Sonderdruck aus der
„Zeitschrift für Pflanzenkrankheiten (Pflanzenpathologie) und Pflanzenschutz"
71. Band, Jahrgang 1964, Heft 2/3
Schriftleiter Prof. Dr. Bernhard Rademacher, Stuttgart-Hohenheim
(Verlag Eugen Ulmer, Stuttgart, Gerokstraße 19)

Will the fight against wheat rust ever end?

By E. C. Stakman

Sixty years ago, in 1904, stem rust, *Puccinia graminis* var. *tritici*, ruined most of the spring wheat of northern United States and Canada. This was a tragic story but not a new one, even for the spring wheat area of the upper Mississippi Basin of the United States and Canada where the extensive conversion of prairie lands into wheat lands had been in progress for only some 30 years. Looking backward and eastward, the story was still older. For more than 200 years stem rust had been periodically and locally destructive wherever wheat was grown in North America. Epidemics certainly became more extensive and spectacular, possibly more frequent also, when vast areas of prairies and plains were converted into vast areas of wheat fields where the sweep of the wind could spread rust fast and far.

Looking still farther backward and going still farther eastward, the rust story is two thousand years old, but the ancient history is interesting historically rather than important scientifically. The modern history of stem rust is only a hundred years old, and the history of really scientific attempts to control it is little more than 50 years old.

Shortly after the epidemic of 1904 a Canadian bulletin summarized the lessons learned from it. In retrospect it is clear that the lessons that needed to be learned were far more numerous and important than those that had been learned. Nevertheless, the epidemic did arouse concern, provoked thought, and stimulated attempts to reduce rust losses. The United States Department of Agriculture established a program of breeding rust-escaping and rust-resistant varieties, initially cooperating especially with the Minnesota and Kansas State Experiment Stations. Canadian wheat breeders also paid more attention to rust resistance and to early-ripening varieties which might escape both rust and frost. It might be logical, therefore, to consider 1904 the year 1 in modern attempts to control wheat stem rust. Of course, it would be necessary to define "modern", and that would be hard to do. Someone might even ask, "Just how modern are our present attempts to control rust?"

How intelligent are our present attempts to control stem rust? Possibly we are still too ignorant scientifically to have a valid opinion. Relative to 1904, of course, there has been tremendous progress in understanding and controlling the rust; but what is our position in 1964 relative to what it should be in 1984? There should be much more progress in the next 20 years than in the past 60 because we know much better now than then what we need to learn in order to progress. At least there now is a science of plant pathology, a science of genetics, and a well-developed art of plant breeding. Past experience has at least shown what needs to be learned, and better methods have been developed for learning it.

How well have we learned our lessons? The greatest lessons that everyone dealing intimately with stem rust should have learned is to not underestimate the vast resourcefulness of this parasitic fungus in its struggle for existence. Even though it is an obligate parasite which can propagate asexually on only a limited number of cultivated and wild species of gramineae, it has been an extraordinarily successful parasite in virtually all areas of the world, including those in which the continuity of successive uredial generations is interrupted by a dry or a cold season. From man's viewpoint, the rust is still too successful despite his attempts to limit its success.

During the past 60 years much has been learned about the great genetic potential of stem rust, the tremendous power of reproduction, the vast capacity for rapid and extensive dissemination, and the varied abilities to survive unfavorable conditions. Although much remains to be learned about all phases of the rust problem and its peculiarities in different regions, a critical question concerns the degree of genetic diversity of the rust in relation to genetic diversity in wheat.

