Virulent New Strains of Rust Fungus Endanger World Wheat

Scientists scramble to protect wheat and other cereal crops from aggressive pathotypes of both stem and stripe rust

Marcia Stone

Four new pathotypes of the deadly Ug99 wheat rust fungus were described this June during a meeting of the Borlaug Global Rust Initiative (BGRI), hosted by Cornell University and held in St. Petersburg, Russia. This new set brings the total of known Puccinia graminis mutants in the Ug99 lineage up to seven. All can overcome a majority of existing stem rust (Sr) resistance genes deployed in commercial cultivars or used in breeding programs. Thus, the evolving pathotypes appear to be an even greater threat to global wheat production than the original Ug99 strain, designated TTKSK.

The emergence and spread of these evolving rust pathotypes is a global issue with enormous implications, say Ravi P. Singh and Arun Kumar Joshi from the International Maize and Wheat Improvement Center, called CIMMYT, in El Batan, Mexico, and Kathmandu, Nepal, respectively. Wheat accounts for nearly 55% of the carbohydrates and 20% of the calories consumed globally, making it one of the most important food crops on the planet. About 90% of wheat varieties are vulnerable to these pathotypes, and it will take a massive, cooperative effort to develop and distribute new rust-resistant wheat varieties.

Stalking Mutant Cereal Killers in Africa and Asia

Two of the newly reported stem rust pathotypes, TTKSP and PTKST, are virtually identical to TTKSF, a common P. graminis strain in South Africa, according to Botma Visser and colleagues at the University of the Free State in Bloemfontein, South Africa, and the University of Sydney in Camden, Australia. Although phenotypically similar, PTKST is less infective than TTKSP in wheat lines carrying Sr21 resistance genes but proves more virulent in wheat with Sr31 resistance genes. Thus, TTKSP appears to be a local mutation, whereas PTKST was likely introduced into South Africa from elsewhere.

This experience in South Africa highlights the vulnerability of local wheat to foreign invasion by resistant wheat rust.

Summary

- Seven P. graminis mutants in the Ug99 lineage overcome most stem rust resistance genes protecting global wheat crops, making these new pathotypes an even greater threat than the parent fungus.
- Although long considered less deadly than stem rust, two new aggressive strains of P. striiformis, commonly known as stripe, or yellow, rust fungus, caused recent epidemics in the United States and Australia and devastated wheat in China, Africa, Asia, and the Middle East.
- Cereal researchers all over the world are collaborating to replace susceptible wheat genotypes with new high-yield, rust-resistant lines.
- Molecular biologists are looking for ways to turn the complex lifestyles of parasitic wheat fungi against them, develop a fuller understanding of rust genetics, and deploy better control strategies.
- The global outlook for wheat remains positive as long as researchers continue to share information and farmers agree to plant genetically diverse varieties.

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pathotypes from other growing regions. “P. graminis is highly adapted to long-distance migration through wind dispersal and rain deposition of its urediniospores,” Visser says. Accidental transport of spores on contaminated clothing or goods also contributes to fungal spread.

Because P. graminis spores disseminate readily, the emergence of rust pathotypes in any locale is instantly a global issue, according to Singh and Joshi of CIMMYT. Since it was discovered in Uganda in 1998, for example, Ug99 or its variants have spread to Kenya, Ethiopia, Sudan, South Africa, Yemen, and Iran. Rust fungi within the Ug99 lineage were also spotted in Zimbabwe, and scientists fear that one or more of these strains will make their way into Punjab, one of the major wheat-producing areas in the world.

The urgent action needed to intercept Ug99 after it was detected in Kenya and Ethiopia launched the Global Rust Initiative (GRI) in 2005, later named the Borlaug Global Initiative to honor Nobel Prize-winning agronomist Norman Borlaug. After years of painstaking cross breeding during the 1960s, Borlaug developed the first P. graminis-resistant, semi-dwarf wheat varieties. Serendipitously, the Sr31 gene that confers resistance to rust also increased crop yields. During the early period of the “Green Revolution,” farmers widely adopted those new wheat varieties, greatly boosting productivity during the 1980s and 1990s.

During the 1980s, Sr31 and other resistance genes kept the stem rust fungus under control, and for the next 20 years many farmers believed that genetic resistance had vanquished this ancient plague. That attitude changed, however, with the discovery of Ug99 in an experimental wheat field by William W. Wagoire from the Buginyanya Zonal Agricultural Research & Development Center in Uganda. Ravi Singh at CIMMYT quickly recognized Ug99’s potential to devastate wheat crops and shortly thereafter it was confirmed as a new strain of P. graminis by Zacharias A. Pretorius from the University of the Free State in Bloemfontein, South Africa.

