Establishment, Distribution, and Pathogenicity of *Puccinia striiformis* f. sp. *tritici* in South Africa

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ABSTRACT

Boshoff, W. H. P., Pretorius, Z. A., and van Niekerk, B. D. 2002. Establishment, distribution, and pathogenicity of *Puccinia striiformis* f. sp. *tritici* in South Africa. Plant Dis. 86:485-492.

Stripe rust, caused by *Puccinia striiformis* Westend. f. sp. *tritici* Eriks., has become an endemic disease of wheat (*Triticum aestivum* L.) in South Africa since it was first observed near Moorreesburg, Western Cape during August 1996. The main objectives of this study were to monitor the occurrence, spread, and the possible development of new variants of the stripe rust pathogen and the susceptibility of grass species to the pathogen. Results of surveys conducted during 1996 to 1999 revealed that rainfed wheat produced in the Western Cape, Eastern Cape, and the eastern Free State, as well as irrigated wheat produced in KwaZulu-Natal and the Free State, are most likely to be affected by stripe rust epidemics. Pathotype 6E16A- with virulence to Yr2, Yr6, Yr7, Yr8, Yr11, Yr14, Yr17, and Yr19 and pathotype 6E22A- with added virulence to Yr25 were detected. The occurrence of pathotype 6E22A- is currently restricted to KwaZulu-Natal and the Free State. Stripe rust isolates found on *Hordeum murinum* L. in the Western Cape were identified as pathotype 6E16A-, and both pathotypes 6E16A- and 6E22A- were collected from *Bromus catharticus* Vahl (= *B. unioloides* H.B.K.) in the eastern Free State. Urediospores from infections similar to stripe rust found on the grass species *Dactylis glomerata* L. (Eastern Cape), *Poa pratensis* L. (= *P. bidentata* Stapf; Western Cape), and *P. annua* and *P. trivialis* L. (eastern Free State) failed to infect wheat cv. Morocco seedlings in the glasshouse. The possible role of grasses in the over-summering of the stripe rust pathogen has not yet been established. Stripe rust infections, however, have been found on summer-sown wheat in the south Western Cape during 1998, volunteer wheat growing in the summer and autumn months in the eastern Free State from 1998 to 2000, and on summer-sown wheat in Lesotho.

Stripe rust, caused by the obligate parasite *Puccinia striiformis* Westend. f. sp. *tritici* Eriks., is one of the most important diseases of wheat (*Triticum aestivum* L.) (48). This forma specialis infects numerous wheat cultivars, as well as a few barley cultivars and certain grass species (48). Historically, stripe rust has been more important in areas with cool and wet environmental conditions and, therefore, occurs regularly in northern Europe, the Mediterranean region, Middle East, western United States, Australia, East African highlands, China, the Indian subcontinent, New Zealand, and the Andean regions of South America (16). Stripe rust also is important in more tropical areas of higher altitude such as the North African countries, the Himalayan foothills of India and Pakistan, and Mexico (32).

In comparison with the leaf rust (*P. triticina*) and stem rust (*P. graminis* f. sp.

tritici) pathogens of wheat, the global distribution of *P. striiformis* f. sp. *tritici* is more restricted. Stripe rust did not occur in Australia until 1979 (38), and was not found in New Zealand until 1980 (5). In central Africa, stripe rust was first reported in northern Zambia in 1958 (1).

The sexual stage of *P. striiformis* has not been encountered and alternate hosts have not been identified (48). Numerous, highly specified pathotypes of *P. striiformis* occur (24) and are probably formed by mutation and somatic recombination (48). Selection for virulence by growing cultivars with pathotype-specific resistance plays a major role in determining the pathotype of the pathogen.

The epidemic that occurred in the Western Cape during 1996 (43) indicated that stripe rust could become an important foliar disease of wheat in South Africa. Crop losses due to disease and higher input costs due to the repeated application of fungicides necessitated the development of more affordable control strategies against stripe rust. Under local growing conditions of predominantly dry-land wheat production with uncertain rainfall (average yield is 2.05 t/ha; 2), breeding for resistant cultivars represents the most cost-effective means of controlling stripe rust. Effective

breeding strategies are, however, dependent on an understanding of genetic variation in both pathogen and host. Of further importance in an effective disease control strategy is an understanding of the epidemiology of the pathogen. For stripe rust, this includes the ability of the pathogen to survive through the noncrop season and the probability of the disease occurring in the different wheat-growing areas of South Africa. The latter will have a limiting influence on the release of susceptible cultivars in areas of high risk and will be an important factor in cultivar selection by wheat producers.

The objectives of this research, which was conducted from August 1996 to February 2000, were to (i) determine the contribution of weather conditions to the successful establishment and subsequent epidemic outbreak of *P. striiformis* in the Western Cape during 1996, (ii) monitor the distribution and virulence of the stripe rust pathogen in local wheat-producing areas, and (iii) determine the susceptibility of grass species to stripe rust infection.

MATERIALS AND METHODS

Disease surveys. Wheat fields and disease nurseries (rust trap nurseries) were surveyed periodically from 1996 to 1999 by researchers of the Small Grain Institute (SGI) to monitor the occurrence, development, and distribution of stripe rust in South Africa. Thirty disease nurseries, planted annually in the important wheat-production areas of South Africa, and commercial wheat fields in the different production areas were visited at least once during the wheat growing season. Disease nurseries included the two wheat cultivars McNair 701 (stem and stripe rust susceptible) and Morocco (leaf, stem, and stripe rust susceptible), a stripe rust differential and supplemental set, several lines carrying different stem and leaf rust genes, a number of commercial wheat cultivars, and advanced breeding lines. Stripe rust severity was recorded on disease nursery entries and in commercial wheat fields in the different wheat producing areas using both the modified Cobb scale (41) and the field response scale for infection type (36,44).

