that the aecial hosts play an important rôle in the propagation of the disease? We do not dare affirm it." Findings in the various countries of Europe bear this out.

In Germany *Thalictrum* has been found to carry aecia only of *Puccinia persistens*, which does not infect wheat (GASSNER and PIESCHEL, 1934; RIEHM and SCHWARTZ, 1927; SCHEIBE, 1930*b*). ROBERTS (1936) reports that *Thalictrum* is not naturally infected in England, RALSKI affirms the same for Poland (1936, 1939), GONZALES-FRAGOSO (1926) considers it doubtful if aecia are formed on *Thalictrum* in Spain, and MARCHAL points out that no alternate host is required in Belgium (1903). In Italy *Thalic-*

trum species are common but even when growing near wheat they bear no aecia referable to *P. triticina* (MONTEMARTINI, 1933, 1934, 1939; PETRI 1926*b*, 1927).

RĂDULESCU (1932), in error, cites SCHEIBE (1930*a*) to the effect that *Thalictrum* while rare in western Europe is common and is heavily infected with wheat leaf rust in southern Europe. Such a statement could not be found in SCHEIBE's paper. Moreover, SĂVULESCU, in later papers (1933, 1938*a*, 1938*b*) states that the *Thalictrum* in Rumania is not strongly attacked by any rust and that not once has an aecium on it proven to be of *Puccinia triticina*.

Against this weighty body of evidence there stands only the single report of D'OLIVEIRA in Portugal. After an extensive search, D'OLIVEIRA succeeded in finding 3 specimens of *Thalictrum* with aecia, one of these being a potted plant, and with the aeciospores he reports that he was successful in infecting wheat. D'OLIVEIRA's report is anomalous in other respects. He found teliospores of the rust in considerable abundance whereas they are rare in other countries of southern Europe, and he succeeded in germinating them in the fall, while other workers agree that they will germinate only after a rest period. D'OLIVEIRA considers this aecial stage rare in Portugal; because of its unique and anomalous character it requires confirmation, and it hardly alters the generalizations of ERIKSSON (1926) and STEINER (1933*a*) that the aecia of *Puccinia triticina* have never been found in nature on *Thalictrum*.

Significance of heteroecism in Puccinia triticina: — We have seen that although the wheat leaf rust fungus has the potentialities of including an alternate host in its developmental cycle in nature, it rarely makes use of its alternate host and in most parts of the world it is highly successful in its perpetuation by the uredo stage alone. Except in eastern Siberia the Ranunculaceous host has little or nothing to do with the epiphytology of the disease. What, then, is the significance, if any, of an alternate host to *P. triticina* and its destructiveness on the wheat plant?

ALLEN (1926) calls attention to several abnormalities or discrepancies of *P. triticina* in *Thalictrum* as compared with other related rusts. These include occasional fusion of appressoria or substomatal vesicles, multinucleate condition of first hyphae formed followed by a regular 3-nucleate condition, the production of 1-nucleate haustoria from 3-nucleate mycelium, occasional hyphal fusions before spore formation, and a return to a more normal 3-nucleate condition in spore production. She raises the question whether these aberrations are to be regarded as an expression of the need of, and an ill-defined attempt at compensation for the excised part of the life cycle.

Some mycologists in the past have entertained the hypothesis that the regular or occasional passage of a rust fungus through a sexual stage on an aecial host serves to rejuvenate the fungus and maintain it in a vigor and virulence that might otherwise be lost in an endless succession of non-sexual, vegetative generations (BOLLEY, 1889*a*; FREEMAN and JOHNSON, 1911), an hypothesis similar to that by which early horticulturists sought to explain a real or fancied degeneration in higher plants that for many years have been propagated by purely vegetative means. The behavior of *Puccinia triticina* testifies against such an assumption. In most areas of

the world there is rather convincing evidence that the alternate host is dispensed with, and that the fungus is perpetuated in the uredinial stage. Yet a comparison of the fury of recent rust epiphytotics with the recorded destructiveness of *Puccinia triticina* in past years clearly indicates that the fungus has suffered no loss in vigor or virulence despite its passage through thousands of vegetative generations without benefit of a sexual phase. We have experimental evidence on this point appearing in the work of FREEMAN and JOHNSON (1911) who carried *P. triticina* through 53 uredial generations without any sign of loss of virulence in the fungus. MEHTA (1940) also observed no alteration in the fungus following 100 successive single-uredospore transfers.

There remain, however, two ways in which the Ranunculaceous host might exert well-marked influence on the development of the rust fungus. In the Lake Baikal area of eastern Siberia, the alternate host, *Isopyrum,* is the only means by which the rust can survive from one season to the next, since there is no winter wheat, and mountain and desert barriers prevent the ingress of rust spores from areas where the rust overwinters on wheat, hundreds of miles away.

In the second place, the sexual phase on the Ranunculaceous host is a point at which new physiologic races of the rust could arise. These might be marked with new degrees and types of virulence, necessitating unremitting efforts of the wheat breeder to overcome such new types of rust virulence. The origin of new races of rust will be discussed in connection with physiologic specialization in *Puccinia triticina* (page 91) and here it is necessary only to point out that, although WATERHOUSE has experimentally produced new rust races on *Thalictrum* (1932), the absence of natural aecial infections on this host, and the occurrence of a functioning aecial stage only in a remote and isolated area of Asia, leads to the conclusion that, for the world as a whole, new races have other origins (as by mutation) than the sexual phase of the fungus.

Chapter VII

PHYSIOLOGIC SPECIALIZATION

Concepts and definitions: — It has been seen that the cereal and grass rusts comprised in the form species *Puccinia rubigo-vera* are morphologically related, and that their greatest differences lie in the fact that each attacks certain species of grains or grasses, and does not attack other *Gramineae* which are hosts of other rusts in the *P. rubigo-vera* complex. Thus, the leaf rust of wheat occurs primarily on wheat and not rye, while the morphologically similar rye leaf rust attacks rye but not wheat. These major pathogenic differences were those involved in ERIKSSON's conception of physiologic specialization, morphologically similar rusts which were specialized on different species of host plants being termed *formae speciales*.

STAKMAN first showed that such a *forma specialis, viz.,* the wheat form of stem rust, could be further subdivided into a large number of physiologic races, similar or identical morphologically and all attacking wheat, but each differing from the others in its capacity to attack certain wheat varieties but not others. Thus if different physiologic races of wheat stem rust are each used to inoculate the 12 wheat varieties used in differentiating stem rust races, no two of the races will behave alike: on one or more of the differential wheat varieties, one of any two races will produce one type of reaction, the other a different type. The same situation applies to wheat leaf rust when its races are inoculated on the 8 wheat varieties used in differentiating this rust.

The 12 wheat varieties used in stem rust race determination, and the 8 in the case of wheat leaf rust have been arbitrarily chosen. If a larger collection of differential varieties is used, we find that different rust collections that behave as a single race on the 8 differential varieties are not the same, and as the number of differential varieties is increased, there is almost limitless possibility of subdividing what are at present termed physiologic races. These finer subdivisions may be termed biotypes. Their significance in relation to *Puccinia triticina* will be discussed later. For the present, it is only necessary to point out that for the principal practical purpose served by race identification, — guidance in breeding wheat for rust resistance —, finer subdivisions of pathogenicity than are detected by our present methods of race identification do not appear to be needed; instead we might profitably reduce rather than increase the present degree of differentiation without appreciable loss in the serviceability of physiologic race study.

GESHELE (1936) suggests that each individual pure culture of rust is a clone, the vegetative progeny of a single spore, genetically homogeneous, comparable to a clone of vegetative progeny of potatoes or fruit trees. The race is a collection of clones that may differ genetically, but react alike within the limits of differentiation which we have chosen by our adoption of an arbitrary group of differential varieties, and arbitrary categories of reaction types. Accordingly, he suggests the term "isoreagent" to apply to the

groups of clones which are customarily termed "races." While GESHELE's position is sound, it is doubtful whether any advantage appertaining to adoption of his terminology would outweigh the disadvantage in replacing a term already well entrenched and understood by plant pathologists and agronomists.

It is manifest that our classification of rust races, as indeed all plant systematics, is, and must remain, man's practical attempt at organizing the multiplicity of living organisms, and if our organization, artificial though it may be, serves our practical ends, it has accomplished its purpose.

VAVILOV (1913, 1919) developed the concept of degree of narrowness of specialization. The wider the host range of a parasitic fungus, *i.e.,* the more species and genera it can attack, the less likely one will be to find resistant varieties in any species of host, and *vice versa.* According to this concept, the wheat leaf rust is narrowly specialized, having few host genera, — for practical purposes only one, and hence many resistant varieties may be expected within this genus. Stem rust of oats is regarded as much less specialized, with crown rust of oats intermediate.

Discovery of physiologic specialization in Puccinia triticina: — Before the discovery of physiologic specialization in wheat stem rust, early workers, such as ERIKSSON, SORAUER, and CARLETON, noted that rust-resistant cereal varieties sometimes behaved as susceptible when cultivated in new environments, and, on the other hand, CARLETON observed that wheat varieties that were badly rusted in the United States behaved as resistant in Australia. This was ascribed to differences in climate or changes in the constitution of the host plant. With the discovery of specialization in stem rust, it became realized that these differences in behavior of a wheat variety in different regions of the world may be due to differences in the rust race constitution in the various regions. Thus, the fact that Malakoff wheat was immune at one point of the United States and showed 70-80% leaf rust at another, was considered a problem in rust race distribution. It was also recognized that specialization complicates rust control by the use of rust-resistant varieties. MELCHERS and PARKER in 1920 pointed to the possibility that more than one race of leaf rust had been present in their Kansas plots from 1914 to 1919 and emphasized the need for caution in interpretation of varietal rust reactions because of this possibility.

In 1921, MAINS and JACKSON reported that during 1919 and 1920 wheat leaf rust cultures obtained from aecia on *Thalictrum* fell into two groups, some to which Malakoff and certain Turkey Bearded Minnesota wheats were susceptible and others to which these wheats were resistant.

In a brief abstract in 1923 these authors reported having assembled leaf rust collections from various parts of the United States and tested them on 200 wheat varieties of which 31 proved to be differential hosts to one or more leaf rust races. On the basis of the reactions of the rust samples on 7 of these varieties, 12 physiologic races of wheat leaf rust were differentiated.

Following this brief report, MAINS and JACKSON published a detailed account of their studies in 1926. By that time 11 differential varieties were being used: Malakoff, Turkey, Norka, C.I. 3778 (later named Brevit),

Webster, C.I. 3756 (later named Carina), C.I. 3747, C.I. 3779 (later named Loros), Mediterranean, Hussar, and Democrat. Subsequently the Turkey and Norka (which behave like Malakoff) and the unnamed C.I. 3747 (with reactions like Webster) were dropped, and the remaining 8 differential varieties remain in standard use today. Their agronomic characters have been described by JOHNSTON and MAINS (1932).

On the basis of reactions on these differential varieties, MAINS and JACKSON distinguished 12 physiologic races, numbered 1 to 12, and gave a key to them together with their respective reactions on the differential varieties.

Subsequent development of physiologic specialization in the rusts: — Following MAINS and JACKSON's description of the first twelve physiologic races of wheat, leaf rust workers in many parts of the world undertook to analyze their local leaf rust populations for race constitution. As a result, many new races were described, until by 1942 the total had reached 129 races. These, with their reactions on the differential wheat varieties, an analytical key for identifying them, and information on their original descriptions and places and years of their discovery or report are given in the "Third Revision of the International Register of Physiologic Races of the Leaf Rust of Wheat," issued by the U. S. Department of Agriculture.

Minor variations in host reactions have been disregarded in assignment of race numbers. In race identification any host reaction from 0 to 2+ is regarded as a resistant reaction, and any reaction from 3— to 4+ is regarded as a susceptible reaction. This is the reason why HUMPHREY and his co-workers have frequently assigned what were considered by their discoverers as new races to formerly known races. If such minor differences as that between a "3" and a "4" reading were to be made the basis of new races, the list of races would become so extensive as to lose thereby some of its usefulness, and in addition these minor variations might easily be due to differences in evaluation of reactions by 2 different workers, rather than to actual differences in the rust materials. Some workers have noted minor differences from the International Register in the reactions of their rust races, as, for example, MEHTA (1940), RASHEVSKAYA and BARMENKOV (1936), and GORLENKO (1936*b*), but they have not regarded their races as new, and have classified them according to the Register.

A number of investigators have experimented with the use of other differential varieties than those on which the International Register is based, as supplements to or substitutes for the standard varieties. WATERHOUSE (1929-30) found that 589 isolations of leaf rust from various provinces of Australia all gave the same reactions on the standard differential wheats. When, however, these were tested on the FARRER wheat, Thew, this wheat variety was resistant to 288 of the isolations and susceptible to 302 of them. WATERHOUSE designated the rust cultures with these contrasting reactions as Australian Form 1 and Australian Form 2, respectively, although according to the International Register they all fell within the new race 26. Later (1932) WATERHOUSE derived two additional races from aecial material, and these, now known as races 96 and 97, were also identical if tested on the

standard differentials, but race 96 gave a "4" reaction on Thew while race 97 had a "0" Thew reaction.

Thew has not been accepted as a differential variety by workers other than in Australia. In Kansas, Thew has been inoculated with 21 important leaf rust races and found completely susceptible to all of them. In Canada, NEWTON and JOHNSON rejected it as being susceptible to all Canadian leaf rust races found in their 1940 survey, as well as to 6 additional races. In Germany, GASSNER agreed that Thew was not needed. RĂDULESCU, in Rumania, tested two lines of Thew and found that they did not react uniformly to rust races, and accordingly did not use Thew in his work.

SCHEIBE and HASSEBRAUK in Germany and BARMENKOV in Russia also experimented with additional differential varieties. BARMENKOV (1938) found that his cultures of races 20 and 65 were heterogeneous, and that they could be divided into sub-races, race 20 by use of the varieties *apulicum* 77/2, Moskovskaya 02453, *melanopus* 037, and *gordenforme* 910, and race 65 by using *apulicum* 77/2, *erythrospermum* 020/430, Kanred × Fulcaster 266321, Argentine H-31, and Fulcaster.

SCHEIBE (1930*b*) has raised the question whether the limited number of standard differentials gives sufficient race distinction. More differentials would increase the number of races and at the same time greatly complicate race study and the use of physiologic specialization as a control in breeding for rust resistance. It cannot be gainsaid that two rust collections which key out to the same rust race by use of the standard differentials may be distinct genetically. SCHEIBE tested 6 collections of race 11 on 17 German and other wheats, and found that only 2 of them reacted alike. He had a similar experience with collections of race 13. Despite these results, however, SCHEIBE held that some compromise was necessary, that an increase in the number of differentials is undesirable and unnecessary for the purposes of wheat breeding, but that we must always keep in mind that races are really groups of similarly but not identically reacting entities, and that, for example, race 11 of America and race 11 of Europe, while belonging to the same race group, are not necessarily identical.

HASSEBRAUK (1940*c*) appears to be the only worker who has gone so far as to discard all of the American standard varieties but one, and adopt a new set of differential varieties which he regards as more suitable for race study in Germany. He points out that certain of the American standard differentials are labile in their rust reactions with changing environments, notably Brevit, Carina, and Hussar. (This is a valid objection which is discussed in detail on page 78 *ff.*) He presents a table of data showing that different collections of race 11 showed notable differences in pathogenicity when tested on 6 European wheat varieties, and he had similar results with collections of race 13, 14, 15, 16, 19, 20, and 94. In certain cases, races that were distinct according to the standard differentials reacted alike on the European wheats.

Because of these objections, HASSEBRAUK undertook studies comparable to the pioneer work of MAINS and JACKSON, but even more extensive. He tested 10 races of leaf rust on 963 varieties of winter wheat. Of these he chose 23 that appeared most suitable as differential varieties, and tested these for their reactions to 140 collections of 15 rust races. Some of the wheats were then rejected because of poor differentiation or because

delayed rust development prevented uniform rust readings at one time. There remained twelve, which were used as differentials for study of physiologic specialization of leaf rust in Germany.

This increase in the number of differentials cannot be regarded as too objectionable, since 12 are used in race study of *Puccinia graminis tritici,* and 16 for *P. glumarum* by STRAIB's technique.

Using these differentials, HASSEBRAUK distinguished 45 leaf rust races, numbered D-1 to D-45 ("D" = Deutschland). That these differentiate rust races to a high degree is shown by the fact that using only 8 of his differentials he obtained 31 races from 140 rust collections. From MAINS and JACKSON's races 9, 10, 13, 19, 20, and 31, he obtained 14 distinct races. In this work only major clear-cut differences in reactions were considered valid for race distinction, — greater differences than that between "2" and "3", which serves to distinguish many races in the International Register.

HASSEBRAUK disagrees with SCHEIBE and with JOHNSTON and MAINS that further subdivisions of specialization would serve no useful end, provided the race differences are sharp, clear-cut, and not unduly subject to variation due to environmental differences. He agrees with SCHEIBE that although two rust collections from different parts of the world key out to the same race, they may still be quite different pathologically, and hence feels that any conclusions based on world distribution of rust races are without value.

Finally MAINS (1932) has used certain grasses in studying specialization of wheat leaf rust, and has found, as may be seen in the following table,

REACTION OF:	GRASS COLLECTION:	WHEAT LEAF RUST RACE: 3	5	9
Aegilops ovata	803	3	3–4	2+
— —	811	3	0–1	0
A. cylindrica	804	1–2	2–3	0
— —	813	0	0	0

that these grasses as well as wheat varieties, serve to differentiate races of the rust.

Methods of study: — With minor variations, workers on race identification have followed the methods outlined by MAINS and JACKSON (1926) and JOHNSTON and MAINS (1932). As soon as possible after collection, fresh uredinial specimens are enclosed in paper packets and placed in a refrigerator where the spores retain viability for several months or even 2-3 years (*see* TABLE 13). Moist or oiled paper should be avoided.

Field collections are usually mixtures of several races. Single races may be isolated from such mixtures by any of several methods, principally by several successive inoculations on susceptible wheat, each transfer involving one isolated pustule (comparable to purification of bacteria by the poured-plate method), by inoculations of single spores, picked up on the point of a needle, or by inoculating the race mixture on differential wheat varieties, which "screen out" contaminating races to which the varieties are resistant, combining this with single pustule transfers. This last has the

advantage of permitting recovery of races that comprise very small fractions of the rust population. Before and after race isolation the rust collection is multiplied and maintained in greenhouse culture, usually on a wheat variety that is susceptible to all known races, such as Little Club or Cheyenne or others listed on page 43. Each pure rust culture is usually protected from contamination in the greenhouse by growing it in a separate moist chamber, cabinet, or greenhouse compartment.

Inoculations are usually made on uniform seedlings on the prophyllum. This is drawn 2-3 times between wetted fingers to remove the waxy bloom, and rust spores are applied with a scalpel or dull spear-headed needle. In certain cases the spores may be sprayed or dusted onto the plants. GASSNER's school of workers have usually applied the spores in a .1% agar solution instead of water; this decreases surface tension and retards evaporation without interfering with spore germination. Refinements or variations of inoculation methods include outlining the site of inoculation with India ink (NAUMOVA, 1935; YARKINA, 1941*a*; RASHEVSKAYA and BARMENKOV, 1936), enclosing individual leaves in tiny, partitioned glass tubes to permit simultaneous inoculation of a leaf with several rust cultures without danger of cross-contamination (BARMENKOV and PANCHENKO, 1935*a*, 1937; RASHEVSKAYA and BARMENKOV, 1936), and inoculating plants hypodermically (ZEHNER and HUMPHREY, 1929; NEWTON and BROWN, 1934).

Scrupulous attention must be given to sterility of hands and equipment, with frequent disinfestation of these with alcohol, use of sterile water or agar solution for preparing spore suspensions, operating in calm air, and having the process of removing the waxy bloom of the leaves performed by an assistant who has no direct contact with the rust.

Immediately after inoculation the plants are placed in moist chambers (bell jars, tanks, iron cylinders, cotton-plugged lamp chimneys, humid incubation cabinets). These may exclude light, but must maintain saturated air humidity at 16°-20° C. For inoculating large numbers of seedlings with a single rust culture, a moist chamber can be devised by building a scaffolding over the greenhouse bench and covering the plants and bench with a large sheet of wet canvas. The writer has had excellent results, in creating greenhouse leaf rust epiphytotics for testing seedling or mature plant reactions of breeding materials to several rust races simultaneously, by the following procedure. Interspersed among the plants to be tested are placed numerous pots of seedlings with good infections of the rust races to be used. In the evening the canvas cover is placed over the plants and a fine, hard spray of water is directed on the plants by inserting the hose under the side of the cover at several points successively until the plants are thoroughly wetted (but not drenched). The spray causes a circulation of air that directs the spores to all parts of the chamber. The cover is then sprayed from the outside until it is saturated. Early the following morning the cover is removed. This procedure, if repeated daily, can result in such a heavy epiphytotic that susceptible plants fail to head. Powdery mildew, *Septoria, Darluca,* or *Helminthosporium* leaf spot have not proven troublesome under these conditions, with greenhouse temperature maintained at 60-65° F. continuously. Although the canvas is wetted but once, in the morning it is regularly still damp, and when the cover is removed the plants are still covered with water droplets.

The inoculated plants should be left in saturated air for about 12 hours, then removed to normal greenhouse air. Longer periods in the moist chambers lead to scalding or wilting of the plants when they are removed. The writer has obtained maximal infections with only 6-8 hours exposure to saturated air after inoculation, and ASUYAMA (1939) also found 6 hours sufficient. That infection occurs in this short time is confirmed by K. D. BUTLER'S finding (1940*b*) that sulphur dust is not a rust protectant if applied later than 3-4 hours after inoculation.

Further culture of the plants is under ordinary greenhouse conditions, at 18°-20° C. Contaminations may be avoided by segregating the plants inoculated with different rust cultures, in separate rooms or compartments, before spores are produced. Muslin-covered lamp chimneys are useful for this.

For each test, 6-30 seedlings of each differential variety are usually used. This is necessary, as the seed of the varieties is not always homogeneous. Any tests showing aberrant results should be repeated and comparisons are valid only when they are made on uniform materials at the same time. The plants are usually grown in 4-inch pots, 3-10 plants per pot, in fertile soil, well supplied with nitrogen.

The plants must be protected from pests and other diseases. Powdery mildew can be checked by applying sulphur paste to the greenhouse pipes, frequent rust transfer, using mildew-resistant wheat varieties for stock rust cultures, and maintaining the greenhouse temperature at 18°-20° C. The hyperparasite *Darluca filum* (*see* page 175) is avoided by not using *Darluca*-infested rust collections for greenhouse culture; timely rust transfer is also an aid in controlling this fungus. It may also be necessary to fumigate the plants with nicotine smoke to control aphids, to screen the ventilators to exclude birds and grasshoppers, and to control mice, which feed on newly-planted seed, with poisoned bait or traps.

Taking data: reaction types: — It is customary to make readings of the types of rust infection on the tenth day after inoculation. Sometimes the pustules are mature enough for reading as early as the eighth day, but in winter, under conditions of low light intensity and short days, 14 days may be required before the infections are sufficiently advanced to permit error-free reading.

In their original paper in 1926 on specialization of wheat leaf rust, MAINS and JACKSON recognized the following types of host reaction, which are the basis of race readings:

Class of host reaction:	*Type of rust infection:*
0 Highly resistant	No uredinia formed; small flecks, chlorotic or necrotic areas more or less prevalent.
1 Very resistant	Uredinia few, small, always in small necrotic spots. Also more or less necrotic areas produced without development of uredinia.
2 Moderately resistant	Uredinia fairly abundant, of moderate size, always in necrotic or very chlorotic spots. Necrotic spots seldom without uredinia.
3 Moderately susceptible	Uredinia fairly abundant, of moderate size. No necrosis produced, but sometimes slight chlorosis immediately surrounding the uredinia.

4 Very susceptible .....Uredinia abundant, large. No necrosis or chlorosis immediately surrounding the uredinia. Infected areas sometimes occurring as green islands surrounded in each case by a chlorotic ring.

JOHNSTON and MAINS in 1932 added the types:

X Heterogeneous or indeterminate....."Uredinia very variable, apparently including all types and degrees of infection on the same blade; no mechanical separation possible; on reinoculation small uredia may produce large ones and *vice versa*. Infection ill-defined" (STAKMAN).
"Tips of leaves often have large, normal uredinia while leaf bases have minute uredinia and flecks" (JOHNSTON).

Intermediate or variable .....Varying from moderately resistant ("2") to moderately susceptible ("3") at different times, but consistent on a given leaf.

To these may be added the descriptive symbols (GASSNER and HASSEBRAUK, 1934*a*):

;	Chlorosis	−−	Traces of uredinia
(;)	Weak chlorosis	−	Small, isolated pustules
.	Necrosis	∓	Subnormal pustules
(.)	Weak necrosis	±	Normal pustules
R	Resistant (Types 0 to 2 ++)	+	Strong attack
S	Susceptible (Types 3= to 4 ++).	++	Very strong attack

Intermediate values between 1 and 2, 2 and 3, etc., are indicated by the symbols —, = ("double minus"), +, and $\overset{+}{+}$ (or ++), so that a complete series would be: 0, 1=, 1—, 1, 1+, $1\overset{+}{+}$, 2=, 2—, 2, 2+, $2\overset{+}{+}$ 3=, ... $4\overset{+}{+}$.

A variable reaction is usually indicated by a hyphen connecting the extremes of variation, *e.g.*, 1-2, 1-3, 2-4+, etc., but some workers use the arithmetical mean of the extremes to express such reactions. Each has its advantages, but the former is more readily understandable to those not best versed in rust work.

NEWTON and JOHNSON (1943) use a method of converting the infection types into numerical values, as follows: Type 1 = 5; type 2 = 10; type 3 = 15; type 4 = 20; types X=, X—, X, X+, and $X\overset{+}{+}$ = 11, 12, 13, 14, and 15 respectively.

A series of Kodachrome lantern slides showing the principal infection types of wheat leaf rust have been reproduced and distributed, by the Extension Service of the U.S. Department of Agriculture, to many of the departments of plant pathology in the United States, where they are available for consultation.

The type "X", — heterogeneous, indeterminate, or mesothetic reaction —, deserves further comment. It has at least 3 possible interpretations: (*a*) that it is an environmentally-conditioned irregularity, as suggested by the authors of the "International Register" since they do not discriminate between it and the variable reaction which is regarded by them as an environmental effect; (*b*) that it is due to genetic instability of fungus or host, not primarily conditioned by environment; and (*c*) that in some cases it may be merely the result of an unrecognized mixture of 2 or more races in

what was supposed to be a pure race culture. Of the various cases involving the "X" reaction in the "Register," there are probably some that represent environmental effects, others that are genetic in nature, and still others that are due to race mixtures.

It is clear that environmental variation may change a resistant or susceptible reaction to an "X" reaction. There is direct proof of this. For example, HASSEBRAUK (1939) inoculated 1000 plants of Carina and Brevit wheats with pure cultures of races 13, 19, 20, and 31. An "X" reaction is not normal for any of those combinations, yet HASSEBRAUK states that the results of these inoculations were often so confusing that he was forced to reject them, due particularly to the frequent appearance of type "X". WATERHOUSE (1929-30) observed a change in Hussar and Carina reactions from susceptible in summer to "X" in winter. Table 8 groups certain races that have been shown experimentally to have given reactions characterizing other races in each group, respectively, under the influence of certain environments. In the table we find a number of instances of races characterized in the "International Register" by one or more "X" reactions, but which, under some environmental conditions give clear-cut resistant or susceptible reactions, or *vice versa.*

That the "X" reaction in other cases may be an expression of genetic instability is in accordance with ALLEN's suggestion (1927), based on her histological studies, that it may be due to an adjustment of the fungus to a resistant host, in which case, if the fungus can survive early stages, progressively greater tolerance is shown by the host. SCHEIBE, who first made use of the "X" reaction in *Puccinia triticina* (1930*b*) held that this combination of all types of reaction on the same leaf must be anchored in the genotype of the fungus, and pointed out that this type of reaction, which is common in the rusts with functioning alternate hosts, *P. graminis* and *P. coronifera,* is less frequent in *P. triticina,* which rarely makes use of an alternate host. JOHNSTON and MAINS (1932) mention that the "X" reaction is often met with in F_1 hybrids and heterozygous segregates from susceptible X resistant crosses, *i.e.,* accompanies genetic instability in the host plant. It is to be expected that sexual reproduction in the alternate host of a rust results in comparable genetic instability on the part of the fungus, whereupon it would follow in turn, that a fungus in which the sexual stage plays an important rôle would be expected to contain a greater percentage of genetically unstable races than a fungus, such as *P. triticina,* in which the races, for the most part, are the result of many years of natural selection, and hence more stable.

We pass to the third possibility: that in some cases the "X" reaction may merely be the result of an unrecognized mixture of 2 or more races in what is supposed to be a pure rust culture. Despite ordinary precautions, there is an ever-present danger of contamination and race mixtures in rust race study. We know that single rust pustules can contain 2 races, though to all outward appearance they are identical with pustules arising from a single spore. If a mixture of two rust races is cultured on the differentials, a new series of reactions is obtained in which the "X" reaction is the conspicuous feature. Without questioning the validity of some of the races characterized by "X" reactions, nor the precautions taken by those who have described them, it may be pointed out that the synthesis of the common races 15 and 2 produces reactions indistinguishable from those of race 34,

race 6 added to race 20 reacts as race 80, race 19 plus race 105 reacts as race 65, and an unsuspected mixture of races 10 and 77 would be recorded as race 115. These are all hypothetical mixtures of common races, and the mixtures in all cases produce reactions indistinguishable from those of different races marked by "X" reactions. Other such illustrations could have been selected. It is too much to hope, considering the number of workers on physiologic specialization in wheat leaf rust, and the variations in their methods, in particular their systems of controls, that all of the "X" reactions in the "Register" conform strictly to STAKMAN'S definition of this reaction, which requires intensive study to determine that the mesothetic reaction is that of an undoubtedly pure culture of rust, and that it is relatively stable under different environments.

Mention should also be made of the anomalous "X" type reaction described by ROBERTS (1936) in which there are many small, crowded pustules on a leaf, the whole surface of which is chlorotic. She found that this sometimes coincided with warm weather. In all probability it is a response to environment and/or state of metabolism of the host plant, and until more is known of it, it should be differentiated from a true, genetically-conditioned mesothetic reaction.

Permanent records of infection types: — It is desirable to have some means of preserving the appearance of infection types for later reference, for comparison of the results of different workers, and for teaching purposes. Any of several methods may be employed.

MAINS, in 1924, considered that the best method was to make herbarium specimens, which, if dried quickly under moderate pressure, retain their color and last for several years. He pointed out that photographing to bring out the important details of reaction types is difficult, and recommended for this purpose the use of Wratten and Wainright panchromatic plates with a B (green) filter, photographing with both transmitted and reflected light, and enlarging the photographs to 2 to 3 times life-size.

With the development of color photography, it is now possible to obtain very faithful and permanent color photographs that bring out the characteristics of rust reaction types in full detail. The writer has had excellent results using indoor (A) Kodachrome film with powerful direct lighting secured through the use of 4 No. 1 photoflood lamps placed about 1 foot from the object.

For permanent, natural color preservation of infected leaves themselves, VACHA'S solution, developed by GERALD A. VACHA, Department of Plant Pathology, Minnesota College of Agriculture, is recommended. In order to determine whether his readings of infection types were strictly comparable to those of other workers, the writer, on one occasion, prepared a series of 21 vials containing wheat leaves with leaf rust infections of types ranging from 0 to 4—, preserved in VACHA'S solution, and sent them with his readings to NEWTON and JOHNSON in Canada. The readings of all three workers agreed closely enough so there was full assurance of comparable data although the writer's readings were based on the leaves before preservation, and NEWTON and JOHNSON'S on the specimens which had been preserved in VACHA'S solution for several weeks.

Variations in reactions due to impurity of differential seed stocks: — Ever since MAINS and JACKSON'S first report in 1926, there has been complaint from workers on wheat leaf rust specialization of genetic impurity in the seed of the differential varieties. For 15 years or more the seed of Mediterranean has been acknowledged to be a mixture of at least 2 or even 3 types, as regards rust resistance, which may be related to the fact that this variety hybridizes freely. RUDORF *et al.* (1933) report that Malakoff showed mixed rust reactions although it was uniform-appearing in the field. They also found genetic impurity in Hussar, and to a less extent in Loros and Brevit (1934). VOHL (1938) had the same experience with the last-named 3 varieties. ROBERTS (1936) found that Loros was lacking in uniformity morphologically (some plants having abnormally hairy leaves) as well as in rust reaction. HASSEBRAUK (1937) also reported segregation in the differentials.

The writer has had trouble of this kind since 1938, particularly with Mediterranean, and it has been his practice in race determinations to use twice the normal number of plants of this variety on this account.

The genetic impurity of seed stocks of the differential varieties contributes unnecessarily to the labor and errors in race identification, because even though an experienced worker can usually recognize aberrant results due to this cause, he would not do so if, through chance, a pot of seedlings happened all to result from seed of the contaminant, and if any considerable percentage of the seedlings were of the contaminating strain, it would be necessary to repeat the test. Since the supply of differential seed needed to furnish workers through the world is relatively small, it should be possible, by growing the wheat in isolated areas, with head-row planting, roguing, and greenhouse control of rust susceptibility, to produce and maintain homogeneous seed stocks of the differential varieties.

Effect of wheat nutrition on reaction type: — MAINS and JACKSON recognized from the outset that the types of rust reactions on certain of the differential varieties are modified by variations in environment. They found that Malakoff, when inoculated with races to which it was resistant, showed uniform resistance under all conditions of inoculation. "On the other hand, to some of the physiologic forms, some varieties, as for example Hussar, showed considerable variation, often being highly resistant when inoculated in the fall or winter and only moderately or slightly resistant when inoculated in late spring, indicating an environmental effect upon the reaction."

The first to make an experimental study of this problem were GASSNER and HASSEBRAUK in 1934. They grew wheat seedlings of the differential varieties in pots of sand to which were added nutrient solutions of different N, P, and K ratios and concentrations. The plants, 6 per pot, were inoculated with race 14 of wheat leaf rust and incubated at 18°-20° with the outcome shown in TABLE 6.

These reactions clearly indicate that soil fertility may influence the type of infection sufficiently to lead to a complete reversal from resistance to susceptibility, and hence lead to a different race identification. If we take each of these columns and attempt to identify the race indicated by the reactions, we find that only column 2 keys out to race 14, while columns 1, 3, 4, and 5 key out to races 26, 107, 71, and 57 (all of which except race

TABLE 6: *Effect of various amounts of N, P, and K on type of reaction of wheat leaf rust race 14 on differential varieties of wheat* (after GASSNER and HASSEBRAUK. For symbols see page 74.) : —

VARIETY	NO N NORMAL K	NORMAL N HIGH K	NORMAL N NORMAL K	HIGH N NORMAL K	NORMAL N LOW K
Malakoff	0 ;	0 ;	0 ;	0 ;	0 ;
Carina	3-2 ; —	2-3 ; —	3 ; —	3(4) ; ±	3(4) ; ±
Brevit	4 ; +	4(3) ; —	4(0, 3) ; ±	4 ±	4 +
Webster	2 ; —	2-3(0) ; —	3(0) ; —	0, 3 ; —	3(0) ; —
Loros	3(0) ; ±	3(0, 4) ; ±	3-4 ; ±	3(4) ; ±	3(0) ; ±
Mediterranean.	0(3) ;	0(3) ;	0(4, 3) ;	0, 3, 4 ; —	3, 4(0) ; +
Hussar.....	3 ; —	3-4 ; ±	3-4 ; ±	4 (;) ±	4 +
Democrat	0 ;	0 ;	0(3) ;	0(4) (;)	3(0, 4) ; —

26, were described by other workers subsequent to the publication of this table).

Certain trends are seen as the proportion of nitrogen to potassium increases from left to right in the table. With increasing nitrogen in the ratio, chlorosis becomes less evident in some varieties, the number of pustules tends to increase, and, the most important from our present point of view, the reaction type tends to pass from more resistant to more susceptible, from "0" to "3" or "4" in the case of Democrat and Mediterranean, and from "2" to "3" in Webster. We note that Malakoff, which is regarded as the most stable of the varieties, is the only one showing no change in infection type with increase of nitrogen amendment. The values in parentheses are not explained in GASSNER and HASSEBRAUK's text, but they appear to indicate some lack of purity in the seed stocks, which, as we saw in the preceding subsection particularly characterized Mediterranean, Hussar, Loros, and Brevit at the time of these experiments.

In later experiments (1939) HASSEBRAUK again noted that increase in nitrogen increased the susceptibility of Hussar and slightly altered the types of reactions of Carina and Brevit. A combination of high humidity and low nitrogen, however, changed the Hussar reaction of race 93 from resistant to susceptible, giving race 17.

That alterations of the reactions by changing the nitrogen level actually play a part in the practice of race determination is seen from NAUMOV's recommendation (1939): "For increasing the strength of reactions it is often advised before working to fertilize the soil, adding to pots 5 cc. of 1.5% NH_4NO_3, or better, $NaNO_3$."

The writer has cultured race 9 of *Puccinia triticina* on a variety of natural soils, without amendments, with all other conditions uniform. The reactions were typical for race 9 on the greenhouse soil mixture normally used for race identification, but on a rich, sandy loam from the Oklahoma Red River valley, the reactions of the varieties Mediterranean and Democrat changed from "0" in the checks to "2-3" and "2" respectively, which gave a series of reactions that keyed out to no known race.

Effect of temperature on reaction type: — The most extensive studies of the effect of temperature in altering the reaction of the differential wheats to races of *Puccinia triticina* have been those of NEWTON and

JOHNSON, reported in 1937 and 1941, and HASSEBRAUK in 1939. Prior to this time, however, a number of investigators had observed such temperature effects.

GASSNER and STRAIB (1931) inoculated a number of commercial and differential wheats with leaf rust race 14 and incubated the plants at various temperatures. There were several cases in which the reaction was reversed, from susceptible to resistant or *vice versa,* with a change in incubation temperature. Thus Malakoff was susceptible at 6.0° C. and resistant at 10.9°, 16.6°, and 18.7° C.; Democrat was resistant at 18.7° and susceptible at the other 3 temperatures; and a similar increase in susceptibility at lowered temperatures was seen in the von Rümkers Sommerdickkopf, Roter Tiroler Speltz, and Norka varieties; the reactions of Webster and of other German wheats toward race 14 were unaffected by culturing at temperatures between 20-22° and 6° C.

DODOV (1931*a*) found that the reactions of durum wheats were very variable with change of environment, and considered that temperature was the principal factor involved. RUDORF and his co-workers in Argentina (1933) found that in several cases the reactions of the differential wheats were weaker at lower temperatures than at higher ones. GESHELE (1936) considered that "race 24 is not sharply distinct from race 13, since at low temperatures some race 13 biotypes give evidence of rust on the varieties Mediterranean and Democrat." ROBERTS (1936) noted instability of the reaction of race 66 on Hussar wheat: with high temperature or with the combination of low temperature and low light intensity there was an atypical production of the "X" type reaction. In many cases, low light with low temperature increased resistance in normally susceptible varieties, while higher temperature and more intense light tend to make normally resistant varieties susceptible.

The earlier reports of NEWTON and JOHNSON (1937) indicate that while 65° F. led to "normal" reactions on all differential varieties, 75° F. increased the susceptibility of Carina, Brevit, and Hussar, and increased the resistance of Webster, Mediterranean and Democrat, while 60° F. operated in the reverse direction, increasing the resistance of Carina, Brevit, and Hussar and the susceptibility of Webster, Mediterranean, and Democrat. The reactions of Loros and Malakoff were constant at all these temperatures.

In their later work (1941) NEWTON and JOHNSON tested 8 races of leaf rust on the differential varieties at 57° or 60°, 64° or 65°, and 69° or 75° F., with different light conditions as well. There were many cases in which the reactions changed from resistant type to susceptible type or *vice versa* with increase in temperature. As a result, the races used gave sets of reactions which were characteristic of entirely different known or undescribed races, as seen in TABLE 7. No two of the undescribed races obtained were alike.

Of the differential wheats, Loros and Malakoff were least affected by temperature. Loros in no case showed reversal of reaction, and Malakoff in only 1 case out of a possible 8 changed from susceptible to resistant with increase in temperature. At the other extreme were Carina, Brevit, and Hussar. These varieties in 53%, 53%, and 67% of the tests, respectively, changed from resistant type at lower to susceptible type at higher tempera-

TABLE 7: *Wheat leaf rust "races" obtained when given races were inoculated on the differential wheat varieties and incubated at the stated temperatures and times* (condensed from NEWTON and JOHNSON, 1941.).

RACE INOCULATED	57° FEB.	60° FEB.	60° MAR.	60° APR.	64° FEB.	65° APR.	69° FEB.	75° FEB.	75° MAR.	75° APR.
9*	New	...	...	...	9	...	20	...	...	...
10	...	New	New	115	...	...	...	49	108	20
11*	New	...	...	...	New	...	66	...	...	...
15*	...	...	...	15	...	15	...	...	...	62
31	...	31	New	27	...	31	...	20	20	20
41*	New	...	...	...	41	...	77	...	...	...
44*	New	...	...	...	44	...	58	...	...	...
52	...	5	New	52	...	...	...	52	New	52
85	...	...	New	New	...	...	...	61	85	12
87	...	New	New	87	...	87	...	26	26	26
88	...	...	44	New	...	88	...	...	12	12
89	...	New	...	New	...	...	...	...	New	77

* In these cases NEWTON and JOHNSON did not give the reactions on Malakoff and Loros It is assumed that, as usual, the reactions on these varieties were normal; if they had varied, the results would have been even more bizarre than those appearing in the table.

tures. Webster, Mediterranean, and Democrat were intermediate in their stability, and the reverse of Carina, Brevit, and Hussar in the direction of the change. These varieties in 40%, 13%, and 13% of the cases respectively, changed from susceptible at the lower to resistant at the higher temperature.

HASSEBRAUK'S results (1939) in general confirm those of NEWTON and JOHNSON. He found that lowering the temperature from 20° to 6° C. increased the susceptibility of Malakoff and to a less extent that of Mediterranean, Democrat, and Hussar, while it increased the resistance of Carina, Brevit, and, to a slight degree, Webster. Loros was unaffected by the temperature change. Commercial varieties of wheat showed similar reaction changes. Carina showed increased resistance when the temperature was lowered only 4° (from 19° to 15° C.).

As a consequence of such variations in reactions, race 94 behaved as race 27 at 8.5° C., race 13 as race 31 at 10° C., and the races 20, 93, 14, 16, and 15 at 6° C., and race 11 at 10° C. in all cases gave groups of reactions that key out to no known race.

CHESTER and JAMISON (1939) observed that in many race determinations in Oklahoma, race 9 occurred almost exclusively in some experiments, while in other experiments, performed at other times, and under other conditions of temperature and light, race 13 predominated. The two races were rarely identified in any one experiment. Over a period of years, race 13 has been the dominant one in Oklahoma by a wide margin, while in Kansas, it is race 9 that is identified in the majority of cases. In two adjacent states with no separation by natural barriers, with uniform wheat culture and varieties, and prevailing winds directly from one state to the other, it is inconceivable that different races would predominate in the two areas.

Further evidence on this point was reported by CHESTER and TEMPLE in 1941 when cultures of rust first determined on different occasions as

races 9, 13, 19, 20, and 31, were cultured side-by-side on different days, so that the experiments were subjected to minor differences in environment during the incubation periods. It was found that in certain of the tests all of the cultures behaved as race 13, in others all behaved as race 31, etc. It was concluded that the differences in the 5 groups of reactions characterizing the so-called races 9, 13, 19, 20, and 31 are due to environmental differences, principally temperature, and that these are merely variations in expression of a single race, or at most of a group of races so closely related that differentiation is impractical and serves no useful purpose.

Effect of light on reaction type: — While the effect of light in altering leaf rust reactions is less marked than that of nutrition and temperature, there are numerous records of reactions being changed from susceptible to resistant or *vice versa* by changes in light intensity.

MAINS and JACKSON (1926) found Hussar more resistant to certain races in the winter than in the summer. DODOV (1931*a*) observed that various wheats exhibited a higher degree of resistance in the longer days of May than in March. ROBERTS (1936) found abnormal production of mesothetic reactions and increase of resistance associated with combined low light intensity and low temperatures. She observed that the reaction of Webster to race 73 varied with the light intensities of the different seasons of the year. With Hussar and races 22, 68, and 70, or Carina and races 73 and 75, low light coupled with low temperature was associated with greater resistance, WATERHOUSE (1929-30) observed that the varieties Hussar and Carina gave susceptible reactions in summer and mesothetic reactions in winter, and that the reaction of Thew changed from susceptible in summer to highly resistant in winter. More extensive studies on this question were made by HASSEBRAUK and by NEWTON and JOHNSON.

HASSEBRAUK (1937) found markedly greater resistance in some of the reactions in July than in tests under comparable conditions in May. In experiments in which plants were artificially darkened (1939) the reactions of the varieties Carina and Brevit were altered, with the result that race 19 behaved as race 10, and races 13 and 31 behaved as race 20 under low light intensity. In experiments of the reverse type (1940*b*) he found that with stronger lighting than was normal for his greenhouse, he obtained a preponderance of race 13 instead of race 20, and race 19 acted as race 9.

NEWTON and JOHNSON (1941) tested the effect of light by maintaining constant temperature and observing changes in reactions associated with the increase in natural light from February through April. They tested 7 rust races on 7 differential wheats during 3 months of different light intensity, at 60° and at 75°. The results are included in TABLE 7. In numerous cases there was a reversal of reaction from resistant to susceptible as day length and light intensity increased. This was expressed, to greater or less degree, by all varieties toward one or more races and by all races toward one or another variety. The reactions that normally are extremes of resistance or susceptibility were less affected by light than those representing only moderate resistance or susceptibility. Since in the experiment both light and temperature were varied independently, it is possible to gain an idea of the comparative magnitudes of the two effects. It was seen that temperature variation was more influential on the reactions than light

variation, and often a significant temperature effect was seen in cases in which variation of light had but slight effect. Thus the reactions of Carina wheat at the three light intensities were "1", "1+", and "1+" at 60° C. and "3+", "3", and "3+" at 75°. In a few cases, the reactions, *e.g.*, those of Webster to race 31 ("3+"), and of Democrat to races 88 and 89 ("3+") were unaltered regardless of the variations in temperature and light. In some cases the effect of low light was sufficient to alter the race identification even at a favorable temperature. Thus in the case of race 52 the Hussar reaction is normally "3". At 60° and with the low normal light of February, the reaction dropped to "1", which would necessitate identifying the culture as race 5 instead of 52. In March this reaction became "X" which, in combination with the other normal reactions of race 52 would indicate no known race. Finally in April the normal "3" reaction was obtained. At 75° this reaction was between "3—" and "3+" at all light intensities. Other illustrations are seen in the table.

Effect of humidity on reaction type: — HASSEBRAUK (1939) compared infection types on differential wheat varieties with and without continuous coverage with bell jars. Although the effect of the high humidity thus induced was not as striking as those of temperature or nitrogen nutrition, in a number of cases the high humidity induced a reversal of reaction, the plants in general exhibiting greater susceptibility under high humidities. Thus, the Brevit reaction of race 13 was changed from "2" to "3-4", which is characteristic of race 20, the Hussar reaction of race 19 changed from "2" to "3", which is also characteristic of races 13 and 20, and a comparable change occurred in the Hussar reaction of HASSEBRAUK's race "C" (=race 94). The combination of high humidity and low nitrogen supply changed the reactions of race 93 to those of race 17. GASSNER and STRAIB (1931), on the other hand, failed to note any difference in reaction of plants under bell jars as compared with those exposed to the low humidities of free greenhouse air.

The writer tested the reactions to race 13 under low, medium and high humidities, and also found an increase in susceptibility with increase in humidity, but limited in this case to the varieties Brevit and Democrat. The difference was great enough, in the case of Brevit, to alter the race identification.

Effect of age of seedlings on reaction type: — HASSEBRAUK (1939) also compared the infection types on the primary leaves of seedlings of different ages. He found that the youngest plants were most resistant (Carina, Brevit) to races 19 and 31 but the reverse was seen with races 20 and 14. The picture was unchanged whether the experiment was performed at normal or low temperature. The writer performed an analogous experiment in which the youngest plants of Brevit and Democrat were less resistant than the older ones, this difference, in the case of Democrat, being sufficient to change the race identification from race 13 to an unknown race.

Race identity in relation to environment, and the concept of group reactions: — The facts brought out in the foregoing sections have a most important bearing on the whole structure of our present system of physiologic specialization in *Puccinia triticina.*

We have seen that differences in greenhouse environment and culture of experimental plants, — temperature, soil, light, humidity, and age of seedlings —, differences such as may occur from time to time in any one greenhouse, and which unquestionably exist if we compare the greenhouse conditions and methods of one worker with those of another, are sufficiently great in the case of each variable that a single pure culture of rust in one environment produces sets of reactions which characterize one race, in another environment reactions which characterize other known or unknown races. It has become apparent to a number of workers that the "International Register" contains numerous examples of 2 or more "races" bearing different numbers, attributed to different workers, and based on supposedly clear-cut reaction differences, which "races" are no more than a single race exhibiting its property of inducing resistant-type reactions on given differential varieties in one environment and susceptible-type reactions on them in another, perhaps only slightly different, environment. What significance, for example, can we attach to the differences between the Register's races 5 and 52 when the same pure culture is identified as race 5 in February and as race 52 in April, the only tangible environmental variable being the difference in light intensity during these two months? Is there any basic difference between races 9, 13, 19, 20, and 31 when such minor environmental differences as characterize successive days in the same greenhouse cause the same pure culture of rust to react as one of these if inoculated on one day and as some other one of the group if inoculated on another day? If we must recognize a rust culture as race 5 in February and as race 52 in April, does not logic also require that we base a new race on the still different set of reactions of the same culture in March, and a host of other new races on the reactions that key out to no known race as seen in TABLE 7? If we do not choose to follow such a procedure, a logical alternative is to introduce, accept, and make use of the concept of environmentally conditioned *race groups*, recognizing as single races those groups of races the reactions of which duplicate those of others of the same group under certain environmental conditions.

The literature gives us ample authorization for doing this, From study of the behavior of certain races under differing environments we have evidence that the following are such race groups: Race 9=10=13=19=20=24=27=31=108=115; race 2=3=15=25=34=62; race 11=14=22=26=66=71; race 21=41=77=89=94; race 12=44=58=61=76=81=84=85=88; race 5=52; race 43=49=50=64=69; race 57=67; race 17=93; race 45=57; and race 68=107 (CHESTER and TEMPLE, 1941; DODOV, 1931*a*; GASSNER and HASSEBRAUK, 1934*a*; GESHELE, 1936; HASSEBRAUK, 1937, 1939, 1940*b*, 1940*c*; JOHNSTON and MAINS, 1932; NEWTON and JOHNSON, 1941; SCHEIBE, 1930*b*; VALLEGA, 1942*a*, *b*; VOHL, 1938). A further careful and extensive study of the effect of environment on the races listed in the "International Register" would unquestionably bring to light many more such cases.

It is noteworthy that with few exceptions the members of any of the groups listed above are quite uniform in their reactions on Malakoff, Webster, Loros, Mediterranean and Democrat wheats, and their environmentally-conditioned instability is confined to their reactions on Carina, Brevit, and

TABLE 8: *Physiologic races of* PUCCINIA TRITICINA *based on reactions on wheat varieties Malakoff, Webster, Loros, Mediterranean, and Democrat. Key: "R" resistant, — infection types 0 to 2+; "S": susceptible, —infection types 3— to 4+; "X": mesothetic, heterogeneous, or indeterminate* (defined on page 75) ; *"V": variable, — infection types 2-3, 1-3, 2-4, etc.:—*

A. *Race groups, of which the members indicated in bold face type have been experimentally shown to react like one another, and other members of which are inseparable except by reactions on Carina, Brevit, or Hussar.*

GROUP	MAL.	WEB.	LOR.	MED.	DEM.	THEW	INCLUDES FORMER RACES:
1	R	R	R	R	R	—	**1, 16,** 53, 63, 120, 123
2	R	R	R	S	S	—	**2, 15, 25, 34,** 59, **62,** 127
	R	R	V	S	S	—	**3,** 102
5	S	R	R	S	S	—	**5, 52**
9	S	S	S	R	R	—	**9, 10, 13, 19, 20, 31**
	S	S	S	R	X	—	**24**
	S	S	S	R	V	—	**27**
	S	S	S	X	X	—	**115**
	S	V	S	R	R	—	*29,* **108**
11	R	R	S	R	R	S	**11, 14, 26,** 38
	R	R	S	R	R	R	95
	X	R	S	R	R	—	**22**
	R	V	S	R	R	—	**66,** 72, 106
	R	V	S	V	R	—	**71,** 75
12	R	R	S	S	S	—	**12,** 32, **58, 61, 84**
	R	R	S	X	S	—	**44**
	R	X	S	S	S	—	**76,** 90
	R	V	S	S	S	—	**85**
	R	X	X	S	S	—	**81**
	R	S	S	X	S	—	**88**
17	S	R	R	R	R	—	**17, 93**
18	R	S	S	R	R	S	18, **68,** 96, **107**
	R	S	S	R	R	R	97
21	S	S	S	S	S	—	**21,** 30, 35, 42, 54, **77,** 122
	S	X	S	S	S	—	**89**
	S	S	S	V	S	—	**94**
37	S	R	S	R	R	—	**37,** 43, 49, 59, 64, 128
	V	R	S	R	R	—	**69**
45	R	S	S	S	S	—	**45, 57**
	R	S	S	S	V	—	*67*

Hussar. The few exceptions are cases in which the environmentally-conditioned differences in reaction are between a variable or mesothetic reaction and resistance or susceptibility.

Many workers have observed that Carina, Brevit, and Hussar are consistently variable in their reactions, much more so than the other 5 differential varieties, and several have expressed the opinion that these three varieties are unsuitable as differentials on this account.

This leads us to a second logical step, — to discard Carina, Hussar and Brevit as differentials. Future work on specialization of wheat leaf rust could then be based on the use of the remaining 5 differentials, or to these 5 could be added certain of the more stable differentials found by HASSEBRAUK.

TABLE 8: *Physiologic races of* PUCCINIA TRITICINA (continued) : —

B. *Remaining races of the "International Register", the relationships of which have not been determined experimentally. Many are probably related to, or inseparable from, one another or from the race groups in part A.*

RACE	MAL.	WEB.	LOR.	MED.	DEM.	INCLUDES FORMER RACES :
4	R	R	S	S	R	4
6	S	R	S	S	S	6, 28, 39, 105, 126
7	S	S	R	S	S	7,60
8	S	S	S	S	R	8
23	X, V	S	S	R	R	23, 70
33	R	R	S	R	S	33, 46, 51
36	V	R	R	R	R	36
40	S	R	S	S	V	40
41	S	S	S	R	S	41, 99, 117
47	S	S	R	R	R	47, 91, 119, 121, 125
48	S	S	S	V	R	48
55	R	V	S	S	R	55
56	R	R	R	S	R	56, 92
65	S	X	S	X	X	65, 80, 101
73	R	S	S	S	R	73, 86
74	R	R	V	R	R	74
78	R	R	S	X	X	78
79	R	R	X	R	X	79
82	S	S	S	X	S	82, 112
83	S	R	S	X	S	83
87	R	S	S	X	X	87*
98	R	R	V	V	V	98
100	X	R	R	S	S	100
103	S	R	X	X	V	103
104	S	V	S	S	S	104, 114
109	S	R	R	R	S	109
110	S	R	V	R	R	110
111	R	R	V	V	S	111
113	S	X	X	S	S	113
116	V	V	V	V	V	116
118	R	S	R	R	R	118
124	R	R	R	R	S	124
129	S	R	S	S	R	129

* Race 87 shows affinities to race 11 (NEWTON and JOHNSON, 1941).

Meanwhile the reactions of Carina, Brevit, and Hussar could be deleted from the "International Register" and the races therein then reduced to the number that can be clearly differentiated by the reactions on the remaining 5 varieties. Such an eventuality was foreseen by MAINS and JACKSON when they stated (1926, p. 102) : "With the study of additional cultures, it may be desirable to modify the characterization of some of the physiologic forms to include cultures which may show but slight deviations. This is especially true of such forms as have been isolated but once and lost after but comparatively little study, including forms 1, 7, 8, and 12." The results of such a procedure are given in TABLE 8.

