

Global status of stripe rust

Colin Wellings

*The University of Sydney, Plant Breeding Institute, 107 Cobbitty Road Cobbitty NSW 2570, Australia
Seconded from Industry & Investment NSW
e-mail: Colin.Wellings@sydney.edu.au*

Abstract Stripe rust, caused by *Puccinia striiformis*, has been an important disease of wheat, barley, rye, triticale and certain graminaceous hosts for centuries. The significance of the disease on cultivated cereals has waxed and waned according to the vagaries of climate, inoculum levels and susceptible varieties. A progressive understanding of pathogen biology has revealed levels of specialisation between and within host groups, and these had varying impacts on the hosts concerned. The most economically important form is *P. striiformis* f. sp. *tritici* (*Pst*), the causal pathogen of stripe (yellow) rust of wheat, which is the major focus of this paper. The recent discovery of the perfect stage of *Pst* on *Berberis* spp. will encourage further work to uncover the potential importance of the sexual stage in pathogen biology in regions where *Berberis* spp. occur. A review of the evolution of pathotypes within *Pst* over the past 50 years reveals recurrent pandemics emanating from a combination of specific virulence in the pathogen population, wide scale cultivation of genetically similar varieties, and agronomic practices that led to high yield potential. When these factors operate in concert, regional stripe rust epidemics have proven to be dramatic, extensive and serious in terms of the magnitude of losses and the economic hardships endured. A review of these epidemics suggests that little progress has been made in containing the worst effects of epidemics.

The current status of stripe rust was gauged from a survey of 25 pathologists and breeders directly associated with the disease. It was evident that *Pst* remains a significant threat in the majority of wheat growing regions of the world with potential to inflict regular regional crop losses ranging from 0.1 to 5%, with rare events giving losses of 5 to 25%. Regions with current vulnerability include the USA (particularly Pacific North West), East Asia (China north-west and south-west), South Asia (Nepal), Oceania (Australia) and East Africa (Kenya).

The resources deployed to contain the worst effects of *Pst* will need to find a balance between training a new generation of breeders and pathologists in host-pathogen genetics, and an investment in infrastructure in IARCs and NARs.

Keywords international status, pathogen variability, *Puccinia striiformis*, yellow rust, wheat

Introduction

It is a long and widely held view that stripe rust (syn. yellow rust), caused by *Puccinia striiformis* West. (*Ps*), is a prevalent but sporadic disease of temperate cereals. Biffen (1931) noted that even an “intense attack” failed to destroy crops in any comparable manner to the “killing power” of stem rust. However history informs us that stripe rust epidemics have been significant in certain geographic regions and the losses incurred required serious financial outlays to address disease control and crop loss mitigation. Several reviews deal with the range of biological issues of importance in understanding the regional nature and distribution of *Ps*, including Zadoks (1961), Stubbs (1985), Line (2002), Chen (2005) and Wellings (2007). This paper will consider some of the regional milestones that characterize the economic significance of the disease, and then attempt to place the current status of stripe rust in a global context. Emphasis is given to wheat stripe rust (caused by *Puccinia striiformis* f. sp. *tritici*, *Pst*) and the remaining *formae speciales* will be given less consideration.

Historical impact of stripe rust

Rust caused great concern to cereal cropping enterprises since the earliest recorded history. References to rust epidemics are found in the Mosaic books of the Old Testament and in the writings of early scholars (Large 1940). Epidemics reported in England in 1725 and Sweden in 1794 may have been stripe rust (Chester 1946).

The principle outcome of stripe rust epidemics is reduced yield and quality of grain. Early studies undertaken by Bever (1937) in greenhouse experiments using a susceptible spring wheat cultivar demonstrated yield losses as high as 65%. The extent of the losses were measured in reduced dry matter production, root growth, plant height, size and number of flowering spikes, and the size and number of grains. These effects were more pronounced with infection beginning at the seedling stage, although infections initiated at anthesis were also associated with reduced root weight and grain yield. Crop loss studies since this early work have essentially served to confirm the magnitude of losses and the physiological mechanisms determining reductions in yield potential.

Infection of spikes by *Pst* is a symptom expression of great concern to growers, and yet has received relatively little attention. Early work by Purdy and Allan (1963) established yield losses of 20% due to spike infection among cultivars resistant to foliar infection. Surveys by Cromey (1989) in New Zealand demonstrated mean grain weight losses of 11%, and noted that the wide range of losses in commercial fields appeared to be related to the timing of infection and the duration of moisture over the flowering period.

Epidemics of national and regional significance

An historical snapshot of the episodic nature of stripe rust epidemics and associated crop losses across various regions of the world is given in Table 1. These examples are not exhaustive, but simply illustrate the significant losses that have occurred in certain regions. Stripe rust epidemics have typically been the outcome of classic interactions between vulnerable host materials, conducive environmental conditions and sufficient quantities of pathogen inoculum. Several examples illustrate these principles.

TABLE 1 HERE

The stripe rust pandemics reported in the 1970s were often associated with the failure of Siete Cerros and related cultivars over a wide area, including North Africa, the Indian Subcontinent, Middle East, east African highlands and China (Saari and Prescott 1985). It is presumed, although not definitively proven, that an important basis of these epidemics was the failure of *Yr2* that is known to be present in the varieties most affected (McIntosh 2009).