A survey was conducted during February 1997 in the Western Cape to determine the role of volunteer wheat and wild

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Accepted for publication 13 December 2001.

grasses in the survival of the stripe rust pathogen during the hot summer months. Similar surveys were conducted in the south Western Cape during March 1998 and 1999 and in the eastern Free State from February to May in 1998 and 1999. The occurrence of stripe rust on summer-sown wheat in Lesotho was monitored from 1998 to 2000 and the susceptibility of wheat cultivars commonly grown in Lesotho was determined at both the seedling and adult plant stages. Procedures followed for the seedling and adult plant evaluation of the Lesotho cultivars are described below.

Pathotype determination. During field surveys, leaves containing sporulating

uredia were collected from wheat fields, disease nurseries, and triticale ($\times$ *Triticosecale* Wittmack), placed in glassine bags, stored in a portable refrigerator (7°C), and transported to SGI at Bethlehem. Additional rust collections were sent to SGI by coworkers responsible for the planting and maintenance of disease nurseries. The date of collection, location, cultivar (if known), and rust severity (41) were recorded. A cyclone collector was used to collect urediospores that were suspended in a mineral oil (Soltrol 170) and sprayed onto the primary leaves of 7-day-old seedlings of wheat cv. Morocco. Morocco seedlings were grown in 10-cm-diameter plastic pots

filled with steam-sterilized soil in a disease-free room at $22 \pm 1^\circ\text{C}$. Upon emergence, these seedlings were treated with a maleic hydrazide solution at 0.3 g liter^{-1} and 50 ml/pot to retard plant growth and stimulate urediospore production. Inoculations were done in an enclosed booth that was rinsed with water between isolates to eliminate contamination. After drying for 2 h in an air-conditioned room, inoculated seedlings were placed in a dew chamber at $11 \pm 1^\circ\text{C}$ and $>96\%$ relative humidity for 30 h. Seedlings then were moved to a glasshouse cubicle where daylight was supplemented with cool-white fluorescent tubes emitting photosynthetic active radiation of $120 \mu\text{E/m}^2$ for 16 h each day. Day and night temperatures were kept at $17 \pm 2^\circ\text{C}$. Seedlings inoculated with different stripe rust isolates were placed in separate glass cages.

After 14 to 16 days, urediospores of each isolate were collected from infected Morocco seedlings and inoculated onto the primary leaves of the world and European differentials (Table 1), placed in the dew chamber, and then moved to a glasshouse cubicle as described above. The cultivars Clement and *Triticum spelta album* were added to the world set of differentials as proposed previously (26,27,52). The seedling reaction of cv. Wembley and 26 supplementary wheat lines also was determined. Seeds of the differential lines and supplementary testers were provided by C. R. Wellings, Plant Breeding Institute, Cobbitty, Australia. Rust reaction of primary leaves of seedlings in the differential and supplemental sets was assessed using the 0-to-4 scale 14 to 16 days after inoculation (36). Pathotype classification was determined according to Johnson et al. (27) and Wellings and McIntosh (52). For adult plant evaluation in the field, differential cultivars and supplemental lines were planted in 1-m rows with 30-cm interrow spacing. Stripe rust spreader rows consisting of a mixture of Morocco and McNair were planted perpendicular to the differentials. The differential cultivars and supplemental lines were assessed for stripe rust at different locations in the field using the modified Cobb scale for measuring rust severity (41) and the field response scale for infection type (36,44).

Susceptibility of wild grass species. Rust samples resembling stripe rust were collected from infected grasses during surveys and tested in the glasshouse for pathogenicity on Morocco seedlings. When infections occurred, procedures followed for pathotype determination were the same as described above. In addition, 17 grasses belonging to six genera were tested in the glasshouse for their susceptibility to an isolate of *P. striiformis* f. sp. *tritici* from wheat.

Influence of weather conditions. Air temperature and precipitation data collected by the ARC-Institute for Soil, Cli-

Table 1. Seedling infection types produced on the World (1 to 9) and European (10 to 17) differentials, and supplemental tester lines (18 to 44) by pathotypes 6E16A- and 6E22A- of *Puccinia striiformis* f. sp. *tritici*

