The Rusts of Wheat, Oats, Barley, Rye

John H. Martin, S. C. Salmon

Wheat, oats, barley, and rye may be attacked by eight distinct species or subspecies of rust fungi.

Wheat is subject to stem rust (*Puccinia graminis tritici*), leaf rust (*P. rubigo-vera*), and stripe rust (*P. glumarum*).

Oats are attacked by a stem rust (*P. graminis avenae*) and by crown rust (*P. coronata avenae*).

Barley may fall prey to the same stem rust (*P. graminis tritici*) that attacks wheat and a leaf rust (*P. hordei*).

A stem rust (*P. graminis secalis*) and a leaf rust (*P. rubigo-vera*) attack rye.

Each of the eight rusts is made up of several or many different races, which may attack certain varieties of a particular cereal crop but not others.

Stem rust of wheat causes the most spectacular and perhaps the greatest losses. Leaf rust of wheat and crown rust of oats occur more frequently, usually affect larger acreages, and so may cause greater average losses year in and year out. Before the extensive use of resistant varieties, stem rust was most destructive in spring wheat in the northern Great Plains. Severe losses sometimes occur in the southern Plains, many Eastern States, California, and occasionally in localities in the Pacific Northwest and Intermountain States.

Leaf rust of wheat and crown rust of oats occur wherever wheat and oats are grown. They cause little damage west of the Rocky Mountains or in the drier parts of the Great Plains. Some damage occurs in the eastern half of the United States nearly every year. Reductions in acre yields are especially great in the Southern and Southeastern States although neither wheat nor oats is grown extensively in much of that area.

Most varieties of barley, some of oats, and all varieties of rye escape considerable damage because of their early maturity as compared with wheat. Stem rust sometimes injures barley seriously. Leaf rust is not usually serious but is sometimes locally destructive on spring barley. The stem and leaf rusts do not cause serious losses in rye. Stripe rust occurs most commonly on wheat but only in special situations in the United States has it caused serious losses.

Wheat stem rust is characterized by pustules that develop and break through the surface of the stems, leaves, and sheaths and often the chaff and beards of the wheat plant. Myriads of brick-red spores escape from the pustules and are carried by the wind to other wheat plants.

The crop is damaged by the growth of the rust fungus on the wheat stems and leaves and by the developing spores, both of which use up the water and nutrient materials needed for developing the wheat kernels. The water requirement in rusted wheat is much higher than in healthy wheat.

As a result, the kernels are badly shrunched, many of them being so light and chaffy that they are blown out with the chaff in threshing. The remaining grains may be shrunken to one-half or two-thirds normal size. Losses range up to 85 or 90 percent; at that point the crop is not worth harvesting and is a total loss. The rusted straw turns brown, becomes dry and brittle, and soon breaks over.

Wheat stem rust also attacks barley and occasionally rye. It attacks many wild grasses, including wild barley or squirreltail grasses (*Hordeum* species); certain wheatgrasses (*Agropyron* species); wild-rye grasses (*Elymus* species); bottlebrush grasses (*Hystrix* species);
and some brome grasses. It does not attack oats.

The rust lives over the summer on volunteer grains and wild grasses in the Southern States and in northern Mexico. These spores and those blown down from the north in late summer and early fall infect fall-sown wheat or barley. The rust lives over winter in the red rust stage in the southern part of the United States and in northern Mexico but not in the Northern States.

If weather conditions are favorable in the spring, the rust multiplies and the spores sweep northward with the advance of the crop season. Thus a heavy rust epidemic in Texas is a threat to the wheatfields of Oklahoma and Kansas, and the latter, in turn, are sources of inoculum for the grainfields in the North Central and Intermountain States.

The red rust spores that spread the disease are about one-thousandth of an inch long. They fall upon a wheat leaf and may germinate in an hour in warm, humid weather or in several hours at temperatures of 40° to 50° F. Germinating spores send out germ tubes, which grow along the surface of the leaf or stem of the plant until they reach a breathing pore (stoma), where they enter, send out branches that grow within the tissues of the plant, draw nourishment from them for a week or longer, and then produce the red pustules with another crop of spores. At low temperatures, or when there is but little sunlight, it may take 2 or 3 weeks from the time the germ tube first enters the plant until the spores form. In warm, moist weather, however, they may reach full development within a week.

Thus a new generation of rust spores may be produced every 10 to 14 days during the spring and summer, starting in Texas and advancing northward with the progressive development of the wheat crop at different latitudes. Since a single rust pustule may produce 350,000 spores, the rust can spread very rapidly. Rising air currents can lift the spores up to altitudes exceeding 10,000 feet and from such heights winds can carry the spores many miles before they fall to the ground.

A heavy rust epidemic on the nearly 4 million acres of wheat in South Dakota could produce about 2 sextillion rust spores. If only one in 10,000 of the spores blew north into North Dakota, four spores would be provided for every wheat plant in the State. Spores carried northward reach young wheat plants that are in a succulent stage, in which they are easily infected with rust. Spores blown southward in early summer fall on ripening or ripe wheat, which is not readily infected with rust. Those blown southward in late summer can attack volunteer wheat, early-sown wheat, and certain grasses. These plants in turn serve as a source of inoculum for fall-sown wheat in the South, where the rust lives over winter.

An additional source of rust menace the wheat in the northern half of the country—rust that develops on the barberry. The production of the brick-red uredospores ceases as wheat approaches maturity and black spores (teliospores) are produced in the same pustules. The latter stage is important only in the Northern States because the spores cannot survive the hot summers in the South.

The teliospores usually will not germinate immediately after they are formed but require a relatively long resting period, somewhat like the hard seeds of alfalfa and clover. They are not blown about by the wind, but remain on straw or stubble throughout the winter and germinate in the spring, especially in moist, cool weather. On germination, they produce small colorless spores (sporidia), which germinate and readily infect certain species of barberry.