The occurrence of virulence for *Yr9* in East Africa and the subsequent migration of this pathotype north and east through the majority of wheat producing regions in the Middle East (Syria, Turkey, Iran) and the Indian Sub continent (Pakistan, India) caused considerable crop damage in the 1990s (Singh et al. 2004). The origins of this series of pandemics is widely considered to be mutation to virulence for *Yr9* arising in the Red Sea region (Ethiopia, Yemen, Eritrea) as early as 1987 (Louwers et al. 1992). However, these authors cautioned that independent single mutational changes in existing pathotypes in Syria and Turkey may also have led to the same pathotype. The situation became exacerbated by the deployment of wheats carrying *Yr9*, notably Seri 82 and derivatives, over large areas in these regions. Similar, although independent, events occurred in China with up to 80% of released cultivars carrying *Yr9* in the late 1980s (Wan et al. 2004), with the result that virulence for *Yr9* in 1985 laid the foundation for the historical epidemic in 1989-1990 (Chen et al. 2009).

Rusts have been significant limiting constraints for cereal cropping in Australia since European colonization. *Pst* was recorded in Australia for the first time in 1979 and caused significant problems throughout the eastern wheat belt in the mid-1980s (Wellings 2007). The failure of the *YrA* resistance in 1981 caused a sudden localized epidemic in certain areas where this gene was deployed in cultivars which unknowingly had minimal supporting adult plant resistance (Wellings et al. 1988). The recent severe epidemics throughout eastern Australia since 2003 were the result of a new

pathotype incursion originating in Western Australia in 2002 (Wellings et al. 2003). New incursions are by nature unpredictable, and a large proportion of contemporary cultivars were vulnerable to this new pathotype. This led to an increased role for chemical control in Australia, and from 2003-2006 there was an estimated \$40-90 million annual expenditure in fungicide applications (Wellings 2007).

Current status of stripe rust

Life cycle

Stubbs (1985) surveyed early attempts, dating from Eriksson and Henning's work in 1894, which failed to establish a role for presumed candidate genera *Berberis*, *Valerianella* and *Mahonia* as alternate hosts. The microcyclic life cycle of *Pst* remained dogma for more than a century. The recent discovery of the sexual host of *Pst* (Jin et al. 2010) was greeted with great surprise and clearly resolved an issue that eluded generations of researchers. Although the nature and extent of sexual recombination in *Pst* in nature remains to be determined, the compelling evidence for recombination based on molecular and virulence diversity reported in certain regions such as China (Enjalbert 2009; Duan et al. 2010) may now be explained by a sexual phase in the life cycle.

International effort will now be directed to *Berberis* species during surveys in regions of interest in order to confirm the role of the host in nature. The host species reported, in particular *Berberis chinensis* (Caucasus barberry), are likely to be distributed in stripe rust prone regions. Jin (these proceedings) predicts that more *Pst* susceptible *Berberis* species are likely to be discovered.

The role of *Berberis* species will include not only the potential for virulence recombination, but also a potentially important means of pathogen survival between cropping seasons. In this respect, it is of interest to note the observation of short dormancy periods in teliospores and rapid production of basidiospores. On this basis Rapilly (1979) predicted that should an alternate host be discovered it would likely play a minor role as disease escape would be frequent in situations where basidiospores are quickly exhausted.

Pathogen nomenclature

Wheat stripe rust (Puccinia striiformis f. sp. tritici [Pst])

Although the predominant host of *Pst* is wheat, a noticeable increase in frequency of isolates recovered from wild *Hordeum* spp. stimulated an investigation of the evolutionary development of *Pst* on this host in Australia. Observations indicated that isolates of standard *Pst* pathotypes showed differential variation on clones of *H. glaucum* and *H. leporinum* (Wellings et al. 2000a). However, it was concluded that pathotype evolution within *Pst* on the weedy *Hordeum* species was independent from, and therefore likely to have little impact on, that occurring on wheat. It was also concluded that while *Pst* can cause stripe rust on rare genotypes of cultivated barley, it was not a threat to production (Wellings 2007).

Barley stripe rust (P. striiformis f. sp. hordei [Psh])

Isolates of the stripe rust pathogen that occur on cultivated barley, were described as *Psh* by European workers in the late nineteenth century. Barley stripe rust caused significant problems in winter barley production, particularly in the UK and The Netherlands in the 1960s (RW Stubbs pers com). The introduction and spread of *Psh* race 24 in Colombia in 1975, and its adaptation and dispersal throughout South America in the 1980s caused crop losses approaching 70% in some regions (Dubin and Stubbs 1986). The disease subsequently spread northwards into Mexico, Texas and western USA resulting in seasonal epidemics and significant economic losses (Marshall and Sutton 1995). *Psh* remains a pathogen of sporadic occurrence and severity, notably in certain seasons in UK, Russia and Europe (Macer 1972); North and South America, Middle East, South Asia (India) and East Africa (Stubbs 1985). A collection of stripe rust from barley stubble in northern Kazakhstan (Wellings 2009 unpublished) may represent an extremity of the geographical range of this pathogen, although the

identity of the isolate remains under investigation (Hovmoller pers comm). Reviews of barley stripe rust in a North American context can be sourced from Brown et al. (2001) and Line (2002).

Barley grass stripe rust (P. striiformis f. sp. pseudo-hordei [Psp-h])

A new form of *P. striiformis* was described in Australia by Wellings et al. (2000a). This form of the stripe rust pathogen first occurred on grassy species of *Hordeum* including the naturalised barley grass communities in eastern Australia. *Psp-h* causes disease on certain barley cultivars and barley breeding lines (Wellings et al. 2000b), and showed very low infection types on all wheat differential testers with the exception of Chinese 166 (*Yr1*). Contrasting isozyme loci and unique molecular phenotypes compared to Australian *Pst* pathotypes (Keiper et al. 2003) provided evidence for a unique *forma specialis* within *P. striiformis* (Wellings 2007). Recent evidence using fingerprinting markers implied that *Psp-h* shares genetic features with *Pst* (Loladze and Karaoglu unpublished). The international distribution of this form remains unclear. McIntosh (2009) predicted from personal observations that *Psp-h* is likely to be common in South America, especially Chile, and also in California, but the actual identities were not confirmed in greenhouse or laboratory studies. The US *Pst* pathotype PST-21, which seems to be very similar in virulence/avirulence phenotype to *Psp-h*, as well as being a constant outlier in molecular studies, was recorded mostly from California (Line 2002; Chen 2005).