Without rust resistant varieties it seems improbable that rust can be controlled economically and permanently in extensive wheat-growing areas which are watered by abundant rainfall and even in certain irrigated areas where fogs and dews enable the rust to become destructive without much rainfall. Barberry eradication has been an effective control measure, either locally or generally in some areas, and it has alleviated the problem in certain large regions such as the upper Mississippi Basin of the United States. Such is the power of the wind to disseminate spores fast and far, however, that wheat may be menaced by distant sources of inoculum even where there are no local sources at the beginning of the growing season. The use of early-ripening varieties, early seeding, proper soil preparation, and the use of appropriate fertilizers have been aids in reducing rust damage under some conditions, but these measures cannot be relied upon to eliminate it completely under most conditions. It may become economically feasible to reduce rust damage by homeopathic doses of protective or therapeutic fungicides if present and future searches for relatively inexpensive and effective ones are successful. It is unlikely, however, that chemicals will be used in the near future to protect the millions of acres of wheat in the larger wheat-growing areas of the world.

No method or combination of methods have yet controlled rust completely in any large area. During the past 60 years each method has had its partisans and still has them. Partisanship has not solved the rust problem, however, and never will; but research on all methods of control will bring it closer to solution. And the solution will come most quickly if there is no partisanship, between the investigators of the different methods nor on the part of the investigators of each method.

Even the strongest partisans, if there are any left, must admit that it is desirable to incorporate as much disease resistance as possible into all kinds of crop plants. Resistance is valuable even if it does not protect plants completely, for every defense that a variety itself has against diseases relieves man of some of the burden of defending it against them. To justify a statement that breeding for rust resistance is essential need not imply that it is now or ever will be the only method of rust control. The importance of resistant varieties is fact;

whether they can permanently defeat the rust is a matter of opinion or speculation. Time may tell, but it has not told us during the past 60 years; will it tell within the next 20 years, or will it never tell?

One of the most important lessons of the past is that scientific agnosticism is more valuable than partisan dogmatism. Even some of those who contributed a great deal to breeding for rust resistance in the past were partisan in their efforts. Without engaging in semantics, it may be more precise to say that some breeders had been subtly affected by certain presuppositions and prejudices regarding the potential virtues of crosses between certain parental varieties as compared with others. Of course, expectation was sometimes based on available evidence, but sometimes intellectual bias and wishful thinking crept in and developed into blind faith in favorite varieties and a dogmatic partisanship for them. The result was that many varieties had limited usefulness and a short life because they had too narrow a base of resistance. Naturally, many of those engaged in breeding programs learned this, often as the result of bitter experience and therefore tried to broaden the base.

There now are many resistant varieties with complex but scientifically synthesized genotypes. And more is continually being learned about the identity and location of genes for resistance and their effects under various environmental conditions. But relatively few varieties are resistant to all known rust races under all conditions.

It is true, of course, that rust-resistant varieties have contributed tremendously to greater and more assured world wheat production, especially during the past 35 years. But it is equally true that it has been necessary to breed continuously in order to replace temporarily resistant varieties with a succession of other temporarily resistant varieties. In some areas the average life of varieties has been considerably less than ten years, although many of them had promised to be resistant for many decades. Indeed, so great was the faith in certain varieties that any intimation that rust might sometime attack them was branded as treason to the cause of plant breeding. Is it wise to be agnostic, even now, about a final solution of so complex a problem as that of wheat stem rust? It probably is.

Even as this is being written, some varieties with a broad genetic base for resistance, which had long been resistant in certain areas of North America, are being heavily attacked by stem rust; and other popular varieties are known to be susceptible to rust races that are now widely distributed but not abundant. The wheats of North America are not yet safe against known rust dangers, and it is likely that some of the most widely-grown ones will succumb when weather and other conditions favor widespread and abundant development of stem rust. This will be a hard blow, but it will not be as stunning as many similar blows of the past because there now is much more scientific sophistication about the possibility of such events than there was a few decades ago. There is now a general opinion that breeding must be continuous in order to checkmate the continual changes in the rust. A common question is, "Will the fight against stem rust never end?"

Can the fight against stem rust ever end? Can the rust break down whatever defenses wheat can set up against it? Can the genes for virulence in the rust prevail over those for resistance in wheat? The rust obviously has tremendous potential for virulence, distributed among thousands of biotypes; and *Triticum* has a great potential for resistance, distributed among thousands of varieties of wheats and their close relatives. What needs to be known is which potential is the more powerful.

