Chapter 6

Development and Impact of Regional Cereal Rust Epidemics

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The rusts are important diseases of many of the cereal crops that comprise a major part of the world's food supply. Historically, epidemics of stem, leaf, and stripe rust of wheat have been among the most devastating of the plant diseases. The pathogens *Puccinia graminis* Pers. f. sp. *tritici*, *P. recondita* Rob. ex Desm. f. sp. *tritici*, and *P. striiformis* Westend. f. sp. *tritici* reproduce asexually and produce large numbers of uredospores that are frequently transported by wind to distances up to thousands of kilometers within a few days. The hosts, various *Triticum* spp., are widely grown. Wheat is self-pollinated, and large areas are often sown to a cultivar or a group of cultivars that may be genetically similar in resistance to one or more of the wheat rusts. When environmental conditions are favorable for disease development and virulent, aggressive genotypes of the pathogen are present, the stage is set for a regional rust epidemic.

Rust epidemics have sometimes been local, affecting only a single field, cultivar, or geograpical entity such as a valley or low-lying area. Failure of local epidemics to become more widespread results from limitations in at least one of the factors of disease (host, pathogen, environment, or time). For this chapter I have arbitrarily defined regional epidemics as those that cover at least 50% of the area occupied by the crop on a continental basis and that cause an average loss of 5% or more.

HOST FACTORS IN REGIONAL EPIDEMICS

Distribution of Susceptible Phenotypes

Regional epidemics are most apt to develop when highly susceptible cultivars are grown over an extensive area. The cultivars need not be of identical, or even similar, genotypes except for the lack of resistance factors effective against the predominant pathogen genotype. In the United States, over 350 different cultivars of wheat are grown annually. Within regions, however, the soils, climate, pests, markets, economic incentives, and cultural practices are similar, so that farmers tend to select from a limited group of cultivars. There are approximately 50 cultivars grown per region annually but 20 cultivars make up roughly 30 to 50% of the national production in any year (Roelfs, 1985b). The cultivars differ widely in some characters and are very similar in others. Diversity for resistance cannot be determined except for individual pathogen phenotypes. For example, Centurk (a cultivar of *Triticum aestivum*) has genes *Sr5, 6, 8, 9a,* and *17* for stem rust resistance, and Lee has *Sr9g, 11,* and *16* but *Puccinia graminis* f. sp. *tritici* race 113-RTQ virulent on *Sr17* is virulent on both cultivars, race 113-RKQ virulent on *Sr17* is virulent on Centurk but not Lee. Race 113-RKQ avirulent on *Sr17* is avirulent on Centurk and Lee, while race 113-RKQ virulent on *SR17* is avirulent on Lee but virulent on Centurk.

Additionally, some hosts seem to be more susceptible than other susceptible hosts. For example, when the susceptible cultivars Baart and Prelude were crossed, progeny were obtained that were more susceptible than either parent (Skovmand et al., 1978). Both of these cultivars are themselves so susceptible to stem rust that they are frequently killed. Some pathogen cultures are more aggressive than others (see Katsuya and Green, 1967). In our greenhouse seedling tests race 15 and 56 produce larger uredia than other cultures from North America.

Spacing of Plants and Fields

Cereal crops are generally grown in rows. Row spacing for wheat varies from about 15 to 30 cm with about 400 tillers per square meter. When farmers increase row spacing they generally increase the seeding rate per linear unit and vice versa. In areas where high numbers of tillers per plant are formed the seeding rate per square meter is normally decreased. Thus, there is little space between adjacent tillers to impede the spread of disease. Multilines (mixtures of phenotypically similar lines with different resistance genes) are being widely promoted and tested but currently make up a minor portion of the world wheat production. Multilines of oats have been developed for crown rust control (Browning and Frey, 1969) as has a multiline of wheat for stripe rust control (Allan et al., 1983). In the People's Republic of China wheat is interplanted with other crops, but this practice is not common over entire regions nor is it used to control rust diseases.

Although relatively little research has been done on the effect of spacing between fields of wheat, the distances between fields must have a significant effect on rust development. Two large wheat growing areas in the United States are Kansas and North Dakota with approximately 5.3 and 4.2 million hectares (ha) of wheat, respectively (Fig. 1). Yet, wheat is grown on less than 20% of the areas of these states.

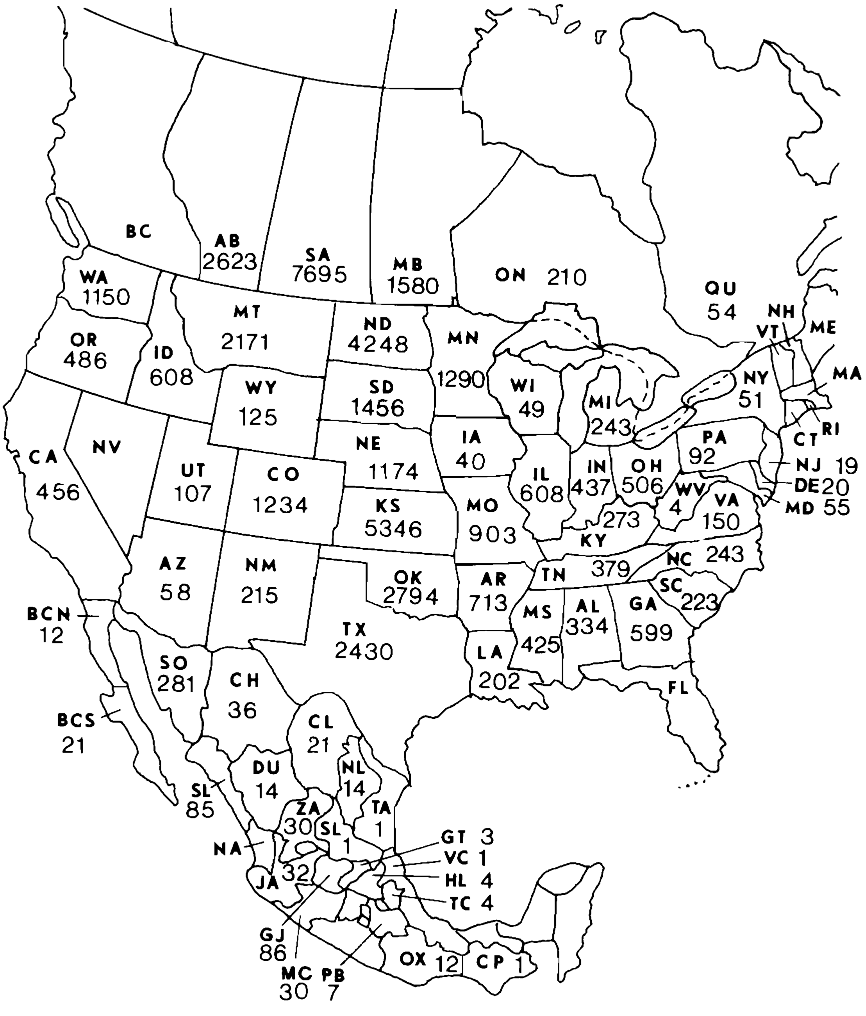

Figure 1 Distribution of wheat in North America. Values are in 1000 of hectares for the period 1978 to 1981.