Cocksfoot stripe rust (P. striiformis f. sp. dactylidis [Psd])

Stripe rust infecting cocksfoot (*Dactylis glomerata*) was described by Manners (1960) as a form with distinctive urediniospore dimensions compared to *Pst*. On this basis it was described as a variety of *Ps*, viz. *P. striiformis* var. *dactylidis*, and by implication *Pst* became *P. striiformis* var. *striiformis*. These distinctions were not widely accepted. Recent molecular fingerprinting suggests that *Psd* diverges significantly from other *Ps* variants in Australia, and may be a distinct species (Loladze, Karaoglu and Wellings unpublished). The global distribution of *Psd* remains uncertain, although it has not been recorded in Western Australia. Pasture improvement programs have focussed on the breeding and selection of *Dactylis glomerata* in Australia's eastern states, and released varieties are currently being evaluated for possible vulnerability to *Psd*.

Stripe rust on Kentucky bluegrass (P. striiformis f. sp. poae [Psp])

Psp was described by Tollenaar (1967) as the pathogen causing stripe rust of Kentucky bluegrass (*Poa pratensis*) in the USA. Temperature optima for urediniospore germination (12-18°C) and the close association between pathogen isolates and the host suggest that this is a distinctive *forma specialis*. The disease is noted to be widespread in western USA (Chen 2007) although the geographic distribution of *Psp* outside the USA remains unclear. Interestingly, it was the observation of stripe rust on *Poa pratensis* following random inoculation with aeciospores collected from *Berberis* spp. that gave the first suggestion of a sexual host for *P. striiformis* (Jin et al. 2010).

Host resistance

Efforts to contain stripe rust have largely focused on breeding for resistance. A review of early literature, including an accessible account of the substantial contributions of German researchers, was provided by Robbelen and Sharp (1978). Progressive genetic studies led to the description and characterisation of resistance genes (e.g. McIntosh et al. 1995; Singh et al. 2004; Boyd 2005; McIntosh et al. 2008), many of which are available in genetic stocks for use in research and breeding programs. Molecular markers associated with nominated resistance genes were summarized by Singh et al. (2004). Minor gene resistances, including QTLs and associated molecular markers, were reviewed by Singh et al. (2004) and Boyd (2005). This paper will not attempt to address the detailed status of genetics and breeding for resistance to stripe rust, and the reader is directed to the well documented literature.

Pathogen evolution

Studies of pathogenic variation in *Pst* trace back to the early work in the 1930s by Gassner and Straib (1932) in Germany. The development of differential host testers was driven historically by interests in pathogen population studies, epidemiology and breeding for resistance. An attempt was made to establish an international system of pathotype nomenclature (Johnson et al. 1972). This was adopted by Stubbs' group in The Netherlands who reported variability in European *Pst* populations and received support to conduct analyses of pathogen isolates internationally. Australian studies were also based on this set, although additions became necessary in order to address important pathogen variability related to commercial cultivars (Wellings and McIntosh 1990). A similar nomenclature and methodology is employed in India (Prashar et al. 2007), Middle East (Yahyaoui et al. 2002) and South Africa (Boshoff et al. 2002). However, current stripe rust research groups in UK, Denmark, France, USA, China, and Mexico use differential sets of varying composition and apply differing methodologies for designating pathotypes. Clearly a unified system for international pathotype designation remains a distant hope.

Despite differences in approaches to differential sets, international colleagues have monitored *Pst* populations over many years and regions. A summary of regional developments in pathogen evolution from the 1970s was provided in Wellings et al. (2009). A detailed review of this work is beyond the scope of this paper, although several common themes are worthy of comment:

1. Long term regional and continental studies consistently reveal the close relatedness of newly emerged pathotypes with pre-existing pathotypes. The evident clonal nature of *Pst* populations leads to the conclusion that single step mutation remains the predominant cause of variability (Justesen et al. 2002; Chen 2005; Wellings 2007; Chen et al. 2009).
2. New pathotypes with specific adaptation facilitated by acquisition of specific single gene virulences, and simple virulence combinations, were major factors underlying regional epidemics. The acquisition of virulence for *Yr2* in the 1970s, *Yr9* in the 1990s, and *Yr27* in recent years contributed significantly to regional and continental epidemics, and crop losses (Wellings et al. 2009).
3. Comparative studies using *Pst* isolates drawn from widely dispersed geographical regions showed distinct genetic contrasts including evidence for putative recombinants (Enjalbert 2009; Duan et al. 2010). Chinese workers frequently reported wide variability in pathogenic features in *Pst* populations in Gansu province (e.g. Chen et al. 2009). While the lack of evidence for a sexual host remained undiscovered, these claims were unsupported. The situation has now clearly changed, and greater emphasis will be placed on determining the distribution and importance of candidate *Berberis* spp. as alternate hosts in these regions.

Pathogen aggressiveness

The apparent aggressiveness of certain isolates of *Pst* has been a subject of speculation for many years. Johnson and Taylor (1972) were among the first to demonstrate that differences in urediniospore yield between isolates of identical pathotype were associated with the cultivar source of the isolate. However the emergence of destructive *Pst* pathogen populations in North America, Australia and elsewhere over the past decade provided the impetus to undertake detailed studies of pathogen aggressiveness in relation to temperature. While earlier European workers suggested that *Pst* may have become adapted to warmer temperatures (Macer 1972; Zadoks 1979), it was the detailed work of Milus et al. (2009) that provided a basis for the claim of temperature adaptation within newly emerging *Pst* populations. This work demonstrated that a recently introduced pathogen population in North America was capable of producing more urediniospores in shorter time periods and at higher temperature profiles. Australian work confirmed a shorter pathogen cycle in aggressive isolates of *Pst* presumed to be of similar origin to those in the USA, but with less clear evidence for adaptation to selected temperature regimes (Loladze et al. 2009).

