THE ROLE OF WILD AND CULTIVATED GRASSES IN THE HYBRIDIZATION OF FORMAE SPECIALES OF *PUCCINIA GRAMINIS*

By N. H. Luig* and I. A. Watson*

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Abstract

Although *Berberis vulgaris*, the alternate host of *Puccinia graminis*, occurs rarely on the Australian mainland, the present studies show that native and cultivated grasses can play an effective part in the evolution of new strains of this pathogen. *Agropyron scabrum* and *Hordeum leporinum* appear to be important as sources of somatic hybrids involving *P. graminis* f. sp. *tritici* and *P. graminis* f. sp. *secalis*. On the Darling Downs of Queensland the former grass species was found to be infected by more than 25 different hybrid strains. The principles governing hybridization between these two formae speciales of *P. graminis* may also be applicable to corresponding events between other rusrs.

I. Introduction

It is now well established that somatic hybridization is a process by which new strains of wheat stem rust, *Puccinia graminis* Pers. f. sp. *tritici* Eriks. & E. Henn., can arise (Nelson 1956; Watson 1957; Watson and Luig 1958*b*). It has been shown further that this process takes place between formae speciales of *P. graminis*, viz. *tritici* and *secalis* (Watson and Luig 1959). Thus, there exists the possibility for new combinations of genes for virulence in the rust population. In order for this to happen, a congenial medium must be available for the growth of *P. graminis tritici* and *P. graminis* f. sp. *secalis* Eriks. & E. Henn. This paper presents data which indicate the part played by wild and cultivated grasses in the origin, selection, and perpetuation of hybrid strains of stem rust.

Waterhouse (1929) reported that several grass species, including *Hordeum murinum* L., were susceptible to two forms of *P. graminis*, viz. wheat stem rust and oat rust, *P. graminis* f. sp. *avenae* Eriks. & E. Henn. At this time no other formae speciales of *P. graminis* had been found by him in Australia. Later he reported (1951) the presence of stem rust of rye grass, *P. graminis* f. sp. *lolii* Guyot & Massenot, and in 1957 the appearance of rye stem rust, *P. graminis secalis*, at Mt. Kosciusko. He thought that this region may play an important part in the origin and spread of new strains of stem rust.

In 1958, rye stem rust was found to be widely distributed in Tasmania, especially on *Agropyron repens* L. (Watson and Luig 1958*a*). Barberry bushes (*Berberis vulgaris* L.) in the vicinity of *A. repens* frequently carried the sexual stage of this pathogen. Since wheat stem rust also occurs in Tasmania, sexual hybridization on the barberry between this rust originating on wheat cultivars and rye stem rust from *A. repens* was considered a strong possibility (Watson and Luig 1958*a*). Both *A. repens* and *B. vulgaris*, however, occur only rarely on the Australian mainland.

* Department of Agricultural Botany, University of Sydney, Sydney, N.S.W. 2006.

II. Materials and Methods

Samples of infected rough wheat grass, *Agropyron scabrum* Beauv., from Queensland were mainly received from Mr. R. G. Rees, Queensland Wheat Research Institute, Toowoomba. Mr. R. J. Flynn, Agronomist, Department of Agriculture, Albury, N.S.W., also contributed many samples of rust-infected grasses. Collections in northern and central New South Wales and in Tasmania were made by one of us (I.A.W.). Other samples were received from several collectors.

Preliminary tests of rust samples from *A. scabrum* were made on the wheat stocks Little Club, W2691,* and Yalta and on Black Winter rye (B.W.R.). In most instances, virulence on B.W.R. and infection types "X", "2 =", and "0" (Watson and Luig 1958*a*) on W2691, Little Club, and Yalta (*Sr11*) respectively, indicated that the collection was rye stem rust. Such cultures were discarded without further testing. On the other hand, avirulence on B.W.R., "2−" or "3+" infection types on Yalta, and virulence on W2691 and Little Club indicated that wheat stem rust was involved. Subsequently, such cultures were tested and the strain involved was determined according to the scheme outlined by Watson and Luig (1966).