This procedure reduces the number of races from 129, many of which are proven duplicates of one another, to 44 (considering the groups in TABLE 8A as single races) and further study of their responses to varying environments will doubtless further reduce the duplication, particularly in those races characterized by mesothetic or variable reactions. We can see

from part A of the table that many of the "races" so characterized are but environmentally-conditioned variants of the 11 races that have been studied in relation to environment. Some of the mesothetic reactions are no doubt due to the presence of 2 or more races in cultures studied; others may be due to environmental effects; and still others may be truly characteristic of certain pure races, relatively independent of environment; and since there is no means, at present, of distinguishing between races based on true mesothetic and variable reactions and those based on reactions from mixed cultures, the races marked by these unstable reactions in part B of the table may be retained provisionally, for the present.

TABLE 8, in grouping the races, attempts to emphasize *resemblances* in races, rather than disregarding these and having in mind only *differences,* of all degrees, between them. This is done in an effort toward simplification of race analysis rather than its further complication in years to come.

The worker with race 9, for example, should have clearly before him the possible relationship between this race and races 23, 48, 65, and 70 (*see* TABLE 8B) as an aid toward ultimate disposal of such related races, — their retention if the "X" or "V" reactions prove constant, and their reduction to synonymy if these reactions are shown to be environmentally-induced fluctuations of the typical race 9 reactions.

TABLE 8A offers strong confirmation of the view that the removal of Carina, Brevit and Hussar from the list of differential wheats results in a logical disposition of races of wheat leaf rust. This is seen in the fact that if we consider the many scores of tests revealing one race behaving as another under altered environment, and then arrange the races in groups each containing races that are duplicates of one another on the basis of these tests, we discover that the arrangement fully harmonizes, as in the table, with the groupings that result from the omission of the differential varieties Carina, Brevit and Hussar. We find no case in which two races shown experimentally to be inseparable fall into two distinct groups according to their reactions on the stable varieties Malakoff, Webster, Loros, Mediterranean, and Democrat, the only variation in reactions on these varieties being the evidently non-significant variation from resistant or susceptible to mesothetic or variable. JOHNSTON and MAINS (1932) have pointed out that when 2 races differ in their reaction on only one variety, — "If this difference is high resistance opposed to high susceptibility it probably is real and constant. If, however, it is between resistance and intermediacy or susceptibility and intermediacy, there is some doubt as to the actuality of the difference."

There is only a single case in the table in which a variety is susceptible to one race and resistant to another race in the same group. This is the case of race 88 in the race 12 group, but in this group the Webster reactions are clearly borderline. With a progression from resistant to susceptible, the majority of the members of the group induce reactions on Webster that are either weakly or moderately resistant, intermediate, or variable, and race 88's reaction is only moderately susceptible. A similar situation may exist in the case of race 87 in TABLE 8B which NEWTON and JOHNSON found to be an environmentally-induced variant of race 11. This is also a case involving a borderline Webster reaction. In this connection it is important to note that the 5 differentials retained are not equally stable in their

reactions, and that of them, Webster is least stable of the 5. (We recall that in NEWTON and JOHNSON'S studies the percentages of environmentally-induced reaction changes were 0% for Loros, 13% for Malakoff, Mediterranean, and Democrat, 40% for Webster, and 53%, 53%, and 67% for Carina, Brevit, and Hussar respectively.)

It is no doubt true that some of the races distinguished only by reactions on Carina, Brevit, or Hussar, may be truly distinct genetically. Only a few of the race groups indicated in the table have been analyzed and their members shown to be different environmentally-conditioned expressions of the same race. Yet we cannot logically consider differentials that are grossly unstable in some well-authenticated cases as suitable in other cases that have not been studied critically.

It must always be kept in mind that the greatest service of the study of physiologic specialization is in providing a guide in the breeding of rust-resistant crop varieties, and the system of race differentiation should be developed with this purpose foremost in mind. If two races differ only in environmentally-unstable reactions on an unreliable differential variety, the recognition of this difference only complicates the testing of breeding stocks without serving any useful end, since we are interested in developing wheats that will maintain their resistance under a broad range of environments, and therefore are concerned only with well-defined, constant, stable factors for resistance.

One is justified in inquiring whether the reduction of 129 races to a much smaller number in the fashion followed in TABLE 8 will not cause wheat breeders to overlook races that are potentially dangerous. The question reduces itself to this: is the resistance or susceptibility of commercial wheats or breeding stocks toward the races that are considered inseparable in any one group of TABLE 8A, governed by the same or by different factors; *i.e.*, will a wheat that carries resistance to race 9 be necessarily resistant to races 13, 19, 20, 31, etc.?

There is experimental evidence that, in those cases where it has been studied, resistance is directed toward the group and does not vary with respect to the different members of the group. DODOV (1931*a*) tested 192 wheat varieties with cultures of 7 races of leaf rust. These include races 13, 19, 20, and 24 which according to TABLE 8 are not separable, all belonging in the race 9 group, and races 15, 17, and 21, all of which fall in groups distinct from one another and from the race 9 group. If our position is tenable, the 192 wheats should have each reacted in the same fashion toward the races 13, 19, 20, and 24, and we might expect in numerous cases that the reactions of a given wheat variety toward races 15, 17, and 21 would bear no relationship to one another nor to those of the 13-19-20-24 group. This is indeed the case, as shown in the representative sample data from DODOV'S tables given in TABLE 9.

Of the 192 wheats only one reacted in such a way as to sharply discriminate between members of the race 13-19-20-24 group, and this proved to be the discarded, unstable Hussar. Meanwhile, as clearly brought out in the table, the reactions of given wheat varieties were often quite independent with reference to races 15, 17, 21, and the 13-19-20-24 group as a whole.

TABLE 9: *Representative reactions of wheat varieties toward the rust races indicated* (discussion in the text, from DODOV, 1931*a*) : —

WHEAT VARIETY:	INSEPARABLE RACES:				DISTINCT RACES:		
	13	19	20	24	15	17	21
Fultz (brown chaff) Sel. M1-7..	R, S	R, S	R, S	R, S	S	R	Int.
Resaca, C. I. 6390-2	S	S	S	S	R	Int.	S
Turkey × Bd. 47-1	S	S	S	S	R, S	S	S
Buford, C. I. 6295-5	R	R	R	R	Int.	R	R
Mindum, C. I. 5296-2	R	R	R	R	Int.	R	R
T. durum fastuosum	S	S	S	S	S	S	Int.
Arnauti 3361	Int.	Int.	Int.	Int.	S	R	Int.
Mavragani argoladanon	Int.	Int.	Int.	Int.	S	S	S
Tounous G. 6544	R	R	R	R	S	R	Int.
Hussar	S	R	S	S	R	Int.	S

DODOV's data thus give strong testimony that for the practical purpose of developing leaf rust resistance in wheat, one is justified in proceeding on the basis of race groups, since there is no evidence, so far as the experiments go, that resistance or susceptibility to one race of a group is dependent on different factors than govern resistance or susceptibility to other races in the same group.

HASSEBRAUK (1940*c*) inoculated 936 winter wheats with races 11, 13, 14, 15, 16, 20, 31, and 94, and his results confirm and extend DODOV's findings. HASSEBRAUK did not tabulate his results, but he came to the conclusion that races 13, 20, 31 (members of a single group), reacted similarly, and were related. Races 11 and 14 (members of a single group but one that is distinct from that containing races 13, 20, and 31) also reacted on the 936 wheats as though they were closely related. Races 15 and 16 (which belong in groups distinct from each other and from the other races listed) reacted in a fashion independent of each other and of all other races studied. The reactions of race 94 resembled those of the race group 13-20-31 which suggests that the major factors for resistance and susceptibility may not only be uniform within a group but at times may even agree with those in a second group, which from the practical standpoint of wheat breeding points toward even greater simplification of the system of races than is proposed here.

The relationship between races 11 and 14, and the distinctness of races 13 and 15 from races 11 and 14 and from each other, is also indicated, though less strikingly, in SCHEIBE's tests of these races on 295 wheat varieties. There were a few cases of marked disagreement between races 11 and 14, perhaps comparable to the unstable reactions of Carina, Brevit, and Hussar, but these were less numerous than the cases of disagreement between the races that fall in distinct race groups.

Further confirmation of these results is seen in the wheat breeding experiments of VOHL (1938) who found that resistance of the wheat varieties Ardito and Varonne toward races 11, 14, and 15, and of Normandie and 3972_{30} toward races 14 and 15 were due in each case to a single factor. "We speak, in this case, of group-resistance, *i.e.*, resistance toward a group of races." As a result of his studies, VOHL states: "The absolute

number of races has no importance to the practical breeder; he is primarily interested in the most important races or race groups. There would be a great reduction in the labor of the plant breeder if he need not consider the 40 races that have been listed for Europe but perhaps deal with only 2 or 3 race groups."

Chapter VIII

PHYSIOLOGIC SPECIALIZATION (*Contd.*)

Origin of races: — It is well known in the case of *Puccinia graminis* that if two physiologic races mate on the barberry, new races unlike their parent races in pathogenicity, spore color, etc., may result. This not only has been demonstrated experimentally but evidently also occurs in nature. The expression of dominance or recessiveness, and segregation in the F_2 generation, in crosses of rust races, follows the well-known laws of heredity in the higher plants. F_2 segregates comprise a variety of types, often including the parent races together with new hitherto unknown ones. As rust lines in nature are often heterozygous, their selfing also may result in the production of new races.

Puccinia triticina has the sexual mechanism to permit this manner of race origin. A single receptive hypha on *Thalictrum* (and presumably on *Isopyrum*) can receive from 1 to 12 male nuclei (ALLEN, 1932) and the feeding of insects on spermagonial nectar can provide ample opportunity for the hybridization of races.

On one occasion new races have been produced experimentally in this manner. WATERHOUSE in Australia (1932) inoculated *Thalictrum* with a mixture of leaf rust telial inoculum. Previous extensive search had brought to light only 2 races of leaf rust in Australia. From aeciospores resulting from these mass inoculations WATERHOUSE isolated 2 races that had not been previously described, and their production was attributed to either hybridization or selfing of heterozygous races on the aecial host.

There is little likelihood that this mode of race origin plays any important rôle today except, perhaps, in eastern Siberia, where, alone, the aecial host is regularly infected in nature. In the early evolution of *Puccinia triticina,* however, it is conceivable that the production of races in this fashion had an important part in the creation of the present diversity of pathogenic types in this fungus. It would be of great interest to determine whether isolated eastern Siberia presents an unusually rich assortment of uncommon or new races, such as might be expected in the only area of the world where sexual reproduction of the fungus is known to occur regularly.

A second possibility is the origin of new races by mutation in the diploid mycelium, such as is known to occur in *Puccinia graminis* and *P. glumarum.* In the latter case, GASSNER and STRAIB detected mutants at the rate of 1.6 per 100,000 to 200,000 uredospores.

In *Puccinia triticina* we have records of two such cases. JOHNSTON in 1930 collected on a resistant wheat strain in Texas an aberrant race, later described as race 27, which appears to have arisen by mutation, because it is constant in reproduction and differs widely from other known races in many respects; the pustules are smaller and light orange rather than orange-red, they require 23 days to reach full development or twice as long as is common for *P. triticina,* no chlorosis or necrosis accompanies the pustules,

which are of type "3-4" despite their small size, and the spore walls are slightly thinner and the spores less regular in shape than those of the common race 9. There is no direct proof that this race arose through mutation, but this is a likely possibility considering the complete absence of the sexual stage of the rust in nature in America.

ROBERTS' discovery (1936) of a mutant race occurred under strictly controlled conditions. In a completely isolated plant of Malakoff wheat which had been inoculated with a pure culture of race 66 (race group 11), to which Malakoff is resistant, there appeared a type "4" pustule which remained constant in reproduction and was determined to be a variant of the unrelated race 10 (race group 9), differing from race 66 in Hussar as well as Malakoff reaction. The mutant was distinct from any race being cultured in ROBERTS' greenhouse at the time and from any other race recorded outside North America up to the present.

We have only conjecture to acccount for the nature of the process by which such mutations arise. NEWTON and JOHNSON note that mutants are usually retrogressive, *i.e.* appear to have arisen by the loss of some character associated with the source race. WATERHOUSE expresses the hypothesis that mutant races may arise from transfer of nuclei through anastomosis of vegetative mycelia of two rust races in the same area of the leaf. There is no cytological proof of this likely possibility.

A third possibility, origin of races by adaptation, carries us back to the Lamarckian and Darwinian views of the origin of species, by adaptation and natural selection, respectively, and to the "bridging host" hypothesis of MARSHALL WARD.

There is no evidence that heritable changes may result in leaf rust races as a consequence of long exposure to abnormal environments. CALDWELL and STONE (1936) cultured several races of the rust through many single uredial generations with all inoculations in darkness (closed stomata), and, separately, many generations inoculated in the light (open stomata). When the cultures were then used to inoculate wheat under uniform conditions of light or darkness, respectively, they saw no sign of adaptation to light or darkness and no evidence of selection for ability to infect in darkness.

The "bridging host" hypothesis, whereby a race of rust that can infect one host variety, but not a second, may gain the ability to infect the second if it is first passed through an intermediate variety, has not been tested with reference to *Puccinia triticina;* there is ample evidence, however, from the extensive experiments of STAKMAN, that this does not apply in the case of stem rust.

While there is no proof that bridging hosts or ecological adaptation play any part in the origin of races, they do play a very important part in changes in the composition of race populations. It is entirely possible that it was the latter effect which MARSHALL WARD mistook for fundamental changes in the pathogenicity of races. A hypothetical example will make this clear:

Let us assume two races of rust, "x" and "y", and 3 varieties of wheat, "A" which is susceptible to race "x" and resistant to race "y". "B" which is immune from race "x" and susceptible to race "y", and "C" which is moderately resistant to race "x" and susceptible to race "y". If varieties "A" and "B" are each exposed to a rust population consisting principally

of race "x" but containing a trace of race "y", variety "A" will react as susceptible and variety "B" as resistant. If variety "C" is exposed to this same rust population it will first behave as moderately resistant, but with repeated exposures, the amount of race "x" will diminish and that of race "y" will increase, until "y" becomes the predominant race in the population, and if the population now is used to inoculate variety "B", the latter will behave as susceptible, — *i.e.* its reaction has been reversed by passing the rust population through a third variety the effect of which was to change the proportions of the two races in rust population.

This is not merely theoretical. There are numerous records of the changing of fungus populations in nature through selective action of given host varieties. When a variety that is resistant to some strains of a parasite and susceptible to others is grown extensively there follows a mass shift in the strain population to those strains to which the host variety is susceptible. This was the case with race 56 of wheat stem rust, the proportion of which in the American rust population increased at a colossal rate from an insignificant beginning when Ceres wheat, which is susceptible to this race but resistant to many others, became cultivated on an extensive acreage. Similar cases are reported by CÂLNICEANU (1934) for bunt, loose smut, and stripe rust. This worker inoculated wheat varieties with mixtures of known proportions of different leaf rust races, and found that regardless of the proportions, each variety acted in such a way as to select and increase those races to which it was most susceptible, at the expense of other races.

Biological characteristics of races other than pathogenicity: — We are accustomed to think of physiologic races of a given fungus as differing from one another to no significant extent beyond their diverse pathogenicities on different host varieties. MAINS and JACKSON, in describing the first 12 races of *Puccinia triticina* found few morphologic differences between the races, but suggested that future tests might show them to differ physiologically, as in temperature requirements for spore germination, winter survival as mycelium, or ability to develop in the host plant under certain environmental influences such as has been shown by HURSH and PELTIER for stem rust. Subsequent work has brought to light numerous differences of these kinds.

Mention has been made of JOHNSTON'S race 27 which differs notably from other common races in pustule size and color, thickness of spore walls, regularity in shape of spores, and size of spores.

WATERHOUSE (1930*a*) tested for statistical significance the measurements of 200 uredospores of wheat leaf rust races 95 and 26. The spores of the two races differed in length by .78 ± .147 μ, in width by 1.10 ± .13 μ and in shape (length : width) by .13 ± .01 μ, the results representing significant differences in each of these categories, since the differences divided by the probable errors were 5.2, 8.5, and 13.0 in the 3 cases respectively. (A value over 3 is generally considered significant.)

Different leaf rust races show well-defined differences in their responses to temperature. We have already seen that the reactions of some races on certain wheat varieties fluctuate with temperature, light, and other factors.

This, according to JOHNSON and NEWTON (1937), is much more characteristic of certain races than others.

NAUMOV (1939) notes that leaf rust races differ in their reactions to temperature as seen in the differences in the reported cardinal temperature points and lengths of incubation periods. It has been pointed out that JOHNSTON's aberrant race 27 (1930) has an incubation period double that of ordinary races. GORYACHEVA (*in* NAUMOV, 1939) found that at high temperatures the incubation periods of different races differed by 1-2 days, although at optimal temperature no difference was seen. The writer has also noted that race 21 had an incubation period one day longer than that of race 9 and other common races under uniform conditions.

The various races of leaf rust also differ in their abilities to overwinter as dormant mycelium. JOHNSTON and MAINS (1932), for example, find race 9 overwintering more readily than other races in the southern Great Plains, so that early spring collections consist of this race exclusively, and STEPANOV (*in* NAUMOV, 1939) has also observed differences in winter- and cold-resistance of the different races in Russia. In New South Wales, one of the two dominant races occurs more frequently, early in the season, than the other according to WATERHOUSE (1938).

In the same way different degrees of drought resistance characterize the different races. According to YARKINA, "race 109S" (race group 1) which is found in dry areas and seasons in Saratov province, has drought resistance that presumably does not occur in other races (implying race groups 9 and 65 which were collected in moister seasons or locations).

Race 17 has been found by Russian workers (MURASHKINSKI *et al.*, 1938; NAUMOV, 1939) to stimulate greater activity of oxidative enzymes and greater transpiration in affected tissues than race groups 9 and 65. They found in addition that race 17 was less able to attack older tissues of the host plant (Brevit) than seedling tissues, but this was not characteristic of the other two races. They also report that different races form teliospores at different times and with differing facility.

FEDOTOVA (1938), in serological tests, determined that the globulin fraction of a given wheat reacts differently toward the globulins of different rust races, indicating protein differences in the races.

STEINER (1930) compared the osmotic values of uredospores of races 11, 13, and 14 (race groups 9 and 11) and reported notable differences in both maximum osmotic values and upper limits (*see* page 59) for the 3 races. His work was repeated under more strictly controlled conditions by HASSEBRAUK (1932*a*) who found no differences in the upper limits but for maximum osmotic values obtained 13.0 atm. for races 11 and 14, and 10.0 atm. for race 13. (We recall that in our simplified classification, races 11 and 14 are regarded as pathologically inseparable.) STEINER drew some far-reaching conclusions from his tests, suggesting a correlation between osmotic value of the spores of a given race and adaptation of that race to regions of specified annual rainfall, and even considered that eventually we may be able to identify rust races by osmotic values alone. Such conclusions are not justified in view of the paucity of STEINER's data and the fact that they could not be confirmed in the more detailed and better controlled experiments of HASSEBRAUK.

TABLE 10: *Frequency of identifications of physiologic races of wheat leaf rust in North America.* (Data for Canada from NEWTON and JOHNSON, (1941), for 1931-1940; data for United States from MAINS and JACKSON, (1926), for 1920-1923, and JOHNSTON and MAINS, (1932), for 1926-1929; data for Oklahoma from CHESTER *et al.* (1939, 1941) for 1938 and 1939 with additional original data for 1940-1943. The table does not include the extensive data accumulated by the U. S. Department of Agriculture and cooperators of the past 12 years, since these have not been released by *bona fide* publication. A study of them, however, indicates that their inclusion in the table would result in no material change in the indicated race frequencies.)

RACE GROUP	MARITIME PROVINCES	ONTARIO, QUEBEC	PRAIRIE PROVINCES	BRITISH COLUMBIA	CANADA, TOTAL	UNITED STATES	OKLAHOMA	GRAND TOTAL
1	13	6	5	8	32	6	1	39
2	41	31	47	19	138	28	26	192
4	..	..	..	..	..	2	..	2
5	3	14	39	..	56	16	12	84
6	1	2	5	..	8	14	21	43
7	..	..	..	..	..	1	..	1
8	..	..	..	..	..	1	..	1
9	10	22	80	2	114	146	188	448
11	1	..	5	20	26	7	..	33
12	55	34	20	6	115	10	21	146
18	..	..	..	..	..	..	4	4
21	3	11	32	4	50	18	46	114
33	..	..	..	..	..	9	1	10
36	..	..	..	..	..	5	..	5
37	..	3	1	..	4	7	1	12
40	..	..	..	..	..	2	..	2
45	..	..	..	..	..	2	..	2
47	..	..	..	..	..	3	..	3
48	..	..	..	..	..	2	..	2
56	5	..	4	1	10	..	..	10
65	1	7	6	..	14	..	..	14
83	..	..	1	..	1	..	..	1
87	..	1	..	2	3	..	..	3
103	1	..	..	..	1	..	..	1
104	1	3	2	..	6	..	1	7
Total	135	134	247	62	578	279	322	1179

Occurrence and distribution of races: — An attempt has been made in TABLES 10 and 11 to present a summary of all published data on the occurrence and relative prevalence of physiologic races of wheat leaf rust. The records have been entered, according to TABLE 8 and pertinent discussion, under race groups, the individual races of any race group having been shown to be separable only by reactions on environmentally unstable differential varieties.

Certain principles of race distribution can be deduced from the data, although the extent of such deductions is limited by the fact that in many important wheat regions of the world the sampling has been too meager for reliable conclusions.

The tables include records of 4,829 race identifications. Two race groups, 9 and 11, account for 64% of all determinations; eight race groups, less than one-fourth of the total number, groups 1, 2, 5, 6, 9, 11, 12, 21 and 37, account for 96% of all determinations; and less than 1% of the determi-

TABLE 11: *Frequency of identifications of physiologic races of wheat leaf rust other than in North America:* — Race group (according to Table 8)

	1	2	4	5	6	7	9	11	12	17	18	21	23	37	45	47	55	56	65	73	74	98	104	109	116	118	Total tests
Germany-Austria	101	157+	..	3	6+	6	293+	370+	2	12	3	57+	..	..	..	..	..	2	..	..	..	..	..	..	..	..	1012+
Belgium	1	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2
Finland	..	3	..	1	1	+	8	1	..	..	..	6+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	20+
Czechoslovakia	1	1	..	..	..	..	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	6
Bulgaria	..	7	..	..	..	..	58	1	..	2	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	70
Hungary	..	1+	..	..	..	..	13	1	..	..	..	2+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	17+
Holland	1	3	..	..	..	..	..	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	7
Italy	..	7+	1	..	..	1	1	2	13	..	..	..	..	..	2	..	1	1	..	1	..	..	..	..	..	..	30+
Greece	..	1	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3
Sweden	..	2	..	..	..	..	28+	3+	..	..	..	5+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	38+
Turkey	..	3	..	..	..	..	4	3	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	11
Poland	..	..	..	..	..	..	13	1+	..	..	..	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	17+
Lithuania	..	..	..	..	..	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2
Latvia	..	..	..	..	..	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2
Estonia	..	..	..	..	..	..	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4
France	..	1	..	..	..	..	3	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	8
Switzerland	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2
Rumania	1	9	..	..	..	..	105+	1	..	5	..	12	..	4	..	..	..	..	2	..	..	..	..	..	..	..	139+
England	+	7+	..	..	..	..	1	1	..	..	3	..	2	1	5	..	..	..	..	1	..	..	..	..	..	..	21+
Portugal	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	+
European Russia	15	..	..	..	..	..	129+	+	..	4+	..	2	..	..	..	+	..	..	++	..	..	..	..	..	3	..	153+
Total Europe.	120	202+	1	4	7+	7+	669+	395+	15	23+	7	88+	3	5	7	+	1	3	2+	2	+	..	..	..	3	..	1564+

TABLE 11: (Continued)

	1	2	4	5	6	7	9	11	12	17	18	21	23	37	45	47	55	56	65	73	74	98	104	109	116	118	Total tests
Russia—																											
unspecified ...	+	..	..	..	..	..	++	..	..	+	..	+	+	+	..	+	..	..	..	..	..	..	..	..	..	+	+
Asiatic Russia ..	..	..	..	..	..	..	31	..	..	..	..	7	..	..	..	..	..	..	..	..	..	1	..	..	..	..	39
Japan	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	+
India	304	..	..	..	..	..	108	3	..	..	8	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	423
Total Asia ...	304+	..	..	..	..	..	139	3	..	..	8	7	..	..	..	..	..	..	..	..	..	1	..	..	..	..	462+
Libia	..	1+	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1+
So. Africa	..	10	..	..	..	..	18	12	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3	..	..	43
Total Africa..	..	11+	..	..	..	..	18	12	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3	..	..	44+
Australia	..	+	..	..	..	..	..	1220	..	..	+	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	1220+
Argentina	..	14+	..	13+	3	..	168	3	..	2	..	+	..	67	1	..	..	..	..	..	..	..	..	..	..	..	271+
Chile	..	16	..	+	+	..	+	+	..	..	39	..	..	+	+	..	..	..	..	..	..	..	12	..	..	..	67
Brazil	..	..	..	..	1	..	5	..	..	..	..	..	..	7	..	..	..	..	..	..	..	..	..	..	..	..	13
Total So. America	..	30		13+	4+	..	173+	3+	..	2	39	+	..	74+	1+	..	..	..	..	..	..	..	12	..	..	..	351+

nations are scattered through 50% of the race groups, most of which are based on races described recently and characterized by variable or mesothetic reactions. We have seen that the 129 described races of *Puccinia triticina* fall into but 44 clearly distinguishable categories and that of these at least half appear to be either unrecognized duplicates of established race groups or of such extreme rarity that they may be regarded as biological curiosities rather than factors for serious consideration in breeding wheat for leaf rust resistance.

These facts also simplify the conception of race origin (*see* page 91 *ff.*). The occurrence of 129 races of a rust, with the almost complete absence of a sexual stage which could serve as a source of new races, suggests an abnormally high degree of mutation in the rust. If, however, *Puccinia triticina* is far less specialized than the description of 129 races implies, as is borne out by the preceding discussion, the origin of new races presents less of a problem.

Comparing one part of the world with another brings out further fundamentals of race distribution. Australia, by far the most isolated wheat region of the world, is characterized by a unique race flora. Its thorough study has shown that race group 9, which predominates elsewhere in the world, and the important race groups 1, 5, 6, 12, and 21, are totally lacking, the leaf rust in Australia consisting almost exclusively of the single race group 11.

The race floras of North America and Europe, which, in general, have also been adequately studied, show striking resemblances. On both continents the principal race groups include 1, 2, 9, 11, 12, and 21, and these account for 82% and 89 % of all collections in the two continents respectively.

Despite these similarities there are certain differences between North America and Europe that are probably significant, judging by the frequency of collections. The race 17 group appears to be peculiarly European; it has been identified there a total of 23 times in 4 countries, while the data contain no records of its occurrence elsewhere in the world except for two collections in Argentina. It is a very well-defined race group and would not easily be confused with other races.

On the other hand, races 5 and 6 appear to be much more prevalent in North America than elsewhere in the world. Race 5 occurs throughout the continent in the Mississippi Valley, Atlantic Seaboard, and the Pacific Northwest, and race 6 from Georgia and Texas to all the divisions of Canada except British Columbia. Other than in North America these races are known only in Europe and South America and are represented by very few collections.

So far as Asia is concerned, the data from India are the only ones sufficiently extensive to warrant discussion. In India race groups 1 and 9 predominate with a trace of race groups 11 and 18 and no others reported. India is isolated from the other wheat-growing areas of the world by mountains, oceans, and the equatorial zone; it is not surprising to find its race flora distinctive in the absence of races common in the northern hemisphere, race groups 2, 12, and 21.

The determinations that have been made in Africa and South America

are also suggestive of intercontinental differences in race flora as seen in the absence from the African reports of race groups 1, 12, and 21, and in South America the absence of race groups 1 and 12, and the higher prevalence of race groups 18, 37 and 104, the latter not occurring elsewhere except in North America.

Several important wheat-growing areas of the world are unexplored insofar as specialization in leaf rust is concerned. We know nothing of the races in China, Spain, and North Africa. In view of the differences of race populations from one continent to another, China might well show important peculiarities in this respect.

As to race differences in different areas of a single continent, there are few data to support the idea of local adaptation and prevalence of a given race in one part of a large land mass, and its absence in other parts of the same land mass. Race group 11 in North America was once thought to be restricted to the Pacific Northwest, but is now known to occur in the Maritime and Prairie Provinces of Canada and in the southern Great Plains. The Canadian data suggest that race group 5 is absent from the Pacific Northwest, but this group has been reported from the State of Washington (JOHNSTON and MAINS, 1932). The major race groups, 1, 2, 9, 12, and 21 occur west of the Rocky Mountains, in the Mississippi Valley, and along the Atlantic Seaboard. The data for the other races in TABLE 10 are too limited to warrant the conclusion that any one of them is localized in North America.

Likewise the European data fail to indicate any significant localization of races within the limits of that continent. The dominant race groups 1, 2, 9, 11, and 21 occur from the Balkans to Northern Europe, and the collections from Sweden and Hungary, for example, yield almost identical race distributions, both being in accord with the more extensive data from Germany.

In the early work on specialization of wheat leaf rust there was a tendency to call attention to the apparent localization of certain races. This was most evident in the European publications. In 1930 SCHEIBE, for example, regarded race 13 (group 9) as being concentrated in eastern Europe and races 11 and 14 (both in race group 11) as predominating in western Europe. The latter were considered to represent less aggressive forms of the rust, since they produce strong infection on fewer differential varieties, and SCHEIBE looked on eastern Europe as a center of leaf rust aggressiveness. RĂDULESCU, in 1932, in general agreed with SCHEIBE that aggressiveness of the European leaf rust races increased to the eastward, the sporadic appearance of "western races" in eastern Europe being attributed to the prevailing west winds.

The later workers, TSCHOLAKOW (1931), STROEDE (1934), HASSEBRAUK (1937, 1940b), and VOHL (1938) all obtained results that failed to bear out SCHEIBE's view of "eastern" and "western" races and a center of aggressiveness in eastern Europe. The "western" races (groups 11 and 2) were found many times in eastern Europe and the "eastern" race group 9 proved to be widely distributed in western Europe. SCHEIBE's premature conclusions were attributed to his too limited data; they consisted of 87 collections which SCHEIBE himself considered only as a "Stichprobe".

A thorough survey of the race populations in the Lake Baikal region of eastern Siberia might have great interest in this connection. There, where an alternate host is functional, is the one place in the world where a unique diversity of races might be expected, though their significance for the rest of the world would be strictly limited by the geographic isolation of the area.

The possibility of a rise in importance of a new race from an insignificant beginning to dominance is well illustrated by the increase of race 56 in wheat stem rust. No comparable rise has been observed in races of wheat leaf rust. NEWTON and JOHNSON state that: "The surveys for physiologic races carried out since 1931 [through 1940] indicate that races of wheat leaf rust have undergone no marked change in respect to identity or relative prevalence during this period in Canada, unless the appearance of race 76, in 1936, in the eastern provinces can be regarded as such. As the surveys prior to 1936, for leaf rust in eastern Canada were rather inadequate, it is quite possible that this race was also present there in earlier years." The European literature also affords no clear-cut indication of decided shifts in race population through the years.

An apparent rise of a new race or marked increase in relative importance of a known race needs to be analyzed from the viewpoint of race groups. To state a hypothetical case, let us assume that over a period of years collections identified as race 10 tend to become fewer and fewer while, at the same time, there is the appearance and progressive rise in frequency of collections identified as race 20. It would be an error to interpret this as indicating, in reality, the waning of one race and the waxing of another. These two "races" are but two environmental expressions of the same race (group 9), and a more probable explanation is that the later determinations were made under higher greenhouse temperatures than the former. (We recall that a rise in temperature results in a more susceptible type of reaction in the differential varieties Carina, Brevit, and Hussar, and races 10 and 20 differ only in the fact that these three varieties exhibit resistant-type reactions toward race 10 and susceptible-type reactions toward race 20.)

The dramatic rise of race 56 of wheat stem rust was associated with the widespread planting of Ceres wheat, which is susceptible to race 56 but resistant to other common races. A comparable wide scale adoption of leaf rust resistant varieties, such as might be expected to result in marked changes of race populations, has not yet occurred.

We have seen that while there are major differences in race populations between certain of the continents, within a given continent there is a fairly homogeneous population, consisting largely of a few dominant races. The reason for the dominance of such is to be found in the adaptation of rust races toward external environment and host plant.

Most cultivated wheats, the world over, are so susceptible to the leading leaf rust races that differences in their susceptibility probably play little part in the race composition. The leading races evidently are able to flourish in a wide diversity of climates. Thus we find race group 9 among the leading races in Canada, Oklahoma, Scandinavia, Siberia, the Balkans, and India.

We have seen, in the preceding section, that leaf rust races differ somewhat in their response to environmental variables, and these differences

undoubtedly are the principal factors in the relative importance of the races. There are few reported tests of these differential responses, and such as there are usually have been confined to comparisons between races which are all of importance.

To take a single illustration of this, JOHNSTON pointed out the long incubation period of his anomalous race 27, and others have also noted differences in lengths of incubation periods of different races. These differences need not be great in order to have importance. For example, if two races have incubation periods of 8 and 10 days, respectively, one can pass through 5 uredinial cycles while the other passes through 4, and the former will accordingly be the more prevalent, other factors being equal. Differences among the races in ability to overwinter, abundance of spore production, resistance of spores to heat, cold, and drying, length of time required to germinate and effect stomatal entrance, these and other such factors will determine the prevalence of any given race, and it is to be expected that the races favored in such respects will become the dominant ones and that the rarer races will be found to be at a disadvantage in these ways.

Practical applications of specialization: — A variety of wheat that is developed for rust resistance must ideally be resistant to all rust races that it is likely to encounter in nature. In practice, if a wheat is resistant to the few races that predominate in the rust population, it will behave as a moderately resistant variety and may be as little injured by rust, practically speaking, as a variety that is resistant to all races in the rust population. Most of the leaf rust-resistant wheats now under cultivation are of this sort. A variety of wheat that is resistant to race group 9, the dominant group in the United States, often behaves as highly resistant in the field, although it may be susceptible to race groups 1, 2, 12, etc.

Judging, however, by the behavior of Ceres wheat and some of the newer oats varieties, there is danger that a wheat that is resistant to only a few major races, if planted on large acreages, may ultimately succumb to epiphytotics of leaf rust in which the former principal races (which cannot multiply on the variety) have diminished and become replaced in the rust population by the formerly minor races which are able to attack the variety.

Hence, for more lasting resistance it is necessary that the new variety be characterized by resistance to all rust races to which it is likely to be exposed. This is less of a problem with leaf rust than with stem rust, with its greater number of races and greater opportunity for the production of new races on the functioning alternate host. The differential wheats themselves, and numerous other breeding wheats contain the genes for resistance to any known leaf rust race, although these are not combined in a single variety.

A knowledge of physiologic specialization, then, first leads us to a wise choice in parents in breeding, selection being made of those parent varieties that tests have shown to be resistant to one race or another.

Again, when time comes for selection of rust-resistant types in heterogeneous F_2 and later wheat populations, physiologic specialization comes to our aid. The plants of small populations can be inoculated in the greenhouse with separate races (race groups) known by surveys to be prevalent

in the area. Larger populations of plants can be inoculated with mixtures of spores of all important races. Selection, following such inoculations, will then be based on resistance to all of the races involved, and will avoid the great possibility of failure to detect susceptibility toward a minor race when the wheat is exposed to natural infection, which may consist of a very great amount of one or two races and relative absence of others.

ERIKSSON in 1895 and KLEBAHN in 1904 both demonstrated that it is possible to secure information on the parentage of hybrids by the reactions of the hybrids and of their parents or suspected parents to species of rust. VAVILOV in 1913 and 1914 developed the concept that fungi, especially if narrowly specialized as is *Puccinia triticina,* serve as good "physiologic reactors" in aiding systematic botany. He gave numerous instances of correlation between morphology of wheat species and their reactions to leaf rust, and pointed out that the wheat relationships indicated by rust reactions agree with the serological relationships of wheats, determined by ZADE.

With the discovery of physiologic specialization in the wheat rusts, there arose the possibility that reactions to races of rusts might aid in the identification of wheat varieties. JOHNSTON and BOWER in 1924 made practical use of this in connection with the certification of Kanred wheat seed. They used a race of stem rust to which Kanred, but no other Kansas wheat, was immune, and in 1923 they determined the purity of many growers' samples of Kanred seed by this method. They report that a corresponding test with leaf rust serves a similar purpose in determining the purity of seed lots of Fulcaster, Mediterranean, and other soft red winter wheats. Purity of Pawnee wheat may be tested by its reaction to race 9.

SCHEIBE (1929) felt that such a method had very limited application in Germany, where few commercial varieties showed distinctive reactions to the known leaf rust races, but considered that in instances in which the different components of variety mixtures reacted differently to certain leaf rust races, the method had promise.

Proposals for improvement in the study of specialization of the rust: — Many workers on physiologic specialization in wheat leaf rust have commented on the desirability of increasing the number of standard differential varieties, reducing their number, replacing them by entirely new differentials, or leaving them as they stand.

RASHEVSKAYA and BARMENKOV in Russia (1936) hold the view that certain races, such as numbers 77 and 115, are being differentiated on too few varieties, and that more differentials should be added to the standard group. They, as well as HASSEBRAUK (1940*c*), contend that the group of differentials selected in America is unsuitable for European use, and advocate the selection of Russian or German wheat varieties (in the two cases respectively) as differentials. This position does not appear to consider that both Russian and German wheats, in general, are uniformly susceptible to leaf rust races, that the standard group of differentials were selected from a world collection of wheats, and are not American commercial varieties, and that results of work in one country could not be correlated with those from other countries unless a common group of differentials is used. Other

foreign workers, *e.g.* DODOV (1931*a*), appear to be fully satisfied with the group.

It is evident that to increase the number of differential varieties would increase the number of races by subdividing present known races. We have seen, however, that this would greatly increase the labor and opportunities for error in the work without increasing the practical usefulness of race identification. The leading American workers in this field, JOHNSTON and MAINS (1932), and NEWTON and JOHNSON (1941) agree that no useful end would be served by adding to the number of differentials, except, perhaps for unusual, and special types of research.

With regard to reducing the number of differential varieties, particularly by removing from the list the environmentally unstable varieties Carina, Brevit, and Hussar, the desirability of so doing has been discussed in detail on pages 84-90. HASSEBRAUK (1939) and VOHL (1938) also subscribe to the view that these varieties add nothing to the usefulness of the work and inject confusion into it. If other differentials were substituted for the 3 unstable ones there would be the serious disadvantage, as pointed out by NEWTON and JOHNSON, of being unable to relate races previously described to new ones, and there would be interference with an important function of race surveying, — the detection of new races.

The adoption and use of the concept of race groups outlined on pages 83-90 would not be subject to this disadvantage, since the original 5 relatively stable differentials of MAINS and JACKSON would be retained without addition. Evidence has been adduced that indicates that the "races" distinguished only by reactions on Carina, Brevit, and Hussar, are the result of environmental differences and are not genetically distinct, and that in wheat breeding it is necessary only to consider the race groups, since resistance or susceptibility in wheat is directed at each group as a unit, and not at the individual members of the group, which are evidently not significantly different from one another, but, at the most, are to be regarded as biotypes of a single race.

For these reasons it is proposed that the race groupings indicated in TABLE 8 be the basis for future analysis of wheat leaf rust races.

The only exception to this regards the use of the variety Thew. This variety is indispensable for race analysis in Australia, and has recently been included in the "International Register" but only with reference to 4 races occurring in Australia. JOHNSTON, NEWTON, and JOHNSON have tested many common American rust races on Thew, finding them all susceptible. If their results were inserted in the "International Register" and made available to other workers, it is possible that, in the future other important race distinctions, based on Thew reactions and comparable to those in Australia, would be made.

A second proposal regards the environment under which tests are conducted. There is no question (*see* pages 78-83) that at present the results of race analysis in one greenhouse are not comparable to those in another, and that this is the principal reason for the many duplications of the same race under different numbers in the "International Register". Much of this duplication will be eliminated by dispensing with the unstable differential varieties, but even the reactions of the relatively stable ones, particularly

Webster, vary to some extent with environment. For this reason, every effort should be made to conduct the work, so far as possible, under conditions that can be duplicated by other workers. JOHNSTON and MAINS have pointed out that finer race distinctions than at present could be obtained, but "only under carefully controlled conditions that could be duplicated by other investigators". If this would be desirable for further refinements of race analysis, is it not even more so for routine race analysis?

Adoption of standard cultural conditions, such as the following, would go far to insure comparable results among different workers: The greenhouse temperature that appears to be most satisfactory is 65° F., and this should not vary more than 3° F. above or below. Inoculations are best made on the prophyllum when the first true leaf is 2 to 3 inches long. This is usually about 12 days after planting. Instead of soil, which varies widely in nutrients and exerts a profound influence on the results, it is suggested that the plants be grown in washed sand and supplied a balance nutrient solution, such, for example as that of BRUCH, which GASSNER and HASSEBRAUK (1931) report results in normal development of wheat seedling and rust, equivalent to that in good soil. The formula is: KNO_3, .5 gm.; $MgSO_4$, .25 gm.; K_2HPO_4, .25 gm.; $CaSO_4$, .25 gm.; dilute $FeCl_3$, 1 drop; NaCl, .005 gm.; in water, 1000 c.c. The plants are grown in ½ liter, 10 × 10 cm. receptacles, 10 plants per receptacle, irrigated once with the nutrient solution, which is buffered by the addition of 2.5 gm. calcium permutite per receptacle, and thereafter supplied with distilled water as needed. Artificial supplementary light should be supplied during short or cloudy days. The plants should be covered with glass lamp chimneys or bell jars only for 24 hours or less after the inoculation, and again for 1-2 days before readings are made, to prevent dissemination of spores to other plants. The routine readings should be made as soon as the pustules are well formed, usually the 9th day after inoculation, although if doubt exists, later readings should also be made.

A third proposal concerns purity of the seed of the differential varieties. It should be possible to remove the contamination that at present exists in the seed stocks, and unless this is done, continued anomalous results must be expected.

Finally, confusion and the indiscriminate describing of new "races" would be reduced if, at some one point there could be maintained pure cultures of all known or available races, comparable to the "Centraalbureau voor Schimmelcultures", with which supposed new races could be compared. If this were done and new races or races nowhere in culture were considered provisional until comparison with the type culture collection had been made, much of the present duplication could be avoided. At the same time, additional confusion would be eliminated if workers would avoid assigning numbers to new races but leave it to those in charge of the "International Register" to assign serial numbers, once the identity and distinctiveness of each new race is determined by comparison with the type cultures.

Chapter IX

FACTORS AFFECTING RUST SURVIVAL AND DEVELOPMENT

Environment and the disease syndrome: — Contrary to a rather general misconception, the external environment that favors the development of one rust disease may be wholly unsuitable for the development of another rust. The history of rust epiphytotics furnishes many instances in which, during a given year, a certain wheat area was visited with a destructive outbreak of stem rust, for example, yet was singularly free from leaf rust, while in other years the same area suffered from epiphytotic leaf rust with negligible stem rust damage. Many such examples might also be adduced from the literature dealing with oats, barley, rye, and the grass rusts. We cannot speak loosely of "rust years"; the particular rust must be specified.

In 10 years of extensive readings of the intensities of 5 cereal rust species, VON KIRCHNER (1916) found no case of 2 rusts in which the years of lightest rust coincided; the two years of most severe stripe rust of wheat were years of the least wheat leaf rust, showing that the same weather affects the different rusts quite differently.

TEHON (1927) also observed great differences in the behavior of the leaf rusts of wheat, corn, rye, barley, and oats. As shown by his figure 23, which is here reproduced as our FIG. 3, we can see that the most favorable season in 5 years for corn rust was the least favorable for oats rust, the most favorable season for wheat leaf rust was least favorable for barley rust, etc. The pattern of seasonal effects on wheat leaf rust was unlike that for any of the other rusts.

In analyzing the effects of environment it is also necessary to keep continually before us the conception, so ably developed by E. FISCHER and GÄUMANN in their "Biologie der pflanzenbewohnenden parasitischen Pilze", of the dual rôle of environmental factors. Each factor operates at the same time on the host plant and the parasite: its effect on the disease is the resultant of its effects on host and parasite. If an environmental factor favors development of the rust but at the same time induces greater resistance in the host, the one effect may largely offset the other, while if the factor at once increases host susceptibility and rust development, the synergic effect may be very great.

We are accustomed to think that the predominating effects of environment are exerted directly on the parasite, but in the case of wheat leaf rust this is not necessarily true. GASSNER (1915*c*), finding no direct correlation between weather and rust in Uruguay, was convinced that in that region the primary influence of weather was not on the fungus ("direct effect") but on the host plant ("indirect effect"). Supporting this view is GASSNER'S observation that in Uruguay winter conditions limited leaf rust on

spring wheats but not on winter wheats. (The reader is referred to GASSNER's detailed discussion, in the paper cited, of the indirect effect of environment on rusts in general.)

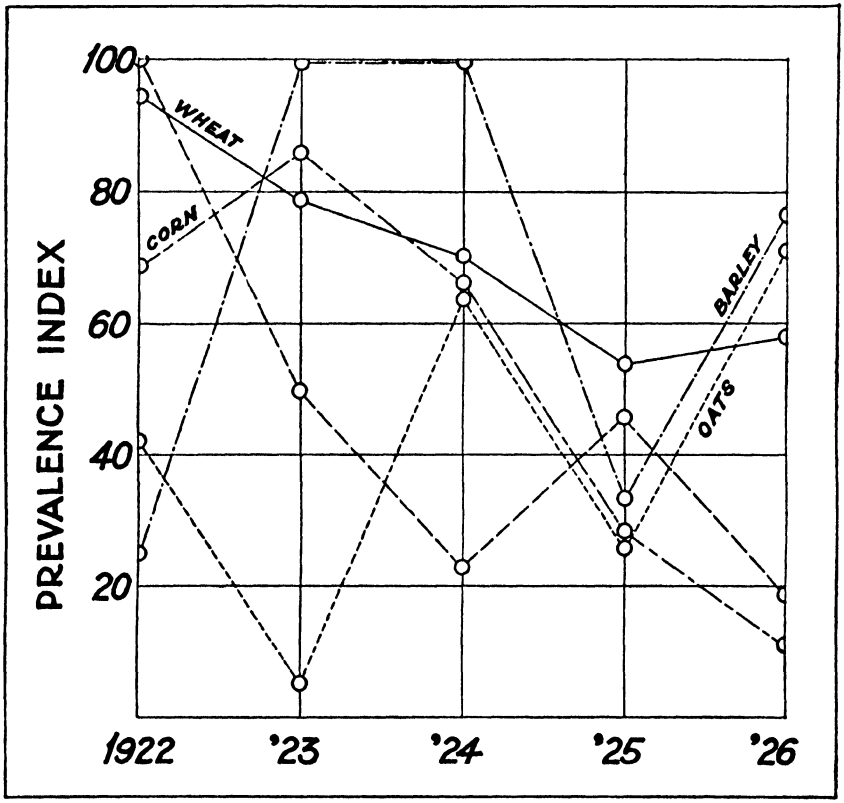

FIGURE 3. — Prevalence of cereal leaf rusts in Illinois, 1922-1926. (*After* TEHON, 1927).

The indirect effects of environmental factors vary with the hereditary constitution of the host plant. One variety will alter its resistance or susceptibility very sharply as a reaction to environment; others retain much the same resistance or susceptibility under different environments. This was illustrated by the behavior of "environmentally unstable" varieties and the "stable" ones used in physiologic race determination, discussed on pages 78-85.

Finally, it must be kept constantly in mind that what we term "environment" is a complex of many factors all of which must be compatible with one another and with the environmental requirements of the disease in order to permit destructive disease development. The modification of any one factor may bring in its train a whole series of changes in other factors. The effect of rainfall, for example, is complex enough if we regard solely its direct effects on the parasite: permitting spore germination which may in turn either favor infection, if spores are in a suitable infection court, or

interfering with infection by precipitating spores from the air or facilitating their germination and consequent destruction before they reach infection courts. But rainfall exerts other influences on development of the disease. It alters the soil constitution, favoring or hindering nitrogen assimilation by the host plant, which, in turn indirectly favors or hinders rust development by modification of the resistance of the host plant. It modifies the resistance of the host by contributing to its succulence and the rankness of its growth. Then rainfall modifies other environmental factors: it cools the air, leading to a whole series of temperature effects on host, parasite, and disease; it is associated with reduced light, which, in turn, has numerous influences on the disease, for example lengthening the incubation period, or inducing lodging, a condition favoring rust multiplication; and it may retard maturity of the crop, so as to increase the extent of rust destructiveness, or, conversely, give the grain more time to fill, thus partially offsetting the effects of rust.

These are but some of the most obvious primary and secondary elements in the diverse effects of a single factor, rainfall, on leaf rust development, dissemination, and destructiveness, — many others might be added. But they serve to illustrate the extreme complexity of environment as it conditions the disease.

Moisture: — The literature is replete with statements to the effect that severe leaf rust is associated with wet seasons, high rainfall and humidity, dews, and fogs. DE CANDOLLE in 1815, referring to rust in general, — "on la trouve surtout dans les lieux et les années humides," expressed the views of farmers for centuries before him, and countless similar statements are to be found in the recent literature.

Yet such generalities give us but little guidance in interpreting the actual relationships between leaf rust and moisture. They fail to take into account the different moisture requirements of rust and the wheat plant at different periods in their respective developmental cycles, or the different effects of the various forms of moisture, from torrential rains to dews and fogs, and they are only comparative, — a "wet season" in a region of low annual rainfall may actually be drier than a "dry season" in a more humid climate.

These are among the reasons why we find such apparently contradictory views as GASSNER'S to the effect that there is no correlation between humidity and leaf rust attack in Uruguay and that of various French and Russian workers who call leaf rust the rust of dry seasons and stem rust that of wet seasons. An attempt is made, at this point, to analyze the various aspects of moisture in relation to wheat leaf rust development.

Since the uredospores are primarily responsible for leaf rust multiplication, particular attention has been given to the effect of moisture on their production, germination, and viability.

MAINS, in 1924, reported that 100% relative humidity was required for leaf rust uredospore germination. This subject was investigated in detail by STOCK, in 1931. He obtained no germination in 24 hours of exposure to 90, 95, and 99% relative humidity, and only a small percentage of germination at 100% humidity unless the spores were actually in contact

with water, in which case good germination resulted. If the germ tubes were in contact with dry glass they were often abnormally gnarled and branched. Spores under water germinated poorly, as had also been noted by MAINS; this is evidently due to lack of aeration, and will be considered later.

STOCK's findings were confirmed in 1933 by those of HEMMI and ABE who obtained profuse germination in saturated air but only 4.29% germination at 99% relative humidity and probably none at 95%. Although they did not find it necessary for the spores to be in contact with drops of water, they conclude that the spores must have a film of water condensed on their surfaces and this condensation occurs only at or slightly below 100% rel. hum.

The writer has found that if dry spores are "conditioned" by exposure to air humidity that is high, but not quite high enough to permit their germination, they become swollen, lighter in color, and noticeably vacuolate, and if these spores are then tested for germination in water droplets, they germinate much sooner than spores which have not been so "conditioned".

Drying of uredospores for a few days after their production, in MAINS' experience (1924), increased their germination percentages, which is not contradictory to the phenomenon noted directly above, but suggests that an after-ripening period is necessary before some spores will germinate.

These experiments have been conducted under artificial laboratory conditions. It has been shown by YARWOOD and HAZEN that for certain plants the relative humidity at leaf surfaces may be as much as 32% higher than the nearby air humidity. If this also applies to wheat, moisture conditions permitting spore germination might exist in nature on the leaf surface even though the relative humidity of the air about the plants is well below 100%.

After spore germination, continued high humidity is necessary if the germ tube is to effect appressorium formation and penetration into the host stoma. Under favorable conditions this period of high humidity need not exceed 8 hours, a length of time well under that of air saturation during a normal dewy night.

The germ tubes of *Puccinia triticina* uredospores are negatively hydrotropic according to BEAUVERIE (1924); when the spores germinate on the surface of water drops the germ tubes grow straight out into the air. This suggests that their entry into the stomata is not guided by hydrotropism, which is only to be expected, since if the air within the substomatal cavity is saturated, and that at the leaf surface must also be saturated in order for the spore to germinate, there would be no humidity differential to enable a hydrotropism to function.

From the moment at which the stoma has been penetrated till the rupture of the uredinial pustules and release of spores, external air humidity has a more minor rôle. HASSEBRAUK (1939, 1940*a*) found that covering infected plants with bell jars, thus maintaining high humidity while other factors were relatively constant, for the most part had little effect on type of infection. He observed only that exposure to high humidity during the first few days or last few days of the incubation period tended slightly to increase the resistance of some varieties.

NAUMOV (1939) states that incubation is relatively independent of

TABLE 12: *Longevity of wheat leaf rust uredospores, in days, when stored at the indicated relative humidities and temperature ranges. Averages of 2 tests in each case except those at 3-11° C. and 9-21° C.* (from RAEDER and BEVER, 1931): —

PERCENT REL. HUMIDITY	TEMPERATURE (°C.)					
	29-30	13-26	9-21	9-13	3-11	—2-5
100	Mold	4, mold	3.0	6.0	6	9.5
76	31.0	26.5	63.0	89.5	118	35.0
49	33.5	34.0	88.0	111.4	124	30.5
25	22.5	27.5	69.0	93.5	105	25.5
1.5	11.0	18.5	42.0	53.5	71	9.5

external air humidity, and that variation of this has no effect on the length of time required for pustule formation. His curves of temperature-humidity-incubation period relationships, however, show that at all temperatures tested the incubation period was regularly about 2 days longer under high humidity than in the plants exposed to average humidity.

A number of workers have observed that high humidity at the time leaf rust pustules are liberating their spores appears to increase the number of spores produced. Pustules in moist chambers appear larger, with more abundant spores than those exposed to dry air, but this may be merely because in moist air the spores are larger, and if protected from air currents they tend to adhere to the pustule, giving the impression of more massive spore production.

From the time the mature uredospores are produced until they chance to be deposited on a wheat leaf under conditions suitable for their germination, they are also subject to the effects of air humidity. We have seen that dried spores, if kept at low temperatures, retain their viability for many months, or even several years. Quite a different situation obtains, however, if the spores are subjected to high humidities during their pre-germination period.

MAINS (1924) warned against loss of viability of uredospores if shipped in moist packets. The subject was later studied in detail by RAEDER and BEVER (1931) and NOVOTELNOVA (1935). The results of RAEDER and BEVER's determinations are given in TABLE 12.

From the table we see that either very low, or especially very high, relative humidities are detrimental to the viability of the spores at all temperatures tested. A relative humidity of 49% was most favorable at all temperatures except those near freezing, in which the spores stored at 76% relative humidity retained their viability longest. The greatest longevity observed was 124 days in spores stored at 49% relative humidity and in temperature range 2-11° C. The increase in longevity with lower storage temperatures will be discussed later.

NOVOTELNOVA found that nearly all viability of the uredospores was lost after storage of 24 hours at 100% relative humidity, while the spores germinated well after 6 hours exposure to humidities ranging up to 89%. Wetting the spores for 4 hours, followed by dry storage, caused a sharp decrease in viability.

We can see that air humidity plays an important part in the survival of

spores from the moment of their production to their deposition on a suitable infection court, and initiation of infection. Their viability is reduced by extremes of high or low humidity, and if they are exposed to 100% humidity or liquid water for as much as 6 hours before reaching a wheat leaf, they will usually germinate and die without effecting infection.

Little information is available on the humidity relationships of the other types of spores in *Puccinia triticina*. Their germination has usually been obtained by exposing them to saturated air or water drops. The germination of the teliospores follows after a period of maturation conditioned primarily by time and temperatures, and this will be discussed later, with only reference in passing to BRIZGALOVA'S observation (1935) that alternate wetting and drying of the teliospores aids in the maturation of these spores.

RUSAKOV and SHITIKOVA, who have devoted much attention to the study of natural variations of environmental factors, and the effect of these (as contrasted with constant levels of the factors such as characterize most laboratory and greenhouse tests, yet never occur in nature) on leaf rust, have stressed the fact that the alternation of high night humidities with low daytime humidities is most favorable to leaf rust development. The daytime dryness facilitates the detachment and dispersal of individual uredospores while high humidity at night enables them to germinate and infect wheat.