The most important susceptible species is the common barberry (Berberis vulgaris), which was introduced from Europe as an ornamental shrub.
Others are wild native species, *Berberis canadensis* in the eastern Allegheny region and *B. fendleri* in the Rocky Mountains. The Japanese barberry (*B. thunbergii*) and the ornamental evergreen barberries are not attacked. The winter spores themselves do not directly cause infection on grains; their sporidia cannot infect grains or grasses, but infect only the barberry. The sporidia germinate on barberry leaves and send out small germ tubes that penetrate the epidermis directly. Only young parts of the plant therefore can be infected, for the germ tubes cannot penetrate the older, tougher parts.

Within a week or 10 days after germ tubes of the sporidia have entered the barberry, small yellowish or honey-colored spots appear on the infected parts, especially the young leaves. The yellow spots comprise the spermatangia, which contain the spermatia. Spermatia function in connection with the sexual reproduction of the rust by means of pycniospores, which may develop new races of the rust as a result of new combinations formed during sexual reproduction. Within a short time the cluster cups (aecia) are produced, commonly on the under surface of the infected leaf. The small cup-shaped structures contain long chains of cluster-cup spores (aeciospores), which are shot forcibly from their cups, especially during moist weather, are blown about by the wind, and initiate the red, or summer, stage of the rust on grains or grasses. The typical life history of stem rust where barberries become infected is, then, as follows: The rust overwinters in the black, or teliospore, stage; the teliospores germinate in the spring and produce sporidia, which cannot infect grains and grasses but do infect certain kinds of barberries, on which the aecial stage subsequently develops. The aeciospores cannot infect the barberry but, falling upon grains and grasses, germinate and induce the uredial stage. This stage may persist and produce successive crops of uredospores until growing conditions become unfavorable, when the teliospores are produced. While the stem rust fungus actually produces five kinds of spores, only the uredospores and aeciospores can infect grains and grasses. The teliospores, by means of which the rust usually survives the winter, are harmless unless there are barberries nearby.

Usually the rust is spreading from barberries to the grainfields some 2 or 3 weeks before the general rust spread arrives from the South. Because of this early start they may cause severe damage to grains growing near infected barberry bushes. The spread from barberries usually can be traced only short distances or up to a few miles; so the damage is largely local. However, they supply additional inoculum to hasten the spread of general epidemics. As many as 70 billion aeciospores may be produced on one large barberry bush.

About 240 parasitic strains or physiological races of stem rust of wheat have been discovered, but not more than a dozen are widely prevalent or are important in any one year. Even fewer recognized races are of common occurrence in South America. These races differ in their ability to attack certain varieties of wheat. For example, some attack Marquis but not Pawnee; others attack Pawnee but not Marquis.

The Little Club variety is attacked by all races. Race 15B attacks all wheat varieties grown on farms in the United States, but does not attack certain varieties from Kenya, Africa.

The same parasitic strains are not always present in a given region in different years, and there may be different strains in several regions in the same year. For that reason a variety may be susceptible to rust in one region and resistant in another; it may be susceptible in a given region in certain years and resistant in others. The development of stem rust on wheat, then, depends not only on the presence of numerous spores early in the growing season but also on the presence of spores of the particular
parasitic strains that normally can attack the variety of wheat grown in that region. Conversely, the particular races that occur in any region depend in part on the variety or varieties of wheat that are grown.

The leaf rust (*Puccinia rubigo-vera tritici*) of wheat usually attacks the leaf blades and sheaths, although it may sometimes occur on the stem proper, especially just below the heads. Sometimes it occurs also on the chaff and awns or beards. The rust pustules are smaller than those of stem rust, are more nearly round, and are less likely to unite. Usually they appear only on the upper side of the leaf. The color of the summer (uredial) stage is orange to orange brown, being brighter than that of pustules of stem rust.

The pustules of the black, or winter, stage (telia) are of about the same size as those of the red stage, but they seldom break through the epidermis of the plant, and the color, therefore, is likely to be lead gray. Leaf rust of wheat is found in nearly every place that wheat is grown. In the United States it is most abundant and destructive in the Southeastern States and in the Ohio and Mississippi Valleys, where weather conditions usually are most favorable for its development. It is less destructive in the hard red winter and the hard red spring wheat areas, although it is usually present to some extent and in favorable seasons may cause considerable damage to certain varieties. It usually is present in the irrigated areas of the West and on the Pacific coast but seldom does extensive damage, although sometimes it may be of importance locally.

Leaf rust may cause much damage to certain varieties of wheat in certain regions, although the damage usually is less conspicuous than that caused by stem rust. Leaf rust seldom shrivels the kernels, but it does reduce their size and number and the quality of the grain. Furthermore, when plants become heavily rusted while still young, the entire plant may be weakened and somewhat dwarfed, and, under such circumstances, the yield may be reduced as much as 90 percent.

This rust may occasionally attack barley to a slight extent, but for practical purposes it may be considered as attacking only wheat and a few species of goatgrasses (*Aegilops* species). The cluster-cup, or aecial, stage of leaf rust occurs on certain species of meadowrue (*Thalictrum*), but this is of no practical importance in the United States, as the species that are native here do not get infected under natural conditions.

The many parasitic strains of the leaf rust of wheat differ in their ability to attack different varieties. More than 140 of these strains are known and 85 have been identified in the United States. New ones are occasionally encountered. The exact manner in which they originate, however, is not known.

