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International surveillance of wheat rust pathogens: progress and challenges

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Abstract Surveillance of wheat rust pathogens, including assessments of rust incidence and virulence characterization via either trap plots or race (pathotype) surveys, has provided information fundamental in formulating and adopting appropriate national and international policies, investments and strategies in plant protection, plant breeding, seed systems, and in rust pathogen research. Despite many successes from national and regional co-ordination of rust surveillance, few attempts were made to extend rust surveillance to international or even global levels. The Global Cereal Rust Monitoring System was established to address this deficiency. It is underpinned by an information platform that includes standardized protocols for methods and systems used in surveys, preliminary virulence testing, data, sample transmission and management at the field and national and global levels, and includes two web-based visualization tools. While considerable progress has been made towards a global system for monitoring variability in the wheat stem rust pathogen, and linking this to the threat posed by this pathogen to regional wheat production, some challenges remain, including ongoing commitment to support rust surveillance, and the ability to share and compare surveillance data.

Keywords Surveys · Pathotype · *Puccinia* · Race · *Triticum aestivum*

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Introduction

Following the demonstration of races (pathotypes) in the wheat stem rust pathogen in the early 1900s (Stakman and Piemeisel 1917), many countries established pathotype surveys, and/or networks of trap plots to assess the presence/absence of rusts and in some cases to provide information on the occurrence of virulence for specific resistance genes (e.g. Wellings et al. 2009). These rust surveillance efforts provide knowledge of the distribution and incidence of rust pathogens and pathotypes, and in regions where there is an understanding of deployed resistance genes, the potential impact of pathotypes on wheat production. This information is fundamental in formulating and adopting appropriate national and international policies, investments and strategies in plant protection, plant breeding, seed systems, and in rust pathogen research.

The genetic control of rusts has had considerable success in regions where pathotype surveys are closely integrated with pre-breeding and breeding efforts targeting rust resistance, and with post-release management of wheat cultivars (Park et al. 2009). This is particularly so in Australia, which along with New Zealand, is known to represent a single (Australasian) rust epidemiological zone (Luig 1983). Long-term monitoring of pathogenic variability in wheat rust pathogens including *Puccinia graminis* f. sp. *tritici* (*Pgt*) across the Australasian region has shown clearly rapid and unimpeded rust migration within this region, and provided arguably the best evidence supporting periodic long-distance intercontinental spread of wheat rust pathogens (Watson and de Sousa 1982; Wellings 2007). The geographic isolation of Australia from other wheat growing areas and its political uniformity permitted a nationally co-ordinated effort in rust control, led by the (currently) Australian Cereal Rust Control Program.

While regional co-ordination of wheat rust surveillance has functioned well in some cases, there have been few attempts to extend this to the international or even global levels. At the First International Congress of Plant Pathology in London, 1968, a resolution was passed recommending that global surveys of several plant pathogens, including *Pgt*, be undertaken to determine regional differences in virulence. Luig (1983) published the results of an international virulence gene survey for *Pgt* that involved 18 countries over 3 years, and interestingly identified the two initial problems in this work as being "the lack of an accepted up-to-date classification system dealing with variation in *Pgt* which was applicable throughout the world", and "our inability to introduce rust cultures from other continents into our laboratory…". Both of these problems, but particularly the second, continue to impede global co-ordination of cereal rust surveillance.

The global cereal rust monitoring system (GCRMS)

The existence of evidence supporting intercontinental spread of rust pathogens reinforces the need to couple efforts on improving understanding and capacity in pathotype analysis with a system that ensures rapid and free sharing of international information. Similar challenges were faced in establishing an international system for desert locust monitoring, which was successfully achieved by developing the Desert Locust Information Service (DLIS), located within the FAO's Emergency Prevention System for Transboundary Animal and Plant Pests and Diseases (EMPRES) (Hodson et al. 2009). The long-term success of DLIS and the ability of FAO to enter into dialogue with UN-member countries provided an excellent framework within which to develop an international rust surveillance system.