Up to the present no known wheat has been immune from all known races of stem rust under all known conditions. Indeed, so inexorable has been the tendency for resistant varieties to succumb to rust after having been grown extensively for a number of years that there seems to be a tendency to revive the old belief in the ability of the pathogen to gain virulence for a variety by association with it. Ward's theory of adaptation and bridging hosts has long been moribund but has never died completely and now seems to be having at least a faint revival. The theory was "disproved" by a mass of evidence, but is it safe to assert that adaptation is an impossibility? It would be a rash assertion indeed to say that something cannot happen in biology because there is no evidence that it does happen. Theoretically, adaptive enzyme systems or other similar adaptive systems might account for adaptation, if there were experimental evidence for adaptation in the sense in which the term was used a half century ago.

But it is not necessary to resort to a theoretical explanation, an explanation of desperation, for the fact that resistant varieties have usually been attacked by rust after having been grown extensively for varying periods of time. In many cases it was known that they were susceptible to rust races that existed in small quantities in the region in which the varieties were grown. The unknown in the situation was simply when, if ever, would these races become prevalent enough to cause damage. The "if ever" is more important than it seems, because the probability that a non-prevalent race may become prevalent depends not only on its virulence but also on other factors for agressiveness and survival ability. Some highly and generally virulent races are handicapped because they can thrive within only a narrow range of ecological conditions; hence the potential destructiveness of rust races depends on their virulence and on their ability to capitalize their virulence under a wide range of environmental conditions.

Although some virulent races of stem rust do not have good survival ability and may disappear completely, there are enough genes for virulence in races that do have good survival ability to explain what has happened to resistant varieties in the past and to create concern for the future.

It is not necessary to state that there are many physiologic races of wheat stem rust; the fact is old and generally known by wheat breeders. But it is important to emphasize the fact that there are far more races than is generally appreciated. The "Identification of Physiologic Races of *Puccinia Graminis* var. *Tritici*" issued by the U.S. Department of Agriculture in 1962 lists 297 races which have been distinguished by their effects on 12 so-called standard differential varieties, but it would be naive to think that this is more than a very small sample of the total number. The races represent groups of biotypes that have some genes for virulence in common and therefore produce similar effects on some varieties of wheat. But it has long been evident that the component biotypes may differ in respect of some genes; hence, many races can be subdivided by the use of supplemental differential varieties. The problem sometimes has been to find additional differentials that distinguish clearly and consistently between similar but not identical isolates. But this is a problem of classification, and it will always exist because of the extensive genetic changes that are continually taking place in the astronomically numerous rust populations. More pertinent to the present question is the total potential virulence of the rust in relation to the total resistance potential of wheat and related plants.

That there are thousands of biotypes of *Puccinia graminis* var. *tritici* must be evident to all who have studied the pathogen thoroughly, and that new ones are continually being produced by mutations and recombinations of various kinds is clear from abundant experimental and circumstantial evidence. It is the writer's opinion that the genetic diversity is comparable with that of *Ustilago maydis*, in which at least 20 thousand biotypes were obtained experimentally by mutation and hybridization among the progeny of two haploid sporidia. The elementary fact that there is vast and changing genetic diversity in wheat stem rust is platitudinous; nevertheless it is also an elementary fact that it has been necessary continually to expand our concepts during the past 60 years regarding the magnitude of that vastness. And we need to expand our conceptual horizons still more in viewing future probabilities, possibilities, and prospects.

What defenses can genes for resistance in wheat set up against the vast virulence potential in the thousands of present and future biotypes of stem rust? There is a high degree of specificity in the interactions between the virulence of individual rust races and individual wheat varieties. Are there specific genes or combinations of genes among wheats which can nullify the effects of specific genes or combinations of genes for virulence among the thousands of biotypes of the rust? Simply but crudely, will it be possible to breed varieties of wheat that have physiologic resistance to all races of rust? Although this may be possible by extensive recombinations or by the incorporation of new genes by means of crosses with non-wheat grasses, it seems improbable that it can be accomplished in the near future. Recognizing this, attempts are being made to solve the problem in other ways.

