Pathotypes of *Puccinia graminis* f. sp. *tritici* with Increased Virulence for *Sr24*

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ABSTRACT

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Pathogenic studies of two pathotypes of *Puccinia graminis* f. sp. *tritici* first isolated during 1984 on the previously resistant cultivars SST44 and Gamka demonstrated that both possessed increased virulence for *Sr24*. These pathotypes, designated 2SA100 and 2SA101, which appeared to be mutations of earlier types, became widespread throughout the South African wheat production areas within two seasons. Seedling and adult-plant response studies indicated genetic vulnerability in 60% of the cultivars. Nine of the 23 recommended cultivars possess *Sr24*, either alone or in combination with other resistance factors. Susceptibility ratings, measured in terms of latent period and uredinium density, separated cultivars into three distinctive groups. Differences in the degree of susceptibility in lines/cultivars having *Sr24* as a major stem rust resistance gene were evident. Pathotypes 2SA100 and 2SA101 or races similar to these constitute a major threat to wheat production in Southern Africa and other regions where *Sr24* is deployed, because they combine increased virulence with aggressiveness and good survival ability.

Stem rust, caused by *Puccinia graminis* f. sp. *tritici* Eriks. & Henn., is an important disease of wheat (*Triticum aestivum* L.) in the winter rainfall regions of South Africa.

The pathogen oversummers on volunteer wheat plants and *Hordeum murinum* Huds., which are supported by periodic summer rains. Moreover, the likelihood of stem rust outbreaks is enhanced because wheat is grown throughout the year in different climatic regions. To reduce the frequency and extent of epidemics, resistant cultivars have been released since the mid-1960s.

In the process of producing new resistant cultivars, wheat breeders and pathologists have exploited the available genetic sources. The resistance genes currently deployed in local cultivars include: *Sr9e* (SST33 and SST66), *Sr24* (SST44, SST102, and Gamka), *Sr31* (Gamtoos), and *Sr36* (Zaragoza and SST107) (J. Le Roux, *unpublished*). By the end of 1984, 54 and 61% of the wheat areas in the winter rainfall region and the Transvaal irrigation areas, respectively, were planted with resistant cultivars. The use of resistant cultivars combined with a serious drought in the summer rainfall region, where more susceptible cultivars are grown, resulted in a sharp decline in the incidence and severity of stem rust during the period 1982–1983.

SST44 (CI 13523/3*TA[Anza]), a high-yielding stem rust-resistant spring wheat released during 1980, became the predominant cultivar in the winter rainfall and Transvaal areas. During 1983, SST44 reached a production peak of 15 and 31%, respectively, of wheat produced in both areas. Although it possesses genes *Sr5*, *Sr8a*, *Sr9b*, *Sr12*, and *Sr24* (R. P. Singh, *personal communication*), only the last conferred resistance to the predominant local strains (J. Le Roux, *unpublished*).

Until recently, *Sr24*, a dominant gene present in a spontaneously translocated chromosome of *Thinopyrum elongatum* (= *Agropyron elongatum* (Host.) Beauv.) to wheat chromosome 3D(2), conditioned resistance in both seedling and adult plants to stem rust worldwide (4,8,11). Only one virulent culture, a putative *P. g.* f. sp. *tritici*/*P. g.* f. sp. *secalis* hybrid, has previously been reported by the University of Sydney Plant Breeding Institute (9). Artificial mutation studies suggested that the avirulence gene corresponding to *Sr24* rarely mutates to virulence (5).

Because of the widespread effectiveness of *Sr24* in controlling stem rust, it has been exploited extensively, e.g., in Australia, where it occurs in Sundor, Skua, Torres, Bass, Sunelg, and Vasco (N. H. Luig, *personal communication*); the United States, where it occurs in Agent (9), Blueboy II, Cloud (6), Sage, Osage, Fox (N. H. Luig, *personal communication*), and Siouxland (13); and South Africa, where it occurs in SST44, Gamka, and SST102 (J. Le Roux, *unpublished*). At present, *Sr24* also serves as a universal resistance tester in pathogen variability surveys worldwide (4,8,11).

This study describes two stem rust pathotypes, 2SA100 and 2SA101, first found in South Africa during 1984 (3). Both are characterized by increased virulence for *Sr24* and are currently still the only pathotypes that have been found to be virulent on commercial cultivars possessing this gene.