Cultivar	Yr gene(s)	Low infection type ^b	Seedling reaction ^a	
			pt. 6E16A-	pt. 6E22A-
Differentials				
1. Chinese 166	1	0;	0;	;
2. Lee	7	;N, 1N	4	4
3. Heines Kolben	2,6	;, N1	4	4
4. Vilmarin 23	3a,4a	;	;N	;N, 1C
5. Moro	10,Mor	0;	;	;
6. Strubes Dickkopf	Sd,25	...	;C, 1CN	;C, 1CN
7. Suwon 92/Omar	4,Su	;	0;	0;, 1C
8. Clement	2,9,25,Cle	0;	0;	;
9. <i>Triticum spelta album</i>	5	0;, ;	0;	;
10. Hybrid 46	4b	;	;	;
11. Reichersberg 42	7,25	;N, 1N	;1CN	4
12. Heines Peko	2,6,25	;N, N1	;N	4
13. Nord Desprez	3a,4a	;	;	;, ;C
14. Compair	8,19	0;, ;	4	4
15. Carstens V	Cv	...	;	;C
16. Spaldings Prolific	Sp	...	0;	0;
17. Heines VII	2,25,HVII	0;, 2	;C	;C, ;1C
Supplemental set				
18. Yr1/6*AvS	1	0;	;	;
19. Kalyansona	2	0;, 2	4	4
20. Yr5/6*AvS	5	0;, ;	0	0;
21. Yr6/6*AvS	6	;, ;N1	3	3
22. Yr7/6*AvS	7	;N, 1N	3	3
23. Yr8/6*AvS	8	0;, ;	3	3
24. Federation/4*Kavkaz	9	0;	0;	0;
25. Yr9/6*AvS	9	0;	0	0;
26. Yr10/6*AvS	10	0;	;	0;
27. Yr11/3*AvS	11	...	3	3
28. Wembley	14	...	3	3
29. Yr15/6*AvS	15	0;	0	;
30. Trident	17	;C, ;1	4	4
31. Yr17/3*AvS	17	;C, ;1	3	3
32. Jupateco R	18	...	4	4
33. Yr18/3*AvS	18	...	4	4
34. Yr24/3*AvS	24	...	;	;
35. TP981	25	...	;	4
36. TP1295	25	...	;	4
37. Yr26/3*AvS	26	...	;	;
38. Selkirk	27	...	1CN, 3	1CN, 3
39. Yr27/3*AvS	27	...	;, 1p=4	;
40. Avocet R	A	;CN1, 2+	;C, 1C	;C, 1C
41. YrSp/3*AvS	Sp	...	;	;
42. Avocet S	...	...	4	4
43. Federation 1221	...	...	4	4
44. Jupateco S	...	...	4	4

^a Seedling reaction types were determined according to McIntosh et al. (36): 0 = no uredia, ; = fleck, 1 = necrotic and chlorotic areas with restricted sporulation, 2 = small to medium uredia with chlorosis and necrosis, 3 = medium-sized uredia with chlorosis, 4 = abundant sporulation without chlorosis, C and N = more than usual degrees of chlorosis or necrosis.

^b Low infection type or resistant reaction for the separate Yr genes as described by McIntosh et al. (36).

mate, and Water in Pretoria were used to determine the influence of weather on the successful establishment, spread, and subsequent epidemic outbreak of stripe rust in the Western Cape during 1996.

RESULTS

Outbreak, occurrence, and distribution during 1996. Stripe rust was first observed on 9 August 1996 on the bread wheat cv. Palmiet in the winter rainfall region near Moorreesburg in the Western Cape (Fig. 1). Subsequent surveys at the time of detection showed that the disease was well established in wheat fields in the western and northern parts of the Western Cape, as well as at Nieuwoudtville in the Northern Cape Province. The initial location and time of outbreak, therefore, could not be determined.

The above-average rainfall together with lower than average minimum and maximum temperatures recorded during August and September 1996 (Fig. 2) contributed significantly to the establishment, spread, and subsequent epidemic outbreak of stripe rust in the Western Cape, and necessitated extensive and often repeated applications of triazole fungicides. Despite these efforts, head infection and destruction of

the foliage resulted in significant losses in grain quantity and quality. Producers spent an estimated 28 million Rand on fungicides to control the stripe rust epidemic during 1996 in the Western Cape Province. The fact that almost all the cultivars grown in this area in 1996 were susceptible to the pathotype that was initially identified contributed to this epidemic.

The disease also spread to wheat-producing areas in the southern parts of the Western Cape and the western and southern areas of the Eastern Cape. Due to hot and dry weather conditions in these regions, the incidence of stripe rust was low and fungicide applications were restricted to the districts of Caledon and Humansdorp. During November 1996, stripe rust was observed on irrigated wheat at Rietrivier in the summer rainfall area south of Kimberley, which proved that inoculum had been disseminated to the interior of the country.

Occurrence and distribution during 1997. During the 1997 wheat season, stripe rust was first observed in early June near Mossel Bay in the southern and Moorreesburg in the western regions of the Western Cape. Unlike the 1996 season, wet and

cold conditions until flowering were more favorable for stripe rust development in the southern areas of the Western Cape and in the western and southern areas of the Eastern Cape. This required the use of fungicides to control stripe rust on susceptible cultivars. The low incidence of stripe rust in the western and northern parts of the Western Cape Province during the 1997 season may be attributed to the widespread cultivation of the stripe rust-resistant cv. SST57 that was grown on more than 60% of the area. Unfavorable weather (dry and hot conditions for most of the season), and prophylactic applications of fungicides on susceptible cultivars contributed to the low incidence of stripe rust.

During August 1997, stripe rust was observed near Wesselsbron in the western Free State and it spread to the rest of the province, and to KwaZulu-Natal, Gauteng, North-West, and Northern Province. Epidemic outbreaks of stripe rust observed during September on the spring wheat cv. Palmiet, which was grown under center pivot irrigation near Bloemfontein, was the most southern report of the disease in the Free State. During October, stripe rust occurred on irrigated wheat at Rietrivier, Vaalharts, and Prieska in the Northern

Fig. 1. Map of South Africa showing the different regions where stripe rust occurs.

Cape Province. Higher day temperatures toward the end of October and early November, however, restricted rust development on irrigated wheat in the Northern Cape. Except for parts of the western, central, and eastern Free State, the incidence of stripe rust on dry-land wheat in the summer rainfall region was low due to dry and hot weather conditions. Producers in the eastern Free State spent an estimated 18 million Rand to control stripe rust during 1997.

