Special Report

Successes in Breeding for and Managing Durable Resistance to Wheat Rusts

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Stripe rust, leaf rust, and stem rust—caused by *Puccinia striiformis* Westend., *Puccinia recondita* Roberge ex Desmaz., and *Puccinia graminis* Pers., respectively—have been considered to be the most widely destructive diseases of wheat (*Triticum aestivum* L.) in the world. Rust epidemics have been common throughout history and have frequently caused severe yield losses. During the first half of the twentieth century, rust resistance was short-lived. Within a few years after the release of a new resistant cultivar, new, virulent races (pathotypes) of the rust pathogens would appear and severely damage the previously resistant cultivar.

Within the last 30 to 40 years, major progress has been made in developing cultivars with superior, more sustainable resistance to the rusts, and in the application of improved methods of managing that resistance. Consequently, rust epidemics have been infrequent, and when they have occurred, damage caused by the rusts has been less severe and less extensive. The following is a brief discussion of some of the successes and a few of the failures in controlling the rusts. The information is based on firsthand knowledge of the rusts and corroborative information from many other rust specialists. Emphasis will be on control of the diseases in North America.

Wheat production and rust development in North America. The environmental conditions that affect wheat production and rust epidemics have a major impact on the strategies and methods of breeding for rust resistance and the management of that resistance. Wheat is grown in many regions of North America under a wide range of environmental conditions. It is the environment within those regions that determines the wheat types and market classes that are grown, the importance of each of the three rusts, and the effectiveness of different types of rust resistance (10). It also is the diversity of environment, market classes, and management conditions that make breeding for rust resistance difficult. Newly developed cultivars of each wheat class and type must be adapted to the environment and management systems of each specific region and must have resistance to other diseases and pests in that region as well as to the rusts. Since rust spores can be wind disseminated long distances, cultivars developed for some regions must also be resistant to races from other regions.

All three rusts are obligate parasites, require free water on the foliage for development of epidemics, and have the ability to increase from a few primary uredia (pustules) early in the growing season to high disease intensities later in the growing season. Each rust species has a unique, optimum temperature range for disease development; stripe rust is a cool temperature rust, leaf rust is a moderate temperature rust, and stem rust is a warm temperature rust. Because of these environmental requirements, stripe rust is most destructive in the West, especially the cool Pacific Northwest, and is sometimes destructive in the south central United States. Stem rust is most destructive in the north central United States and adjacent Canada, can be destructive in the Pacific Northwest, and is infrequently destructive in the southern United States. Leaf rust epidemics can occur in all of the wheat growing regions of North America.

In the Pacific Northwest, stripe rust and leaf rust start in the fall, increase slowly during the winter, and increase rapidly in the spring (10). Stripe rust develops most rapidly during the cooler temperatures of early spring. Leaf rust develops most rapidly during the warmer temperatures of late spring. Stem rust epidemics, which start from inoculum produced on barberry leaves, develop most rapidly when the weather is hottest during the late spring and summer. In the southern United States, all three rusts usually survive during the winter, but the spring temperatures are often too high for development of severe stripe rust epidemics, and the crop usually matures before severe stem rust epidemics develop. In the north central and northeastern United States and adjacent Canada, winter survival of the rusts is rare; the primary inoculum usually originates from wheat in the southern United States and arrives in the region in late spring when temperatures are too high for stripe rust epidemics.

Resistance to stripe rust. In the late 1950s and early 1960s, stripe rust caused losses in excess of 70% in the Pacific Northwest (12). Those epidemics were the impetus for a major effort in breeding for stripe rust resistance. Of the various types of resistance that have been identified, seedling resistance and high-temperature, adult-plant (HTAP) resistance are the most important (3–6,11,14,15,17). Seedling resistance is characterized by race specificity and low infection types at all stages of plant growth and a wide range of temperatures. When used extensively over time and space, new races usually circumvent the seedling resistance within 3 to 4 years after the release of cultivars with that resistance (9,11). Managing the seedling resistance has extended the life of the cultivars. Use of the race-specific seedling resistance in a multiline cultivar has provided protection for more than 10 years. Use of cultivar mixtures also has extended the duration of the effective use of seedling resistance.