Leaf rust of wheat, like all other rusts, is caused by a very small parasitic fungus that enters the wheat plant through its breathing pores. The red, or summer, stage continues as long as the wheat plants are green and growing. The orange-colored pustules that develop on the wheat contain thousands of summer spores (uredosporcs), which are easily blown about by the wind and are capable of causing rust on other wheat plants. During warm, moist weather, this red stage may recur every week; therefore the rust can increase and spread rapidly. When conditions become unfavorable for the growth of the wheat and for the development of the red stage, the black, or telial, stage appears.

The red stage is capable of surviving the winter in most of the wheat-growing regions of the United States. It can be found at all times of the year in the Southern States and in some years in the Northern States. If weather conditions in late summer and early fall favor rust development—that is, if there is considerable moisture—the red stage attacks volunteer wheat plants and fall-sown wheat, where it may remain and even increase somewhat during the winter.
In the spring it increases rapidly if weather conditions are favorable. The spores then may be carried long distances by the wind and infect wheat plants in regions where the rust may not have survived the winter. The destructiveness of the epidemic will depend on the earliness with which plants are attacked in the spring.

When there is abundant rainfall or heavy dews in the spring and early summer, following a winter that has favored the survival of the red stage of the rust, abundant early infection may occur. If the weather continues warm and moist, there is danger of a destructive epidemic. As in the case of stem rust, warm, moist weather is most favorable for the development of leaf rust, but this rust seems able to develop under a wider range of conditions than does stem rust.

Stripe rust, *Puccinia glumarum*, has been commonly known as yellow rust because of the yellow or orange-yellow pustules of the summer stage. Stripe rust seems a better name, however, because one of its main features is the arrangement of the pustules in rows of various lengths, giving the appearance of fairly narrow yellow stripes.

Stripe rust attacks wheat, barley, rye, spelt, emmer, and more than 60 species of wild and cultivated grasses. In the United States it is most prevalent on wheat and certain wild grasses. It is seldom found on barley and rarely on rye. It is especially common on some of the wild barleys and bromegrasses and on a species of goatgrass.

Stripe rust develops most abundantly on the glumes or chaff, on the leaves, and on the leaf sheaths, but it may also attack the stems and the kernels. On seedling plants, and sometimes on older plants, the stripes are not distinct, but the yellow color distinguishes the rust from other cereal rusts.

If the attack of stripe rust is heavy, especially on the necks and glumes, considerable damage is likely to result, particularly if plants have become rusted during the milk stage or earlier. Under such conditions the kernels may be shriveled and the yields considerably reduced. Often, however, stripe rust is most abundant in seasons that are so favorable to wheat that high yields are obtained despite the damage from the disease.

The black stage of the rust is formed after the red, or summer, stage but may develop at any time during the growing season and at any stage in the development of the host. The black pustules (telia) also are produced more or less in rows that look like long, narrow, dark-brown, or black stripes. They may appear on all above-ground parts of the plant, including even the kernels.

Stripe rust is the commonest and most destructive grain rust in many regions of Europe. It occurs also in Africa, South America, Japan, China, and India. Stripe rust has been in the United States at least since 1892 but was not recognized until 1915. It occurs sporadically over the western half of the United States and at corresponding longitudes in Canada and Mexico.

The several physiologic races of stripe rust differ in their ability to attack certain varieties of wheat and other grass species. A special race attacks only a wild barley (*Hordeum murinum*). Both the summer, or yellow-spore, stage and the black stage of stripe rust are produced in the United States. An alternate host and therefore the cluster-cup (acacial) stage are unknown. The exact conditions under which the yellow stage overwinters most abundantly are not known, although it persists throughout the winter under a variety of climatic conditions.

Epidemics of stripe rust are most likely to occur when there has been abundant infection in late summer and fall of the previous year, when a large number of summer spores and abundant mycelium have survived the winter, and when spring and summer conditions, such as cool nights, warm days, heavy dews, and abundant sun-
shine, prevail during the growing season. Unlike some of the other cereal rusts, stripe rust seems to thrive best at low temperatures; in fact, its development is likely to be checked by hot weather.

While stripe rust is extremely destructive in some foreign countries, it has caused relatively little damage in the United States, except in limited areas where susceptible varieties are grown and where weather conditions are very favorable.

Stripe rust has not become established in the principal grain-growing regions of the Mississippi Valley. Experience in other countries, however, indicates that it might be destructive to some varieties of wheat under favorable weather conditions.

When the upper part of the stems, chaff, and kernels become rusted during the milk or early dough stage of kernel development, the grain may be considerably shriveled. Yields then are smaller and the wheat is of inferior quality. Badly rusted grain may germinate poorly, but infection is not transmitted to plants grown from such diseased seed.

**Stem Rust on Oats (Puccinia graminis avenae)** looks like the stem rust on wheat. Stem rust is darker in color than crown rust and usually produces longer pustules and is more abundant on the necks of the plants. The color of the summer stage of stem rust usually is brick red; that of crown rust is a bright yellow or yellow orange. This disease attacks oats, a number of the wild grasses, orchardgrass, some of the fescues, meadow foxtail, and bluejoint. Normally it does not attack wheat, barley, or rye. Its life history and methods of spread are like those of the stem rust of wheat.

**Crown Rust of Oats (Puccinia coronata)**, often known also as leaf rust or orange leaf rust of oats, occurs principally on the leaves, although it is frequently present also on the leaf sheaths and sometimes on the stems and panicles. The most destructive disease of oats, it often cuts the yields 20 to 50 percent. Crown rust is particularly destructive in the South and in the North Central States. More than 80 species of grasses may be attacked by one or another of several varieties of crown rust. Among them are quackgrass, reedgrass, redtop, meadow fescue, ryegrass, and bluegrass. The variety of crown rust most prevalent on oats also attacks several grasses and a number of different kinds of buckthorn. The oats variety of crown rust comprises in turn a number of distinct parasitic strains, which differ in their ability to attack different varieties of oats. More than 100 physiologic races of crown rust have been identified in the United States.