The experiments initiated by Borlaug on multilineal varieties may contribute much to a practical solution of the rust problem. By using a "composite" or "multilineal" variety comprising a number of lines of wheat that are similar agronomically but each of which has specific resistance to different rust races or groups of races it should be possible to counteract the effects of changing populations of rust races by changing the components of the variety accordingly. The success of such procedures presupposes prior knowledge regarding the population trends of races, the early detection of new races, and the availability of lines that are resistant to them. The production of composite varieties is, of course, an attempt to broaden the base of resistance while maintaining flexibility in fighting the shifting populations of races. Whatever the future of this scheme, it represents conceptual progress.

"Lest we forget!" About 35 years ago statements were freely made by several wheat breeders to this effect: "We no longer worry about physiologic races of stem rust because we now have mature plant resistance which is effective against all races." And again, in effect: "The performance of Blank variety negates the talk about physiological races." Of course, these statements now seem hyperbolic and even absurd. It would have been wiser to put them into the subjunctive mood rather than the indicative. But there was evidence at the time that some wheats had functional and morphological characters by virtue of which they had a certain degree of generalized resistance in the field. When it became evident that this generalized resistance did not give complete protection, however, there was tendency to think that it gave no protection at all. And this was another mistake.

Has there been a tendency to neglect the potential practical value of "non-specific" or "generalized" resistance? Without answering the question categorically, it certainly is true that some wheats are much less easily infected than others, that the incubation period is longer in some than in others, that there are much smaller pustules on some than on others, that there are more subepidermal pustules on some than on others, and that some can carry a heavier rust load than others without breaking down. And these differences exist between varieties that have the same specific reaction to certain physiologic races. As an example, extensive experiments have shown that when certain varieties are inoculated in exactly the same way with the same rust race, large pustules may appear on all of them at the same time, but there are from three to fifteen times as many on some than on others at a given time. The final number may or may not be the same; but it is evident that there are wide differences in the degree of "infectability", which may be important under many conditions and extremely important under some conditions. The stomatal or other characters that account for such differences should be determined and utilized in breeding programs.

It is not necessary to describe the many morphological characters, such as lignified epidermis, strategically distributed sclerenchyma, small collenchyma bundles, and other known characters that are barriers to the rapid or extensive growth of the rust fungus. These characters are now scattered among a number of different varieties. Attempt should be made to combine them in a single variety, which could then be used in breeding programs as a donor of generalized resistance to reinforce specific resistance to as many physiologic races as possible.

The charge may be made that emphasis on the potential value of functional and morphological characters is a revival of ancient history — of Cobb's theory of mechanical resistance, which was once accepted, then discarded, and then revived in modified form. Whatever the vicissitudes of the theory, the fact is that there are many non-specific characters which are known to have some value in resistance, but how much value they would have when combined is still unknown. These characters have been studied to explain resistance rather than to increase it. They represent a relatively unexploited resource in breeding against rust.

Will the fight against wheat stem rust ever end? Or will it never end? The modern fight against it coincides with the life span of Dr. Fuchs, in honor of whom this little piece is written and with whom the writer once had the honor of discussing many such questions as this. The fight against stem rust may never end completely, but the rust can probably be put under guardianship if all available knowledge, methods, and materials are combined in fighting it and if each method is improved by adequate research.

Summary

The fight against stem rust is probably as old as the extensive cultivation of wheat. The rust problem is an old one, even in "the New World". The problem in North America probably was aggravated when vast areas of prairie lands in the United States and Canada were converted into wheat lands. Following a devastating epidemic in 1904, efforts at control were intensified. Early attempts to produce resistant varieties were necessarily empirical because little was known about the genetics of wheat and of the rust. As scientific knowledge accumulated, it became apparent that the problem was even more complex than it had seemed.