Ug99’s Greatest Strength May Prove Its Biggest Weakness

Ug99 is well established in Kenya where, because farmers cannot afford fungicides, it has already killed between 60 and 70% of the wheat crop, says Joshi of CIMMYT. Thus, wheat researchers are racing to defeat this pathogen by blocking steps within its own complex biochemistry. “P. graminis represents a class of destructive plant pathogens that share a biotrophic lifestyle; that is, they rely entirely on living host tissue for completion of their life cycle,” says one of those researchers, Peter N. Dodds, from the Commonwealth Scientific and Industrial Research Organization, in Canberra, Australia. The biochemistry needed for its elaborate parasitic relationships, effector proteins in particular, “may be the source of this pathogen’s own undoing,” he says.

When it infects a wheat plant, P. graminis taps into host nutrients by penetrating the plant cell wall with specialized structures called haustoria, Dodds continues. Plants that can fend off such attacks do so in part by recognizing proteins, called effectors, that transfer from haustoria into host cells during infection. “Effector proteins are emerging as the prime weapon of plant parasites and also as targets for host recognition and immunity,” he says. An understanding of pathogen effectors is not only revealing fascinating insights into biotrophic lifestyles and plant-microbe coevolution, it could also lead to innovative disease-control measures.

Other plant pathogens form haustoria. For example, during the first stage of infection, the oomycete of Phytophthora infestans, the pathogen that caused the Irish potato famine, makes these structures. “Surprisingly,” says Dodds, “oomycete effectors seem to share common features with those of the human malaria pathogen, although this may be accidental.” Nonetheless, P. graminis research will undoubtedly affect a number of plant diseases and may even have repercussions for human diseases such as malaria.

Dodds and his collaborator Ralph Panstruga at the Max-Planck Institute for Plant Breeding Research in Köln, Germany, are working on several fungal resistance strategies, including efforts to block effector delivery mechanisms, to modify host targets to shield plants from effector recognition, and to design synthetic immune receptors to detect other parasite effector proteins. Furthermore, natural variation among effectors could provide a valuable diagnostic tool, says Dodds, who is collaborating with U.S. De-
partment of Agriculture (USDA) scientists on this research.

“Eventually the devastating Ug99 stem rust fungus will reach North America and Europe,” says W. Ronnie Coffman at Cornell University in Ithaca, N.Y. Farmers all over the world urgently need to replace most of their current wheat with newer rust-resistant strains, he warns.

USDA Acts to Pre-Empt Spread of Wheat Rusts

Two Ug99 pathotypes are particularly worrying to wheat experts at the USDA. One of them can overcome Sr24, a favorite resistance gene of North American wheat producers, and the other overcomes Sr36, which is widely used to protect winter wheat varieties grown in the Great Plains states.

Les J. Szabo and his colleagues from the USDA Cereal Disease Laboratory at the University of Minnesota in St. Paul are collaborating with Christina Cuomo and her group at the Broad Institute in Cambridge, Mass. The Broad Institute group sequenced the Ug99 genome and four different members of its lineage. Now the two groups are cloning effector genes, dissecting functions of those involved in *P. graminis* pathogenicity, and planning to monitor their expression during disease development.

“The availability of cloned effector genes will likely result in ways of rapidly screening wheat germplasm for specific resistance genes without the need to use live *P. graminis* cultures,” Szabo says. The research is also enabling development of PCR assays to identify stem rust pathogens and to distinguish one member of the Ug99 lineage from another. These assays will be deployed to regional labs in the United States and around the world to detect specific Ug99 pathotypes and enable rapid interventions against them.

“Because of its destructiveness and the economic importance of its cereal hosts—which include barley, oats, and rye in addition to wheat—*P. graminis* is one of the most widely studied of all plant pathogens,” says Szabo, who works at one of two research facilities in the world permitted to handle exotic cereal rust pathogens and where live-culture experiments are allowed only in December through February each year. The other lab authorized to work on live rust pathogens is in Winnipeg, Manitoba, Canada. Both facilities were sited to ensure that escaping spores would be unlikely to survive in icy, barren neighboring fields.