Occurrence and distribution during 1998. During the 1998 season, stripe rust incidence was low in the Western and Eastern Cape Provinces. The first symptoms were observed during the last week of July near Swellendam in the south Western Cape. This low incidence was attributed to the planting of resistant cultivars that prevented the rapid build-up and spread of the disease. Furthermore, environmental conditions were not conducive for stripe rust development during most of the season. Only a trace of stripe rust was observed near Cradock in the Eastern Cape and at Rietrivier in the Northern Cape.

In the summer rainfall region, stripe rust was observed during mid-September in KwaZulu-Natal and later near Vrede in the northeastern Free State. The development of a new stripe rust pathotype in the eastern Free State was mainly responsible for

the stripe rust epidemic experienced in this region during 1998 (6). The new pathotype, identified as 6E22A-, differed from the initially identified pathotype, 6E16A- (discussed below), in its ability to infect cvs. Hugenoot and Carina in both seedling and adult plant growth stages. In 1998, these two cultivars were grown on an estimated 20% (42,000 ha) of the total wheat hectareage in the eastern Free State because of their resistance to pathotype 6E16A-. Wheat producers spent an estimated 8 million Rand on chemical control of stripe rust in the eastern Free State during 1998, and yield losses were estimated at 5 million Rand.

Occurrence and distribution during 1999. As in 1998, stripe rust was observed in the Western Cape later during the 1999 season. In the western areas, the first symptoms were observed near Porterville and Piketberg at the end of July. Isolated epidemics occurred on cv. SST 66 in the Piketberg area during mid-September. In this region, chemical control of stripe rust was required in commercial fields planted to susceptible cvs. Adam Tas, SST 66, and SST 75, and moderately susceptible cv. SST 65. Throughout the rest of the western and northern areas of the Western Cape, the incidence of stripe rust was low and restricted to cv. Morocco, which was included in disease nurseries. In the southern parts of the Western Cape, the first stripe rust symptoms were found during the first week of August in commercial fields near Bredasdorp and Caledon. This region experienced the worst drought in decades, with abnormally high temperatures during June and July. Chemical applications in this region were restricted to cv. SST 75 in fields near Caledon. As in other areas, the occurrence of *P. striiformis* f. sp. *tritici* remained restricted to susceptible entries in disease nurseries planted near Caledon, Riviersonderend, and Napier.

In the summer rainfall areas, stripe rust infections were observed on breeders' plots

near Pongola in KwaZulu-Natal during the third week of June. During the second week of July, stripe rust was found on the lower leaves of wheat near Bloemfontein. In the eastern Free State, stripe rust infections were common starting in September on lower leaves of susceptible cultivars in the districts of Reitz, Kransfontein, and Harrismith. Chemical control was restricted to wheat fields planted to cv. Hugenoot near Reitz and Kransfontein. Stripe rust was also observed for the first time near Groblersdal in northern Mpumalanga on the cv. Morocco that was being grown under irrigation for seed production. In the Northern Cape, the incidence of stripe rust on irrigated wheat was low. Symptoms that were restricted to the cv. Morocco used as a stripe rust spreader in SGI trials were reported during the first week of October at Rietrivier.

Survival during summer and autumn.

Stripe rust symptoms were not observed on summer-sown wheat, volunteer wheat, and wild grasses in the Western Cape during February 1997. Nevertheless, the first stripe rust symptoms were observed in June 1997 on wheat seedlings at the three-leaf stage near Mossel Bay and during early July on volunteer wheat near Moorreesburg.

During March 1998, stripe rust infections were observed in a summer-sown wheat trial near Riviersonderend in the Western Cape. In addition, volunteer wheat plants that could serve as potential bridging hosts occurred in the latter region, most likely due to above average summer rains during the 1997–98 season. Stripe rust was observed on volunteer wheat near Bethlehem during the autumn of 1998, which indicates that the pathogen also successfully over-summered in the summer rainfall region.

During a survey conducted in March 1999 in the Western Cape, stripe rust symptoms were not found on summer-sown and volunteer wheat plants. In the

Fig. 2. Minimum and maximum temperature and rainfall during April to November 1996 compared with 11-year means at Moorreesburg, Western Cape, South Africa.

Table 2. Seedling infection type and field response of wheat cultivars planted in Lesotho to pathotypes 6E16A- and 6E22A- of *Puccinia striiformis* f. sp. *tritici*

Cultivar	Seedling reaction ^a		Field response to 6E22A- ^b
	6E16A-	6E22A-	
Moholotsane (Mother of the birds)	4	4	80 MS
Bolane (Ou Boland)	3	3	30 MS
Mant's Tlala (Tugela)	;, 1C	3+ ^c	T,5 MS ^d
Telu Nts'o (Black beard)	3	3	20 MS

^a Seedling reaction types were determined according to McIntosh et al. (36): 0 = no uredia, ; = fleck, 1 = necrotic and chlorotic areas with restricted sporulation, 2 = small to medium uredia with chlorosis and necrosis, 3 = medium-sized uredia with chlorosis, 4 = abundant sporulation without chlorosis, C and N = more than usual degrees of chlorosis or necrosis.

^b Field response reactions (0 to 100) represent the highest percentage of infection recorded on the flag leaves for each entry during the growing season. Field response types were determined according to McIntosh et al. (36), Roelfs et al. (44), and Peterson et al. (41): S = susceptible, with large compatible uredia with little or no chlorosis and necrosis; MS = moderately susceptible, with moderate-sized uredia that are mostly surrounded by chlorosis; R = resistant, with miniature or no uredia with chlorosis and necrosis present; MR = moderately resistant, with small uredia that are surrounded by either chlorotic or necrotic areas; T = trace; and 0 = no visible signs of disease.

^c Susceptible in the seedling stage to pathotype 6E22A- which indicates the presence of Yr25.