MATERIALS AND METHODS

During the annual rust survey, stem rust samples collected from each of the various localities were inoculated onto 7-day-old seedlings of wheat (cultivar McNair 701), treated with maleic hydrazide to enhance urediniospore production. After 10–12 days, urediniospores from two single uredinia were collected separately and increased. The subsequent cultures were inoculated onto the following differential testers: Reliance (with gene *Sr5*), ISr7bRa (*Sr7b*), ISr8Ra (*Sr8a*), W2402 (*Sr9b*), Vernal (*Sr9e*), Acme (*Sr9g*), Festiquay (*Sr30*), W2691 + Sr36 (*Sr36*), ISr6Ra (*Sr6*), Renown (*Sr7b* + *Sr17*), Agent (*Sr24*), SST44 and Gamka (local *Sr24* testers), Yalta (*Sr11*), TAF2d (*A. intermedium*, unnamed gene), and Enterlago de Montijo (unnamed gene). Inoculated seedlings were placed in an incubation chamber held at 100% relative humidity for a 14-hr dark period followed by 3 hr of gradual drying at a light intensity of 10,000 lux. Temperature inside the chamber was maintained at 20 ± 2 C. Plants were then moved to a greenhouse, where they received natural daylight supplemented with illumination from cool-white fluorescent tubes for 14 hr each day. Temperature was controlled at 22 ± 2 C. Infection type responses (IT) were recorded after 10–12 days according to the method of Stakman et al (14).

After the demonstration of two new pathotypes, seedlings of an extended differential host series (Table 1), including all previous designated genes, were assessed.

Additional *Sr24* testers. In a subsequent test, in addition to Agent (9), two independently produced translocation stocks designated 3D/Ag1 and 3D/Ag3, three lines having *Sr24* in a Baart background, and seven lines with *Sr24* as a possible resistance factor selected from nurseries distributed by CIMMYT (International Maize and Wheat Improvement Centre) (Table 2) were tested as seedlings. Two *P. g.* f. sp. *tritici* cultures viz. 2SA48 and 2SA52, avirulent and virulent, respectively, on stocks with

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Sr9g, and avirulent for *Sr24*, were included to represent the pre-1984 stem rust spectrum with the two pathotypes virulent for *Sr24*.

Seedling responses in South African cultivars. Because resistance derived from Agent has been used extensively in local wheat breeding programs to control stem rust, it was imperative that recommended South African winter and spring wheats be evaluated for reaction to the new pathotypes. Accordingly, eight cultivars (Table 3) were inoculated with 2SA48, 2SA52, and the two *Sr24*-virulent pathotypes.

Table 1. Comparison between line/cultivar seedling responses to *Puccinia graminis* f. sp. *tritici* pathotypes virulent (2SA100, 2SA101) and avirulent (2SA48, 2SA52) for *Sr24*