Pathogen movement

Pathotype surveys were used in Australia to demonstrate important aspects of disease epidemiology. The early seasonal occurrence of the disease, frequently involving different pathotypes recovered from distant locations, provided evidence for the independent localized survival of *Pst* within major wheat growing regions. In Australia, there is no evidence for specific survival areas.

In Europe, various studies demonstrated clonality in *Pst* populations with clear evidence for long distance dispersal. Justesen et al. (2002) demonstrated extinction (1996) and re-colonization (1997) of *Pst* in Denmark using molecular and pathogenicity markers. Hovmoller et al. (2002) provided further evidence to indicate that *Pst* populations in northwestern Europe frequently migrate across the region. These, and other studies, argue strongly for a co-ordinated regional and continental approach to disease control.

Documentation of rapid and long distance dispersal in *Pst* is relatively recent. The first detection of *Pst* in Australia in 1979 was considered an outcome of inadvertent urediniospore transfer from Europe (Wellings et al. 1987). A similar mode of introduction presumably led to the discovery of *Pst* in South Africa in 1996 (Pretorius et al. 2007) since the initial pathotype was more closely related to North Africa and the Middle East than prevailing pathotypes in west Africa. The occurrence of a new pathotype lineage in North America in 2000 (Chen et al. 2002; Chen 2007) and detection of a near-identical pathotype in previously stripe rust free Western Australia in 2002 (Wellings et al. 2003) highlight the potential for rapid international transfer of *Pst* pathotypes. Hovmoller et al. (2008) compared a set of *Pst* isolates representing recently emerged (post 2000) near identical pathotypes collected from various continents and regions. They concluded that two subsets, or strains, of the apparent widely dispersed pathotype could be distinguished based on AFLP fingerprints: Strain 1 was common to USA and Australia, and Strain 2 was recovered from Eritrea, West Asia (Iran, Azerbaijan) and Central Asia (Kazakhstan, Uzbekistan, Kyrgystan).

The widespread international occurrence of this newly emerged *Pst* lineage is cause for concern. International travel must play a significant, although currently unmeasured, role in cross boundary plant pathogen transfer. International tourism has grown from 25 million passenger movements per annum in the 1950s to 760 million in the current decade (R. Delane pers comm). These challenges must be embraced by agriculturalists and policy makers concerned with implementing effective disease management strategies.

Current international stripe rust status

Singh (2004) presented an overview of the relative importance of the three cereal rust diseases, and concluded that stripe rust was currently the most damaging cereal rust across international locations. In order to update and further clarify this conclusion, an attempt to gauge the current status of *Pst* was undertaken for the purposes of this paper. Colleagues with experience in wheat stripe rust were contacted and asked to assess the incidence and severity of the disease over the period 2000-2010 in the regions for which they had immediate knowledge. Assessments were based on a simplified method for disease incidence, adapted from Murray and Brennan (2009), using scores to express the frequency of epidemics and the approximate wheat production area affected during an epidemic (Table 2). Assessment scores for stripe rust severity (Table 3) were based on an average expectation for crop losses encountered in nominated regions.

TABLE 2 HERE

TABLE 3 HERE

Assessments provided by 25 colleagues are summarized in Table 4. Although comparisons were not sought with other wheat diseases, the survey provides evidence for the widespread incidence and severity of stripe rust in major wheat production zones of the world. The most 'at risk' regions for

stripe rust could be considered those where epidemics are experienced in most seasons with expected regional losses ranging from 5 to 25%. These regions include the USA (Pacific North West), East Asia (China north-west and south-west), South Asia (Nepal), Oceania (eastern Australia) and East Africa (Kenya). A majority of regions have stripe rust incidence on a regular basis (incidence scores of 3 and 4) with estimated losses of 1 to 10%. This survey was brief and would clearly improve with greater attention to assessments for more precisely defined regions. Should this development occur, then it may be possible to arrive at regional estimates of the current costs incurred by stripe rust and other significant wheat diseases, thereby developing a basis for prioritizing R&D investments. The work of Murray and Brennan (2009) in Australia, who estimated the current national losses due to stripe rust at \$AUD17.82 per hectare or \$AUD127million across the national wheat growing regions, could serve as a basis in developing an international economic assessment of the impact of stripe rust on world wheat production. Such projections are likely to generate a staggering estimate of the economic magnitude of the stripe rust problem internationally.

Conclusions

This brief survey and overview of published work on stripe rust strongly supports the conclusion that wheat stripe rust continues to be a major limiting factor in world wheat production. Despite the regular and significant impact of the disease, there appears to be a limited international capacity to respond to epidemics, much less to anticipate and proactively prepare farming communities to minimise the effects. With few exceptions, there appears to be a lack of regionally co-ordinated R&D programs that link active pathogen monitoring with known deployed resistances in farmers fields and resistance breeding programs. The international rust trap nursery system implemented and co-ordinated by IARCs (CIMMYT and ICARDA) has been helpful in monitoring variety responses to local *Pst* populations, and the application of NILs has added a useful dimension to this work (Wellings et al. 2009). The recent establishment of a Global Reference Centre for Yellow Rust at the University of Aarhus, Denmark, is a significant step towards sealing the vacuum that occurred when IPO Wageningen ceased international testing and training. The latter program, which was eminently led by RW Stubbs and colleagues and continued until the early 1990s, was an invaluable assistance to those monitoring *Pst* in developing countries. Experience informs us that new and important pathotypes are generally recovered initially at low frequency, and if these can be identified and their significance can be interpreted, opportunities are presented for timely responses to minimise crop losses. The Global Reference Centre for Yellow Rust will provide valuable support, but is unlikely to have the capacity required to manage large sample numbers from regional epidemics. Investments in resources and training for regional centres of expertise in cereal rust pathology and breeding should be a priority if we are to gain maximum advantage from global IARCs.