There is general agreement that of all forms of moisture, dew is the most important in permitting uredospore germination and wheat infection. This is because of the comparative frequency of dews, their formation in tiny droplets that expose the greatest water surface to the spores without at the same time washing them to the ground, their customary duration, due in part to the calm night air, for a period long enough to allow infection to take place, and the fact that they are usually associated with cool night temperatures within the range favoring spore germination.

The importance of dews to wheat leaf rust is illustrated in RUSAKOV'S reference (1929*a*, 1929*d*) to the severe rust outbreak in Yeisk in 1926, when "*Puccinia triticina* . . . . showed its amazing drought resistance; aided by only two inconsequential rains and 20 very light and transitory dews, in a month from the time of its appearance it developed to a strength of 3-3¼ units . . . . and at harvest time showed an infection of 3-4 units."

RUSAKOV (1922 and other references) has emphasized the fact that the weather conditions recorded in standard instrument boxes, 6 feet above the soil surface, give an inadequate and often highly erroneous picture of the conditions in the zone of the plants themselves. In particular this applies to humidity, and he has noted that dew, indicating 100% relative humidity, formed on wheat leaves when the weather box recorded only 42-65% relative humidity.

In most of the reports on rust in relation to moisture, it has been the practice to attempt correlations between rainfall and rust development. It would doubtless lead to much more consistent and intelligible conclusions if rust and dew were to be correlated. Direct observation of the presence of dew in wheat fields at sunrise would not only suffice but even be preferable to records from the standard weather instruments, for reasons given above. It was gratifying to learn that in their rust reports for 1944 the collaborators

of the "Cargill Crop Bulletin" were urged to include daily notations on the presence of dew.

Rain, in itself, unless very light, is more of a detriment than an aid to leaf rust development. It cleanses the air of spores, washes the spores on wheat leaves to the ground, and permits them to germinate there where they are harmless. SCHAFFNIT (1909) reported no viable spores remaining after rains.

The common association of severe rust with rainy weather is due to the secondary effects that follow rains, — raising the air humidity and lowering the temperature so as to permit dew formation, and promoting rank, succulent wheat growth that is particularly susceptible to rust and that forms moisture-holding air pockets among the plants. These indirect effects are so important that they account for the fairly high correlation between monthly rainfall and rust occurrence.

Morning rains, especially if of short duration, of the thundershower type, are likely to be followed by such quick evaporation and lowering humidity (with rise in temperature) that there is not time to permit spore germination. Evening rains are more effective, as they are followed by many hours of high humidity. In general, fine, light, drizzling rains or mists have a greater direct effect in permitting spore germination than heavy rains. The replies to a questionnaire sent by RUSAKOV to many Siberian wheat growers (1927*c*), often associated rust with "rain as through a sieve," the Russian expression for rain composed of tiny droplets.

The effects of rains, as of any environmental variable, must be considered in the light of mutual effects of other factors. Rains in cool climates have a greater effect on rust than those in warmer areas, since in the first case their effects are more prolonged. Frequency of rainfall, even if light, is more important than total rainfall, except in dry-land areas where the absolute amount of precipitation is a limiting factor to the development of both the wheat plant and its rust.

Fog, as another manifestation of high relative humidity, is often associated with destructive leaf rust development, especially in wheat fields near large bodies of water, where fogs are commonest and heaviest. The subject is discussed in detail by ERIKSSON and HENNING (1896). GASSNER found fog a factor, though one of indeterminate importance, in rust near the lake-like mouth of the La Plata River; D. D. CUNNINGHAM and PRAIN in India (1896) and RUSAKOV in Russia (1927*c*) have made similar observations. RIVERA and CORNELI (1929) found rust to be less severe on the banks of the Tiber than somewhat inland, but point out that the highest humidity is usually at some distance from a large river. In all these cases the references are to cereal rusts in general, and not to leaf rust in particular. In Bulgaria, severe epiphytotics of leaf and stem rusts in 1928, 1930, and 1932 were associated with frequent heavy fogs which were lacking in the light rust year, 1931 (DODOV, 1933).

The effects of soil moisture are indirect, through modification of the susceptibility of the host plant, alteration of the air humidity near the soil, and induced guttation.

In wheat plants grown in the greenhouse in soils of different moisture contents there appears to be little correlation between soil moisture and

rust development. STEINER (1933*b*) observed very little difference in type of leaf rust pustule in wheats growing in soils containing moisture to the extent of 20, 40, 60, and 80% of their moisture capacities. The pustules on wheat in the driest soil were merely somewhat less luxuriant than on that in the wetter soils. HASSEBRAUK (1934) had a similar experience, the only correlation between rust and soil moisture consisting in a slightly longer incubation period associated with 50% soil moisture capacity than at 25 or 75%. These negative results are partly explainable by the fact that the experiments were not designed to bring out the effect of soil moisture in raising the air humidity, or to reproduce indirect effects of soil moisture such as occur in nature (devitalization of the host plant by prolonged drought, or delaying of maturity and leaching away of nitrogen by excessive soil moisture, for example).

In contrast to these greenhouse experiments, observations of wheat under more normal conditions indicate that at times soil moisture may have an important effect on leaf rust development. It has often been noted that rust is worst in low, undrained fields. STEFANOVSKII (1936, 1937) recorded the amount of leaf rust on a large number of wheat varieties grown with and without irrigation, other growing conditions being equal and favorable. In the irrigated wheat, 97.3% of the strains showed heavy rust (4 Russian units) and none showed light rust (1 Russian unit), while in the non-irrigated wheat 52.6% of the strains were lightly rusted and only 13.1% heavily rusted. FRIEDRICHSON (1937), in the semi-arid region east of Saratov on the left bank of the Volga, also found that irrigation, from 7 days before tillering to 7 days after heading of wheat, increased the susceptibility of susceptible varieties. Numerous comparable records of the effect of irrigation on leaf rust are to be found in the "Plant Disease Reporter".

If soil moisture drops so low that the plants wilt (or if the same effect is obtained by subjecting them to hot, dry air), instead of normal, susceptible-type rust pustules, only small necrotic spots are obtained (DOAK, 1930). This is but a transient change in reaction, however, for such plants later produce normal pustules if their turgescence is restored.

The production of water of guttation, which is often noted on wheat seedlings, depends to a great extent on high soil moisture. Droplets of guttation water probably act as dew drops in permitting rust spores to germinate and infect wheat.

Temperature: — For many years it has been known that the uredospores of *Puccinia triticina* are able to retain their viability for long periods of time under favorable conditions. In 1891, BOLLEY mentioned obtaining profuse germination from uredospores that had been 2 days in the mails, and then exposed to outdoor, June temperatures, but protected from sun and rain, for 7 days. They also germinated well after a month's exposure to August temperatures, outdoors but protected from sun and rain, and 50% germination was obtained after a similar exposure, but without protection from such direct sunlight as was transmitted through the walls of glass tubes. FREEMAN and JOHNSON (1911) mentioned frequently obtaining good germination from uredospores that had been shipped from Texas to Washington and then exposed to room temperatures for several days

before testing germination. In physiologic race determination in the United States, it is the routine practice to send uredospore-bearing wheat leaves for long distances without refrigeration, and although several days are often consumed in transit, there have been no complaints of serious frequent losses of viability in material so treated.

TABLE 13 lists the recorded data on retention of viability of wheat leaf rust uredospores when exposed to or stored at given temperatures from —53° C. to +52° C. The data are not entirely comparable, since they are influenced to some extent by other variables, such as humidity (*see* TABLE 12), light, condition of spores at the start of the experiment, etc. Yet they clearly show the trend, with greatest retention of viability when the spores are stored at 0° to 10° C., marked, progressive loss of this as the temperature rises to 52° C., and less marked loss of viability as the temperature is lowered from 0° C. to —53° C. The remarkable resistance of the spores to temperature is seen in their retention of some viability in the ten-minute exposures at points 101° C. apart, +52° and —53° C., and in their very considerable survival for nearly 3 years at 5° C. Throughout a broad range from about —10° C. to +35° C., which essentially includes the temperatures to which wheat is exposed during its vegetative period, the spores will survive, insofar as temperature is concerned, for at least several days, which is an important factor in the adaptation, and coexistence with the wheat crop, of *Puccinia triticina*. But during the periods between wheat crops, the winter in spring wheat areas and the summer in the warmer winter wheat areas, the temperatures not uncommonly lie outside this range for many hours or days, and the spores cannot survive such extremes of temperature, so that the new wheat crops must receive their first infection from outside sources, or, in rare cases, through the functioning of the aecial host.

The data support J. BECKER's conclusion (1928) that the optimum temperature for conservation of viability of the uredospores is 0 to 5° C. at a relative humidity of 50-60%.

That longevity of the spores varies with the condition of the spores themselves is seen in MENCACCI's report (1929) that spores from resistant wheat varieties retain their viability longer (49+ days) at room temperature than those from susceptible wheats (22-25 days), and that of SĂVULESCU (1941) that spores collected in May were more long-lived at 15-20° C. than those collected at other times of year.

While the uredospores may retain their viability to some extent after being frozen in ice (BOLLEY and PRITCHARD, 1906), SCHAAL (1925) found that such spores were somewhat less long-lived than those subjected in a dry state to the same sub-freezing temperatures. In nature it would be a common occurrence for the spores to be frozen in ice, or under snow for extended periods, and STEPANOV (*in* NAUMOV, 1939), who determined temperatures by the use of thermocouples under the snow, found that in Russia the uredospores survived in this condition from early fall at least until February, at which time the tests were discontinued.

The germinating spores and germ tubes are much less resistant to cold than are the ungerminated spores, according to GASSNER and PIESCHEL (1934). They are killed in 1-2 days at —5° to —7° C. if not "hardened",

but these workers suggest that they might prove somewhat more resistant to these temperatures if they were to be exposed to them by gradual degrees.

In contrast to these extensive data on uredospores we have very few regarding temperature and the viability of teliospores, sporidia, and aeciospores. Under natural or uncontrolled conditions the teliospores are known to retain their viability for at least 2 years (SĂVULESCU, 1940, and others).

Since these spores are adapted to survival between wheat crops, and, in fact, do not normally germinate until they have passed a period of dormancy in which they are often subject to temperature extremes, it is probable that they are at least as resistant to temperature extremes as the uredospores, and, by analogy with the spores of other rusts, probably even more so.

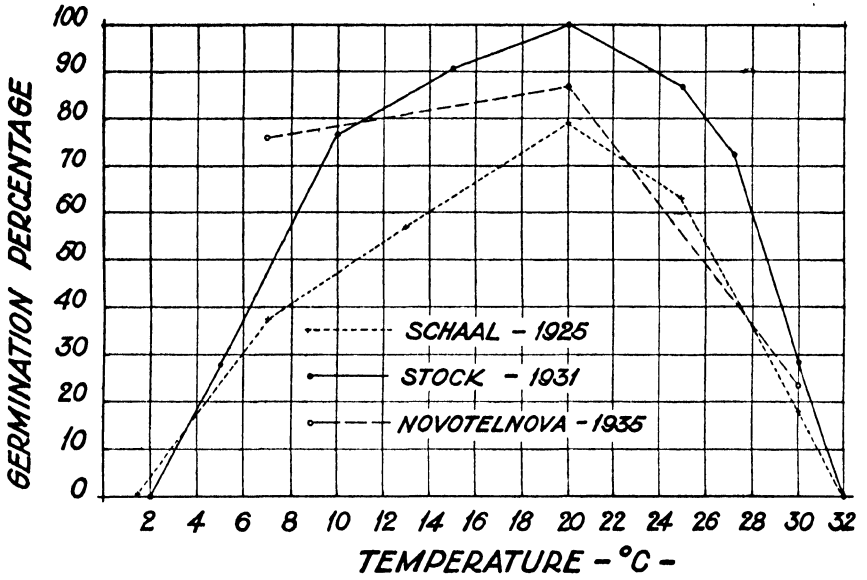

FIGURE 4. — Relation of wheat leaf rust uredospore germination to temperature. (*After* STOCK, 1931, SCHAAL, 1925, and NOVOTELNOVA, 1935).

SIBILIA (1931) has reported their withstanding 65° C. without loss of germinating power, which is well above the maximum for uredospores. MAINS (1924) found that aeciospores gave excellent germination after 5 days and slight germination after 28 days if dried for 2 days at 27° C. and then stored at room temperature in dry packets.

Besides this direct evidence on the temperature resistance of *P. triticina* spores, we will find that there is much supplementary, indirect evidence, in the actual overwintering and oversummering of the rust, a subject to be discussed later.

The principal published data on temperature in relation to germination of spores of *P. triticina* are presented in TABLE 14 and FIGURE 4.

We can see from the table and figure that the uredospores germinate over a wide range, from about 2° to 31° C., with optimum germination at about 20° C., while relatively good germination occurs through the zone from about 8° to 28° C.

TABLE 13: *Retention of viability of wheat leaf rust uredospores on exposure to or storage at the stated temperatures: —*

TEMP. (°C.)	TIME (da.)	SURVIVAL (%)	AUTHORITY
—53	.007	5.3	SCHAAL, 1925
—26 to +3	67	10.0	CHRISTMAN, 1904
— 9 to —8	1.83	+	ABE, 1933
— 6	2	12.1	SCHAAL, 1925
— 5	several	+	PLOWRIGHT, 1889
— 5 to —2	49*	+	RAEDER, BEVER, 1931
0 to 2	150	+	STROEDE, 1934
3 to 11	124*	+	RAEDER, BEVER, 1931
5	300	88†	Original
5	660	25†	Original
5	1020	18†	Original
Refrig.	158	+	ASUYAMA, 1939
Refrig.	90-120	+	YARKINA, 1941a
?	235	+	DUCOMET, 1925
5 to 10	90+	+	MEHTA, 1940
6	90-180	+	RASH., BARM., 1936
9 to 12	159	+	MAINS, 1924
9 to 13	118*	+	RAEDER, BEVER, 1931
9 to 21	88*	+	RAEDER, BEVER, 1931
9 to 22	180	+	SCHILCHER, 1932
10	6	67.9	NOVOTELNOVA, 1935
10	15	27.5	NOVOTELNOVA, 1935
10	30	0	NOVOTELNOVA, 1935
"cool cellar"	60	0	SCHEIBE, 1928
13 to 26	35*	+	RAEDER, BEVER, 1931
20	6	56.1	NOVOTELNOVA, 1935
20 to 26	90	+	SCHILCHER, 1932
"Room"	25	+	MENCACCI, 1929
"Room"	240	0	SCHILCHER, 1932
28	.75	50	MEHTA, 1929
29 to 30	35*	+	RAEDER, BEVER, 1931
30	6	19.3	NOVOTELNOVA, 1935
32	.17	50	MEHTA, 1929
35	6	6.1	NOVOTELNOVA, 1935
35	15	0	NOVOTELNOVA, 1935
45 to 47	.75	0	MEHTA, 1929
47	.17	30	MEHTA, 1929
52	.17	2	MEHTA, 1929

Notes: "+", viability retained but percentage not stated; *, highest value obtained at any humidity tested· see Table 12 for fuller details; †, percentages are of samples with some viability, not of spores.

The teliospores, and particularly the aeciospores, are distinguished by lower optimum and especially lower maximum temperatures for germination, reflecting their adaptation to germination in early spring.

The results of the various workers are in sufficient agreement, such minor differences as exist being doubtless due to differences in techniques, adequacy of temperature control, use of different rust races, etc. SCHAAL, for example, used race 52 while STOCK's rust was of race 14.

Temperature exerts an important influence on spore germination not only as seen in percentage of germination, but in its energy, as measured

by the speed and character of germination. Thus, SCHAAL (1925) found that at the optimum temperature, 20-21° C., 10.9% of the uredospores germinated within 50 minutes and 45.2% within 60 minutes. At 6-8° C. only 1.7% of the spores germinated in 60 minutes, and it required 70 minutes for 30.8% of them to germinate. At 30° C. no spores had germinated

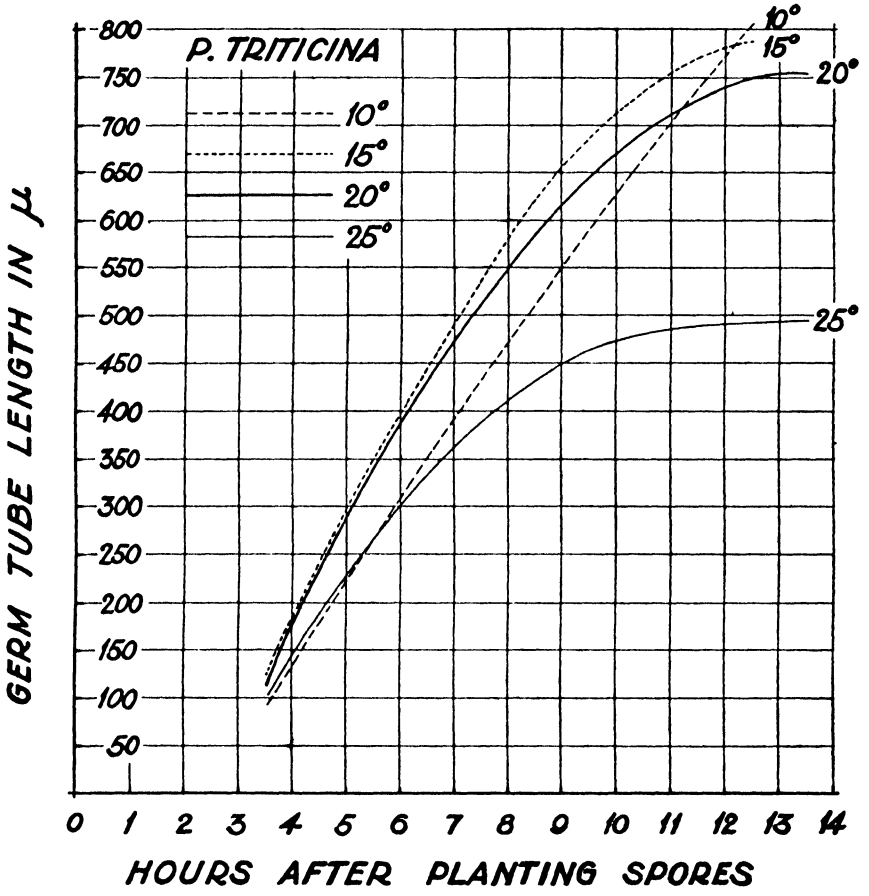

FIGURE 5. — Relation of germ tube growth of wheat leaf rust uredospores to temperature. (*After* STOCK, 1931).

after 75 minutes and only 4.6% after 90 minutes, while 120 minutes were required for 12.4% of them to germinate. Similarly BRIZGALOVA (1937*b*) found that spores which required 1½ hr. for germination at 15-18° C. consumed 6 hr. in the same process at 3-5° C. She also reported that aeciospore germination occurred in 5 hr. at the optimum temperature but required 8-14 hrs. at lower temperatures, and that teliospores produced basidia in 9 hr. at 6-19° C., but only after 48 hr. at 2° C., while above 20° C. they germinated but produced no basidia at all.

SCHAAL'S results shown in FIG. 4, illustrate a common finding, that the maximum germination obtained with collections of uredospores is often well below 100%. SCHAFFNIT (1909) contended that good germination of

uredospores requires that they be fully ripened and that this ripening or maturation can occur only before the spore is detached, and is associated with warm, dry, windy weather, conditions quite distinct from those which favor spore germination. The fully-matured spores can be recognized by their dark color. SCHAAL (1925) found that spores which could be dusted off the pustules germinated to the extent of 80.6%, while those which required scraping off showed only 59.4% germination. In accord with this is BEAUVERIE's observation (1924) that uredospores collected in late summer gave the highest percentages of germination. PLOWRIGHT found that germination percentages could be increased by exposing the spores to a temperature of —5°, but SCHAFFNIT was unable to increase their germination percentages by any of a variety of treatments, once the spores had been detached from the sorus.

The relationship between temperature and growth of uredospore germ tubes has been studied in greatest detail by STOCK (1931). His results are summarized in his figure 7 which is reproduced here as FIG. 5. The figure brings out two important features of the effect of temperature on uredospore germ tube growth. First, it is seen that the rate of growth is most rapid at 15° and 20° C. while it is notably slower at 10° and 25° C. In the second place, the length ultimately attained by the germ tubes progressively decreased from 10° to 25° C., and while the rate of germ tube growth at 10° and 25° C. is nearly the same at first, the final length of the tubes at 25° is apparently not over half that of the tubes at 10° C. This may be explained as due to the greater use of food resources for respiration at the higher temperatures, while at the lower ones more are available for growth.

The optimum temperature for germ tube growth of *P. triticina,* 15-20° C., is close to that for uredospore germination. At temperatures of 27.5° C. or above, the germ tubes are often very short and flat at the ends, and sometimes the protoplasm pours out of the spores without forming germ tubes.

At 25° C., germ tube growth was completed in about 10 hours, and at 15° and 20° this occurred in about 12 hours.

SĂVULESCU's determinations of the cardinal points for germ tube growth (1938*a*) agree closely with those of STOCK, namely: minimum, 5-6° C.; optimum, 16-20° C.; and maximum 31° C.

ASUYAMA (1939) has furnished us with details on the relation of temperature to the infection process. The optimum temperature was 18-25° C., with invasion occurring in 3-6 hours. At 23° C. the uredospores germinated in an hour, appressoria began to form in 3 hours, and stomatal invasion was occasional after 4 hours, frequent after 6-9 hours, and relatively complete after 24 hours. The first infection hyphae were produced 9 hours, and haustoria 20 hours after inoculation. At 13° C. stomatal invasion required 9 hours, and at 8° C. infection was very slow, with infecting hyphae not being developed from the substomatal vesicles until 24 hours after inoculation.

These time-temperature relationships are of the greatest importance in the development of the fungus, since at this critical period — from spore germination to invasion of the wheat plant — the relative humidity must remain close to 100%. If the temperature is optimal, invasion may occur in 3-6 hours, but if it is not, the time required for invasion may be so

extended that it exceeds the period during which the air, in nature, is saturated, and infection thus cannot occur.

Similarly the time-temperature relationship in this period determines the length of time during which experimentally inoculated plants must be retained in moist chambers. GASSNER and APPEL (1927) have submitted

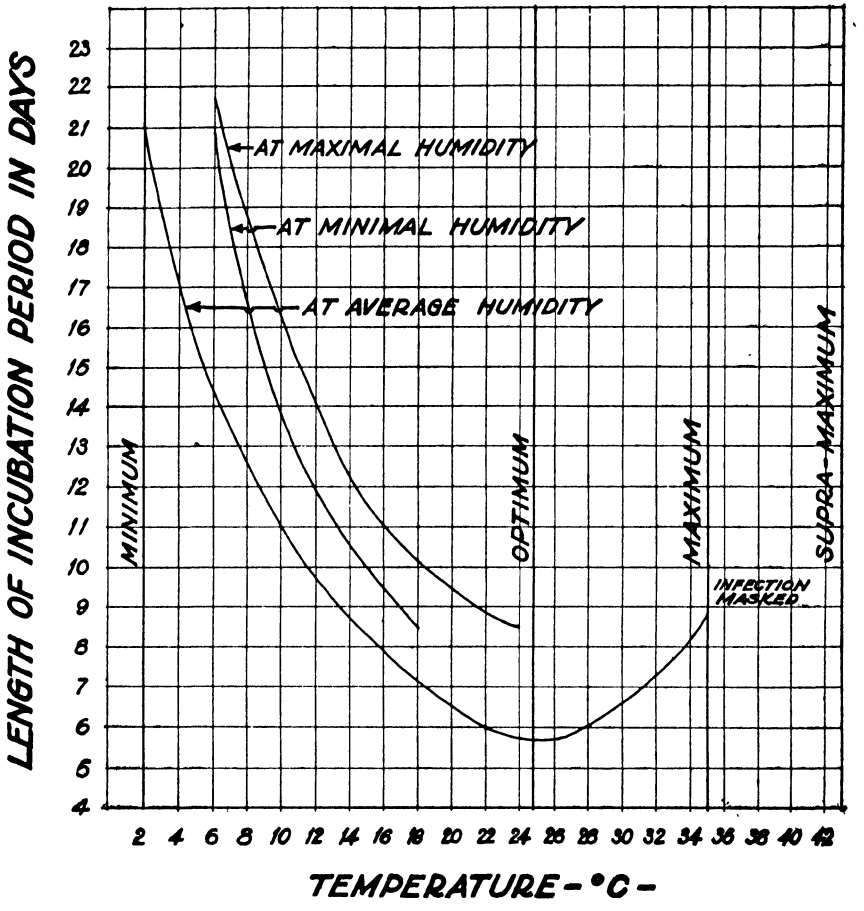

FIGURE 6. — Relation of length of incubation period of leaf rust in wheat to temperature. (*After* NAUMOVA, 1935).

data showing that 24 or 48 hours retention of inoculated plants in moist chambers at 10° or 15° C. was required in order to permit essentially the same amount of infection as occurred in a 12-hour moist chamber exposure at 20° C.

The temperature requirements for the infection period (as distinguished from those for the incubation period) may be studied by placing plants in moist chambers for 24 hours following inoculation, at given temperatures, and then exposing them for the duration of the incubation period, to optimal conditions for infection. NAUMOVA (1935), following this procedure, observed that no infection resulted if the temperature for the first 6 hours

after inoculation was 35° C. The optimum temperature for the first 24 hours was 19.4° to 22.8° C. This corresponds with SCHAAL's report of maximum infection when the temperature for the first 48 hours after inculation was 18°-20° and 24°-25° C., *i.e.* in a range of 18°-25° C. The writer found that if inoculated plants were placed in moist chambers at 27° C. for 24 hours after inoculation, and then incubated at the optimum temperature, no infection resulted, while comparable control plants, kept at the optimum temperature throughout, became abundantly rusted. This failure to obtain infection at 27° C. agrees with the data on slower growth of the germ tubes and invasion at higher temperatures, but may also involve progressively greater difficulties in maintaining saturated air, even in a moist chamber, with increase in temperature.

The foregoing data bring out the fact that the cardinal points of temperature for uredospore germination almost exactly coincide with those for germ tube growth and invasion of the host plant, namely 2°, 20°, and 31° C.

The most extensive and critical studies of temperature in relation to the incubation period of leaf rust in wheat have been those of NAUMOVA (1935). Her data, which have been shown to be statistically significant, are the basis of the curves showing the relationship between average temperature and length of incubation period given in FIG. 6.

The figure reveals the important fact that the optimum and maximum temperatures for incubation, *i.e.* the development of the infection once the fungus has invaded the host, are several degrees higher than the optimum and maximum temperatures for spore germination, germ tube growth, formation of appressoria, and invasion of the host. This point can only be fully seen when infection is allowed to proceed for about 24 hours at a standard, favorable temperature, and the plants are then subjected to different temperatures for the remaining period, until pustules appear, the procedure followed by NAUMOVA.

As the incubation temperature departs from the optimum, the incubation period is lengthened, and this is particularly noticeable in the range of low temperatures. It also occurs in the range from the optimum of 25° C. up to about 35° C., but when the incubation temperature reaches this point the infection becomes masked. No symptoms develop, but the fungus remains alive, and if at any time such plants are returned to a favorable temperature, pustules develop promptly (NAUMOVA, 1935; CHESTER, 1942*c*). An analogous phenomenon has been noted when infected plants are incubated at low temperatures, but here it is difficult to distinguish masking of symptoms and a very extended incubation period. ZIMMERMANN (1925) has reported that under certain conditions in Germany, the incubation period may be as much as 5-6 weeks in length, and, as we will see later, it is common for wheat leaf rust to overwinter as nonsporulating, dormant mycelium in the dormant wheat plant in which the infection may be regarded either as masked or as undergoing a very extended incubation period.

The data of NAUMOVA are in general agreement with the more fragmentary data on temperature and the length of the incubation period of other workers, although a few discrepancies may be seen in some of the reports. Thus a number of workers have stated that the maximum temperature for incubation is 30° C. This is evidently because 30° is the upper

limit for spore germination and infection, and therefore this temperature limits the entire process from inoculation to spore production if the tests have not discriminated between infection period and incubation period. Variation in the records of length of incubation period, in relation to tem-

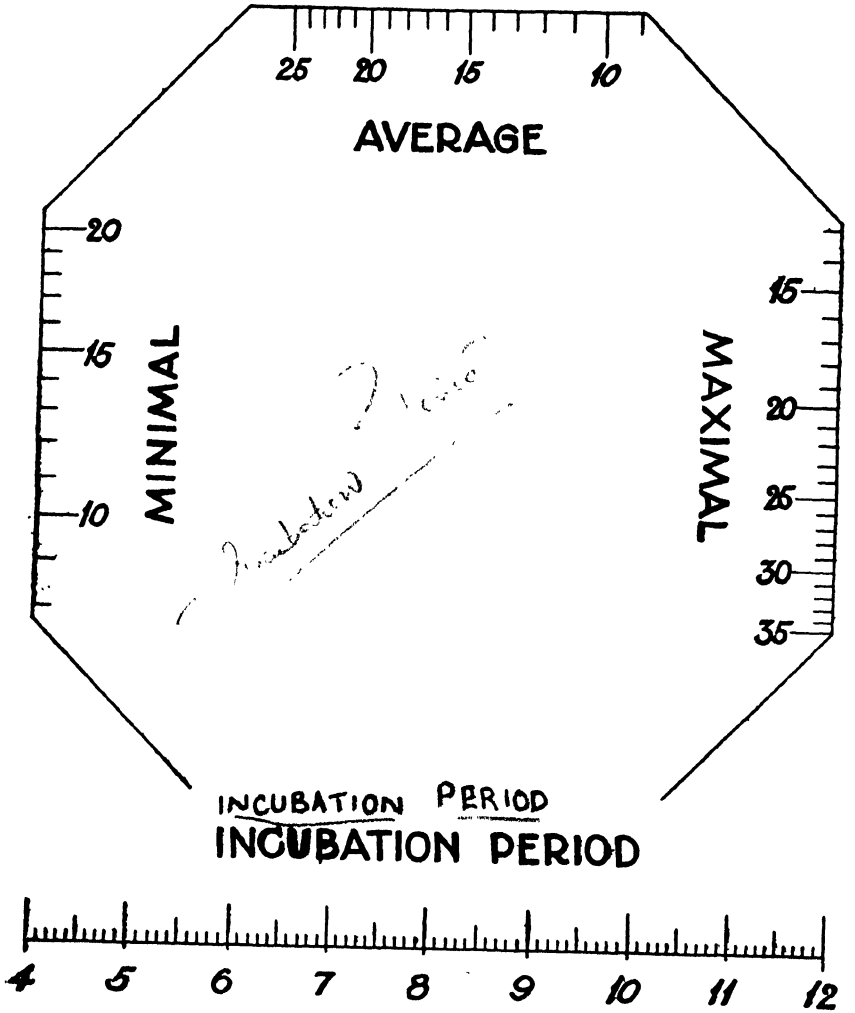

FIGURE 7. — "Nomogram" for determining length of incubation period of *Puccinia triticina* in wheat, in relation to temperature. Prepared by Prof. POMORSKI. (*After* NAUMOVA, 1935).

perature, to some extent may be due to differences in the point of rust development arbitrarily selected as marking the end of the incubation period. Finally, it is difficult to account for the low optimal temperatures for incubation reported by some workers (STOCK, 1931: 10°-15° C.; JOHNSON, 1912: 12°-17° C.; MAINS and JACKSON, 1926: 16°-20° C.). In part at least, this is evidently explained by failure to distinguish the different temperature requirements of infection and incubation periods, but other factors, such as

differences in races of leaf rust, in wheat varieties, and in humidity, may also partly be responsible for these discrepancies.

GASSNER and APPEL (1927) were unable to alter the length of the incubation period by fluctuations of temperatures in any manner other than that resulting from comparable constant temperatures, but NAUMOVA found that sharp daily fluctuations in temperature, as between 21.8° and 46° C., stimulated the mycelium and shortened the incubation period.

By keeping her plants at optimum temperatures except for certain definite portions of the incubation period, NAUMOVA was able to determine the effect of temperature at various stages in the developing infection. This revealed that the most critical periods, once infection has occurred, are at the beginning and slightly before the end of the normal incubation period. The temperatures of the first 3 days of the incubation period influence the number of pustules ultimately formed.

Although NAUMOVA found that the length of the incubation period (at temperatures below the optimum) is inversely proportionate to the temperature, whether the latter is expressed as the sum of average daily temperatures or as the average of daily maximum plus minimum temperatures, she found no correlation between the length of the incubation period and the total number of degree-hours. The latter was fairly uniform (2728-3544 degree-hours) for incubation periods of different lengths, with constant or fluctuating temperatures. There was more correlation between the length of the incubation period and the minimum temperature than with the average or maximum temperatures.

From her data it was possible to construct a "nomogram" by use of which one can calculate the length of the incubation period, knowing the minimum, average, and maximum temperatures for the period. Such a "nomogram" is illustrated in FIG. 7.

In its use, two lines, intersecting at right angles, are ruled on a piece of transparent paper. As an example, let us assume that in a given case the average, minimum, and maximum temperatures are known to be 19°, 11°, and 24°, respectively. If the paper with the intersecting lines is placed over the nomogram in such a way that the upper, left, and right arms of the cross pass through these respective temperature points, the lower line intersects the lower scale at 8; *i.e.* with these temperatures the incubation period will be 8 days. In the same fashion the length of the incubation period can be determined for any other combination of average, maximum, and minimum temperatures represented in the nomogram.

The preceding pages have been concerned primarily with the effect of temperature on the length of the incubation period. Temperature during the incubation period also has a marked effect on the type of pustule produced. This subject has already been treated (pages 79-82), and here the discussion will be limited to the *modus operandi* of temperature in relation to infection type.

GASSNER and FRANKE (1934*b*) grew wheat plants of 6 varieties at different temperatures but otherwise in constant environments, and found an increase in protein content of the plant associated with decrease in temperature. In lowering the temperature from 20° C. to 5° C. the protein increased 203 to 261%. GASSNER and his coworkers, in other experiments,

have shown that increased plant protein is correlated with increased rust susceptibility (*see* pages 129-133) and we have also seen (page 80) that a decrease in temperature below the optimum in many cases is associated with an increase in rust susceptibility. These findings of GASSNER and FRANKE provide a link in the chain by showing that a reason for this increased susceptibility is the temperature-induced increase of protein in the host plant.

Workers agree that leaf rust develops most rapidly in wheat fields when the mean temperature is in the range of 15°-22° C. This is in good agreement with the optimal temperature for spore germination and wheat infection (20° C.), for greenhouse rust culture (18°-20° C.) and for growth of the wheat plant itself. It is well correlated with many observations on the development of rust in relation to monthly temperature, such as BRIZGALOVA's finding (1935) that in Siberia, June temperatures determine rust development, it being necessary that they be above the average of 15°-16° C. to permit dangerous outbreaks. In Oklahoma the month of March is most critical (CHESTER, 1943, 1944) ; there the average March temperature is 10° C. (50° F.). If this is exceeded by a few degrees, the foundation is laid for extensive rust development in later months, while if the average March temperature is below this point, development of the disease is inhibited.

In nature the diurnal temperature oscillates about the mean, and it has already been pointed out that alternation of low night with higher day time temperatures, about the optimal mean, is even more favorable for the development of rust than a constant optimal temperature.

Most workers agree that the tempo of increasing leaf rust is greater in the spring than in the fall. Other factors being equal the principal difference in the two seasons lies in the fact that in spring the crop is developing during a progressive rise in temperature, while the reverse is true in the fall. A possible explanation of the more rapid tempo of rust development in the spring is seen in the fact that the optimum and maximum temperatures for rust incubation are a few degrees higher than those for spore germination and infection. It follows that for any given case of infection, the ideal condition is for there to be a rise of a few degrees of temperature as the infection and incubation processes proceed, a condition that often obtains in the spring, while the reverse is true in the fall.

While the optimal temperatures for development of rust and of its host are similar, there are differences in the maxima and minima for the two organisms. RUSAKOV (1922) has pointed out that temperatures of 4°-8° C. permit wheat to grow while inhibiting the rust, and at slightly higher temperatures (such as often obtain in the Kamenoi Steppes even in summer) the wheat plant can drive on in its growth ahead of the weakly-functioning fungus.

Light: — BOLLEY (1891, 1898) was the first to investigate the effect of light on the viability of uredospores of *Puccinia triticina*. In his first tests he found that the spores germinated well after outdoor exposure in test tubes in the shade during the whole of August, while if the tubes were placed in direct sun they showed 50% germination after the same period

of exposure. His later tests seem to indicate that direct sunlight has little effect in lowering the viability of the spores. Thus, he obtained 90-100% germination from spores exposed to direct sun on dry glass for 5 days, and the same germination from spores similarly exposed for the same length of time in the shade, both at 38° C. Spores exposed to direct sun for 12 days gave 80-100% germination, and those exposed for 21 days gave 5-10% germination.

Similarly, GASSNER and STRAIB (1928) found that 4 hours of exposure to direct sunlight at 30°-35° C. did not injure uredospores of *P. triticina* although it killed those of *P. glumarum*.

In general, HWANG's results (1942) are in agreement with the foregoing. There was little difference in loss in viability of spores on wheat leaves exposed up to 8 hours in full sun or in the shade, although spores exposed as much as 20 hours to full sun germinated to the extent of 25% as compared with 52% for spores in the shade, while after 48 hours exposure to direct sunlight (100 hours total exposure) germination dropped to 2% as compared with 36% in the shaded controls. As is true of other organisms, the ultraviolet rays proved to be particularly involved in such loss in viability as does occur: germination of *P. triticina* spores was reduced to 64-65% following irradiation with ultraviolet light for 15-20 minutes.

The results of these different workers agree in that the uredospores of *P. triticina* are relatively insensitive to such direct sunlight as normally occurs during several days, and that they will retain some viability for a longer period,—up to 3 weeks in BOLLEY's tests. This has an important bearing on the survival of spores in nature, since it indicates that insofar as light is concerned, the uredospores can retain their viability for sufficiently long periods to enable them to produce infection after having been windborne for hundreds of miles, or after having survived a number of days of dry weather, on the surface of a wheat leaf, before the occurrence of moisture and temperature conditions permitting spore germination and infection.

There is evidence that strong light, quite apart from being harmful, may be actually beneficial in connection with the ripening of uredospores. MAINS and JACKSON (1926) noted that uredospores found in periods of low light intensity germinate poorly (only 10%) unless after-ripened for a few days in the laboratory, and HWANG (1942) confirms this in his report that spores formed in the greenhouse in November and December (Minnesota) germinated more poorly (30-70%) than those formed in other months (75-95%).

A number of workers have shown that the presence or absence of light has no effect on the germination of wheat leaf rust uredospores and infection, by their germ tubes, of wheat. We recall that infection occurs through the stomata. According to CALDWELL and STONE (1936), these are open in daylight but close so tightly in darkness that no slit is apparent. They never open in darkness regardless of the humidity. All of the stomata of a leaf act similarly. When inoculated plants were placed in the dark, 85.3% of the appressoria formed effected entrance through the closed stomata, while in plants in the light, entrance was effected by 89.8% of the appressoria, — hardly a significant difference. Infection regularly occurred at night if plants were inoculated at 4:30 P.M., as shown by dusting them with sulphur early the following morning to prevent further infection in daylight. More-

over, certain workers use light-tight containers as moist chambers, with good infection results. Similarly HART and FORBES (1935) obtained 87.9% infection with 84% heavy infection, in the darkness and 83.4% infection with 64.3% heavy infection in the light.

STOCK (1931) showed that the germ tubes of *Puccinia triticina* uredospores are negatively phototropic, and this was later confirmed by FORBES (1939), who found in addition that this phototropic response is due primarily to blue and violet rays. However, judging by the equal success of infection in light and in darkness, this tropism appears to have little importance in determining the success of infection.

There is general agreement that decreasing the amount of light from the optimum lengthens the incubation period of wheat leaf rust. This is observed if the incubation period during the short days of winter is compared with that in summer. SCHAAL found that the incubation period extended from 8 to 18 days under such low light that the plants showed etiolation, and GASSNER and APPEL were able to shorten the incubation period by 3 days, through supplementary lighting in winter.

SEMPIO (1939) and later HASSEBRAUK (1940*a*) investigated the effect of light in different parts of the incubation period. SEMPIO found that exclusion of light in the first third of the period only, led to stronger rust development; darkness in the middle third of the period extended the incubation period without altering the rust reaction; while exclusion of light in the last days of the incubation period led to a greatly reduced rust attack. This last was a permanent effect and not masking, since no rust developed when such plants were returned to the light. In general, HASSEBRAUK's findings confirm those of SEMPIO, although HASSEBRAUK found the situation more complicated than would appear from SEMPIO's results. Great differences were noted in the light reactions of different wheat varieties. Moderately resistant varieties and highly resistant but unstable varieties behaved as SEMPIO had described, but with very susceptible varieties, darkness either had no effect or darkening in the later stages of the incubation period increased the resistance of the plants.

While increase in light from suboptimal to optimal amounts shortens the incubation, further increase to an excessive level again causes an extension of the incubation period, seen in leaves exposed to full, intense sunlight, according to SCHEIBE (1930*a*).

Not only is the incubation period lengthened by suboptimal light, but the character of the rust reaction is also altered. This subject has been discussed (pages 82-83) and we need only recall here, that the reaction may at times be changed from a resistant to a susceptible type as light intensity and day length are increased. With some rust races and wheat varieties total darkness during the incubation period entirely inhibits rust development (GASSNER and APPEL, 1927; original).

The increase in resistance with low light intensity is generally regarded as due to inadequate photosynthesis in the poorly lighted plants (GASSNER, 1927; SIBILIA, 1928; HASSEBRAUK, 1939). This is also borne out by the fact that rust develops on plants in the dark provided they are fed sugar (MAINS, 1917; GASSNER and STRAIB, 1929; POHJAKALLIO, 1932). GASSNER covered areas of wheat leaves with light-tight coatings and in such cases

normal rust pustules were formed in the etiolated spots resulting, indicating that the green parts supplied the etiolated portions with sufficient metabolites to permit normal rust development.

There are many reports that severe rust is associated with cloudy weather. We have just seen that low light intensity does not favor rust development. It follows that while cloudiness is not a favorable factor for rust, insofar as light is concerned, it is regularly associated with high humidity, the rust-favoring effect of which much more than compensated for the concomitant effect of low light.

Air: — Judging by the data of GASSNER and STRAIB (1929) and of STOCK (1931) uredospore germination and germ tube development are relatively insensitive to variations in the CO_2 content of the air within rather wide limits, although they respond more strongly to lack of O_2. We have seen that spores under water germinate more poorly than those on the surface of water droplets, and this is evidently due to oxygen response. Further evidence of this response to O_2 is seen in the report of HITCHCOCK and CARLETON that uredospores in weak H_2O_2 (liberating O_2) germinate better than those in pure water.

GASSNER and STRAIB noted no difference in germination of uredospores in atmospheres containing .03% to 7.5% CO_2, or in water containing CO_2 at 1.65 to 3.5 atm. pressure. Also plants inoculated in the presence of high CO_2 concentration and then incubated in normal air became rusted in normal fashion, showing that the CO_2 did not interfere with germ tube penetration.

STOCK obtained equally good germination in pure O_2, N_2 + 2% O_2, and air, and there was no difference in germ tube length in these three types of atmosphere. In N_2 with only a trace of O_2, germination was reduced only from 25% (in air)to 8%, indicating that the O_2 need of spores is very small. Germination was delayed by large amounts of CO_2 in the atmosphere. It began in 1 hr. in air, 1.5 hr. in 5% CO_2, 2 hr. in 10% CO_2, 3 hr. in 15% CO_2, and 6 hr. in 20% CO_2. In all these cases, however, full germination eventually occurred. Likewise the rate of germ tube growth was reduced by so little as 1% CO_2, but eventually the germ tubes in CO_2-air mixtures reached the length of those in pure air, since they continued growth for a longer time than in air.

In contrast, the exposure of infected plants to different CO_2 levels during the incubation period elicits a much more marked effect on rust development. In preliminary observations in 1927, GASSNER observed that the strongest rust development resulted from increasing the normal air content of CO_2 (.03%) to .15%, but that the rust became weaker with further increase of CO_2 (.75%, 3.75%). When the plants were entirely deprived of CO_2, rust development was retarded or eventually inhibited. These results were confirmed the following year by SIBILIA who also found that moderate CO_2 increases favored rust, while an increase to 1.1% CO_2 notably diminished susceptibility.

Proceeding from these preliminary observations, GASSNER and STRAIB in 1929 made a more detailed study of the CO_2 relationships of leaf rust-infected wheat seedlings. Their results are summarized in TABLE 15.

We can see from these data that the optimal CO_2 level for wheat

seedling development (.15 — 1.5%) is considerably higher than that of air. In this range susceptible wheat shows its greatest susceptibility, and wheat with an intermediate reaction becomes more susceptible, but the resistance of a resistant variety is reinforced. Still higher CO_2 levels result in poorer plant growth and increased rust resistance. These results were obtained under normal May-September light. In the winter months the CO_2 effect was less striking.

TABLE 14: *Cardinal points for germination of wheat leaf rust spores, as determined by various workers* (°C.): —

SPORES	MINIMUM	OPTIMUM	MAXIMUM	AUTHORITY
Uredospores	1.5°	12-17°	31°	E. C. JOHNSON, 1912
—	2°	15-22°	26°	BRIZGALOVA, 1937*b*
—		20°		BEAUVERIE, 1924
—	2-3°	5-20°	29-30°	MEHTA, 1923
—	2.5°	12 5-25°	30°	STOCK, 1931
—	(7°)*	20-25°	30°	NOVOTELNOVA, 1935
—	2-3°	10-22°	30-32°	SĂVULESCU, 1938*a*
—	2.5°	22-25°	30+°	NAUMOV, 1939
—	(6-8°)*	20-21°	31°	SCHAAL, 1925
Teliospores	2°	14-19°	20°	BRIZGALOVA, 1937*b*
—		12 5-25°		NAUMOV, 1939
Aeciospores†	2°	5-9°	20°	BRIZGALOVA, 1937*b*

* Minimum evidently somewhat below the point indicated, but temperature intervals a few degrees below this point not tested.
† Aeciospores from *Isopyrum fumarioides*.

These results, in conjunction with those of the preceding section on light, indicate that in both cases the effects operate through altering the photosynthetic activity of the host plant rather than directly affecting the fungus. Further evidence of this is seen in GASSNER and STRAIB's observation that plants in which rust development has been inhibited by high CO_2 concentrations, if returned to air, promptly produce normal rust pustules, showing that the high CO_2 content has not injured the fungus, but that the latter has lain dormant in the plant, the carbohydrate metabolism of which has been disrupted by the excess of CO_2. It is worthy of comment that the greatest rust susceptibility occurs at CO_2 levels that stimulate the most vigorous growth of the host plant, in accordance with many other types of observations indicating that high rust susceptibility and a high state of vigor of the wheat plant are positively correlated.

The work of GASSNER and STRAIB was carried out on seedling wheat plants. Later SCHEIBE (1930*a*) performed analogous tests on older plants with results in general agreement with those of GASSNER and STRAIB. The greatest susceptibility and shortest incubation periods were in plants exposed to .3% CO_2 or 10 times the normal amount in the air.

Moving air has opposite effects on wheat leaf rust. Winds are unfavorable to rust development insofar as they cause rapid evaporation of condensed moisture or that from light rains, and lower the relative humidity, which interferes with spore germination and infection. Winds also are said to encourage a more resistant type of wheat growth, and to hasten maturity,

in both respects being unfavorable to rust development. On the other hand, winds not only are instrumental in dislodging spores, but also serve as the principal means of dissemination of rust, locally and to great distances. The alternation of calm nights (for infection) and windy days (for dispersal) is particularly favorable for the rust. From this it follows that in humid areas, wind motion, and in dryer areas, calm air are in general most favorable.

TABLE 15: *Effect of CO_2 content of the air on leaf rust reaction of wheat seedlings* (after GASSNER and STRAIB, 1929) : —

CO_2 IN ATMOSPHERE	NORMAL REACTION OF WHEAT VARIETY			PLANT GROWTH
	SUSCEPTIBLE	INTERMEDIATE	RESISTANT	
Air	Susceptible	Intermediate	Resistant	Vigorous
CO_2 0.03%	Resistant	Intermediate	Resistant	Retarded
— 0.15%	Susceptible	More susceptible	Very resistant	Very vigorous
— 0.30%	Most susceptible			Very vigorous
— 0.75%	Susceptible	Less susceptible		Very vigorous
— 1.50%	Intermediate			Very vigorous
— 3.00%	Resistant			Retarded
— 4.50%		Very resistant	Very resistant	Retarded
— 6.00%	Resistant			Retarded; injured

These opposite influences of winds are reflected in reports on the occurrence of rust in areas protected by forests or other windbreaks, as compared with rust in more exposed places. Some workers report greater rust intensity in protected areas, others in more exposed ones.

Such reports are not referable to wind effects alone. For example, in the calm areas near a windbreak, snow accumulates to a greater depth and is more persistent, — hence, the rust overwinters more readily and there is more inoculum available in the spring. Since in nature it is characteristic for there to be a well-mixed assortment of conditions of air movement, it is doubtful if lack of adequate air movement or calm often plays an important rôle in interfering with rust development and dispersal.

The function of winds in dissemination of wheat leaf rust is discussed in detail in Chapter XI.

Topography: — It is very generally accepted that rusts in general, and wheat leaf rust in particular, develop more abundantly and destructively in valleys or other low-lying sites than on hillsides, upland sites, and plateaus. So axiomatic is this that a regular part of standard recommendations for rust control is the avoidance of bottom sites for wheat culture. However, there are exceptions to this rule as is seen when an analysis is made of the various factors relating to topography.

It is natural for moisture to be abundant in low sites, and for it to evaporate less readily than in exposed places. If, as is often the case, the amount of moisture is the leading factor conditioning rust development, rust has an advantage in low locations, and this is the principal basis for the generalization expressed above. Furthermore, it is also customary for low sites to be characterized by richer soil. This favors a ranker, more succulent

and luxuriant type of wheat development, which in turn makes the wheat particularly liable to rust.

Occasionally rust is observed to be more destructive on upland locations, for a number of reasons. SHITIKOVA-RUSAKOVA (1928) in a comparison of two experimental wheat fields, one of which was 150 m. lower than the other, found the greater amount of rust on the upper field, which she attributed partly to the fact that in the lower field the wheat was so rank that competition killed the lower leaves, bearing early rust, and partly to the fact that on the upper, more exposed field, wheat maturity was regularly later, so that the rust had more time to act on it, and accordingly was more destructive than on the lower field. Also in the upper field the rust overwintered better under a more persistent snow cover and the temperatures were regularly cooler and humidity higher. In East Siberia, BRIZGALOVA (1935) likewise observed heavier leaf rust on high sites, but in this cold climate, temperature, rather than moisture is the principal factor limiting rust development, and in the valleys and depressions, where cold air collects, which are more subject to frosts, and which are last to receive warmth from the sun, the rust is at a disadvantage as compared with higher locations. She found that in warm, dry seasons, northern slopes showed the most rust because of slower evaporation of moisture, while in wet, cool years rust on southern slopes had the advantage, because of higher temperatures. The windward sides of slopes in any case are in better position to receive airborne rust spores.

Russian workers in particular (RUSAKOV and SHITIKOVA-RUSAKOVA, 1928; BRIZGALOVA, 1935; FEDORINCHIK *in* NAUMOV, 1939) have called attention to the differences in the amount of leaf rust, due to small depressions and elevations, such as furrows and wheel or cattle tracks in otherwise uniform fields. These have their greatest importance in aiding rust hibernation and as foci for early initiation of rust epiphytotics. Such depressions favor rust hibernation by holding the snow cover, and its development by providing little pockets of humid air which facilitate spore germination and infection.

Barriers, ranging in size through small hedges, forest strips, hills, and mountain ranges, affect rust primarily as they deflect winds disseminating rust spores. Specific cases of their effects are discussed in Chapter XI.

FACTORS AFFECTING RUST SURVIVAL ANI DEVELOPMENT (*Contd.*)

Vigor and succulence of the host plant in relation to its rust: — Observations of many agronomists, plant pathologists, and growers are uniform in associating severe rust with rankness or luxuriance of the wheat plant. Any environmental factors which favor this type of vegetation indirectly favor the disease, and this fact is the key to the following sections, since the properties of the soil are foremost factors in determining the vigor of the host plant.

Together with the primary relationship between succulence and host response to rust are a number of secondary relationships. Thus, (*a*) ranker, more vigorous plants have a greater leaf area exposed to rust spores which facilitates rust multiplication, (*b*) such plants by forming a denser plant cover, tend to maintain a humid layer of air about themselves, which favors spore germination and infection, (*c*) this type of vegetation tends to mature later than less succulent plants, which extends the time during which the destructive work of the rust can progress, and (*d*) a high degree of succulence may operate in the reverse direction insofar as hibernation of the rust is concerned, since plants or leaves so characterized are most liable to winterkilling, which in turn destroys the overwintering mycelium of the rust.

Soil type and physical condition: — We have few observations and experimental data for evaluating the effects of soil type (considered apart from soil fertility) on wheat leaf rust. BOLLEY (1905) and BOLLEY and PRITCHARD (1906) reported that rust is most destructive in wheat on poorly drained heavy clay soils, gumbo and alkaline spots in lighter lands, light sandy soils that are too deficient in nutrients to permit early maturity of the crop, on loamy soils containing an excess of organic matter, and on soils that are not properly compacted.

ERIKSSON and HENNING (1896) and SĂVULESCU (1934) concluded that soil texture has no direct effect on rusts although indirect effects are seen in the influence of soil texture on earliness or lateness and on vigor of the crop. GASSNER (1915*c*) arrived at the same conclusion with reference to wheat leaf rust following observations and experiments in Uruguay. Among the latter, he grew wheat in soils composed of various proportions of loam and quartz sand, but with the same levels of moisture and fertility, and found no variation in the strength of leaf rust attack. SĂVULESCU observed that wheat is more severely attacked by rust on neutral to alkaline soils than on acid soils, but acid soils are less favorable for vigorous wheat growth, judging by the fact that wheat in general is grown on neutral to slightly alkaline soils.

Chemical constitution of the soil: Major elements: — Early workers stressed the importance of avoidance of nitrogenous fertilizers and

recommended the application of phosphate fertilizers to reduce rust damage. Nitrogen tends to delay maturity of wheat, while phosphorus has the opposite effect, and these recommendations were based on the principle of avoiding rust damage by hastening the maturity of the crop. As we will see, below, nitrogen also plays a major part in increasing the susceptibility of the wheat plant, while phosphorus has the opposite effect. That these recommendations with reference to rust and the major nutrient elements represented scientifically sound advice, has been borne out in recent years by many field observations, field experiments, and controlled tests with plants growing in nutrient solutions or sand cultures with definite mineral composition of the nutrient fluids.

GASSNER, who, with his associates, has contributed more than any other to the experimental study of the relationship between nitrogen and wheat leaf rust, began with field experiments in 1915. A wheat field that was rich in Ca and K and tolerably so in N, was fertilized with various amounts and proportions of Ca, K, P, and N. Leaf rust developed to equal extent on all the plots, which GASSNER considered might be due to the fact that the field already contained sufficient N to permit maximum rust. There was only an apparent rust-favoring effect of N in retarding maturity (and teliospore formation) and in stimulating a denser stand which was associated with high humidity in the plant cover. Later, in 1934, GASSNER and HASSEBRAUK confirmed their greenhouse tests (discussed below) by fertilizing wheat in the field with various proportions of N, P, and K. Leaf rust was more severe whenever K was deficient in the ratio.

In 1924, STAKMAN and AAMODT reported the outcome of fertilizing wheat with acid phosphate, $NaNO_3$, and KCl, at different rates. While the results were not wholly satisfactory because the wheat varieties used were somewhat rust resistant and little rust developed during the experiments, there was some indication that infection was increased by decreasing phosphate and increasing nitrate. Results with manures were not significant.

SCHILCHER in 1933 found that the nitrogenous fertilizer, calcium cyanamid, promoted the severity of leaf rust, as did N in general, while K and P retarded infection.