The pustules of the red, or summer, stage of crown rust are usually more or less circular. They rupture the epidermis and release uredospores. Later in the season the black, or winter, stage appears. The black pustules usually do not rupture the epidermis. The cluster-cup stage of crown rust develops on a number of species of buckthorn (Rhamnus). The first stage (spermagonium stage) appears on the upper surfaces of the leaves or on young twigs as small bright-yellow or orange spots. Opposite these spots, usually on the under surface of the leaf, the cluster-cup stage appears.

The life history of crown rust is similar to that of stem rust except that the cluster-cup stage develops on buckthorns instead of on barberries. The summer spores overwinter in the South and are spread to other plants and fields in the spring. In the Northern States the red, or summer, stage does not overwinter commonly, and epidemics result from summer spores that may be blown in from the South or from the development of the cluster-cup stage on buckthorns.

Warm, moist weather is most favorable for the rapid development and spread of crown rust. Moisture from dews or rains is likely to be held longer in dense stands of oats; that favors the
development of rust. Epidemics are most likely to develop when there are many spores in the spring and when weather conditions favor the development of the rust. In the fields of winter oats in the South, where the summer spores survive the winter, the rust gets an early start in the spring. The amount that overwinters depends on the amount of infection in the previous season and on weather conditions; mild winters are particularly favorable for the survival of the rust. In the Northern States the amount of infection on buckthorn bushes determines how early and how good a start the rust gets. If the weather in the early spring has been favorable for abundant infection on the buckthorns, there may be considerable crown rust if the subsequent weather conditions are also favorable. Summer spores blown into the Northern States from the South may also cause widespread epidemics. All buckthorn bushes in the northern oat-growing States should be destroyed because inoculum from them causes severe losses to oats in the vicinity and provides inoculum for an early spread of crown rust.

Barley is attacked by both the wheat and rye strains of stem rust and the development and spread of the disease on barley is the same as for those crops.

**Leaf rust of barley** is seldom of economic importance in areas where spring barley is grown but is sometimes destructive locally to winter barley. At times it is so abundant as to prevent the proper heading of infected plants and may sometimes reduce the yields and the quality of the grain.

The pustules of the summer stage of leaf rust of barley appear on the leaf blades and sheaths of the barley plant. They are yellow or yellowish brown, small, and round. The black stage follows the red stage and produces lead-gray pustules, which do not rupture the epidermis of the plant.

Leaf rust attacks cultivated varieties of barley, although under some conditions it may develop weakly on some of the other cereals and on several wild grasses.

The life history of leaf rust of barley is similar to that of the leaf rust of wheat. The rust survives the winters in the red, or summer, stage, particularly in the winter regions. The spring, or cluster-cup, stage, when it is produced, develops on the star-of-Bethlehem (*Ornithogalum umbellatum*), and a closely related species (*O. narbonense*). Although those plants are fairly common in certain parts of the United States, they rarely become rusted.

**Stem rust of rye** (*Puccinia graminis secalis*) has a life history similar to that of wheat rust. However, stem rust of rye attacks barley but does not develop on the wheat and oats, except under specially favorable experimental conditions. In addition, it attacks many of the same grasses as does wheat stem rust from wheat but particularly quackgrass, which is not commonly attacked by wheat stem rust. Because of the early maturity of rye and the fact that it is grown but little in the South, severe attacks of stem rust on rye are rare except where there are barberry bushes. The eradication of barberry is the only control measure needed.

**Leaf rust of rye** (*Puccinia rubigo-vera*) is similar to the leaf rust of wheat; so similar, in fact, that it is considered as belonging to the same species. It may occur wherever rye is grown. In the South, where rye is sometimes used for winter pasturage, it may become so abundant as to kill the plants during the winter. It may also cause considerable losses in the northern rye-growing regions. It attacks *Sécale montanum*, a wild species of rye. Some wild grasses may occasionally become infected if the conditions are favorable, but the rust generally is restricted to rye.

It usually attacks the leaf blades and sheaths. It may occur also on the necks and glumes of severely rusted plants. The pustules of the red stage
are scattered more or less irregularly and are orange brown to cinnamon brown. They are usually small but may unite to form fairly large pustules. The pustules of the black stage are gray to black and remain covered by the epidermis until it decays or falls away. The rust persists during the winter in the red, or summer (uredial), stage. The spring, or cluster-cup, stage can develop on some plants of the borage family, but it is seldom found in nature in the United States and is therefore of no importance in the life history of the rust.

The development of epidemics occurs under conditions similar to those that promote epidemics of leaf rust of wheat. The degree to which the summer stage persists during the winter depends on weather conditions. In the spring, new infections occur; if the weather is warm and humid, the rust may become epidemic.

Rainy weather or cool, dewy nights and warm, humid days are most favorable for the development of the rust. No variety of rye is uniformly highly resistant to leaf rust. Rye is cross-pollinated and no varieties are uniformly pure. Certain pure inbred self-fertile strains are highly resistant to leaf rust but are not vigorous and are therefore useful only as resistant breeding stocks.

Three methods of controlling leaf and stem rusts of wheat, rye, oats, and barley have been suggested— the use of resistant varieties, eradication of the alternate host, and dusting with fungicides. Early varieties and such cultural practices as early seeding and use of phosphate fertilizers that hasten ripening may help to escape rust but do not prevent damage in bad years. Their effect is indirect rather than direct. In general the recommended control measures are much the same for both leaf and stem rust and for all small grains with some modifications, depending on the particular crop or alternate host.