With the remaining collections from *A. scabrum*, B.W.R. was heterogeneous (in nearly all cases, the majority of B.W.R. seedlings exhibited intermediate "2−", "X", and "2+" infection types), Yalta was resistant ("0", "0;" infection types), while W2691 and Little Club were less resistant than to cultures of *P. graminis secalis*. Cultures of this group, hereafter referred to as "scabrum rust", were subjected to further tests in which the main studies were on 23 testers, the majority of which were chosen because of their differentiating abilities shown in earlier studies involving hybrid cultures with many unusual genes for avirulence (Watson and Luig 1962*a*, 1962*b*). The following wheat stocks were used: (1) **standard differentials**—Little Club W1, Marquis W2 (*Sr7b*), Einkorn W292, Vernal Emmer W11 ($Srdv_1$); (2) **supplementary differentials**—Yalta W1373 (*Sr11*), Eureka W1325 (*Sr6*), Norka W578 (*Sr15*); (3) **other testers**—Brevit W972, Loros W974, Thew W203 (*Sr15*), Federation W107, Koala W1577, Transfer W2382, Mona W1168, Vernstein W3196 ($Srdv_1$), Purple Straw W1816 (*Sr18*), Line SA (*Sr11*), Pusa W801, Soft Baart W628, Morocco W1103, and W2691. The two ryes were B.W.R., and line 5, a B.W.R. selection susceptible to certain strains of *P. graminis tritici*.

Samples collected from grasses other than *A. scabrum*, e.g. *Hordeum leporinum* Link (barley grass), *Dactylis glomerata* L., *Lolium perenne* L., *A. repens*, *Phalaris tuberosa* L., and *Deyeuxia quadriseta* Benth., were first tested on wheat (Little Club), rye (B.W.R.), oats (Algerian), barley B.240), *Lolium temulentum* L., and *D. glomerata*.

III. Results

(*a*) *Studies on Probable Hybrids between* P. graminis tritici *and* P. graminis secalis

In 1963 we observed a strip of heavily rust-infected *A. scabrum* at St. Ruth, Qld. On either side the wheat cultivars Spica and Mengavi were free of rust. The observation was surprising as this grass was known to be a frequent source of wheat stem rust, and the prevalent strains at that time were virulent on either Spica or Mengavi. Consequently, the rust on *A. scabrum* was sampled and investigated in detail. The majority of the wheat cultivars tested, including those which possessed no known genes for resistance to wheat stem rust, were resistant to this rust. Of the 12 standard differentials, Little Club was intermediate ("3−" infection type), Marquis gave a mesothetic ("X") reaction, and the other 10 were highly resistant. This first unusual culture from *A. scabrum* was designated strain 71–O of wheat stem rust; however, on many wheat cultivars it resembled the somatic hybrids obtained earlier from mixtures of *P. graminis secalis* and *P. graminis tritici* (Watson and Luig 1959).

Since 1967, 107 rust cultures grouped during preliminary tests as scabrum rust by the methods described above, were tested on the 21 wheat and 2 rye cultivars

* W numbers refer to the Sydney University Wheat Accession Register.

TABLE 1

INFECTION TYPES PRODUCED ON 21 WHEATS AND ON BLACK WINTER RYE BY STRAINS OF *PUCCINIA GRAMINIS*

Accession numbers given in parenthesis. S, showing segregation for susceptibility (i.e. approximately 60% of the plants give 2, 2+, 3, or 3+ reaction); MS, markedly susceptible (i.e. approximately 90% of the plants give 2, 2+, 3, or 3+ reaction); R, resistant

Host	Strains of "scabrum" rust								Wheat S.R. (21—2Y)	Somatic hybrid (NL)	Rye S.R. (69090)
	A (67149)	B (68232)	C (67344)	D (67347)	E (67177)	F (69096)	G (69346)	H (69106)			
Little Club	; 2 =	3,3+	2 = 2−	2 =	2 =	2	2	2	3+	2−	2 =
Marquis	;	; 1	X	;	2−, 3	; 2 =	X	2 =	3+	2 =	0;
Einkorn	;	;	;	;	;	;	;	;	; 1	;	;
Vernal Emmer	;	; 2 =	;	0 ;	3	;	;	;	; 2 =	;	;
Yalta	;	;	0;	0;	;	; 1	0;	X−	3+	X−	0;
Eureka	;	X−	; 2−	X+	X =	2+3−	; 1−	X	X+	X+	2X =
Norka	; 1	X	;	X+	;	X+	; 1+	; 1	X+3	2+3	0;
Brevit	3	X+	2 = 2−	3	2	;	2 =	; 1++	3+	;	2 =
Loros	; 2 =	X+	;	;	2−	; 2 =	; 2 =	2 =	3+	;	;
Thew	;	;	0;	;	; 1 =	;	X	;	X+	;	0;
Federation	; 2−	2+,3[c]	3	; 2−	3[c]	2+3−	3[c]	2	3+	2+3	; 1 =
Transfer	; 2 =	2+3	3[c]	; 2 =	1+	2−	3−3	2 =	3+	2 =	; 2 =
Koala	X	X+3	2+3−	; 1−	2−3−	2+3−	2 =	X+3−	3+	2+3−	; 2 =
Mona	;	X+	3	;	;	2 =	2+3−	2 =	3+	2 ≡	0
Vernstein	;	;	;	;	3	;	;	;	2 =	;	;
Purple Straw	2 =	3,3+	3,3+	; 2 =	3+	2	3,3+	2 =	3+	2−	;
Line SA	;	; 2 =	;	; 2 =	; 2 =	X	;	3+	3+	3	;
Pusa	;	3	3	0;	X+	0;	; 1+	;	3+	;	0;
Soft Baart	; 2 =	2	2 =	; 2 =	2	2+3−	2−	2+3	3+	2+3−	X−
Morocco	; 2 =	2+3	2 =	2 =	2−	2	2 = 2−	23−	3+	2−	; 1 =
W2691	2+3	3,3+	2+3	3	2+,3	3+	X3−	3+	3+	33+	X+
B.W.R.	S	S	S	S	MS	MS	S	S	R	S	3+
B.W.R. line 5	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+