A review of historic and contemporary experiences with stripe rust in global wheat production zones inevitably results in a cascade of apparent unresolved issues. Why is it that we seemingly remain vulnerable to successive waves of pathotype lineages across entire regions and continents? Where does the pathogen survive in vulnerable locations and what can be achieved in designing containment strategies that seek to reduce the dangers of early infection in these locations? What can be done to strengthen national programs to effectively monitor *Pst* populations in the context of locally deployed resistant genotypes? How can we synchronise informative and timely pathotype data with a whole-of-industry approach to resistance breeding and post release management of varieties? These are not new questions!

Biffen (1931), buoyed by early success in the application of Mendelian genetics in breeding for stripe rust resistance, predicted that 'the solution of the most important problems of rust control is in sight'. Forty years later, Manners (1969) referred to Biffen's statement as 'perhaps still true, but the view is more distant than Biffen anticipated'. Johnson (1992) reflecting on a further thirty year period in stripe rust research found some agreement with Manners but added his own personal view: 'although one can still optimistically look forward to the final solution, it is rather seen through the

wrong end of a telescope'. If the light of solutions to stripe rust indeed resides at the end of a tunnel, it would seem that we still have a good deal of work to do to ensure the train is heading towards us and not in the opposite direction. If this is viewed as a light hearted conclusion, then we should be galvanised to action by the thought that without continued effort and resources, international wheat productivity clearly remains at serious risk from recurring stripe rust epidemics. Currently, stripe rust is spreading rapidly in a region stretching from Turkey, Syria and northern Iraq to southern Uzbekistan; the potential for crop loss is in the billions of dollars (Abdallah et al. 2010).

Acknowledgements Colleagues gratefully acknowledged for contributing to the survey include: Ayele Badebo, Rosemary Bayles, Wanquan Chen, Xianming Chen, Claude de Vallavielle-Pope, Antonin Dreiseitl, Kerstin Flath, Silvia German, Mogens Hovmoller, Alma Kokmetova, Ricardo Madariaga, Brent McCallum, Zafer Mert, Alexei Morgounov, Kumarse Nazari, Guillermo Ortiz-Ferrara, Maria Pasquini, Mohinder Prashar, Shynbolat Rysaliev, Atef Shahin, Sarala Sharma, Davinder Singh, Ravi Singh, Galina Volkova, and Amor Yahyaoui.

References

- Abdallah O, Nazari K, Clarke E (2010) ICARDA calls for action to tackle wheat stripe rust threat to Middle East breadbasket. ICARDA media release. (<http://icardablog.wordpress.com>)
- Bayles RA, Channell MH, Stigwood P (1989) Yellow rust of wheat. UK Pathogen Virulence Survey, 1989 Annual Report, pp.11-17
- Bever (1937) Influence of stripe rust on growth, water economy and yield of wheat and barley. *J Agric Sci* 1:4-48
- Beresford RM (1982) Stripe rust (*Puccinia striiformis*), a new disease of wheat in New Zealand. *Cereal Rusts Bull* 10:35-41
- Biffen RH (1931) The cereal rusts and their control. *Trans British Mycol Soc* 16:19-37
- Boyd LA (2005) Can Robigus defeat an old enemy? – yellow rust of wheat. *J Agr Sci* 143:233-243
- Boshoff WHP, Pretorius Z, van Niekerk BD (2002) Establishment, distribution, and pathogenicity of *Puccinia striiformis* f.sp. *tritici* in South Africa. *Plant Dis* 86:485-492
- Brown WM, Hill JP, Velasco VR (2001) Barley yellow rust in North America. *Annu Rev Phytopathol* 39:367-384
- Chen WQ, Wu LR, Liu TG, Xu SC (2009) Race dynamics, diversity and virulence evolution in *Puccinia striiformis* f.sp. *tritici*, the causal agent of wheat stripe rust in China from 2003 to 2007. *Plant Dis* 93:1093-1101
- Chen XM (2005) Epidemiology and control of stripe rust (*Puccinia striiformis* f.sp. *tritici*) on wheat. *Can J Plant Pathol* 27:314-337
- Chen XM (2007) Challenges and solutions for stripe rust control in the United States. *Aust J Agric Res* 58:648-655
- Chen XM, Moore M, Milus EA, Long DL, Line RF, Marshall D, Jackson L (2002) Wheat stripe rust epidemics and races of *Puccinia striiformis* f.sp. *tritici* in the United States in 2000. *Plant Dis* 86:39-46
- Chester KS (1946) The nature and prevention of the cereal rusts as exemplified in the leaf rust of wheat. *Chronica Botanica*, pp269
- Cromey MG (1989) Occurrence and effects of stripe rust in wheat spikes in New Zealand. *NZ J Crop and Hort Sci* 17:155-158
- Duan X, Tellier, A, Wan A, Leconte M, de Vallavielle-Pope C, Enjalbert J (2010) *Puccinia striiformis* f.sp. *tritici* presents high diversity and recombination in the overwintering zone of Gansu, China. *Mycologia* 102:44-53
- Dubin HJ, Stubbs RW (1986) Epidemic spread of barley stripe rust in South America. *Plant Dis* 70:141-144
- Duveiller E, Singh RP, Nicol JM (2007) The challenges of maintaining wheat productivity: pests, diseases, and potential epidemics. *Euphytica* 157:417-430