In 1935-1937 a series of field experiments were carried out in Russia (NAUMOV, 1939). MAKLAKOVA'S tests, in Gorkovsk, resulted much as those of GASSNER, perhaps for the same reasons. In contrast, FRIEDRICHSON in the Trans-Volga region, PRONICHEVA in Krasnodar, and FOMIN and NOZDRACHEV in the Ukraine all found that P and K applications reduced the amount of leaf rust, while N increased it. P or K, if combined with N, tended to offset the rust stimulation of N alone. Numerous wheat varieties were involved in these tests, and it was observed that the response of rust to these elements differed somewhat from one variety to another. The differences in rust intensity were sometimes quite striking, as in PRONICHEVA'S tests, in which the varieties Ukrainka, Cooperatorka, Stepnyachka, and Stavropolka 328, when in plots fertilized with N alone, showed 94, 100, 93, and 86% rust respectively, while the same varieties in plots with K fertilization developed only 49, 34, 45, and 39% rust. The rust intensities in the plots receiving only P or those with N + P, N + K, P + K, or N + P + K had intermediate amounts of rust, from 62 to 73%.

A particularly striking example of the N-rust relationship was observed

by the writer in 1942 in Oklahoma Experiment Station plots of Turkey wheat with and without N fertilization. Soon after the flag leaves formed, those in the plots with N fertilization became heavily rusted, while the flag leaves of adjacent plots that had not been so fertilized remained relatively uninfected and green, so that the N plots could be readily detected from a distance as reddish-yellow strips in an otherwise green field.

As a result of such experiments and observations, it is now generally accepted that leaf rust may be reduced in severity by reducing the proportion of N in the N:P:K ratio, and this is reflected in recommendations of recent years. Only rarely does one encounter such a conflicting statement as that of VALLEAU in the "Plant Disease Reporter" (19:134. 1935): — "Specimens of wheat making poor growth, light in color, and heavily rusted have been received from Marion County. Almost continuous rains have probably reduced nitrification to a minimum in heavy, poor soils resulting in starvation of the developing wheat." The abundant experimental data show that nitrogen starvation and heavy rust are incompatible, and the statement is evidently based on an inadequate understanding of the cause of the yellowing and of the nitrogen-rust relationship.

Experiments to study N:P:K — leaf rust relationships under controlled greenhouse conditions were initiated by WEISS in 1924, followed by DOAK in 1931, and GASSNER and his co-workers in a series of papers from 1930 to 1939.

In WEISS' experiments, which were conducted on too limited a scale to be of more than orienting value, Marquis wheat with leaf rust was grown in nutrient solutions containing various proportions of N, K, Ca, and Mg. The amount of rust ranged from 32% in the plants receiving the most N to 2, 4, and 6% in the plants receiving K, Ca, and Mg, but not supplementary N, respectively.

DOAK grew rusted wheat in sand cultures with different N, P, and K levels. High N increased susceptibility, resulting in larger primary uredinia and more secondary ones, with little chlorosis. High P increased chlorosis; it did not affect the size of primary uredinia but decreased or inhibited the occurrence of secondary ones. High K increased chlorosis and decreased the size of primary uredinia. In wheat varieties of intermediate rust reaction, high N increased the number of pustules, and the reverse resulted from low N or high P or K.

The more detailed work of GASSNER and his associates consisted of experiments with sand cultures and nutrients of various N:P:K contents, and others in which the leaves of wheat plants were immersed in solutions which permitted them to absorb these minerals directly, and observations were made both of amount and type of rust development and of the N-content of the plant tissues.

The sand culture experiments (GASSNER and HASSEBRAUK, 1931, 1934*a*; HASSEBRAUK, 1930, 1939), were conducted with seedlings of very susceptible, intermediate, and very resistant wheat varieties. The intermediate or moderately resistant varieties were most useful, as it was not possible to alter the reactions of highly resistant or susceptible varieties by altering the nutrient supply. The supply of N, P, and K was varied from none or 1/20 normal to 5 or 10 times normal. The use of seedlings has the advantage of eliminating error from "apparent resistance" due to nutrient-condi-

tioned differences in maturity of the plants as seen in field experiments, although it also slightly increases possible error due to failure to exclude salts present in the seed endosperm of the seedlings. The results obtained with *Puccinia triticina,* which were entirely comparable to those obtained with other rusts, *P. glumarum, P. graminis, P. coronifera, P. dispersa,* and *P. simplex,* were as follows:

Nitrogen favored rust development, the more so as it was in excess over P and K. This effect also depended on the P:K ratio and the anions in the salts furnishing N, P, and K. Thus, with the neutral *p*H used, NH_4^+ salts were most active in favoring rust, $CaNO_3$ was less effective, $NaNO_3$ still less effective, and KNO_3 least effective of all. An excess of $NaNO_3$ or KNO_3 could even increase resistance due to the greater effect of the Na^+ and K^+ as compared with the NO_3^- ion. The period of spore production was lengthened by increasing the N supply; K and P had no effect on this.

With increasingly deficient N the incubation period was shortened and the rust reaction moved progressively to the resistant side, with as numerous but smaller pustules and more chlorosis, so much so that at times it was difficult to determine the infection type. The effect of N and K in altering the reaction types of the differential wheats used in rust race identification was discussed on page 79, and TABLE 6 shows that the reactions may be varied at will from highly resistant to highly susceptible, with all intergrades, by increasing the proportion of N in the N:K ratio.

Potassium in general has the opposite effect of N; as K is increased the rust reaction is displaced to the resistant side, other elements being constant. When N and P were simultaneously varied, the rust-depressive effect of K increased with increasing excess of K over N and P. The K effect was also dependent on the N:P ratio. The effects of KCl and K_2SO_4 were similar, now one and now the other being more effective in increasing rust resistance. When K was entirely lacking there was such injury to the plants that the results were unreliable. With a wheat variety of weak rust resistance, the reaction could be shifted from type "4" to type "1-2" by increasing the proportion of K (FIG. 8, page 147).

Phosphorus has less clear-cut effects, which depend upon the simultaneous presence of K and N and on the K:N ratio. According to the ratio P:K:N, phosphoric acid can heighten either susceptibility or resistance. If P > K, N, resistance is increased and if P < K, N, susceptibility is increased; these P effects differ with the different varieties and research conditions. The relatively insoluble P-salts were less effective than the more soluble ones. With the K-phosphates and possibly the Na-phosphates, the cations had effects which must be considered. Increase of K-phosphate greatly increased resistance but this effect was apparently mainly due to the K cation.

We see that the elements of the N:P:K ratio are closely interlinked and effective in opposing directions, so that it is not always possible to determine whether a given rust response is due to the relative excess of one of these elements or to the simultaneous relative lack of another.

Because of a possible objection in work with sand cultures that the root systems might exhibit selective action in taking up nutrient salts, GASSNER and HASSEBRAUK (1933; HASSEBRAUK, 1930) verified their sand culture experiments by tests in which seedlings were permitted to take up

mineral salts directly through the leaves. The salts were used in 1/32 molar solutions, and the fact of their absorption was demonstrated by the production of chlorophyll in iron-free plants the leaves of which were immersed in iron salt solutions. Immersion was for a few hours daily, and, in general, no injurious effect on the plants was observed. The following were the principal results of these tests:

Nitrogen salts increased susceptibility to rust, as seen in larger and more numerous pustules with reduction of the amount of chlorosis, and the period of fructification was lengthened by several days. These effects were most striking following the use of NH_4 nitrate, chloride, and sulphate, and glycocoll, less so with Ca and Mg nitrates and asparagin, and least so with K and Na nitrates and especially ammonium phosphate (due to the antagonistic effect of the K and P ions). With strong solutions of KNO_3 there was increased resistance to rust (K^+ effect), and with weaker solutions, increased susceptibility (NO_3^- effect).

Potassium salts increased the resistance of both moderately and highly susceptible varieties, with K_2HPO_4, KH_2PO_4, $KHCO_3$, and K_3PO_4 most effective, KNO_3 least effective (counteracting effect of the NO_3^- ion), and KCl, K_2SO_4 and KBr intermediate.

Phosphorus increased rust resistance but the effect was sometimes difficult to demonstrate because of the insolubility of some P-salts and the counteracting effect of the cation in others. The greatest effect was obtained with K_2HPO_4, K_3PO_4, and Na_2HPO_4, due to the combined action of the phosphate ion with the K^+ or Na^+ ions, while no effect was obtained with $(NH_4)_2HPO_4$, due to the opposite actions of the N and P. These effects were obtained with both moderately and highly susceptible varieties.

Chemical constitution of the soil: Minor elements and miscellaneous substances: — The data relating leaf rust severity to minor soil constituents are meagre and ill-assorted.

In connection with the work of GASSNER and HASSEBRAUK, reported above, these workers noted that KCl and to less extent NaCl increased rust resistance while MgCl and $CaCl_2$ were without effect. K_2SO_4 increased resistance, Na_2SO_4 less so, and Mg_2SO_4 not at all. After allowance is made in these cases for the action of the K ions, there is little indication in these tests that the chloride, sulphate, magnesium, calcium, and probably sodium ions have any substantial effect on rust response. Yet it is pertinent, in this connection, to recall the early prescriptions for rust control by applications of salt, and to call attention to NOZDRACHEV's (1936) recent experiments in Russia. This worker reported that applications of NaCl to wheat fields in the spring sharply reduced leaf rust infection, both in seedling and later stages, and this was accompanied by increased yields on some soils, although the salt applications were harmful on others.

GIGANTE (1935) has published the results of experiments in which rusted wheat plants have been tested for response to boron. Plants receiving from none to 14.8 mg. of sodium borate per 150 c.c. of soil showed type "4" infection, those receiving 29.6 mg., type "2-3", and those receiving 59 mg., type "3" infection. These differences are hardly great enough to carry much significance, especially in view of the very high dosages used (57 mg./150 c.c. of soil corresponds approximately to 128 lbs./acre, which

is far in excess of the amount of boron usually used to elicit plant responses), and field tests with *Puccinia triticina* were not conducted, although GIGANTE states that in the field boron applications of .5 to 5.0 gm. per sq. meter were followed by reduced intensity of *P. glumarum,* and increased yields, test weights, and seed vitality. Later HASSEBRAUK (1938) reported that in his experience boron applications sometimes strongly repressed leaf rust, but that its action was unpredictable because of environmental effects.

In the same paper, HASSEBRAUK reports the results of treating soil with 16 organic substances containing nitro-groups or sulphur. Complete rust control resulted in plants growing in soil treated with o- and p-toluolsulphonamide, but these were apt to cause some plant injury. This was not true of picric acid, which was moderately effective in rust control. The action of p-toluolsulphonamide was uniform on 25 wheat varieties. Addition of organic material to the soil reduced or eliminated the rust-toxicity of some of the most promising compounds. Carbolineum and other tar-oil products strongly repressed rust, but their action was unpredictable because of environmental effects.

The effect of lithium on wheat leaf rust has been studied by WORTLEY (1936) and KENT (1941). Both workers found the intensity of leaf rust somewhat decreased by lithium applications but only by amounts of lithium salts that were injurious to the wheat seedlings. It is very probable that in both these cases the effect of lithium was to impair the health of the host plant, with attendant loss in rust susceptibility.

SEMPIO (1936) observed the effects of a number of drugs and metals added to the soil, on wheat leaf rust and powdery mildew. Strychnine (.3/1000) and nickel (M/7500) markedly reduced rust infection, apparently as the result of a direct effect on the fungus. Caffeine, theobromine, and codeine were without effect. When plants were inoculated with both leaf rust and mildew, those with soil amendments of cadmium (M/7500) developed only abundant rust, while those treated with strychnine (.22/1000) developed only abundant mildew, showing the differential action of these two substances on the two diseases.

Effect on rust of modification of the soil composition by cultural practices: — GASSNER has cautioned that the results from greenhouse tests with pure nutrients in controlled environments cannot be applied directly to fertilization and cultural practices for rust control in the field, because these practices have independent effects in affecting yields and rust, and a benefit from fertilization, for example, in increasing vigor and yield capacity of the whole plant, might more than offset a simultaneous increase in rust. Also the clear-cut results obtained in greenhouse experiments, under controlled conditions, may not always be equalled by tests of fertilization and other cultural practices in the field where the availability of nutrients is modified by *p*H and other characteristics of the soil. Nevertheless, broadly speaking, we do find that fertilization and cultural practices that modify the soil composition do affect leaf rust development in a manner roughly comparable to that observed in more precise experiments.

With reference to the effect of previous cropping practices on subsequent leaf rust development, the literature is somewhat inconsistent, as might be expected considering the complexity of the effects of cropping practices

(selective removal of the different soil elements by different crops; different contributions to the soil by different crops; effect of the preceding crop in advancing or retarding wheat maturity; etc.).

Generally speaking, cropping practices that add nitrogen to the soil (use of legumes) have the same effect as nitrogen fertilization, *i.e.*, favor rust, while cropping in such a manner as to lower the nitrogen proportion has the opposite effect. We see good evidence of this in DOWSON's report (1921) from East Africa, where soils are normally quite rich in nitrogen. Here some measure of leaf rust control is attained by preceding wheat with a crop that is a heavy nitrogen feeder, as flax. According to BOLLEY (1889*a*), many farmers believe that wheat rusts badly after clover. SORAUER (1909) received reports that rust is most destructive in wheat following clover, and although he interpreted this in terms of moisture relations, it is more likely that the nitrogen-fixing property of the clover was responsible for the rust effect. STAKMAN and AAMODT (1924) observed a higher degree of infection in wheat following alfalfa than in that following clover or cabbage, although there is question as to the significance of this difference. RUSAKOV (1929*a*) advises avoidance of previous crops that delay maturity in wheat, but does not relate this to soil nutrients. Finally GASSNER (1915*c*) could observe no differences in the amount of rust in fields previously cropped in alfalfa, corn, barley, and wheat.

It is safe to say that continuous cropping of land with wheat has little direct effect on leaf rust development, but insofar as the vigor of the wheat plant is affected by continuous cropping, its response to rust will be altered.

Nutritional aspects of the pathogen: Teliospore production: — From the distribution of the teliospore stage and from such facts as the abundance of this stage in India during certain years (E. J. BUTLER and HAYMAN, 1906), although it is usually rare or absent, we can conclude that the appearance of telial sori is conditioned by the climate as it operates on the host plant. The facts indicate that the lack of teliospore production, where this is noted, is associated with a curtailment of the growing season, either by intense heat (Plains of India), by drought, or by a very short growing period, in the coldest climates in which wheat will grow. In favorable climates when the rust infestation develops late in the season, teliospores may form soon after infection.

In his early work with leaf rust, GASSNER (1915*b*) adopted MAGNUS' "exhaustion" (Erschöpfungs) theory of teliospore production. He pointed out that teliospore production regularly occurs shortly before heading, and that it does not occur in wheat varieties which, because of varietal characteristics, fail to head, even though heading varieties are producing teliospores at the same time. He regarded the production of teliospores as the result of depletion of food reserves in the leaves and leaf sheaths of the wheat plant, when such foodstuffs accumulate in the heads, incident to the filling of the grain. The first teliospore production on the uppermost leaves and leaf sheaths was interpreted as the result of their being closest to the head and hence first "exhausted." This same view was shared by RUSAKOV and SHITIKOVA in 1929.

In later years, as a result of his intensive study of the metabolism of rusted cereal plants, GASSNER abandoned the "exhaustion" theory, and

expressed a diametrically opposite point of view (GASSNER and FRANKE, 1938). We have seen that rusted wheat plants have a much higher proportion of nitrogen than comparable healthy plants (page 37). As the wheat plant approaches maturity and its rust infection advances in age and destructiveness, the nitrogen content of the plant becomes higher and higher, until a point is reached at which teliospore production begins. Thus, in two experiments the ratios of soluble nitrogen in healthy : rusted plants were 1.2 : 21.8 and 2.4 : 37.8 respectively. At the same time the ratios of water content were 90 : 25 and 93 : 27 in the same 2 cases. We see that not only has the nitrogen content greatly increased, but at the same time the abnormal loss of water in the rusted plants has concentrated this highly nitrogenous foodstuff so that the plant, instead of being "exhausted" contains, on the contrary, an extraordinarily rich supply of highly nitrogenous food material at the fungus' disposal; — then the rust mycelium ceases production of uredospores, and begins production of the teliospores, which, considering their structure and function, might well require richer nutrition for their formation.

The greater production of teliospores on the upper leaves is also explainable according to this view. The lower leaves are infected first, but at that time nitrogen accumulation has not reached a point high enough to allow teliospore formation. Later, when this high nitrogen level is reached, the lower leaves have passed the point at which rust activity is possible, hence teliospores develop principally or only on the upper leaves.

The hypothesis of GASSNER and FRANKE also explains teliospore production on moderately resistant varieties. According to these workers, as well as to RUSAKOV and POKROVSKI (1928), teliospores are formed in smaller amounts on resistant than on susceptible varieties, and GASSNER and FRANKE have shown that the nitrogen excess in rusted, as compared with healthy plants, is less in resistant than in susceptible wheat plants.

Seeding and stands: — Many workers have called attention to the relationships between date of planting and resultant rust. In general, these are in agreement that the most abundant rust in the fall develops on early-planted winter wheat, while with spring wheat, early plantings mature sooner than later plantings and hence tend to escape the most destructive rust. These observations are reflected in recommendations for the reduction of leaf rust losses by altering planting dates so that they are later in winter wheat areas, and earlier in spring wheat areas.

While late fall and early spring planting is a general rule for rust evasion, this rule must be qualified under some circumstances. In the fall, it sometimes happens that rust develops more strongly on wheat of middle or average date of planting, since early plantings are in poor condition due to heat or drought. In other cases repeated observations through the fall show that although the rust first develops intensely on the earlier planted wheat, later it becomes even more abundant on wheat of middle and late sowing dates.

When local leaf rust epiphytology is regularly characterized by a wave of severe infection at a given time of year, as in some spring wheat areas (BRIZGALOVA, 1935) or where conditions for wheat vegetation prevail the year around, with one season particularly marked by rust intensity, as in

Australia, early planting to enable wheat to escape the rust is particularly important. Because of the ready ability of the rust to spread from one field to another, early planted fields may prove dangerous sources of infection for nearby, later planted fields, which has led to stressing the importance of a common planting date for whole communities, and the avoidance of having early and late plantings close together.

The planting date of spring wheat is definitely correlated with the date of maturity, which, in turn, is one of the major factors in rust damage. Thus the spring planting date may play a major rôle in determining the loss from rust. On the contrary, there is very little relationship between earliness or lateness of fall planting and time of maturity of the crop the following spring. The importance of the fall planting date, from the standpoint of rust, is related principally to such rust damage as may occur in the fall and to overwintering of the wheat plant and the rust. Since there may be little correlation between the amount of rust in the fall and that the following spring (*see* page 171), it follows that the fall planting date has, for the most part, only a minor and indirect influence on the destructiveness of leaf rust during the danger period as the crop passes through the heading stage and approaches maturity.

Density of stand relates to leaf rust development in two principal ways. Dense stands provide conditions of humidity that favor the germination of uredospores and infection. Widely spaced stands avoid this danger but introduce another: wide spacing is associated with delayed maturity of the crop, and we have seen that this is a most important factor in increasing rust damage. Also in denser stands, rust-bearing lower leaves are killed by competition, which retards epiphytotic rust development. Recommendations of past years advising reduced planting rates as a feature in rust control were evidently based on theoretical grounds, and more recent studies have shown that the retarded maturity associated with thin stands is more dangerous, from the standpoint of leaf rust, than the conditions of humidity in more dense stands. GASSNER (1915*c*) found no difference in the amount of leaf rust developing in Uruguay in wheat sown at various rates from 30 to 160 kg./ha., but showed that the wheat had a tendency to regulate its stand to a uniform density, regardless of sowing rate, by producing more tillers on widely separated plants. However, even when he regulated stand density by hand thinning he still failed to note differences in rust intensity correlated with differences in stand density, and he attributed this to the uniformly favorable moisture conditions in Uruguay. On the other hand, SHITIKOVA-RUSAKOVA (1932*b*) in Russia (Amur) experimented with plant spacings of from 10 × 10 cm. to 30 × 40 cm., secured by hand thinning, and found that when the distance between plants was doubled, rust increased by 150% and when the spacing was tripled, the rust intensity was 800% of that in closer stands. RUSAKOV (1929*a*) made analogous observations.

These relationships are the general rule, but there are exceptions. For example, sparse stands of wheat may not occupy the ground sufficiently to control the weeds, and the resulting plant cover of wheat and weeds may behave, with reference to rust, as a dense wheat stand (RUSAKOV and SHITIKOVA, 1929). This is not uncommon with volunteer or self-sown stands. In cases where deficient moisture is a limiting factor in rust develop-

ment, the retention of moisture by a dense stand may outweigh in importance the later maturity of a thinner stand.

Optimal planting dates and rates, which, like other agricultural practices, have often evolved without recognition of the underlying factors, represent compromises or resultants of various yield factors, some beneficial, some harmful, which, on the average, result in the best yields. In this evolution of optimal planting dates and rates, rust damage is one, but only one factor. It follows that, in general, the date and rate indicated by experience as most favorable for high yields, will be likely to be followed by as much rust evasion as is compatible with other requirements of the developing crop.

It is a generally accepted principle that any factor which advances the maturity of the wheat crop favors evasion of leaf rust damage. Reference to FIG. 2 shows that when rust intensity has reached a point at which the average wheat plant has been defoliated, the loss from rust will be only 10.2% if the wheat is in the wax to dough stage, while it is nearly double that if the wheat is in the milk stage and more than triple if it is only blossoming. Not many days separate these consecutive stages, so that the importance of even a few days advance in maturity of the crop is clearly indicated.

We will see, in considering the recommendations for leaf rust control in Chapter XII, that much emphasis is laid on the use of early-maturing varieties and adoption of cultural practices that favor early maturity. This is also one of the reasons for the rust-stimulating effect of excess of N in the N:P:K ratio. In addition, other factors which favor early maturity of wheat are freedom from winter injury, lack of excessive moisture as the crop approaches maturity, vernalization of the seed, certain features of the topography, soils, and weather, certain types of crop rotations, methods of tillage, and other agronomic practices.

The influence of topography on wheat maturity and incidence of rust, is illustrated by observations of SHITIKOVA-RUSAKOVA (1928) who has made a detailed analysis of the differences in two experimental fields of the Stavropol Agricultural Experiment Station. On one, which is 150 m. higher than the other, the wheat crop is regularly 1-2 weeks later in maturing and regularly suffers more from leaf rust, in comparison with the lower field.

In Russia, vernalization of wheat seed is recommended in connection with wheat leaf rust control since the practice usually accelerates maturity of the crop by 1-5 days. This, in turn, is associated with reduction in damage from leaf rust, as shown, for example, in tests in Odessa in 1932 (NAUMOV, 1939) in which wheat from vernalized seed showed 78% leaf rust as compared with 98% rust in wheat from untreated seed, under otherwise comparable conditions. STEFANOVSKII (1937), however, has shown that this effect differs with the wheat variety and time of sowing and that with early-sown wheat, that from vernalized seed may actually become more heavily rusted.

Other plant hazards in relation to rust: — In 1934, MAINS and JOHNSTON independently reported that the presence of powdery mildew (*Erysiphe graminis*) causes the development of leaf rust pustules of a highly

susceptible type in wheats normally showing resistance to the races of leaf rust in question. The effect is limited to the chlorotic zones surrounding the mildew pustules and containing mildew mycelium. The same phenomenon was later observed by ROBERTS (1936) and K. D. BUTLER (1940*b*). MAINS' view was that "apparently the cells of the host invaded by the mildew were more favorable for the development of the mycelia of the rust than uninfected cells," while JOHNSTON considered it probable "that the mildew fungus splits some complex compounds which the fungus is unable to use into simpler compounds upon which it is able to subsist."

There seems to be no other clear-cut record of a distinct wheat disease favoring leaf rust development. CÂLNICEANU (1934) reported that infection of wheat seedlings with bunt (*Ustilago* sp.) did not alter their subsequent reaction to leaf rust, and that infection of the plants with one race of leaf rust had no effect on their later infection with another leaf rust race. This report conflicts with a later one of PARKER-RHODES (1939) in which he states that plants that are resistant to leaf rust lose this resistance when infected with bunt. In 1906 BOLLEY and PRITCHARD had recommended bunt control as a rust-preventive measure, since the smut was considered to favor rust by retarding plant development.

There are at least 3 ways in which other wheat diseases might interfere with leaf rust development: by devitalizing the plant so that it shows increased leaf rust resistance, by first occupying tissues that might otherwise be available to the leaf rust, or by destroying tissues harboring the leaf rust. Examples of each of these can be cited.

An example of the first type is seen in wheat plants attacked by foot rot (*Helminthosporium sativum*). In this case the writer has observed a greater degree of leaf rust resistance in such weakened plants than in nearby specimens not suffering from root rot.

With reference to the second type of antagonism, when wheat leaves are first attacked by stem rust, stripe rust, or *Septoria tritici*, the leaf rust fungus is unable to invade the tissues first occupied by these other pathogens.

The behavior of *Fusarium nivale* and *Septoria tritici* represents the third type of antagonism in which leaf-rust-infected leaves are destroyed, and with them the rust. In Europe, *F. nivale*, the snow mold of cereals, develops under the snow cover, destroying the rusted leaves of overwintering wheat. *Septoria tritici* is regularly active from late fall till early spring and sometimes this activity continues until heading stage of wheat. The writer has described (1944*b*) the race between this fungus and the leaf rust in early spring, the latter being, at times, barely able to multiply fast enough to replace infections wiped out by the rapidly advancing *Septoria*. Later in the spring, when abundant foliage is available to both fungi, *Septoria* sometimes destroys the lower leaves while the leaf rust attacks the upper ones, thus much intensifying the loss attributable to either fungus by itself.

Wheat insects may either favor or be antagonistic to leaf rust. Leaf-feeding insects, such as grasshoppers and army worms, destroy rust-bearing wheat foliage, reducing leaf rust inoculum and infection courts. Another group of insects, including chinch bugs, green bugs, cut worms, brown mites, white grubs, wireworms, false wireworms, and the Hessian fly, destroy wheat seedlings in the early stages of their development. This has the

principal effect of thinning the stand, which, as we have seen above, results in delayed maturity of the crop, attended by increased leaf rust damage. The reverse effect, intensification of insect damage as a result of the presence of leaf rust, is desscribed on page 27. SORAUER (1909) has suggested that insects may also favor rust by stimulating the development of an excessive number of late-formed tillers, on which the rust flourishes.

Wind-blown sand by covering or cutting to pieces young wheat plants, reduces stands, and thus delays the crop, and results in a greater or less degree of lodging, and lodged wheat has been shown to be a particularly favorable location for leaf rust multiplication. The same effect follows from other causes inducing lodging, *e.g.,* insufficient light, excessive nitrogen in the soil, excessive moisture, flooding, frost injury, attacks of insects or diseases at the culm bases, and inherent lack of adequate mechanical strength in the culms. Drought, in addition to its direct effect in retarding multiplication of the rust fungus, has the secondary effect of reducing the vitality of the wheat plants, and with this, their susceptibility to leaf rust; flooding may have the same result.

Hibernation of the rust in the uredinial stage: — It is a well established fact that throughout the greater part of the winter wheat areas of North America, wheat leaf rust is able to overwinter in the uredinial stage in the wheat plant. Such overwintering is usual in the southern half of the wheat belt and not uncommon in the northern part.

BOLLEY (1889*a, b*) in Indiana was the first to prove this mode of overwintering when he demonstrated dormant mycelium of the rust in dormant wheat plants, microscopically. In 1905 he mentions having found *P. triticina* freely overwintering in Minnesota and N. Dakota, as well as in Illinois, Texas, and Mississippi. BOLLEY's findings were followed in 1893-1899 by those of HITCHCOCK and CARLETON who concluded that the rust normally overwinters in the mycelial stage in North America south of the 40th parallel (which separates Kansas from Nebraska and bisects Illinois, Indiana, and Ohio).

That wheat leaf rust actually may overwinter far to the north of this parallel, in accordance with BOLLEY's views, was indicated by CHRISTMAN in 1904 and FREEMAN and JOHNSON in 1911. CHRISTMAN, in Wisconsin, found viable uredospores in exposed places after the temperature had fallen to —14° F. Such collections were made in November, January, February, and March. Some of the spores collected were presumably at least 67 days old. FREEMAN and JOHNSON, after finding viable uredospores under snow and ice in November, December, and January stated: "It is a fact easily observed in almost any wheat area of the United States, at least as far north as St. Paul, Minn., and Fargo, N. D., that the uredostage exists through the winter months in the severest winters, and the rust may thus live independent of an aecidial host."

Again, far north of the 40th parallel, K. D. BUTLER (1940*b*) proved that the rust overwinters in Ithaca, New York, both by mycelium (shown by bringing plants indoors in midwinter and demonstrating pustule production), and by uredospores (which he collected in a viable state in March, before the snow had melted). Furthermore, SCHAAL (1925), who worked in Minnesota, reports the disease overwintering as far north as the Canadian

border, while SANFORD, in the "Annual Summary of Plant Diseases in Canada" for 1930 found secondary infections on April 10 in Alberta, which he interpreted as indicating overwintering of the rust that far north.

Likewise the overwintering of wheat leaf rust in the manner indicated has long been recognized abroad. BOLLEY's pioneer work in North America was antedated by NIELSEN (1875, cited by CHRISTMAN) who concluded that in Denmark the rust passes the winter as mycelium in green leaves, retaining its vitality as long as the leaves are green; SORAUER in Germany made similar observations.

Since these early reports, many workers abroad have observed or demonstrated the hibernation of wheat leaf rust in the uredinial stage actively vegetating, as dormant mycelium, or, with apparently greater difficulty, as hibernating uredospores. Thus, in England, Germany, Holland, France, Rumania, Sicily, Austria, Italy, and Belgium, viable uredospores have been found in wheat fields throughout the winter. Overwintering as dormant mycelium has been shown to occur in Germany, Austria, Rumania, Poland, and France. Usually this was demonstrated by the prompt production of uredinia on dormant wheat plants brought into the greenhouse in winter.

Uredinial overwintering as hibernating mycelium or as spores, protected by snow cover, has been observed in many parts of Russia. Only in Amur government and in certain other parts of eastern Siberia where spring wheat prevails, and where there is not always a protective snow cover, is overwintering in the uredinial stage usually absent. Here, although there may be rather rare hibernation by uredospores formed the previous season, the principal sources of spring infection are the alternate host, *Isopyrum fumarioides* (in Za-Baikal region), and wind-borne spores from the South (Amur region).

In Australia and in the La Plata area of Argentina and Uruguay, even south of the 35th parallel, the rust may be found actively vegetating and producing uredospores the year around.

Many years ago, BARCLAY (1892) expressed the hypothesis that leaf rust overwinters in India as perennial mycelium in the roots of grasses. This has not been confirmed, with reference, at least, to the leaf rust of wheat, in which grass hosts have little rôle. More recently MEHTA (1929, 1931*a*, *b*, 1934) has conclusively shown that *Puccinia triticina* survives the winter in India as hibernating mycelium in winter wheat but at lower altitudes only (*e.g.*, Almora, 5400 ft.; Simla, 7000 ft.; and poorly at Muktesar, 7600 ft.).

In summary, with few exceptions, ARTHUR appears to be justified in his statement (1929) that wheat leaf rust overwinters in the uredinial stage throughout its range.

Winter temperature, in itself, is less a factor in this mode of overwintering than concomitant factors such as depth and constancy of snow cover, relief, winter survival of the host plant, and amount of rust present the preceding fall.

The snow cover is outstanding among these factors. Indeed it frequently is the case that leaf rust can overwinter better at points where there is a heavy and continuous snow cover than at points farther south (in the northern hemisphere) where the snow cover disappears, from time to time, during the winter. We have seen that at temperatures near 0° C., leaf rust

uredospores will retain their viability for many months. Under a deep snow cover that overlies frozen soil are conditions not unlike those of refrigerator storage. We have no exact data on the temperature requirements of dormant mycelium, but there is indication that any low temperatures that can be withstood by the dormant wheat plant can be endured by the leaf rust mycelium within it, and the favorable condition for winter wheat survival under a continuous, deep blanket of snow, is well known. In Russia, particularly, it has been frequently observed that overwintering of the rust occurs, even when the temperature drops to —50° C., provided the snow cover is deep and continuous, while if the winter is open, and the snow cover does not persist throughout the winter, both wheat plant and rust are destroyed by temperatures well above this. Hence leaf rust would be expected to overwinter successfully under two contrasting climatic conditions: (*a*) in warmer latitudes, where winter temperatures are not low enough that a snow cover is needed to assure survival of the crop and its rust, and (*b*) in cold but fairly humid regions where the snow cover is deep and persists throughout the winter; in such regions mild winter weather may be detrimental rather than beneficial to rust survival. Between these two zones, or in dry areas such as western Kansas and Nebraska or Amur Province in Russia, where there is no benefit of continuous snow cover, even moderately low temperatures can prevent the hibernation of the rust in the unprotected wheat plant.

But the depth and persistence of the snow cover are determined not only by climate but by features of the macro- and micro- relief and by windbreaks. The relation of these to rust hibernation has been considered particularly by Rusakov and Shitikova (1928, 1929), who found that there was no overwintering of the rust on exposed steppes, while near forest edges, at the edges of fields, and near windbreaks of corn- or sunflower-stalks, the snow was persistent, and the rust overwintered. Overwintering was favored on gently sloping hillsides, protected from the prevailing winds, where snow accumulates and persists, and to such an important extent in slight soil depressions, as cattle hoof-tracks, that the grazing of wheat in the fall by cattle was regarded as a dangerous practice.

It must be borne in mind that the conditions permitting hibernation by uredospores are even more exacting than those allowing mycelial survival. A single warm, moist period in midwinter may permit the overwintering spores to germinate. If this period is of sufficient duration to allow infection to occur, not only survival but increase of the rust results, whereas if the period is too short (as is likely at relatively low temperatures) the germinated spores will die without effecting invasion of the wheat plant, and are thus eliminated as means of hibernation.

Any other factors which interfere with the survival of the wheat plant, or those of its leaves that are rust-infected in the fall, will, in turn, determine the extent to which the rust survives as hibernating mycelium. The winter-survival of wheat is determined by many factors: variety, soil, rate and date of planting, relief and exposure, etc. Each of these is indirectly correlated with rust survival. Thus, if the crop is heavily fertilized with nitrogen, it is more susceptible to the rust, but, in turn, the succulent growth resulting is particularly liable to winter-killing, and hence does not favor hibernation of rust mycelium. Very mild late fall weather followed suddenly

by a sharp drop in temperature has a similar effect in destroying the non-"hardened" wheat leaves. The Russian workers (NAUMOV, 1939; RUSAKOV and SHITIKOVA, 1929; SHITIKOVA-RUSAKOVA, 1928) have observed the best overwintering of rust on well-fertilized land, in dense stands, sometimes in early plantings and at other times in late ones, depending on the season, and in varieties which lose their leaves least readily in winter, such as Ferrugineum 117 and Cooperatorka.

Ordinarily the rust mycelium has been found to overwinter on the 2nd to 4th youngest leaves (NAUMOV, 1939). If these are killed back, the mycelium may still be found in their bases (BOLLEY, 1889*b*) or, given favorable periods for multiplication in the winter, it may pass to the newly formed leaves. This last is particularly important when, as commonly occurs in the southern Great Plains, throughout the late fall, winter, and early spring the older leaves are progressively destroyed by *Septoria tritici* (CHESTER, 1944).

There are many notes in the literature associating severe rust in the spring with mild winters which permit abundant overwintering of the rust, and the converse, unseasonably cold winters resulting in low levels of rust during the growing season. It must be borne in mind, however, that this is only one, and a relatively minor one of the factors conditioning the amount of rust in spring and early summer. Because of the enormous capacity for reproduction in *Puccinia triticina,* given favorable weather in early spring, the number of plants with overwintered rust need not be great in order to initiate widespread rust development. GASSNER and PIESCHEL (1934), for example, have shown that a single rusted plant (stripe rust in this case) served to infect 10,000 plants in 10 weeks. And in addition the rust is not solely dependent on local hibernation for spring renewal, which can also be due to air-borne inoculum blown in from distant points.

Aestivation of the rust in the uredinial stage: — Although *Puccinia triticina* hibernates successfully throughout most of its range, its oversummering is often more difficult, particularly in regions with long, hot, dry summers. We need consider only winter wheat areas, since in spring wheat regions aestivation is in an active stage on the developing wheat crop.

In the northern part of the North American wheat belt, oversummering of leaf rust regularly occurs, on volunteer wheat or in spring wheat fields. Farther south its oversummering is irregular. For example, workers in Kansas and Indiana report oversummering of the rust during some years but not in others. Failure to oversummer may be associated with the absence of volunteer grain. Oversummering on volunteer grain is also reported from Kentucky (VALLEAU, 1923) and, with difficulty and only at higher altitudes, in Texas (FREEMAN and JOHNSON, 1911). The writer's observations and those of BROWN (1938) indicate that in Oklahoma aestivation of the rust is unusual, as volunteer wheat cannot ordinarily be found in the long, dry, and very hot summers in that State. HITCHCOCK and CARLETON'S generalization (1894) that the rust oversummers in the active state throughout the United States clearly needs qualification.

In Europe, the rust is reported to aestivate in an active, vegetative state in Austria, Poland, Sicily, Italy, Rumania, and England. It is active the year around in Australia. In India, it cannot survive the summers in the

plains, where the temperature reaches 110° F. in the shade for several weeks, but there it aestivates in the hills at altitudes of 3500 ft. to 5400 ft.

Saprogenesis of the teliospores: — Some confusion resulted, with reference to saprogenesis of wheat leaf rust teliospores, in the early years of rust study, as a result of failure to discriminate between the leaf rusts of wheat and rye, but in 1899 ERIKSSON made it clear that the teliospores of the wheat leaf rust, in contrast with those of the rye leaf rust, require a rest period (winter) before they will germinate. This has since been confirmed by numerous workers.

Apparently, overwintering, in itself, is not necessary, but it is evidently true that a rather long rest period is required and also that teliospore maturation is aided by subjecting the spores to such shocks as result from alternate freezing and thawing or wetting and drying (BRIZGALOVA, 1935; MEHTA, 1940).

Exceptions to the general rule that overwintering is necessary before the teliospores will germinate are apparently explainable by the climates in regions where such exceptions have been noted, and by a certain degree of variation, in respect to this requirement, in the spores themselves.

MAINS (1924) succeeded in germinating leaf rust teliospores on December 10, but this was several months after they had been formed and in nature they would have been subjected to repeated alternative wetting and drying, and to at least a month of fluctuating winter temperatures.

BRIZGALOVA (1935, 1937*a*) found that some spores formed in Siberia in the spring would germinate the following fall. This is an indication of variation in this property in the spores themselves. It agrees with ARTHUR'S statement (1929) that in some species of rusts all the teliospores are developed as resting spores, but in others (*"e.g., Puccinia triticina"*) only part of them. The writer has made analogous observations. Oversummered teliospores collected in Oklahoma late in October, when examined, showed that a considerable number of the cells had germinated at some time between their formation and the date of their collection. This was indicated by empty cells, sometimes proximal and sometimes distal, with well-marked holes in the cell walls through which the promycelia had emerged. These were evidently the teliospores which, according to ARTHUR, do not require long rest periods. But those normal-appearing spores which had not germinated by late October could not be germinated in the laboratory even after freezing and subjecting them to different germination temperatures, *i.e.*, these evidently required further maturation.

BRIZGALOVA observed summer germination of teliospores that was subject to quite a different explanation: they were spores that had been formed a year before and had remained in the resting stage, in nature under Siberian conditions, from one July till the next. Fall germination of teliospores in Siberia is associated, according to BRIZGALOVA, with fall rains, alternating with sunny days, and temperatures that may compare with winter temperatures in warmer climates. But if the spores are not subjected to this alternate wetting and drying in the fall the maturation process is not accomplished in the winter (since the spores are protected from alternate freezing and thawing or wetting and drying under a deep snow cover), and this becomes completed only after further exposure to alternate wetting and drying in

late spring or early summer. These exceptional features of teliospore germination in Siberia have epiphytological importance, because they determine whether or not the alternate host, *Isopyrum fumarioides,* can become infected in the fall (the rust overwintering as aecial mycelium) or the time at which this host can become infected in the spring.

D'OLIVEIRA, in Portugal (1940*b*) reports good germination of teliospores, collected the preceding summer, in October. It is difficult to evaluate this report in view of the limited data and the unusual character of the observations in this and other respects (*see* page 66). It is known that teliospores of *Puccinia triticina* will withstand heating to 65° C. without loss of viability (SHITIKOVA-RUSAKOVA, 1932*a*), and it is not impossible (although there is no evidence on this point) that in Portugal a long period between crops in the summer and high summer temperatures might result in maturation of the spores, comparable to that resulting from overwintering.

Hibernation of the rust as aecial mycelium: — The practical significance of this possibility is limited to eastern Siberia, the only region in which the alternate host of *Puccinia triticina* functions in the annual cycle of the rust. In the preceding subsection it was noted that in eastern Siberia leaf rust teliospores sometimes germinate in the fall and this leads to fall infection of the host *Isopyrum fumarioides.* This is followed by a deep snow cover which persists all winter. BRIZGALOVA (1937*a*) observed that on the melting of the snow the aecia formed in the fall were on tiny dead spots on the leaves, but surrounding each was green tissue in which circles of pycnia promptly developed about the old aecia. The general appearance of aecia from new, spring infections did not occur until 10 days later, and these were on new leaves, which had not overwintered, and from these facts and the position of the pycnia, surrounding the old aecia, BRIZGALOVA concluded that the pycnia had developed on overwintered aecial mycelium.

Hibernation or aestivation of the rust with seed: — The scientifically and practically important question of whether cereal rusts can be carried from one crop to the next on or in cereal seed, received much attention from the early workers in this field. Three hypotheses have been advanced in support of the view that such seed transmission is possible. Two of these, ERIKSSON'S "mycoplasm" theory and PRITCHARD'S "seed-infection" hypothesis have historical interest only, and will not be discussed. LEVINE (1919) has given us a good summary of the status of these hypotheses and of the evidence on which their rejection is based. The third hypothesis, dealing with the possibility of race transmission of wheat leaf rust by uredospores adhering to the wheat seed coat, deserves more attention.

We have seen that seed from a heavily rusted wheat crop may be coated with so many thousands of uredospores that the seed has an obvious orange color, and we know that these spores are relatively long-lived if protected from heat. What is the possibility that rarely, under very exceptional conditions, one of these spores does succeed in infecting a plant of the new crop? One infection could suffice to introduce the rust to a new area.

As NAUMOV (1939) points out, the odds are greatly against this happening. The plant tissues with which the spores would have greatest opportunity to be in contact, coleoptiles, roots, etc., are not susceptible to rust.

The interval of time before susceptible green tissues are available is long enough so that the majority of spores, under most conditions, would die, and this would be particularly true of spores in the soil, exposed to enough moisture to permit the wheat seed to germinate. Furthermore the position of spores adhering to the seed in the soil, and of the only susceptible tissues aboveground would be a great mechanical impediment to successful infection of the leaves by these spores. Even with smuts of the seedling-infection type, where the coleoptile is susceptible to the fungus, only one spore in tens of thousands succeeds in producing infection; seed heavily infested with smut ordinarily produces a relatively small percentage of smut in the field, and that only under favorable environmental conditions.

Yet, rare as is the possibility that a uredospore can remain viable until the seedling leaves are formed, and then by remotely possible accident be placed on such a leaf and under conditions suitable to infection, this possibility cannot be considered excluded, and there is some indication that this may have occurred in the past. If volunteer wheat is present at planting time, spores could very conceivably become separated from seed grain, and drifting onto the volunteer wheat produce initial infections.

When GASSNER went to South America in 1907-1910 there was much evidence that *Puccinia glumarum, P. dispersa,* and *P. anomala* were not present there. *P. dispersa* was introduced about 1913, evidently on rye seed from France. *P. glumarum* was evidently introduced between 1919 and 1928 and this may also have been associated with importation of seed, as suggested by HUMPHREY and CROMWELL (1930).

As NAUMOV points out, this theoretical possibility of intercontinental transfer of rust becomes more likely when we consider the many years of grain commerce between the continents, the millions of introduced seed that have been planted, and the fact that a single successful spore, in a favorable environment, would suffice to establish the disease in its new home.

Studying, analyzing, and expressing combined environmental factors: — GASSNER (1915*c*) has emphasized the necessity of considering the "law of the minimum" in interpreting rust epiphytology. According to this law, the effect of varying a factor is seen only when the factor is present in a quantity or intensity below the minimum for normal response. For example, if moisture adequate to rust spore germination is constantly present, variations in this moisture level will have little effect on the rust. If the soil is well supplied with nitrogen, further addition of nitrogen may have no effect. As an analogy, if a beam balance is heavily overloaded on one side, the addition or subtraction of considerable weight on this side will not cause the balance to tip.

The law of the minimum is important to us in two ways. It often explains why one investigator, working with a variable below its threshold for normal response, finds a correlation between the variable and rust development, while another, working in a range above the minimum, observes no such correlation. Secondly, in studying the effect of a variable, all variables except the one under study should be above the minimal threshold.

STAKMAN, with reference to stem rust, and others, working with leaf rust, have emphasized that in studying the effects of environmental variables on rust, it is best to use varieties that are neither highly resistant nor highly

susceptible, but intermediate in their rust response. This, in a sense, is another aspect of the law of the minimum. It is well illustrated in FIG. 8, from the work of GASSNER and FRANKE (1934*a*), which shows the rust response of a susceptible, an intermediate, and a resistant variety of wheat

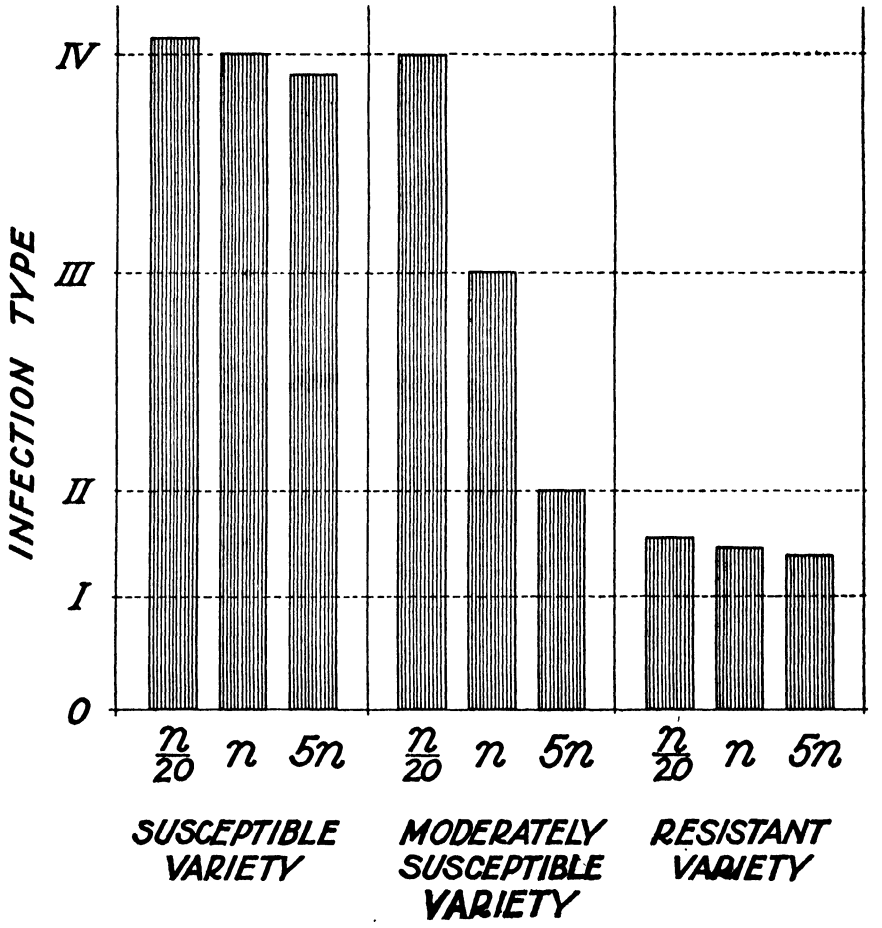

FIGURE 8. — Change in leaf rust resistance of various susceptible wheat varieties in relation to potassium nutrition (KCl). (*After* GASSNER and HASSEBRAUK in GASSNER and FRANKE, 1934*a*).

to three levels of potassium nutrition. The susceptible and resistant varieties hardly alter their reaction types when K is varied from .05 to 5.0 normal, while the wheat that was intermediate in reaction changes from reaction type "4" to type "2" with increase of K.

A third principle in interpreting environment as related to rust development concerns the temperature, moisture, air currents, and light in the zone of the plant cover, among the plants themselves, as compared with those recorded by standard weather instruments, in an enclosure 6 feet above the soil and plants.

This subject has been studied in particular by RUSAKOV (1922, 1924),

who also cites relative data from KLAUSS, SCHUBERT, LUBOSLAVSKI, RUDOVITZ, VANGENHEIM, and SIRIUSOV, whose tests have shown clearly not only that very considerable differences exist in the weather at the two zones in question, but even at different levels from the base to the top of the wheat plant, and that these differences alter in amount and character at different times of the day and night, and in different seasons. These differences have been found to be as great as 10° C. and 15% relative humidity or even more. The features of the plant cover which are associated with these differences include: proximity to soil which accumulates heat from the sun during the day and releases it at night and which is a source of humidity, obstruction of air currents so that humidity is not readily dissipated, increase in humidity as a result of transpiration, decrease of light with increasing distance down into the plant cover, and lowering of temperature through evaporation of condensed moisture. The denser the vegetative cover, in general, the more pronounced are these differences; in thin stands, and especially with decreasing distance from the Equator, where the sun's rays are more vertical, there is greater penetration of the plant cover by the sun. With increasing departure from the vertical direction of the sun's rays, the stratum of the plant zone which is directly warmed by sunlight is nearer the tops of the plants.

There may be many nights during which the air is saturated (and hence favorable to spore germination) in the plant cover near the soil, while the instrument box records humidities well below saturation. The night humidity is progressively less at higher points in the plant cover, but even 60 cm. from the soil, halfway up the headed wheat plant, the air may remain saturated from midnight to 7:00 A.M. when the air outside the plant cover is drier, and these 7 hours can suffice for spore germination and infection. Dew forms more heavily on the upper and middle leaves than at the bases of plants, except in dry seasons, and as the rust spores are often intercepted by leaves before they fall to the lower parts of the plant cover, conditions in the upper and especially the middle parts of the plant zone are more favorable for rust infection than at the base of the plant, where daytime absorption of heat by the soil results in a relatively lower humidity in the early hours of the night. Because of those conditions in the plant cover, in some seasons the disease may begin in the lowest leaves and gradually progress up the plant, while in other seasons it may appear to skip certain ranks of leaves and develop most intensively on the uppermost ones.

These differences between the "microclimate" in the plant cover and that recorded by the standard weather instrument box have two important applications in connection with rust epiphytology. First, they lead us to regard with caution conclusions based on instrument box weather records. It is quite certain, for example, that saturated air and temperatures conducive to rust infection often occur at wheat leaf surfaces, when, judging by the standard weather instruments, infection could not take place. Secondly, in future critical studies of rust epiphytology it is clearly desirable to record the weather *in the plant zone* and base correlations with rust development on these records, rather than those of the standard instrument box. Even such a simple procedure as the daily recording of dew in the plant zone may give information more directly related to rust development than that obtained from the standard weather box.

Averages, summations, and daily fluctuations of weather: — It is common practice to attempt to correlate rust development with monthly averages of temperature and monthly rainfall totals. In Europe this is often somewhat refined by using the corresponding values for each 10-day period ("decade") of the month. In some cases the comparison is made with the total of "degree-hours" for an extended part of the growing season. The point to be considered here is whether these procedures are adequate, or whether the daily temperature ranges and precipitation records must be analyzed in order to interpret rust phenomena.

At the one extreme we have attempts to correlate rust development with *annual* mean temperatures and total rainfall, a feature in TEHON's (1927) analysis of rust epiphytology, and at the other extreme RUSAKOV's (1922) contention that one must deal individually with 5-day or even 24-hour periods at times when the weather is critical for the disease.

RUSAKOV feels that the interpretation of rust development cannot be based on monthly rainfall or temperature averages or totals, beyond a limited extent, because short-time fluctuations of the weather may have an important bearing on rust development and their summation or averaging obscures this. In preceding sections we have had illustrations of the rust-favoring effects of short-time alternations of temperature and moisture. For example, spore germination and wheat infection proceed best at 20° C., while the incubation period is shortest at 25° C., and although infection is favored by calm and saturated air, uredospore detachment and dissemination best proceed in dry, windy weather, so that a frequent alternation of these conditions is most favorable of all. Or we may consider the effects of a light rain at different times of the day or night. If it is a morning shower, it may soon evaporate, and the rust has no opportunity for multiplication, while if it comes in the evening, the moisture may persist through the night, and infection can occur. Such effects are overlooked in dealing with averages.

If we now pass from daily or monthly weather averages to annual ones, it usually becomes more difficult to relate rust development to the weather record. Wheat and its leaf rust occur in coastal regions where the climate is uniform the year round, in continental regions where periods of torrential rainfall may be succeeded by severe droughts, without regularity, and in regions where well marked rainy seasons, alternating with equally well marked dry periods, are regular features of the climate. It might easily be shown that regions of these 3 types could have the same annual total rainfall, but its effect on the development of rust throughout the wheat growing season would vary enormously according to the day-by-day and month-by-month distribution of rainfall in each case. In the same way, two regions may have the same average annual temperature, but in one case it is a fairly constant temperature the year round, while in the other it is the mean of extremely hot summers and cold winters.

Wheat leaf rust is severe in the regions of Benares, India, and Kharkov, Russia, but the climates of the two differ enormously. Benares has an annual rainfall of nearly 40 inches for the year, while Kharkov has less than 20. The temperature extremes in Benares are 120° and 30° F. (mean of these, 75° F.) while Kharkov has extremes of 99° and —34° (mean, 31° F.). The annual mean temperatures would be quite useless in interpreting rust epiphytology in these two regions. So far as rainfall is con-

cerned, Benares, with 39.54″ annually has only slightly more than Uruguay, but in Benares this is received in mean amounts varying from .19″ to 11.72″ in the different months, while the mean monthly extremes in Uruguay are 2.46″ and 4.62″. Thus rust in wheat can perpetuate the year round in Uruguay while in the Indian Plains a season of wheat growth and rust alternates with one in which neither can survive. It is thus clear that the most diverse annual means and totals can obscure comparable periods in the year, during which the rust can flourish, while similar annual means and totals can be associated with gross seasonal differences. Although these annual means and totals might have some limited value in comparing one rust year with another in a given location, they may have very little meaning in comparing rust development in one area with that in another.

Furthermore, if we avoid the difficulties associated with comparing annual meteorological records in regions with quite different climates, by comparing successive years in a single region, we encounter the problem of uneven monthly distribution of temperature and rainfall in any two years. A year with a mild winter and cool summer might have the same annual mean temperature as one with a colder winter and hotter summer, yet the effects on rust development would be quite different in the two cases. The same can be said for comparison of two years with equal annual total rainfall, one of which had a dry spring and wet fall, and the other, the reverse.

The use of annual means and totals assumes that the weather in each month of the year is of equal importance in rust development. This is far from the case. Fall weather and the amount of rust in the fall have little influence on spring rust development (*see* page 171), and each year contains a number of months between growing seasons in which the weather is either unrelated to rust or has effects quite at variance with those in the growing season. For example, either a hot summer or a warm spring would raise the annual mean temperature, but in the first case the higher temperature would be injurious to aestivating rust while in the second, it would favor its spring development.

It has been pointed out that summation of rainfall over extended periods gives a misleading picture of the effects of rainfall on rust, because of failure to consider the distribution of the rainfall in time. The same can be said for summation of temperature in degree-hours. Furthermore, we have already seen that a number of the activities of the leaf rust fungus have optimal temperatures, and that either above or below these optima, such activities decrease. Although 20 hours of activity at a suboptimal temperature might have the same result as 10 hours of activity at the optimal temperature, 5 hours at a corresponding supraoptimal temperature (which would have the same importance in summating degree-hours) would produce quite a contrary effect. Thus, NAUMOVA's conclusion (1935) that summated degree-hours had no correlation with length of the incubation period of *Puccinia triticina* might be expected to apply to activities of the leaf rust fungus in general.