When the pathogen race involved is virulent on only some of the cultivars, the relevant measure of spacing must be calculated for distance between fields of susceptible cultivars. If two or more pathogen races are involved, then the spacing may vary for the different pathogen races. Likewise, when a host resistance functions only under some environmental conditions, then spacing changes as conditions change.

Life Cycle of the Host

Wheat is an annual crop with a growing period of 3 to 11 months. Thus, the cereal rusts cannot survive from one year to another on the same plant, as occurs with perennial crops. In areas with mild winters wheat is planted in the fall and harvested in late spring or summer. Where winters are severe wheat is seeded in the spring (Figs. 2 and 3). Thus, in most areas of the world there is a period when wheat is not grown. Exceptions exist where the date of sowing of winter wheat overlaps the harvesting of the previous crop (e.g., a small area of the Pacific Northwest of the United States) or where elevation changes greatly over short distances (e.g., Kenya). Here rust may spread directly from the mature to the newly sown crop with favorable environmental conditions. Where self-sown wheat occurs between cropping seasons a "green bridge" of host material is provided on which the pathogen can survive between seasons.

Alternate Hosts

The alternate hosts for *P. graminis* are several species of *Berberis* and *Mahonia* (Roelfs, 1985a). For *P. recondita* alternate hosts are species of *Thalictrum, Isopyrum, Anchusa,* and *Clematis* (Samborski, 1985), while for *P. striiformis* there is no known alternate host (Stubbs, 1985). The alternate host and the

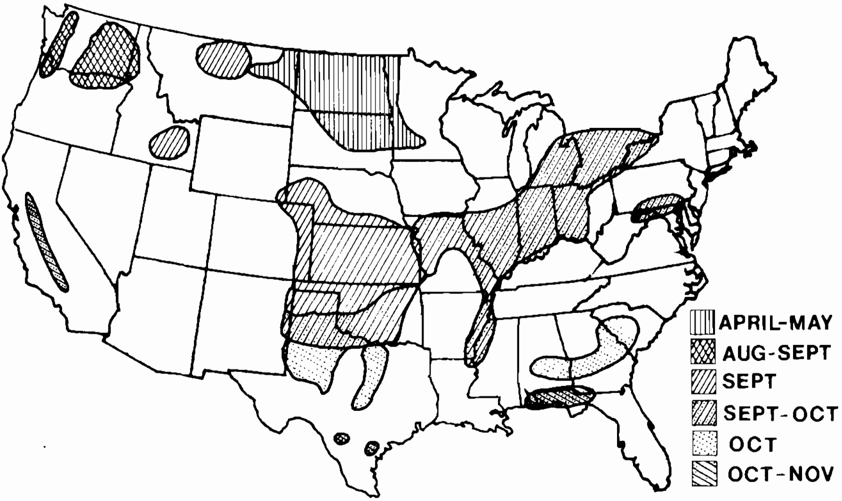

Figure 2 Wheat planting periods for the various areas of the United States.

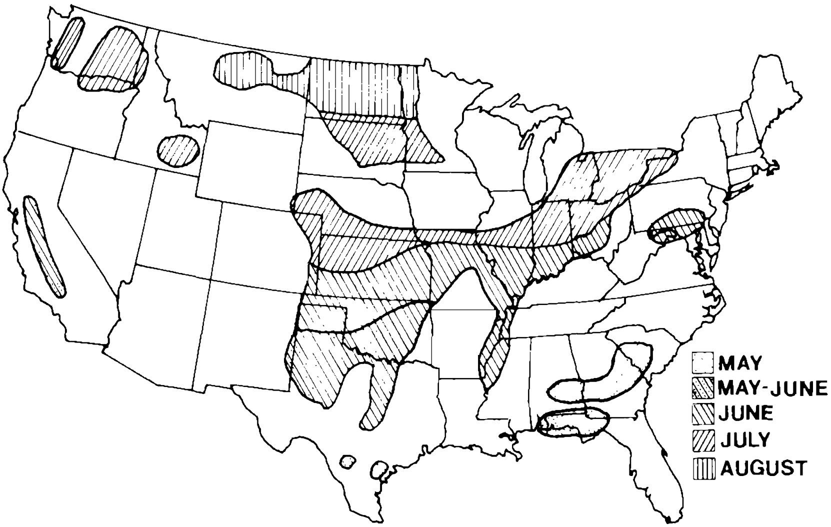

Figure 3 Wheat harvesting periods for the various areas of the United States.

teliospores provide a mechanism for the pathogen to survive the winter and reinfect wheat in the spring. The sexual cycle occurs during the transition from teliospores to aeciospores on the alternate hosts, so they provide not only a local source of inoculum at the early stages of the wheat growth, but also an opportunity for genetic recombination of virulence types.

The major stem rust epidemics in North America (which occurred in the years 1878, 1906, 1916, 1935, 1937, 1953, and 1954) show no evidence of being the result of aeciospores spread from barberry. They all seem to have originated from air-borne uredospores from the south (Craigie, 1945; Roelfs, 1982). Many local epidemics have resulted from aeciospores spread from barberry in Minnesota, North Dakota, and Wisconsin (Roelfs, 1982). A local epidemic and its associated loss is shown in Fig. 4. Such epidemics were eliminated in Denmark by barberry eradication (Hermansen, 1968).

The only area where sexual reproduction occurs regularly in *P. recondita* is in eastern Siberia (Chester, 1946, pp. 62-67; Saari and Prescott, 1985). The role of the alternate host in epidemics and the effects of the alternate host on diversity in virulence are discussed in Roelfs and Groth (1980) and Groth and Roelfs (1982).