A comprehensive outline of the GCRMS was provided by Hodson et al. (2009). It is underpinned by an information platform that includes standardized protocols for methods and systems used in surveys, preliminary virulence testing, data, sample transmission and management at the field, national and global levels. The foundation of the entire system is the field surveys and associated sampling undertaken by a coordinated international network of rust surveillance teams. Field surveys are focused on commercial fields, with geo-referenced assessments of rust disease (stem rust, leaf rust, stripe rust) incidence being made every 20–30 km. Relatively standardized survey routes are used covering the main wheat growing regions of each country. Collected stem rust samples are sent under permit to two international specialist rust laboratories for pathotype analysis, but increasingly the expectation is that national laboratories will take over this role. A coordinated network of rust trap

nurseries is now being established by ICARDA and CIMMYT, which include an international stem rust trap nursery and an international "Ug99" stem rust trap nursery. These trap nurseries have been deployed in multiple locations in 24 countries and data integration with the GCRMS is in process. An important part of establishing these trap nurseries has been the generation and distribution of correct, pure seed of each nursery entry. The maintenance and distribution of nursery entries is undertaken by staff at ICARDA.

In order to provide access to stem rust information in a timely fashion, an information portal named Rust SPORE has been established (http://www.fao.org/agriculture/crops/rust/stem/en/). This web portal includes situation updates, country surveys, visualization tools e.g. RustMapper developed by CIMMYT (http://www.cimmyt.org/gis/RustMapper/index.htm or http://www.cimmyt.org/gis/rustmapper/RustMapper_Web.html), and a pathotype tracker. Integrated data management is achieved through a centralized database managed by Aarhus University, Denmark. The tools and database are updated on a routine basis, hence delivering the most recent information relating to stem rust in a timely manner.

Success of the GCRMS is dependent on the international exchange of quality information. To assist in this, four workshops involving training in cereal rust survey (including sampling) techniques were held (Syria, Central Asia, India and Egypt), at which GPS units were distributed to ensure geo-referencing of survey data. By the end of 2009, data from over 3,000 survey sites were incorporated into a centralized database, with 15 countries regularly submitting standardized field data. Stem rust pathotype summaries from 14 countries in 2008 provided an initial baseline dataset. These achievements represent significant progress towards the establishment of the foundations for an operational GCRMS. It is hoped that within 10 years, the GCRMS will provide information that is used routinely by national partners to guide decisions regarding control and management of stem rust in at least 30 countries, and that it will also be used by these countries to assess the effectiveness of stem rust mitigation efforts.

Forecasting is considered important as the GCRMS evolves and matures. Existing use of wind model information has already provided useful indications of likely migration routes for the "Ug99" lineage. Initial predictions made in 2005–2006 (Hodson et al. 2005; Singh et al. 2006) have largely been supported by subsequent field observations. Additional climate-based disease suitability models will be evaluated and included if shown to provide reliable value-added information at the national or regional scale. However, implementation of site-specific decision support tools to guide short-term chemical control of cereal rusts is considered unlikely in the near-future within the GCRMS.

Variability in rust pathogens and the "Ug99" lineage

The detection of virulences for the stem rust resistant wheat cultivars Eureka (*Sr6*), Gabo (*Sr11*), Spica (*Sr17*) and Festival (*Sr9b*) soon after their releases in Australia was attributed by Waterhouse (1952) and Watson (1958) to independent mutational changes in *Pgt* that resulted in the pathogen acquiring virulence for each resistance gene. Although the precise molecular basis of this process in *Pgt* remains unknown, it is generally accepted that mutation to virulence occurs in nature and that most new pathotypes identified in Australia over the past 80 years, for example, were generated by this process. This is consistent with experiments under controlled greenhouse conditions that demonstrated the acquisition of virulence for resistance genes following exposure to the chemical mutagen ethyl methane sulphonate (EMS) (Luig 1978). Long term studies of pathogenic variation in *Pgt* (90+ years; Watson 1981; Park 2007), *P. triticina* (90+ years; Park et al. 1995) and of *P. striiformis* f. sp. *tritici* (30+ years; Wellings 2007) provide the best evidence of clonal lineages comprising closely related pathotypes in wheat rust pathogen populations, derived from periodic incursions of exotic pathotypes acting as "founding ancestors" that in time, underwent sequential mutations in genes conferring pathogenicity.