^d Plants displayed variable reactions.

eastern Free State, volunteer wheat plants showing stripe rust symptoms were observed during March and April in the districts of Petrus Steyn, Reitz, Kranzfontein, Harrismith, Danielsrus, and Bethlehem.

In Lesotho, wheat is sown during October and November and harvested toward the end of March. During a survey conducted in Lesotho, stripe rust was found on wheat planted by subsistence farmers during March 1999 and on volunteer wheat during June 1999. During February 2000, a stripe rust epidemic occurred on wheat in the Mokhotlong district in Lesotho. The cultivar Moholotsane had the highest levels of stripe rust. The seedling and field reactions (flag leaf) of Lesotho wheat cultivars were evaluated and are summarized in Table 2. Based on the severity data, Moholotsane was the most susceptible cultivar. Although stripe rust development was slower on cvs. Bolane, Telu Nts'o, and Mants'a, the pathogen sporulated on all the wheat cultivars grown in Lesotho.

Virulence of *P. striiformis* f. sp. *tritici*.

Over the 4 years, 231 *P. striiformis* isolates were tested on the differential set (Table 3). Isolates were collected from commercial wheat fields, disease nurseries, triticale cultivars and lines, barley (*Hordeum vulgare* L.) cv. Clipper, barley breeding lines, and several wild grass species. Most isolates originated from the Western Cape ($n = 124$), followed by the Free State ($n = 65$), Northern Cape ($n = 16$), Lesotho ($n = 13$), Eastern Cape ($n = 7$), and KwaZulu-Natal ($n = 6$).

P. striiformis samples obtained from the initial epidemic in the Western Cape in 1996 were identified as pathotype 6E16A- (Table 1). The seedling infection type of pathotype 6E16A- on the World (1 to 9) and European (10 to 17) differentials, and a set of supplemental lines (18 to 44) are presented in Table 1. The field response (flag leaf) of these lines at different locations in South Africa is presented in Table 4. Disease severity ratings represent the maximum development of the disease in the adult plant. Pathotype 6E16A- is characterized by avirulence to the differential cultivars Chinese 166 (*Yr1*), Vilmorin 23 (*Yr3a* and *Yr4a*; 35), Moro (*Yr10* and *YrMor*; 13), Strubes Dickkopf (*YrSd* and *Yr25*; 9), Suwon 92/Omar (*Yr4* and *YrSu*), Clement (*Yr2*, *Yr9*, *Yr25*, and *YrCle*; 9,13), *Triticum aestivum* subsp. *spelta* var. *album* (*Yr5*), Hybrid 46 (*Yr4b*) (12), Reichersberg 42 (*Yr7* and *Yr25*; 9), Heines Peko (*Yr2*, *Yr6*, and *Yr25*; 9), Nord Desprez (*Yr3a* and *Yr4a*), Carstens V (*YrCv*), Spaldings Prolific (*YrSp*), Heines VII (*Yr2*, *Yr25*, and *YrHVII*; 9,13), Avocet R (*YrA*); and virulence to Heines Kolben (*Yr2* and *Yr6*; 10), Lee (*Yr7*), Compair (*Yr8* and *Yr19*; 11), and Trident (*Yr17*).

In stripe rust surveys conducted in the major wheat-producing areas in South Africa during 1996 and 1997, only

pathotype (6E16A-) was detected. During 1998, stripe rust infection reached epidemic proportions on the widely grown cvs. Hugenoot and Carina in the eastern Free State. These two cultivars are resistant to pathotype 6E16A-. Avirulence and virulence characteristics of the isolates of *P. striiformis* f. sp. *tritici* collected from Hugenoot and Carina were determined on the standard stripe rust differential wheat lines and 25 supplementary testers. The wheat lines TP981 and TP1295 (supplied by R. Johnson, Cambridge, UK), which have a major resistance gene in common with the differentials Heines Peko, Reichersberg 42, Strubes Dickkopf, Clement, and Heines VII (9,34), also were included. Isolates obtained from Hugenoot and Carina differed from pathotype 6E16A- based on virulence to Reichersberg 42 (*Yr7* and *Yr25*), Heines Peko (*Yr2*, *Yr6*, and *Yr25*), TP981 (*Yr25*), and TP1295 (*Yr25*). The new variant, designated as 6E22A- (Table 1), also was identified in collections from KwaZulu-Natal. The previously resistant cvs. Hugenoot, Carina, Tugela, and Tugela-DN are the only local cultivars infected by pathotype 6E22A- in seedling tests. The data presented in Table 3 demonstrate a regional difference in pathotype distribution, which indicates that stripe rust pathotypes survive independently at several locations in South Africa during the summer months.

Susceptibility of wild grass species.

During 1997, stripe rust was found on *Bromus catharticus* Vahl (= *B. unioloides* H.B.K.) in the eastern Free State and on *Hordeum murinum* L. in the Western Cape. Rust isolates ($n = 20$) sampled from both species were identified as pathotype

6E16A-. During 1999, stripe rust collected from *B. catharticus* in the eastern Free State was identified as pathotype 6E22A-. Urediospores from infections resembling stripe rust from leaves of *Dactylis glomerata* L. (Eastern Cape), *Poa pratensis* L. (= *P. bidentata* Stapf) (Western Cape), and *P. annua* and *P. trivialis* L. (eastern Free State) failed to infect cv. Morocco seedlings. Seedling infection types of 17 grass species to an isolate of *Puccinia striiformis* f. sp. *tritici* are presented in Table 5. *B. arenarius* and *B. oxydon* showed compatible seedling reactions and *B. trinii* (accession 25528) showed both resistant and susceptible reactions.