Gene (*Sr-*)	Line/cultivar	Accession number	*P. g.* f. sp. *tritici* pathotype[a]			
			2SA100	2SA101	2SA48	2SA52
5	Reliance	CI 14159	4	4	4	4
	ISr5Ra	CI 14161	4	4	4	4
6	McMurachy	···	4	4	4	4
	ISr6Ra	CI 14163	3+	4	4	4
7a	Marquis + *Sr7a*	···	2+3	3	3	3
	Mq *Sr7a* EG101 sel.	CI 15083	2+3	3	3+	33+
7b	Marquis	CI 3641	3+	3	3+	4
	I*Sr7b*Ra	CI 14165	2++3	2++3	33+	2++3
	CSHope 4B	···	33+	33+	33+	3+
8a	Mentana	···	4	4	4	4
	I*Sr8*Ra	CI 14167	4	4	4	4
8b	Barleta Benvenuto	···	X=cn	X=cn	;1++n	;1++n
9b	Line AA	CI 17386	4	3+	3+	3+
9d	Arnautka	CI 1493	4	4	3+	4
	Mindum	CI 5296	4	4	4	4
	Spelmar	CI 6236	4	4	4	4
9e	Vernal	CI 3686	;cn	;cn	;1−n	;1−n
	PI 192334	CI 8155	;1−cn	;1=cn	;1−	;1−
9g	Acme	CI 5284	;cn	4	;cn	4
	Kubanka	CI 2094	;cn	4	;cn	4
10	Federation	···	4	4	4	4
	Line F	CI 17388	4	4	4	4
11	Yalta	···	4	4	4	4
	I*Sr11*Ra	CI 14171	3	3+	4	4
12	Line R	···	4	4	3+	3+
	Bt*Sr12*	CI 17783	4	4	3+	3+
13	Line S sel	CI 17387	12=	12=	;1	;1
	Marquis + *Sr13*	CI 15088	12=	12=	;1	;1
14	Line A	···	4	4	4	4
	Line A (new)	···	4	4	4	4
15	Norka	···	X−n	X−n	X	X
	W2691/+*Sr15*	···	X−n	X−n	X	X
16	Marquis + *Sr16*	···	4	4	4	4
17	Renown	···	4	4	4	4
18	Mq-A	···	4	4	4	4
19	Mq-B	···	4	4	4	4
20	RL-C	···	4	4	4	4
21	Einkorn	CI 2433	1+	1+	;1+c	;1+
	Triticum monococcum derv.	···	1++	1++	1++2	1++
22	SW*Sr22*TB 11-70-565-resel.		1++	2	2	2
23	Selkirk	CI 13100	3cn	X++cn	3cn	3cn
24	Agent	CI 13532	2++3−	2++3	12=	12=
25	Ars-3 sel	CI 17473	1+2	1−	1+	1
	Agatha	···	1−	1	;1−	;1−
26	Eagle	PI 365582	;1−	;c	1−	1−
	Avocet	···	;1−	;c	;1=	1
27	WRT 238-5	CI 14141	;n	;	;n	;n
28	Kota	CI 5878	3+	4	4	4
	Line AD	···	3+	3+	4	4
29	RL6046 *Sr29*	···	2+	2	2++	2+
	Tc6+/Etiole de Choisy	RL6045	2+	2−	1++	1
30	Festiquay	PI 330957	1+	1++	2++	2+
	Bt + *Sr30*	···	2	2	2+	2+
31	Veery#3 Gamtoos	···	;12=	;1=c	0;	0;
32	CS + *Sr32*	···	1	1+	1++	1++
	W3598	···	1+	1+	1	1
35	82.2692	Univ. Sydney	;1−	0;c	;	;
36	Line C	CI 17385	1n	;n	;	;0
	Mengavi	···	0;	0;	0;	;
37	W2691 + *Sr37*	Univ. Minn.	;n	;	;1=n	;1=
Tt3	74-3452	···	2+3−	Xcn	1++c	1++
Gt	Bt + *SrGt*	PI 329230	2++3	2	3−	1++3−
	Gamut	···	2++	12−	3	1++3−
dp-2	Medea Ap9d	3255	2	2	;1−	;1=
	Golden Ball deriv.	W 3504	2	2	;	;c
	Agropyron intermedium	···	1+	12−	1+	1+
	Enterlago de Montijo	192847	1++	1+	1	1
	Rosner Triticale	15013	;n	;n	;n	;n
	Morocco	W 1107	4	4	4	4
McN	McNair 701	···	3+c	3+c	3+c	3+c

[a] South African designation for *P. g.* f. sp. *tritici* cultures. For avirulence/virulence formulas, see text.

Adult-plant responses in South African cultivars. To determine the relationship between seedling and adult-plant response, six South African cultivars (Table 4) believed to possess *Sr24* were inoculated with pathotypes 2SA100 and 2SA48. Tillers at growth stage 60 (16) of each test plant were quantitatively inoculated with a 0.11-ml (3 mg urediniospores per milliliter) suspension (in Soltrol 130) with an Andres inoculator (1). The trial consisted of 12 replicates, each consisting of one plant. Plants were arranged in a randomized block design within the same greenhouse cubicle. This procedure was repeated for each cultivar-pathotype combination.

Inoculated adult plants were exposed to the same incubation procedures as described for seedlings. Latent period (LP) was determined on the terminal two internodes of adult plants by counting sporulating uredinia daily after inoculation until no more erupted. The LP was calculated by linear regression as the time from inoculation until the stage at which 40% of uredinia had erupted. Uredinium density (UD) was determined as the number of uredinia per centimeter of stem length when all had erupted. The significance of differences in LP and UD among cultivars and pathotypes was tested by analysis of variance ($P \leq 0.05$) and Tukey's procedure (15).

Prevalence of *Sr24* virulence during 1985. After abnormally high summer rains in the wheat production areas of the southern and eastern Cape, a rust survey to assess oversummering of inoculum was conducted during the beginning of March 1985.

RESULTS

During March 1985, stem rust survived on volunteer wheat plants and *H. murinum*, furnishing an adequate inoculum level for the following wheat season.