mentioned earlier. About 95% of these cultures came from Queensland. We were able to differentiate them into 27 different strains. Infection types of eight typical strains (A–H) are presented in Table 1.

Of the hosts shown in Table 1, Einkorn was fully resistant to all cultures. This result was unexpected as two somatic hybrids synthesized earlier (Watson and Luig 1959) produce intermediate reactions on this standard differential. The infection types observed on the other testers indicate that the strains could have had a hybrid origin. The data also suggest that the majority of the wheat testers possess more than one gene for resistance to the scabrum strains; and when such multiple resistances condition intermediate infection types only, and the gene effects involved are additive rather than epistatic, they allow for maximum differentiation. In this respect, the wheat testers resemble the 12 standard differentials. However, because of the genetic complexity of such testers, little information regarding the host–pathogen gene-for-gene relationships was obtained. If such information in regard to the scabrum rust strains is of interest, isogenic lines will have to be developed and employed. At present we are transferring by back-crossing all known single genes concerned in resistance to *P. graminis tritici*, *P. graminis secalis*, and their hybrids into a line (W3498) which is very susceptible to all strains of scabrum rust and to the majority of strains of *P. graminis secalis*. Sanghi (1968) and Sanghi and Luig (1971) have demonstrated the presence of many hitherto unknown genes for resistance to hybrid rusts.

Line 5, a selection from B.W.R. susceptible to wheat stem rust, was also susceptible to all cultures of scabrum rust. It is inferred that the resistance of commercial B.W.R. to scabrum rust is expressed as a result of the presence of genes for avirulence in the pathogen which have been derived from wheat stem rust.

As shown further in Table 1, strain A is avirulent on nearly all testers, while strain B is virulent on a majority of them. Strains E and F, on the other hand, combine genes for virulence on both rye and wheat.

As will be shown later, wheat stem rust was found frequently on *A. scabrum* in Queensland, especially at the end of the wheat season. Rye stem rust was recovered from nearly all those areas where scabrum rust was found. About 50% of samples of *P. graminis secalis* came from *A. scabrum*, another 20% from barley, and the remainder from commercial rye. Although wheat stem rust attacks some rye plants, somatic hybrids between this rust and rye stem rust, originating on rye, would have no advantage as commercial rye is highly susceptible to *P. graminis secalis*.

Commercial barley is also a host for both wheat and rye stem rust, but the former is more pathogenic on it. Like *A. scabrum*, barley can serve as a medium for somatic hybridization between these two formae speciales. However, there would be little chance of survival for such hybrids since in competition with *P. graminis tritici* they would be eliminated. Thus, the most interesting evidence for the hybrid origin of scabrum rust was the frequent recovery of rye stem rust from *A. scabrum*.

By contrast to the situation in Queensland, a higher percentage of *P. graminis secalis* occurred in the samples collected from *A. scabrum* in New South Wales, a lower percentage of *P. graminis tritici*, and very few instances of scabrum rust. Notable exceptions were in collections at Cabramurra and Adaminaby in the southern highlands: they comprised mixtures of *P. graminis secalis*, *P. graminis tritici*, and scabrum rust.