What, then, are we to conclude as to the best method of treating weather records in relation to rust? RUSAKOV's day-by-day, or even hour-by-hour correlation is unquestionably the most accurate and revealing, but it yields data that are too detailed to be condensed without difficulty into a form

suitable for comparing seasons or regions. At the other extreme, we can see that annual averages, while simple to manipulate, are wholly misleading, because with their use, even the gross details of weather, in relation to rust are lost.

Admitting the inadequacy of our present methods of analyzing weather in relation to rust, it appears to the writer that we can best follow the course of using the detailed methods of RUSAKOV (correlation of the weather in the plant zone, throughout 24-hour periods, with rust development) in studying the finer details of rust activity in nature, and correlating these with the results of laboratory and greenhouse tests under controlled conditions, following the practices of KEITT and his co-workers, in studying the course of rust development during periods of a few months, and using monthly, or preferably 10-day averages, with maxima and minima indicated, for correlating rust development with weather in comparing one season or locality with another.

The "critical month": — In three articles in the "Plant Disease Reporter" (1942*a*, 1943, 1944*b*) the writer has developed the thesis that the intensity of development of wheat leaf rust on winter wheat in the spring is determined primarily by the temperature and precipitation during the early spring month in which the mean temperature is close to 50° F. (March in Oklahoma, April in Illinois and Iowa, April 15-May 15 in New York). The reader is referred to these publications for a detailed discussion of this thesis and the evidence on which it is based. As operating in Oklahoma, it can be summarized as follows.

There is little correlation between the amount of rust in the fall and that of the following spring (*see* page 171). Our starting point is midwinter, in which there is regularly some leaf rust overwintering in the mycelial stage, and reproducing during occasional mild, moist winter periods. By late winter this rust concentration is normally quite low. Not more than one rust pustule per 3000 wheat leaves may be present.

There is no considerable leaf rust reproduction at temperatures below 50° F. (due to poor germination of uredospores and long periods required for infection and incubation). Above this "critical temperature" the rust multiplies readily, and the difference between favorable and unfavorable temperatures is a matter of only a few degrees.

For an increase of the rust from the low late-winter level to epiphytotic proportions, the rust must reproduce itself about thirty millionfold (from .0003 to 1000 pustules/leaf with a 10-fold increase in leaf tissue). The great number of spores produced in each rust pustule is offset by the failure of the majority of these to produce infection, hence this colossal increase in rust intensity requires a number of consecutive uredinial generations each consuming about 10 days. The first generations, that increase the rust intensity from one pustule per 3000 leaves to one per leaf, are ordinarily unobserved, but they are as necessary for epiphytotic rust development as the obvious generations that raise the rust population from one pustule per leaf to one thousand. Moreover, the essential early generations must occur at a time when temperatures hover near and often dip below the threshold that will permit significant rust reproduction (50° F.). Therefore the temperature, and necessarily associated moisture conditions, of the first

month after winter in which the temperatures approximate 50° F. are most vital of all to the future development of the fungus, and the month concerned is the "critical month" in determining the extent of the epiphytotic to follow. To a less important extent, winter temperatures are also involved, since they affect the concentration of rust present, whether 1 pustule per 100, 1000, or 10,000 leaves, at the beginning of the "critical month."

Once this "critical month" is passed, the weather for the remainder of the growing season is poorly correlated with rust development, since, even with marked departures from normal, it is still within the range favoring rust multiplication, and these later months also usually have adequate rainfall for rust even when the rainfall is below normal. For Oklahoma, where March is the "critical month," rust epiphytotics have occurred regardless of whether April, May, and June were relatively wet or dry, warm or cool,—the essential requirement is that March temperatures and precipitation be normal or above normal. An analogous situation exists in Illinois, Iowa, and New York.

A number of unsuccessful attempts have been made to correlate the weather of the months after the "critical month" with rust development. This is not unexpected since these later months are those in which the rust actually becomes noticeable; the error is due to overlooking the fact that weather during these later months is regularly in a favorable range for the rust, regardless of seasonal variations, while the vitally important early uredinial generations must proceed in the presence of weather that varies about the threshold permitting rust infection. If these generations do not occur, there is not time enough remaining, before maturity of the crop, for rust multiplication to destructive proportions, regardless of the favorable environment. In a sense we are dealing with the "law of the minimum"; the months before the "critical month" are so unfavorable and those after it are so favorable for rust reproduction that seasonal variations in these months do not markedly alter the course of rust dormancy or activity respectively.

Chapter XI

RUST DISSEMINATION; ANNUAL CYCLES; EPIPHYTOTICS

Disjunction and survival of spores: — The spores which are almost exclusively responsible for the dissemination of wheat leaf rust, the uredospores, evidently have no special mechanism for their expulsion from the uredinia. On maturity, however, they are very easily dislodged by the lightest of air currents (.36 m./sec. or less) or vibrations.

We recall that these are characterized by a high degree of resistance to temperature. In the temperature range to which the spores would be normally exposed during air-dissemination in the wheat-growing season (10°-35° C.), they can, under certain conditions, retain at least some viability for periods ranging from 6 days to as much as 3 months (at 20°-26° C.; SCHILCHER, 1932). Since the spores may be wind-borne hundreds of miles in a single day, and they can withstand temperatures somewhat higher and much lower than 10°-35° C. for that length of time, their destruction by unfavorable temperatures in transit is not a serious limiting factor to their long-distance dissemination. This is in marked contrast to the limited viability of certain other types of spores, *e.g.*, rust basidiospores or conidia of downy mildews.

A much more important limiting factor is seen in the relation of the spores to moisture. In its wind-borne flight if a uredospore passes into a cloud it may germinate and thus lose its ability to infect if it is later deposited on an infection court. Many "empty" spores are found on slides exposed to the wind, and this is doubtless a principal reason. Furthermore, if the air-borne spore encounters rain it is promptly washed to the ground where it germinates or at least is not in a suitable position for later air transport.

Uredospores drifting in the wind high in the air are particularly subject to the action of strong direct sunlight. Yet they will endure up to 3 weeks of normal daily direct sunlight exposure at earth level, and although we know from the experiments of HWANG (1942) that ultraviolet light is injurious to uredospores, it is doubtful that this is a serious limiting factor to their long-distance aerial transport, considering the relatively short time requirements, and the fact that the majority of air-borne spores are found at no great height from the earth's surface and therefore protected from undue ultraviolet radiation by the air density and frequency of clouds above them.

Spore-fall in relation to wind dispersal: — The behavior of leaf rust uredospores in the air can be visualized by comparing them with motes of dust in a beam of sunlight. The spores are much smaller than such motes and hence more subject to being wafted about by gentle currents of air, or being borne for long distances by winds before coming to rest.

UKKELBERG in 1933 was the first to make a precise study of the rate of

free fall of leaf rust uredospores in calm air. His procedure was to introduce the spores, by means of a dust gun, at the upper end of a 6-foot vertical cylinder, and count the spores which had fallen on microscope slides at the lower end of the cylinder, removed at definite time intervals after the spores were introduced. Falling spores were also observed directly, as are motes in a sunbeam, by use of a strong beam of light. He found much variation in the rate of fall of individual spores. Those of *Puccinia triticina* required 90-150 sec. to fall 180 cm., the rate averaging 12.62 mm./sec.; at this rate of fall it would take a leaf rust uredospore 6 hr. 43 min. to fall 1000 ft.

STEPANOV, who made an intensive study of the rate of fall and distance to which spores may be wind-borne (1935), with methods comparable to those of UKKELBERG, determined the rate of fall of *Puccinia triticina* uredospores to be 18 mm./sec., which is of the same order of magnitude as UKKELBERG'S figure.

STEPANOV carried out further experiments in which he determined the velocity of an ascending current that would suffice to hold a spore suspended, without falling or rising; any greater upward velocity of air would cause them to rise. These showed that the "floating velocities" in general were somewhat higher than the rates of fall (probably because of inability to distinguish single spores and spore clumps in determining "floating velocity"), but even so they were very small in absolute terms, usually 6-8 cm./sec. Ascending currents of air sufficient to rustle leaves of trees have been observed in nature, and these would need to have velocities much greater than 6-8 cm./sec.

Ascending currents of air are almost always present in nature. Particularly in the morning when the earth's surface becomes unevenly heated by the sun, strong ascending currents of air are created, and these, being much greater than the "floating velocity" of the spores, can carry them upward to great heights. PETERSEN (cited *in* NAUMOV, 1939) has reported that spores can be carried upward in this fashion for 2 km., and the absolute heights at which they have been recovered are much greater than this.

Thus with their capacity for being carried upward, and their extremely slow rate of fall, the uredospores are at the mercy of winds for the many hours or days that suffice to bear them away to great distances.

Supply of spores at their point of origin: — By the laws of dilution with the square of distance from their source, and corresponding decrease in probability of infection with increasing distance, air-borne spores could not be highly effective in long-distance dissemination of rust were it not for the colossal number of spores produced.

We have seen that in leaf rust epiphytotics, such clouds of uredospores are produced as to stain clothes and all nearby objects with a red spore coating. To attempt to gain some faint conception of the enormous number of spores produced at a source of infection, we need only recall that each uredopustule produces some 2000 spores each day for about 2 weeks, and a heavily infected wheat leaf may have more than 1000 pustules. Assuming 2 such infected leaves per tiller and 40 tillers per sq. ft., an acre of heavily infested wheat would produce, in 2 weeks, about 100,000,000,000,000 spores. If such an infestation extended over the wheat acreage of Oklahoma, in

combination with south winds, there would be produced in 2 weeks about 8 million spores for every leaf of wheat in the wheat States north of Oklahoma to Canada. To this must be added the spores originating in Texas and those produced by secondary infections in the more northern states, and the duration of time must be increased to much more than 2 weeks, in order to present the entire theoretical possibilty of this source of spores in the southwestern United States.

But the great majority of the spores will not fall on susceptible wheat leaves. Some of those which do will have lost their viability. Others may be deposited on wheat leaves but lack the environmental requirements for germination and infection. The enormous production of spores is counteracted by the failure of the vast majority of them to accomplish infection. Were this not so, wheat might long ago have become extinct.

The incubation period of wheat leaf rust is only about 10 days. After that period secondary spread can greatly increase infection from one or a few primary infections. As NAUMOV (1939) has pointed out, the likelihood that a single plant, at a great distance from the source of infection, will receive a primary infection from that source, is almost zero, but if the plant is one of a large association — a single wheat plant in hundreds of acres of wheat—, the chances become very much greater that some other plants of the association will receive primary infection from the original source of rust, and that the plant will become infected as a result of secondary rust spread.

Similarly, the chances may be remote that a wheat field 500 miles from a source of rust spores will be infected primarily by spores from that source, but they are much greater that the distant field will be infected by spores from a secondary source, between the distant points and the original source, the secondary sources having received their inoculum directly from the primary source.

Theoretical extent of dissemination of rust by wind: — There are numerous data showing that small bodies comparable to rust uredospores have been carried 1000 miles or more by winds. STAKMAN *et al.* (1923) have demonstrated the presence of wheat leaf rust uredospores at elevations of 16,000-16,500 ft. in the air. Knowing the altitude of spores, their rate of fall, and the wind velocity, one can calculate the theoretical distance to which the spores could be carried before coming to rest at the earth's surface. Thus, UKKELBERG (1933) has shown that theoretically a wheat leaf rust uredospore at 5000 ft. elevation in a 30 mi./hr. wind, would travel 1000 miles of horizontal distance before reaching the ground. NAUMOV (1939) considers the theoretical limit of dissemination of *Puccinia triticina* uredospores to be 1200-12,000 km. STEPANOV (1935) has calculated the "average limit of dissemination" of the rust as 641 km. and the "absolute limit of dissemination" ("that which is seldom exceeded") as 1282 km. His empirical determinations support these calculations.

Study of rust spore dissemination by use of spore traps: — Investigators of the epiphytology of the cereal rusts have devoted considerable attention to the study of air-borne spore dissemination, by the use of adhesive slides or other forms of "spore traps" for sampling the air. With par-

ticular reference to wheat leaf rust, the most extensive of these studies have been those of MEHTA in India and RUSAKOV and SHITIKOVA-RUSAKOVA in Russia. The Russian work indicates the following relationships between aerial dissemination of rust spores and the environment.

Several times more spores are caught during the day, when spores are rising, than in the evening or at night, when they are falling. This is explained by the greater spore precipitation and reduced spore transport at night, due to the calm, humid air, with few convection currents, and to the fact that spores caught at night may be washed away by dew.

Most spores are caught in dry weather. Few or none are deposited on the slides during steady rains, but with intermittent rains the spore catch may be very high a few hours after a rain. The spore catch increases approximately as the square of the wind velocity. RUSAKOV (1929*a*), for example, reports trapping an average of 127 spores in a 15 m./sec. wind and only 30 in an 8.5 m./sec. wind.

The number of spores caught is correlated with nearness to their source, vertically and horizontally, and with the size of that source. Since most spores caught are usually of local origin, the catch will increase with the increasing local intensity of the disease, usually reaching a maximum between the heading and dough stages of the crop, and then, as telial pustules replace the uredinia, and the infected leaves die, the numbers of spores caught rapidly fall. In wheat areas where both leaf and stem rusts are prevalent, the maximum catch of spores of the former is usually a few weeks before that of the latter.

Relation of leaf rust dissemination to topography: — The effects of windbreaks and barriers are well indicated by the spore catch. RUSAKOV and SHITIKOVA-RUSAKOVA (1928, 1929, 1932*b*) found that comparatively few spores were caught at the edges of forests or in fields separated by forests.

On a larger scale, extensive regions may be protected from the introduction of rust spores from outside, by mountains. Thus, according to NEWTON and JOHNSON (1941), the mountains separating British Columbia from the rest of Canada serve as a good barrier against introduction of rust, according to the results of physiologic race surveys. HAUMAN-MERCK (cited by GASSNER, 1916) found 3 places in Argentina where there were no grain rusts, which were protected against spores from other grain areas by the high Cordillera Mts. as well as by distance. Similarly, K. D. BUTLER in New York (1940*b*), which is separated from the main wheat areas by distance and low mountains, found no evidence from his spore-trapping that there were present in the air rust spores other than those from local sources; spores were not caught until the infection was well established locally. Large bodies of water, being cooler than the land in late spring and summer, would serve as barriers by being sources of descending air currents. Fields of snow or ice may have the same effect.

Local leaf rust dissemination: — Despite the emphasis laid on long-distance transport of rust uredospores, the vast majority of all infections are from local sources. The principles governing this local spread of rust are quite apparent: the concentration of air-borne spores, and the quantity

of infections resulting from them is greatest near the source of spores and decreases with distance from the source, at first sharply then more gradually. The principal spread is in the direction of the prevailing winds, and here barriers of no great size play an important part in determining the characteristics of the spread. These may be unevennesses in the terrain, hedges, weeds, groups of trees, buildings, etc.

It is a matter of common observation that in early stages of rust renewal there are islands or foci of infection (single pustules or single infected plants) which soon become surrounded by plants with secondary infections, and, as they enlarge, they blend with others, until the field is uniformly infested and the primary foci can no longer be detected. GASSNER (1915*c*) demonstrated this by setting individual rusted plants in rust-free fields. After 13 days (one incubation period) the rust had spread in circles, 2-3 m. in circumference about the foci of infection, and after 3 weeks, infection was so general that the original spots could not be found. RUSAKOV and SHITIKOVA (1929) observed a similar concentration of leaf rust about areas protected by cornstalks which permitted the rust to overwinter: 14 ft. from the source of rust there was ½ as much rust, at 245 ft., ¼ as much, and at 700 ft., only ⅛ as much rust as at the source. GALLOWAY (1893) noted that early in the season there were groups of 25-30 rusted plants together, surrounded by rust-free plants, evidently the result of local spread from small foci of infection. Finally, NAUMOV (1939) cites GORLENKO's report in 1934 of the decrease in percentage of leaf rust in spring wheat, from 6.6% in wheat adjacent to the source of infection, winter wheat, to 2.6% at a distance of 60 meters from the source.

Data from the study of other rust diseases, particularly stem rust, agree with observations such as those mentioned above, in showing that the concentration of rust decreases by geometric proportion as the distance from a small focus of infection increases by numerical proportion. This in turn is correlated with a similar geometrical decrease in air-borne spore concentration with increasing distance from the source of the spores, as shown by STAKMAN *et al.* (1923) for stem rust. The regularity of the decrease in infection with increasing distance from its source is somewhat disrupted by one-sided wind influences, so that instead of there being concentric circles of diminishing rust concentration about the focus of infection, they may be ellipses, or even assume the form of a comet's tail with the focus of infection as its head, the tail extending out in the direction of the prevailing wind, as was observed many years ago with reference to the pattern of new stem rust infections from barberry bush sources.

A good example of the characteristics of local rust dissemination is seen in two experiments of BOEVSKI (1936). In the first of these (*see* FIG. 9) the source of infection was a field of winter wheat on which leaf rust had overwintered, in the windward direction of an uninfected field of spring wheat, and separated from the latter by a strip of trees 25 meters wide with shrubby undergrowth, broken only at one point. In the field of spring wheat, at points indicated by the numerals 1-8 in the figure, adhesive slides were exposed to determine the deposition of rust spores from the field of winter wheat. When the wind was south (the prevailing direction) the greatest number of spores was caught on slide 1, and progressively smaller

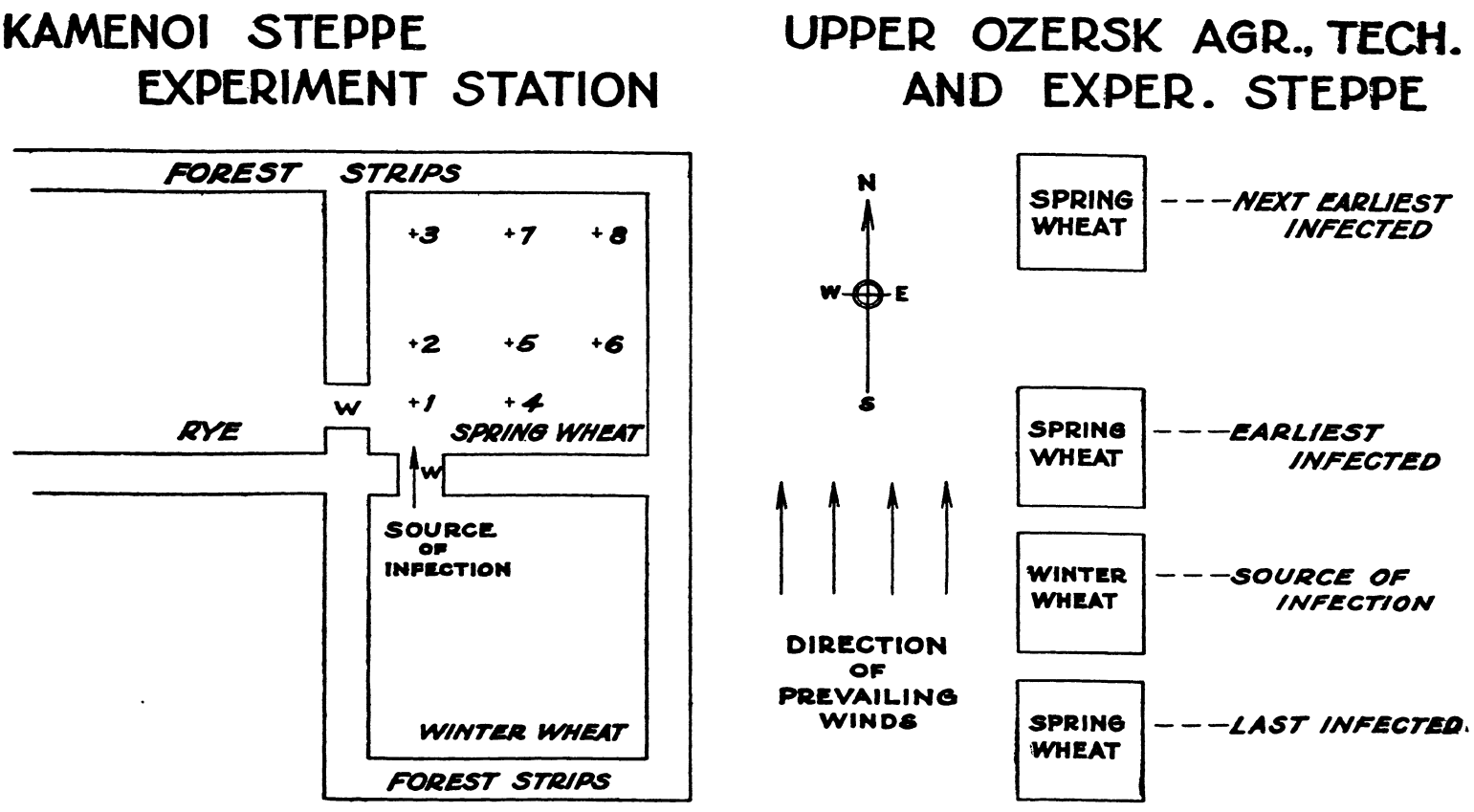

FIGURE 9. — Relation of local dissemination of rust to barriers and prevailing wind direction. (*After* BOEVSKI, 1936).

numbers on slides 2, 3, 5, and 7; this order was 1, 4, 5, 6 (the spores being of rye rust) when the wind was west. The most wheat leaf rust developed, about 10 days after the spores were observed, on the plants at position 1, with progressively decreasing amounts at positions 2, 3, 4, 5, 6, 7, and 8. As the spring wheat approached maturity this same order of rust intensity at the different locations was preserved.

The results of the second experiment are apparent from the figure. A field of spring wheat near the rust source and in the leeward direction of it was first infected, next a field of spring wheat 2.5 km. from the source but on the leeward side, and last of all a field close to the source but on the windward side. This relative situation persisted through the season. On June 22, for example, the fields, in the order named above, had 41.3, 6.1, and 1.1% of rust respectively, on July 1, 58.7, 15.3, and 9.3%, and on July 22, 100, 75.5 and 63.7%.

It can be clearly seen from this example, and others might be cited, that the direction of a wheat stand relative to a source of infection is fully as important as its distance from the source of infection, and it illustrates the effectiveness of barriers in preventing local rust dissemination.

Dissemination of the rust from wheat debris to the alternate host by means of basidiospores, and from the alternate host back to wheat by means of aeciospores, in the limited region (eastern Siberia) where this occurs, is purely a matter of local dissemination, judging by the ecological relationships of the two hosts and what is known of dissemination of these types of spores in other rusts. In general, aeciospores do not have pathological significance at distances greater than about 5 miles from the place of their origin, and usually this distance is much less, while basidiospores are even less suited to producing infection at a distance. The aecial host, *Isopyrum*, is a small weed, common in eastern Siberian wheat fields, and its infection from the wheat stubble, and passage of the infection back to wheat in most cases would involve distances measured in feet rather than in miles.

Spring rust renewal in the North American Great Plains: — The North American Great Plains, extending from the northern half of Texas to the Peace River valley in Canada, is a continuous wheat belt, uninterrupted by any important natural barriers. The prevailing winds are southwest in the summer, northwest in the winter, and cyclonic in spring and fall. It has been well established that uredospores of stem rust from fields in the southern part of this area borne north by the winds, are the principal source of inoculum for the northern parts of this belt, where stem rust does not overwinter in the uredinial stage. While little special attention has been given to wheat leaf rust in this regard, it has been assumed that the same situation applies to this disease as to stem rust. We will see that this is not entirely the case.

In the first place, leaf rust overwinters in the uredinial stage much farther north than stem rust, even occasionally in Canada (*see* page 140). This overwintering of leaf rust may often be undetected by any but an exhaustive search of many hours. Yet in Oklahoma the writer has observed that such overwintered rust, in trace amounts, can result in the establishment of abundant infection before spore traps show any significant intro-

duction of wind-borne rust spores from the south. In such a case the wind-borne spores only serve somewhat to intensify the infestation late in the season.

It cannot be determined how much farther north there is the same situation, in which overwintered rust plays the major rôle and introduced uredospores the minor one, in establishment of leaf rust infestation in the spring. There is little doubt that in the extreme northern part of the Great Plains, wind-borne uredospores are the principal source of spring inoculum. In Canada, uredospores are regularly present in the air 1-2 weeks in advance of infection of the wheat crop (NEWTON, 1938; CRAIGIE, 1939), and air-borne uredospores from the South also appear to be the usual source of the first spring infections in North Dakota (BOLLEY and PRITCHARD, 1906).

But three factors, none of which has received adequate attention in the past, point to the secondary importance of long distance wind transport of leaf rust throughout most of the Great Plains; these are: *a*) overwintering of the rust to a greater extent than has been recognized; *b*) the lack of prevailing south winds at the time leaf rust is abundant in the South; and *c*) the relatively greater effectiveness of locally-produced uredospores compared with introduced spores.

As has been shown, overwintering of leaf rust in trace amounts is adequate to result in intensive late-season rust, without the necessity of showers of spores from a distance. To determine the occurrence of such overwintering requires intensive and frequent searches, correlated with slide exposures, such as have not been made in most of the Great Plains, at least so far as the literature shows. There is no reason to believe that the situation in Oklahoma is unique; it probably has its counterpart, but in progressively less degree, as far north as the rust overwinters.

Secondly, it must be borne in mind that leaf rust appears and disappears earlier in the season than stem rust. The latter, occurring late in the season, is well timed for northward spore dissemination by the winds which have become prevailingly south. Leaf rust becomes abundant in the South in April and May, in the period of cyclonic weather, when the winds blow from all directions, and there is no reliable northward wind current.

Finally, given an equal amount of locally produced and introduced inoculum, the former is more favored for producing rust, since the spores are fresh, while many of the air-borne ones may have lost vitality, and the locally-produced spores are in the plant zone, in the most favored position for reaching infection courts, and constantly present to produce infection whenever the environment permits. It should also be considered that a few locally-produced rust spores early in the season, each of which is a potential ancestor of several successive generations of rust during the growing season, have far more destructive effect than wind-borne spores that are introduced later and hence can serve as progenitors of fewer uredinial cycles before the rust season is past.

Much study is needed before we have a reasonably complete picture of the spring renewal of leaf rust in the Great Plains. From the foregoing discussion we can only conclude that it is unsound to transfer knowledge of stem rust renewal to that of leaf rust, as has too commonly been done, and that there is good *a priori* indication that the major importance of leaf

rust overwintering and the minor rôle of introduced spores, as observed in Oklahoma, may have its counterpart rather extensively over the southern and central Great Plains.

Fall rust renewal in the North American Great Plains: — In the northern parts of the Great Plains the summers are favorable for the growth of planted or volunteer wheat and the reproduction of leaf rust. Hence there is inoculum at hand for wheat in the fall, and long distance introduction is not necessary. Farther south, the fields are often quite barren of wheat during the hot summer months in which neither host nor pathogen can exist in the vegetative state.

FREEMAN and JOHNSON in 1911 first suggested that the original fall infections in the southern Great Plains may result from uredospores that have been produced in the North and blown southward. Confirmation of this was obtained in Oklahoma in the fall of 1938 (CHESTER, 1939*a, b, d*; BROWN, 1938). That year no evidence of oversummered wheat or leaf rust could be found. Slide exposures from airplanes showed the first concentration of leaf rust spores in the air over Oklahoma in the fall on Oct. 20-29. Ten days to 2 weeks later the first fall infections appeared in 60% of the fields examined over a wide area of the State. There were no further spore showers up to Nov. 20, but two weeks after the first pustules appeared there had been abundant secondary spread, and the fall infestation was well established. The spore shower coincided with the first fall north winds, continuous from Canada to Oklahoma, and the spores had evidently originated far to the north on late-harvested or volunteer wheat.

This evidence, confirmed by reports from Texas, appears to justify the conclusion that wind-borne uredospores from the North are a major source of fall leaf rust infection in the southern Great Plains. Under exceptional circumstances (in a very mild summer, in protected situations), the fungus might oversummer to some extent in this area, but these cases are believed to be the exception and not the rule.

Long-distance rust dissemination in Europe: — In some seasons leaf rust overwinters with difficulty in parts of the Russian granary. This was true in the winter of 1926-1927 in Yeisk, according to RUSAKOV (1929*a*). When the rust did appear, in May, it bore no relation to overwintering of wheat and, in fact, appeared more strongly on spring than on winter wheat. The pustules appeared here and there over the fields "as though they had fallen from above", bearing no relation to edges of fields or plants of *Thalictrum*. The first infections appeared May 13-14, and exposed slides caught the first leaf rust spores April 30-May 1. There was dew and a trace of rain at that time, and the temperatures were low enough for the rust to require a 2-week incubation period. During the next 4 weeks, not a single leaf rust uredospore was caught, which RUSAKOV interprets as showing that local infections of less than 1% intensity are not registered on the slides. Finally, May 30, spores were again caught, and these were traced to secondary infections from the pustules that appeared May 13-14.

In an arc from NNE to SW of the Yeisk station on the west side there were only a few dozen wheat fields and thence, 2-3 versts away, the Sea of

Azov stretches away for 50 km. and to the north for 250 km. No spores were trapped when the winds were NE, but abundant spores were deposited on the slides when the winds were blowing directly across the Sea of Azov. The slides also caught pine pollen when the nearest pines were dozens of km. away (SHITIKOVA-RUSAKOVA, 1932*a*). In No. Caucasus, in 1929, leaf rust spores were first trapped where the rust had overwintered (Gronozii), then in regions 300 km. away (Otrada Kubanskaya, Krasnodar), and later still farther away (Yeisk, Rostov). All of this led RUSAKOV to conclude that the spring renewal of the rust can result from long-distance transport of uredospores. NAUMOV (1939), while questioning the conclusiveness of RUSAKOV's findings with reference to dissemination of spores across the Sea of Azov, considers that his correlation of air-borne spores with infection 2 weeks later is good evidence that the first infections were due to spores brought in from a distance.

SĂVULESCU (1933, 1934, 1938*b*) holds that although leaf rust ordinarily overwinters in Rumania, after cold winters or rust-free fall seasons it is brought in from such areas as Bulgaria, Italy, So. Russia, and the Balkan Peninsula by NE, E, S, SE, and W winds. A certain degree of correlation was seen between the frequency of such winds in April and May and the intensity of leaf rust development in years in which the spring rust renewal was not related to local rust hibernation following fall rust development (1933, FIG. 4).

ROBERTS (1936) described a number of physiologic races of wheat leaf rust in England that she considered distinct from those of continental Europe. She associated this with the fact that during the season in which the prevailing winds are east, from the Continent to England, leaf rust is not prevalent in northern and central Europe. Considering the nearness of England to the Continent it would be remarkable if there were not sufficient rust dissemination across the English Channel to result in a uniform distribution of races in England and on the mainland, and when allowance is made for environmentally-conditioned variations of ROBERTS' reactions, her "English races" must all be relegated to races that do exist on the European mainland.

Long-distance rust dissemination in Africa and Asia: — BURTON (1931*b*) has considered that since wheat leaf rust occurs in Abyssinia (Ethiopia), and the prevailing winds in Keyna Colony are N by E, Abyssinia can serve as a source of wind-blown leaf rust inoculum for Kenya; however, this is unnecessary, since in Kenya the temperatures are uniform and equitable the year round, and the wheat rusts can perpetuate without the need of alternate hosts or long-distance wind dissemination.

E. J. BUTLER and HAYMAN in 1906 and E. J. BUTLER in 1918 were perplexed as to the origin of wheat leaf rust infections following hot summers in the Indian plains through which neither wheat nor its rust can survive. MEHTA solved this problem in a series of studies from 1929-1940 in which he showed that winds from the hills, where the rust oversummers, carry the infection to the Plains. This explanation of the annual migration of leaf rust in India was verified by analysis of the spore content of the air.

Two regions in eastern Siberia have been studied in this connection,

the Amur-Primorsk region in the southeastern corner of Siberia, and the Irkutsk region in the south-central part of Asiatic Siberia, west of Lake Baikal. The study of long-distance dissemination of wheat leaf rust in the Amur region, with the aid of spore traps, is reported in a number of papers by RUSAKOV (1925, 1927*b*) and SHITIKOVA-RUSAKOVA (1932*a* and particularly 1927). According to SHITIKOVA-RUSAKOVA, there are no local sources of spring rust renewal in Amur, where only spring wheats are grown. *Thalictrum* plants are numerous, but the weather is too dry to permit them to function in spring rust renewal.

In 1926, the first air-borne leaf rust uredospores were deposited on spore traps June 19. Dew was present and temperatures favorable for spore germination and infection. Nine days later, the normal length of the incubation period of leaf rust, the first rust pustules appeared in the fields. The spores were caught only in SE winds, indicating that they had been brought from Manchuria, where much wheat is grown, where the crop is 2 weeks earlier than in Amur, and where leaf rust was known to be prevalent. No more spores were trapped after the Manchurian wheat had matured, and none were brought in by west winds. (A chain of mountains lies to the west of the Amur Station at Blagovestchensk.) Later in the season, after spore transport from the SE had ceased, spores were trapped in north winds, the result of late season rust infestation north of the Amur Station.

The Irkutsk massif is one of the most isolated wheat growing areas in the world. On the east it is separated from the wheat area of Amur by Lake Baikal, mountains, and great distance, on the south it is bounded by mountains and the Gobi Desert, to the north lies a vast expanse of forests and frozen tundra, and to the west there are the Caucasus Mountains and a distance of 1000 km. before a wheat region is reached. As further evidence of its isolation, wheat stem rust does not occur in the region west of Lake Baikal, although it is present and widely distributed in Manchuria and eastward across the Yablonoi Mts. in Sretensk, as well as in western Siberia and European Russia. This indicates that rust uredospores are not introduced into the Irkutsk region from outside.

BRIZGALOVA (1935) who studied leaf rust in this isolated region, exposed spore traps to obtain further evidence relative to the spring renewal of rust. She caught no appreciable number of spores until leaf rust appeared in the fields, and those caught bore no relation, according to wind direction, to any distant source of inoculum. Thus, the Irkutsk region appears to be a clear-cut instance of a geographic area with total protection from long-distance wind dissemination of viable leaf rust spores.

Long-distance rust dissemination in Australia and South America: — Australia represents another geographic region that appears to be totally protected against introduction of rust by long-distance wind dissemination. The Australian wheat region is in the southwestern and southeastern parts of the continent, in Western Australia, Victoria, and New South Wales. There is also a little wheat grown in New Zealand, which is part of the same geographic area. The nearest wheat regions are across the equator, thousands of miles away, in India, Burma, and China. Even more distant,

across the Indian Ocean, is the minor wheat area of South Africa. Here, if anywhere in the world, we would expect to find freedom from wind-borne rust from the outside, and that this is actually the case is strongly indicated by the physiologic races present in the Australia-New Zealand area.

Examination of TABLE 11 shows us that the race 9 group, which predominates in all other wheat areas, was totally absent in WATERHOUSE's very extensive race analyses, as were also the fairly common race groups 1, 17, and 21. Furthermore, half of his collections failed to give susceptible reactions on Thew wheat, which, according to JOHNSTON and NEWTON, is susceptible to all leading North American races (which, in turn, are representative, in general, of the races of the northern hemisphere.)

In South America, the Argentine wheat area is almost as isolated as the Australian, with the nearest wheat, except for very insignificant amounts in the mountainous areas of Bolivia, Peru, and Columbia, in North America and South Africa. Its race flora is not quite as unique as that of Australia, but it is noteworthy (TABLES 10, 11) that leaf rust race group 1, which is prevalent in North America, Europe, and Asia, and race 12 which occurs in North America and Europe, have never been recorded from South America.

Thus, in Australia and Argentina, as in the Lake Baikal region of Siberia, we evidently have regions which are so separated from other wheat areas by natural barriers, mountains, oceans, deserts, and vast distances, that for all practical purposes they may be considered as totally isolated from the rest of the world, insofar as the introduction of wind-borne rust is concerned.

Rust dissemination by insects: — COBB (1890–1894) and COBB and OLLIFF (1891), drew attention to the activity of insects in the local, plant-to-plant spread of wheat rust. They pointed out that there are several species of *Ceciodomyidae,* presumably of the genus *Diplosis,* the larvae of which feed exclusively on rust spores of wheat and other plants, and that "insofar as these larvae devour the rust they do good, but they have an unfortunate habit of daubing themselves all over with spores, and are in consequence active agents in spreading the rust fungus". *Diplosis* larvae crawling over rusted plants had an average of 1,121 rust spores adhering to each larva, and when such larvae were placed on paper they dropped 250 spores in moving an inch in 2-3 minutes. The spores were shown to be viable. Much later, BARNES (1936) described *Hyperdiplosis triticina,* which feeds on the spores of wheat leaf rust in Kenya and Egypt.

Another early report was that of WEBSTER, in India (1890), who observed the larvae of a small robust springtail (*Sminthurus* sp.) feeding on uredospores of *Puccinia triticina* when the rust first appeared in the fall. These appeared to be efficient vectors in spreading rust, since their bodies were covered with bristles to which adhered great quantities of spores.

E. C. JOHNSON, in Texas (1911) found thrips on wheat bearing rust spores and concluded that, as these are very active and numerous, they must be important in spreading the rust over plants and from plant to plant. Later AYYAR (1928) described the new species *Anaphothrips fungorum,* which feeds on "rust of wheat" in India.

Finally, the writer has often seen tiny beetles of the *Phalacridae* (*Phalacrus politus*) apparently feeding on wheat leaf rust spores (as well as spores of wheat bunt, *Tilletia* sp.), and as these beetles are very active, they appear to be capable of being agents of local rust dissemination.

Thus, it would appear that a number of rust-feeding insects, as well as insects that frequent wheat plants for other purposes, can serve as vectors of rust, aiding in the local increase of the disease; there is no evidence that they are involved in long distance rust dissemination.

Rust dissemination by seed: — This subject was discussed in connection with hibernation and aestivation of the rust (pages 145-146), and it was concluded that leaf rust is not disseminated by seed except, perhaps, in very rare cases, which have no significance with reference to annual rust renewal, although they may be of importance in the first introduction of rust species or races into new areas. This, in turn, would only have practical application to areas, such as Australia and Argentina, that are protected against rust introduction by long-distance wind dissemination.

Rust dissemination by airplanes: — In the past, when intercontinental commerce was restricted to maritime shipping, the odds were greatly against the long-distance transport of rust by this means, because the time consumed in bringing goods to a seaport, loading, passage, unloading, and distribution of the goods would greatly reduce or destroy the viability of uredospores accidentally contaminating merchandise, and because the ship itself normally touches only at congested seaport dock areas, far from the nearest wheat fields.

With the intercontinental transport airplane the situation is quite otherwise. Passage is a matter of a day or two, and airports are located outside the cities, often in close proximity to fields of crops. Under these conditions the plane and its contents could easily become contaminated with large quantities of uredospores at the point of departure, considering the vast numbers of spores present near heavily rusted wheat fields. The passage, at low temperatures of the upper air, would favor retention of viability of the spores, and at the end of the trip they could be liberated in a favorable position for reaching and infesting nearby wheat fields. While this would not normally relate to the annual renewal of rust at the destination point, it could have great significance as a means for the introduction of rust races to new areas. This applies also to other fungous diseases of plants, and warrants serious consideration of the desirability of surrounding airports with crop-free zones, the form and extent of these to be determined by the laws of dilution of air-borne inoculum with distance from its source, prevailing winds, and other factors involved in local disease dissemination.

Annual cycles of rust in North America: — FIG. 10 gives the dates on which leaf rust normally becomes evident in the various parts of the Great Plains during the spring and summer. In southern Texas, along the Rio Grande, the rust is normally in a vegetative state, reproducing, in midwinter. In northern Texas the rust is usually dormant for a few weeks in the winter but resumes vegetation in March. The period of spring rust renewal is progressively later, passing northward, to the latter half of June

FIGURE 10. — Dates on which wheat leaf rust usually becomes noticeable in various parts of North America

in Manitoba. As we pass northward the rôle of overwintered rust, in spring renewal, progressively decreases, and that of wind-borne spores from the southward areas increases, until in Canada the introduced inoculum from the South is the chief source of the spring infections. It is difficult to determine at what point, passing northward, overwintered rust first loses its major rôle in initiating spring rust, but since we know that normally leaf rust will overwinter as dormant mycelium under any conditions permitting winter wheat to overwinter, it would appear that the principal source of spring inoculum is overwintered rust in winter wheat in an area extending northward to include Nebraska and Iowa.

Whether or not overwintering leaf rust is normally observed in these States is immaterial unless thorough searches have been made, and the course of rust renewal in the spring has been studied in detail, and in most cases this has not been done.

In all of this territory, from Texas to Manitoba, leaf rust can become epiphytotic as the crop approaches maturity, and often does. In the cool summer of the northern latitudes the rust oversummers on volunteer wheat or on the crop itself, and in the fall we have the exact reversal of the spring picture, with oversummered rust providing the principal inoculum for fall infections in the northern part of the Great Plains, and a progressive decrease of this, and increase of dependence on spores, carried south by the winds, for providing the fall inoculum in the southern Great Plains.

A word should be said, at this point, on the significance of "first dates" on which rust is apparent. This term is very loosely used: to one observer the "first date" is that on which rust becomes obvious from a casual glance at the field, — it may represent a concentration of many rust pustules per plant; to another the "first date" is that on which a few minutes' search brings to light a few pustules; to a third, the first date is that on which a very extended search reveals even a single pustule. Because of these irregularities, the data of Fig. 10 are only rough approximations.

TEHON (1927) suggested that the "first dates" for leaf rust in Illinois follow HOPKINS' bioclimatic law, and the data of FIG. 10 indicate that this is roughly true of the North American wheat areas as a whole, excluding the southernmost area where the rust is more or less prevalent throughout the winter.

There is limited winter wheat culture from New York to South Carolina and from Washington to California. Both of these coastal regions are isolated from the Great Plains by mountains. Here, as in all North America, no alternate host of leaf rust is functional. The source of spring rust inoculum is primarily spores from mycelium that has overwintered in the wheat. These regions may be regarded as self-sufficient, insofar as rust is concerned, the rust hibernating as dormant mycelium and aestivating in volunteer wheat, which is more favored here than in the southern Great Plains, because of the tempering effect of proximity to the oceans, higher altitude, and, in general, more northern latitudes.

Annual cycle of rust in Europe: — In many respects the annual cycle of leaf rust in Europe resembles that in North America. There is no reliable evidence than an alternate host is functional in Europe. The rust

has been shown to overwinter in the uredinial stage throughout Europe from Sicily to Poland and in European Russia from the Black Sea region to Leningrad (*see* page 141). As the continent is broken up by mountain ranges, its central and northern parts might be compared, in this respect, with such areas as Pennsylvania, New York, Washington, and Oregon, and the Mediterranean area with southern Texas. Long-distance dissemination of rust spores, for the most part, is not a factor, except in the movement of rust from the Black Sea area northward in European Russia, and perhaps northward into Rumania. In general, in this region, summer temperatures are temperate enough to permit rust survival on volunteer wheat, or, in the northern part of Europe, on the wheat crop itself.

The dates of rust development are progressively later as we pass northward. In Italy leaf rust usually becomes epiphytotic in March and April, but sometimes in February or in May-June; it is often abundant in the fall. In France it ordinarily becomes evident in June, although it may be as early as April or be delayed to early July. It is common from Oct. 25 to the end of the year. In Rumania, if there is abundant overwintering of the rust, it becomes noticeable in April or May, but if this is not the case, and spring renewal is dependent on spore transport from more southern regions, the renewal may be delayed till June or July. Leaf rust usually appears in Austria in April-May; it becomes abundant in May-June, as it does in Poland. Mid-June is the period of rust intensity in England. Finally in northern Germany, and as we pass into the spring wheat area, in the nearby southern tip of Sweden, July or even early August is the time of severe leaf rust. In European Russia, the rust first appears at southern points (Yeisk, Kiev) in April, and farther north (Kursk, Voronyezh) in May-June. Here, in the Russian granary, the rust reaches its epiphytotic stage in June and July.

Both winter and spring wheats are grown in European Russia, and the winter wheats, in which leaf rust readily hibernates, often serve as sources of spring wheat infestation. Rust overwintering on winter wheat is associated with strong rust development in Sept.-Oct. and a protective snow cover. We also have seen that rust spores developing on winter wheat at times may be borne by the wind to Russian spring wheat areas (as from Rostov) thus serving as sources of air-borne spring infection.

Annual cycles of rust in eastern Siberia:—Here we must distinguish two regions, the Irkutsk massif, west of Lake Baikal, and the Amur district.

In the Amur district only spring wheat is grown, and alternate hosts do not function. The rust does not survive the long, cold winters. Spring infection, which is noticeable in June, is due to uredospores brought in by south winds from areas where the rust overwinters and develops earlier, *viz.*, Manchuria and the Coastal (Primorsk) province. Oversummering of the rust occurs in a vegetative stage on wheat.

Quite a different situation obtains in the Irkutsk massif. This area is completely isolated from any other wheat area by mountains, desert, and great distance. Spring wheat is grown almost exclusively; there is a slight amount of overwintering of rust on volunteer wheat and the very few

hectares of winter wheat, but the principal source of spring inoculum is from the functioning alternate host, *Isopyrum fumarioides*. This wheatfield weed sows itself in July, emerges in August, and passes the winter as small rosettes showing natural *Puccinia triticina* infections sometimes in the fall and always in the spring. By means of aeciospores the rust passes from this alternate host to wheat where it becomes apparent during June.

Annual cycle of rust in India: — Here wheat is grown north of a line connecting Bombay and Calcutta. It is planted in Oct.-Nov. and harvested in Mar.-Apr. or 1-2 months later in the hills. Ninety-five per cent of the crop is grown in the Indo-Gangetic Plain where the summer temperatures are 100° to 110° F. for weeks at a time. During this summer there are no volunteer wheat plants, and no rust survives on the Plains. There is no evidence, from extensive investigations, of the functioning of an alternate host.

At higher altitudes, however, in the hills where only 5% of the Indian wheat is grown, temperatures are low enough so that the rust can vegetate through the summer. This is at altitudes of 3000-5500 ft., as at Almora, where the rust can survive from May through February. In the Nilgiris and Palni hills, where wheat is sown in April-June, leaf rust may be found in abundance the year around, and particularly during the summer when there is no rust in the Plains. Overwintering of the rust is accomplished on wheat in the hills at moderate altitudes, where it reproduces from September to November, but, due to the cold weather is relatively inactive during November-January. This delays infection in the Plains till January, although in the Plains the wheat is up and growing from November onward. In January, uredospores are normally wind-borne to the Plains where they initiate the first rust on the main crop, accomplishing this by a series of stepping stones, — from the higher to the lower hills, to the nearer parts of the Plains, and thence to more distant parts of the Plains.

Annual cycle of rust in South America and Australia: — The climate of Uruguay is subtropical with a mean annual temperature of 16° C., winter mean temperature of 10° C. (4°-18°), and summer mean temperature of 23° C. (14°-35°). The average relative humidity is 82% in the winter and 63% in the summer. The average rainfall is 762 mm., and this is evenly distributed through the year. As a result of such an equitable climate, wheat may be found vegetating in all stages of growth at any season of the year; although the crop is principally planted in July and harvested in December, volunteer wheat may be found at all times. It follows that leaf rust may be found at all seasons; its "cycle" is a perpetual series of uredinial generations. There is no evidence of the functioning of an alternate host, nor is there need for one. Here wheat has been cultivated for 500 years, and there is evidence that it has suffered from leaf rust at least since 1860 (Gassner 1915*a, b, c*).

According to Rudorf *et al.* (1933) a similar situation exists in Argentina with wheat and rust both vegetating the year round, and with no functioning alternate host.

In Australia according to Cobb (1890-1894) and Waterhouse (1934) wheat is sown in the autumn (Apr.-May), and harvested in early summer

(Nov.-Dec.). Heavy rust in late winter in the coastal regions provides inoculum for later wheat in the main wheat belt. On the cultivated crop or on volunteer wheat the rust persists throughout the year in a vegetative stage, with some intensification of its activity in May-Oct. (winter and spring).

Conclusions derived from rust epiphytotics of past years: — An analysis of the occurrence or absence of leaf rust epiphytotics down through the years affords data from which we are justified in drawing some conclusions:—

(i) The record of recent years indicates that a leaf rust epiphytotic extending throughout the North American Great Plains is likely every 4 years, and a very serious epiphytotic about once in 10 years. Severe epiphytotics occurred, between 1915 and 1944 in 1919, 1922, and 1938, and there were other important outbreaks of leaf rust in 1916, 1927, 1932, 1935, and to less extent in 1943.

(ii) In North America there are at least 3 very distinct and independent regions, respecting leaf rust, the Great Plains, the Atlantic Coastal States, and the Pacific Northwest. The intensity of the disease in one of these regions appears to bear no relationship to that in the others. Thus, in 1917 and 1933 leaf rust was epiphytotic in the Atlantic States and minor in the Great Plains, and in 1922 and 1935 it was epiphytotic in the Great Plains and nearly absent from the Pacific Northwest.

(iii) While the North American Great Plains usually are fairly homogeneous as to leaf rust intensity, there are occasional years in which leaf rust begins with great destructiveness in the South and becomes inconsequential in the North, as in 1926, 1929, 1934, and 1945, and others in which the disease does little damage in the southern Great Plains, but becomes epiphytotic in the North, as in 1925.

(iv) There is no evident correlation in leaf rust intensity during a given season between any two of the leading continental wheat areas of the world. In 1922 the disease was epiphytotic in North America and Europe and almost absent in India; in 1924 it was epiphytotic in Europe but minor in North America, in 1927 it was epiphytotic in North America and inconsequential in Australia and in European Russia; the European epiphytotic of 1930 coincided with a very low level of rust in North America; etc.

(v) There is a suggestion of a cyclic behavior of leaf rust in the Great Plains. This is illustrated in FIG. 11. There is a regular tendency for years of leaf rust epiphytotics to be preceded and followed by years of moderate and not low rust intensity, and for years of light rust also to be preceded and followed by years of moderate and not epiphytotic rust intensity. The period of time is too short, and, above all, the data are too limited, to permit any far-reaching conclusions. At this point we can only remark on the apparent cyclic behavior of the rust and suggest its further study.

(vi) It is noteworthy that, as seen from the figure, epiphytotic leaf rust years are isolated, *i.e.* they do not appear in groups of two or three consecutive epiphytotic years, and the years of minor rust are similarly isolated. This point applies in the Great Plains where there is an average

moderate leaf rust intensity. In areas, such as certain of the Atlantic States, where the rust is regularly epiphytotic, there are often several successive epiphytotic seasons, and the reverse is true in regions where the rust is normally of very minor consequence. Isolation of epiphytotic years is indicative of a lack of year-to-year carryover of rust intensity. Thus it appears that if leaf rust is epiphytotic this year, that fact gives us no basis for assuming that the great quantities of inoculum present this year will result in another serious outbreak next year. The climatological hazards from one spring to the next have such great influence as to virtually nullify the direct effect of rust intensity of one season on that of the next. Some concrete examples will bring this out.

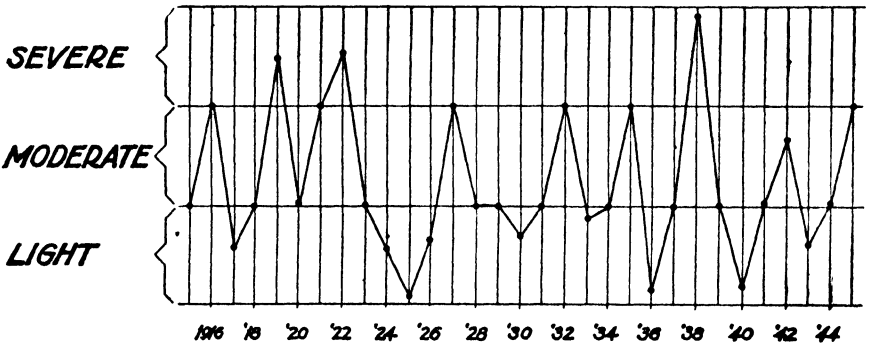

FIGURE 11. — Intensity of wheat leaf rust in the Great Plains, 1915-1944, as concluded from the United States and Canadian plant disease surveys.

TABLE 16 relates the fall rust in Kansas, during 8 years in which fall rust was heavy, to the rust of the preceding and following springs. We can see that in 4 out of 8 cases the heavy fall rust occurred in years in which the preceding spring had been one of light rust, and in 6 out of 8 cases the heavy fall infestation was not associated with severe rust the following spring. It appears clear that an unfavorable winter can nullify the effect of a rust epiphytotic in the fall, and while it is entirely possible that in some cases heavy fall rust, favored by a mild winter, could result in early, abundant rust infections in the spring, this is not the normal occurrence. Wheat leaves that are rusted in the fall usually die before rust renewal is under way in the spring, and the important factor is not so much the survival of the fall rust, as the opportunities for rust reproduction in the winter and early spring, independent of the gross amount of rust present in the fall. Similar reasoning applies to survival of rust in the summer.

It has also been shown for the southern Great Plains (CHESTER, 1943, 1944*b*) that the fall weather is not correlated with rust the following spring, while a close relationship does exist between the late winter weather and spring rust development. Thus, three different approaches, — the apparent cyclic behavior of rust, the lack of correlation between spring and fall rust, and the lack of correlation between fall weather and spring rust development—, all lead us to the same conclusion, that the carryover effect of rust from one season to the next is negligible. For practical purposes, the rust

TABLE 16: *Relation of heavy fall rust in Kansas to that in the preceding and following spring season: —*

HEAVY RUST IN THE FALL OF:	FOLLOWED SPRING INFESTATION WHICH WAS:	PRECEDED SPRING INFESTATION WHICH WAS:
1925	Less than usual; from none to 5-20% occasionally	Severe
1926	Late but severe in So. and Central Kansas; elsewhere light	Severe
1927	Very heavy	Late; only a trace May 20
1930	Late but heavy in central Kansas; lighter in E. and W. Kansas	Lighter than usual
1931	Lighter than usual	Lighter than usual
1938	Severely epiphytotic	Late and light
1940	Very light as late as June 10	Very mild
1941	Very mild	Very late, not severe

potentialities of each new spring may be looked upon as being unrelated to the intensity of rust the previous year or even the previous fall.

Prediction of wheat leaf rust epiphytotics: — In Chapter X is a discussion of the "critical month" in relation to subsequent leaf rust development in the spring. After this month temperatures and moisture conditions are usually such that rust development proceeds normally without serious hindrance from the weather; before this month temperatures are regularly too low for spring rust renewal. If, during the "critical month", the weather permits the first cycles of rust renewal, the disease has enough of a "head start" so that epiphytotic development follows; if these, usually unobserved, early cycles do not occur during the "critical month", there is not enough time during the growing season for the rust to multiply to epiphytotic proportions until the crop is sufficiently advanced that crop loss from rust is fairly light. Thus the weather during the "critical month", and the behavior of the rust during that month provide the basis for forecasting the spring rust intensity 2½ months before harvest. This situation, worked out for the conditions of Oklahoma, also appears to apply in Illinois, Iowa, and New York, *i. e.* it may have rather general application in winter wheat areas. Moreover, in areas which depend principally on wind-introduced uredospores for their spring rust renewal, the situation in the area of the source of these spores should serve as a basis for forecasting the future rust intensity in the area dependent on spore showers.

The practical value of forecasting is seen, for example in the case of a farmer in Oklahoma whose wheat planting has resulted in a rather poor stand. If the crop is doomed to any considerable amount of rust damage it will amount to failure at harvest time in June. The land could still be planted with corn in April, or with cotton, or summer legumes in May. If, on the other hand, the crop is not subjected to heavy rust damage, even the poor stand of wheat may still yield a more profitable return than a summer crop (considering that the wheat requires no further cost than that of harvesting). To such a farmer a reliable rust forecast, based on sound scientific principles, in early April or even early May, would enable him to gain the

most benefit from the use of his land and the most profit from his labor and expense.

An understanding of the relationship between leaf rust and the weather of the "critical month" has applications with reference to control of leaf rust by sulphur dusting and to practices for increasing rust intensity in rust nurseries. GREANEY's extensive work on sulphur dusting in Canada was directed primarily at stem rust which develops later in the season than leaf rust. His dustings were usually started in mid-July. Reference to FIG. 10 shows that leaf rust normally first becomes apparent in Canada in June. If the "critical month" applies to Canada, the early rust cycles upon which later epiphytotic rust development depends occur in May. We can conclude that for leaf rust control in Canada the dustings would need to begin at least 2 months before mid-July.