- Enjalbert J (2010) Clonality and recombination footprints in wheat yellow rust genetic structure. Abstract p 49, 12th Int7 Cereal Rusts & Powdery Mildews Conf, 13-15 October, Antalya, Turkey
- Gassner G, Straib W (1932) Die Bestimmung der biologischen Rassen des Weizengelbrostes (*Puccinia glumarum* f. sp. *tritici* (Schmidt) Eriks. And Henn.). Arb Biol Reichsanst land Forlswirtsch 20:141-163
- German S, Barcellos A, Chaves M, Kohli M, Campos P, de Viedma L (2007) The situation of common wheat rusts in the Southern Cone of America and perspectives for control. Aust J Agric Sci 58:620-630
- Hovmoller MS, Justesen AF, Brown JKM (2002) Clonality and long distance migration of *Puccinia striiformis* f.sp. *tritici* in north-west Europe. Plant Pathol 51:24-32
- Hovmoller MS, Yahyaoui AH, Miles EA, Justesen AF (2008) Rapid global spread of two aggressive strains of a wheat rust fungus. Mol Ecology 17:3818-3826
- Jin Y, Szabo LJ, Carson M (2010) Century-old mystery of *Puccinia striiformis* life history solved with the identification of *Berberis* as an alternate host. Phytopathology 100:432-435
- Johnson R (1992) Reflections of a plant pathologist on breeding for disease resistance, with emphasis on yellow rust and eyespot of wheat. Plant Pathol 41:239-254
- Johnson R, Taylor AJ (1972) Isolates of *Puccinia striiformis* collected in England from the wheat varieties Maris Beacon and Joss Cambier. Nature 238:105-106
- Johnson R, Stubbs RW, Fuchs E, Chamberlain NH (1972) Nomenclature for physiologic races of *Puccinia striiformis* infecting wheat. Trans Br Myc Soc 58:475-480
- Justesen AF, Ridout CJ, Hovmoller MS (2002) The recent history of *Puccinia striiformis* f.sp. *tritici* in Denmark as revealed by disease incidence and AFLP markers. Plant Pathol 51:13-23
- Keiper FJ, Hayden, MJ, Park RF, Wellings CR (2003) Molecular genetic variability of Australian isolates of five cereal rust pathogens. Mycol Res 107:545-556
- Large EC (1940) The Advance of the Fungi. Jonathan Cape, London, pp 488
- Line RF (2002) Stripe rust of wheat and barley in North America: a retrospective historical review. Annu Rev Phytopathol 40:75-118
- Loladze A, Druml T, Wellings CR (2009) Differential adaptation of Australian and New Zealand stripe rust isolates to high temperature. Abstract p22, 12th Int Cereal Rusts & Powdery Mildews Conf, 13-15 October, Antalya, Turkey
- Louwers JM, van Silfhout CH, Stubbs RW (1992) Race analysis in wheat in developing countries, Report 1990-1992. IPO-DLO Report 92-11, 23 pp
- Macer RCF (1972) The resistance of cereals to yellow rust and its exploitation in plant breeding. Proc Royal Soc London 181:281-301
- Manners JG (1960) *Puccinia striiformis* Westend. var. *dactylidis* var. nov. Trans Brit Mycol Soc 43:65-68
- Manners JG (1969) Presidential address. The rust diseases of wheat and their control. Trans Brit Mycol Soc 52:177-186
- Marshall D, Sutton RL (1995) Epidemiology of stripe rust virulence of *Puccinia striiformis* f.sp. *hordei* and yield loss in barley. Plant Dis 79:732-737
- McIntosh RA, Yamazaki Y, Dubcovsky J, TRogers J, Morris C, Somers DJ, Appels R, Devos KM (2008) Catalogue of gene symbols for wheat. 11TH Int Wheat Gen Symp Brisbane <http://wheat.pw.usda.gov/GG2/Triticum/events/11IWGS/MacGene2008.20080808/Documents/Catalogue/Catalogue2008.htm>
- McIntosh RA (2009) History and status of the wheat rusts. In RA McIntosh (ed) Proc Borlaug Global Rust Initiative 2009 Technical Workshop BGRI Cd Obregon, Mexico, pp11-23
- McIntosh RA, CR Wellings, RF Park (1995) Wheat rusts: an atlas of resistance genes. CSIRO Publications, Victoria, Australia, 200pp
- Milus EA, Kristensen K, Hovmoller M (2009) Evidence for increased aggressiveness in a recent widespread strain of *Puccinia striiformis* f.sp. *tritici* causing stripe rust of wheat. Phytopathol 99:89-94

