

# Historic overview of stem rust research

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## SUMMARY

Major events of relevance to stem rust over the past 150 years are briefly reviewed. Because stem rust has not been a significant problem for many years, other breeding objectives have taken priority. The occurrence of virulence for the widely used *Sr31* in a pathotype with several important additional virulence factors is a cause for concern. The potential for this pathotype to spread over much of Asia, if not elsewhere, and the fact that it has already mutated to virulence for two potentially useful resistance genes raises important questions in regard to future wheat production throughout the area.

## LANDMARKS IN CEREAL RUST RESEARCH

Major events in the history of stem rust research include:

- A description of the complete life cycle of cereal rust fungi, including heteroecism in *Puccinia graminis* by de Bary in the 1850s
- Separation of '*formae speciales*' within pathogen species by Eriksson and co-workers in the 1890s
- Further subdivision based on pathogen specialisation in virulence to specific host genotypes by Stakman and co-workers in the 1910s. These phenotypic groupings were described as physiologic races, races, strains or pathotypes. Stakman also led a campaign to eradicate barberry, and initiated studies of spore dispersal and pathotype variation in North America. His research and training activities at the University of Minnesota had a huge influence on subsequent rust research worldwide
- Production and deployment of resistant cultivars starting with Kanred and Ceres in the early 1900s
- Production of the landmark rust resistant cultivars Hope and H-44 by McFadden, and of Marquillo and Double Cross (Thatcher) by Hayes in the 1920s and 1930s
- Demonstration of sexuality in *P. graminis tritici* (Pgt) by Craigie in 1927
- Recognition and study of both sexual and asexual hybrids in *P. graminis* by students at the University of Minnesota and continued in Australia by Watson and Luig

- Although not based on cereal rusts, the gene-for-gene relationship in the flax rust system described by Flor in the 1940s and 1950s had a huge impact on cereal rust research, setting the stage for all subsequent research and thinking on plant disease systems
- An international gene virulence survey undertaken by Watson and Luig enabled a worldwide comparison of pathotypes (Luig, 1983)
- The isolation of aneuploid series in Chinese Spring wheat allowing genes to be located and mapped on chromosomes
- The production of near-isogenic lines by Knott, and later by Watson and Luig in Australia, provided reference host genotypes for international comparisons
- The use of resistance in agriculture often led to resistance 'break-down' at variable times after deployment – the average life of a resistance gene in wheat was estimated to be about three years. To overcome the resultant 'boom and bust' cycles, different research groups suggested a range of strategies usually based on personal experiences with different crops. For example, wheat stem rust workers sought rapid replacement of susceptible genotypes and the potential of gene combinations, whereas stripe rust workers emphasised the value of the very widespread sources of post-seedling resistance. These examples led to widely differing views on so called specific or vertical resistance versus non-specific or horizontal resistance
- The DNA sequencing of *Pgt* must be judged as the most recent landmark whose benefits are yet to be realised

## PATHOTYPE DESIGNATIONS AND SURVEYS

A race or pathotype is a clonally reproducing entity described by an arbitrary number of phenotypic traits – usually a series of host differentials. Cultures may be derived from single spores or may comprise bulks usually selected for uniformity of response on a differential set. Since pathotypes are limited phenotypic descriptions, different research cultures require permanent identities. Because of the current complicated naming systems, 'common'

names for agriculturally significant pathotypes are often preferred. For example, the Australian *Pgt* 'Cook' pathotype describes one or more variants with virulence on cv. Cook, and the *Pst* 'WA' pathotype refers to one or more entities resulting from the 2002 *Pst* incursion in Western Australia, just as UG99 has a distinct meaning to which we can all relate. On the other hand TTKS or Unkown (Kota (*Sr28*)-avirulent)-1,2,3,5,6,7,8,... may have meaning to North American or Australian workers, respectively, but little meaning is conveyed to other scientists or laymen. Neither designation conveys the fact of virulence for *Sr31* and avirulence for *Sr28*. For detailed comparisons such designations must at least be converted to binary nomenclature, and even then important phenotypic details may be lost. Watson and Luig (1968) described progressive changes in virulence whereby pathotype groups could be distinguished by their actual infection types produced on reference lines with genes such as *Sr6* or *Sr15*. Such details that are important in evolutionary comparisons are lost in binary notation systems.

Pathotype surveys are undertaken with most cereal rusts in most geographical areas and they vary from simple monitoring of trap plots dispersed throughout growing regions to systematic sampling and screening of single spore isolates or bulk collections on chosen sets of differentials. The type and value of data coming from surveys not only depends on the conditions of the test and technical knowledge of the people involved, but also on how the sampling was undertaken. Because different questions are being asked variable results are obtained.

A survey of relevance to UG99 should comprise trap plots of adapted genotypes possessing at least *Sr31*, *Sr26*, *Sr24*, *Sr30* and perhaps *Sr28*, selected resistant accessions and a susceptible control. These plots and cropping areas can be sampled for laboratory tests utilizing available or future facilities.

### LOCAL DISEASE CYCLES

Systematic surveys provide information on the presence and prevalence of rust on an annual basis, permitting the identification of 'hotspots' indicative of overseasoning areas. The presence of barberry, wild wheat relatives and wild and cultivated barleys might also be important as ancillary hosts. Pathways of spore movement may also be important in some regions, but in these considerations the importance of local survival is probably under-rated as exemplified by the long term survival of *Pst* in Australia, with no

mountainous areas of wheat cultivation and no known contributory ancillary hosts, and despite very extended drought periods.