The importance of the weather of a "critical month" has also been suggested by observations in other parts of the world. In eastern Siberia, BRIZGALOVA (1935) considers June weather to be critical for leaf rust development. This month corresponds phenologically to April in Oklahoma or May in Iowa or Illinois. It is possible that an even greater importance would be found in May weather in eastern Siberia, although the functioning of the alternate host of leaf rust in that region (Lake Baikal area) may result in marked differences in the relationships between early spring weather and rust, in comparison with areas where the rust overwinters in the uredinial stage. In India, MORELAND (1906) and E. J. BUTLER and HAYMAN (1906) found that January weather is critical, and that there is no relationship between October rainfall and rust development the following spring. January in the Indian Plains is the month in which the first leaf rust infections normally occur and although in this case the source of rust is wind-borne spores from the hills and not overwintered rust in the Plains, January in India appears to correspond to the "critical month" in the Great Plains.

Finally, it has been shown (page 171) that there is no regular connection between fall rust and that in the spring or between the amount of rust one year and that the next year. Therefore rust intensity at these times could not serve as the basis of rust predictions.

Chapter XII

NATURAL, REGULATORY, AND CULTURAL RUST CONTROL

Control by the physical environment: — When we think of natural control of a plant disease, we are prone to think primarily of the checking of the disease-causing organism by its competition with other organisms, or its inhibition or destruction by hyperparasites or predatory animals. Yet we must not lose sight of the fact that the pathogen is subject to controlling forces far more important than these, the forces of the physical environment. We have recounted the limits of environmental variables within which the leaf rust fungus can survive and multiply at the expense of its host plant, and here it is only necessary to call attention to the fact that once any of these variables departs from the range favoring the rust, the latter is subjected to natural control of a common and absolute type. Wide as is the tolerance of *Puccinia triticina* to environmental variations, as compared with many other plant pathogens, its limits of tolerance are well marked and often passed, so that, even in wheat-growing areas, for many months of the year the fungus is often inactive, or even unable to exist, and there are vast areas of the globe, in the polar and equatorial zones, in deserts and at high altitudes in which natural control of the fungus by the physical environment is so absolute that its development is wholly impossible, and even when we pass to the more favored areas where wheat is grown, every season or location of "light rust" exemplifies the dominant rôle of the physical environment in preventing the rust from free expression of its parasitic abilities, a rigid natural control which only relaxes occasionally and permits the rust to develop in epiphytotic fashion.

Since the effects of the physical environment on leaf rust have been treated in detail in Chapters IX and X, we will omit any further discussion of them, beyond these orientative remarks, and pass to the subject of the natural control of leaf rust by biological agents.

Control by competition with other fungi: — On page 139 attention was called to the fact that the activity of certain other wheat pathogens may limit that of the leaf rust fungus, by devitalizing the host plant so that it becomes more resistant to leaf rust (*Helminthosporium* foot rot), by occupying the wheat tissues before the rust can invade them (stem rust, stripe rust, *Septoria tritici*), or by destroying leaves that harbor leaf rust (*Septoria tritici, Fusarium nivale*). In all of these cases but one, that of *Septoria,* the harm done by the antagonism of other fungi is regularly worse than any good they might accomplish through reduction of leaf rust. But the action of *Septoria tritici* in destroying rust-bearing leaves of overwintering wheat at times plays a very important part in reducing the leaf rust inoculum available in the spring (CHESTER, 1944) and thus may be a decisive factor in the ensuant rust intensity. *Septoria tritici* is responsible for much de-

struction of wheat tissue, but the harm thus done may possibly, in some cases, be outweighed by the beneficial effect in retarding spring renewal of leaf rust.

Control by Darluca filum: — *Darluca filum* is a not uncommon fungous hyperparasite of the wheat leaf rust fungus. It sometimes becomes a serious pest in greenhouses where pure cultures of leaf rust are being studied. In nature it is not usually abundant, but often can be found in small amounts on rusted wheat. TRAYLOR (1940) examined 300 collections of wheat leaf rust made in Oklahoma in the epiphytotic year 1938 and in 1939, and found a single specimen parasitized by *Darluca,* — this was on one of the 1939 collections. In the fall of 1941, *Darluca* was found occasionally in Oklahoma on leaf rust which at that time was scattered but fairly abundant. On April 14, 1942, when rust was slow in developing, and the weather was very wet and the temperatures cold to moderate, *Darluca* was found on 4% of leaf rust specimens at Stillwater, Oklahoma. On grass rusts, *Darluca* is often found in much greater abundance, especially in the autumn.

KEENER (1934) considers it very possible that *Darluca filum* includes many physiologic races or strains. It is found on a considerable number of rusts, including rust species that have little systematic relationship to one another. KEENER successfully cross-inoculated *Darluca* on species of *Colcosporium, Frommea, Kuhneola, Puccinia,* and *Uromyces,* and the writer obtained luxuriant *Darluca* infection on wheat leaf rust using as inoculum *Darluca* from the cottonwood rust, *Melampsora medusae.* KEENER (1934), FEDORINCHIK (1939), TRAYLOR (1940), and HARDISON (1942) have all shown that *Darluca filum* freely cross-infects various grain and grass rusts, but KEENER'S experiments indicate that any two given collections of *D. filum* may differ somewhat in their rust host ranges, *i.e.* they exhibit physiologic specialization.

Darluca filum is recognized as clumps of tiny, spherical, black, shiny pycnidia seated among the uredospores of leaf rust (and also among the teliospores in the cases of some other rusts). The pycnidia have circular openings through which ooze out long tendrils of colorless spores, 12-18 $\times$ 3-5μ in size, oblong and straight, with one crosswall. They may or may not be equipped with bristles at the ends. When young, the pycnidia are paler, smoky colored at the opening, with the color progressively more dilute downward. There may be 6 or more on a single leaf rust uredinium. The wall of the pycnidium is quite firm, and not fragile. KEENER gives further details of the morphology of the fungus.

The hyperparasite develops best on large, luxuriant rust pustules of "4" type. On resistant-type pustules, pycnidia appear if there is no necrosis accompanying the rust pustule. HARDISON has noted unusual rust symptoms on leaves and stems, when the rust is parasitized by *Darluca.* Sometimes sporulation of the rust is almost or entirely prevented.

In its environmental relations, *Darluca filum* is fairly tolerant of variations. According to FEDORINCHIK the spores of *Darluca* begin to germinate in 3 hours at 15°-25° C., with optimum germination at 20°-21° C. and many germinating between 10° and 26° C. These are temperatures that are also favorable for growth of both wheat and leaf rust. The spores withstand heating to 30° C. for 20 days, which is a means of freeing *Darluca*

spores from those of leaf rust. FEDORINCHIK recorded the incubation period of *Darluca filum* as being 4-7 days at 8-35° C. and 5-6 da. at 22.4° with 70-100% relative humidity. The incubation period is usually regarded as the lapse of time between inoculation and the appearance of the first noted reaction to the parasite, and if this was FEDORINCHIK's conception, his incubation periods are much longer than those obtained by the writer. At room temperature the period from the time of inoculation of uredinia with *Darluca* spores till maturity of the *Darluca* pycnidia and release of the first conidia was as short as 65 hours, while at the end of 87 hours long tendrils of conidia were oozing out of the pycnidia. This is a remarkable fact when one considers that the *Darluca* spores can germinate, the germ threads can infect the rust mycelium or spores, withdraw from the rust sufficient material for production of fruiting bodies and spores, develop relatively elaborate pycnidia, and within them conidiophores, abstract conidia from these, and discharge the latter to the outside, all within the short space of 65 hours.

The life of a leaf rust uredinium is normally about two weeks, and we can understand the necessity that its hyperparasites have a very brief cycle of development as an adaptation to the short life of its substrate, but the extreme brevity of this is none the less remarkable.

The necessity for a short developmental cycle is also indicated by the fact that *Darluca filum* appears to be an obligate parasite, capable of living only at the expense of living rust. The writer has made numerous attempts to culture *Darluca* on laboratory media without any success, nor would the spores infect healthy wheat leaves. FEDORINCHIK could inoculate wheat with a mixture of *Darluca* and leaf rust spores, obtaining *Darluca,* but inoculations of *Darluca* alone were without result. The writer attempted to demonstrate parasitism of *Darluca* promycelia on leaf rust promycelia without definite results, although very rarely a *Darluca* hypha would make one or two coils about a rust hypha. SAPPIN-TROUFFY (cited by KEENER, 1934) has demonstrated *Darluca* hyphae entering rust uredo- and teliospores in water drop mounts. The depauperate growth of *Darluca* on rust uredinia of resistant types is also in conformity with the view of its obligate parasitism.

Before leaving the subject of the parasitism of *Darluca,* attention might be called to a phenomenon involving *Darluca,* which, although it does not directly relate to leaf rust, appears to be a relatively unknown and yet very remarkable instance of secondary hyperparasitism, and therefore worthy of additional record. SPEGAZZINI in "Mycetes Argentinenses" (Part 4, No. 367 An. Mus. Nac. de Buenos Aires, 12, 1909) cites a case in which the grass, *Andropogon condensatus,* was rusted by *Puccinia andropogonicola,* which was hyperparasitized by *Darluca australis,* which last, in turn, was parasitized by *Didymella darluciphila.*

Finally we come to the question of the function of *Darluca filum* in controlling wheat leaf rust in nature. The hyperparasite is widely distributed, yet is not very damaging to leaf rust on a wide scale. This cannot be explained by its temperature relationships, but may relate to moisture requirements. In the greenhouse *Darluca* is only troublesome when humidities are kept high, and FEDORINCHIK points out that it develops best where there is high humidity in moist sites. He appears to be the only worker

who has made deliberate attempts to control leaf rust by spraying fields of wheat with *Darluca* spores. (The original paper has not been seen, and the abstract gives no information on the outcome of this experiment.) While it would be well to have further data on this possibility, it appears somewhat unlikely that this could develop into a practical means of rust control, since *Darluca* inoculum is regularly present, yet there appears to be no case on record in which the hyperparasite has shown any effective degree of control of the rust. The activity of *Darluca* is limited by environmental conditions over which man has no control, and his efforts at supplementing the inoculum already present could hardly be expected to change this situation.

Control by other hyperparasitic fungi: — HASSEBRAUK (1936, 1937) has reported some difficulty in keeping greenhouse leaf rust cultures free from hyperparasitism by *Verticillium nivcostratosum.* This imperfect fungus covers the pustules with abundant, white, somewhat crusted mycelium which renders the rust spores incapable of germinating. It also attacks pustules of other cereal rusts. As it is dependent on very high moisture, and only succeeds in parasitizing slowly developing uredinia, HASSEBRAUK was able to control it by aeration and supplementary lighting.

HASSEBRAUK also recorded a number of other hyperparasitic fungi with similar habits. These included *Cephalosporium acremonium, Verticillium fungicola,* another fungus of verticillate growth, and one that was probably a *Fusidium* or a *Spicaria* or *Cylindrium* species. None of these was found doing important damage to rusts in nature, yet all were parasitic on the rusts and incapable of spreading to healthy leaf tissue or infecting it if inoculated directly on it. They can probably be disregarded in relation to any significance in controlling leaf rust in nature.

LEVINE, GRANOVSKY, and LEACH (1932) found that stem rust spores which had passed through the intestines of slugs produced infections that were often parasitized by an unidentified fungus and bacterium, neither of which would attack healthy plants. They reported that "all of the cereal rusts are apparently susceptible" to these hyperparasites. High humidity was necessary for the fungus but not for the bacterium. Again there is no evidence that these have any importance in nature.

Control by predatory insects, snails and slugs: — On page 164 there is an account of several species of insects (*Cecidomyidcae,* spring tails, thrips, and Phalacrid beetles) which feed on leaf rust uredospores. There is no indication that any of these have economic importance in the natural control of leaf rust, and, in fact, the harm they do by disseminating rust spores may outweigh any benefit from the reduction of rust inoculum.

To these cases may be added that of D'OLIVEIRA (1940*b*) in which the activity of aecia of rusts (including by implication, aecia on *Thalictrum* which may have been those of wheat leaf rust) in the fall was checked by the partiality of snails and slugs to the pustules. Again, this may be regarded as one of the many interwoven factors which contribute to make up the balance of *Puccinia triticina* with its biological environment, but not one to which may be ascribed economic importance.

Control by regulation: — The leaf rust inoculum for over two million acres of wheat in the Plains of Peninsular India (Hyderabad, much of Bombay-Deccan) must come, each year, from some 3400 acres of wheat in the Nilgiri and Palni hills (*see* page 169). Therefore MEHTA (1940) has recommended that the wheat sown in the hills in April-June be suspended, and that sowings of July-August in Chitaldwog and Bellary be delayed, since these act as secondary foci of infection. He considers that leaf rust outbreaks in the great Indo-Gangetic Plain could be checked effectively by prohibiting August-September sowings in Nepal, allowing sowing there only at the usual time in October-November. Most effective of all would be to suspend wheat culture for 2-3 years in the hills at altitudes of 3000 ft. and above, where, alone, the rusts oversummer. MEHTA considers that such a plan would be difficult to carry out, since these small sources of infection are under the control of different governments, the cooperation of which would be necessary. Americans, who have experienced crop control regulation governing countless millions of acres, might find it difficult to understand the problem of restricting wheat production on these 3400 dangerous acres. It certainly appears that MEHTA's proposal is sound and that the prospective gain would enormously repay the cost of the regulation, even if the hills farmers were reimbursed 100% for the wheat taken out of cultivation.

An analogous situation exists in spring wheat areas of Russia where small patches of winter wheat serve as sources of infection for great acreages of spring wheat. RUSAKOV and SHITIKOVA-RUSAKOVA (1929, 1932*a*) have advocated the elimination of winter wheat in such areas, which, under Russian government, should be easily accomplished.

It has been suggested that the planting of rust resistant wheat varieties exclusively in a barrier zone a few hundred miles wide in the southern Great Plains would largely prevent the annual northward migration of leaf and stem rusts and result in a marked reduction of rust losses in the North, as well as in the barrier zone itself. Such an undertaking assumes that well-adapted rust-resistant wheat varieties are available for the southern Great Plains, which has not been true in the past, but is gradually being realized. It also assumes the means for compelling the planting of new rust-resistant wheat varieties by many farmers who have not been educated to the value of them, but this is not as radical a step as some of those already accomplished by the Agricultural Adjustment Act. Furthermore, this is a quantitative matter, — it might not be necessary to have rust resistant wheats on all the acres in the barrier in order to realize benefits of having them on most of the acres. But a serious flaw in such a proposal is the assumption, without the proof insofar as leaf rust is concerned, that the main source of inoculum for the northern half of the Great Plains is uredospores from the South. In the north-central United States, air-borne rust spores are regularly caught in spore traps after but not always before the rust is already well established in the northern fields. It is entirely likely that the majority of these spores which are viable are not from the South at all, but of local origin, and that more extensive searches than have yet been made will reveal the source of the primary inoculum in hibernating rust to a much greater extent than has heretofore been realized. We have

seen in a number of instances in earlier pages, that the principles of stem rust epiphytology cannot be freely applied to leaf rust epiphytology, as has commonly been done, and this is a case in point.

NAUMOV (1939) has suggested that "to biotypes of rust fungi there should be applied all of the principles and practices of quarantines . . . . were it not for the technical difficulties involved." He refers in particular to the possibility of introduction of rust races into areas in which they have not before existed, by means of very rare seed transmission. If such regulation involved examination of seed and identification of rust races thus found, the technical difficulties would, indeed, be practically insuperable. NAUMOV did not mention another, much more practical alternative, namely the surface disinfestation of seed wheat intended for long-distance transshipment. The world distribution of leaf rust races has already been shown to be such that, in general, such a requirement would need to apply only to intercontinental shipments, because of the relative homogeneity, with a few exceptions, of the race floras within given continents. There are few data on the effect of seed disinfestants on seed-borne rust spores, but these could easily be obtained. Quite apart from the rust aspect, such disinfestation should be compulsory for intercontinental shipment of seed grain from the point of view of possible dissemination of other seed-borne pathogens.

NAUMOV has made another useful suggestion, namely that seed wheat from the area in which *Isopyrum fumarioides* functions as an alternate host of leaf rust be examined and declared free from *Isopyrum* seed before it is permitted to be sent to other areas.

Primitive rust "control" practices: — In the centuries following the ancient attempts at rust prevention by prayer, sacrifices, and feasts, there doubtless were many empirical recipes for this purpose of which little record remains. In 1620, WORLIDGE (cited by WATERHOUSE, 1938) suggested prevention of the "noxious dew" by smudge fires or by making the crop obnoxious to the "distemper" by placing in it woolen rags steeped in salt of tartar solution or white wine vinegar, or treated with pepper. He also made the interesting recommendation of having two men stretch a rope between them and drag it through the field. This practice was later mentioned by OLIVIER DE SERRES (ERIKSSON and HENNING, 1896), who recommended that the dew be thus removed from the plants, one hour before sunrise. From his questionnaire addressed to growers in Amur province of Siberia, RUSAKOV (1927*c*) found that as recently as 1925, farmers there were still following the practice of knocking off the dew with ropes or whips or a horse-drawn leveller, or spraying the fields with water to "wash off the rust". It was reported by farmers that "the ropes shook off the rust from the heads, and there was no damage". GASSNER (1915*c*) tested this practice in Uruguay, but no difference in the amount of rust in treated and untreated plots was observed. During the 19th century there were also many recommendations of burning the rusted straw and of treating fields with such substances as salt, herring or herring brine, and iron salts. The effect of salt is mentioned on page 133, and modern knowledge of the rusts does not bear out the value of the other primitive practices noted above.

Selection of planting site: — For more than half a century, it has been recommended that the greatest losses from rusts in general, and wheat leaf rust in particular can be avoided by choice of well-drained, somewhat exposed upland sites for wheat culture. It is a common observation that the greatest rust damage is in low, wet lands, and furthermore it is good farming practice to use such lands for other crops which are favored by such locations.

We have seen that in many cases volunteer wheat from the previous crop is an important breeding place or means of survival of rust which thus provides inoculum for the succeeding wheat crop. This is the principal reason for danger to wheat from a previous wheat crop; surviving uredospores are of minor importance and the surviving teliospores are normally non-functional. A general recommendation to avoid planting wheat directly following wheat is hardly justified on the basis of leaf rust danger (although it may be warranted on other pathological grounds), since the problem of volunteer grain may be largely solved by tillage, and agronomic practices in wheat-growing areas and the economics of farming in such areas will often prevent such alternation of crops.

A second consideration on land use concerns the growing of wheat following a leguminous crop. The latter adds nitrogen to the soil, and we have seen that high nitrogen in the soil predisposes wheat to rust. Again, no general recommendation can be given. There are areas where soils are already well supplied with nitrogen and in such cases a leguminous crop might best be followed with a crop that draws heavily on the nitrogen, before planting wheat (*see* page 135). In other cases the danger of the nitrogen effect on rust might be offset by fertilization with K and P. In soils deficient in nitrogen, the use of a leguminous crop might benefit the wheat to an extent greater than is offset by increasing its predisposition to rust.

Finally from the standpoint of leaf rust, the rotation systems to be preferred are those which favor early maturity of the succeeding wheat crop. On the other hand, some of the recommendations that occur in the literature are quite meaningless, as that of "rotating for better growth" or "judicious rotation and fallowing".

In the spring wheat areas of North America (Bolley and Pritchard, 1906) and Russia (Grooshevoi and Maklakova, 1934; Boevski, 1936; Naumov, 1939) it has been emphasized that no winter wheat, not even trial plots, should be grown near spring wheat. Boevski soundly adds that where winter and spring wheat are both grown in a given area, the spring wheat fields should be located as far as possible from winter wheat fields and on the prevailingly windward side of them, and that insofar as possible adjacent fields should be planted alternately with wheat and other crops. Volunteer wheat in fields near to those planted in wheat should be eradicated by tillage.

Rows of trees on the windward sides of wheat fields have some value in protecting wheat from air-borne uredospores but this value is limited by the fact that much wheat is grown on treeless plains, and that spores borne in by the wind from a distance are of less importance in the leaf rust cycle than local sources of infection where the rust has survived in the wheatfield itself. Yet one can conceive of cases in which the choice of a protected

field rather than an unprotected one, other factors being equal, could perceptibly reduce rust damage by delaying the time of its intense development.

Seed: — It has long been recognized that disinfestant seed treatments have no value in leaf rust control. Disinfestant treatments for smut control will kill rust spores on wheat, but we have seen that these spores have no rôle in the annual recurrence of rust, and common observation shows the complete lack of correlation between smut treatments and leaf rust.

Yet, until quite recently, seed treatments have been held by some growers to be related to rust control. RUSAKOV's questionnaire of 1925 (1927*c*) revealed that it was still considered possible to control rusts in Russia by washing the seed with water, disinfesting it with formalin, or washing it with lime and water, and in SORAUER's collection of recommendations for rust control (1909), the use of old seed was included. In 1917 some interest was aroused in the "Wolfryn Electrochemical Process" exploited by DE-WOLF and FRY in England, and claimed to increase yields 20-30% and reduce losses from rust, bunt, and wire worms. The process consisted in immersing the seed in a salt solution and passing an electrical current through it for several hours. Experiments in several countries failed to bear out these claims, and LEIGHTY and TAYLOR (1924) actually found in tests in the severe rust years 1921 and 1922 that the yields gave 96:1 odds in favor of untreated seed.

The Russian practice of vernalizing seed to accelerate maturity of the crop and thus avoid rust damage is discussed on page 138.

Finally, the use of plump seed from a rusted crop was advocated as early as 1821 by ELIAS FRIES and since by BOLLEY and PRITCHARD (1905, 1906), MCALPINE (1896), COBB (1890-1894) and others. The value of this is considered in connection with mass selection for rust resistance, on page 218.

Preparation of soil: — The general recommendations for rust control often include advice to sow the seed at a uniform depth in a well-prepared seedbed. This is a good agronomic practice, but it is difficult to see any direct connection between a well-prepared seedbed and subsequent rust development, unless such preparation hastens maturity of the crop. Insofar as good seedbed preparation favors vigor and succulence in the crop, it predisposes the plants to rust. It would be more effective, in making recommendations for control of rust (or other diseases), to avoid such generalizations as have no important bearing on the subsequent development of the disease, in order not to lose emphasis on the really important control measures, regardless of the agronomic value of the generalizations.

We have seen that a high proportion of nitrogen in the N:P:K ratio in the soil leads to increased rust destructiveness both by increasing the susceptibility of the wheat plant and by delaying its maturity. The latter of these two effects has been generally recognized since the time of the early work of COBB, BOLLEY, MCALPINE, and ERIKSSON, and is the basis of the standard recommendations in all wheat-growing areas, of avoiding excessive nitrogen fertilization (manures, commercial nitrogenous fertilizers, leguminous crops), and correcting relatively excessive nitrogen in the soil by amendments of potassium and phosphorus. However, such recommendations should be clearly qualified, as has not usually been done, by relating

the fertilization practice to local soil and climatic conditions and to the effect of the fertilization on wheat growth and yields apart from its effect on the rust. It is entirely possible that a certain procedure of fertilization might, in a given case, lead to increase in the damage from rust, but at the same time so raise the general level of production that the rust loss is more than offset by the salutary effect on wheat growth and productiveness. It follows that although the principle of rust reduction by decreasing the nitrogen in the N:P:K ratio is sound, it must be applied only with due consideration of the other agronomic effects of the fertilization, so as to effect the greatest economic gain. Particularly is this true when rust resistant wheat varieties are used.

No other type of soil amendment can at present be recommended as an aid in rust control. The negative, harmful, or inconsistent results of treating soils with a variety of substances were recounted on page 133.

Since leaf rust is more destructive in low wet lands, it naturally follows that drainage will assist in reducing its destructiveness, and this has been sometimes included in the recommendations for rust control. It should be pointed out, however, that soils and locations that are naturally so wet as to require drainage are probably more suited for vegetables, alfalfa, or other crops, than for wheat, which is more economically grown on naturally well-drained upland sites where drainage practices will rarely be necessary.

Weed control is another of the indefinite rust-control recommendations that are sometimes encountered. Without specific elaboration it means little. Some of the relationships between weeds and rust can be mentioned, however. Insofar as weeds act as hosts of the rust, they may in general be discounted, except in the case of volunteer grain and of the weed alternate host of the rust in Siberia alone. Weeds in wheat cannot be eradicated by cultivation, and their control by practices to insure good stands (seed treatment, attention to approved agronomic practices with reference to seed quality, and date, rate, and depth of planting) is only indirectly related to rust control, — it can be recommended for encouraging strong crop development, such as can withstand rust attack without undue loss, but not as a specific rust-preventive measure.

Planting date, rate, depth, and method: — The effects of planting practices on incidence of rust were analyzed on pages 136-138. From this analysis it follows that leaf rust damage is reduced by avoiding early sowing of fall wheat and late sowing of spring wheat. Where winter injury is common, winter wheat should be sown on a medium rather than a late date, since the latter predisposes the wheat toward winter injury, which in turn delays maturity of the wheat in the spring, thus favoring rust damage. It is emphasized that spring wheat should be sown as early as good local agronomic practice permits. The benefits of sowing at the most favorable time for rust evasion are enhanced if, insofar as possible, all the wheat in a given community is planted at approximately the same time, and if the varieties planted in the community are relatively homogeneous in their period of maximum rust attack and of maturity.

With reference to rate of planting, the analysis in Chapter X indicates that practices that result in either unusually wide or close plant spacings,

particularly the former, should be avoided from the standpoint of rust control. The optimal rate and depth of planting for each locality, as determined by trial and error over past years, are associated with highest yields, since they tend to avoid the most damaging effects of environmental hazards, insects, and diseases, including rust, and any considerable departure from these local optima can be expected to result in lowered yields, either through increased rust destructiveness or as a consequence of other hazards.

Care of the crop: — In general wheat is not considered to require tillage, and once the crop is planted it is undisturbed until harvest time. An exception is seen in Russian recommendations (RUSAKOV, 1926*b*, NAUMOV, 1939) that winter wheat be harrowed in early spring to destroy leaves on which rust has overwintered, break up the crusted soil, and invigorate the crop.

Very little scientific attention has been given to the effect of fall pasturing on subsequent leaf rust development in winter wheat, yet this has an important influence on the crop, and in some wheat areas the value of the pasturage is regarded as being equal to or even greater than that of the grain yield. Wheat that is planted with the intention of pasturage as well as grain production, is usually sown early, sometimes as much as a month in advance of the optimal date. We have seen that such early-sown wheat is sometimes heavily rusted, which indicates the importance of the development and use of wheat varieties that are resistant to leaf rust *in the seedling stage,* where pasturage is a consideration, and early planting is necessary.

It seems to be agreed that when wheat is planted early, a judicious amount of pasturing is beneficial to avoid undue vegetative development which leads to winter-killing. Such pasturing will also remove a considerable amount of rusted foliage that might otherwise overwinter and serve as a source of early spring infections. But, on the whole, the effects of pasturing on rust damage are probably only incidental to the purely agronomic aspects of this practice. Insofar as pasturing promotes vigorous wheat growth, it increases the predisposition of wheat to the rust, but this may be more than offset by a general raising of the level of yield, and evasion of the most serious consequences of rust by shortening the period to crop maturity.

An exceptional case is that in the spring wheat culture of eastern Siberia, where pasturing of the infrequent fields of winter wheat is discountenanced, since the cattle tracks favor overwintering of the rust and, from it, infection of the main spring wheat crop (RUSAKOV and SHITIKOVA-RUSAKOVA, 1928).

As most wheat is grown without irrigation this point need not be ordinarily considered, with reference to leaf rust control. In the few areas where wheat is irrigated it should be remembered that leaf rust may, at times, be unusually destructive in irrigated wheat, and that therefore the use of rust-resistant wheat varieties is particularly essential in this case.

A few points with reference to harvesting wheat have a bearing on leaf rust control. Harvesting, by whatever method, should avoid, insofar as possible, the scattering of grain in the field, not only because of the waste involved, but because the volunteer wheat resulting is an important means

of survival of the rust between crops. In Russia it is recommended that threshing be carried out at a distance of no less than ½-1 km. from fields of winter wheat to avoid infection of the latter by spores released in threshing. Where wheat is combine-harvested, either this danger does not exist, because of the time interval between harvest and emergence of the new crop, or if it does exist, spread of the rust from the mature crop to the new one would occur naturally, regardless of precautions in harvesting.

ERIKSSON and HENNING (1896) mention the practice, many years ago, of burning rusted wheat stubble and straw for rust control. BOLLEY (1889*a*) considered that this was necessary to kill the teliospores, and COBB (1890-1894), with some doubt as to its efficacy, thought that possibly burning the stubble might help to keep down rusts. Some Russian growers were practicing burning of wheat stubble for this purpose as late as 1925 (RUSAKOV, 1927*c*), and destruction of stubble by deep plowing or burning was advocated by GROOSHEVOI and MAKLAKOVA in 1934.

Others have stressed the importance of turning wheat stubble under soon after harvest and not using rusted straw as fertilizer for cereal fields. We now know that uredospores in dead stubble and straw play little part in infection of the following crop if the spores have been exposed to the weather for even a relatively short time, while the teliospores are normally functionless. There is no purpose in destroying the straw and stubble for this reason. Such destruction robs the soil of organic matter that it should receive, and in some cases it must be left on the land as protection from erosion of the fallow land. From the standpoint of rust control, the only important point involved is the elimination of volunteer wheat by such tillage as is warranted, considering the desirable agronomic practices for each area. "Stubble mulching", in which the surface of the soil is disturbed without plowing, is likely to favor volunteering of wheat, and in this respect it favors rust survival.

An exceptional case is that in eastern Siberia where spring wheat may become infected both by overwintered uredospores from the last crop and by the functioning of the basidiospores. Here destruction of the stubble and old straw is very essential, and the recommended practice includes two plowings, one just after harvest and the other just before planting (BRIZGALOVA, 1935).

Eradication of wild hosts: — Although a few grasses closely related to wheat sometimes show a moderate degree of infection by *Puccinia triticina*, these are so slightly infected in nature that their eradication as a measure for wheat leaf rust control has no practical significance. This has been recognized generally since the time of ERIKSSON's early work.

On the other hand, we have seen that the eradication of volunteer wheat by cultivation is a practice of considerable importance in rust control. This is a general recommendation in the United States, Europe, Russia, India, and Australia.

Eradication of *Thalictrum* species for leaf rust control is probably justified nowhere in the world. While the great local importance of *Isopyrum fumarioides* in the annual cycle of leaf rust in eastern Siberia is recognized, its eradication is considered out of the question (NAUMOV, 1939), as with

cruciferous weed hosts of other rusts, because the plant is tiny, biennial, and very abundant as a wheatfield weed.

Salvage of rusted crops: — It has sometimes been suggested that the loss from rust may be reduced if a badly rusted crop is cut before full maturity. While this may apply to stem rust, it does not avail in the case of leaf rust. BOLLEY (1905) conducted experiments to test this point and found that if rusted wheat was cut at various times from the early dough stage till maturity, the 1000-kernel weight was progressively greater the later the cutting. GREANEY (1931*a*) obtained similar results. Delay in harvesting may result in lodging of some of the rusted culms, but in this case, according to BOLLEY, the lodged grain is mainly shrivelled and of little value in any case. NAUMOV (1939) also indicates that there is no advantage in harvesting a rusted wheat crop before its full maturity but emphasizes that this applies to leaf rust and not to stem rust.

We recall (pages 36-39) that rusted wheat is non-toxic and palatable to livestock and that it contains much more protein than healthy wheat hay. One can conceive of cases in which the use of a rusted crop for hay would have definite advantages and would result in a salvage of part of the loss due to the rust. Thus a farmer with a fair to poor stand of wheat, if heavy rust is indicated for the future, might profit by cutting the crop for hay and preparing the land for a summer crop. The rusted crop might equally well be used for forage, especially since, in the early springtime in question, green pasture is not plentiful, and this would give livestock the benefit of the leaves close to the ground, when wheat is in the rosette stage, before mowing could be accomplished.

Chapter XIII

RUST CONTROL BY THE USE OF FUNGICIDES

In the latter part of the 19th century, with the advent of spraying as an effective means of controlling some plant diseases, it was quite natural that scientists investigating the cereal rusts, and anxious to test any imaginable means of lessening their destructiveness, should direct their attention to fungicidal spraying, however remote its practical application might seem. So we find a number of attempts in this direction in the 90's. For the most part the results were not promising, so that it was not until thirty years later, following the development of sulphur as a fungicide and of dusting in place of spraying, that attention was again directed to chemical control of the cereal rusts, this time with more success. We will consider first the early and more recent tests of various fungicides on leaf rust spore germination and then take up the results of field experiments in rust control.

Response of the rust to fungicides: — Between 1891 and 1894, COBB in Australia, HITCHCOCK and CARLETON in the United States, and WÜTHRICH in Germany tested a number of chemicals for their efficacy in preventing the germination of leaf rust uredospores. Copper, mercury, and zinc salts were found effective in fairly high dilution. Certain alkaloids and other salts were not highly toxic to the spores. BEAUVERIE in 1924 had less striking results with the copper salts.

The efficacy of sulphur in preventing leaf rust uredospore germination was shown by GREANEY in 1928 and 1934. Spore germination was largely inhibited by the sulphur preparations Kolodust, Sulfodust, and Electric Sulphur, as well as by $CuCO_3$ and $CuSO_4$-lime dusts, but not by chalk, talc, or china clay, substances used as fungicidal dust carriers. Kolodust was the most effective of the sulphurs tested, probably because it was the finest. Oxidizing the sulphur did not increase its effectiveness.

HITCHCOCK and CARLETON (1893) led the way in greenhouse tests of fungicides. They sprayed greenhouse wheat plants with various chemicals and then noted the reactions of the plants to the chemical and to rust. The chemicals were used at rather high concentrations (1:50-1:200) and all ($FeSO_4$, $K_2Cr_2O_7$, $CuSO_4$, $FeCl_3$, $ZnCl_2$, $CuNO_3$, $HgCl_2$, and $CuCl_2$) were injurious to the wheat leaves at these concentrations. Some effectiveness in rust control was noted in the cases of all but $K_2Cr_2O_7$ and $CuNO_3$. Results were also negative or unsatisfactory with boric acid, NaCl, and $Pb(C_2H_3O_2)_2$. A principal difficulty was in thoroughly wetting the waxy surface of the wheat leaves.

GREANEY (1928) supplemented his spore germination tests with greenhouse experiments in which wheat plants were dusted with sulphur and then inoculated with leaf rust. Kolodust and Sulphodust gave good rust control, but if the sulphur was applied immediately after rust inoculation, 15-22% infection resulted.

PETIT (1932*a,b*) was successful in controlling wheat rusts in greenhouse tests involving the use of colloidal sulphur sprays, and dusts of sulphur, or sulphur (10%) + cyanamide (1%) + paraformaldehyde (1%) + lime (88%). Moderately good results were also obtained with sulphur (68%) + copper arsenite (30%) + saponin (2%); talc (78%) + copper arsenite (20%) + saponin (2%); talc (68%) + copper arsenite (30%) + saponin (2%); lime or gypsum containing 5% paraformaldehyde; and lime (48%) + decyanurized precipitated sulphur (48%) + formaldehyde (4%). While the dusts were effective, no liquid treatment appeared promising for practical use.

In a search for new fungicides that might be used in control of leaf rust and other fungi, STRAIB (1941) sprayed greenhouse plants, at varying times after inoculation, with a number of organic substances. Picric acid was more effective as a fungicide than ortho- or para-toluolsulphonamide, acridin, or .2% borax. The acidity of the picric acid seemed to be its chief factor in toxicity to uredospores, but the toluolsulphonamides and acridin had toxic value in addition to their *p*H. Picric acid and acridin, each at .1%, killed all rust spores tested in 24 hours, at 20° or 14° C., but .4% toluolsulphonamide was effective only against *Puccinia glumarum*. STRAIB got absolute control of wheat leaf rust by spraying with .1% para-toluolsulphonamide if applied immediately after rust inoculation, but applications 2-4 days after inoculation were less successful. Acridin at .4% was moderately effective against wheat leaf rust. Both the sulphonamides and acridin injured the wheat foliage at fungicidal concentrations; picric acid was less harmful but injured some plants.

On the basis of these tests it can be concluded that sulphur and certain salts of the heavy metals, particularly copper, are effective fungicides against *Puccinia triticina* if applied before infection occurs. The organic substances tested by STRAIB do not appear to satisfy the qualifications of good fungicides, and since, in addition, the toluolsulphonamides are expensive and the picric acid is toxic and explosive, one cannot see any future possibilities in them as practical means of leaf rust control.

In discussing fungicides for *Puccinia triticina* mention should be made of KIASHKO's finding (1935) that the rust on wheat leaves was killed by 72 hours' exposure to 300 gm. of H_2S in 1 cu. m. of air. This has only theoretical interest at present, but it appears to be a unique case of killing of the rust after infection has been established.

Since sulphur has been used almost exclusively in the successful field tests of rust control, a word as to its mode of action is not irrelevant. The subject, with reference to rusts, has been reviewed by GREANEY (1928) and RUSAKOV (1930), and these works can be consulted for further details.

The effect of sulphur is purely prophylactic. It can prevent spore germination or destroy the germ tubes, but once infection has been accomplished the rust mycelium appears to be relatively unaffected by sulphur on the leaf surface. Because the leaf area occupied by a rust spore and its germ tube is very small, the dust must be fine enough to insure good coverage of the leaf surface; its fineness also favors its adhesion to the leaf.

There is lack of agreement as to the chemistry involved in the toxic property of sulphur. In moist air it evidently forms pentathionic acid,

a S + H_2O oxidation compound, or oxidizes to form SO_2. If germ tubes are formed, the toxic product weakens their development; they show large vacuoles, and are usually unable to infect the wheat plant. According to GREANEY, the finer the dust, the greater its toxicity; high humidity greatly reduces the effectiveness of sulphur; high temperatures are less important; and the effect of the sulphur is mainly due to its chemical properties, not to physical changes of the sulphur on the wheat leaf.

Field experiments in protecting wheat with fungicides: — Between 1891 and 1896 there were a number of attempts at rust control by fungicidal spraying in the United States, Sweden, and Australia by BOLLEY (1891), KELLERMAN (1891), COBB (1891), PAMMEL (1892*b*, 1894), HITCHCOCK and CARLETON (1893), GALLOWAY (1893), and ERIKSSON and HENNING (1896), chiefly involving the use of copper, zinc, and iron salts. The negative or indifferent results obtained in these early attempts at chemical rust control account for the stagnation in this direction during the next 30 years. These men were leaders of thought on the rusts, and their ideas dominated work in the years that followed. We can now see some of the reasons for their discouragement with this means of rust control: the difficulties in making sprays adhere to wheat foliage; the expense of the materials and of spraying on a wide scale; the unsuitability of spray equipment for closely drilled crops; inadequate timing and frequency of applications; and the burning effect of the spray materials on the wheat foliage. With the later substitution of dusting for spraying, of cheap sulphur for the more expensive spray materials, and of improved methods of application, including the use of the airplane, in place of heavy spray equipment, these difficulties are largely overcome.

KIGHTLINGER and WHETZEL in 1926 revived the subject of chemical control of leaf rust and demonstrated in New York that where leaf rust alone was a factor, the yield was increased an average of 18.5% or 6 bu./acre (6.8-48.2%; 2.7-17.1 bu./acre) by sulphur dusting. Where both leaf and stem rusts were involved, the average yield increase from dusting was 19.6% (8.6 bu./acre) with maximum increase of 35.1% (19.6 bu.) and minimum of 6.6% (2.6 bu.).

At almost this same time other workers in the United States became interested in the possibilities of sulphur dusting for leaf rust control. MAINS in Indiana (1927b, 1930) increased the yield of Trumbull wheat 10.9% (3.5 bu./acre) and of Illinois No. 1, 24.3% (4.8 bu.) by dusting to control leaf rust of 70-100% intensity, with a little stem rust. BROADFOOT in Minnesota (1931) raised the yield of wheat 27% (7.65 bu.) by sulphur dusting to control stem rust. Leaf rust was well controlled by dusting in Kansas and North Carolina. In North Dakota BOLLEY, who, we recall, had been unsuccessful in his spraying experiments 37 years earlier, was able, by sulphur dusting, to increase yields by 15% (5 bu./acre) when leaf rust was controlled, and 8 bu./acre when both leaf and stem rusts were involved (BOLLEY and PRITCHARD, 1928), and he concluded that large scale tests were worthy of trial.

At about this time, GREANEY and BAILEY began their very extensive tests of sulphur dusting in Canada. We will consider these separately.

From 1934-1939 there were reports of sulphur dusting experiments from Indiana (CALDWELL *et al.*, 1934), Texas (DECKER, 1935; WATKINS, 1938; Anon., 1939), Kansas (JOHNSTON, 1937), and New York (K. D. BUTLER, 1940*a*, *b*). Some of these were entirely successful; others were less favorable but for reasons that do not invalidate the general effectiveness of this means of rust control. BUTLER'S tests, which, in a sense, are a continuation of those of KIGHTLINGER and WHETZEL, deserve special comment.

BUTLER'S experiments in 1937-1939, in which years leaf rust was not complicated by stem rust, were extensive and carefully designed for determination of statistical significance. He usually used 2-3 applications of sulphur dust at the rate of 30 lbs. per acre per application, and timed the application by the use of spore traps. In 24 tests, the dusted wheat yielded an average of 8.3 bu./acre more than the undusted, representing a profit of $2.90 to $7.26 per acre over the cost of dusting. The grade of the dusted wheat was also superior to that of the undusted control plots.

The work of GREANEY and BAILEY on control of cereal rusts by sulphur dusting in Canada is very extensive and detailed and directed primarily against stem rust, with leaf rust studied incidentally. For these reasons it is not possible, within the limits of the present work, to do more than bring out some of its more important results. The reader will be well repaid by detailed study of the original publications concerned (BAILEY and GREANEY, 1925, 1926, 1928; GREANEY, 1930, 1931*a*, 1934*a*; GREANEY *et al.*, 1941; and especially GREANEY, 1934*b*, which summarizes much of the earlier work).

The experiments were carried out at several points in Canada, in replicated plots and on farm fields, with use of hand dusters, horse-drawn dusters, and airplanes. Sulphur, usually Kolodust, was applied at rates from 12 to 60 lbs. per application per acre, in 2 to 24 applications at 2 to 14 day intervals. The results are analyzed for statistical significance and are expressed in terms of both quantity and quality of the yield.

Leaf rust was commonly a factor in the yield reductions of undusted plots, and it was usually reduced in amount by dusting; however, it is impossible to interpret the results strictly from the standpoint of leaf rust. This is partly due to the fact that stem rust was regularly a complicating factor, and partly because the dusting schedules were planned with stem rust control uppermost in mind, and therefore the applications were timed much too late for full effectiveness in leaf rust control. However there is no question that a substantial part of the yield increases was due to leaf rust control.

These increases usually ranged from 5 to 15 bushels per acre, and in some instances were 20 to 30 bushels per acre, or even more in exceptional cases. The dusted grain regularly was one to several grades higher than the undusted in quality. The profit from the treatment ranged from $1.34 to $11.81 per acre. As might be expected, the yield increase varied directly with the number of applications and amount of sulphur applied. The most profitable procedure involved a moderate number of applications with a moderate sulphur poundage per application. For example, in 1930 the most economical practice was 9 applications of 15 lbs. of sulphur each, this

increasing the yield from 6.6 bu. of "Feed" grade wheat to 19.9 bu. of "No. 1" grade wheat per acre.

GREANEY'S work is also an important contribution from the standpoint of the techniques and of the economics of cereal dusting, which will be considered later.

These experiments have been supplemented by tests of PETURSON and NEWTON in Canada in 1939. They were intended to secure a measure of loss from leaf rust and not as a practical test of rust control by sulphur dusting; for this reason 18 applications, of 30 lbs. of sulphur per acre, were used. By working with varieties of wheat that were susceptible to leaf rust but resistant to stem rust, it was possible to rule out the effect of stem rust and obtain a measure of leaf rust damage alone. In the 3 tests, the dusted plots yielded 51% (12.2 bu.), 30% (7.3 bu.), and 37% (11.7 bu.) more than the undusted controls, and the grade of the grain in each case was one point higher in the dusted plots. We can deduce, from these results, the part that was played by leaf rust in GREANEY'S experiments.

Apart from a few negative results of SCHILCHER in Austria (1935*a*, 1936), involving the use of calcium cyanide dust, which is toxic to wheat, the foreign work on chemical control of wheat leaf rust has been concentrated in Italy, Russia, and Australia.

FRAIPONT (cited by PETRI, 1929) evidently initiated the work in Italy with tests of spraying wheat with "Protector", which by controlling leaf and stem rusts, increased wheat yields from 3200 to 4200 lbs. per ha. Less favorable results were obtained with "Protector" mixed with $CuSO_4$ and sulphur. PETRI (1926*a*, 1929) treated wheat with $CuSO_4$ and with sulphur dust in 2-3 applications at 3 stations, and got effective rust control with both materials. SIBILIA (1927, 1934, 1935*a*, 1937) carried on experiments in dusting wheat with copper and sulphur dusts from 1927-1937. Three applications of sulphur at 15-day intervals gave good results. Eight applications of sulphur with a horse-drawn motor duster gave a profit of 20 lire per ha., and 4 applications of "Asporitol" (a copper dust) with a hand duster, by controlling all 3 of the wheat rusts, increased the yield from 20 q. of grain, with a specific wt. of 78.3 to 23.7 q., of 79.1 sp. wt., amounting to a profit of 439.25 lire per ha. He did not consider dusting practical unless rust was heavy. MENCACCI (1928) dusted wheat with a mixture of 97% S + 3% $CuSO_4$ and by controlling leaf and stem rusts increased the yields 58%, 13%, and 5% in 3 tests, with increases of specific weight from 72., 72.8, and 73.5 to 78.2, 73.9, and 75. respectively. He advised 3 applications in normal years, when the wheat is ripening. DEL GIUDICE (1931) reported success with sulphur dusting for leaf rust control, but MONTEMARTINI, in Sicily (1933) was unable to control leaf rust by this means.

The Russian work on fungicidal control of leaf rust was begun by RUSAKOV and SHITIKOVA. In 1927, RUSAKOV (1929*a*, *e*, 1930) was able to increase the yield of wheat in North Caucasus 18% over lightly rusted controls as a result of dusting with sulphur flowers. The following year at Omsk, sulphur dusting reduced the amount of rust by ½, although the work was started late in the season. In 1930, using 15 applications of sulphur dust, at the rate of 45 kg. per ha., leaf rust was reduced by 75% and yields increased 27-29%, the results being shown to be statistically

significant. RUSAKOV recommends dusting at 5-day intervals, beginning with the appearance of the first rust pustules, and continuing through the milk stage of the crop, at the rate of 15 kg. per ha. per application. When rust was unimportant, as at Otrada-Kubanskaya in 1930 and Krasnodar and Otrada-Kubanskaya in 1931, no significant yield increase was obtained by sulphur dusting (NAUMOV, 1939).

Mme. SHITIKOVA-RUSAKOVA, working with RUSAKOV and with POLYAKOV, also contributed to our knowledge of the effect of sulphur dusting on leaf rust and wheat yields (RUSAKOV and SHITIKOVA-RUSAKOVA, 1929; SHITIKOVA-RUSAKOVA and POLYAKOV, 1937; NAUMOV, 1939). In 1927, Preparation No. 12 of the All-Russian Institute of Plant Protection (5% sodium silico-fluoride + 93% fine clay + 2% thin lubricating oil to eliminate burning) was tested and found to equal sulphur in rust control. Dusting was not started until wheat was in the milk stage, and hence the differences between dusted and undusted plants were not great. In 1929 RUSAKOV and SHITIKOVA, dusting wheat with sulphur flowers at 15 lbs. per acre thrice weekly in 7 applications, almost completely eliminated rust with a 4-fold yield increase over the undusted checks. When there was little rust in 1934 in the Ordzhonikidzevsk region, sulphur dusting led to little yield increase. Similar results were obtained by LOBIK (1930) in North Caucasus in 1929, a year of light rust. Trials of a spray of sodium arsenate and lime under the same conditions showed that this mixture is injurious to wheat. With 6 applications of sulphur at the rate of 5 to 45 kg. per ha., ZAITSEV and POLOVA (1932) reduced leaf rust from 64% to a minimum of 7.4%. KIKOINA (1935), working in the Azov-Black Sea region, showed in 1933 that 8 sulphur dustings, of 40 kg. per ha. each, reduced leaf and stem rusts from 11.3 to 4.1% after heading, from 50.7 to 18.6% after blossoming, and from 60 to 46.6% at the milk stage, increasing the number of grains by 21% and the yields by 84.4%. GROOSHEVOI and MAKLAKOVA (1934) reported that airplane dusting with sulphur was often satisfactory in some parts of Russia, with rust damage reduced to 40-50%, although in other regions it was economically unwarranted. Finally BRIZGALOVA, who worked in eastern Siberia (1935), in experiments from 1932-1934, used 9 applications of sulphur flowers at the rate of 40 kg. per ha. In spite of the fact that dusting was begun too late in all cases, and that, as a result, the dusted plots were far from being free of rust, she measured yield increases from dusting of 32.5, 45.3, and 21.2% in 1932, 6.9 and 22.1% in 1933, and 9.7% in 1934.

In Australia, PHIPPS in 1938 used a colloidal sulphur spray with a spreader, in 4-7 applications, when unsprayed plots showed 85% leaf rust intensity, and increased yields by 7.3 bu. per acre (12%) and test weights 1½ lbs. per bu.

Dusting materials: — NAUMOV (1939) considers that a good fungicidal dust must be as fine as possible; have the highest possible sticking property; have a lasting period of toxicity; have small or insignificant solubility in water; have suitable aerodynamic properties; and retain its particulate nature during the time of its activity. On the whole, finely divided sulphur has these properties. NAUMOV's first point is open to question, as stated, —

there is undoubtedly a limit of fineness beyond which there is loss, not gain, in effectiveness.

It would seem, from the literature, that the standard dusting sulphurs now on the market are suitable for cereal dusting. GREANEY (1931*b*, 1934*a*, *b*) reported good results with Kolodust, Electric sulphur, Koppers dust, Koppers lime dust, and Sulfodust, but the best result with Kolodust and the finest of the other sulphur preparations, of 300-mesh fineness; 200-mesh sulphur was less suitable. K. D. BUTLER (1940*b*) saw no difference in Kolodust, Texas Gulf sulphur very finely ground, Swan sulphur, and other similar brands. Purity is a factor, according to DEL GUIDICE (1931), who found pure windblown sulphur more effective than windblown raw natural sulphur. The addition of an oxidizing agent ($KMnO_4$), slightly improves the fungicidal efficiency of sulphur according to BAILEY and GREANEY (1928). Although the Russian work on sulphur dusting in general shows marked rust control and consequent yield increases, it should be noted that Russian workers commonly used flowers of sulphur for dusting; this is a very coarse product compared with 300-mesh dusting sulphurs, and for this reason the maximum value of sulphur dusting may not be apparent in much of this work.

The effect of sulphur on the soil and on the wheat plant: — If a sulphur-dusted crop outyields a non-dusted crop, we naturally wonder whether beyond rust control, the sulphur exerts any direct effect on the soil or the wheat plant such as might influence yields. All of the evidence available indicates that there is no appreciable effect of this sort with the amounts of sulphur used for rust control.

GREANEY's review of the literature on this subject (1934*b*) was confirmed by his own findings. When rust was not a factor, even 5 applications of 45 lb. of sulphur per acre had no effect on wheat yields. No such effect resulted from the addition to the soil of 45 lb. of Kolodust per acre at 7-day intervals from the boot stage to maturity of wheat, although there was a very marked effect when, in a rust year, the same amount of sulphur was dusted on the crop. Even the addition of 765 lb. of sulphur per acre showed no fertilizing action reflected in crop yields. There was also no effect on rust from sulphur volatilizing at the soil surface. These findings were again confirmed in later tests (GREANEY *et al.*, 1941).

Likewise PHIPPS (1938), K. D. BUTLER (1940*b*), and BROADFOOT (1931) found that sulphur had no effect on yields of rust-resistant wheat varieties. BUTLER applied sulphur to the soil at a rate of 100 lbs. per acre without altering plant growth or *p*H of the soil. This last, he considers, may be due to the presence in the sulphur of tricalcium phosphate which is used in many sulphur dusts as a conditioner, and which may neutralize the acid effect of sulphur on soil.

Equipment for sulphur dusting of wheat: — For experimental dusting of small plots of grain, knapsack-type hand dusters are suitable. These will dust a swath about 4 feet wide and are particularly useful in small, replicated plots in studies of the effect of rust on yield. They have no place in rust control on a farm basis.

Horse-drawn dusters have been shown by BAILEY and GREANEY (1928) to be practical. Those available have been designed for row crops, and are not suitable for cereals without modifications, but the effectiveness even of improvised horse-drawn dusters led BAILEY and GREANEY to conclude: "It is certain that this method of rust control will be widely introduced and extensively used as soon as a thoroughly satisfactory cereal duster is developed." Such a duster should throw a swath 50 ft. wide without serious mechanical injury to the crop.

K. D. BUTLER (1940*b*) improvised a cereal duster by mounting a cotton duster on an old-model truck with high axles and narrow wheels. He used a 20 ft. or even a 40 ft. boom, capable of being folded back to permit passage through gateways. In the boom there were holes 1½" to 3" apart, and ⅛ - ⅜" in diameter, smallest in the center. These were tested for pressure and enlarged or made smaller as necessary. BUTLER emphasizes that good results are obtained only when the dust is applied with force. The truck was adequate, but BUTLER felt that a smaller, lighter model would be more efficient. It was operated at 4 miles per hour. If half the working time were spent in loading and other operations incidental to dusting, and the machine was actually in action only half the time, its capacity with a 40 ft. boom would still be 10 acres per hour — a practical amount for use on considerable acreages. According to BUTLER, his equipment is also suited for dusting vegetables, which would reduce that part of the cost due to depreciation.

Some mechanical damage to the crop results from the use of this type of equipment. BUTLER found that about 7% of the plants were killed or broken over, but that adjacent plants profited by this, so that the net crop loss from this cause was only about 1 bushel per acre. This was higher than desired, but not considered a serious obstacle to cereal dusting.

The specially designed Niagara tractor power duster illustrated by GREANEY (1934*a*, FIG. 24) appears to be well adapted to cereal dusting. The wheels are narrow and there is no cross axle, so that the machine passes over standing grain without injury, provided the wheels are kept between the drill rows.

In some respects the airplane is the ideal machine for dusting cereal fields. Mechanical damage to the crop is ruled out, under favorable conditions it is possible to dust 100 acres per hour, and the dust is applied with force due to the back draft of the propeller, which increases the effectiveness of its application. Some of the disadvantages in airplane dusting can be overcome. The cost is greatly increased by the expense of "ferrying" the plane from its home base to the fields to be dusted, but with the post-war airplane and airport development and with increasing demand for cereal dusting, this is a constantly diminishing factor. Other disadvantages cannot be easily avoided: for example the dusting airplane is unsuited for use in small fields; it cannot be operated by the farmer at his convenience or during a short period of favorable weather; and it is inefficient if the wind velocity is more than 10 m.p.h., which would mean, on open, windy plains, there would be difficulty in having the plane for operation at the infrequent times of relative calm. But in spite of these obstacles, the dusting airplane has been used successfully for cereals in Canada (BAILEY and GREANEY,

1928; GREANEY 1934*b*), and Russia (GROOSHEVOI and MAKLAKOVA, 1934), and doubtless has an important future for this purpose. In GREANEY'S experiments, dusting was accomplished by a plane flying at 100 m.p.h., about 15 ft. above the ground, with straight dusting flights of ½ mile proving satisfactory. Men on the ground signalled the paths the plane was to traverse. The construction and operation of horse-drawn and airplane dusters are described and well illustrated in the papers of BAILEY and GREANEY (1928) and GREANEY (1934*b*).