Pathotype identification. From the rust survey, two new pathotypes were identified and designated 2SA100 and 2SA101 (2 identifies *P. g.* f. sp. *tritici*, SA = South Africa, and 100 = record number for each distinctive pathotype). The avirulence/virulence formulas were as follows: 2SA100 (*Sr8b,9e,9g,13,15,21,22,25,26,27,29,30,31,32,35,36,37,Tt3,dp2,* TAF2d, Enterlago de Montijo/*5,6,7a,7b,8a,9b,9g,10,11,12,14,16,17,18,19,20,24,28*) and 2SA101 (*8b,9e,13,15,21,22,25,26,27,29,30,31,32,36,37,Tt3,dp2,* TAF2d, Enterlago de Montijo/*5,6,7a,7b,8a,9b,9g,10,11,12,14,16,17,18,19,20,24,28*). Detailed IT responses for 70

differential lines, representing 46 single host genes, for resistance to *P. g.* f. sp. *tritici* pathotypes 2SA100, 2SA101, 2SA48, and 2SA52, are presented in Table 1. Data indicated that 2SA100, standard race 222 on the Stakman et al key (14), and 2SA101, standard race 34 (14), only differ in avirulence and virulence, respectively, for *Sr9g* (Acme). Comparing 2SA100 and 2SA101 with selected pre-1984 pathotypes, we found that 2SA100 could not be distinguished from 2SA48 nor 2SA101 from 2SA52, except for their *Sr24* response. A further characteristic of the 2SA100 and 2SA101 pathotypes was their moderate virulence to host lines with *Sr7b*(Marquis). Variable IT scores, 2+3, 3c, 33+, and 3+c, led Le Roux (3) to conclude that 2SA100 was standard race 343 (14). The present study showed, however, that both 2SA100 and 2SA101 were relatively virulent on Marquis, ISr7bRa, and CS Hope4b (Table 1) compared with pathotype 2SA10 (standard race 98), which produced IT 2− on the stocks.

Pathotypes 2SA100 and 2SA101 constituted 58 and 5%, respectively, of survey cultures during 1984. A similar situation prevailed during 1985, when the corresponding frequencies were 55 and 6%. The distribution of 2SA100 and 2SA101 for 1984 and 1985 is indicated in Figure 1. Pathotype 2SA100 was confined to the wheat production areas of the southern Cape, Natal, Transvaal, and eastern Cape during 1984 but spread to the adjacent areas of the southwestern Cape, eastern Cape, and Orange Free State in the following season. Yield losses as great as 75% were experienced in the Albertinia region of the southern Cape. In contrast to 2SA100, pathotype 2SA101 occurred only in the southern Cape in 1984, then spread to the eastern Cape region and Transvaal in 1985.

Responses of Agent and related genotypes to pathotypes virulent for *Sr24*. The seedling responses of Agent and 12 other lines with *Sr24* to pathotypes 2SA100 and 2SA101 and those from which they in all probability were derived, 2SA48 and 2SA52, are given in Table 2. Increased virulence for *Sr24* in 2SA100 and 2SA101 was clearly indicated by the responses of 12 lines representing six genetic backgrounds. Two response groups were evident. Lines Bt*Sr24*Ag, 3Ag#1, 3Ag#3, Agent/6*Inia, Agent/7*Ska, Bt*Sr24*Agent, and Agent/4*Yecora70 responded with fully susceptible reactions, clearly confirming the full virulence of the pathotypes for *Sr24* and also the presence of *Sr24* in these lines. The second response group included Agent (CI 13532), Agent/5*Yecora70, and Agent/2*Yecora70 and gave distinctly less susceptible responses with 2SA100 and 2SA101. All lines carrying *Sr24* gave typically low responses for *Sr24* when inoculated with the avirulent pathotypes (Table 2).

Table 2. Seedling infection types produced by Agent and related genotypes inoculated with four *Puccinia graminis* f. sp. *tritici* pathotypes

Line/cultivar	Source of seed[a]	*P. g.* f. sp. *tritici* pathotype[b] 2SA100	2SA101	2SA48	2SA52	*Sr24*
Bt*Sr24*Ag (Baart Ag-2)	Univ. Minn.	4	3+[c]	2−	2−	+
Bt*Sr24*Ag (resel)	Univ. Minn.	4	33+	1+	1+	+
3AG#1	Univ. Sydney	4	3+	12−	12−	+
3AG#3	Univ. Sydney	4	3+	12−	12−	+
Agent/6*Inia66	1984LRRM/124	33+	3+	12=	12=	+
Agent/6*Inia66	1984LRRM/125	3+	3+	12=	12=	+
Agent/7*Ska	1984LRRM/144	3+	3+	;1=	1−	+
Agent/7*Ska	1984LRRM/145	3+	3+	12=	12=	+
Baart*Sr24*Agent	1984ISWRN/13	4	4	12−	12−	+
Agent/4*Yecora70	1984LRRM/80	3+	4	;12=	12=	+
Agent (CI 13532)	Univ. Sydney	2++3−	2++3	12=	12=	+
Agent/5*Yecora70	1984LRRM/79	3	1++3	;12=	;12=	+
Agent/2*Yecora70	1984LRRM/81	3	1++3	12=	12=	?
Morocco		4	4	4	4	−