Accessory Host

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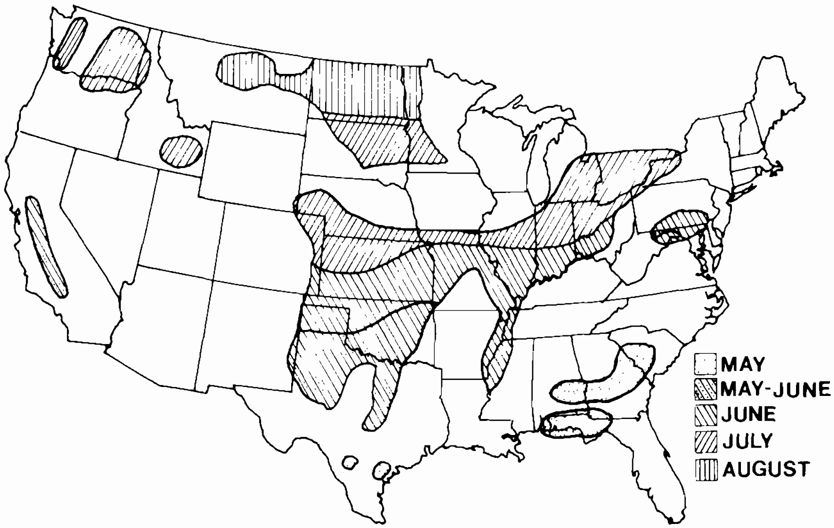

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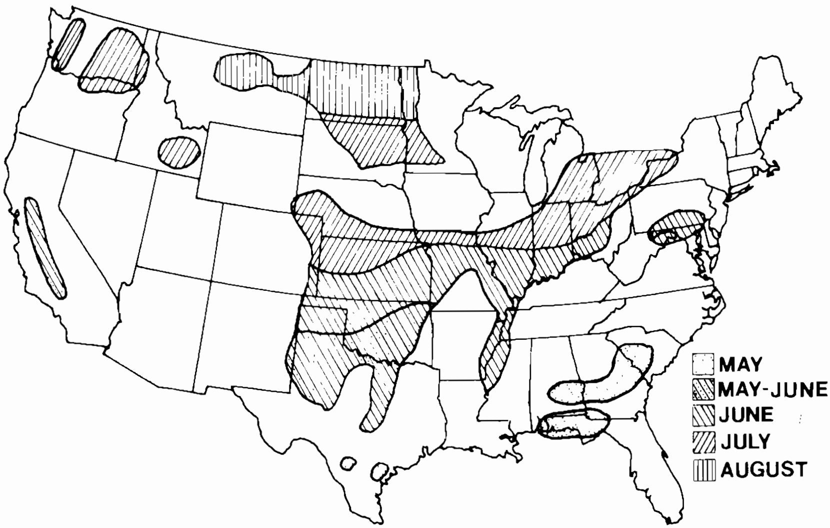

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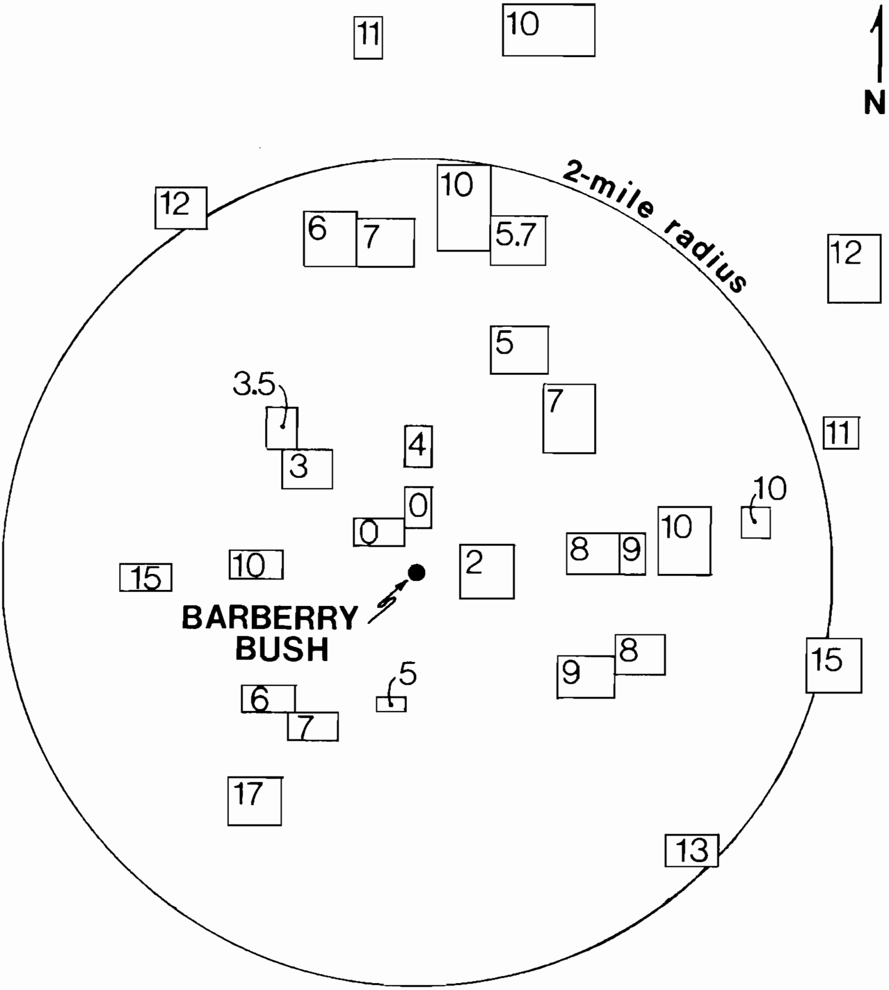

Figure 4 Wheat yield in bushels per acre in the immediate vicinity of a barberry bush near Alert in Decatur County, Indiana. Yields outside the rusted area were 15 to 25 bushels per acre. *(Adapted from Beeson, 1923.)*

well understood in cereal rust epidemiology in most areas of the world. Interesting reviews are available for Israel which is part of the area of origin of wheat (Anikster and Wahl, 1979; Wahl et al., 1984). In North America, the wild, noncultivated *Hordeum jubatum* L. is often infected with *P. graminis* but most inoculum is from uredospores produced on wheat rather than on *H. jubatum*. After wheat harvest in Nebraska, stem rust is often common on *H. jubatum*; however, it is not known whether this forms a green bridge to the fall sown wheat. An accessory host such as *H. jubatum* may also be infected with *P.*

graminis f. sp. *secalis*, which is avirulent on wheat. Stripe rust is common on wild *Hordeum* spp. in Chile, but these cultures are generally avirulent on wheat. Often where accessory hosts are infected, self-sown plants of the crop are also infected and occur in greater numbers nearer to newly sown fields. The pathogen races present on accessory hosts may differ in relative frequency from their occurrence on the cereal crop, as with *P. graminis* Pers. f. sp. *avenae* on wild oats, *Avena fatua* L., in the United States.