The Escalating Threat of *P. striiformis*

“While the world remains in fear of stem rust, large-scale epidemics caused by new virulent and aggressive strains of yellow rust fungus, also known as stripe rust, now pose a severe threat to the world’s wheat supply,” warn Mogens Støvring Hovmøller, Stephanie Walter, and Anнемarie Fejer Justesen at Aarhus University in Slagelse, Denmark. Since 2000, Australian and U.S. wheat farmers have suffered severe stripe rust epidemics, they note. Even more alarming,
they say, is that this particular rust devastated major wheat-producing areas in China, northern and eastern Africa, western and central Asia, and the Middle East in 2009.

Two pathotypes of *P. striiformis*—PstS1 and PstS2—were recently identified on five continents, Hovmøller says. “This appears to be the most rapidly and expansive spread ever of an important crop pathogen.” Moreover, its rapid spread is likely to continue because stripe rust strains tolerate relatively high temperatures, and the world is getting warmer.

A pathotype recently introduced into North America, for example, produces urediniospores more quickly at higher than at lower temperatures. Australian researchers confirm a shorter pathogen cycle in these more aggressive isolates, but their adaptation to selected temperature regimes is yet to be established. The U.S. and Australian *P. striiformis* strains are presumed to be of similar origin.

“Many winter wheat cultivars that performed well against stripe rust in the central plains of the U.S. became susceptible for the first time in 2010,” according to Robert L. Bowden at the USDA’s Agricultural Research Service in Manhattan, Kans., who notes that the unexpected shift in the stripe rust pathogen population surprised growers. The pedigrees of almost all the new pathotypes were traced to the cultivar Jagger which carries the Yr17 resistance gene. It now appears that *P. striiformis* strains with virulence against Yr17 are firmly established in the central plains, and only a few local wheat varieties are highly resistant to the new pathotypes. “Breeders and pathologists are working to play catch-up and develop new resistant varieties with more durable resistance,” says Bowden.

Recent stripe rust research “strongly supports the conclusion that *P. striiformis* continues to be a major limiting factor in world wheat production,” says Colin Wellings from the University of Sydney Plant Breeding Institute in Cobbitty, Australia. There is still a good deal of work to do, he notes, because stripe rust is currently a major problem in many of the world’s major wheat-producing regions. The 2010 epidemic reached from North Africa and included Turkey, Syria, northern Iraq, and Uzbekistan. Specific regions in the U.S. were also severely affected and early indications point to the potential for another epidemic in eastern Australia this coming spring. “This year has been a historically significant one for rust stripe globally,” he adds. “The cost in terms of crop loss and additional fungicide expenditures is in the billions of dollars.”

USDA researchers, who are actively studying the life cycle of *Puccinia striiformis*, recently identified shrubs in the *Berberis* genus that are an alternative host for these pathogens. “In areas where wheat and susceptible *Berberis* species coexist, sexual recombination likely played an active role in pathogen variability,” say Jin, Szabo, and Martin Carl-

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**Facts about Wheat Rust**

**Stem rust**, *Puccinia graminis f. sp. Tritici*, appears as reddish pustules on the stems or leaves of the wheat or other plants. This pathogen has caused intermittent famines since wheat was domesticated about 2,000 years ago. “A crop that appears healthy 3 weeks before harvest can be devastated by an explosive buildup of stem rust if sufficient inoculum arrives from a heavily infected wheat crop in some distant region,” note Kurt J. Leonard and Les J. Szabo from the USDA Cereal Disease Laboratory at the University of Minnesota in St. Paul. Even moderately infected fields can produce 10^{11} spores per hectare, and spores can travel thousands of kilometers by wind or hitchhiking on human or animal travelers.

**Stripe (or yellow) rust**, *Puccinia striiformis f. sp. Tritici*, forms long stripes of small yellowish orange spore-containing pustules on leaves and is sometimes confused with stem rust. Once considered less virulent than stem rust, highly aggressive new strains such as PstS1 and PstS2 are forcing scientists to reconsider. Last year several wheat research centers established a stripe rust research facility and the Global Rust Reference Center began banking stripe rust genes to facilitate resistance breeding and research.

**Leaf rust**, *Puccinia triticina* typically causes small orange pustules that erupt through leaf surfaces. As leaves age, the spores resemble black tar spots along lower leaf surfaces and sheaths. Although leaf rust can initiate tiny orange spots on wheat culms and heads, unlike stem rust, leaf rust does not form large, open pustules.

son. Developing a fuller understanding of this pathogen, they contend, should lead to novel strategies for its control.