### CONTINENTAL MOVEMENT OF RUST PATHOGENS

Pathways of spore movement in various regions of the world are well illustrated in the literature. Stubbs (1988) provided maps defining distinctive populations of *Pst* across Africa and Asia; many of the regions were adjacent or overlapping but the implication was that migration between regions was less frequent than within regions. The postulated movement of a *Pst* race virulent for *Yr9* from East Africa to South Asia has been substantiated by meteorological data, and the spread of UG99 to Yemen and Iran appears to follow the same pattern. The possibility of human-borne spread is more random.

### INTERNATIONAL RUST NURSERY

The 15B epidemics in North America in the 1950s had similarities with the UG99 situation, in that a number of suspected sources of resistance were overcome at the same time, and widespread losses ensued. A significant outcome was the establishment of the International Rust Nursery (IRN) co-ordinated by USDA and later largely replaced by CIMMYT nurseries. Breeders worldwide were encouraged to provide materials and/or to receive and test materials distributed by the program. Data were pooled as a means of global assessment. Information on all entries was compiled and distributed for use by collaborators. Materials were freely provided and there were no restrictions on the use of the germplasm in local breeding activities. Clearly, those conditions of free use of germplasm are less likely to be achieved at the present time. The IRN allowed the identification of germplasm that was widely effective worldwide and, especially so, in disease hotspots. Genetic analyses of lines with the broadest resistances identified genes such as *Sr12* and *Sr2* in combination with other well known genes for specific resistance justifying the suggestion that durability of resistance might be achieved through gene combinations. This approach was not unlike many recent studies analysing the basis of effective adult plant resistances to leaf rust and stripe rust. High levels of resistance under field conditions were achieved through combinations of genes which individually conferred lower levels of resistance.

## GENETIC VULNERABILITY

Because *Sr31* was so widely used, and provided effective and durable resistance, it undoubtedly contributed to reduced inoculum over wide areas and probably contributed to the view that stem rust was no longer an important disease. We became complacent. In retrospect, this led to a situation of genetic vulnerability, and although many of the cultivars with *Sr31* had additional resistance genes, such as *Sr30*, there was no realization of the potential threat of a pathotype that had only to overcome *Sr31* in order to become such a widespread threat. This was because we assumed such a mutation was unlikely because of the apparent durability of *Sr31* and other breeding priorities prevailed. One of the problems with genetic vulnerability is that we become wise only after the event, as was the case with T cytoplasm in maize and with the lack of the important 2R chromosome with its stem rust resistance genes in the case of the substituted 2D(2R) triticales in Australia in the 1980s. The current increasing use of *Yr26/Yr24* in China is a potential vulnerability.

## ADDRESSING THE FUTURE

Field testing has shown that some of the germplasm that was effective in early IRNs is still resistant. Most of it involves the ‘*Sr2* complex’ and/or derived from FKN (Frontana-Kenya-Newthatch; Newthatch being a Hope/Thatcher derivative). *Sr2* alone (e.g., CS (Hope 3B)) is not highly effective, with grain weight reductions of at least 50% in the presence of stem rust, but in other genetic backgrounds *Sr2* can be highly effective and its use over time should lead to reduced inoculum levels. North American workers have repeatedly shown the presence of a stem rust resistance suppressing gene in chromosome 7DL in Canthatch and other Thatcher derivatives, e.g., nulli-7D Canthatch plants are more resistant than Canthatch. The presence of *Lr34/Yr18/Pm38* in chromosome 7DS has been described as an anti-suppressor, and its presence in the Thatcher background, but not in many other backgrounds, such as CS, Condor or WW15, leads to enhanced stem rust resistance relative to Thatcher. According to Gavin Vinegas et al. (2008) interactions with the ‘minor’ genes *Sr12* and *Sr16* may contribute to the resistance. In any case it is not simply inherited. As pointed out by these authors Thatcher is not as resistant as its Lumillo durum donor, nor is it as resistant as the primary derivative, Marquillo. Since the D genome of Marquillo should be that of Marquis, and Thatcher is 50% Marquis a testcross analysis Marquis/Thatcher with Tc + *Lr34* might be an

appropriate cross for further study of this potentially important source of resistance.

Other potential sources of resistance require very careful assessment before widespread use in breeding programmes. While *Sr26* is considered a source of durable resistance based on the Australian experience there is no assurance of its continued effectiveness, even if alleged linkage drag problems can be overcome. *Sr24* from the same alien source continues to be effective after more than 25 years of deployment in Australia, but has already been overcome in India and South Africa as well as by a mutant derivative of UG99. In the short term breeders need to exploit the known durable sources while discovering and developing new resistant germplasm from within wheat itself (e.g., sources suggested in Jin and Singh, 2005; Bonman et al. 2007), and from secondary and tertiary gene pool relatives. A search for APR based on additive minor resistance genes as in the case of many recent studies on leaf rust and stripe rust resistances should be undertaken, but with the knowledge that reports of such resistance to stem rust are much less and that any source of such resistance needs to be separated from what we already know about Hope and Thatcher.

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