Similar results are now being obtained with what has become known as the "Ug99" lineage, comprising at least seven pathotypes that differ for virulence to resistance genes *Sr21*, *Sr24*, *Sr31* and *Sr36* (Table 1; Fig. 1; Jin et al. 2008, 2009; Pretorius et al. 2010). Studies using microsatellite markers showed that most of these pathotypes have identical

Table 1 Wheat stem rust pathotypes identified within the "Ug99" lineage

Pathotype[a]	Standard race[b]	Differs from "Ug99" (TTKSK)		Known geographic distribution
		Virulence	Avirulence	
PTKSK	143		*Sr21*	Kenya, Ethiopia
PTKST	143	*Sr24*	*Sr21*	Kenya, South Africa
TTKSK	218	–	–	Uganda, Kenya, Ethiopia, Sudan, Yemen, Iran
TTKSF	218	–	*Sr31*	South Africa, Zimbabwe
TTKSP	218	*Sr24*	*Sr31*	South Africa
TTKST	218	*Sr24*	–	Kenya
TTTSK	218	*Sr36*	–	Kenya

[a] According to the North American system for pathotype designation in *P. graminis* f. sp. *tritici* (Jin et al. 2008)

[b] According to Stakman et al. (1962)

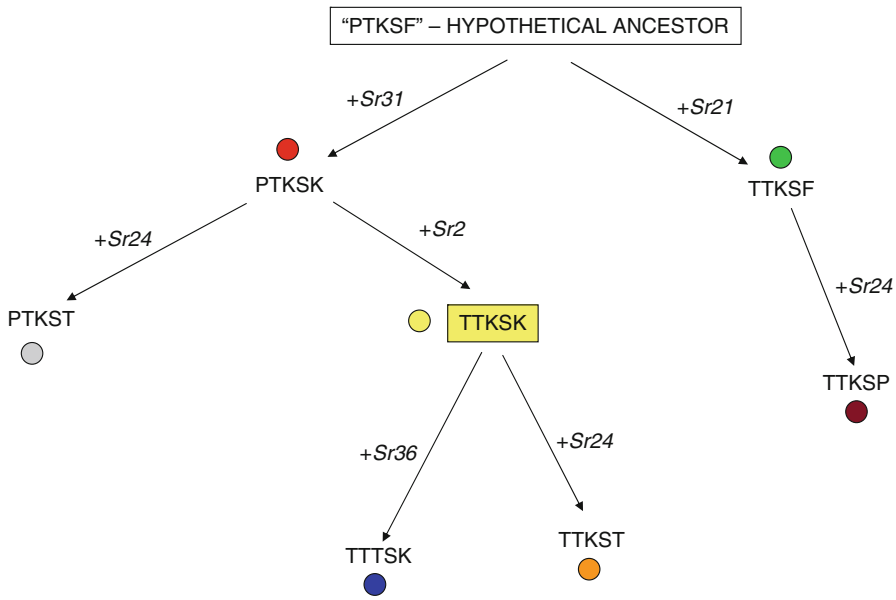

Fig. 1 Putative evolutionary pathways for the development of known pathotypes of *P. graminis* f. sp. *tritici* within the "Ug99" lineage

fingerprints, consistent with them having arisen from a common ancestor via single-step mutation (Pretorius et al. 2010). Significantly, surveys in Turkey, Egypt, Pakistan and India over recent years have failed to detect any of these pathotypes, and three *Pgt* isolates collected from Pakistan in 2009 were clearly shown to differ from pathotype TTKSK in their SSR fingerprint (Karaoglu and Park unpublished) and virulence profile (Fetch unpublished). Regular and ongoing monitoring of *Pgt* pathotypes is considered to be of vital importance.