Late seeding, especially of spring grains, delays ripening and is likely to increase the damage because it provides a longer period for the development of the rust organism. Farmers generally recognize the advantages of early seeding and usually do their seeding as early as possible. Phosphorus often hastens ripening and thereby reduces rust damage. Heavy applications of barnyard manure or of nitrogen, on the other hand, may delay ripening and also may produce a heavy vegetative growth that retains moisture and favors the development of rust.

Extensive trials have shown that stem and leaf rusts of wheat and presumably those of other cereals can be prevented by dusting with sulfur or other suitable fungicides. Usually three or more treatments during the season are necessary. More are needed if the fungicide is washed off by frequent rains. Dusting should begin before rust damage appears, but that is wasted effort in seasons in which rust development is light and the cost generally is too great to be practical in the United States. Some of the newer fungicides may be more effective than sulfur.

Eradication of the common barberry (the alternate host of stem rust of wheat, rye, oats, and barley) and of buckthorn (the alternate host of crown rust of oats) has been widely practiced. Damage from stem rust has been greatly reduced since eradication of the barberry was started. At the same time an aggressive breeding program has sought to produce resistant varieties, especially of wheat. In the more humid sections of the northern Great Plains where stem rust has been most destructive, practically no varieties of wheat susceptible to the ordinary races of stem rust (other than race 15B) have been grown since about 1938. It is certain that eradication of the barberries did not prevent the widespread distribution of race 15B in 1950 and again in 1952 nor infection of susceptible varieties in experimental plots at several locations in recent years. The reason doubtless is that wind-
blown spores from rust overwintering in Mexico and southern Texas were carried to northern wheatfields in the late spring and early summer. Eradication of the barberries in some years has delayed the onset of rust infection and thereby reduced damage in local areas below what it otherwise would have been.

The discovery that rust may hybridize on barberry bushes and thus produce new races is an additional reason for continuing the eradication campaign. Varieties formerly considered to be resistant, including Ceres, Vernal emmer, and Iumillo durum, were attacked later by races of rust believed to have originated on the barberry. Despite this menace from new races, Iumillo durum retained its resistance to rust in the field in the United States for nearly 50 years and Vernal emmer probably for 75 years, and both for an unknown period elsewhere before finally succumbing to race 15B. We have evidence also that new rust races may be produced by mutations in the absence of barberry bushes. Whatever the answer may be, the past losses and future potential losses are so great that no promising method of control should be neglected. Eradicating the common barberry and breeding resistant varieties both fall in this category.

Breeding resistant varieties is certainly one of the most promising methods for controlling all rusts of small grains. It takes a long time, however, and often is difficult. Since stem rust has been most destructive on wheat, most of the outstanding examples of successful breeding for resistance to this disease relate to wheat. Outstanding progress also was made in breeding oats resistant to crown rust.

Both stem and leaf rust of wheat were recognized as among the more important hazards in growing wheat in many sections of the United States before 1900. About 1890 B. T. Galloway of the Department of Agriculture conducted spraying experiments that showed that rust could be reduced by fungicides, but he concluded that resistant varieties, if available, would be a more practical method of control. No markedly resistant varieties were known at that time. M. A. Carleton, who was employed by the Department of Agriculture in 1894, sowed an extensive collection of wheats from many countries at Garrett Park, Md., that fall, in a search for resistant varieties. It was known then that soft winter varieties grown extensively in Texas, Kansas, and southern Nebraska were more susceptible than the hard winter wheats then being adopted in those States, but even the latter were severely damaged in years when rust was bad. Some of the durums were known to be resistant to leaf rust, but they had not been used to any material degree as parents in crosses.

By 1900 Mr. Carleton and others had introduced from Russia and other countries a number of varieties of durum wheat and emmer, which were widely grown in experimental plots throughout the Great Plains. In 1902 and again in 1904 at Brookings, S. Dak., John S. Cole observed that certain varieties, specifically Yaroslav emmer from Russia and Iumillo durum from Italy, were almost completely immune to attacks by stem rust.

They were not satisfactory commercial or bread-making wheats, but they provided rust-resistant parents for hybrids and thereby the basis for an effective breeding program. Their usefulness is attested by the fact that practically all varieties grown in 1953 in Minnesota, the Dakotas, Wisconsin, and Canada, many of those grown in California, and some of those grown in the Eastern States carry resistance genes from one or both of those two early introductions. The job has by no means been completed—as proved by the widespread invasion of race 15B, which attacks all commercial varieties.

Losses from rust have been greatly reduced; even more important per-
haps are the lessons that have been learned and the confidence in ultimate success that has been generated as a result of this experience. Such progress as has been made is the result of more than 60 years of research. Many difficulties have been met and overcome. A brief account of some of the problems and the ways in which they have been solved may be of value.

Crosses between commercial varieties of common wheat and Iumillo durum and Yaroslav emmer were made by Mr. Cole at Brookings almost immediately after the resistance of the latter was discovered in 1904 or 1905. But the crosses were lost before anything useful was derived from them because of changes in personnel. Similar crosses were made at the University of Minnesota about 1907 and at other places in later years. Serious difficulties were at once encountered because of a high degree of sterility and of linkage of rust resistance with undesirable characteristics from the durum and emmer parents. As a result it was nearly 30 years before any really satisfactory variety was derived from such crosses. Other sources of resistance had been discovered in the meantime and used in crosses to produce some commercially desirable common wheats.

The first of the latter to become really important was Ceres, produced by L. R. Waldron of the North Dakota Agricultural Experiment Station and distributed to farmers in 1926. Ceres was derived from a cross between the famous Marquis variety from Canada and Kota, a rust-resistant common wheat found mixed in a durum wheat that had been introduced from Russia by H. L. Bolley in 1903. Ceres was resistant to the prevailing races of stem rust. It was also moderately early and resistant to drought. It was soon grown throughout the northern Great Plains until after 1935, the year in which it was severely damaged by race 56, to which it is susceptible and which first appeared in epidemic proportions in that year.