(b) *A Somatic Hybrid Synthesized from Two Strains Present in Queensland*

Although earlier work had clearly demonstrated that somatic hybridization occurs between wheat stem rust and rye stem rust, we repeated this process in the laboratory with two strains originating from Queensland, viz. 21–2 (a yellow mutant) of *P. graminis tritici* and culture 69090 of *P. graminis secalis*. Using procedures outlined by Watson (1957) seedlings of several wheat varieties including Morocco and Transfer were inoculated with a mixture comprising the two cultures. Despite a relatively high back-mutation rate from yellow uredospore colour to wild type (red) in the wheat stem rust culture (Luig 1967) which made it extremely difficult to handle mixed reactions, we isolated two intermediate-type infections on Morocco and Transfer respectively. When inoculated on the differential set used for scabrum rusts, these two cultures (CL and NL) produced reactions quite distinct from those obtained with Queensland cultures of such rusts. At the time of conducting the somatic hybridization experiments, all cultures of scabrum rust had shown complete avirulence ("O" or ";" infection type) on Yalta (*Sr11*), while cultures CL and NL conditioned mesothetic infection types. Subsequently, a culture was received from Queensland (culture H, Table 1) which, although distinct from CL and NL, showed a similar reaction on Yalta. It is difficult to explain the resistance of this latter to nearly all cultures of scabrum rust. However, we established that culture 69090 is avirulent on *Sr11* when present in a W2691 background (line SA), whereas cultures of rye stem rust collected in New South Wales were virulent on seedlings of this tester line.

(c) *Studies on Adult Plants of* A. scabrum

A. scabrum plants raised from seeds collected from Toowoomba, Qld., and from various parts of New South Wales were grown to maturity and inoculated with a mixture of strains of *P. graminis tritici*. In all cases only resistant reactions were observed. A similar result was obtained when rye stem rust and oat stem rust were used as the inoculum on the same plants. However, when strains of scabrum rust were employed, all plants originating from Queensland were susceptible whereas susceptibility was shown by only some of the plants raised from seed collected in New South Wales.

(d) *Distribution of Strains of Scabrum Rust*

When the different strains of scabrum rust found in Queensland were classified according to the area of collection it was apparent that distribution was not at random. For example, three strains distinguished from the others by virulence on Vernal Emmer, were recovered 10 times in a triangle (Cecil Plains–Malu–Millmerran) west of Toowoomba. This area is relatively small, the longest distance between any two points measuring about 35 miles. The three strains were not found outside this area.

Frequently several different strains of scabrum rust were recovered from the same locality. The differences recorded between such strains on the testers shown in Table 1 were so great that mutation was ruled out as the source of their origin. It is suggested that different strains occurring in the same area have arisen by different hybridization events.

(e) *Seasonal Fluctuations of the Various Rusts on* A. scabrum

Although the present study has indicated that the heterogeneous population of *A. scabrum* is more susceptible to scabrum rusts than to wheat stem rust or rye stem

rust, the last two were frequently recovered from this grass towards the end of the season. *A. scabrum* is a perennial and remains green during the summer; it is thus a receptive host for spores resulting from the massive build-up of rusts on cereals. However, sampling from *A. scabrum* in Queensland during the remainder of the year has revealed a distinct shift towards the scabrum rusts, thus confirming that they are more specialized on this host than either wheat or rye stem rust.

When the relative frequencies of individual strains of wheat stem rust recovered from *A. scabrum* during a given year were compared with those for the same strains recovered from wheat crops, it was clear that this grass plays an important part in the survival of strains which were prevalent in the eastern wheat belt some 10 or 15 years ago. Strains of wheat stem rust having a greater number of genes for avirulence reached their peak in frequency at the beginning of each growing season and it is suggested that these strains are better adapted to *A. scabrum* than the strains which possess a greater number of genes for virulence on modern wheat cultivars.

(*f*) *Stem Rust on Barley Grass*

The majority of 19 rust samples collected from barley grass in Queensland, New South Wales, Victoria, Tasmania, and New Zealand were identified as wheat stem rust with a high proportion of strains having many genes for avirulence, e.g. 21–5, 34–0, 34–2, and 21–2. *P. graminis avenae* and *P. graminis lolii* were also found, and one sample which came from Cudgewa, Vic., proved to be scabrum rust. This is good evidence that barley grass as well as rough wheat grass can participate as a mutual host in the hybridization of formae speciales of *P. graminis*. Waterhouse (1929) reported barley grass as a host of *P. graminis secalis* and our seedling and field tests have confirmed this.

(*g*) *Grass Stem Rusts which are Avirulent on All Wheats*

Rust collected from *Lolium* sp. invariably proved to be *P. graminis lolii* and this attacks certain oat species and a percentage of cocksfoot plants (*D. glomerata*). *P. graminis avenae* is also common on this latter species. *P. graminis lolii* appears to be widespread, especially in southern New South Wales, Victoria, and Tasmania.