DISCUSSION

Since the detection of *P. striiformis* f. sp. *tritici* for the first time on bread wheat in the Western Cape during August 1996, the pathogen has spread to all the important wheat-production areas in South Africa. Stripe rust subsequently has become established as an endemic disease with a significant impact on wheat production in the western and southern areas of the Western Cape, the Eastern Cape, areas of the eastern Free State, and KwaZulu-Natal. The 500,000 ha of wheat planted in these regions account for approximately 47% of the total area sown to wheat in South Africa annually. Wheat produced under dryland conditions in the western, central, southeastern, and southern Free State largely escaped stripe rust epidemics. Factors that contributed to the escape are less dense stands due to low seeding rates (15 to 30 kg/ha), low humidity, and drought conditions during early growth stages, followed by high day temperatures after

Table 3. Pathotypes of *Puccinia striiformis* f. sp. *tritici* detected in South Africa from 1996 to 1999

Year and region	Number of isolates	Pathotype	
		6E16A-	6E22A-
1996			
Western Cape	47	47	0
Northern Cape	8	8	0
Total number	55	100%	...
1997			
Western Cape	42	42	0
Northern Cape	2	2	0
Eastern Cape	6	6	0
KwaZulu-Natal	2	2	0
Free State	14	14	0
Lesotho	11	11	0
Total number	77	100%	...
1998			
Western Cape	15	15	0
Eastern Cape	1	1	0
Northern Cape	1	1	0
KwaZulu-Natal	2	0	2
Free State	21	7	14
Total number	40	60%	40%
1999			
Western Cape	20	20	0
Northern Cape	5	5	0
KwaZulu-Natal	2	0	2
Lesotho	2	2	0
Free State	30	6	24
Total number	59	56%	44%

the first spring rains. Wheat produced under irrigation in the Northern Cape, North-West, Gauteng, Northern Province, and Mpumalanga also escaped stripe rust epidemics. High day temperatures experienced during October and November in the irrigated areas along with high levels of resistance present in most of the cultivars grown in those areas may have contributed to the absence of disease.

Park (39) defined days as being stripe rust favorable when the mean temperature falls within the range of 12.4 to 18.4°C, and the minimum between 7.3 and 14.6°C. Both minimum and mean temperatures in Moorreesburg during August and September 1996, when the stripe rust epidemic was at its peak in the Western Cape, fall

within these ranges. The highest rainfall in 11 years recorded for Moorreesburg during August (90 mm) and September (100 mm) 1996 contributed to the establishment and epidemic development of stripe rust. The higher rainfall not only lowered temperatures and prolonged leaf wetness, but may have played a significant role in the spread of the disease, because rain splash is an important mechanism of stripe rust dispersal (20).

Surveys identified two stripe rust pathotypes in South Africa. Yield losses caused by pathotype 6E16A- in the eastern Free State during 1997 shifted cultivation to the resistant cvs. Huguenot and Carina the next year. The high selection pressure evidently resulted in the development of pathotype

6E22A-, which appears to be a single-step mutation event in 6E16A- that resulted in additional virulence for Yr25. Pathotype 6E16A- was previously detected in East and North Africa, the Middle East, and Western Asia (3,29). With several resistance genes not being reflected in the classification of pathotypes globally, it is possible that some variation within this pathotype may occur elsewhere. With the available data, it is not possible to speculate as to the likely origin of pathotype 6E16A-.

Virulence was detected for the seedling genes Yr2, Yr6, Yr7, Yr8, Yr17, Yr19, and Yr25. From the field data, it is evident that the differential cvs. Compare, Kalyansona, and Trident and the supplemental line

Table 4. Field response of the World (1 to 9) and European (10 to 17) differentials and supplemental lines (18 to 43) to pathotypes 6E16A- and 6E22A- of *Puccinia striiformis* f. sp. *tritici* at different locations in South Africa during 1998 and 1999^a