Time, rate, and frequency of dusting: — It is usually considered that dusting should begin when rust first becomes apparent in the fields or at least before it becomes abundant. This time will vary with the locality and season. In Russia NAUMOV (1939) advises beginning when plants are still in the rosette stage. In Canada, GREANEY (1931*b*) indicates that the proper time to begin is usually when 10 to 50% of the plants are headed; in this case, however, he is referring to dusting for stem rust control; dusting for leaf rust should necessarily begin much earlier. NAUMOV, with some justification, questions whether the moment at which pustules first become noticeable is not too late to start dusting for best results. In this connection the essential rôle of uredinial cycles before rust becomes noticeable (from 1 pustule per 10,000 leaves to 1 per 1000 leaves to 1 per 100 leaves, etc.; *see* p. 151) should be remembered. We have seen that this is a very vulnerable stage in the annual cycle of the rust; the effect of dusting in the "critical month", before rust actually becomes noticeable, has never been studied, yet theoretically it should be greatest of all at that time. Certainly the majority of workers with this method have waited until the rust has already reached a relatively advanced stage (even a few pustules per plant is an advanced stage considering the number of reproductive cycles required to raise the rust intensity from an overwintered trace to this amount) before beginning, and for this reason the maximum benefit to be realized by dusting has probably not yet been realized. The longer the delay before starting dusting, the greater may be the mechanical injury to the plants, the amount of dust required (because of larger plant areas to be covered) and the less the fungicidal effectiveness (since late in the season the weather is normally more favorable for rust infection than earlier). Instead of concentrating dust applications in the heading to milk stages, it is important to establish whether or not equal or greater protective effectiveness might be attained by the same number or fewer applications in the "critical month", or at least in the period from the rosette stage to heading.

SHITIKOVA-RUSAKOVA (1931, 1932*a*) timed the first dustings by determining the moment of the first introduction of wind-borne uredospores, with the use of spore traps. This would be a valuable guide to dusting time in regions where long-distance air transport of spores is the predominant means of establishing the first spring infections (Canada, Amur region of eastern Siberia), but would have little significance where the spring rust renewal depends largely on locally overwintered rust. Thus BUTLER (1940*b*) timed his applications by the use of spore traps, but since he has shown that in New York, long-distance wind transport of rust is not an important feature of spring leaf rust renewal, he was doubtless observing

locally-produced spores in his traps, and since RUSAKOV (1929*a*) has shown that rust must reach a concentration on the plants of 1% locally before it is registered in spore traps, the use of spore traps by BUTLER was probably superfluous, and direct examination of the fields would have given a better guide to the timing of the first dust applications.

There appears to be no record of tests of fall dusting of winter wheat in relation to rust development the following spring, and NAUMOV considers that, theoretically, this should have value. Early fall dusting for the protection of fall wheat pasture might possibly be useful during seasons of heavy fall rust, but since there appears to be comparatively little relation between the amount of rust in the fall and that in the following spring, it is doubtful whether fall dusting would be justified as a means for reducing inoculum for the spring growth.

GREANEY (1934*b*) advises dusting every year because rust cannot be predicted, even though it is actually needed only during seasons when the rust is heavy. He was thinking in terms of stem rust; we have seen that there is a basis for predicting leaf rust (page 172), and therefore this, after its further development, promises to indicate whether or not dusting is likely to be required in any given season, and thus reduce waste of time and money in unneeded applications.

It is generally agreed that the dust should be on plants before rains, and that since a heavy rain washes most of the dust away, such rains should be followed, as soon as practicable, with a dusting to serve as a protection until the next heavy rain. BAILEY and GREANEY (1925) found that such a schedule was more effective than arbitrarily dusting at weekly intervals, even though the same number of applications was used in both cases. This is a point in favor of airplane dusting, since wet soil may prevent the use of ground equipment for several days after a heavy rain, during which time there are likely to be numerous dews, and a consequent marked increase in infection. It has been pointed out that leaf rust infection of wheat often requires no more than 6 hours, which indicates that sulphur dust, to be effective, must be on the plants before or very soon after their leaves are moistened by rain or dew in order that infection be prevented. K. D. BUTLER (1940*b*), for example, inoculated wheat plants with leaf rust and then dusted the plants with sulphur after different lapses of time. His results showed only a trace of infection if dusting were done within 1 hour of inoculation, 17% infection if there was a lapse of 4 hours before dusting, 31% if the lapse was 6 hours, and 86% if it was 10 hours, as compared with 93% infection in the undusted controls.

Since dew usually remains on plants more than 6 hours in a night, this indicates that dusting, to be effective, should anticipate dew formation. As to time of day for dusting, the air is usually most calm in the early morning and evening hours, and these are the hours for most effective dusting, or even the only hours at which satisfactory dusting can be accomplished in windy plains regions.

For stem rust control GREANEY usually obtained the most satisfactory results with applications of 30 lbs. per acre, or even 45 lbs. when the rust was severe (1931*b*). Evidently leaf rust is more amenable to the treatment (perhaps because vertical stems are more difficult to cover with dust than

partly horizontal leaves), for K. D. BUTLER (1940*b*) found that 20 or 30 lbs. per acre was no more effective than 10 lbs., and RUSAKOV (1930) gives 15 kg. per ha. (13.4 lbs. per acre) as the recommended dosage in Russia.

Most workers have recommended 3 to 6 applications, usually at 5 day intervals, but BUTLER found that 2 were as effective as 3 or 4, and in any case the optimal number of applications for economical rust control will vary from season to season and from one locality to another; if there are frequent heavy rains the number must be increased.

Simultaneous control of other diseases and insects: — GREANEY'S work amply demonstrates that both leaf and stem rusts can be controlled by sulphur dusting, but where both diseases are destructive, the optimal schedule for stem rust is not entirely suitable, because stem rust develops later in the season than leaf rust. For best control of both rusts it would probably be better to use a schedule including 2-3 applications earlier than those required for stem rust alone.

GREANEY (1934*a, b*) has shown that the stem rust schedule of dusting simultaneously controlled wheat scab, black chaff, "smudge", and minor leaf diseases. In one test, scab was reduced from 80 to 13% by the dusting. K. D. BUTLER reports that the sulphur dust had no effect on insect populations but that powdery mildew of wheat was controlled by the dust, although perhaps not to quite the same degree as leaf rust. The total effect of sulphur dusting against incidental diseases, in addition to rust, should be included in the economic evaluation of this control method, and at times this will be an important entry on the "credit" side of the ledger.

Economic considerations: — Of the various experimenters with sulphur dusting for rust control, only GREANEY (1934*b*) and K. D. BUTLER (1940*b*) have computed the cost of the operation and related this to the profit from dusting.

GREANEY has supplied data on the cost of dusting and the profit from the practice between 1926 and 1930 at Winnipeg and Graysville, Manitoba, where both leaf rust and stem rust were involved. At Winnipeg in 1927, the profit from application of 240 and 225 lbs. of sulphur per acre in 8 and 15 applications respectively, was $15.28 and $13.27 per acre. In 1926, 1929, and 1930 when the rusts were less severe, 2 to 5 dust applications of 30 lb. per acre each returned profits of $1.07, $1.72, and $.65 per acre. At Graysville, six 30 lb. applications in 1927 yielded a profit of $11.87 per acre; 3 in 1928, $3.04; 4 each in 1929 and 1930, $1.34 and $5.93 profit per acre. The depreciation of the dusting machine was not included in these calculations.

K. D. BUTLER in New York found the cost of dusting was $2.15 per acre for 2 applications and $3.16 for 3. In 1937 and 1939, 3 applications netted a profit of $7.26 and $2.90, and in 1938, 2 applications gave a profit of $4.81 per acre, cost of the equipment included. These figures would have been still higher if the depreciation of the machine could be shared by other farm jobs for which it could be used, and if quality as well as quantity of yield increase had been considered.

Prospect of future usefulness of fungicides in rust control: — GREANEY (1934*b*) concluded that the cost of 3 dustings in Manitoba was prohibitive, but that 2 might be feasible. He recommends the practice as of value to seed growers, grain exhibitors, and experimentalists (1931*b*, 1934*a*). GROOSHEVOI and MAKLAKOVA (1934) felt that the treatment could be financially sound only in regions where the rusts are particularly severe and in years of epiphytotics. Their objection that methodical dusting in Russia would require thousands of planes, "exceeding any practical possibility", was made in 1934, and the war years have entirely changed the picture with reference to availability of planes and pilots.

New York is a region where wheat leaf rust is regularly quite destructive, this often being increased by powdery mildew damage, and K. D. BUTLER's figures encourage the view that sulphur dusting might be economically sound as a regular practice in that State.

There are a number of reasons why the margin of profit in favor of dusting wheat for leaf rust control may be expected to increase in the future:—

(i) great increase in post-war local availability of planes, pilots, and landing fields, with corresponding decrease in cost of sulphur applications;

(ii) concentration of the treatments in seasons and locations of severe rust, thanks to increasing ability to forecast rust epiphytotics;

(iii) more efficient use of the dust due to increasing knowledge of the most effective times, rates, and materials for application.

Thus, economical and profitable sulphur dusting for leaf rust control on a commercial basis is not beyond expectation, although increasing success in leaf rust control by the use of varietal resistance in wheat is unquestionably a more economical means of reducing rust losses, and it is to be hoped that this will ultimately advance to the point at which sulphur dusting need not be considered in ordinary wheat culture.

Chapter XIV

CONTROL BY RUST RESISTANCE

SORAUER's remark in 1909: "Die Rostfrage ist also in Zukunft eine Züchtungsfrage," was both analytical and prophetic. Adjustment of time of sowing, fertilization, destruction of volunteer cereal plants, applications of fungicides,—these are but adjuncts to the fundamental solution of the cereal rust problem: the breeding of cereal varieties that are resistant to rust,—at once the most certain and effective, and the most economical means of checking the ravages of the cereal rusts. No one who has worked intensively with plant diseases can exclude the necessity of some degree of prophylactic and therapeutic measures, now and in the future, but plant pathologists in general will agree that the development of inherent disease resistance in plants is, in the last analysis, the suicidal goal of plant pathology. And nowhere is this more evident than in the efforts at control of the cereal rusts. The disproportionate emphasis that has been laid on stem rust has interfered with the development of leaf rust resistance in wheat, with disastrous results as seen, for example, in the leaf rust epiphytotic of 1938, which found American farmers wholly unprotected with resistant wheat varieties, and in which Thatcher wheat, that had been bred for stem rust resistance and occupied millions of acres was wiped out, as an important commercial variety, by its susceptibility to leaf rust. But despite this ideological obstacle in addition to the technical difficulties in any cereal breeding work, progress has been made in the production of leaf rust resistant wheat varieties, and the control of the disease in the future, by this means, is most promising.

The use of rust-escaping varieties: — It has already been shown that any practice which favors early maturity of the wheat crop, lessens the destructiveness of leaf rust. It naturally follows that wheat varieties that are naturally early-maturing will, in general, suffer less from leaf rust than medium or, especially, late-maturing varieties. This fact has been common knowledge for many years, and has been the basis for worldwide recommendations on the use of early maturing varieties to control rust.

The scientific validity of these recommendations is seen in tests of HAYES, AAMODT, and STEVENSON (1927) in which the coefficient of correlation between advanced date of heading and leaf rust intensity was $+.19 \pm .09$ for 50 spring wheats and $+.23 \pm .12$ for 50 winter wheats.

But no general recommendation on the use of early-maturing varieties and the avoidance of later-maturing ones can be made without qualification. At times there are even more important considerations than leaf rust escape which indicate hazards in the use of early-maturing varieties. Thus, in the southern Great Plains, the variety Early Blackhull is not recommended in preference to the standard Blackhull, which matures 10 days later, and the early variety is not eligible for seed certification. The reason is that in this

region late spring frosts frequently occur when the heads of the early variety have already been formed, with the result that the sexual organs are sterilized. Early-maturing varieties may also be less productive as the result of a shorter growing season. Finally, although early varieties will escape the greatest destructiveness of leaf rust, they still may suffer considerable damage. For example, reference to FIG. 2 shows that if varieties of average time of maturity at the time when leaf rust intensity causes defoliation, are in the milk stage and suffer a crop loss of 18.7%, early varieties in the wax-dough stage at the same time would have 10.2% yield reduction.

From this it can be concluded that while the use of early-maturing varieties is of some assistance in evasion of the greatest damage from leaf rust it cannot be considered an effective control measure, and is only to be regarded as a temporary aid when suitable rust-resistant varieties are not available. Furthermore, the use of early-maturing varieties for this purpose should not be advised until it has been determined that their culture is agronomically a sound practice in any locality concerned.

The nature of leaf rust resistance: — There are several possible relationships between the leaf rust fungus and its host plant. The host plant may be functionally rust-escaping or klendusic: it is fully susceptible but because of its habits of growth or behavior (*e.g.*, earliness) it may escape the most serious effects of rust. At best this is only a partial escape; some rust damage is sustained. On the other hand the host plant may have a greater or less degree of resistance. At the extreme, there is the condition of immunity, in which the plant is totally exempt from disease attack. But immunity is not needed in order to solve the rust problem by breeding for rust resistance. If resistance is great enough that the fungus cannot reproduce itself freely, the plants, as a population, are not appreciably damaged by rust. The greater the population of such plants, and the area they occupy, the more this is the case. For example, a few plants of a highly resistant variety, if growing in the midst of many susceptible plants, may be materially injured by the many tiny necrotic lesions produced by spores from the neighboring plants, but if the resistant variety occupies many acres, there is no local rust reproduction, and the necrotic lesions are rare,— the plants are essentially free from rust damage.

Resistance may be based on different properties of the host plant. It may be a consequence of some peculiarity in the behavior of the host (functional resistance); it may depend on structures of the plant that impede rust invasion (waxy coatings which do not favor the standing of water droplets on the leaves, etc.), in which case it is termed morphological resistance; or it may relate to the chemistry and physiology of the host plant. In any case it may be associated with responses to external environment (*cf.* variations in reactions of wheat plants under different conditions of soil nutrition, page 129 *ff.*) or it may be inherent in the germ plasm of the wheat, heritable, and relatively independent of environment. It is with this last, solid, environmentally-stable, and heritable type of resistance that we are primarily concerned.

Still another concept deserves mention,—rust tolerance. LUKYANENKO (1934) has pointed out that two wheat varieties may be infested with iden-

tical amounts of rust, at the same growth stage, yet one variety suffers much more from the effects of this infection than the second. His table 3 shows that lines of some hybrid families with 65-100% rust suffered 44.5% yield reduction while other families with the same amount of rust lost only 9.5% yield. In the plants with 25-40% rust, the loss varied from 4 to 34%. The behavior of Fulhard wheat in the experiments of MAINS *et al.* (1934) shows a similar anomaly. This introduces a complication in the estimation of rust damage from known rust intensity, and adds still another factor to the already complicated problem of evaluating resistance in wheat. It may invalidate any comparison between different wheat varieties in which rust intensity is assumed to be a measure of rust damage.

Functional factors in rust resistance: — We have just seen that early maturity in wheat is associated with reduced losses from leaf rust. This is an expression of leaf rust evasion, rather than resistance, due to a functional cause,—the behavior of the host plant. A more characteristic form of functional resistance, the behavior of the stomata in relation to rust invasion, has been investigated by CALDWELL and STONE (1932).

They have shown experimentally that invasion by the rust regularly proceeds through closed stomata. When an appressorium forms over a stoma the latter normally closes tightly, and the appressorium appears to be an organ with the function of applying pressure between the guard cells and thus forcing the stoma to open and permit entry of the infection thread.

From this it follows that the behavior of the stomata does not represent a form of functional resistance of wheat to leaf rust and that if two varieties differ, for example, in the time of day at which the stomata open and close, this would not have any necessary relationship to differences in rust response of the two varieties.

MELCHERS and JOHNSTON (1939) have called attention to a peculiarity in Chiefkan wheat which might be regarded as a form of functional resistance. This variety regularly displays a chlorotic marbling of the foliage as the wheat matures, and leaf rust infections do not readily occur on the marbled leaves. The marbling does not appear, in itself, to be a serious detriment to the wheat plant, since Chiefkan is a high yielding wheat in the area of its adaptation, although the possibility is not excluded that its high yields are due to the fact that the beneficial results of its rust resistance more than offset the detrimental effects of the leaf marbling.

Morphological factors in leaf rust resistance: — For a starting point in interpreting the different reactions of cereal varieties toward rusts, it was quite natural that attention was directed at the more obvious morphological protective structures of the plants, and until the middle 1890's it was generally considered that these structures were responsible for rust resistance. A principal exponent of this view was COBB (1890-1894), who made measurements of structures of a few rust-resistant and rust-susceptible wheat varieties. The resistant varieties differed from the susceptible ones in having stiff, upright, narrow leaves, thicker cuticle, smaller epidermal cells, greater resistance of the leaves to breaking, and more, smaller stomata. The leaves of susceptible varieties were broader, flabby,

and pendant. COBB considered that cuticle thickness was a factor in rust resistance which prevented bursting forth of the pustules, although it was not regarded as interfering with infection. The cuticle on the lower side of the leaf was thicker than that on the upper side, which COBB correlated with less rust than on the upper side, regardless of whether the leaf was upright or twisted. No correlation was seen between resistance and thickness of the internal cell walls or pubescence, although COBB considered that hairs on the leaf surface aid in preventing rust spores from reaching cells at the leaf surface. The size of the stomata was evidently not a factor in resistance, since even the smallest permitted germ tube entry. In wheats with well-developed, waxy layers on the leaves, on the contrary, COBB showed experimentally that the wax layer so nearly covered the stomata that the germ tubes were unable to enter.

Beginning with ERIKSSON and HENNING in 1896, evidence began to accumulate that when a sufficiently large number of varieties are studied, differences in resistance and susceptibility cannot be explained, wholly or even mainly, by the morphology of the varieties, and as the concept of physiologic specialization began to take form, and reach a higher and higher level of development, it became increasingly necessary to look for the basis of resistance in the chemistry and physiology of the host plant, rather than in its structure.

ERIKSSON and HENNING (1896) in their studies of stripe rust concluded that "differences in susceptibility cannot be explained purely by mechanical causes, as thickness of outer epidermis wall, toughness of the leaf, number of stomata, waxy coating of surfaces, etc., but by a very complicated physiological process, the explanation of which has not yet been found. D. D. CUNNINGHAM and PRAIN, in 1896, found leaf rust resistance independent of the width of the wheat leaf. In a study of 186 wheat varieties, LITVINOV, in 1912, found no relationship between the kind and manner of hairiness and reaction to leaf rust. A year later VAVILOV reported no correlation between size and number of stomata in 18 varieties of *Triticum vulgare, T. dicoccum* and *T. monococcum* and resistance or susceptibility of the varieties to leaf rust. Resistant varieties had a waxy bloom but so did many very susceptible varieties. The *durum* wheats were all resistant and, in general, these differed from the susceptible wheats in having a smooth, thick cuticle and epidermis.

More recently, workers in Indiana and Kansas have been able to find no correlation between morphology and susceptibility or resistance of wheat varieties. Morphologically similar Turkey strains had very different rust reactions, and Turkey and Norka, though similar morphologically, reacted very differently to leaf rust. SCHEIBE (1930*a*) cites data of HEUSER and supplies original data showing that the more resistant upper leaves of wheat plants have smaller and more abundant stomata, smaller mesophyll cells, and thicker vascular bundles than the lower, more susceptible leaves. The smaller cells suggest greater mechanical interference with spread of the rust mycelium, but while SCHEIBE considers that such morphological characteristics have some part to play in resistance of the wheat leaf, this is minor in comparison with the major effects of host plant metabolism. DUFFAS (1927), from a detailed histological examination of the wheat leaf, con-

cluded that "rust" resistance is not mechanical in nature, since the number of stomata was less in susceptible than in resistant varieties, while the cuticle was of constant thickness in both.

SĂVULESCU (1938*a*) has found the greatest resistance in wheat varieties with small narrow leaves, and those with thin culms, in which the epidermis, cuticle, assimilating tissue, and the sclerenchyma are poorly developed, but one is led to wonder whether these are not simply indicators of varieties with relatively poor vigor and low metabolic rates, which are less susceptible by virtue of this lack of vigor, rather than because of the morphological changes accompanying it. Such lack of vigor is associated, among other things, with wheat culture in saline soils, and it is pertinent to recall HARTER'S experiments (cited by FREEMAN and JOHNSON, 1911) in which plants growing in saline soils showed deposition of waxy bloom on the leaves, thickening of the cuticle, and reduced size of epidermal cells.

There is also indirect evidence that mechanical barriers play little part in rust resistance. We know that susceptible and resistant wheat plants are invaded by rust in the same fashion, but in the one case a successful nutritional regime is established, and in the other it is not (*see* page 52). In both cases such barriers as may be represented by hairs, wax, cuticle, and stomatal structure are successfully passed. According to CALDWELL and STONE (1936) a rust which has no natural biological relationship to wheat whatsoever, such as clover rust, can enter the wheat leaf and proceed in its invasion up to the substomatal vesicle stage, passing all external morphological barriers, before its advance is wholly checked.

Moreover, the waxy coating of wheat leaves cannot have any great protective value (other than in repelling water) since naturally resistant plants regularly exhibit their resistance when artificially inoculated with rust by the usual technique which involves rubbing off the waxy bloom with the fingers before inoculation, to improve water adherence.

D'OLIVEIRA (1940*a*) reports that the strong cutinization of the epidermal walls of some species of *Thalictrum* protects these from attack by sporidia of wheat leaf rust, but we have no convincing demonstration of this, and in any case it can hardly have any rôle in nature, because of the unimportance of *Thalictrum* species as hosts of leaf rust.

In summary we can see that while mechanical protective structures may play some part in determining the resistance of wheat varieties toward leaf rust, this is undoubtedly a very minor part, and we must seek the principal answers to the complex display of resistance phenomena in the chemistry and physiology of the host plant.

Certain physiological-chemical factors in rust resistance: — Inability to explain rust resistance and susceptibility in wheat on the basis of morphological peculiarities of the host plant, naturally led to a search for the key to this problem in the chemistry and physiology of the host. Attempts were made to find the explanation in such properties and constituents of cells as *p*H, osmotic value, carbohydrates, aromatic organic compounds, and enzymes. The studies of these shed a little light on the problem, but they are inadequate to explain the complexity of rust resistance and the phenomenon of physiologic specialization. We still are far

from having this explanation, but with the evolution of GASSNER's hypothesis of the dependence of rust resistance on specific proteins, and the relation of this to antibody reactions in the rust relationship, we appear to be making some progress toward an understanding of this basic riddle of parasitism.

It was suggested by DRAGHETTI (1928) and SĂVULESCU (1938*a*) that high osmotic pressure of the cell sap is associated with resistance of wheat to rust, but there is no convincing proof of this, and the high osmotic values may simply be an expression of lack of vigorous growth, which we have seen to be correlated with reduced rust susceptibility.

Three independent workers, HURD (1923), DRAGHETTI (1928), and KARGOPOLOVA (1936, 1937) are all in agreement that there is no correlation between *p*H of the wheat cell sap and resistance or susceptibility to leaf rust, and VON KIRCHNER (1916), who analyzed for the presence of acids in a few leaf rust resistant and susceptible wheats, also found no correlation indicating that the acids condition leaf rust resistance.

There is a steadily mounting literature with reference to the protective value of phenols and tannin derivatives against plant disease fungi. The function of such substances in relation to wheat leaf rust resistance has been investigated by KARGOPOLOVA (1936, 1937), who worked with 40 specimens of different species and varieties of wheat, differing in rust reaction from very resistant to susceptible, in seedling and milk stages. When the contents of phenolic compounds in the acetic-ethyl fraction of the plant extracts were determined with the use of the Dubosque colorimeter, very resistant or immune varieties gave values of 39-32, resistant varieties 24-20, and susceptible varieties 10-0. From these results, and the known fungicidal or protective properties of phenolic compounds, she concludes that these may be considered as diagnostic indicators of leaf rust resistance. Direct confirmation of the effect of phenolic compounds on *Puccinia triticina* was obtained by tests of spore germination in solutions of pure phenols and in extracts of the phenolic compounds of the wheats. The extracts of resistant varieties were much more toxic to spore germination (percentage of germination and length of germ tubes) than those of susceptible varieties, and in tests with the pure phenols the pyrocatechin phenols were most toxic, the pyrogallols least so. This last was well correlated with the analysis of the phenolic compounds contained in the wheats, the resistant forms (*Triticum timopheevi, T. monococcum,* and very resistant forms of *T. durum*) containing a predominance of pyrocatechins, and the susceptible ones, of the chemically less active pyrogallols.

Very recently, STRAIB and NOLL (1944) and NOLL (1944) have found a curious relationship between supramaximal temperatures, wound gums, and leaf rust resistance. If susceptible wheat plants were dipped in hot water (2-15 hrs. at 30°; 1-5 sec. at 50° C., etc.) a few days after inoculation, the resultant rust reactions were of resistant types with marked chlorosis and necrosis or inhibition of pustule formation. Heat treatment before inoculation (*e.g.,* 40 sec. at 50° C.) increased the susceptibility of very resistant wheat varieties. These changes in reaction are associated with the production of defensive wound gums, which are induced by heat-

ing after inoculation and inhibited by heating before inoculation; these gums appear to check the growth of the rust mycelium.

Fifty years ago, COBB (1890-1894) called attention to reports that wheats yielding more silica in their ash were more resistant to rusts. The very recent work of STRAIB and NOLL revives this point, as they have shown histologically that a more or less marked deposition of silica in infected tissues is associated with resistance to leaf and stripe rusts in wheat.

With reference to enzymes we have only the finding of KARGOPOLOVA (1936, 1937) that no correlation existed in the wheats studied between peroxidase activity of the cell sap and resistance or susceptibility to leaf rust.

SUKHORUKOV and OVCHAROV (1937) report a correlation between the amount of NH_3 in wheat species and their resistance to leaf rust. The greatest amount was in the very resistant *Triticum timopheevi*, the least in the very susceptible *T. lutescens* 062, with intermediate amounts in wheats of intermediate rust reaction. They conclude that rust resistance in wheat is a direct function of NH_3 content, which is an hereditary character, modified by environment.

If we consider the results of attempts to determine a simple chemical basis for leaf rust resistance, the studies reported above still leave us far from the solution. There is evidently no relationship between the osmotic pressure or the *p*H of the wheat cell sap and leaf rust resistance, and, with the exception of the phenolic compounds and wound gums, no others, except carbohydrates and proteins, which are considered below, have been investigated sufficiently to give any clue to the nature of rust resistance.

KARGOPOLOVA's findings with reference to the phenolic compounds appear to be sound and in accordance with what is known of these compounds in other connections. Such compounds may well serve to mark off the broad categories of resistance and susceptibility to leaf rust, considered as a species, *i.e.*, to function in the general display of resistance in durum and einkorn wheats as compared with the more general susceptibility in common wheats. The wound gums may have a similar rôle. But these substances cannot explain the phenonema of resistance and susceptibility that characterize physiologic specialization in wheat leaf rust.

Resistance-susceptibility factors required for interpretation of physiologic specialization: — At first thought, the mosaic of resistance and susceptibility relationships of a number of wheat varieties toward many physiologic races appears so complex as to defy any interpretation except on the theoretical basis of a very large number of R-S factors, so large, in fact, that a number of workers, including the writer, have felt that no category of substances other than the species-specific, serologically distinct proteins could be the basis of this great diversity of reactions. (For brevity the term "R-S factor" is used to indicate a factor determining resistance or susceptibility, whatever its nature.) With more extended study; however, the picture becomes clearer. The complexity is not as great as at first appears. This is brought out by the following line of reasoning:

TABLE 17 gives the rust reactions of the 5 relatively stable differential varieties of wheat toward 11 principal races of leaf rust. Let us assume that

TABLE 17: *Reactions of the more stable differential varieties of wheat against leading races of leaf rust* (R = resistant; S = susceptible): —

DIFFERENTIAL VARIETY	*Puccinia triticina* physiologic race:									
	1	2	12	45	8	9	5	109	7	21
Mediterranean	R	S	S	S	S	R	S	R	S	S
Loros	R	R	S	S	S	S	R	R	R	S
Webster	R	R	R	S	S	S	R	R	S	S
Malakoff	R	R	R	R	S	S	S	S	S	S
Democrat	R	S	S	S	R	R	S	S	S	S

Mediterranean wheat has an R-S factor which we can designate as F_1, by virtue of which it is resistant to race 1 of leaf rust. Mediterranean wheat is susceptible to race 2; therefore race 2 is unaffected by F_1. But Loros wheat is resistant to race 2. This cannot be through the effect of F_1 but must involve a second R-S factor, which we may designate as F_2. Both of these wheats are susceptible to race 12, but Webster wheat is not; this requires us to attribute to Webster a third R-S factor, F_3. In the same way, Malakoff has a fourth, F_4 and Democrat a fifth, F_5. We need not go beyond this point for the moment: all reactions in the table are explainable on the basis of these 5 factors.

In this analysis we are attempting to find the least complicated explanation of the reactions; as in any scientific study the simpler hypotheses should first be exploited before proceeding to more complex ones. We can therefore assume that the reaction of Mediterranean wheat to race 9 is also due to the same R-S factor as conditions its resistance to race 1, F_1. If this is true, Loros, Webster, and Malakoff wheats all lack F_1. The reasoning up to this point indicates that:

Variety	*Possesses*	*Lacks*
Mediterranean	F_1	F_2, F_3, F_4, F_5
Loros	F_2	F_1, F_3, F_4, F_5
Webster	F_3	F_1, F_4, F_5
Malakoff	F_4	F_1, F_5
Democrat	F_5	———

Continuing the same type of reasoning, if the reaction of Loros toward race 7 is due to the factor F_2, then this factor must be lacking in all of the other varieties; if the reaction of Webster toward race 5 is due to F_3, there can be no F_3 in Mediterranean, Malakoff, and Democrat; if the reaction of Malakoff to race 45 is due to F_4, this must be lacking in Democrat; and if Mediterranean's reaction to race 109 is due to F_1, Democrat does not possess this factor. From this reasoning we come to the situation:

Variety	*Possesses*	*Lacks*
Mediterranean	F_1	F_2, F_3, F_4, F_5
Loros	F_2	F_1, F_3, F_4, F_5
Webster	F_3	F_1, F_2, F_4, F_5
Malakoff	F_4	F_1, F_2, F_3, F_5
Democrat	F_5	F_1, F_2, F_3, F_4

Now let us look at this situation from the standpoint of the fungus. Each physiologic race has a different spectrum of reactions on the 5 differ-

ential varieties. The races included in TABLE 17 behave as is indicated below:

Race:	*Is inhibited by the toxicity of, or by the necessity for,* factor:	*But not by the toxicity of, or the necessity for,* factor:
1	F_1, F_2, F_3, F_4, F_5	———
2	F_2, F_3, F_4	F_1, F_5
12	F_3, F_4	F_1, F_2, F_5
45	F_4	F_1, F_2, F_3, F_5
8	F_5	F_1, F_2, F_3, F_4
9	F_1, F_5	F_2, F_3, F_4
5	F_2, F_3	F_1, F_4, F_5
109	F_1, F_2, F_3	F_4, F_5
7	F_2	F_1, F_3, F_4, F_5
21	———	F_1, F_2, F_3, F_4, F_5

In the same way, the reactions of every physiologic race that can be distinguished by these 5 differential varieties can be shown to be due to the presence or absence of these 5 R-S factors.

At this point the question naturally arises: but considering all possible differential varieties, could not the number of R-S factors be greatly increased? It could doubtless be increased but probably not to a great extent. The 8 differential wheat varieties used in leaf rust race discrimination were chosen as the most distinct, in this respect, from a survey of many hundreds of wheat varieties, the great majority of which were discarded because they did not differentiate leaf rust races (*i.e.*, lacked R-S factors) or duplicated others (*i.e.*, possessed no new R-S factors), of these 8, 3 have been discarded because they are environmentally unstable. The 5 remaining varieties thus represent as wide an assortment of stable R-S factors as it has been possible to assemble after a very extended search, involving all major types of wheat known. Therefore it is unlikely that any considerable number of new R-S factors are to be found in wheat. It would not be unreasonable to set the maximum at a dozen, and possibly fewer.

By definition, each physiologic race of rust has a different requirement with reference to these few R-S factors, but this, too, is less complex than appears at first view. When the questionable and unreliable races (those based on reactions on unstable differential varieties) are removed from the list, there remain but a score or two of well-defined physiologic races of leaf rust. Each of these differs from the others in its ability to develop in the presence of some combination of 5 R-S factors. We have no need to resort to higher mathematics or to predicate a nutritional and/or toxicological situation unparalleled in nature to formulate a conception of a situation of this order. Each plant and animal has definite requirements with reference to its needs and hazards to its existence. In the case of the rust, these requirements may be less obvious than they are in the case of the infant or the asparagus plant, as is to be expected of an obligate parasite, but this is no indication that they are unreasonably complex. It is, perhaps, the unreasonable complexity of reports on physiologic specialization of rusts, rather than of the specialization itself, that is responsible for this conception. In any case there is no necessity of falling back upon a more complicated interpretation until it is shown that a simpler one such as proposed above does not apply.

A suggestion as to the nature of factors for resistance and susceptibility: — We pass now to the question of the nature of the R-S factors. They might be structures, substances, or conditions inhibitory to or favoring the successful life of the fungus, they might be deficiencies or adequacies in its nutritional requirements, or they might be one or the other in different cases. In the past, attention has been directed almost exclusively to the former possibility; we have regarded the resistant plant as one which has some sort of defensive mechanism to ward off the parasite. Without denying that such mechanisms may play a part in rust resistance, it might be instructive to examine the opposite viewpoint.

In the case of higher plants and rusts, resistance is commonplace; susceptibility is the rare exception. If we search for factors of resistance, they are legion; if we search for factors of susceptibility, our search is narrowed down to certain varieties of a few, very closely related species of plants, and to the differences between closely related varieties. If we attempt to interpret the reactions of leaf rust in terms of factors for resistance, our explanation must be so broad as to include all vegetation except for the few susceptible varieties, but if we direct attention at factors for susceptibility, we need only search for the requirements of rust development that characterize these varieties. It is not so much a question of what defenses all other plants have that these susceptible varieties lack, as of what positive qualities these varieties have that all other plants lack.

The wheat plant provides the general framework of a substrate, as soil for a seed, blood for a trypanosome, the intestinal tract of a warm-blooded animal for a tapeworm; beyond that there are a certain limited number of requirements. The tapeworm cannot develop in any mammalian intestine, nor the rust in any wheat plant, but in each case only in that host in which certain required substances are available. These required substances must be highly specific to the host, since they are not found elsewhere in nature,— the obligate parasitism of both rust and tapeworm attest this. There is no class of nutrient substances known to belong to certain organisms, exclusive of all others, save the proteins. The analysis of the situation from this viewpoint leads us to search for the key to rust susceptibility in the presence, in certain wheat varieties, of substances required by the rust, rather than to search for the key to rust resistance in all plants but these few susceptible varieties.

From this standpoint, susceptibility of certain wheats, but no other plants, to leaf rust, and physiologic specialization of the rust in wheat, both trace down to the presence in wheat of a general pattern of protein metabolism favorable for the rust, and, in certain varieties of wheat, of a few specific proteins required by the rust, the number of which is not large. This is entirely compatible with what is known of the serology of plant proteins: plant genera are characterized by protein groups distinct from those of other genera, and species and varieties by protein sub-groups distinct from those of other species and varieties. The distribution of more or less specific proteins within the genus has the same pattern as the systematic relationships of the species, and as rust host ranges within a species.

At this point it is desirable to examine the relationship of this view of rust resistance and susceptibility to certain well-known features of rust

activity, namely the fact that rust susceptibility is associated with a high state of vigor in the host plant, and the behavior of rust in a resistant plant.

As to the former, increased vigor and metabolic activity increases rust susceptibility. It is natural to infer that this is related to increased production of metabolites that favor the rust,— *e.g.*, nutrient materials. If the R-S factor is an inhibitory substance, increased vigor of the host plant might be expected to increase this inhibitor, with the opposite result from that which actually occurs insofar as rust infection is concerned.

Regarding the behavior of rust in a resistant plant (*see* page 52 *ff.*), the fungus first invades a few cells, then the invaded cells and the fungus die. Various theories have been advanced to explain this. If the fungus survives it appears to gain strength and becomes less and less unfavorably affected by the host. Such a situation is compatible with the view of resistance as an absence of suitable nutrients. The fungus has sufficient foodstuffs received from the spore to permit invasion of a few cells. If it then is unable to obtain food, it starves, dies, and since it is intracellular, its degenerative products kill the host cell. If, on the other hand, it obtains nourishment it survives, the host cell is not destroyed, and growth of the fungus continues.

It is freely admitted that the views set forth above are purely in the nature of an assumption. But as such, they appear to explain the situation adequately and much more simply than the more elaborate hypotheses based on an intricate system of inhibitory substances. They are proposed merely in the hope that they may serve as a theoretical basis for further progress in revealing the nature of rust parasitism.

Specific proteins as the basis of susceptibility to the rust: — GASSNER has made the most thorough studies directed at the nature of leaf rust susceptibility and resistance, and these led him to the conclusion that the factors for susceptibility are specific proteins, although he regarded these as acting as antitoxins rather than as nutritive substances. We can trace the evolution of GASSNER'S views as follows:

In Chapter X it was made clear that increase in the nitrogen supply to plants increases their susceptibility to rusts while increase in potassium supply has the reverse effect. That increase in soil nitrogen supply is, in turn, reflected in an increase in the nitrogen content of the wheat tissues, has been borne out by the researches of GASSNER and FRANKE (1934). Using 3 wheat varieties supplied with nitrogen at $\frac{1}{20}$ normal, normal, and 5X normal dosage, and then analyzing the leaves for nitrogen, they found that increase in soil nitrogen led to increase in both protein and soluble nitrogen.

It has also been seen that high rust susceptibility is associated with a high degree of vigor in the host plant. Increased vigor is expressed in increased carbohydrate metabolism which is associated with leaf rust susceptibility and is a connecting link between high soil nitrogen and high plant protein. It is a matter of common observation that nitrogen fertilization leads to increased chlorophyll production, as seen in the darker green color of plants fed nitrogen. This in turn results in increased photosynthesis, expressed in the luxuriant growth of such plants and in their in-

creased carbohydrate content. The sugars thus formed provide energy for the synthesis of nitrogenous compounds, in particular proteins, and with this whole process there is an increase in susceptibility. Data from various types of study support this interpretation.

On page 124 it was pointed out that plants deprived of light ordinarily show increased resistance to leaf rust, but if at the same time they are fed sugar, rust development is stimulated. A similar effect is seen in plants which are fed sugar although not deprived of light, according to POHJAKALLIO (1932), who greatly increased rust sporulation by supplying maltose or dextrose. Normally resistant plants could be made susceptible in this manner. COMES (1913) without particular reference to leaf rust, called attention to this relationship between soil nitrogen, sugars, and disease susceptibility; he explained the latter as being due directly to the better carbohydrate nutrition of the parasite. This may apply in the case of organisms that can feed saprophytically, but in the case of leaf rust there appears to be an added stage necessary, the elaboration of nitrogenous substances dependent upon both the energy and the chemical constituents of the carbohydrates.

GASSNER and HASSEBRAUK (1938), increased leaf rust susceptibility by treating wheat plants with chloroform. It is natural to suspect that this might be due to the narcotic effect of chloroform, inhibiting active defense reactions of the host plant. But this explanation does not seem to apply. Ether had no similar effect. The chloroform treatment led to accelerated growth and a darker green color in the plants due to increased chlorophyll production, as demonstrated by analyses. At the same time the chloroform-treated plants contained large quantities of soluble and protein nitrogen. It appears from this that the increased susceptibility of such plants is not due to inhibition of defense mechanisms by the chloroform, but to its influence in stimulating photosynthesis which, in turn, increases the synthesis of nitrogenous compounds.

Another factor involved in photosynthesis is availability of CO_2, and we have seen that moderate increases in CO_2 concentration of the air are associated with increased rust susceptibility.

On the contrary, factors which interfere with the anabolic processes of the plant are associated with increased rust resistance. Deficiency of light, deficiency of CO_2, supraoptimal temperatures, suboptimal temperatures, and increase in soil potassium all lead to reduced metabolic activity in the plant and all are associated with reduced rust susceptibility.

In a susceptible variety of wheat, according to GASSNER (1932), the developing plant normally expresses its susceptibility up till the time of formation of the flag leaf, during which period metabolic activity is high. Then a wave of resistance appears to pass through the plant, during a period of mobilization and transport of foodstuffs in the plant, associated with reproductive rather than vegetative activity. This stage lasts until blossoming or after, and is succeeded by another susceptible period during which foodstuffs are again regarded as being available to the rust.

We can summarize this interplay of factors as follows: Increase in soil nitrogen relative to soil potassium results in increased metabolic activity of the wheat plant. There follows an increase in plant sugars which provide

additional energy for nitrogen uptake (favored, in turn, by nitrogen availability in the soil) and energy and materials for synthesis of nitrogenous compounds. Any other factor favoring metabolic activity contributes to the process. This whole process is associated with increase in rust susceptibility, and leads us to analysis of susceptibility and resistance in terms of that class of metabolites that alone has the chemical diversity to underlie the pattern of rust reactions — the specific proteins.

In 1919, GASSNER expressed the hypothesis that resistance and susceptibility toward rusts is referable to specific proteins of the host plant. This view was developed in 1934 by GASSNER and FRANKE. Since (in the case of stripe rust) varietal differences in rust reaction were not correlated with nitrogen assays, varietal reaction was regarded as being due, not to quantitative but to qualitative differences in the protein compounds ("specific individual proteins"), the proportionate differences in amount of these being independent of external environment. In varieties of moderate resistance or susceptibility, improved nitrogen nutrition increases these specific proteins, together with the total proteins, but without changing their proportion in the total protein. In immune varieties no specific proteins related to rust susceptibility are present, hence no amount of nitrogen nutrition can increase them. In very resistant varieties the amount of these specific proteins is so small that it cannot be materially increased by nitrogen nutrition, and in very susceptible varieties, the amount of rust-specific proteins is so great, even under conditions of low nitrogen nutrition that no measurable increase in them occurs on the addition of nitrogen to the soil.

This hypothesis of GASSNER and FRANKE appears to be capable of illustration as follows: Let us assume that with 3 units of specific protein the wheat plant shows a "1" reaction to rust (very resistant), 6 units a "2" reaction (moderately resistant), 9 units a "3" reaction (moderately susceptible), and 12 units a "4" reaction (very susceptible), and also that an increase in nitrogen fertilization from $\frac{1}{20}$N to 5N doubles the amount of total protein in the plant. Since the rust-specific proteins are in constant proportion to the total protein, the situation resulting would be:

Normal	*Specific protein units present:*		*Resultant rust reaction:*	
Rust reaction	*At low N level*	*At high N level*	*At low N level*	*At high N level*
Immune	0	0 x 2 = 0	0	0
Very resistant	1	1 x 2 = 2	1-	1-
Moderately resistant ..	6	6 x 2 = 12	2	4
Very susceptible	12	12 x 2 = 24	4	4

Thus doubling the total proteins, and with them the rust specific proteins, leads to no alteration of rust reaction in rust-immune, very resistant, and very susceptible wheat varieties. It does lead to a shift from resistance to susceptibility in a variety that normally is only moderately resistant. This fully accords with the experimental results of nitrogen fertilization (*see* pages 79 and 129) and coordinates the hereditary and environmental factors of resistance. The rust specific proteins are lacking in non-suscepts of the rust; in suscepts they vary in proportion with the innate responses of the varieties to rust, and the effect of these proportions can be so altered

by environment as to modify the rust reaction, provided the proportions are not too high or too low.

Specific proteins are not distinguishable by ordinary chemical analysis, but they can be distinguished by serological means. This approach has not yet been adequately exploited, but such data as are available are in accordance with the GASSNER hypothesis. EDGECOMBE in 1931, using the precipitin test with purified globulins of several species of wheats, obtained specific and group reactions that were well correlated with the resistance or susceptibility of the wheats toward leaf rust. The conclusion was reached that "resistance-susceptibility characters . . . seem to have their basis in the constitution of globulins or globulin complexes . . . " Further serological study on this problem was made in 1938 by FEDOTOVA, who also used globulins of different wheats, and of rust races as well. She found that the globulins of different varieties of wheat reacted differently toward the globulins of a given rust race, and those of a given wheat variety reacted differently with globulins of several rust races. These serological results agreed almost completely with the results of infection tests using these rust races and wheat varieties in the greenhouse and field.

This much, then, can be said for the GASSNER hypothesis of specific proteins as factors of leaf rust reactions: the proteins are the only group of chemical constituents of the wheat plant sufficiently plastic to account for the obligate parasitism of the rust, and, at the same time, sufficiently diverse to account for its physiologic specialization; their assumed rôle harmonizes with the experimental facts relating host plant nutrition and metabolism to rust reaction; assumption of their function leads to a harmonious interpretation of both fixed and environmentally labile rust reactions; there appear to be no objections to this interpretation of rust reactions; and the occurrence of specific proteins in wheat and rust races, correlated with the rust reactions of the wheats, is serologically demonstrable. We can now turn to the more difficult problem of the nature of action of these specific proteins.

Here a clear distinction must be drawn between GASSNER's hypothesis of the relation of rust reactions to specific proteins, as recounted above and his ideas relative to the nature of action of these substances. In 1919, when he proposed the existence of these factors of resistance or susceptibility he did not indicate what their function might be, but at the same time he discounted the possibility that *resistance* to rusts is due to specific antitoxins in the host plant. An alternate suggestion was made by GASSNER and HASSEBRAUK in 1938, when they proposed that not resistance but *susceptibility* is determined by the ability of the host plant to produce antitoxins which neutralize toxins of the fungus. If these toxins were not counteracted, according to the hypothesis, the fungus would soon destroy invaded cells, and, being deprived of living host cells, would die. Neutralization of these toxins by the antitoxins of the susceptible host plant prevents the fungus from destroying its host cells, and therefore permits its further development, expressed as susceptibility on the part of the host. Resistance depends on the inability of the wheat plant to neutralize the fungus' toxins; it is a negative, not a positive property of the host. A similar view had been proposed earlier by STAKMAN and by ALLEN (1927).

This hypothesis is in harmony with most of the observed facts, particularly in placing the emphasis on susceptibility as the dynamic condition, rather than resistance, since we know that heightened metabolic activity increases susceptibility, not resistance. Antitoxins are considered to be proteins, and the correlation of increased nitrogen, increased protein, and increased susceptibility accords with this theory. It assumes that the failure of the rust in hypersensitive, resistant hosts is due to an unneutralized poisoning of the host protoplasm by the fungus.

HASSEBRAUK, in later papers (1939, 1940*a*), concluded that the GASSNER-HASSEBRAUK antitoxin hypothesis was inadequate because increasing temperature made Carina and Brevit wheats more rust-susceptible and others more rust resistant, which, he felt, was not in accordance with the dependence of the antitoxin theory on metabolic activity of the host plant, and because a *decrease* in the metabolic activity of Carina and Brevit wheats was associated with greater rust susceptibility. It is a question, however, how much importance should be attached to the behavior of these two wheat varieties, which are notably erratic in their rust reactions.

There is little direct evidence of the presence of a toxin-antitoxin reaction in cases of rust infection. GRETSCHUSHNIKOV (1936) found urea and a high concentration of NH_3 in rust-infected plants, and regarded these as toxins produced by the fungus. Such substances, however, would not be sufficiently diverse, chemically to elicit the specific host reactions that are required by the antitoxin theory of GASSNER.

PARKER-RHODES, in 1939, reported tests of the effects of extracts of healthy and rusted wheat tissues on germination of rust uredospores. His rather limited data suggest that extracts of wheat infected with *Puccinia triticina* are more toxic to uredospore germination of this fungus than extracts of healthy wheat or of wheat infected with *P. glumarum*. The effect, which was regarded as due to host antitoxins, is difficult to interpret; it calls for the assumption of a defensive mechanism in the susceptible wheat directed at the fungus ,and not at its toxins, which is the reverse of GASSNER'S view that the immunity phenomena in the susceptible plant aid rather than interfere with the fungus.

An alternative hypothesis that may be suggested has the advantage of greater simplicity, and would equally well conform to the facts, namely that the specific proteins are foodstuffs. Increased metabolism and synthesis of nitrogenous compounds would increase them, thus increasing susceptibility, which in this case is regarded as availability of specific food materials required by the fungus. Immune plants lack them entirely, therefore they cannot be increased by stimulated metabolism; highly susceptible varieties already contain an over-supply so that their increase is not registered in more rust activity; very resistant varieties contain so little that their proportionate increase is still inadequate for nutrition of the fungus; while in moderately resistant varieties the supply of these foodstuffs is subthreshold, and by stimulated nutrition it can be increased to the point that.a moderate degree of susceptibility results. The species- and variety-specific character of plant proteins serves to explain the restriction of leaf rust susceptibility to a few hosts, and their diversity would permit them to be the R-S factors responsible for race specialization. It is impossible to extract many plant pro-

teins in unchanged forms, since they are chemically altered on separation from the living protoplasm, and this may lie at the root of the obligate parasitism of the rusts. The behavior of the rust in a resistant host may be explained by starvation as well as by toxic effect on the host cell. If the haustorium obtains an inadequate supply of its specific food it must die, and in dying within the host cell, its morbid products would account for disruption and death of the host cell. ALLEN's description (1927) of the behavior of leaf rust in a resistant host at times suggests such a process, as when, on page 704, she mentions a dead and partly disorganized haustorium in a host cell which is living but shows marked disturbance, and in her references to the fact that there is little disruption of the host cells in the immediate vicinity of infected cells. (In cases in which fungus toxins are involved, the host injury usually extends far beyond the seat of infection.) However, the data from the cytological study of rust infections is not sufficient to support strongly one hypothesis against the other.

It does appear, at the present, that the evidence is in favor of susceptibility to leaf rust being dependent on R-S factors that are of the nature of specific proteins. Whether these act as antitoxins against toxins of the fungus or are specific foodstuffs, or, indeed, whether they are of an unknown third category, must be decided by future research.

Ontogenetic factors in resistance to the rust: — Many workers have observed that wheats that are susceptible to leaf rust as seedlings may become resistant as they become older. JOHNSTON (1937) has called this the "maturative type of resistance", seen, for example in Tennarq wheat. Other important commercial wheats with this type of resistance include the Hybrid 622 in Russia (LUKYANENKO, 1934) and 38MA in Argentina (G. J. FISCHER, 1929). The effect may apply, in given wheats, to certain rust races only. It can appear very early in the development of the wheat plant, the second, third, and fourth leaves formed showing some resistance as compared with the first leaf (JOHNSTON and MAINS, 1932).

There are also many cases in which the seedling reaction is a faithful index of mature plant reaction, seedling-susceptible plants being equally susceptible in later life, and seedling-resistant plants maintaining their resistance throughout life. For example, the same reactions that distinguish the two leading Australian rust races, are seen in both seedling and mature stages of the wheat plant (WATERHOUSE, 1934).

In contrast there are no clear-cut cases of varieties that are leaf rust resistant as seedlings but become more susceptible with increasing age. In testing a large number of wheats for leaf rust reaction in the seedling stage and in older plants in the field, RUDORF *et al.* (1933) observed only two cases in which a seedling-susceptible reaction was followed by a more resistant reaction. But these were in the varieties Carina and Malakoff, which differentiate rust races, and it is entirely possible that the plants were attacked by different rust races at the two stages of maturity, since there was no control of races in the field.

SCHEIBE (1930*a*) has called attention to an important law that appears to apply in this connection, namely that if a variety is very resistant or very susceptible to leaf rust, there is no change in reaction as the plant ages,

while the change from seedling susceptibility to mature plant resistance is found only in varieties that exhibit a moderate degree of susceptibility or an intermediate rust reaction. This is also brought out by the fact that in crosses of susceptible and resistant wheat varieties, the homozygous F_2 progeny are either resistant or susceptible throughout life, while the heterozygous F_2's may be susceptible as seedlings and resistant in later life.

Thus, resistance in seedlings is correlated with mature plant resistance, and susceptibility in the seedling stage may be followed by either susceptibility or resistance in the mature plant. This has practical importance in connection with breeding for leaf rust resistance, in view of the information that may be obtained by inoculating seedlings, under controlled conditions and with a minimum of time and expense. A resistant reaction in the seedling stage shows us at once that the wheat strain may be depended upon to be resistant throughout life to the rust races tested. On the other hand, a susceptible reaction in the seedling stage may or may not be followed by field resistance, and care must be taken not to cull out new strains of wheat on the basis of their seedling susceptibility to rust, since in so doing, valuable, field-resistant strains may be lost.

A second manifestation of resistance in relation to ontogeny, is seen in the fact that different organs or parts of organs may differ in their rust reactions at one and the same time. It has been shown by JOHNSTON and MELCHERS (1929), SCHEIBE (1930*a*), and NEWTON and JOHNSON (1943) that, at times, the different leaves on a single plant show different leaf rust reactions, and that in such cases the upper leaves are generally more resistant than the lower ones. JOHNSTON and MELCHERS noted occasional cases in which resistant and susceptible leaves appeared at random over the plant, except that the flag leaf was regularly most resistant. The differences seen were sometimes great, as from a "0" reaction on the top leaf to a "4" reaction on the lower ones.

These workers also observed differences in reaction of the different parts of a given leaf, as has also been shown by GASSNER (1932), and RASHEVSKAYA and BARMENKOV (1936). This may be explainable by the manner of growth of the wheat leaf from its base, such that the leaf tip is composed of older tissues than the leaf base (*cf.* definition of "x" reaction on page 75).

In his second trip to Uruguay in 1927, GASSNER made a particular study of rust reaction in relation to age and stage of development of the wheat plant (GASSNER and APPEL, 1927). He found, when dealing with varieties of labile rust reactions, that a wave of resistance passes through the plant just before the blossoming stage, preceded and followed by susceptibility. This wave of resistance simultaneously affects the seedling leaves when they are old, the top leaves when they first appear, and the middle leaves at an intermediate age. GASSNER interpreted this wave of resistance as the result of migration of foodstuffs from leaves to heads, so that temporarily the leaves are less suitable substrata for the rust, because of low food supply and disturbed water and salt relations, a condition that is later relieved. GASSNER and KIRCHHOFF (1934), further developing this view, pointed out that wheat plants are more resistant in the jointing stage than before or

after, and that this wave of resistance is seen first in the middle leaves and later in the uppermost ones.

We have seen that wheat plants may retain a uniform leaf rust reaction through life, may become more resistant with age, may be characterized by a wave of resistance, separating juvenile and adult susceptibility, or may show varied reactions in different tissues at a given time. While there are numerous possible sources of error in reaching such conclusions (attack of different rust races at different stages of development of the wheat plant, different environments at the different growth stages, etc.), the experiments, particularly of the German workers who inoculated plants of different ages at one time, show clearly that these ontogenetic variations in rust reaction do exist, and this indicates the necessity of understanding these ontogenetic responses in appraising wheat varieties for rust reaction. If GASSNER's explanation is correct, they also lend further support to the view that resistance and susceptibility of wheat varieties depend primarily on the nutritional relationships between host plant and rust.

Ecological factors in resistance to the rust: — Wheat varieties are characterized by basic, hereditary responses toward leaf rust races or race groups. This fundamental property of the wheat variety, termed by GASSNER "Disposition aus inneren Ursachen", may be so firmly entrenched in the genotype of the wheat that it is little affected by growth phase or external environment, as seen in varieties that are very resistant or very susceptible, respectively, at all growth stages and under wide variations of environment. But in wheats of moderate resistance or susceptibility, and in the differential varieties Carina, Brevit, and Hussar, the hereditary rust response is less fixed and unalterable, and is more readily shifted by changes in the environment, or metabolic changes during the vegetative life of the wheat plant. Such changes are attributed by GASSNER to "Disposition aus äusseren Ursachen".

We have abundant evidence of the modifications of the inherent rust response, due to environmental factors, in Chapter VII, and those based on ontogenetic changes in the preceding section. It should be emphasized, as GASSNER has done, that there are not two distinct mechanisms of rust resistance, the one hereditary, the other environmentally conditioned, but that a given pure line of wheat has a congenital property of rust response which may be very fixed and unaffected by internal or external environment of the plant, or which may be relatively plastic and capable of being shifted toward the resistant or susceptible side under the influence of metabolic changes within the host plant due to its growth phases or to external environment.

The greater this plasticity, the less reliable will be the resistance in wheats developed for rust resistance, and an aim in breeding for rust resistance is to secure as stable inherent resistance as may be possible considering the other purposes, limitations, and requirements of wheat breeding.