In North America, there is no available evidence to indicate that regional epidemics arise from initial inoculum generated on accessory hosts. However, accessory hosts can maintain a green bridge between crop seasons, and in the areas with mild climates they may provide a continuous source of inoculum. In studies of virulence changes and their causes in the cereal rusts one should be aware of the potential effects of accessory host, especially during periods of low pathogen population levels.

PATHOGEN FACTORS IN REGIONAL EPIDEMICS

Virulence Combinations

Resistance in cereals and virulence in rust fungi interact in a typical gene-for-gene relation. Most of the current wheat cultivars have at least one gene for stem rust resistance even though it may be ineffective. In areas where stem rust has historically been severe, most cultivars have three to six genes for resistance. These combinations of resistance genes normally consist of some that are ineffective against all local pathogen strains, some that are effective against different portions of the pathogen population, and often one resistance gene that is effective against the entire pathogen population. Thus, in the study of regional epidemics it is essential to know the specific virulence combinations in the pathogen, their frequency, and their distribution. A regional epidemic is normally caused by a single pathogen genotype that makes up most of the pathogen population. Local spread from a single focus also generally involves a single pathogen genotype; however, when environmental conditions are favorable over a large area and many foci overlap, then several pathogen phenotypes occur together. During an epidemic in the southeastern United States in 1972 nearly every overwintering location sampled had a different pathogen race (Roelfs and McVey, 1973).

Aggressiveness

Little is known about variation in aggressiveness among field cultures of rust fungi. However, in an F_2 population of *P. graminis* there was great variation in latent period length (7 to 14 days), number of spores produced, and number of uredia per unit of inoculum. In greenhouse tests, cultures of race 15 and 56 can be distinguished from cultures of other races on a susceptible host by the numerous large, erumpent uredia. In several field tests in the northern Great Plains with above-normal temperatures, race 151-QSH of *P. graminis* created a more severe epidemic than race 15-TNM which normally produces the more severe epidemics. Greater aggressiveness of race 15B-1 than race 56 at prevailing temperatures was in part responsible for the prevalance of race 15B-1 between 1950 and 1961 (Katsuya and Green, 1967). *Puccinia striiformis* genotypes that were studied in Europe from less polluted areas have been reported to be more sensitive to air pollution than the native European cultures (Stubbs, 1985).

These mostly inadequately tested observations lead me to believe that cultures differ in aggressiveness, and that the differences may be sufficient to affect development of regional epidemics. This may be why stem rust epidemics in North America have been caused by a few of the many races that existed, and why the epidemic causing races were not always those with the greatest number of virulence genes.

ENVIRONMENTAL CONDITIONS IN REGIONAL EPIDEMICS

Favorable environmental conditions are necessary for disease development, but they may differ for different diseases. For instance, optimal temperatures for infection are 20, 20, and 11° C for leaf, stem, and stripe rust of wheat (Hogg et al., 1969). Stripe rust tends to be more important in the cooler periods of the year and in wheat grown at high elevations. Leaf rust is more important where the fall and/or spring and early summer are warm and moist. Stem rust is important in warmer areas when frequent free water (usually dew) is available on the wheat leaves for spore germination and infection. The rust pathogens generally have a wide range on both sides of the optimal temperature at which near maximum development occurs, with a rapid reduction in development to the minimum and maximum limits (see Fig. 2 in Roelfs, 1985b).

Environmental conditions directly affect host resistance, infection frequency, length of the latent period, and the rate and duration of fungal sporulation. Free water, most frequently as dew, is required for spore germination. Dew formation is usually heaviest on clear, still nights when the leaf temperature decreases considerably from heat radiation to the sky. Rain and, near large bodies of water, fog may also be frequent sources of free water. *Puccinia recondita* can infect in 3 to 4 h, whereas *P. graminis* requires 6 h under optimal conditions. For germination of uredospores of *P. graminis* free water must be present for 6 h at air temperatures around 18° C, and this must be followed by 3 to 4 h of continued free water combined with a light intensity of more than 10,000 lux and a gradual temperature rise to 26° C (Rowell, 1984).

For wheat rusts the latent period between inoculation and sporulation by the pathogen is 7 to 10 days under optimal environmental conditions. However, latent periods can be as long as 30 days for stem rust when night temperatures are cool (1 to 5° C) and daytime temperatures are less than 10 to 15° C. The latent period for leaf and stripe rust may be even longer when plants are infected late in the fall and sporulation does not occur until spring.

Cereal rust fungi produce large numbers of uredospores. *Puccinia graminis* can produce 5000 uredospores per uredium per day during active sporulation, resulting in up to 5 million uredospores per day from a severely infected tiller. Rust uredia commonly sporulate for 21 days or more under favorable conditions. Thus, a hectare of heavily infected wheat can produce 1.5 trillion uredospores per day for several weeks. Senescence of leaves as plants mature can reduce the length of the sporulation period. Early senescence can be induced by severe rust infection or by environmental stress. Conversely, under cool conditions the accumulation of nutrient reserves around the uredium can prolong the life of that portion of the leaf and the uredium for several weeks.

Strong winds at 1 to 3 km altitude blowing from the disease source toward less mature crop are conducive to long-distance spore transport. Ideal conditions for deposition occur when rain falls through spore-laden air scrubbing out the uredospores. Following such a rain, conditions are often favorable for infection (Roelfs et al., 1970). The terminal velocity of a uredospore is approximately 1 cm/s in still air. Thus, sedimentation from 1 to 3 km in still air requires 24 to 36 h. Of course, downdrafts could bring spores down faster.

Viable uredospores are often transported regionwide but fail to initiate epidemics. The host cultivars in the region may be resistant to the predominant pathogen genotypes, the environmental conditions following dissemination may be unfavorable, or the spores may arrive too late in the growing season to allow an epidemic to develop before the host matures. Wheat stem rust epidemics often fail to develop in some areas because the temperatures are too cool. Conversely, stripe rust development in the Great Plains of North America is retarded by the hot summer weather. Wheat is grown in areas that are usually too arid for rust development. The line of demarcation between areas conducive to rust and those not conducive varies from year to year depending upon rainfall patterns. Regional epidemics often have one or more of their boundaries along such environmental limits.