Six cultures collected from *D. glomerata* and *Anthoxanthum odoratum* L. were very virulent on the former species, but avirulent on *L. perenne*, *L. temulentum*, and Algerian oats. They tentatively were classified as *Puccinia graminis* f. sp. *dactylidis* (Guyot and Massenot 1957). The first collection was made north of Cranbrook on the east coast of Tasmania. Another sample from this State came from the grounds of Hagley Church of England west of Launceston. The remaining four were sent from separated places in New South Wales: Albury in the south, Port Macquarie on the north coast, and Wentworth Falls on the Blue Mountains.

A culture (69968) established from infected *Phalaris* sp., sent from Bowna in southern New South Wales, proved to be virulent on the three *Phalaris* species: *tuberosa*, *canariensis* L., and *paradoxa L.* This ability to attack these species makes it a distinct rust. However, it attacks many oat varieties and is also weakly pathogenic on the wheats W2691 and W3498, which would suggest that it could have arisen as a hybrid between *P. graminis avenae* and *P. graminis tritici*. Further evidence for such

an event in the origin of culture 69968 is its virulence on several barley varieties which are susceptible to *P. graminis tritici* but resistant to *P. graminis secalis*.

A rust sample (69243) isolated from the native grass *D. quadriseta* at Mullengandra, N.S.W., resembled culture 69968 on Algerian oats by producing infection types "1++, 3−"; however, *Phalaris tuberosa* was not attacked. The results of comparative tests with these two cultures on many oat genotypes suggest that culture 69243 may be another hybrid rust.

Many grass species were tested with cultures 69968 and 69243, and with *P. graminis tritici*, *P. graminis secalis*, *P. graminis lolii*, and *P. graminis dactylidis*. Several species were hosts for two or more of these rusts but *P. graminis dactylidis* showed a very narrow host range attacking only *D. glomerata* and a selection of *Phalaris paradoxa*.

IV. Discussion

About 75 years ago the principle of host specialization was established for *P. graminis*, and although later work showed that occasionally sexual hybridization takes place between the formae speciales, no increased fitness was apparent for such hybrids. For example, cereal rye is fully susceptible to rye stem rust, and hybrids between this rust and wheat stem rust which attack only certain rye genotypes would be at a definite disadvantage on cereal rye when in competition with rye stem rust. The present work demonstrates a different situation with regard to wild and cultivated grasses among which resistance is widespread. Hybrids which could overcome the most common resistance genes of a prevalent grass species would have an increased survival ability, especially when the host is a perennial or grows during the whole year. Assuming that the cereal rusts have evolved from grass rusts (Leppik 1970), specialization on *A. scabrum* of hybrids between *P. graminis tritici* and *P. graminis secalis* would constitute the first step towards the more "primitive" state.

Since *A. scabrum* and *H. leporinum* appear to be the main grass hosts infected by *P. graminis tritici* and *P. graminis secalis* in Australia, it is likely that they play the major part as hosts enabling the hybridization between these two rusts. However, it is possible that other grasses, e.g. the *Bromus* species *tectorum* L., *hordeaceus* L., *arenarius* Labill., and *racemosus* L., reported as susceptible to the two formae speciales by Waterhouse (1929), are also involved.

A rust pathogenic on *Agropyron* species and not unlike the scabrum rust has been reported from India, and it has been named *P. graminis agropyri* Mehta & Prasada (Prasada 1947). Although all small grain cereals were reported as resistant, it is apparent that not many wheat or barley genotypes have been tested. Hence, we are unable to determine if this rust and the scabrum rust are the same.

Most strains of scabrum rust are avirulent on commercial wheat and rye, but attack certain barley cultivars. Comparisons between strains of wheat stem rust and scabrum rust have ruled out the possibility that in the case of the latter we are dealing with *P. graminis hordei* a hitherto unrecognized forma specialis of *P. graminis*, suggested by earlier rust workers (Cotter and Levine 1939). In nearly all instances where a difference in infection type was noticed, *P. graminis tritici* was more pathogenic. This would discount a hypothesis which postulates specialization on barley cultivars of newly formed hybrid strains. On the other hand, inoculations of the

same barley varieties with strains of scabrum rust and with rye stem rust showed that the latter was less pathogenic on barley. Scabrum rusts thus occupy an intermediate position between wheat stem rust and rye stem rust when barley is the host and this is further evidence for their hybrid origin.

Little is known of the hybridization processes which give rise to the scabrum rusts, but the data in Table 1 clearly indicate that a continuous variation between the two formae speciales of stem rust exists and that many combinations of genes for virulence are possible. This has serious implications for the breeding of stem-rust-resistant wheats, especially when use is made of genes for resistance transferred to wheat from rye or a grass species.

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