The second resistant common wheat to be developed from a cross was Hope. It was first distributed to farmers in 1927. It was never widely grown, largely because of its susceptibility to heat and drought and low relative yields in the absence of rust. It is of great interest, however, because it or its near relatives have entered into the parentage of most of the resistant varieties now generally grown (except Thatcher) and because of the somewhat unorthodox manner in which it was produced.

Hope was derived from a cross between Yaroslav emmer and Marquis wheat made in 1915 by E. S. McFadden, then employed by the South Dakota Agricultural Experiment Station as an undergraduate student assistant. Because of the high degree of sterility, only a few poorly developed seeds were secured from the cross. From them developed a single plant. The first of the subsequent generations consisted of nondescript, unpromising plants, which were grown in bulk at the Highmore Substation in order “to permit natural selection to eliminate some of the undesirable combinations. . . .” An important feature was the strict elimination of shrunken seed by screens and strong blasts of air in a fanning mill. Another was the relatively large population of plants which could be grown by this method.

Marquillo was the first commercially grown variety to be derived from crosses involving Iumillo. It was distributed by the Minnesota Agricultural Experiment Station in 1928. Like Hope, it was never extensively grown, mostly because of the yellow color of the flour produced from it. It and sister strains have been useful, however, as parents in other crosses.

The famous Thatcher variety, distributed by the Minnesota Station in 1934, was derived from a double cross involving a sister strain of Marquillo and a selection from a cross between Marquis and Kanred winter wheats. As Kanred is resistant to some races of stem rust, it is generally considered
that the resistance of Thatcher is due to genes both from the Iumillo durum and from Kanred.

Thatcher was first grown by farmers in 1934. In the severe stem rust epidemic of 1935 it often outyielded Marquis and Ceres by 20 to 30 bushels an acre. In subsequent years its acreage increased as rapidly as seed supplies permitted. It was highly resistant to the prevailing races of stem rust, ripened early, had short, stiff straw, and produced grain of excellent quality. By 1939 it was the most important variety of spring wheat in the United States.

Thatcher, however, is very susceptible to leaf rust. It was severely damaged by that disease in 1938 and 1941. In the meantime, other new varieties resistant both to leaf and stem rust had been produced and distributed to farmers. The principal ones are Rival and Pilot, distributed in 1939; Regent, released in Canada in 1939; Newthatch, released in 1944; Mida, in 1944; Rushmore, in 1949; and Lee, in 1951.

The acreage of Thatcher began to decline after 1940 and since then has practically disappeared in the eastern half of the northern Plains of the United States, although it continued to be grown in the drier western sections and in Canada. All of the newer varieties, except Lee, derived most of their resistance from Hope or H-44, a sister selection of Hope.

Hope and its derivatives fortunately were resistant to the prevailing races of leaf rust as well as stem rust. About 1944 a new race of leaf rust that attacked most previously resistant varieties appeared generally in farmers' fields throughout the Great Plains. That meant that varieties resistant to the new race and to the older races were needed.

Lee was produced in Minnesota from a cross between Hope and Timstein. Timstein is a selection from a cross between Triticum timopheevi, a wheat relative, and Steinwedel, a common wheat, made by J. T. Pridham of Australia and brought to the United States by his associate, S. L. McIndoe. Lee is highly resistant to most prevailing races of leaf and stem rust except stem rust race 15B.

Interest in 1953 centered in the production of new varieties resistant to 15B as well as to other races of stem rust. The race now known as 15B was identified as early as 1939, and attention was at once directed to discovering new sources of resistance. Since the widespread onset of 15B in farmers' fields in 1950, these efforts have been greatly intensified. Much progress has been made and it is reasonably certain that new varieties will be produced that are resistant to all the prevalent races both of leaf and stem rust and which are satisfactory or superior in other respects.

Considerable control of stem and leaf rust in the southern Great Plains has come about indirectly, and to some extent perhaps unexpectedly, through the development of early maturing varieties. Many of the newer ones carry genes for resistance derived from various sources. Even more important has been the discovery that early ripening varieties are generally superior throughout much of the region even in the absence of rust. Unfortunately these early varieties are not so winter hardy as the old Turkey and others they largely replaced and hence are not suitable for the colder areas. Some notion of the importance of this development may be gained from the fact that early or moderately early varieties, including such important ones as Pawnee, Comanche, and Wichita, occupied more than 75 percent of the wheat acreage in Kansas in 1952.

Much progress has also been made in California in breeding new varieties resistant to the races of stem rust that prevail in that State. The California program is unique in that the backcrossing technique has been used exclusively in producing new varieties resistant not only to stem rust but also to bunt and hessian fly. This technique
insures that the new varieties are very similar to the old varieties except for the addition of the resistant genes. Hence there is not the usual uncertainty regarding yield performance, quality, and other characteristics of the new varieties. Consequently less extensive tests for yield and quality are believed to be necessary. Out of this breeding program have come such varieties as Baart 38, Baart 46, White Federation 38, Ramona 44, and Big Club 48, which occupy some 85 percent of the wheat acreage of California.

Breeding for resistance to leaf rust and in some cases also for resistance to stem rust has been an important objective in several Eastern States—Indiana, Illinois, Kentucky, Georgia, and North Carolina—and by the Department of Agriculture at Beltsville, Md. Several new varieties resistant to leaf rust and in some cases to stem rust have been released to farmers. The more important of these are Vigo in Indiana; Saline in Illinois; Chancellor in Georgia; Atlas 50 and Atlas 66 in North Carolina; Anderson in South Carolina and North Carolina; and Coastal in South Carolina.