Environmental conditions also have dramatic effects on certain types of resistance. For instance, the resistance conditioned by the host genes *Sr6* and *Sr15* becomes ineffective at temperatures above 22 and 20° C. Resistance conditioned by *Sr13* functions best above 26° C, especially with intense light (Roelfs and McVey, 1979).

The development of regional epidemics of rust requires that environmental conditions be favorable for disease development over large areas. It is not essential that the environmental conditions are always optimal; an epidemic can develop if the conditions are frequently favorable. A 10-fold increase in disease in 5 days is common, and with ideal conditions wheat stem rust can increase 100-fold in 3 days (Rowell, 1968). Thus, in 9 days of ideal conditions, stem rust may increase from an almost undetectable level of one uredium per 100 tillers to 100% severity (1000 pustules per tiller). Yield losses of 50% commonly occur if the disease severity reaches 100% before the mid-dough stage of host development. Fortunately, environmental conditions this favorable rarely occur daily, but they can occur several times per growing season in the northern Great

Plains. In general, for regional epidemics to develop, spore transport must occur early enough so that the crop throughout the region receives initial inoculum 30 or 40 days before normal leaf senescence for leaf rust or before plant maturity for stem rust. Earlier spore transport is required for stripe rust, because it develops best at cooler temperatures.

TIME IN REGIONAL EPIDEMICS

Much more time is required for development of regional epidemics than for local epidemics. The pathogen must spread to the top of the crop canopy in the source area. In south Texas, this may require more than 2 months. Inoculum must be transported throughout the region early enough for serious disease to develop before crop maturity in the target area. An entire region may be infected from a single episode of spore transportation and deposition or from consecutive episodes. When an entire region receives inoculum from a single source, then the time required for multiple episodes is only the length of time between the first and last transportation-deposition episode. If the first effective dispersal affects only a portion of the region and must provide the inoculum for a second effective dispersal to the rest of the region, then time is also generally required for disease increase after the first episode. Long-distance dispersal generally results in infection densities of about one uredium per 10 m of row. Generally, infections that occur during active growth of the host plant are within the canopy when they sporulate, restricting spore escape.

The wheat stem rust fungus begins to increase from overwintering uredia in central and northern Texas in April. By early May in favorable years adequate inoculum is available at the top of the canopy for effective long-distance transport. Spread of the epidemic to a distance of about 1500 km can occur in 55 days (Fig. 5).

CULTURAL PRACTICES AFFECTING REGIONAL EPIDEMICS

Green Bridges between Seasons

A number of cultural practices can enhance epidemics if they result in self-sown plants growing during the period between normal wheat crops. In Parana, a state of Brazil, self-sown wheat is a common weed in the summer soybean crop. Rust inoculum moves from late maturing wheat fields to self-sown plants in adjacent fields that were harvested a month or more earlier and planted to soybeans. After the late wheat field is tilled and planted to soybeans, self-sown wheat plants appear. Inoculum then moves from self-seeded wheat plants in the early soybean fields to those in late seeded fields. Rust then spreads back to the early seeded wheat fields following the early soybean crop. Weather conditions during the summers are favorable for rust, and the distance the spores must travel varies from a few meters to a kilometer, which eliminates the need for long-distance transport. A green bridge also exists in many areas of the world with self-sown

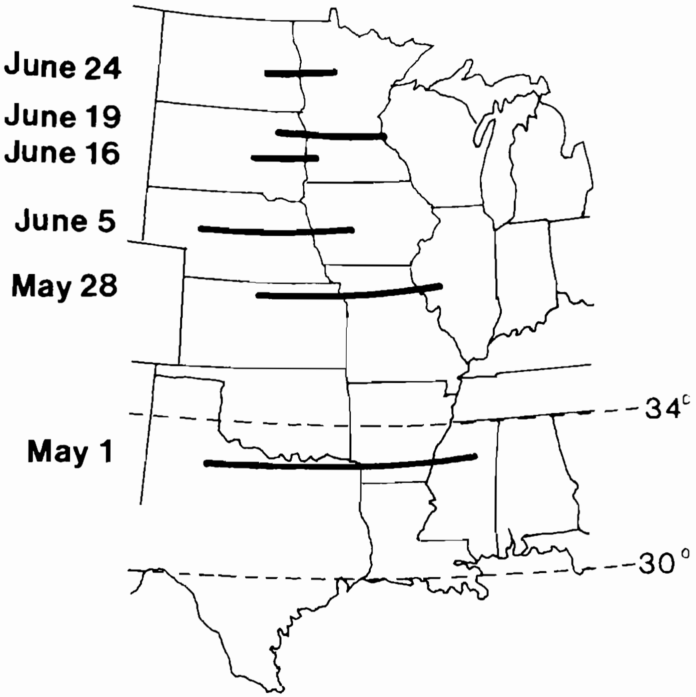

Figure 5 The normal advance of wheat stem rust across the United States. Overwintering may occur north to the 34th parallel and almost always in trace amounts to the 30th parallel. *(Data, in part, from Hamilton and Stakman, 1967.)*

plants along roadsides, irrigation ditches, threshing floors, fences and hedge rows, and in fields not in production for a season.

Irrigation Practices

Irrigation can enhance epidemic development by direct addition of free water on the foliage and by maintaining soil moisture and promoting dense foliage which is favorable for dew formation. There are large areas of irrigated wheat production, however, that have not been the source of inoculum for a regional epidemic. This may be partly because of the generally low relative humidity in areas where irrigation is practiced. Sprinkler irrigation during the day may provide spores with enough moisture to germinate but inadequate time for infection. Also large water drops may eliminate inoculum by dislodging spores and washing them to the ground. One example in which irrigation aided in the development of a local leaf rust epidemic was in the Mayo and Yaqui valleys of Mexico (Dubin and Torres, 1981). In the north China Plain where irrigation is extenisve, it is felt that irrigation helps the pathogen to survive between seasons on the self-sown plants. Irrigation canals and ditches often provide ideal sites for survival.

A possible source of stem rust inoculum for the United States and Canada is northeastern Mexico, but only 50,000 ha of wheat is grown during the dry winter period. The wheat cultivars currently grown are highly resistant to stem rust and only traces of stem rust have been observed. In a limited area small fields, primarily of barley, are grown under irrigation for forage. These fields have occasionally been found to be infected with traces of wheat stem rust. Although the Mexican crop in the spring currently has little role in epidemiology of rust epidemics in the rest of North America, barley could serve as a green bridge through the summer for reintroduction of stem rust into the southern United States in the fall.