Even after the discovery that there were many physiologic races of the rust, there often was unjustified optimism and partisanship with respect to the permanence of resistance. But it became increasingly clear that the variety *tritici* of *Puccinia graminis* comprises an indefinite number of biotypes with a vast potential for virulence and that new biotypes are continually being produced by mutation, hybridization, and other genetic changes. Barberry eradication has alleviated the

situation in some areas and has obviously reduced the number of prevalent physiologic races in Northern United States, but no combination of control methods has prevented destructive outbreaks of rust.

Whatever present or future methods of control are used, resistant varieties must play an important part in the combined fight against the rust. So far, however, virtually all resistant varieties have succumbed sooner or later. This raises the question whether the genes for specific resistance in wheats can enable wheat to withstand the effect of the many genes for specific virulence in the rust. It is urged that fuller use should be made of non-specific functional and morphological characters to reinforce the specific resistance against some races with generalized resistance against all races.

By intelligent use of all known methods and the improvement of each by research, stem rust can probably be demoted to a minor role in many countries within a few decades and in most of them within a few additional decades.

Zusammenfassung

Der Kampf gegen den Schwarzrost ist wahrscheinlich ebenso alt wie der ausgedehnte Weizenanbau. Das Rostproblem ist alt, sogar in der „Neuen Welt". In Nordamerika trat wahrscheinlich dann eine Verschärfung dieses Problems ein, als riesige Flächen des Prärielandes in den Vereinigten Staaten und in Kanada für den Weizenanbau erschlossen wurden. Nach einer verheerenden Epidemie im Jahre 1904 wurden die Bemühungen um Abwehrmaßnahmen intensiviert. Die ersten Versuche zur Züchtung resistenter Sorten waren notwendigerweise empirisch, weil wenig über die Genetik des Weizens und des Rostes bekannt war. Als die wissenschaftliche Erkenntnis zunahm, wurde offenbar, daß das Problem noch komplexer war als es zunächst ausgesehen hatte.

Auch nach der Entdeckung, daß viele physiologische Rassen des Rostes vorhanden waren, gab es ungerechtfertigten Optimismus und Voreingenommenheit hinsichtlich der Beständigkeit der Resistenz. Aber es wurde mehr und mehr klar, daß die Form *tritici* von *Puccinia graminis* eine unendliche Menge von Biotypen enthält mit einem gewaltigen Potential an Virulenz und daß ständig neue Biotypen durch Mutation, Hybridisierung und andere genetische Veränderungen gebildet werden. Die Ausrottung der Berberitze hat die Situation in einigen Gebieten erleichtert und hat offensichtlich die Zahl der vorherrschenden physiologischen Rassen in den nördlichen Vereinigten Staaten vermindert, aber keine Kombination von Schutzmaßnahmen hat bisher vernichtende Ausbrüche des Rostes verhindern können.

Welche gegenwärtigen oder zukünftigen Schutzmaßnahmen auch immer angewendet werden, resistente Sorten müssen eine wichtige Rolle im vereinten Kampf gegen den Rost spielen. Bis jetzt sind jedoch eigentlich alle resistenten Sorten früher oder später befallen worden. Dies wirft die Frage auf, ob die Gene für spezifische Resistenz in Weizensorten dem Weizen ermöglichen können, den Auswirkungen der vielen Gene für spezifische Virulenz im Rost zu widerstehen. Es wird dringend vorgeschlagen, daß ein stärkerer Gebrauch von nicht-spezifischen funktionellen und morphologischen Eigenschaften gemacht werden sollte, um die spezifische Resistenz gegen einige Rassen durch allgemeine Resistenz gegen alle Rassen zu verstärken.

Durch geschickten Einsatz aller bekannten Methoden und durch deren weitere wissenschaftliche Verbesserung kann der Schwarzrost wahrscheinlich in vielen Ländern in wenigen Jahrzehnten, in den meisten anderen Ländern in einigen zusätzlichen Jahrzehnten bis zur Bedeutungslosigkeit zurückgedrängt werden.