The history of breeding for rust resistance in the durum wheats is similar to that for the hard spring, but is less involved. Most of the introduced durums at the time of their release were moderately or highly resistant to the prevailing races of both rusts. New or previously unimportant races, especially stem rust races 17 and 21, to which they are susceptible, soon appeared, however.

Among the earliest attempts to obtain resistant varieties were crosses made in Minnesota between durums of good quality and the poor but highly resistant red durum, Pentad. No suitable progenies came from the cross, and attention was then concentrated on Vernal emmer as a source of resistance. Stewart and Carleton, produced in North Dakota from a Min- dum x Vernal emmer cross and distributed in 1943, are resistant to these and older races. Stewart has since become the leading variety of durum wheat. Vurnum and Nugget, also produced in North Dakota, were released to farmers in 1947 and 1951, respectively. None of these newer varieties nor the old ones is resistant to 15B. Resistance to 15B has been found in certain poor-quality durums from Portugal and Spain, and they have been crossed with the leading commercial varieties. Promising selections are being increased.

All commercially grown varieties of durum are even more susceptible to 15B than are the common wheats. Moreover, the durums generally ripen later and hence favor the development of this race of stem rust to an unusual degree. Although the immediate outlook is rather unfavorable, we believe that satisfactory resistant varieties will be developed.

The experience since 1900 helps to explain why the creation of new varieties is often a slow and uncertain process. Sterility and linkage are always a problem in dealing with intergeneric crosses, but plant breeders know better how to deal with them than they did a generation ago.

In oats more than in any other major crop, there has been a parade of new varieties and frequent and complete changes in varieties in the past 50 years. Breeders have been successful in producing high-yielding, rust-resistant varieties widely grown by farmers. As new or previously unimportant races of the rust organisms have appeared, still other varieties resistant to them have been developed. The introduction and creation of early maturing varieties that escape much rust damage have also been important factors.

At the beginning of the century only late or medium-early varieties and only rust-susceptible varieties (with a few exceptions) were available. The main exceptions were the late or comparatively late White Russian and Green Russian varieties, which were resistant to stem rust but highly
susceptible to leaf rust, and Red Rustproof and Burt, in the Southern States. It is now known that the Red Rustproof types are better designated as late rusters rather than as rustproof, since they are not resistant.

The first important step in avoiding damage from oat rusts in general consisted of the introduction of the Kherson and Sixty Day varieties from Russia, the first by the Nebraska Agricultural Experiment Station in 1896 and the second by the Department of Agriculture in 1901. Neither is resistant to stem or crown rust, but they matured early and escaped much damage that otherwise would have occurred. Widely adapted throughout the central United States from the Atlantic almost to the Pacific coast, they soon became the dominant varieties, especially in the Corn Belt.

Another important introduction was Swedish Select, brought to the United States from Russia in 1899. It also is not resistant to either stem or crown rust but matured somewhat earlier than many of the varieties it replaced in the northern United States. Burt, an early-maturing crown-rust-escaping selection from Red Rustproof, made in 1878, has been widely grown throughout the South and sparingly in the southern part of the Corn Belt. Another important early but rust-susceptible variety was Fulghum, selected about 1900 from Red Rustproof by a farmer, J. A. Fulghum of Warrenton, Ga. Kanota, often regarded as a synonym of Fulghum, was distributed in 1919 by the Kansas Agricultural Experiment Station. Because of its early maturity, it did much to reduce crown rust damage in Kansas and nearby States.

The importance of breeding for resistance to stem rust apparently was first recognized about 1918 when White Russian was crossed with Victory in Minnesota. From it the resistant variety Anthony was produced. Anthony was distributed to farmers in 1929. Richland and Logold were selected at the Iowa Agricultural Experiment Station from Kherson in 1906 and distributed to farmers in 1914 and 1926, respectively. Rainbow, highly resistant to stem rust and moderately resistant to crown rust, was selected at the North Dakota Agricultural Experiment Station in 1925 and distributed to farmers in 1930.

One of the first definite attempts to produce varieties resistant to crown rust was made in 1928 when Rainbow, resistant to stem rust and moderately resistant to crown rust, was crossed with Markton at Aberdeen, Idaho. Selections later were grown at Ames, Iowa, and Arlington Farm, Va., where they were tested for resistance to rust, for yield, and for other characteristics. One of them, Marion, was distributed to farmers in 1941.

Several severe epidemics of crown rust and the discovery of the high degree of resistance of two varieties to the disease centered the attention of oat breeders on crown rust resistance as an important objective. One, Victoria, had been introduced from Uruguay in 1927. The other, Bond, came from New South Wales in 1929. Neither was satisfactory for growing on United States farms but appeared to be just what the oat breeders wanted as parent material.

Victoria was crossed with Richland in 1930. In subsequent years 30 varieties were selected from it and other Victoria crosses and distributed to farmers. They were soon the dominant varieties in all Corn Belt States and were important also in the Northeast and South. They were grown on approximately 30 million acres—about two-thirds of our oats acreage—in 1946. They produced high average yields, had short, stiff straw, and did not easily lodge, a characteristic almost unique among varieties adapted to the Corn Belt and highly prized by farmers who use combines.

Helminthosporium blight, a previously unimportant disease, caught up with the oats crop in 1946. Victoria and selections from crosses in which Victoria was a parent were especially
susceptible and were seriously damaged. Fortunately Bond was resistant; in the meantime it had been used extensively as a parent and a number of selections were then in the yield-testing stage. Seed supplies of a few of them had been increased to be distributed if and when their superiority should be demonstrated. The widespread damage from helminthosporium blight emphasized their potential value and stimulated more extensive tests for yield and other characteristics. Out of this work have come such outstanding varieties as Clinton, Bonda, Andrew, Benton, and Mindo, now widely grown in the Corn Belt; and Camellia, Taggart, and Delair, which are grown to some extent in the Southern States. These new varieties, derived from crosses in which Bond was one parent, are resistant to the helminthosporium blight and generally to crown rust and are fully equal to the Victoria-derived varieties in yield, stiffness of straw, and quality.