Wheat has been grown in Kenya since the beginning of the twentieth Century (Martens 1975), and although all three rusts caused considerable damage to susceptible cultivars, stem rust was identified as historically the main threat by Luig (1983). Pathotype identification in *Pgt* in Kenya began in 1928 (Luig 1983), with detailed published accounts available of analyses made in 1968 (Green et al. 1970) and 1969 and 1970 (Harder et al. 1972). Martens (1975) examined virulence dynamics in *Pgt* in Kenya over the 14 year period 1957–1971, and concluded that "virulence in the pathogen, relative to the host, has not changed as rapidly as the literature suggests".

"Ug99" is avirulent for *Sr28* (Singh et al. 2008), present in the stem rust differential Kota, which also carries *Sr7b* and *Sr16*. Virulence analyses of isolates of *Pgt* from many countries by Huerta-Espino (1992) reported significant levels of avirulence for *Sr28*

among isolates from Ethiopia and Nepal, but in other regions, virulence for this gene was common. Using the nomenclature of Stakman et al. (1962), pathotypes TTKSK, TTKSF, TTKSP, TTKST and TTTSK all key out to standard race 218, and pathotypes PTKSK and PTKST as standard race 143. Harder et al. (1972) reported five races as avirulent on Kota, one of which was standard race 143 (aka EA17) isolated on one occasion from Tanzania in 1970. Although it is impossible to know if this or other pathotypes identified in this work are the progenitors of "Ug99", it is plausible that the "Ug99" lineage has been present in eastern Africa since at least the early 1970s and that pathotype TTKSK was derived via sequential acquisition of virulence over the intervening years. However, while previous studies suggested that barberry was non-functional in the life-cycle of *Pgt* in Kenya (Guthrie 1966, cited by Green et al. 1970), recent reports of aecial infections on this host in Kenya (Jin unpublished) could mean that sexual recombination in *Pgt* may occur there. Interestingly, reports of aecial infections of barberry have also been made from New Zealand (Waipara et al. 2005), and Azerbaijan (Nazari unpublished), Georgia (Sikharulidze unpublished), India (Prashar unpublished), Iran (Nazari unpublished), Kazhakstan (Park unpublished), Nepal (Thapa pers. comm.) and Turkey (Mert pers. comm.). These observations suggest that sexual recombination within *P. graminis* may not be rare; however, further work is needed to determine the pathogen species, or *forma specialis*, present on barberry in these countries, especially in view of the recent finding that barberry is also the alternate host of *P. striiformis* (Jin et al. 2010).

Challenges in global rust pathogen surveillance

Despite the progress that has been made in establishing the GCRMS to date, many challenges remain. The incidence of rust pathogens varies between years, making it difficult to sustain funding for ongoing surveillance. A global decline in the incidence of stem rust over the past 40 years, attributable at least in part to resistance breeding and the widespread deployment of the resistance gene *Sr31*, led to many countries abandoning stem rust surveillance and an alarming reduction in the global skill base in rust pathotype analysis and general rust pathology. The lack of capacity and resources to undertake rust surveillance and monitoring are a major challenge being faced in establishing the GCRMS, as are barriers limiting the exchange and free-flow of surveillance information and rust isolates. Significant initial investments are considered necessary to replace the lost capacity to undertake rust surveillance and monitoring, but subsequent maintenance and operational costs are likely to be low in comparison to the costs of controlling serious rust epidemics. The huge costs incurred by the Australian wheat industry resulting from an incursion of a single exotic stripe rust isolate in 2002 illustrate the impact such events can have. In this case, annual chemical control from 2003 alone was estimated in the range AUD$ 40–90 million (Wellings 2007).