Cultivar/line	Yr gene(s)	Bethlehem 1998 (pt. 6E16A-)	Greytown 1998 (pt. 6E22A-)	Bethlehem 1999 (pt. 6E22A-)	Riviersonderend 1999 (pt. 6E16A-)	Burgershall 1999 (pt. 6E16A-)	Greytown 1999 (pt. 6E22A-)
Differentials							
1. Chinese 166	1	0	0	0	0	0	0
2. Lee	7	90MSS	30MS	80S	10MS	20S	50MS
3. Heines Kolben	2,6	80MSS	50MRMS	80S	10MS	20S	50R
4. Vilmorin 23	3a,4a	0	10R	5MS	0	0	TR
5. Moro	10,Mor	0	...	0	0	0	...
6. Strubes Dickkopf	Sd,25	0	...	0	0	0	...
7. Suwon 92/Omar	4,Su	0	0	0	0	0	0
8. Clement	2,9,25,Cle	0	0	0	0	0	0
9. <i>Triticum spelta album</i>	5	0	10R	0	0	0	0
10. Hybrid 46	4b	0	0	0	0	0	0
11. Reichersberg 42	7,25	0	10MR	20MS	0	0	0
12. Heines Peko	2,6,25	0	15R	20MS	0	0	10R
13. Nord Desprez	3a,4a	0	TR	TR	0	0	0
14. Compare	8,19	0	0	5MS	0	0	0
15. Carstens V	Cv	0	0	0	0	0	0
16. Spaldings Prolific	Sp	0	0	0	0	0	0
17. Heines VII	2,25,HVII	0	0	0	0	0	0
Supplemental set							
18. Yr1/6*AvS	1	0	0	0	0	0	0
19. Kalyansona	2	5MS	10R	10R	5MS	0	5R
20. Yr5/6*AvS	5	0	0	0	0	0	0
21. Yr6/6*AvS	6	...	...	100S	80S	100S	100S
22. Yr7/6*AvS	7	100S	70S	100S	60S	100S	100S
23. Yr8/6*AvS	8	30MR	15R	20MR,80MS	5MS	TMS	TR
24. Federation 4/Kavkaz	9	0	0	0	0	0	0
25. Yr9/6*AvS	9	5R,40MS	0	0,20MS	0	20MR	30MRMS
26. Yr10/6*AvS	10	0	0	0	0	0	0
27. Yr11/3*AvS	11	...	...	80S	50S	80S	60MR-MS
28. Wembley	14	90MRMS	30MR	80MS	...	40S	30MR
29. Yr15/6*AvS	15	0	0	0	0	0	0
30. Trident	17	20MS	20R	40MS	5MS	20MS	30MR
31. Yr17/3*AvS	17	90MS	40MSS	90MS	20S	40MS	80MSS
32. Jupateco R	18	20MR	5R	20MRR	10MR	10MRMS	20R
33. Yr18/3*AvS	18	...	...	30,80MS	...	20MS	20MR
34. Yr24/3*AvS	24	...	...	20R,70R	...	...	70MR
35. Yr26/3*AvS	26	...	...	20R	...	...	5R
36. Selkirk	27	10R	40RMR	20R	10R	TR	10R
37. Yr27/3*AvS	27	...	...	10R,80S	0	0,100S	0,20MS
38. Avocet R	A	20MS	5R	30MR,80MS	0	10MS	TR
39. YrSp/3*AvS	Sp	...	...	0	0	0	0
40. Federation 1221	...	80S	80S	100S	30S	80S	80S
41. Avocet S	...	...	...	100S	60S	100S	100S
42. Jupateco S	...	100S	...	100MS	10S	100S	90MSS
43. Morocco	...	100S	100S	100S	80S	100S	100S

^a Field response reactions (0 to 100) represent the highest percentage infection recorded on the flag leaves for each entry during the growing season. Field response types were determined according McIntosh et al. (36), Roelfs et al. (44), and Peterson et al. (41): S = susceptible, with large compatible uredia with little or no chlorosis and necrosis; MS = moderately susceptible, with moderate sized uredia that are mostly surrounded by chlorosis; R = resistant, with miniature or no uredia with chlorosis and necrosis present; MR = moderately resistant, with small uredia surrounded by either chlorotic or necrotic areas; T = trace; 0 = no visible signs of disease; ... = not tested.

*Yr8/6*Avocet-S* carry an additional gene or genes that result in different levels of adult plant resistance against pathotypes 6E16A- and 6E22A-. The low adult plant response obtained for the differential cvs. Reichersberg 42 and Heines Peko at Greytown and Bethlehem, where pathotype 6E22A- was present during 1999, may be attributed to escape of infection; however, adult plant resistance in Reichersberg 42 and Heines Peko can not be excluded. The gene *Yr27* present in Selkirk (35) produced a compatible seedling reaction when scored 12 to 14 days after inoculation, but this infection type became incompatible (necrotic) when scored 3 to 4 days later (glasshouse data). Based on the latter and field data, it is clear that the seedling gene *Yr27* is still effective. Supplemental lines exhibiting heterogeneous field reactions were *Yr8/6*Avocet-S*, *Yr9/6*Avocet-S*, *Yr18/3*Avocet-S*, *Yr24/3*Avocet-S*, *Yr27/3*Avocet-S*, and *Avocet-R*. The absence of most of the effective seedling genes from commercial cultivars (42) and the resulting low selection pressure preclude any predictions of their durability to local stripe rust pathotypes. Seedling genes with a hypersensitive response to avirulent isolates of *P. striiformis* are well known for their vulnerability to the development of more virulent pathotypes (17,30,33,45,52). Over a 10-year period, 15 different stripe rust pathotypes were detected in Australia and New Zealand adding virulence to seven seedling genes, initially effective against the pathotype introduced to Australia in 1979 (52). Furthermore, the seedling genes *Yr5*, *Yr8*, *Yr27*, and *YrSp* have become ineffective due to changes in the pathogen population without the presence of these genes in Australasian wheat (33,52). Adult plant resistance against *P. striiformis* has been known to last longer than seedling genes (8,25,30,33,40). The adult plant gene *Yr18* present in Jupateco R and *Yr18/3*Avocet-S* exhibits intermediate to high levels of resistance under South African conditions. Although the adult plant genes *Yr11* and *Yr14*, present in *Yr11/3*Avocet-S* and cv. Wembley (23), respectively, showed a relative level of resistance compared with the susceptible Avocet S, their responses are not expected to provide adequate crop protection.

