CSIRO PUBLISHING
www.publish.csiro.au/journals/ajar *Australian Journal of Agricultural Research*, 2007, **58**, 854–857

Sustained genetic control of wheat rust diseases in north-eastern Australia*

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Abstract. Control of wheat rusts in north-eastern Australia has been based on resistance breeding since the early 1920s. It has been an enduring journey of discovery, disappointment, and achievement, which has culminated in a pool of knowledge and expertise upon which today's plant breeders can efficiently target durable resistance to the major rust diseases. This paper outlines significant advances in genetic control of rusts in the region, with particular emphasis on the invaluable role played by the University of Sydney rust control program and its influence on wheat breeding in the region and throughout Australia.

The region

The wheat-growing area of north-eastern Australia occurs mostly in the subtropics to the west of the Great Dividing Range from ~32°S latitude and extends north beyond the Tropic of Capricorn to around 22°S. It embraces northern New South Wales and Queensland, and is characterised by fertile clay soils and summer-dominant rainfall. Spring storms may occur and usher in periods of high humidity when wheat crops are filling grain and receptive to rusts. In addition, summer rains support the growth of volunteer wheat plants and grass hosts between seasons, which may provide year-round, local inoculum. The area has a history of stem rust epidemics since white settlement, yet there has not been a similar significant event for over 20 years.

Introduction

It appears that wheat rusts were present in Australia before white settlement (Waterhouse 1939). It is likely that the diseases co-existed on indigenous grass species *Elymus scaber* (Labill.) A. Love and *Hordeum murinum* L. before bread wheat was ever introduced into the country. In a new colony, production of food was essential and wheat cropping a priority; however, crops often failed. The varieties were poorly adapted to their new environment, being long-season wheats, and obviously lacked adequate rust resistance. The first recorded rust epidemic in wheat in Australia was in 1795 when it was reported that 'Cape wheat was not worth the labour of harvesting through blight and rust' (Waterhouse 1929).

Despite the continual threat of rust, wheat growing expanded with settlement and it seemed that growers were prepared to continue growing the crop knowing full well that it could be destroyed by the rust menace. Serious epidemics occurred on average one in every 6 years throughout the 1800s. The gravity of the rust problem through that period is demonstrated by the Queensland Government's response to the epidemic of 1879. In the following year, the Legislative Assembly offered a reward of £1000 for the discovery of a cure for rust in wheat (Rees 1988). It appears that the reward was never claimed and no real progress in rust control was made until Farrer's entry into wheat breeding and selection in the late 1800s.

Genetic control

As early as 1882, Farrer recognised the potential to develop varieties that would satisfactorily resist rust (Farrer 1898). In his own words, '. . . whenever well-directed attention is given to the improvement of a domesticated plant in any quality in which it is variable, that quality can be increased and developed to an indefinite extent. I saw that the wheat plant varied in the amount of resistance it offered to the different rust parasites and that it was for that reason capable of being improved for that quality'.

Although Farrer did not achieve success through developing rust resistance *per se*, he did develop varieties that were earlier maturing and thereby often escaped the warm, moist conditions often present in late spring during grain filling, conditions so favourable for rust development. It is interesting to note that Farrer considered it was only worthwhile to select for the summer rust resistance (stem rust *Puccinia graminis* f. sp. *tritici*), although spring rust (leaf rust *Puccinia triticina*) was common, and this opinion drove rust resistance breeding for several decades.

Rust epidemics continued to occur and it was estimated that the losses to rust in the epidemic of 1916 were in the order of £2 000 000. Furthermore, Waterhouse (1936) estimated that rusts in NSW had cost an average of £250 000/year for the past 20 years.

*This paper is part of 'Global Landscapes in Cereal Rust Control', see *Aust. J. Agric. Res*. Vol. 58, no. 6.