Those achievements do not, however, justify complacency. Crown rust races 45 and 57 attack Bond and most of its derivatives. More recently crown rust race 101 has been discovered; it attacks both Victoria and Bond and their derivatives.

Two otherwise poorly adapted varieties, Landhafer and Santa Fe, which are resistant to those races and also to helminthosporium blight, have been crossed with Bond and Victoria derivatives to produce varieties with the necessary resistance to both diseases. Two such varieties, one produced at the Iowa Agricultural Experiment Station and the other at the Indiana Station, were to be made available for general growing in 1954. Floriland, a new variety that is resistant to crown rust race 101, was distributed in Florida in 1953. Other varieties resistant to one or more of these races and used as parents in crosses are Ukraine, Trispernia, and Klein.

Stem rust came again into the picture with races 6, 7, and 8, to which most of the new varieties are susceptible. Race 8 is widespread and abundant. Race 7 appears to be rapidly increasing. A new, more virulent biotype, 7A, has been reported from Canada. Race 6 occurs infrequently.

Segregates from crosses designed to combine resistance to those races with resistance to other races of stem rust, crown rust, and the helminthosporium blight were in the yield-testing stage in 1953.

**Rusts of barley** were not generally considered important enough to justify intensive breeding for resistance to them until about 1935, when many fields in the North Central States and western prairie regions were severely damaged by stem rust. It is now generally recognized that leaf rust may do damage generally in all humid barley-growing areas but principally on winter barley in the Eastern and Southeastern States. Resistance to both rusts has been an important objective in most barley-breeding programs in those areas.

The most important commercial variety resistant to stem rust was found by a farmer, S. T. Lykkens of Kindred, N. Dak. In 1935 he decided to plow up his field of Wisconsin Pedigree 37 because of severe damage by stem rust. He observed a single plant that was free of rust, saved the seed, planted it in his garden the next spring, and in subsequent years sold seed to his neighbors. By 1942 it was a recognized commercial variety. Its resistance has since been verified by others. It has been included in numerous yield trials and tests of quality. Although it has some defects, such as weak straw, it has compared favorably with other varieties in most important respects. It has been named Kindred and is now grown more extensively for use in malting than any other variety in the principal barley-producing area of the United States.

Other commercially grown varieties resistant to stem rust are Peatland, Mars, Plains, Feebar, and Moore.
Fifty or more other varieties, most of them from the world collection of barley from various foreign countries and as selections from farmers' fields known to be resistant to stem rust, are valuable sources of resistance for use by plant breeders, even though they are not grown commercially. Progress has been made also in breeding varieties resistant to leaf rust, but only one, Goliad, had been released in 1953. Goliad is also resistant to stem rust.

The large number of physiologic races (240 or more of stem rust of wheat, for example) has sometimes seemed an insurmountable obstacle to the successful breeding of resistant varieties. Nevertheless a great deal of progress has been made. From the years of experience has come a better understanding of their relation to breeding programs.

Our concept of a large number of races stems mostly from the manner in which they are identified. Because of technical difficulties, it is not generally feasible to determine the ability of each of a large number of collections of rust spores to infect each of a large number of varieties in an advanced stage of growth in the field. Yet this is the information that is needed. The nearest approach to this so far devised for identifying races is to infect young plants, usually seedlings, growing in a greenhouse. Only a few varieties, often not more than a dozen, are included in the tests, and they are usually the same year after year. They are known as host testers. It is hardly to be expected that results from the tests could be applied directly to breeding without due consideration of the conditions under which they are obtained.

One important fact is that resistance or susceptibility in the seedling stage in the greenhouse does not necessarily mean resistance or susceptibility when a plant is in an advanced stage of development in the field. A physiologic race that infects a given variety in the seedling stage but not when the plants are approaching maturity is not likely to be a serious menace to that variety, but it may add to the number of physiologic races.

Another fact that makes breeding for resistance to all prevalent races less formidable than it may seem to be is that many varieties are resistant to several races. It is known, for example, that Kanred in the seedling stage is resistant to 11 races of stem rust. Hope is resistant to at least 17 races, Red Egyptian to 26, Kenya-Gular to 30, and certain other Kenya derivatives to at least 35. They may be and probably are resistant to a larger number in advanced stages of growth in the field, although, as we indicated, the exact situation would be hard to determine.

Somewhat the same applies to leaf rust of wheat and to the rusts of oats and barley. In most cases it is possible on the basis of known information to choose a small number of varieties of each crop that collectively are resistant to all known races of a given rust. If this resistance were to be concentrated in a single variety, and no new races appeared, the job of producing resistant varieties would be finished except as there might be need for resistant varieties for other areas or for other reasons. And this, of course, is what cereal breeders for rust resistance have been trying to do for some 75 years with considerable success.

From this point of view, the appearance of a new physiologic race does not mean defeat. Rather, it should be regarded as a warning of danger: A highway sign is designed not to frighten but to be respected.

John H. Martin is an agronomist in charge of sorghum investigations in the division of cereal crops and diseases at the Plant Industry Station, Beltsville, Md. He has written many bulletins, circulars, and other publications on cereal culture.

S. C. Salmon is an agronomist in charge of investigations of wheat in the same division. Before he joined the Department of Agriculture in 1930 he was on the staff of Kansas State College.