HTAP resistance is characterized by a range of infection types and a shift in the range of infection types depending upon temperature and stage of plant growth (17). As plants with HTAP resistance become older, they become more resistant at higher temperatures, but they remain susceptible when grown at low temperatures. Seedlings of cultivars with HTAP resistance are susceptible at all temperatures. At higher temperatures, flag leaves are most resistant. HTAP resistance can be considered to be a type of "slow rusting" resistance, since it decreases the rate of rust development. Currently, more than 90% of the cultivars grown in the Pacific Northwest have HTAP resistance. The cultivars with HTAP resistance have remained resistant for more than 30 years, even when grown extensively in the region and exposed to numerous races of the pathogen. The durable, HTAP resistance incorporated into adapted cultivars has prevented major stripe rust epidemics and widespread losses and has prevented mul-

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timillion dollar losses in the western United States as well as in other regions of the world.

Resistance to leaf rust. Highly race-specific seedling resistance, adult-plant resistance, and slow rusting resistance have been studied and used extensively to control leaf rust in North America (1,2,8,13,16,18–21). Seedling resistance, which also is effective in adult stages, has been used primarily in southern United States. In most cases, the resistance has remained effective for only a few years before new races have circumvented that resistance. This occurred even when the resistance came from nonwheat species. Because of ineffective seedling resistance, leaf rust recently caused major losses in Kansas and significant losses in other states of the south central United States.

In contrast, adult-plant resistance has proven to be highly effective for about 30 years in Canada and the north central United States. Combining two adult-plant resistance genes or combining adult-plant and seedling resistance genes has provided even greater leaf rust resistance (8,19,20). Leaf rust has caused only slight losses since the extensive use of adult-plant resistance in that region. Prior to the use of adult-plant resistance, leaf rust caused major losses. Adult-plant resistance to leaf rust also has proven to be effective in Mexico.

Slow rusting resistance has been used to control leaf rust of winter wheat in some areas of the southeastern United States and leaf rust of spring wheat in the Pacific Northwest (13,16). Results of studies in the Pacific Northwest indicate that the slow rusting resistance may be adult-plant resistance and/or the interaction of adult-plant and seedling resistance. In some cases, slow rusting has showed a moderate level of race specificity, but to date, the slow rusting resistance continues to provide protection.

Resistance to stem rust. It has often been stated that pyramiding race-specific genes does not provide durable resistance to rust. However, pyramiding race-specific genes has been highly effective in controlling stem rust in Canada and the north central United States for about 40 years. During the same period, the weather in that region has been frequently favorable for stem rust, and yields of cultivars without the pyramided genes have been greatly reduced by stem rust. In other regions, stem rust has severely damaged cultivars that do not have the pyramided genes. Some genes for stem rust resistance appear to provide more durable protection than others, especially when the gene for resistance is temperature sensitive (7,8,18,21). Combining the race-specific genes appears to provide additional resistance.

General conclusions. Sustainable agriculture can be defined as an agricultural management system that minimizes cost, purchased inputs, and adverse environmental impact; sustains production and profit; and maintains a stable rural community. The use of durable resistance to rusts has been a mainspring of sustainable wheat production in North America. The incorporation of superior types of resistance to stripe rust, leaf rust, and stem rust into locally adapted wheat cultivars of high quality and the effective management of those types of resistance has successfully prevented severe rust epidemics in North America and other regions of the world for 30 to 40 years. In addition to preventing extensive losses, the use and management of durable types of resistance has reduced the need for fungicides, enabled more efficient use of fertilizer and water inputs, enabled use of alternative crop managerial practices to reduce wind and water erosion, and helped to sustain stable, profitable wheat production. Many genes for resistance to the three rusts have been identified, and their characteristics, inheritance, genetic interactions, and chromosomal locations have been determined. Undoubtedly, further progress in the use of rust resistance will be possible as we learn more about the resistance. New methods of studying resistance and using genes for resistance should provide even greater sustainability of wheat production in the future. The successful control of the wheat rusts does not mean that further research is not needed. Without a diligent monitoring program, further research on understanding rust resistance, and the incorporation of highly effective resistance genes into new, improved cultivars, wheat production could revert to the unstable conditions of the first half of the twentieth century.

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