10.1071/AR07122 0004-9409/07/090854

A milestone in the genetic control of rusts in wheat was achieved with the appointment of W. L. Waterhouse as the Walter and Elisa Hall Research Fellow in 1918 and later (1921) to the position of Lecturer and Demonstrator in Plant Pathology, Genetics and Plant Breeding and Agricultural Botany at the University of Sydney (Watson and Frankel 1972). Waterhouse appreciated that for success in breeding for resistance, it was necessary to study both the genetics of the host and the genetics of the pathogen. He had established strong links with the Department of Plant Pathology at the University of Minnesota, St Paul, and with Dr E. C. Stakman and M. N. Levine who were involved in rust research there. Driven by his own enthusiasm and the need for rust control, a scientific approach to genetic control of wheat rusts in north-eastern Australia began.

One of the first tasks undertaken by Waterhouse was to study the Australian population of *Puccinia graminis tritici*. He concluded that there were 6 physiologic forms of *P.g. tritici* (Luig 1985), which led him to report that 'the state of specialisation of the wheat stem rust in Australia is remarkably simple and stable. The position is one which makes the outlook for the plant breeder particularly hopeful' (Waterhouse 1939).

Armed with the knowledge of virulences in the Australian stem rust population, Waterhouse developed a line that combined resistances from 2 of Farrer's wheats (Watson and Butler 1984). The variety Euston was resistant to all strains of stem rust at that time; yet with the exotic incursion of race 126-5,6,7,11 in 1925, the variety was rendered susceptible. The outlook for the plant breeder had suddenly become less hopeful.

With the arrival of race 126, new sources of resistance had to be found. These were identified in a diversity of sources from overseas, which had been introduced by the N.S.W. Department of Agriculture: varieties of *Triticum durum*, bread wheats from Kenya, and Webster, Hope, and H-44 from North America. This germplasm was to provide the basis of rust-resistant varieties for northern Australia for the next 30 years. From this material, the stem rust resistance genes *Sr6*, *Sr9b*, *Sr11*, *Sr13, Sr17*, and *Sr30* were identified. Each of these was used individually to develop new varieties for the region.

The wisdom of this approach to resistance breeding was challenged by the breakdown of *Sr6* resistance in the variety Eureka in 1942. What had been a very effective resistance gene was overcome by a new variant of the pathogen. Race 126-5,6,7,11 had undergone a single-step mutation to 126-1, 5,6,7,11. This ushered in a period of 'bust, boom, and bust' wheat breeding in Australia (Stanton 1984) between 1938 and 1964 (Zwer *et al*. 1992).

Breeders were releasing varieties protected by a single gene only to find that the resistance was being overcome rapidly as the variety was grown on a broader scale. Often, resistances broke down within 5 years of release (*Sr6*, *Sr11*, *Sr9b*), and the variety Mengavi *Sr36* was rusted in its first year of commercial production. As Zwer *et al*. reported, it was a period of release of cultivars with single resistance genes followed by the identification and increase in frequencies of pathotypes with matching virulence genes. While it might seem that the use of single-gene resistance breeding was an abject failure, the approach provided invaluable knowledge of the pathogen's ability to acquire new virulences through step-wise mutation.

It was clear that this strategy too could not provide effective rust control in the region. A more enduring solution was required. The use of resistance gene combinations or broad-base resistance was proposed by Watson and Singh (1952) and evaluated by Luig and Watson (1970). The apparent success of this approach has guided the Sydney University rust program to the present day. The new strategy resulted in the release of varieties with a suite of resistance gene combinations that provided longer lasting control of the disease. Most of the gene combinations used included genes that had been defeated when exposed alone in superseded varieties, e.g. the variety Gamut combined resistance genes *Sr6*, *Sr9b*, *Sr11*, and *SrGt*. Gamut maintained resistance for 10 years even though all genes but *SrGt* had been defeated in previously released varieties. Similarly, the Australian variety Mendos (*Sr7a*, *Sr11*, *Sr17*, *Sr36*) proved highly resistant in North America despite the presence of virulences for individual genes in the resistance combination, and Timgalen (*Sr5*, *Sr6*, *Sr8a*, *Sr36*) maintained resistance to stem rust in Australia for almost 20 years.