Chapter XV

CONTROL BY RUST RESISTANCE (*Contd.*)

Early efforts in development of leaf rust resistant wheat varieties: — Breeding of wheat for rust resistance may be said to stem from the pioneer work of FARRER in Australia, at the close of the last century. In 1882 he had a controversy with the newspaper, "The Australasian", regarding the possibility of securing rust resistant wheat varieties. Accepting the challenge, in 1886 he began the first extensive and intensive breeding and selection for rust-resistance in wheat, and was so successful that even today many of his hybrids are of agricultural significance in the British Empire and in the United States (*e.g.,* Federation). By 1894, according to the report of the 4th "Rust-in-wheat Conference", rust resistance was well established in Australia as a means of rust control. It should be pointed out, however, that the work was directed at rust in general, with little emphasis on leaf rust; it was not until many years later that the comparative importance of leaf rust was recognized in Australia. Not long after this, BIFFEN in England applied the principles of newly rediscovered Mendelism to the breeding of wheat for stripe rust resistance. HITCHCOCK and CARLETON in 1894 had also recognized that the breeding of "rust proof" wheats offered the most promising means of rust control, and it was not long before the breeding of wheats for rust resistance got under way in America, with outstanding results in the control of stem rust, but, until recently little attention to resistance to leaf rust. The development of this work, in America and abroad, is brought out in the following subsections.

Sources of resistance: — Any wheat variety showing resistance may be regarded as a potential parent in breeding for leaf rust resistance, and in the following sections there are many examples of resistant wheats used for this purpose. The sources of resistance comprise members of resistant species of *Triticum* (*T. timopheevi, T. durum,* etc.), resistant varieties of common wheat, and resistant individuals selected from predominantly susceptible but heterogeneous wheat varieties. A few of the most important of these will be given special mention at this point.

The wheats which have had the greatest importance as parents in recent breeding programs directed at stem and leaf rust control are Hope and its sister selection H-44. These wheats resulted from a cross of Yaroslav emmer (*Triticum dicoccum*) × the spring wheat Marquis, made by MCFADDEN (1930) in 1915. A single F_1 plant resulted. Selection was difficult in the F_2 and F_3 generations, and in the F_4, of some 5000 plants, 6 were selected as rust-free. Their progeny were reselected, giving attention to resistance against other diseases, and to protein content, and one selection from the F_9 generation was named "Hope".

Hope has *Triticum vulgare* characters. It is highly resistant to leaf and stem rusts, and also has resistance to tip blight, bunt, powdery mildew,

loose smut, and wind and hail injury. It has easily loosened bran and a high tillering capacity. Its weak points include susceptibility to black chaff, anthracnose, and root rot, rather low yields, low test weight, susceptibility to spring frosts, heat, and wet weather damage, and uneven shrinkage of the endosperm.

However, by crossing Hope and H-44 with rust susceptible but otherwise desirable wheats, there have been developed many rust resistant, desirable commercial wheats in North America (TABLE 19) and abroad.

In Texas, MCFADDEN and SEARS, through colchicine treatment of F_1 hybrids, have obtained a series of hybrids of various *Triticum* species with species of *Aegilops,* several of which have a high degree of resistance to leaf rust and other diseases, and have promise of being useful parents in crosses with common wheats.

Triticum timopheevi is a Russian species of wheat that is resistant to the 3 wheat rusts, powdery mildew, bunt, loose smut, "white spot", *Fusarium* (*nivale*?), and certain insects (YAKUBTSINER, 1934). Although unsuitable for culture, it offers immense possibilities as a breeding parent. Its use as a parent has been limited by difficulty in crossing *T. timopheevi,* which has 28 chromosomes, with *T. vulgare,* which has 42, but early failures in this direction have been followed by more recent successes. VAVILOV made a successful cross of *T. timopheevi* with *T. vulgare erythrospermum,* but did not test its disease reactions. KOSTOV (1938) produced the amphidiploid *T. timococcum* with 42 chromosomes by doubling the chromosomes in the F_1 hybrid of *T. timopheevi* (N=14)×*T. monococcum* (N=7). This, which has been called "the most immune wheat known", should be compatible with *T. vulgare* (N=21). SHANDS (1941) was recently successful in crossing *T. timopheevi* with various varieties of *T. vulgare,* obtaining fertile progeny. PRIDHAM, in New South Wales (1939), has crossed *T. timopheevi* with Steinwedel wheat and produced promising new rust-resistant strains of the *vulgare* type. In Russia, YAKUBTSINER (1934) has found several natural hybrids of the *T. timopheevi* type, and other Russian workers, by using KOSTOV's method of building up chromosome numbers, have crossed *T. timopheevi* with *T. dicoccoides* and *T. aegilopoides.* A final, spectacular accomplishment has been ZHEBRAK's production of the amphidiploid *Triticum sovieticum* by crossing *T. timopheevi* with a durum wheat. This has grains almost 3 times as heavy as those of ordinary wheats and is extremely resistant to disease. ZHEBRAK has also been successful in hybridizing *T. timopheevi* with *T. vulgare,* and the resulting hybrid is being tested on a large scale in Russia. Thus it appears that *Triticum timopheevi* has promise of playing an important part in the development of rust resistant wheats of the future.

Certain Chinese wheats show a high degree of leaf rust resistance and have been used as parents in breeding for rust resistance in China, England, and Argentina.

Good sources of resistance are the differential wheats used in wheat leaf rust identification, since these have been selected from a large number of wheat varieties because of their display of resistance-susceptibility responses. Thus we find Mediterranean and Malakoff being used for this purpose in America, and Webster in Argentina.

Other wheats with leaf rust resistance, that are used as sources of resistance in wheat improvement, include durums, Pentad × Marquis, and Marquillo in Australia, Marzuolo Todaro 87 in Italy, 38MA, Mentana, Ardito, Chino 166 and Lin Calel in Argentina, and Sabwani in Kenya. In Russia, a very extensive collection has been made of the leading wheats of the world, and this offers an opportunity to make use of any of a great number of genotypes. Some of the leaf rust resistant American varieties appear to be particularly useful in Russian wheat breeding.

Mass selection for increasing rust resistance: — Selection and multiplication of rust resistant individuals from standard rust susceptible wheat varieties is a method for increasing rust resistance that has been used to advantage by a number of workers, including those in Kansas, Indiana, and Argentina. A more fruitful procedure is to select from crosses made to yield progeny with many combinations of rust reaction and other characters, and this is the standard practice today, but before discussing it, mention should be made of mass selection for rust resistance as suggested many years ago by COBB (1890-1894) and BOLLEY and PRITCHARD (1905, 1906).

Mass selection is based on the assumption that if a wheat crop is so heavily rusted that the yield is greatly reduced, the grain harvested will be mainly from the plants least affected by the rust. If this grain is then graded to separate out the plumper kernels, these may be presumed to have been produced on the plants least damaged by rust, and hence, will be carrying some rust resistance.

At the time when this was recommended, there was little else that could be done by farmers in combatting rust by wheat resistance, but the method is slow, of questionable effectiveness, and cannot be used except in years following those of severe rust epiphytotics, and today, with the growing availability of leaf rust resistant wheats, this practice has only historic interest.

Methods of breeding wheat for resistance to the rust: — The technique of hybridizing wheat is described in standard works on plant breeding, such as H. K. HAYES and F. R. IMMER, "Methods of Plant Breeding", McGraw-Hill Co., 1942, and need not be considered in detail here.

Preliminary phases of the breeding program may be carried out in the greenhouse. This has certain advantages over field culture. The valuable early generations of hybrids can be protected from natural hazards; the plants may be grown under optimal conditions of soil, light, moisture, and temperature for seed increase and for rust susceptibility; they can be inoculated with pure races of rust and thus exposed to a greater variety of rust races than might be prevalent in the field; the reaction to each rust race can be determined; and in the greenhouse there is no danger that plants may be classed as resistant when they have merely escaped infection due to lack of sufficient natural inoculum at a suitable stage of plant growth and under environmental conditions suitable for infection.

On the other hand, greenhouse culture of new hybrid materials has disadvantages which require that the later generations, at least, be grown

in the field. One of these is the fact that greenhouse tests may indicate a much higher degree of rust susceptibility than the plants will show under field conditions. In the second place, any new rust-resistant hybrid wheat, if it is to be commercially useful, must combine this resistance with climatic and soil adaptation, some resistance to natural hazards, and such characters as good tillering capacity and freedom from lodging and shattering, and greenhouse plants give no index of these characters. Finally, in the advanced stages of breeding the number of plants is so large, and the space requirement so great, that greenhouse culture is uneconomical, although it is a good practice to culture small duplicate groups of the field-planted materials in the greenhouse, for continued study of reactions to pure rust races during the entire period of developing new hybrids.

The F_1 hybrid generation should, as a rule, be grown in the greenhouse, to protect the few potentially valuable plants from natural hazards. This generation should not be exposed to leaf rust, since if rust resistance is inherited as a recessive character, all of the F_1 plants will be susceptible, and are likely to be lost from the intensity of the rust attack under greenhouse conditions. Selection begins with the F_2 generation and should be repeated in each generation, usually until about the F_7, in order to establish sufficient genetic purity of the hybrid lines.

Considering the length of time required to develop hybrids, attention should be given to the possibilities in accelerating this process by growing more than one generation of wheat per year in the early filial generations. This is possible if the experimental greenhouse can be artificially cooled as well as heated, and if a sufficient quantity of artificial light can be supplied. It has been shown that it is possible to produce 3 successive crops of wheat in a year; one grown in the field and two in the greenhouse with supplementary or even continuous light. At present such a device is adapted to only the first filial generations, in which the numbers of plants are small. However, with modern air transport it might be possible to extend this principle to the later generations, for example by growing the generations alternately in suitable locations in the northern and southern hemispheres, at the rate of two field generations per year, retaining small portions of the seed of each generation in the hemisphere of its origin, for such tests of rust-susceptibility, adaptability and yield as are required. Vernalization of the seed, in this case, might be an added means for accelerating maturity of the crop.

In greenhouse tests of the F_2 and later generations it is desirable to inoculate the plants with pure cultures of all rust races known to occur in the area for which the wheat is intended. If the concept of race groups is followed, each locally present group should be included; the total number of these would not be great. GESHELE (1936) recommends mass infections since he considers that a few spores of a comparatively rare race have no practical importance in a large population of common races. But if a new wheat variety that is susceptible to the rare race but resistant to the more common races is grown on greater and greater acreages, the common ones will tend to disappear from the rust population, while the rare one, lacking competition and having large numbers of susceptible plants on which to develop, will multiply until it becomes the dominant race, and the new

wheat will no longer show rust resistance. For this reason new wheats should be bred for resistance to all of the races with which they are likely to come in contact, major and minor, and this can best be accomplished by subjecting the selections to greenhouse inoculations with all known races (race groups) known to be present in the area concerned, and using the results as the basis for selection.

A satisfactory procedure in the writer's experience has been to test all selections against all available races, when the plants are in the seedling stage, and later, as the greenhouse plants are heading, to subject them to a mass inoculation by the method described on page 73, using a mixture of all local races in approximately equal concentrations in the mixture.

In field tests of selections we are applying the principle of "survival of the fittest", and it is therefore imperative that the plants be subjected to as intense a rust attack as possible,— at least as intense as they can be expected to encounter in nature. Various devices are used to secure this high intensity of rust attack.

The land chosen for the trial field should preferably be a low location, with rich soil, high in nitrogen, and well supplied with moisture. Fertilizers that tend to increase rust resistance (P, K) should be avoided. In dry climates it may be necessary to irrigate the wheat in order to raise the humidity to a point favoring rust development.

If spring wheats are being studied, delaying their planting date will subject them to more intense late season rust, especially if they are planted near winter wheats, on which rust has overwintered, or early-sown, rust-susceptible spring wheats. In the case of fall-sown wheats, rust development can be encouraged by having the plants adjacent to early sown, rust-susceptible wheats.

For favoring the overwintering of leaf rust and its early spring development, NAUMOV (1939) recommends the use of snow fences, to protect the crop and rust in the winter, and breaking the soil crust in the early spring by watering or raking, not by harrowing since this destroys rust-infected leaves.

Wheats for selection are usually interplanted with "spreader rows" of rust-susceptible wheats, to provide abundant inoculum for the adjacent selections. Varieties of wheat that are used for this purpose in different regions are listed on page 43.

The spreaders, or the entire planting, are often inoculated with rust spores in order to make sure that all locally important rust races are present in the planting, and to encourage early rust development. Various methods of introducing inoculum are used. Some workers prefer to spray the plantings with uredospore suspensions. These are prepared in water or in .1% agar and applied with a knapsack sprayer or, if a large area is involved, with a tree-sprayer. It is generally recommended that the spray be applied in the evening when dew is forming.

A somewhat more satisfactory means of artificial inoculation of field plants is by use of infection centers. Here and there in the plot susceptible plants are inoculated, or heavily rusted potted plants are set out, and these serve as sources of natural rust spread. PAINTER *et al.* (1940) had good

success inoculating spreader plants hypodermically; hundreds of infection centers could thus be created in a short time.

It is desirable to make several readings of rust intensity during the season, since the wheat strains may reach the climax of infection at different growth stages, and these differences have an important bearing on rust damage. In order that the readings may have absolute significance in the records, the amounts of rust should be estimated with the use of one of the rust intensity scales (page 21).

Once a selection has proven its value and the work has reached the point at which the selection is to be multiplied for large scale tests and ultimate release to farmers, the work is guided by two objectives,— to keep the line as pure as possible, and to increase it as rapidly as possible.

The means for achieving these purposes for the most part, are readily apparent. Wheat does not readily cross-pollinate, but it is nevertheless desirable to have increase plantings well separated from other wheat. They should be on land not contaminated with volunteer wheat. Off-type plants should be rogued out during the growing season, and extreme care used in harvesting, threshing, packaging, labelling, and storing, to prevent accidental contamination with other seed.

Russian workers advocate vernalization of the seed to aid increase of new varieties. Other practices that are desirable in this connection are disinfestant seed treatment to aid seedling development, use of a lower rate of planting than is usual (even a rate too low to be economical of land in farm fields, but not low enough to introduce serious weed competition), choice of rich, well-watered land that is not foul with weed seed, best possible preparation of the soil with plowing well in advance of planting to allow the seedbed to become firm, conformance to the local optimal date of planting, and timely harvesting with care not to waste the grain in this process.

Basic pattern of inheritance of resistance: — In general, resistance to leaf rust is inherited in simple Mendelian fashion when hybrids from pure lines of wheat are tested for their reaction to pure rust races. In many cases resistance is governed by a single dominant factor, and in an almost equal number of cases the single factor is recessive. Frequently the single factor is only incompletely dominant or intermediate, so that heterozygous progeny are more resistant than the susceptible parent but more susceptible than the resistant parent. When the rust employed consists of two physiologic races, two resistance factors may be involved, independently inherited, in which case the inheritance follows the simple Mendelian pattern of a dihybrid cross. These various cases, with references to the literature concerned, are given in TABLE 18.

From this situation we can see that the genetic background of the inheritance of leaf rust resistance is such as to offer much promise in the breeding of rust-resistant wheats. This is all the more true in view of the fact that a single factor, dominant or recessive, frequently governs inheritance to several races, or, making use of the concept of race groups, resistance to a race group is inherited as a unit. Hence the number of factors required in a practically resistant wheat is not great.

TABLE 18: *Inheritance of resistance to wheat leaf rust* (Factors for resistance: "R", "S" = resistant, susceptible): —

MONOHYBRID DOMINANT: Cross	Ref.*	MONOHYBRID RECESSIVE: Cross	Ref.*	MONOHYBRID INTERMEDIATE: Cross	Ref.*
Malakoff (R) × several S varieties	1	Malakoff × C. I. 3778 (R) Race 5	1	Kanred (R) × several S varieties	1
Malakoff (R) × C. I. 3778. Race 12	1	Kanred × Fulcaster	13	Malakoff (R) × several S varieties	1
Norka × C. I. 3756. Races 5, 12	1	Harvest Queen × Fulcaster	13	Malakoff × Webster (R)	1
Webster (R) in various crosses	2	Harvest Queen × Kanred	13	Fulcaster (R) × Kanred	1
Rimpaus r. Schlanstedter × Normandie (R)	3	Ardito (R) × San Martin	10, 14	Vulgare Chinese × dicoccum (R)	19
1014 × Normandie (R) Race 15	3	Ardito (R) × various S varieties	15	Webster × Mediterranean (sometimes)	4
Webster × Mediterranean	4	Varonne (R) × various S varieties	15	Malakoff × R varieties	5
Malakoff (R) × S wheats	5	Normandie (R) × various S varieties	15	037 × Cooperatorka	9
Canaberra × Thew (R) Austr. 1	6	Dinkel × emmers (usually)	16	Marquis × lutescens 0329, etc.	18
Riverina × Thew (R) Austr. 1	6	Durum × vulgare	16		
Gluyas × Thew (R) Austr. 1	6	Turgidum × compactum	16	*Dihybrid double dominant:*	
Japanese bearded (R) × Federation Austr. 1	6	Polonicum × spelta	16	Norka × C. I. 3756	1
Norka (R) × Ceres Race 3	7	Malakoff × C. I. 3778 (R), Race 5	8	12H × 38 MA (R)	14
Malakoff (R) × several vars. Races 12, 3	8	S vars. × Democrat, Mediterranean 35.27	17		
Vulg. 037 × Ukrainka, Poltavka	9	Kanred × Fulcaster, etc.	18	*Dihybrid double recessive:*	
Hope (R) × Leap's Prolific	11	Hope (R) × Ukrainka	18	Vulgare 037 × Minhardi	9
Hope (R) × Fulcaster	11	Marquis × Ukrainka	18	Vulgare 037 × Belaya Tserkov 6182	9
Purplestraw × Hope (R)	11	Odessa 0719 × Mediterranean (R)	18		
Peragis × Normandie (R) Race 15	12	Chino 166 (R) × Lin Calel	10	*Dihybrid dominant + recessive:*	
Blausamtiger Kolben × Peragis (R) Race 15	12	Kanred (R) × several S varieties	1	Malakoff (R) × C. I. 3778	1

* *References:* 1, MAINS *et al.*, 1926; 2, Anon., 1930; 3, ISENBECK, 1931; 4, MAINS, 1926; 5, LEIGHTY, 1926; 6, WATERHOUSE, 1930*b*; 7, MAINS, 1934; 8, LEIGHTY, 1929; 9, GORLACH, 1937; 10, RUDORF *et al.*, 1933; 11, ADAMS, 1939; 12, HUBERT, 1932; 13, Anon., 1924; 14, RUDORF and JOB, 1934; 15, VOHL, 1938; 16, TOCHINAI and KIHARA, 1927; 17, RĂDULESCU, 1939/40; 18, cited by NAUMOV, 1939; 19, GUARD, 1938.

Modifications of the basic pattern of inheritance of resistance: — Variations in techniques are responsible for some of the modifications of the basic pattern of inheritance of rust resistance, complex situations, or discrepancies reported in the literature. If a hybrid wheat progeny is exposed, in the field, to all rust races that may be present, its display of resistance may appear to be very complex and incapable of resolution, particularly if there is no companion study of the rust race flora. A second source of misinterpretation lies in the natural variation in rust intensity in the field, from one season to another. In cases of relatively light rust intensity there is a tendency to regard hybrid progenies as more resistant than is actually the case. A third, and very important source of discrepancies, is the lack of uniformity in classifying rust reactions. There is no arbitrary line separating resistance from susceptibility, but instead there is a graded series of reactions, passing gradually from high resistance to high susceptibility. Each worker must select an arbitrary point in the series of rust reactions to separate resistance from susceptibility, and different workers have selected different points.

Even more conducive to discrepanies is the practice of classifying plants according to the percentage of rust infection, since this varies in susceptible varieties with the season, and since the arbitrary point chosen to separate resistant and susceptible reactions differs with different workers. It can readily be seen that of two workers, scoring the same plants with different arbitrary classifications, one could conclude that resistance is dominant, the other that it is recessive. Of the various classifications, those based on reaction type, as contrasted with rust percentage, are most likely to give reliable results, since reaction type is a function of host plant and rust that is more independent of external environment than rust intensity.

Infrequently, transgressive segregation of factors for leaf rust resistance is seen in wheat crosses. SHEKHURDIN (1936) crossed two susceptible wheats (*lutescens* 2075 × Cooperatorka) and obtained resistant progeny. WISMER (1934), from a cross of Oro, which is very susceptible to leaf rust, × Tenmarq sel. Kans. 2637, which is moderately susceptible, obtained numerous F_4 lines which were very resistant in a leaf rust epiphytotic. The results indicate that in these cases the parents are carrying recessive factors for leaf rust resistance, and the mode of inheritance can best be explained on a multiple factor basis.

At times genetic behavior of wheat toward rust is obscured or complicated by differences in manifestation of rust reaction with different stages of development of the plant. As examples of this, a larger percentage of resistant lines may be found when the plants are adult than in the seedling stage, plants may show resistance in the heading stage but susceptibility in the milk stage, resistance may act as partly dominant in the seedling stage but intermediate later on, resistance may appear to be recessive in seedlings and dominant in adults, or the type of resistance may be regarded as one which is more strongly expressed in adult plants than in seedlings. These manifestations, which are variously attributed to heterozygosity, modifying factors, or conditioned dominance, appear to be different aspects of the same phenomenon, namely the changes in rust reaction associated with the different metabolic states of the plant as it passes through its successive

phases of life activity, a subject that has been discussed on page 213 *ff.* While these changes sometimes increase the difficulty in determining the manner of inheritance of rust resistance, and require special attention in this work, they do not necessarily imply any unusual complexity in the genetics of inheritance of rust resistance itself, but only illustrate the complications resulting from the fact that genotypic expression is conditioned by the physiology of the host plant and its parasite.

When wheats with different chromosome numbers are crossed, the genetic picture becomes more complicated. Very abnormal ratios may be the result of sterility in the F_2 and F_3 generations as seen by JOHNSTON (1937) in crosses between *Triticum vulgare* and *T. turgidum* or *T. dicoccoides.* The hybrids from a given cross have various numbers of chromosomes and this may be associated with their rust reactions, as seen in the following examples:

ABE and MATSUMURA (1939) crossed the rust resistant *T. durum* (N=14) with susceptible *T. vulgare* (N=21). In the progeny, with 2N chromosome numbers from 28 to 35, susceptibility was progressively higher with increase in the chromosome number ($r = + .4021 \pm 0.0504$). However not much correlation was seen in the progeny of the backcross of *T. polonicum* × *T. spelta* with *T. polonicum.*

TOCHINAI and KIHARA (1927), in a series of crosses involving *Triticum vulgare, dicoccum, durum, turgidum, compactum, polonicum, spelta,* and dinkel wheat obtained progeny with varying chromosomes up to 2N = 41. The F_1 hybrids were generally susceptible, *i.e.,* resistance was recessive, and in the later generations the segregates reacted toward rust similarly to the parent which they most resembled in morphology and chromosome number.

GUARD (1938) crossed the seedling-susceptible *T. vulgare* Chinese (N = 21) with the resistant *T. dicoccum* (N = 14). The F_1 plants showed mesothetic or "X"-type reactions, and had 14 bivalent and 7 univalent chromosomes. In the F_2 to F_6 generations, the plants with 14 chromosomes were all rust resistant, and those with 21 had ratios of 11 resistant to 6 susceptible.

Passing finally to intergeneric crosses, wheat-rye hybrids are normally susceptible to wheat leaf rust in the F_1 generation, hence resistance is recessive. An exception was seen in GUARD's crosses between *T. vulgare* Chinese (N = 21) and Abruzzes rye (N = 7) or *Secale montanum.* He obtained amphidiploids with 28 chromosomes, in which wheat leaf rust resistance was dominant.

Application of these genetic principles: — The foregoing data show that the resistance of wheat varieties to given races or race groups of leaf rust is heritable, readily transferred from parent to hybrid progeny, and usually governed by a single Mendelian factor. This factor, in any given case, may be dominant, recessive, or intermediate, and it is often conditioned by the developmental stage or the metabolic state of the host plant. Cases in which such clear cut and simple inheritance of resistance is not seen are usually referable to exposure to several rust races or race groups at once, as occurs in field trials. Although abnormal ratios may result, due to

partial sterility of the progeny, it has been shown that rust resistance may be transmitted to the progeny in interspecific crosses between very distinct species of *Triticum* even when the chromosome numbers of the parent species differ. It has also been seen that genes for resistance to several races or race groups of the rust may be combined in a single hybrid.

All of this indicates a most promising genetic situation with reference to the development of leaf rust resistance in wheat, and this is borne out by the successes that have already been attained in this direction. In the many cases in which resistance is recessive the problem is simplified and breeding is accelerated by the fact that each resistant selection from a hybrid progeny is homozygous for resistance, while those cases involving dominant resistance show us the necessity for rigid genetic control in the development of new rust resistant varieties, to prevent breakdown of the resistance due to segregation of homozygous susceptible wheat types in heterozygous resistant populations. The display of transgressive segregation of factors for leaf rust resistance indicates that programs for the development of rust resistant varieties should not disregard the possibilities of securing rust resistant varieties from the crossing of two susceptible varieties.

The fact that a single gene may govern resistance to several rust races, the simplification of the situation with reference to numbers of leaf rust races, and the limited number of race groups in any major geographic area, all indicate that it is not necessary to combine large numbers of distinct genes for resistance in a single wheat in order to secure a practical degree of field resistance. Finally, as is shown in the following section, the genes for leaf rust resistance are not ordinarily so linked to undesirable wheat characters as to introduce difficulty in combining leaf rust resistance with other desirable wheat characters, a problem that complicates breeding for resistance to certain other plant diseases, *e.g.,* common smut of corn.

Correlation of resistance with other plant characters: — If leaf rust resistance were linked to any obvious morphological character in inheritance, a great advantage would result in breeding, since under conditions of low rust intensity or absence of rust it would be possible to select rust-resistant lines by selecting those with the correlated morphological character. If mature plant resistance were limited to a morphological character of the seedling, it would become possible to discard many strains in the seedling stage without the labor, time, and expense of growing the plants to maturity only to find them rust susceptible. If leaf rust resistance were linked to an undesirable plant character, the difficulties in breeding rust-resistant varieties of otherwise desirable types might be greatly increased, or this might be facilitated if resistance were correlated with one or more desirable plant characters. For these reasons, considerable attention has been given, in wheat breeding, to the occurrence of linkage between leaf rust resistance and other morphological, physiological, and ontogenetic characteristics of the wheat plant.

On page 200 *ff.* attention was directed to the possible function of various features of plant morphology in protecting the wheat plant against leaf rust, and it was seen that, in general, there is no correlation between rust

resistance and such morphological features as leaf structure, thickness of cuticle, pubescence, presence of waxy bloom, and structure and number of stomata.

If we now extend this comparison to include morphological characters that do not have any likely function as defense mechanisms, we also find little or no evidence of correlation with rust reaction.

LITVINOV (1912) found no correlation between the presence or absence of awns and rust reactions, and this has been substantiated by later observations of VON KIRCHNER (1916) and MAINS and JACKSON (1926). DRAGHETTI in 1928 asserted that osmotic activity and rust resistance decreased in correlation with a series of wheat head characters: awned, loose heads; awned, compact heads; awnless, loose heads; and awnless, compact heads, and gave illustrations of this, but in 1930 he abandoned this viewpoint on finding that these correlations did not obtain when the wheats are grown under a variety of environmental conditions.

If we compare several wheat varieties of different leaf rust reactions, it may be seen that the resistant varieties differ morphologically, in one or more respects, from the susceptible ones. Thus, VAVILOV (cited by VON KIRCHNER, 1916) observed that Turkestan and Samara emmers, which were rust-susceptible, had lemmas with blunt, straight teeth, while western European varieties that were resistant had teeth that were pointed and incurved. Also a very resistant "Persian wheat" (*Triticum vulgare* var. *fuliginosum*) differed from all other wheats in having a stalk that was even more pithy than those of *durum* wheats, a rare character in *T. vulgare,* and hairy nodes, a head much thinner than those of most wheats and smooth, with both outer and inner glumes awned. But it would be a mistake to conclude that there is any necessary correlation between such characters and leaf rust reaction in view of the lack of data on their linkage in segregation.

FAVOROV (*in* NAUMOV, 1939) found a very high degree of correlation (up to $r = +.94 \pm .001$) between type of head and leaf rust resistance in *Triticum durum* × *T. vulgare* crosses. This is evidently a special case that does not, in fact, contradict the findings of others. *T. durum* and *T. vulgare* have different chromosome numbers, and the segregates have characters, including rust reaction, that resemble those of one or the other of the parents in the degree in which the chromosome number of the segregate approaches that of the parent. However, as segregation proceeds it is possible to obtain *vulgare* types with the resistance of the *durum* parent, so that the resistance of the *durum* parent is not linked with *durum* morphology (STEVENSON, 1930) nor with the *durum* chromosome number ($r = +.0651 \pm .0467$, ABE and MATSUMURA, 1939).

MAINS and JACKSON (1926) reported that leaf rust resistance of Mediterranean wheat is not linked with winter habit, purple stem, glabrous brown glumes, or soft red kernels, nor was any correlation seen between resistance and morphology in Turkey and Norka wheats.

In Chapter III it was seen that leaf rust attack is associated with many injurious effects on the wheat plant, physiological and morphological. While it can be shown that there is a correlation, often high, between rust attacks and yield factors, as HAYES, AAMODT, and STEVENSON (1927) have done,

these yield factors are not inherited as such but are the result of devitalization of the plant by rust; they are effects of the rust and not heritable factors correlated with the inheritance of rust resistance.

There are a number of hereditary factors for leaf rust reaction, and a survey of the literature suggests that in some cases these are correlated with factors for susceptibility or resistance to other wheat diseases. Data on varietal susceptibility of wheat to its different diseases and pests (leaf rust, stem rust, stripe rust, bunt, flag smut, scab, powdery mildew, nematode, and Hessian fly), in general indicate that resistance to leaf rust is independent of resistance to any of these other diseases or pests. In hybrid progenies there has been noted independent segregation for reaction to leaf rust and bunt, leaf rust and powdery mildew, leaf rust and stem rust, leaf rust and stripe rust, leaf rust and Hessian fly, leaf rust and flag smut, and leaf rust and black chaff.

On the other hand, WATERHOUSE (1930*b*, 1939) and WATSON and BAKER (1943), in crosses of Federation, Kenya, Canaberra, and Gullen × Thew wheat, have found in Thew a dominant factor for resistance to leaf rust race 16 which is closely linked to or identical with a factor for resistance to one of the 3 races of powdery mildew in New South Wales; HAYES *et al.* (1934) observed correlation of leaf rust and stem rust resistance in crosses of H-44 × several leaf rust susceptible varieties; HAYES, AAMODT, and STEVENSON (1927) noted the opposite, — correlation of leaf rust susceptibility and stem rust resistance in other wheats; and RUDORF (1930) in several wheat varieties, found resistance to leaf rust correlated with resistance to several races of stripe rust. HUMPHREY (1938) found no false black chaff present in leaf rust resistant wheats although it was regularly present in susceptible ones, which suggests that resistance to these two diseases may possibly be correlated.

The foregoing data show that, in general, leaf rust reaction is not correlated with any morphological characteristic such as would aid in the selection of resistant strains. However, an advantage results from the fact that no linkage between leaf rust resistance and undesirable plant characters has been found. This permits the breeding of rust-resistant varieties of desirable agronomic characters, and since there is no appreciable correlation between leaf rust resistance and susceptibility to other plant diseases and pests, the genetic situation is such as to permit the combination of resistance to several of these hazards in a single improved strain of wheat. Indeed, this possibility has already been realized in a number of the recently developed leaf rust resistant wheat varieties, as will be seen in the following section.

Results of breeding and selection for resistance to the rust in North America: — In the United States a program of wheat breeding for rust control was initiated in the principal wheat State, Kansas, in 1911, and in Indiana in 1916, the States coöperating with the U. S. Department of Agriculture.

The point of departure of the Kansas work was Kanred wheat, which, from a single head selected by the Botany Department of the Kansas Station in 1906 had come to occupy 50,000 acres by 1918 and 1½ million by

1939. In 1911, tests of the more promising strains were undertaken and by 1917 its rust resistance had been determined and it had been named Kanred. This has served as a source of resistance for breeding experiments in many parts of the world.

In 1926, several thousand F_2 and F_3 progeny of Kanred × Fulcaster were being studied for their leaf rust resistance in Kansas, and selections with high-quality grain and stiff straw had been made. Leaf rust resistance combined with earliness and stiff straw was also found in crosses of Kanred × Hard Federation and Kanred × Prelude.

Meanwhile physiologic specialization of wheat leaf rust had been discovered, and by 1929 JOHNSTON, in Kansas, was using greenhouse tests with pure rust races and had made 200 selections, from 27 standard varieties, of wheat strains resistant to the dominant leaf rust race in Kansas, race 9; some, however, were susceptible to race 5 which is not without importance in this area (JOHNSTON, 1929).

The Annual Report of the Kansas Station for 1930 speaks of several new, promising rust-resistant wheat hybrids, which had not yet been tested agronomically. By 1932 JOHNSTON had secured many hybrids and selections that were resistant to at least some of the common rust races. The best of these were F_3 and F_4 progeny from the cross (Kanred × Fulcaster) × Tenmarq, but those from crosses of Kanred × Kawvale, Kanred × Fulcaster, Mediterranean × Webster, and Fulcaster × Marquis were also promising (JOHNSTON, 1932). Kawvale, itself, a useful wheat for production and breeding, with some leaf rust resistance, was a Kansas production from a selection of Indiana Swamp, made in 1918 and released in 1932. In 1934 JOHNSTON reported resistant and agronomically desirable strains from Kanred × Kawvale, Kawvale × Blackhull, Kawvale × Tenmarq, and Hard Federation × Kawvale. Compound crosses yielded even more resistant lines, as (Kanred × Fulcaster) × Tenmarq or Iobred. Fairly resistant soft wheats had been obtained by selection from Kawvale, Fulcaster, Fultz, and Mediterranean.

By 1936 JOHNSTON's plantings contained many resistant selections of Mediterranean (from Texas), Fultz, Illini Chief, and Shepherd, and also many resistant segregates from hybridizations such as those indicated above. Resistance to both leaf rust and stem rust had been combined in progeny of Kanred × Kawvale, Hard Federation × Kawvale, and especially Hope × Kawvale, Mediterranean × Hope, and Hope × Hussar (JOHNSTON, 1937). Next, the bunt-resistant Oro and such stem rust resistant spring wheats as Marquillo, Thatcher, Renown, Apex, and H-44 in addition to Hope and the durum, Mindum, were crossed with hard red spring wheats, as Tenmarq, or hybrids of these, such as Oro × Tenmarq or Kawvale × Tenmarq, and selections with promise had been made in 1938 (JOHNSTON, 1938*a*).

By 1940, the Kansas workers had obtained F_5 lines from crosses of the Hessian fly and rust resistant Marquillo with moderately rust resistant varieties or hybrids, as Kawvale, Tenmarq, and Kanred × Hard Federation, some of which combined resistance to leaf rust, stem rust, Hessian fly, and bunt, or to two or three of these. Forty-six leaf rust resistant strains gave good doughball tests, with yields well above those of the standard

TABLE 19: *Recently introduced American wheat varieties with various degrees of resistance to leaf rust: —*

VARIETY	CLASS[1]	R. to l. r.[2]	OTHER PRINCIPAL CHARACTERS	ORIGIN
Cadet	HRS	R[3]	R to stem rust; high yields; high quality	Merit × Thatcher
Coronation	—	VR	VR to stem rust; MR to loose smut; MS to bunt; fair quality	Pentad × Marquis
Henry	—	R	R to stem rust; high yield; fair quality	Ill. No. 1-Hope × Webster-Res
Mercury	—	R	R to stem rust and bunt	Ceres × Hope-Florence
Merit	—	R	R to stem rust, powdery mildew, and bunt	H-44 × Ceres
Mida	—	R	R to stem rust and bunt; high yield, test wt.; good flour	Ceres × Hope-Florence
Pilot	—	Int.	R to stem rust; MR to bunt; high yields; good milling and baking	Hope × Ceres
Regent	—	R	R to stem rust, bunt; good yield, milling, and baking	H-44 × Reward
Renown	—	MR	VR to stem rust, bunt; MR to loose smut; good quality	H-44 × Reward
Rival	—	R	R to stem rust; MR to bunt; high yields; good quality	Ceres × Hope-Florence
Vesta	—	MS	R to stem rust; high yield	Ceres × Hope-Florence
Austin	HRW	VR	VR to stem rust, loose smut; stiff straw; non-shattering	Hope × Mediterranean
Comanche	—	MS	High yield; good test wt.; early; stiff straw	Oro × Tenmarq
Pawnee	—	MR	MR to stem rust; VR to loose smut; R to bunt and Hessian fly; high yield, test wt.; stiff straw; winter hardy	Kawvale × Tenmarq
Westar	—	VR	VS to stem rust; of Tenmarq and Comanche type, with high yields, test weight, good milling and baking qualities, stiff straw, satisfactory winter hardiness	Kanred × Hard Federation × Tenmarq
Wichita	—	MS	Early; high yield	Early Blackhull × Tenmarq
Denton	SRW	MS	Stiff straw; high yields	Sel. from Mediterranean
Prairie	—	Int.	R to mosaic	Sel. of Ill. No. 2
Red Chief	—	MS	R to loose smut	Redhull × Chiefkan (?)
Sanford	—	MR	Higher yields than Purplestraw	((Purplestraw × Kanred) × Purplestraw) × Purplestraw
Wabash	—	VR	R to mosaic; high yields	Fultz × ?
Carleton	Durum	R	R to stem rust; strong straw; good quality	Vernal emmer × Mindum
Stewart	—	R	R to stem rust; high yield; good quality	Mindum × Vernal

[1] HRS: Hard red spring; HRW: Hard red winter; SRW: Soft red winter.
[2] Reaction to leaf rust.
[3] R: Resistant; VR: Very resistant; MR: Moderately resistant; Int: Intermediate; MS: Moderately susceptible.

winter wheats, and with elimination of the undesirable creamy flour color of Marquillo (PAINTER *et al.*, 1940).

As one of the practical outcomes of the Kansas work, the new variety Comanche, with limited rust resistance, was released in 1943 and by 1944 was receiving favorable attention in the hard red winter wheat region of the Southwestern Great Plains. Another recent Kansas production, Wichita wheat, is rust susceptible, but may escape rust injury due to its early maturity. The parentage and principal characters of these and other recently released leaf rust resistant wheats are indicated in TABLE 19.

In coöperation with the U. S. Department of Agriculture and the Kansas Agricultural Experiment Station, the Indiana Station initiated work toward the production of leaf rust resistant soft red winter wheats in 1916. At first the effort was to combine the rust resistance of Kanred and Malakoff with soft wheat characters, and by 1926 a number of promising selections from such crosses had been obtained.

Following the Indiana work on leaf rust specialization, attempts were made to incorporate resistance to a number of rust races in hybrids, and in 1929 this had been accomplished in crosses of the differential varieties Malakoff × Brevit.

By 1930 numerous leaf rust resistant selections of various crosses had been made. The resistance of Warden was added to that of Norka and Carina, and that of emmers and rye had been transferred to bread wheats.

A year later it was reported that selections with high leaf rust resistance had been secured from Fultz × Michigan Amber, and that crosses had been made between these and varieties of outstanding winter hardness and scab resistance.

By 1933 (Anon., 1933) two leaf rust resistant selections from a natural Fultz hybrid had been found to produce good pastry flour. Meanwhile the very important cross Hope × Hussar had yielded progeny resistant to leaf rust, bunt, loose smut, powdery mildew, and three races of stem rust, to provide the basis for many future compound crosses. Resistance to bunt, leaf rust, loose smut, and powdery mildew had been combined in several soft wheat hybrids.

By 1935 the breeding materials in Indiana included selections of Chinese wheat × rye which were very resistant to both rusts and to mildew, and these had been crossed with commercial soft wheats. Also good Indiana commercial wheats hybridized with Hussar or Hungarian wheats had yielded lines resistant to leaf rust and 11 races of bunt, combined with good adaptation and yields.

Next (CALDWELL and COMPTON, 1938) strong Hessian fly resistance was combined with a high degree of leaf rust resistance in soft red winter wheats with good promise. In 1938, the new leaf rust resistant variety Wabash was released, the product of a natural Fultz hybrid (*see* TABLE 19).

In recounting the accomplishments of breeding for leaf rust resistance we recall the achievement of MCFADDEN in South Dakota, in the production of Hope and H-44, from a cross of emmer × Marquis (*see* page 216). This was fundamental to present day success in such breeding as seen in TABLE

The neighboring State, North Dakota, was also active in this work, in cooperation with the U. S. Department of Agriculture. Its important leaf rust resistant wheat productions include the spring wheats Pilot and Rival which were grown on limited acreages in 1939, but, on account of the damage of leaf rust to susceptible wheats, showed great increases in acreage in 1942. This was followed by the release of Carleton and Stewart in 1943, Mida in 1944, and Vesta. TABLE 19 gives the origin and outstanding characters of these.

In Minnesota, attention has been directed more at stem rust than at leaf rust resistance, but the failure of the stem rust resistant Thatcher wheat, due to the leaf rust epiphytotic of 1938, led the Minnesota Station, in cooperation with the U. S. Department of Agriculture, to the production of its leaf rust resistant counterpart, Newthatch, which was increasing in 1943. By 1944, however, Newthatch was exhibiting high susceptibility to leaf rust, presumably because of a change in the rust population from races that cannot damage Newthatch to others, to which Newthatch is susceptible.

Federal and State cooperation in Nebraska resulted in the release of Pawnee wheat in 1943, and the recent releases also include Prairie from Illinois in 1940, Sanford from Georgia, and Carala (which is not leaf rust resistant but escapes the most severe damage due to its earliness) from North Carolina. The North Carolina work is reported in the Experiment Station Reports from that State from 1932-1940.

The Texas Station undertook breeding, including attempts to develop leaf rust resistance, in 1930, with Federal cooperation beginning 5 years later. Particular attention was given to Hope × Mediterranean backcrosses for combining resistance to both wheat rusts with desirable agronomic qualities. The accomplishments include the recent release of the hard and soft red winter wheat varieties Austin, Denton, and Westar.

A fundamental contribution to this problem was made by SHANDS in Wisconsin (1941), in his successful crossing of *Triticum timopheevi* (*see* page 217) with common wheats to produce homozygous segregates of *T. vulgare* type with resistance to leaf and stem rusts. The Arkansas Station has recently been active in this field and has obtained uniformly resistant selections from a cross, made in Indiana, of Red Rock × Hope, which outyielded leaf rust susceptible varieties by 50%.

Finally, in the United States, breeding for leaf rust resistance has been an activity at the Oklahoma Agricultural Experiment Station since 1938. An outstanding selection, tentatively designated "Okla. 21", from a cross of Oro X Mediterranean-Hope has been very resistant to leaf rust and stem rust. The original hybrid was made in Kansas. It has good qualities with reference to earliness, stiff straw, stooling capacity, head size and uniformity, is characterized by high yields under Oklahoma conditions (up to 45 bu. per acre in 1944, as compared with an average State yield of 12 bu.), and has been satisfactory with reference to vitreous nature of the grain, test weight, protein content, and milling and baking qualities. Selection for leaf rust resistance has been based on greenhouse tests of seedlings and adult plants inoculated with the principal rust races occurring in the Southwest, and on field behavior, exposed to natural epiphytotics

and to artificially-induced ones, in which they have been inoculated with the principal leaf rust races of the area. "Okla. 21" was being increased on 2½ acres and was included in competitive tests throughout the United States hard red winter wheat area in 1946.

The Dominion Rust Research Laboratory at Winnipeg has been active in breeding wheat for rust resistance, and while the principal emphasis has been on stem rust, some of the more recent spring wheat releases, such as Coronation, Regent, and Renown are from moderately to very resistant to leaf rust. Dr. NEWTON and her associates in 1940 reported success in combining resistance to the two rusts in the progeny of crosses of Kenya R.L. 1373 and McMurachy × H-44.

Work in Australia: — The work in Australia is particularly noteworthy, since it was here that FARRER led the world in his pioneering and successful attempts at wheat breeding. In recent years, WATERHOUSE (1930*b*, 1939) has been particularly responsible for the breeding progress which includes attention to the development of leaf rust resistance. In 1930 he had produced lines resistant to both leaf and stem rusts from a cross of Thew × Canaberra. Later he reported selections of the durum wheat, Gaza, which were resistant to both rusts and to flag smut, and lines from Federation (FARRER'S production) × Thew that combined resistance to leaf rust and powdery mildew. In 1939-40 WATERHOUSE was testing about 200 hybrid strains for rust resistance, and in 1941 was reported the release of Fedweb I, from Federation × Webster, which is moderately resistant to leaf rust and resistant to all known Australian races of stem rust. Meanwhile PRIDHAM, in New South Wales (1939) has contributed to the problem by crossing *Triticum timopheevi* with Steinwedel, a common wheat, and producing strains that in the F_5 generation were homozygous for leaf rust immunity.

Work in Argentina: — According to BIFFEN and ENGLEDOW in 1926, BACKHOUSE in Argentina used a very resistant Chinese wheat to produce leaf rust resistant wheats suitable for Argentina. G. J. FISCHER (1929) reports that the variety 38MA, which was bred for Argentina conditions, has practical leaf rust resistance, although it is susceptible in early stages, and combines earliness with good yields; it is also resistant to the other wheat rusts and immune from loose smut.

RUDORF, JOB, and ROSENSTIEL, in 1933, reported the behavior of F_2 progeny of numerous crosses involving 38MA, Heines Kolben, Mentana, 12 H_3, Chino, and Lin Calel, all of which are resistant to one or more of the wheat rusts, and San Martin, which is rust susceptible but well adapted. By selection to eliminate rust susceptible segregates, many lines with resistance to one or more of the rusts were obtained. In addition, numerous other crosses, in progress, were aimed at combining resistance to the three rusts with loose smut resistance.

Finally, ARZUAGA (1940) in 1939 obtained a wheat with moderate resistance to leaf and stripe rusts combined with satisfactory yield and baking tests, from a cross of Ardito and Lin Calel.

Work in Africa and India: — In these regions breeding for resistance to the rust is still in early stages. BURTON, in Africa (1931*a*, 1932) has obtained F_4 segregates that are very resistant to leaf rust, from a cross of Kenya Standard, which is adapted, with high yields and quality, but susceptible, with B.F_4.3.B.10.V.1(L). KALE in 1938-1939 reported a breeding program at Potchefstroom, but at that time the work had not progressed beyond the F_3 generation.

In India, also according to KALE, testing and selection have been in progress at Simla, Agra, Delhi, Lyallpur, Bharatpur, and Bombay, and some native selections, *e.g.*, from the variety Pusa, with resistance to the Indian leaf rust races, have been secured. One of the problems is to obtain strains with resistance to both leaf and stem rusts, and efforts are being made to combine the stem rust resistance of Khapli with the leaf rust resistance of local selections (PAL, 1936; MEHTA, 1940).

Work in Europe, exclusive of Russia: — Attention has already been called to BIFFEN's fundamental work in England on the genetics of rust resistance. Practical breeding for rust resistance in that country has dealt almost exclusively with stripe rust, and the result has been the production of some good varieties, as a result of crossing stripe rust resistant American Club with English varieties, but these are susceptible to leaf rust. Only the Little Joss variety is mentioned by KALE (1938-1939) as an English wheat with leaf rust resistance.

In Italy, Rieti, which is very resistant to "rust" but has weak straw, has been hybridized with other varieties to produce hybrids resistant to both rust and lodging. The variety Cologna Veneta escapes rust by its earliness and this quality has been transmitted to hybrids with other varieties (PETRI, 1927). STRAMPELLI's production, Rieti II, is resistant to all 3 wheat rusts, and Mentana to leaf and stem rusts.

At Halle, in Germany, an intensive program in wheat breeding was begun about 1920. The most important leaf rust resistant productions have been selections from crosses of the rust resistant Blausamtiger Kolben and Normandie with the very susceptible Peragis. One segregate of the latter cross, in the F_2 generation, was resistant to leaf rust, stripe rust, and lodging (CÂLNICEANU, 1934; ROEMER, 1933). According to KALE (1938-1939) the German work has included very strict selection, with trials in France, Holland, Sweden, etc., from varieties with resistance to German rust races: Marquis, Thatcher, Hope, Garnet, 38MA, Vencedor, and Hard Taganrog. At Halle and Müncheberg these have been hybridized with local German varieties and some rust resistance has been transmitted to the progeny.

KALE, in 1938-1939, reported that Sampo, a variety resulting from the crossing of Thule II Svalöv with a Finnish local wheat, with resistance to all rust races in the Jokioinen area of Finland, had been recently released. According to the same source, a selection, "American 17", has been found resistant to all Rumanian races of the rust. In Bulgaria wheat breeding has involved crosses of durums and einkhorns, which are resistant to the Bulgarian races.

Work in Russia: — In Russia there has been a well-organized and highly successful program of wheat breeding, giving full consideration to

the importance of leaf rust, and based on the "world collection" of wheat varieties assembled about 1930. Principal breeding and testing stations, under the direction of the All-Russian Institute of Plant Protection at Leningrad, were located, prior to the war, at Krasnodar, Otrada Kubanskaya, Beloi Tserkov, Murtazovo, Voroshilovsk, Grosnie Maikop, Buinaksk, Ordzhonikidze, and Yeisk (NAUMOV, 1939). Much of the work has involved selections from crosses of foreign, principally American, varieties with locally adapted but rust-susceptible varieties. A stimulus to this program was undoubtedly the earlier work of VAVILOV (1913, 1914, 1919, 1935), in testing the disease reactions of many wheat varieties in Russia.

Up to 1934 there were few, if any, good Russian commercial wheats with satisfactory rust resistance (GROOSHEVOI and MAKLAKOVA, 1934). Ukrainka, the standard wheat of the Caucasus, suffered severely from leaf rust. In that year, LUKYANENKO reported successful breeding for control of this disease. An attempt was made to combine the better qualities of Marquis and Kitchener wheats (rust resistance, stiff straw, high yields of high quality grain, non-shattering quality) with the drought resistance of local wheats of the botanical varieties *ferrugineum, nigroaristatum,* and *lutescens.* The new rust resistant hybrids produced outyielded Ukrainka from 50 to 200% in 1932. They were generally earlier than Ukrainka, and were free from lodging and shattering. The best of these was Hybrid 622 (Marquis × *ferrugineum* 013, a local wheat widely grown in the Kuban). This was seedling-susceptible, but highly resistant to leaf rust in later growth stages. In two years it outyielded Ukrainka by 95% and Cooperatorka by 85%. It was also superior to Ukrainka in kernel weight, grain size, vitreousness, protein content, milling and baking properties, and flour yield. Another production, Hybrid 1568 (Kitchener × *nigroaristatum* 0264) outyielded Ukrainka by 63% in the presence of heavy leaf rust, but was outyielded by it when rust was unimportant. LUKYANENKO'S hybrids have also been distinguished by their stem rust resistance.

Tests of 1933-1935 in this region also showed marked superiority in yields over Ukrainka in Kanred × Fulcaster and Illini Chief (STARKOV, cited by NAUMOV, 1939). Leaf rust resistant selections of the botanical varieties *ferrugineum, erythrospermum, caesium,* and *lutescens,* made at Krasnodar, and others made at Beloi Tserkov all indicated potential agricultural importance for Russia. Particularly important were the leaf- and stem-rust resistant Krasnodar selections H45, H56, and H51 (NAUMOV, 1939).

By 1936, SHEKHURDIN had obtained lines combining resistance to leaf rust, stem rust, and loose smut, from crosses of *lutescens* or *caesium* with Marquis, Kitchener, Cooperatorka, etc. The following year GORLACH reported resistant lines from *lutescens* × Ukrainka which showed a 50% yield advantage over Ukrainka in the leaf rust epiphytotic of 1935.

New lines of attack, reported in 1938, were the use of crosses involving lines from a collection of 800 Chinese wheats, and rust-resistant but poor-yielding wheats from the Amur region (MURASHKINSKI et al., 1938).

Finally, the Russian workers have given particular attention to the use of interspecific or even intergeneric crosses in development of their breeding program. On page 217 were mentioned their highly significant crosses in-

volving the rust-immune *Triticum timopheevi,* and in addition, DERZHAVIN (1938), from a cross of *T. durum* × *Secale montanum* obtained 6 lines, out of thousands, with stiff straw, freedom from smuts, immunity from stem and stripe rusts, and high resistance to leaf rust; these are compatible with varieties of *T. vulgare.* The war did not entirely disrupt the important Russian wheat breeding program, as witnessed by the production of the remarkable *Triticum sovieticum,* announced in 1944 (*see* page 217); much may be expected of this program in the future.

Direction of future efforts: — Despite the achievements in breeding for rust resistance pointed out above, we are still far from our goal of universal rust control by this means, and much work lies ahead.

In many important wheat-producing regions of the world, little, if any, progress has been made toward the control of leaf rust by breeding. Such regions include China, North Africa, Spain and Portugal, the Balkans and Asia Minor, France, the Low Countries, Poland, and Chile. Rust resistant genotypes to furnish resistance to wheats otherwise adapted to each of these areas are available, and judging by the results in North America, Russia, Australia, and Germany, rich opportunity for wheat improvement lies ahead in the regions in which breeding for rust resistance has so far made little progress.

But even in the United States the work is far from accomplished. This is particularly true of the southern wheat States, where there is great need for leaf rust resistant soft winter wheats. It is entirely possible that southern humid areas now considered unsuited for wheat culture, would be capable of high wheat yields if disease resistant varieties were available.

Many of the rust resistant varieties that are available display mature plant resistance but seedling susceptibility. The latter is an undesirable character in regions where pasturage of the young wheat is an important reason for its cultivation. MELCHERS, CHRISTENSEN, and MURPHY (1942) have pointed out that seedling wheat for pasturage is a cash crop in western Kansas where Colorado sheep are shipped in for winter grazing. In the southern Great Plains there was a heavy leaf rust epiphytotic in the fall of 1940, another in 1942, and the most severe of all in 1944, such that wheat pasture was seriously damaged. This clearly implies that future breeding must give attention to including seedling as well as adult plant resistance in commercial wheats for such areas.

Some of the rust resistant wheats are lacking in other needed characters, for example resistance to foot rots and to speckled leaf blotch. Combination of rust resistance with such valued characters is an outstanding need in future breeding programs, and the new interspecific and intergeneric breeding materials may contribute substantially to efforts in this direction.

Our present leaf rust resistant commercial wheats are far from being rust-immune. They are commonly susceptible to a number of less prevalent rust races. The minor race of rust to which a wheat is susceptible can become the major race when that wheat is planted on large acreages for a number of years, so as to change the field reaction of the wheat from resistant to susceptible. Resistance to all races must be an objective of

breeding, those that are minor at present and those which may arise in the future. From this point of view the control of rust by breeding may never be a completed task.

Finally, the problem of breeding for rust resistance is an international problem: rust inoculum is freely carried by the wind from one country to another; the genotypes needed for a breeding program in any one country must come from other countries; the results of breeding should be tested at many points over the world to determine their possible usefulness in other regions than that for which they were bred. As suggested by KALE this international problem can only be solved by international cooperation, aimed at the prevention, through breeding of rust resistant, adapted, high quality wheats, of the most destructive disease of the world's greatest food crop.

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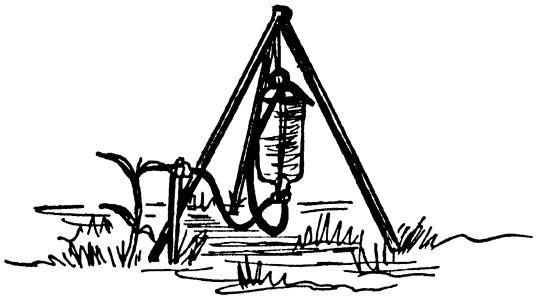

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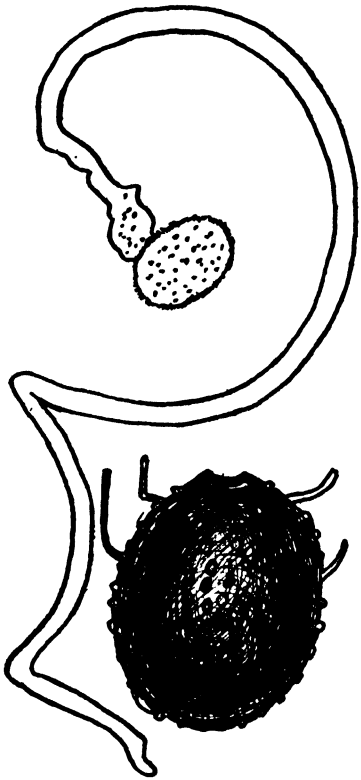

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