Building capacity for in-country pathotype analysis

Biosecurity concerns have and will continue to make the exchange of rust isolates between countries more difficult, meaning that comprehensive pathotype analyses will in most cases require building in-country capacity. Declining support to agriculture has left many, but not all, national systems without the resources or capacity to undertake even cereal rust field surveys on a regular basis, let alone implement pathotype analysis. A final area of concern relates to the in-country/regional capacity and the will to undertake reliable and routine pathotype analysis. Considerable progress has been made in some countries, but a sustained effort over a long period is required to achieve the overall goal. Developing in-country capacity for rust pathotype analysis at its simplest level involves equipping scientists with the required skills and ensuring the provision of adequate infrastructure. Establishing a Global Reference Center for stem rust, as has already been done for stripe rust (Høvmoller et al. 2009), will overcome these problems to some extent, but in-country capacity for pathotype analysis will still be needed because it is expected that such a center would not be able to serve all countries in which rusts are an important constraint to wheat production. Developing capacity for in-country pathotype analysis is challenging because of a lack of commitment by some countries both in providing ongoing infrastructure and personnel (particularly problematic when rust incidence is low), the

time taken to train scientists in pathotype analysis (at least 3 months), and the promotion or movement of trained personnel into other areas. Successful ongoing pathotype analysis is usually typified by long-term commitment of the scientists undertaking such research. For example, in Australia and North America some scientists have been doing this work for more than 20 years.

Sharing information

The GCRMS can only be successful with broad agreement on the timely sharing of information on the incidence of rusts and the pathotypes present. Political sensitivity, especially with respect to the "Ug99" lineage of *Pgt*, is one factor limiting the free exchange of information. The role of FAO as an international neutral broker with the ability to assist member countries over potentially sensitive rust issues is considered to be vital, and advances have already been made in this regard.

Comparing information

The appearance of *Yr9* virulence, initially in east Africa and then progressively throughout Asia in the 1990 s, suggests that much of this region comprises a single rust epidemiological unit (Singh et al. 2006). However, very little information concerning the *Pst* pathotype(s) present in the region at that time is available and as convincing as the hypothesis of migration of a single *Yr9*-virulent pathotype may seem, supporting scientific evidence is lacking. Where information on pathotypes actually present is available, disparities in the differential genotypes, and to a lesser extent, the pathotype nomenclature systems used by laboratories undertaking pathotype analyses, have made precise comparisons of pathogen variability between regions difficult. For example, the origins of 11 exotic wheat rust isolates identified in Australia since 1925 are largely unknown (Table 2), as are most entry pathways. These knowledge gaps reinforce the importance of obtaining and sharing information that can be compared if long-distance spread of rust pathotypes is to be tracked. It must be stressed, however, that two isolates of a given pathotype may not in fact be the same genotype. For example, three isolates of *Pgt* pathotype 21–0 isolated from Australia in 1954, 1994 and 2006, were shown to have different SSR fingerprints (Zhang, Park and Karaoglu unpublished).

Despite inconsistencies in the differential genotypes being used by laboratories involved in pathotype analyses, the data that emerged from recent stem rust surveillance in east Africa and beyond has already provided valuable information for stem rust control efforts in identifying countries where members of the "Ug99" lineage are present, as well as providing useful insight into migration of rust pathogens. The utility of DNA-based marker systems such as SSRs in confirming the genetic relatedness of *Pgt* isolates has also been clearly established in this process (e.g. Visser et al. 2009). A uniform set of differential genotypes and one system for naming pathotypes would add significant precision to international efforts to track rust migration. The

Table 2 Documented incursions of exotic isolates of wheat rust pathogens into Australia from 1925 to 2005

Disease/Pathogen	Year detected	Possible origin	Reference
1. Wheat stem rust/*Puccinia graminis*	1925	?	Waterhouse (1952)
2. Wheat stem rust/*P. graminis*	1945	Africa?	Luig (1977)
3. Wheat stem rust/*P. graminis*	1969	Africa?	Watson and de Sousa (1982)
4. Wheat stem rust/*P. graminis*	1969	Africa?	Watson and de Sousa (1982)
5. Wheat stripe rust/*P. striiformis*	1979	France?	Wellings and McIntosh (1990)
6. Wheat leaf rust/*P. triticina*	1981	New Zealand	Luig et al. (1985)
7. Wheat leaf rust/*P. triticina*	1984	?	Park et al. (1995)
8. Wheat leaf rust/*P. triticina*	1996	New Zealand	Park (unpublished)
9. Wheat stripe rust/*P. striiformis*	2002	USA?	Wellings et al. (2003)
10. Wheat leaf rust/*P. triticina*	2004	?	Park (unpublished)
11. Wheat leaf rust/*P. triticina*	2005	?	Park (unpublished)

difficulties in achieving this were addressed by several rust workers (e.g. McIntosh et al. 1995; Fetch et al. 2009; Pretorius and Nazari 2009). Without a standard set of differential genotypes and agreement on analytical procedures, it is not possible to have a single pathotype nomenclature system.