- Moghaddam ME, Kamali MRJ, Aghaee M, Afshari F, Roustali M (2009) Status of wheat rusts in Iran. In RA McIntosh (ed), Proc Borlaug Global Rust Initiative 2009 Technical Workshop BGRI Cd Obregon, Mexico pp 155-158
- Murray GM, Brennan JP (2009) The current and potential costs from diseases of wheat in Australia. Australian Grains Research and Development Corporation report, 69 pp (<http://www.grdc.com.au>)
- Murray GM, Ellison PJ, Watson A, Cullis BR (1994) The relationship between wheat yield and stripe rust as affected by length of epidemic and temperature at the grain development stage of crop growth. *Plant Pathol* 43:397-405
- Prashar M, Bhardwaj SC, Jain SK, Datta D (2007) Pathotypic evolution in *Puccinia striiformis* in India during 1995-2004. *Aust J Agric Res* 58:602-604
- Pretorius ZA, Pakendorf KW, Marais GF, Prins R, Komen JS (2007) Challenges for sustainable rust control in South Africa. *Aus J Agric Res* 58:593-601
- Purdy LH, Allan RE (1963) Seedling and mature plant reaction of wheat to stripe rust. *Plant Dis Rep* 47:797-799
- Rapilly F (1979) Yellow rust epidemiology. *Ann Rev Phytopathol* 17:59-73
- Saari EE, Prescott JM (2005) World distribution in relation to economic losses. In: Roelfs AP, Bushnell WR (eds) *The cereal rusts Vol II*. Academic Press Inc, Orlando, pp259-298
- Singh RP (2004) The cost to agriculture of recent changes in cereal rusts. Proc 11th Int Cereal Rusts and Powdery Mildews Conf., 22-27 August 2004, John Innes Center, Norwich UK
- Singh RP, William HM, Huerta-Espino J, Rosewarne G (2004) Wheat rust in Asia: meeting the challenges with old and new technologies. In: 'New directions for a diverse planet', Proceedings 4th Int Crop Science Cong, 26 Sep-1 Oct 2004, Brisbane Australia p 1-13 (www.cropscience.org.au)
- Slovencikova V, Bares I (1978) Epidemic of stripe rust in Czechoslovakia in 1977. *Cereal Rusts Bull* 6:15-18
- Stubbs RW (1985) Stripe Rust. In: Roelfs AP, Bushnell WR (eds) *The cereal rusts Vol II*. Academic Press Inc, Orlando pp61-101
- Tollenaar H (1967) A comparison of *Puccinia striiformis* f.sp. *poae* on bluegrass with *P. striiformis* f.sp. *tritici* and f. sp. *dactylidis*. *Phytopathology* 57:418-420
- Vallega V, Zitelli G (1979) Epidemics of yellow rust in Italy. *Cereal Rusts Bull* 6:17-22
- Wan A, Zhao Z, Chen X, He Z, Jin S, Jia Q, Yao G, Yang J, Wang B, G Li, Bi Y, Yuan Z (2004) Wheat stripe rust epidemic and virulence of *Puccinia striiformis* f.sp. *tritici* in China in 2002. *Plant Dis* 88:896-904
- Wellings CR (2007) *Puccinia striiformis* in Australia: a review of the incursion, evolution, and adaptation of stripe rust in the period 1979 – 2006. *Aust J Agric Res* 58:567-575
- Wellings CR, McIntosh RA (1990) *Puccinia striiformis* f. sp. *tritici* in Australasia: pathogenic changes during the first 10 years. *Plant Pathol* 39:316-325
- Wellings CR, McIntosh RA, Walker J (1987) *Puccinia striiformis* f.sp. *tritici* in eastern Australia – possible means of entry and implications for plant quarantine. *Plant Pathol* 36:239-241
- Wellings CR, McIntosh RA, Hussain M (1988) A new source of resistance to *Puccinia striiformis* f.sp. *tritici* in spring wheats (*Triticum aestivum*). *Plant Breeding* 100:88-96
- Wellings CR, Burdon JJ, McIntosh RA, Wallwork H, Raman H, Murray GM (2000a) A new variant of *Puccinia striiformis* causing stripe rust on barley and wild *Hordeum* species in Australia. *Plant Pathol* 49:803
- Wellings CR, Read B, Moody D (2000b) Stripe rust affecting barley in Australia – current and potential threats. In: Proc 8th Int Barley Genet Symp, Adelaide, Australia, September 2000, Vol III, pp197-199
- Wellings CR, Wright DG, Keiper F, Loughman R (2003) First detection of wheat stripe rust in Western Australia: evidence for a foreign incursion. *Aust Plant Pathol* 32:321-322

- Wellings CR, Singh RP, Yahyaoui A, Nazari K, McIntosh RA (2009) The development and application of near-isogenic lines for monitoring cereal rust pathogens. In: McIntosh RA (ed) Proc Borlaug Global Rust Initiative Technical Workshop, BGRI Cd Obregon, Mexico, pp77-87
- Yahyaoui AH, Hakim MS, El Naimi M, Rbeiz N (2002) Evolution of physiologic races and virulence of *Puccinia striiformis* on wheat in Syria and Lebanon. Plant Dis 86:499-504
- Zadoks JC (1961) Yellow rust on wheat. Studies in epidemiology and physiologic specialization. T.Pl.-Zeikten 67:69-256
- Zadoks JC (1979) Strategies in combating cereal diseases in Europe, with special reference to yellow rust of wheat. In: Proc Rice Blast Workshop, Laguna, Philippines, pp183-198
- Zadoks JC, Bouwman JJ (1985) Epidemiology in Europe. In: Roelfs AP, Bushnell WR (eds) The cereal rusts Vol II. Academic Press Inc, Orlando, pp329-369

Table 1 Historical review of major stripe rust epidemics with comments on severity and losses

Region	Period	Nature of epidemic and losses	Reference
United Kingdom	1966 1969 1988-1989	Rothwell Perdux epidemic Joss Cambier epidemic Sleijpner, Hornet epidemic	Macer 1972 Johnson 1992 Bayles et al. 1989
Australia	1983-1986 2002-2010	Losses up to 80% Annual fungicide expenditure \$AUD 40-90m (2003-2006)	Murray et al. 1994 Wellings 2007
New Zealand	1980-1981	60% crop loss	Beresford 1982
Iran	1993	National losses: 1.5 m tonne	Moghaddam et al. 2009
Chile	1976-1988, 2001	Regular epidemics	German et al. 2007
USA	1957-1958 1960-1964 2000 2003	Widespread in 10 states \$USD15-30m losses (Wa State) Widespread in 20 states National losses 3.4% or 11.7m tonnes	Chen et al. 2002 Line 2002 Chen et al. 2002 Chen 2005
China	1954, 1964, 1990, 2002	6.00 m tonne loss 3.20 m tonne loss 2.65 m tonne loss 1.40 m tonne loss	Chen et al. 2009 Wan et al. 2004
Spain, North Africa	1978	Siete Cerros epidemic	Zadoks and Bouwman 1985
Republic of South Africa	1996-1999	Annual fungicide expenditure ZAR5- 28m	Boshoff et al. 2002
India	1994-2004 2001	Recurrent epidemics PBW343 (<i>Yr27</i>) failed	Prashar et al. 2007
Pakistan	2005	\$USD100m losses (NWFP)	Duveiller et al. 2007
Italy	1977-1978	Undetermined; widespread epidemic with susceptible cultivars	Vallega and Zitelli 1979
Czechoslovakia	1977	30% loss in susceptible cultivars	Slovencikova and Bares 1978