Variations in Planting and Harvesting Dates

Earlier planting dates may advance the harvest time enough to escape epidemics when favorable conditions for disease or arrival of inoculum normally occur late in the plant's growth cycle. Mexican farmers had successfully avoided rust epidemics by early planting prior to the introduction of resistant cultivars (Borlaug, 1954). Adjustment of seeding date may be used to weaken the green bridge between crops, by timing the transfer of inoculum from crop to self-sown plants or vice versa so that it occurs during periods unfavorable for pathogen spread or increase. In Brazil the multiple green bridge would be weakened by reducing the time between the earliest and latest planting dates for both soybeans and wheat in an area. In Kansas winter wheats that matured 2 weeks earlier than the original Turkey types were developed to reduce the likelihood of hot dry winds at flowering. Additionally, the earlier wheats eliminated the last cycle of rust increase, greatly reducing local disease severities as well as the amount of inoculum that might be transported northward.

DISEASE FACTORS IN REGIONAL EPIDEMICS

Critical Month

The critical month was described by Chester (1946) for wheat leaf rust in Oklahoma. Wheat is planted in Oklahoma in September and October and by the end of fall it is often infected with leaf rust. Fall severities vary greatly among locations and years. During early winter the disease level generally remains constant, or in severe winters, decreases. By the beginning of March, temperatures increase and conditions again become favorable for disease development. April starts the period in Oklahoma when weather is nearly always within the range favorable for disease increase. Thus, the weather in March determines if the pathogen can move successfully from the surviving overwintering uredia on the lowest leaves to the newly produced leaves. Temperatures are marginal for infection during most dew periods and freezing temperatures may occur. The plant grows during warm periods and the old infected leaves senesce. Chester (1946) described the "critical month" as the first 30-day period in the spring for which the average daily temperature exceeds 10° C. This system of estimating disease severity of wheat leaf rust in Oklahoma was used for many years to predict losses. If such a system was developed for stem rust the "critical month" would be the 30-day period in which the mean daily temeperature for the preceding month was 15° C. A similar system has been recently developed for stripe rust in the Pacific Northwest area of the United States (Coakley and Line, 1981).

Detection Thresholds

The difficulty in detecting single uredia on widely scattered plants in the approximately 1 million ha area where stem rust on wheat has overwintered at least once in the past 15 years has forced us to develop various techniques for detecting overwintering foci. A highly susceptible cultivar is planted in dispersed sites. Plot shape has not been important, but at least 10 m of row has been necessary. Overwintering disease usually is reported only from commercial fields in areas where we detected overwintering in our plots. Plots are inspected during April and early May when the disease has had adequate time to develop a focus up to 1 m in diameter.

Outside the stem rust overwintering areas, the arrival of inoculum and the detection of disease is monitored annually. Trap plots of highly susceptible cultivars are planted. In areas where the disease may appear rarely or at very low intensity, large stips 1 m wide and 100 m long are most effective. In areas where stem rust has historically been important, 10 m of linear row is generally adequate. Surveys are made of these plots and commercial fields with stops every 32 km. Crop growth stage, disease severity and incidence (percent of tillers infected) are recorded. Experience has shown that in the case of stem rust we can detect an infection frequency from exogenous inoculum at a frequency of one uredium per 1000 tillers. Detection of single uredia in overwintering areas is more difficult because the uredia occur low in the canopy and often on dying leaves or those infected with other diseases.

Inoculum has also been detected by trapping uredospores on 5-mm-diameter glass rods used as impaction traps placed about 15 cm above the crop canopy. Rod traps are more efficient than glass microscope slides (Roelfs et al., 1968) and will detect locally produced inoculum from disease levels of approximately one uredium per 1000 tillers of either stem or leaf rust. Impaction traps are not efficient enough for detecting exogenous inoculum, which is best detected in rain samplers (Roelfs et al., 1970). Because most exogenous inoculum is rain deposited (see the earlier section in this chapter, Environmental Conditions in Regional Epidemics), rain samples are very useful in predicting the effective establishment of wheat rusts after long-distance transport (Roelfs et al., 1970; Nagarajan and Joshi, 1985). Data from spore traps must be interpreted with caution, especially for exogenous inoculum, since not all spores trapped are viable and uredospores of different rust pathogens may be very similar morphologically. Spores exposed to rain, sunlight, and varying humidities, and mixed with other spores, pollen grains, and a range of other organic and inorganic materials are especially difficult to identify. Spore identification is normally done at 100× magnification to permit evaluation of samples from large numbers of locations, replicates, and treatments which increases the problems of identification.

Exogenous inoculum can arrive in amounts below the threshold of detection. The resultant infections are apparent only later as foci develop. This can lead to an error of one generation time (14 to 21 days) or more in estimating the initial infection date, which in turn can cause either the amount of exogenous inoculum or the disease increase rate to be greatly overestimated. Additionally, errors in estimating the arrival date of exogenous inoculum can affect conclusions about the apparent source of the inoculum.

Onset Time

Regional epidemics of rust develop only when the initial infections occur at or before flowering. Under ideal conditions disease onset of a week earlier can double the severity of wheat stem rust. Historically the date of the first observation of wheat stem rust in the United States has been recorded (Hamilton and Stakman, 1967) (Fig. 5). A more meaningful observation would include the stage of host development at disease onset. In Minnesota, about 40% of the variation in loss of spring sown oats (*Avena sativa* L.) due to stem rust was explained by date of onset (Roelfs and Long, 1980). Had these disease onset data been improved by including host growth stage they would surely have explained more of the variation in disease loss. The most severe losses were always in fields planted later than the average planting date.

Rate of Disease Increase

Because the latent period varies with temperature, a single event of spore deposition and infection occurring over a large area can become apparent as sporulation initiated over a period of days. The initial sporulation occurs in the warmer areas first and then progresses to the cooler areas over the period of a few days to a few weeks. To the untrained observer this process appears to be a continuous wave of disease spread with daily infections.

Disease increase is normally expressed as the change in percent disease (using a modified Cobb scale, Peterson et al., 1948) over time in days. When rust epidemics are to be compared where the host growth cycle varies greatly in length there is an advantage to using a host growth stage scale as the measurement of time (Calpouzos et al., 1976).