Luig (1983) commented 'Breeding for complex resistance and employing genes that are individually of little value will produce genotypes capable of displaying world-wide resistance'. Unfortunately, the value of the combinations cannot be predicted (Watson and Butler 1984) and the development of gene combinations has to be supported by intensive screening with a wide spectrum of rust virulences before their use in a breeding program can be supported.

Almost 60 years after Waterhouse made his first crosses for rust resistance, the sustained approach to genetic control of stem rust in the region was proving effective. Yield losses through this period of resistance breeding were significantly reduced. Varieties were maintaining rust resistance for longer, which was a product of improved resistances *per se* supported by widespread adoption of practices that maximized the duration of effectiveness of those resistances.

The Sydney University rust program had gained great credibility through their achievements in rust control. Personnel had developed a strong rapport with the grower community and wheat breeders within the region, so that recommendations emanating from the program enjoyed a ready uptake. This resulted in the rapid exit of susceptible varieties from cultivation, promoted the minimisation of over-seasoning opportunities for the pathogen, and gained collective agreement that only varieties resistant to stem rust should be released in the region. The net effect was a marked reduction in inoculum levels, which reduced the number of mutational events contributing further to the longevity of resistances.

The success of the program was highlighted during the rust epidemics in 1973–74. In that year, losses estimated at $300 million occurred in southern Australia, while in the north-eastern region, no serious damage occurred despite favourable environmental conditions. The benefits of genetic control of rusts were demonstrated to the nation.

The focus of the Sydney University program up to this time had been north-eastern Australia, and the success there prompted industry leaders to call for expansion of the program

to include other states/regions of Australia. This manifested in the establishment of the National Rust Control Program in 1975. The national program was structured into 3 main components:

- pathotype surveys and pathogenic variability;
- host variability, sources, and genetics of resistance;
- germplasm screening and enhancement (McIntosh 2007).

What had been achieved in the north was extended to rust workers in other states with the addition of a back-cross program that incorporated desirable resistance genes into adapted germplasm for use as parents or for selection as new cultivars. What was established as the National Rust Control Program is now the Australian Cereal Rust Control Program, which continues to provide invaluable service to breeders and growers of wheat, barley, and oats throughout Australia.

It seemed that wheat growing in north-eastern Australia was no longer under threat from stem rust and resistance could offer long-term control of the disease. However, one instance in recent history served to remind industry that resistance alone was not enough to protect crops from attack. In 1976, the resistance in cv. Oxley (*Sr5*, *Sr6*, *Sr8a*, *Sr12*) was overcome by the arrival of a new pathotype 343-1,2,3,5,6. From a rust-control perspective, this should have resulted in the withdrawal of Oxley from cultivation; yet the variety was particularly well suited to some cropping areas in Queensland and, the lack of a suitable replacement, saw the variety recommended for a further 6 years without the occurrence of a significant epidemic. However, a sequence of favourable seasons in the early 1980s saw increasing amounts of stem rust in Oxley crops. In 1983, this culminated in widespread epidemics in Queensland caused by the Oxley pathotype (343-1,2,3,5,6). Some severe yield losses occurred; yet fortunately, less than 10% of the area in NE Australia was sown to Oxley. Of much greater consequence was the development of a single-step mutant during this epidemic, of a pathotype (343-1,2,3,4,5,6) with virulence for *Sr36* (Luig 1984). This gene had remained effective in the region for 24 years and was still being used widely in breeding programs.

Virulence for *Sr36* rendered the popular variety Cook susceptible. Cook occupied 20% of the area sown in the region in 1984 and, to curb the development of future epidemics, industry agreed that the variety must be withdrawn from cultivation. So effective was the response from growers that in the following season the area sown to Cook declined to 11% and the variety had virtually disappeared from cultivation the next year. The removal of Cook (and other varieties protected only by *Sr36*) from cultivation saw a corresponding decline of the new pathotype in the population. This has allowed the gene to be recycled and incorporated in modern gene combinations to good effect.