Table 2 Descriptions and scores for stripe rust incidence (adapted from Murray and Brennan 2009)

Score	Description	Incidence	
		Epidemic years (%)	Production area affected (%)
0	Not recorded.	0	0
1	Rare. Generally 1 season in 10 over scattered locations.	20	25
2	Localised in some seasons. Approximately 2 seasons in 5 over 25% of wheat growing area.	40	25
3	Present in most seasons but localized. Occurring 2 seasons in every 3 over 25% of wheat growing area.	67	25
4	Widespread in some seasons. Approximately 2 seasons in 5.	40	100
5	Widespread in most seasons. Approximately 2 seasons in 3.	67	100

Table 3 Severity and associated crop loss estimates for stripe rust (adapted from Murray and Brennan 2009)

Score	Crop loss classification	Estimated Percent Loss
0	No losses	0.0
1	Negligible	0.1
2	Light	1.0
3	Moderate	5.0
4	Severe	10.0
5	Very severe	25.0

Table 4 Incidence and severity¹ of wheat stripe rust across cereal producing continents and regions provided by collaborator assessments for 2000-2009

Continent	Region, Zone	Incidence	Severity	Collaborator
North America	Canada –western prairies (Alberta)	3	2	B McCallum, X Chen
	Canada – eastern prairies (Manitoba, Saskatchewan)	2	1	B McCallum, X Chen
	Pacific North West USA	5	3	X Chen, R Singh
	Great Plains USA	4	2	X Chen, R Singh
	South West USA, Mexico	4	2	X Chen, R Singh
South America	Bolivia, Columbia, Peru, Ecuador	4	4	R Singh
	Chile	4	4	R Madariaga
	Argentina, Brazil, Uruguay, Paraguay	1	3	S German, R Singh
Western Europe	UK – eastern England	4	2	R Bayles, M Hovmoller
	UK – other areas	2	1	R Bayles
	Germany	3	2	K Flath, M Hovmoller
	Denmark	2	2	M Hovmoller
	France - north	3	2	C Pope, M Hovmoller
	France – south, Spain	2	1	C Pope, M Hovmoller
	Italy	1	1	M Pasquini, M Hovmoller
Eastern Europe	Romania, Poland, Ukraine, Yugoslavia	2	2	X Chen
	Czech Republic	3	1	A Dreiseitl
	Russia – north Caucasus	2	2	G Volkova
	Russia – Siberia, north Kazakhstan	1	2	A Morgounov, C Wellings
West Asia	Syria, Iran, Iraq, Afghanistan	3	4	R Singh, K Nazari, A Yahyaoui, A Morgounov
	Turkey – south/south east	2	3	Z Mert
	Turkey – Central Anatolia	3	4	Z Mert, A Morgounov
	Turkey – north	2	2	Z Mert
	Iran – north, west, south, central	3	2	K Nazari
	Iran – east	1	2	K Nazari

BGRI 2010 Technical Workshop, 30-31- May 2010, St Petersburg, Russia
Wellings, Global status of stripe rust

Central Asia	Kazakhstan – south/south-east	3	4	S Rysaliev, A Kokmetova, C Wellings, A Morgounov
	Kazakhstan - north	1	3	A Kokmetova, C Wellings
	Uzbekistan	4	4	K Nazari, A Morgounov, R Singh, C Wellings
East Asia	China	4	4	R Singh
	China – north west	5	5	W Chen, X Chen
	China – south west	5	4	W Chen, X Chen
	China – south east	3	2	W Chen
South Asia	India, Pakistan	4	3	M Prashar, K Nazari
	Nepal - eastern foot hills/river basin	5	4	S Sharma, G Ortiz-Ferrara
	Nepal - eastern lower and mid elevation hills	4	3	S Sharma, G Ortiz-Ferrara
	Nepal – central valleys and hills	4	4	S Sharma, G Ortiz-Ferrara
	Nepal – western foot hills/river basin	4	3	S Sharma, G Ortiz-Ferrara
	Nepal – western mid elevation hills	5	4	S Sharma, G Ortiz-Ferrara
	Nepal – far west mid/high elevation hills	3	3	S Sharma, G Ortiz-Ferrara
Oceania	Australia – eastern states	5	3	C Wellings
	Australia - west	4	3	C Wellings
	New Zealand	4	3	C Wellings
North Africa	Morocco, Tunisia	2	4	A Yahyaoui
	Egypt	1	2	A Shahin, K Nazari
East Africa	Kenya	5	4	D Singh, K Nazari
	Ethiopia	4	4	D Singh, K Nazari, A Badebo
	Yemen	4	3	D Singh, K Nazari
	Tanzania	3	3	D Singh
	Uganda	3	3	D Singh
Southern Africa	South Africa, Zimbabwe	3	3	Z Pretorius, R Singh

¹ Scores from 0 to 5 for incidence and severity are based on scales described in Tables 2 and 3.