Initial disease severities are generally lower than the 1% on the modified Cobb scale. They can be quantified by converting the percent scale to a number of uredia per tiller. For wheat stem rust 1% severity is equivalent to 10 pustules per tiller. The conversion factor for leaf rust is: 18 pustules per tiller equal 1%. Estimating severity of stripe rust due to its semisystemic nature must include some estimation of lesion size.

Inoculum Density

Although each uredospore produced by the cereal rust fungi has the potential to cause an infection, not all do. When single uredospores of *P. graminis* with a germination rate near 100% are placed on susceptible host tissue under ideal conditions for spore germination and infection only 1 of 10 will result in an infection (see Rowell 1984, for details of the infection process). *Puccinia recondita* uredospores under similar conditions may produce up to one uredium per three uredospores.

Additionally, the effectiveness of host resistance may depend in part on the amount and quality of inoculum produced on surrounding plants (Roelfs et al., 1972). The stem rust resistance of the cultivar Thatcher is illustrative. In plots with heavy infection (high inoculum level) terminal severities of Thatcher averaged 86%, with a susceptible host response. Thatcher had a mean terminal severity of 2% with a moderately susceptible host response a few kilometers away in a similar geographic area (low inoculum level). In this experiment, adequate spores were present so that the susceptible check cultivar Baart had a terminal severity of 90% in both areas (Nazareno and Roelfs, 1981). Thatcher was damaged by stem rust during the epidemic years 1953 and 1954 when most of the wheat area was planted to cultivars more susceptible than it. In the late 1960s and early 1970s Thatcher was undamaged when most of the cultivars grown were resistant.

IMPACT OF REGIONAL EPIDEMICS

Loss in Yield

Rust can greatly reduce the amount of grain produced by a plant. A severe early natural infection of stem rust or leaf rust at St. Paul, Minnesota can result in a 50% loss compared to a rust-free check in 2 out of 3 years. It appears that this is the maximum loss possible under current levels of inoculum in this area with spring wheat. The major portion of this loss is due to a reduction in grain size. The number of tillers and florets per spike are generally determined before the rust becomes severe, particulary for spring wheats. Occasionally, however, any of the three wheat rusts can become severe enough to kill the entire field prior to grain formation. A reduction in the number of grains can occur, when severe rust kills tillers that would normally survive to produce seed or when lodging and stem breakage occurs and the grain, although formed, cannot be harvested mechanically.

The history of rust epidemics worldwide was reviewed by Chester (1946) and Hogg et al. (1969). The regional epidemics since 1918 in the United States are shown in Table 1. Although the total is very variable, about 29 million ha of wheat are grown annually in the United States. Losses greater than 50% on a statewide basis are infrequent but have occurred. Since 1918, the greatest statewide losses due to stem rust were 56.5 and 51.6% in 1935 for North Dakota

Table 1 Losses resulting from regional epidemics of wheat stem and leaf rust in the United States since 1918

	Losses due to stem rust										Losses due to leaf rust, 1938	
	1923		1935		1937		1953		1954			
State	**%**	**Tonnes**	**%**	**Tonnes**	**%**	**Tonnes**	**%**	**Tonnes**	**%**	**Tonnes**	**%**	**Tonnes**
CO	10.0	55,576	6.0	12,079	Tr	Tr	0.6	7,211	Tr	Tr	2.0	10,710
IL	1.5	26,476	1.0	9,477	11.0	160,434	0.3	4,876	Tr	5,209	15.0	199,942
IN	Tr	Tr	Tr	Tr	12.0	142,849	1.0	12,712	0.5	5,801	3.0	23,858
IA	1.0	3,829	6.5	13,413	19.0	101,212	6.0	4,857	15.0	10,271	1.0	3,567
KS	1.0	23,321	12.0	252,570	6.6	305,904	1.5	60,082	3.0	152,561	12.0	585,867
MI	2.0	8,858	0.5	2,618	2.5	13,745	Tr	Tr	Tr	Tr	1.0	5,373
MN	15.0	114,851	51.6	607,042	10.0	107,454	13.4	68,045	18.0	62,324	8.0	90,158
MO	—	—	4.0	32,122	30.0	507,371	2.0	22,835	1.0	11,348	20.0	236,269
MT	18.0	293,986	0.6	5,624	0.0	0	3.0	96,352	2.0	46,121	Tr	Tr
NE	4.0	36,938	15.0	185,351	6.0	81,870	2.0	48,712	5.0	85,650	20.0	404,144
ND	12.0	258,262	56.5	1,939,554	25.0	535,554	37.7	1,605,878	42.9	1,417,012	2.0	43,110
OH	2.0	22,740	1.5	19,876	2.0	27,046	1.0	18,717	2.0	26,149	2.5	32,435
OK	—	—	Tr	Tr	1.0	18,714	1.0	19,497	2.0	39,390	27.0	622,145
PA	Tr	Tr	Tr	Tr	3.0	22,478	0.2	1,189	0.2	1,066	10.0	66,641
SD	10.0	83,744	29.0	306,049	12.0	58,974	35.2	484,961	21.0	190,972	—	—
TX	2.0	9,174	10.0	35,555	Tr	Tr	Tr	Tr	Tr	Tr	5.0	50,624
VA	0.2	5,264	3.0	7,432	2.0	5,438	2.0	4,301	3.0	5,967	5.0	12,513
WA	Tr	Tr	—	—	—	—	Tr	Tr	Tr	Tr	0.1	1,481
WV	Tr	Tr	Tr	Tr	2.0	1,380	2.0	706	2.5	8,045	—	—
WI	1.0	6,109	1.5	9,873	19.8	14,105	2.9	1,388	1.2	5,427	Tr	Tr
WY	Tr	Tr	10.0	6,112	Tr	Tr	3.2	6,150	Tr	Tr	0.5	4,691
U.S.	4.6	20,713,145	16.7	17,133,463	8.1	23,834,018	7.2	31,895,018	7.3	26,448,572	8.7	25,088,536

Tr = trace.

and Minnesota, respectively. Durum wheat losses due to stem rust were 66% in 1953 for the 746,000 ha and 79% in 1954 for 523,000 ha grown in Minnesota, North Dakota, and South Dakota. Leaf rust resulted in a 50% loss in Georgia in 1972 (Roelfs, 1978).

Rust losses in Australia have been substantial, but loss estimates are not available. Scattered rust oversummers in the moister areas of Australia. Epidemics have occurred when new combinations of pathogen virulence were introduced or developed through parasexualism or mutation (Luig, 1985).