Differential genotypes For pathotype information to be relevant to local wheat breeding programs, the differential genotypes used must include lines carrying deployed resistance genes, which are often different between regions. Because of this, and the impracticality of including all known resistance genes in a differential set, there will always be regional differences in the genotypes used to fully characterise the pathogenicity of rust isolates. McIntosh et al. (1995) proposed the use of an internationally agreed set of differentials for use in the international exchange of information, to which researchers could add local differential testers. This issue was further addressed by Fetch et al. (2009), who proposed adopting 20 standard differential genotypes, which carry the 20 stem rust resistance genes currently used in North America to characterise pathotypes of *Pgt*. If agreement is reached on a core set of international genotypes for pathotype identification, ensuring the purity of each will be of paramount importance.

Pathotype nomenclature Providing a simple name for a new rust pathotype that conveys something of its features is important in getting a clear message across to the wider community. For example, in 1968, influenza type A strain H3N2 killed about 40,000 people world-wide. The virus was commonly referred to as the "Hong Kong flu", in the same way as we have referred to pathotype TTKSK as "Ug99". The latter term has been used widely in the press, probably because it is easily remembered and conveys the origin and year of description of rust pathotype TTKSK. Similarly in Australia, new pathotypes have at times been named after the cultivar first affected, or most affected, to assist in extension. For example, a new pathotype of stripe rust with virulence on triticale, first detected in 2008, was called the "Jackie" pathotype because of its virulence on cv. "Jackie" (Wellings unpublished). The identity of the resistance gene(s) in "Jackie" for which this pathotype is virulent is not known.

In addition to proposing 20 standard international differential testers, Fetch et al. (2009) suggested adopting the North American system of naming pathotypes of *Pgt*, which uses alpha characters and was originally proposed by Roelfs and Martens (1988). An advantage of this system is that it condenses a great deal of information into a concise "code", as does the octal system originally proposed by Gilmour (1973). The brevity of both of these systems, however, make it very difficult to infer evolutionary relationships between pathotypes, and impossible to convey information about features such as intermediate levels of virulence (Watson and Luig 1968). Should the North American code system be accepted in international exchange of information on rust pathotypes, virulence/avirulence formulae should also be provided to allow firstly communication of virulence for resistance genes that may only be present in local differential testers, and secondly in simplifying the ability of non-specialists to assess the threat of pathotypes to commercial wheat cultivars.

Making it work—surveillance and rust control

Where pathotype surveys have been conducted in a robust and relevant way, they have provided both information and pathogen isolates that have underpinned rust control efforts, from gene discovery to post-release management of resistance resources. Information generated by pathotype surveys has been used to devise breeding strategies, indicate the most relevant isolates for use in screening and breeding, define the distribution of virulence and virulence combinations, allow predictions of the effectiveness/ineffectiveness of resistance genes, and issue advance warning to growers by identifying new pathotypes (both locally evolved and introduced) before they reach levels likely to cause significant economic damage.

Although constrained to some extent by a lack of markers, particularly those not subject to natural selection, surveys have also provided considerable insight into the dynamics of rust pathogen populations, including the evolution and maintenance of virulence, and migration pathways, together with periodic long-distance migration events. Reaching global agreement on the composition of a core set of differential testers for stem rust should make it easier to track rust migration over large distances, improving our understanding of how these pathogens move

around. It should be noted, however, that two isolates identified as the same pathotype may in fact be different genotypes, and because of this, DNA-based genome profiling of isolates will be an important part of global rust surveillance. Combined rigorous DNA fingerprinting coupled to virulence phenotyping has already proved useful in the detection of global dispersal events for *Pst* (Høvmoller et al. 2008).

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