Rust Proofing World Wheat

“The best strategy to protect wheat from the menace of Ug99 is replacement of susceptible genotypes with new high yielding and resistant varieties,” says Joshi of CIMMYT. His organization, the International Center for Agricultural Research in Dry Areas, and BGRI are collaborating with national research centers from several countries where wheat is under direct threat to develop high-yield, rust-resistant plants.

This program recently began releasing Ug99-resistant wheat varieties in Afghanistan, Bangladesh, Egypt, Ethiopia, Pakistan, Iran, and the especially hard-hit Kenya. Seed stocks of Ug99-resistant wheat strains are being expanded in Nepal, Afghanistan, Egypt, Ethiopia, and Pakistan, and breeders expect them to be distributed to farmers shortly.

Like the rust-resistant wheat varieties that Borlaug developed several decades ago, the new lines not only tolerate rust—in this case, Ug99—but also increase crop yields, providing an added incentive for farmers without direct experience dealing with wheat rust. Having a mix of resistance genes is critical, stresses Singh of CIMMYT, who recommends using wheat varieties with different genotypes to “enhance genetic diversity in farmers’ fields and thus reduce the risk of pandemic.”

The first Stem Rust Resistance Screening Nursery was assembled by CIMMYT, in part by using data generated at the Kenya Agricultural Research institute (KARI) in Njoro in 2005. Its charge is to search for Ug99 resistance in elite strains of CIMMYT wheat lines, says Peter N. Njau of KARI. Since then, plant scientists have been sending elite wheat cultivars and experimental lines from their countries to Njoro for testing against Ug99 and its mutant pathotypes. At last report, only 78 of 1,768, or 4.4%, of heirloom wheat varieties survived infection with mutant stem rust fungi. However, that figure is more than could be expected from randomly selected accessions, say the scientists.

In addition to this testing program at Njoro, seedlings from four consecutive growing seasons beginning in 2005 had their DNA analyzed in the USDA Cereal Disease Laboratory greenhouses in St. Paul, where Yue Jin and his team discovered that two species-specific genes, designated Sr24 and Sr25, confer resistance to the original TTKSK strain of Ug99. However, the mutant pathotype TTKST overcomes Sr24.

Although 30% of the screened lines were susceptible in the seedling stage, they displayed various levels of adult plant resistance in field tests,” says Singh. Only those wheat lines with high levels of adult plant resistance, or slow rusting resistance genes, appear likely to provide durable resistance to mutating P. graminis. Sr2 conferred only moderate levels of resistance when present alone; however, its presence is highly relevant in the company of other resistance genes.

The trick will be putting together the right combination of genes. Although none is fully protective against every P. graminis variant when alone, once assembled, they could provide almost complete resistance to virtually all current and evolving rust pathogens, Singh says. “A Mexico-Kenya shuttle breeding scheme has

Global Wheat Production and Estimated Pricing

- Wheat makes up approximately 30% of global grain crops, and estimated global production in 2009 was 682 million tons—putting wheat production third in cereals after maize and rice.
- On average, every individual consumes 68 kg of wheat per year, accounting for up to one-half the minimal energy requirements for most adults. In West Asia, North Africa, and Central Asia, wheat provides more calories than all other grains combined.
- Middle Eastern and North African countries consume 50% more wheat than they produce, making them heavily dependent on imports.
- Approximately 220 million hectares of land are used to produce wheat each year, and nearly half the world’s wheat is grown in developing countries.
- The 2009 U.S. wheat crop of 60 million tons was worth approximately $12 billion; the global crop was worth roughly $134 billion, assuming an average worldwide price of $5 per bushel.

Sources: The BGRI 2010, the Food and Agriculture Organization of the United Nations Trade and Marketing Division, and A.K. Joshi of CIMMYT.
been initiated by CIMMYT in an effort to incorporate high levels of complex adult resistance into high-yielding wheat varieties, and the resulting new lines could further help reduce genetic vulnerability to wheat rusts while enhancing yields.

“Ug99 has shown us how vulnerable wheat is,” says Robert Park at the University of Sydney Plant Breeding Institute in Camden, Australia. Overcoming wheat’s vulnerability to this fungal pathogen “is a problem that will not be solved quickly,” he says. “Ug99 research, monitoring, and plant breeding demand an ongoing effort; an arms race that must be supported by sustained funding.” Also key to this effort, he and others contend, is the continued rapid and free sharing of information about wheat varieties and the pathogens that threaten them.

SUGGESTED READING