Epidemics have occurred in India and Pakistan (Nagarajan and Joshi, 1985), but the extent of annual losses is unknown. Rust survives the hot dry summers in the southern hills of India and in the foothills of the Himalayas in the northern areas of both countries. Losses occur when cultivars are susceptible, the inoculum arrives early in the season, and environment is especially favorable.

Losses in China were fairly common in the periods of political turmoil during the 1950s through the mid-1970s. Control of volunteer plants, timely planting, and use of resistant cultivars have all resulted in reduced losses in recent years (Roelfs, 1977; Hu and Roelfs, 1985).

Losses due to rust in Europe are usually local and erratic. Epidemics are associated with early arrival and/or increase of inoculum in the spring. Stripe rust is an important disease in winter cereal areas, with Great Britain and The Netherlands particularly threatened (Zadoks and Bouwmann, 1985). Hogg et al. (1969) reported no epidemics of stem rust after 1958, and leaf rust resulted in fewer epidemics and less loss. No major leaf rust losses have occurred since 1961. Fungicides are currently used along with resistant cultivars to control stripe rust in northwestern Europe (Stubbs, 1985).

In South America, the cereal rusts occur but seldom result in more than local or areawide epidemics. Losses are difficult to estimate in some of the areas because of the severity of many other foliar diseases. Epidemics are associated with high initial levels of inoculum and with years in which the winters are mild and moist.

Loss in Grain Quality

Nearly all crops have some quality standards by which they are judged and which affect their market value. Test weight (weight per volume) of wheat is such a quality standard in much of the world. Shriveled grain, a common result of severe rust epidemics, often reduces test weight enough to result in a much lower price. Grain produced during a severe rust epidemic can be of such poor quality that it is useful only for animal feed, which means its price is determined in the United States by the price of corn and sorghum, the predominant feed grains. Although shriveled grain tends to have higher protein content, a desirable trait, shriveled grain also has a lower flour extraction, an undesirable trait.

Rust epidemics can also indirectly lower the grain quality by forcing growers to use a lower quality resistant wheat in place of a high quality susceptible wheat. The 1953 and 1954 rust epidemics destroyed the United States durum crop.

Growers turned to the resistant cultivars Wells and Lakota that had small seed (undesirable durum quality) because the large-seeded Langdon and the Yuma durums were too susceptible to grow economically. It required 14 years to develop the large-seeded resistant cultivar Leeds (Lebsock et al., 1966).

Losses in Forage

In some areas of the world, including the southern Great Plains of the United States, fall planted wheat is important as fall and winter forage for cattle and sheep. The value of forage in this area is often the profit margin for growing wheat. Winter sown oats in the Gulf Coast states is often planted only for forage. Rust decreases the amount of forage directly by killing the leaf tissue, and indirectly by weakening the plant and reducing its growth. Severe epidemics can result in losses of 100%. Additionally, the uredospores of the rusts can be a physical irritant to the grazing animals, resulting in watery eyes and runny noses.

Economic Impact

When disease destroys a portion of the crop, the price for the remaining crop increases. Thus, growers that produce some wheat may receive nearly a normal income. Growers with severe disease loss suffer while other growers with little or no disease loss may profit from the higher prices. The total supply of grain may be adequate following a rust epidemic, but the amount of grain in the high-quality grades may be in very short supply. This usually results in an unusually large price differential between grades. Currently with a surplus of wheat in the United States it would take a very serious epidemic to produce a major change in price. In areas of the world where the population consumes the entire harvest to meet just the basic food needs, even local epidemics can have a significant impact on both prices and survival.

Rust epidemics have changed grain exporting and grain self-sufficient countries into importers, for example, Pakistan (Hassan, 1978) and Mexico (Dubin and Torres, 1981). As a result of the serious stem rust epidemics of North America in the 1950s pasta products were made from bread wheat rather than from the high-quality durum wheats.

Prevention of losses due to rust is costly. Plant breeders must make crosses and select for resistant lines, reducing the available gene pool for commercial production. Good lines otherwise may have to be reentered in the crossing block to obtain rust resistance. Time and space are required for evaluation of rust resistance. The cost of evaluation varies with the level, type, and genetic complexity of the resistance required and the severity of the disease in the area. Many breeding programs spend from 10 to 20% of their time on rust resistance. The breeding program usually involves local, national, and international pathologists. Field surveys of disease intensity and severity, physiological race surveys, basic studies on the pathogen, basic and applied studies on the disease, searches for resistant germplasm, basic and applied studies on the nature of resistance, basic and applied studies on genetics of resistance, germplasm classification, improvement, and storage all are necessary to provide the inputs that result in a constant flow of improved resistant cultivars to the grower. As these items are funded by various groups, the entire cost to be assigned to each cultivar is not readily available. But in 1984, perhaps 250,000 dollars per rust-resistant cultivar would be a reasonable estimate in the United States.

The following example illustrates the time and problems in developing a rust-resistant cultivar. Thatcher was developed by a cross made in 1914 between an adapted cultivar of a hard red spring wheat (Marquis) and a stem rust resistant durum wheat cultivar (Immillo). A line selected in 1918 was released to growers in 1928 as Marquillo. This cultivar never was important; however, in 1921 a sib line of Marquillo had been crossed by a Marquis/Kanred derivative. Kanred/Marquis cross had been made in 1918 to obtain the immunity of Kanred to certain *P. graminis* races in a hard red spring wheat. The line (later named Thatcher) was selected in 1925 and released to growers in 1934. Although it took 20 years to develop, it was among the most successful resistance sources ever developed (Schafer et al., 1984). It provided spectacular resistance to the epidemics of 1935 and 1937. Although it was damaged in the epidemics of 1953 and 1954, it still is widely used as a background for stem rust resistance in the hard red spring wheats.

Chemical sprays are used either alone or in combination with host resistance to control stripe rust in Europe (Stubbs, 1985) and in the Pacific Northwest of the United States (Line, 1982) and to control leaf rust in Brazil and Paraguay. Obvious costs are the price of the chemical and its application. The cost of the chemical is usually adjusted to include the cost of developing and testing the chemical. However, other costs are not as obvious. Ground-drawn rigs can reduce the yield by 2 to 4% by direct damage to the crop. Aircraft sprayers eliminate this loss but usually are more expensive. Monitoring systems are necessary to determine if and when spraying is required even in years when the disease is absent (Rowell, 1968). Most, like Epimul (Kampmeijer and Zadoks, 1977), have been developed at public expense.

Although I have avoided assigning a value to the cost of cereal rust epidemics, it is substantial. Worldwide, the equivalent of hundreds of years of scientific investigation are spent on rust control annually.

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