The ability of the stripe rust pathogen to survive near wheat fields through the non-cropping season plays an important role in disease onset and the increase of inoculum during early growth stages. The data presented in this study show that stripe rust survives independently during the summer months in the summer and winter rainfall areas of South Africa. The summer and autumn survival of the stripe rust fungus in other countries is dependent on susceptible volunteer or self-sown wheat plants and, to a lesser extent, on grass species (18,37,46–48,51). Virulence on grasses provides

greater opportunity for the survival and increase of stripe rust (33) and may play a role in the occurrence of epidemics (31). In this study, *B. catharticus* and *H. murinum* were identified as hosts and *B. arenarius* and *B. oxydon* were susceptible as seedlings, whereas *B. tritici* was heterogeneous for seedling reaction. *B. catharticus*, commonly found during the spring, summer, and autumn months along river banks, roads, and agricultural fields throughout all the wheat-growing areas, is perennial to weakly annual, depending on the growing conditions (21,50). *H. murinum*, found along commercial fields, roads, and waste areas in the Western Cape as well as in the mountainous southern parts of Lesotho, is a winter-active annual and uncommon during the summer months in the Western Cape (21,50). Sporulation of *P. striiformis* on leaves of both these grasses is abundant under environmental conditions conducive to stripe rust development. Stripe rust was not found on susceptible grasses during the summer and autumn months. The possibility that susceptible grasses plays an important role in the over-summering of stripe rust in the mountainous region of the Western Cape, Eastern Cape, eastern Free State, KwaZulu-Natal, and Lesotho cannot be excluded and warrants further investigation.

As in previous studies, urediospores obtained from infections on *Poa pratensis*

and *D. glomerata* were avirulent on wheat (22,28). Stripe rust found on *P. pratensis* and *D. glomerata* has previously been classified as *Puccinia striiformis* f. sp. *poae* and *P. striiformis* f. sp. *dactylidis*, respectively (7,49). *H. murinum* (= *H. leporinum* Link), *B. unioides*, and *Poa trivialis* also previously have been found to be susceptible to stripe rust pathotypes originating from wheat (22,28,37). Infection of *B. arenarius*, *B. oxydon*, and *B. tritici* seedlings also could serve as hosts for local *Puccinia striiformis* pathotypes. The latter species currently do not occur naturally in South Africa, but are planted for grazing (21).

Unusually mild and rainy weather during the off season promotes the build-up of stripe rust inoculum and is closely associated with subsequent levels of stripe rust observed in commercial crops (4,14,19,39). In the eastern Free State, stripe rust infection on susceptible volunteer wheat serves as an inoculum source for the onset of early season infections. The higher elevation areas of Lesotho, which have a different growing period than the main wheat areas in South Africa, provide a zone for the over-summering of stripe rust. These sources of inoculum can be minimized by planting resistant cultivars, especially in the eastern Free State and Lesotho where summer rain and mild summer temperatures can significantly

Table 5. Pathogenicity of an isolate of *Puccinia striiformis* f. sp. *tritici* (pathotype 6E16A-) from wheat to 17 grass species belonging to six genera occurring naturally or used for grazing purposes

Grass species	Origin	Infection type ^a
<i>Bromus arenarius</i> acc. W209 ^b	DPQC ^c	3
<i>B. carinatus</i> acc. 1599 ^b	DPQC	0
<i>B. carinatus</i>	Riviersonderend	0
<i>B. catharticus</i> Vahl (= <i>B. unioides</i> H.B.K.) ^d	Bethlehem	3
<i>B. catharticus</i> acc. 80270 ^b	DPQC	3
<i>B. diandrus</i> Roth	Malmesbury	;N
<i>B. japonicus</i> Sensus (= <i>B. pectinatus</i> Thunb) ^d	DPQC	0
<i>B. mollis</i> L. cv Catapico ^b	DPQC	;
<i>B. oxydon</i> acc. 28124 ^b	DPQC	2+3
<i>Bromus</i> sp. ^b	DPQC	;N
<i>Bromus</i> sp. cv 14789 ^b	DPQC	1N, 2
<i>B. tritici</i> cv 25531 ^b	DPQC	1N, 2
<i>B. tritici</i> cv 25528 ^b	DPQC	1C, 4
<i>B. unioides</i> H.B.K.	DPQC	3
<i>Dactylis glomerata</i> L.	Eastern Cape	0
<i>Hordeum capense</i> Thunb. (= <i>H. nodosum</i> auctt., non L.) ^d	Porterville	;N, 1N
<i>H. murinum</i> L.	Elsenburg	0;
<i>H. murinum</i> L.	Hopefield/Piketberg	4
<i>H. murinum</i> L.	g	
<i>Lolium multiflorum</i> Lam.	Gouda	;C
<i>Lolium</i> sp.	Malmesbury	0
<i>Poa pratensis</i> L. (= <i>P. bidentata</i> Stapf) ^d	Porterville	0
<i>P. trivialis</i> L.	DPQC	0
<i>P. annua</i> L.	Bethlehem	0
<i>Secale cereale</i> L. cv Cool Grazer ^b	Bethlehem	0
<i>S. cereale</i> L. cv M/71/128 ^b	DPQC	0, ;C
	DPQC	0, ;C

^a Seedling reaction types were determined according to McIntosh et al. (36): 0 = no uredia, ; = fleck, 1 = necrotic and chlorotic areas with restricted sporulation, 2 = small to medium uredia with chlorosis and necrosis, 3 = medium-sized uredia with chlorosis, 4 = abundant sporulation without chlorosis, C and N = more than usual degrees of chlorosis or necrosis.

^b Used only for grazing.

^c Directorate of Plant and Quality Control, South Africa.

^d Gibbs Russel et al. (21).

contribute to the summer survival of stripe rust.

Factors that may lead to the rapid evolution of aggressive pathogen races are increased fecundity and a microclimate more conducive for disease development (15). Stripe rust control strategies in South Africa should be directed at reducing the probability of epidemics and reducing the magnitude of losses. The latter may be obtained by avoiding the release of cultivars containing only genes for seedling resistance and the planting of stripe rust-resistant cultivars in the more rust-prone areas. It is important to continue to monitor the stripe rust population for pathotype changes so that new pathotypes with the potential to overcome resistance genes currently deployed can be detected early.

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