This experience highlighted several salient points, namely:

- the risk of growing susceptible varieties in the region;
- the vulnerability of single-gene resistance (*Sr36* alone was protecting Cook);
- the ready acceptance by growers of industry advice.

The event was a curt reminder. If durable resistance was to be achieved, it was obvious that targetted resistance breeding must be supported by measures to minimise inoculum levels. Over 95% of the area is now sown to varieties resistant to stem rust.

Effective gene combinations continue to be the cornerstone of host resistance in the region and there are several genes that feature in several of those combinations. *Sr2*, *Sr9g*, *Sr24*, *Sr26*, *Sr30*, *Sr36*, and *Sr38* are the main genes currently in use (H. S. Bariana, pers. comm.) All but *Sr30* have been derived from alien sources (McIntosh *et al*. 1995). While some of these resistances were first deployed in the region over 40 years ago, they continue to provide useful resistance when used alone and very effective resistance in combinations, e.g. *Sr2*, *Sr26*.

Discussion has focussed on the genetic control of *P.g. tritici* with no reference to the other problem rusts in the region. Stem rust was the priority and deservedly attracted the lion's share of attention. It threatened the sustainability of wheat production in the region. Through the program's achievements in genetic control of stem rust, a template was set for future work with other cereal rusts. It clearly demonstrated the success of a relentless approach to resistance breeding supported by sound epidemiological principles to minimise inoculum within the region. The wheat/stem rust system in north-eastern Australia is currently very stable, which has enabled increased efforts in developing improved resistance to leaf and stripe rusts. The mould has been cast for successful genetic control and it is reasonable to expect that similar gains can be made for these diseases in a much shorter time-frame. It is not the authors' intention to document resistances being used to combat these other rusts because they are adequately covered by others (Bariana *et al*. 2007; Wellings 2007).

Due recognition must be given to the Sydney University program in achieving genetic control of rusts in north-eastern Australia. The battle against rusts was waged by learned people who applied established and innovative scientific methods to study both the pathogen and the host. When approaches to resistance breeding appeared to fail, workers were able to devise new strategies, often based on knowledge generated from within the program, to combat the rust. They recognised the importance of industry support and established strong relationships with breeders and leading growers in the region. The program has worked closely with rust laboratories in the USA, Canada, Mexico, South Africa, and Germany and these networks continue to expand and develop.

The persistence of staff in pursuing host resistance for control cannot be overstated. The rapid breakdown of resistances that occurred in the formative years of the program and later during the boom and bust years must have been disheartening and questioned the validity of the methods being adopted. However, staff was able to respond to these setbacks by adopting new strategies that offered a higher probability of success and matching these with an analysis of the pathogen population to understand the effects and implications of the strategies adopted.

Conclusions

The success in controlling stem rust resistance in north-eastern Australia was attributed by Watson (1981) to 3 lines of approach:

- parents were selected on the basis of the diversity of their resistance genes and for a broad spectrum of effectiveness against many rust strains;

- use of the gene *Sr2* conferring durable resistance;
- the use of alien species as sources of rust resistance genes.

The use of broad-base resistance has further enhanced rust control in the north. Luig reported that the results of his International Gene Virulence Survey unequivocally demonstrated the value of complex resistances, and recent experience in Australia would support this claim. While these practices have carried industry to a position where stem rust is not currently a serious threat, Watson warned that continuous genetic research on both the host and the fungus must be carried out to remain successful.

The sustained genetic control of wheat rusts in north-eastern Australia has given security to the industry in the region. It has also provided extensive knowledge of the pathogen, the host, and the genetics controlling resistance. What has been achieved through sustained genetic control of wheat rusts in the region has been a triumph of global significance for plant pathology and plant breeding.

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Manuscript received 26 March 2007, accepted 8 June 2007