[a] LRRM = leaf rust resistant material nursery, CIMMYT. ISWRN = International Spring Wheat Rust Nursery.
[b] South African designation for *P. g.* f. sp. *tritici* pathotypes. For avirulence/virulence formulas, see text.
[c] + = Present and − = absent.

Table 3. Seedling infection types of South African wheat cultivars inoculated with *Puccinia graminis* f. sp. *tritici* pathotypes virulent and avirulent for *Sr24*

Cultivars	*P. graminis* f. sp. *tritici* pathotype 2SA100	2SA101	2SA48	2SA52	*Sr24*
Gamka	4	4	12−[a]	12−	+
SST44	33+	2++3	;1=	;1=	+
SST25	3	2++3	12=	12=	+
Palmiet	33+	33+	;1+	;1+	+
Kinko	33+	3+	1+2	1+2	+
SST102	33+	2++3	12−	12=	+
Wilge	1++3	2++	2−	2−	?
Karee	1++3−	1++3−	1−	1−	?
Morocco (check)	4	4	4	4	−

[a] + = Present and − = absent.

Responses of South African wheat cultivars to pathotypes virulent for *Sr24*. The seedling reactions of eight South African commercial cultivars to pathotypes 2SA100 and 2SA101 and the pathotypes from which they were in all probability derived, are presented in Table 3. Significantly increased virulence of 2SA100 and 2SA101 compared with that of 2SA48 and 2SA52 provided evidence of the presence of *Sr24* in Gamka, SST44, Kinko, Palmiet, SST25, SST102, and possibly, Wilge and Karee.

Although Palmiet, SST25, and SST102 responded with a significantly increased seedling IT, these cultivars were only moderately susceptible (20% severity) at the mature-plant stage. In contrast, the adult-plant response of Gamka and SST44, when compared with seedling IT, increased from 40% moderately susceptible to 70% susceptible. Yield losses in these two cultivars ranged between 17 and 75%.

LP and UD responses. Virulence enhancement, as indicated by the seedling data, was confirmed during the adult-plant stage by calculating the corresponding effect on the LP (Table 5) and UD (Table 6) of Agent, SST44, and Gamka by pathotypes 2SA100 and 2SA48. Because Kinko, Palmiet, and SST25 did not support sporulation when inoculated with the *Sr24*-avirulent pathotype (2SA48), their LP and UD responses to pathotype 2SA100 with those of Morocco, Gamka, SST44, and Agent are presented separately (Table 4).

Table 4. Latent period (LP) and mean uredinium density (UD) responses of South African wheat cultivars inoculated with a *Puccinia graminis* f. sp. *tritici* culture (2SA100) virulent for *Sr24*[y]

Cultivar	LP (hr)	UD
Morocco (check)	138.56 a[z]	9.61 a
Gamka	158.38 a	9.72 a
SST44	160.26 a	8.35 ab
Agent	213.49 b	6.25 cd
Kinko	226.19 b	7.48 bc
Palmiet	234.47 b	7.03 c
SST25	267.16 c	5.64 d

[y] LP = number of hours from inoculation to 40% uredinia formed and UD = number of uredinia per centimeter of stem length.
[z] Values are means of 12 replicates. Means followed by the same letter are not significantly different ($P = 0.05$) according to Tukey's procedure.

When compared with 2SA48, pathotype 2SA100 reduced the LP of Agent, SST44, and Gamka by 38, 33, and 37%, respectively ($P \leq 0.05$). SST44 and Gamka responded to these pathotypes with LPs similar to Morocco, the susceptible check. Although susceptible in terms of lesion size, Agent had an LP significantly longer than that determined for SST44 and Gamka. Considering the pathotype means, 2SA100 significantly increased the UD (Table 6). The UDs of SST44 and Gamka were increased by 47

and 39%, respectively. In contrast to LP, the UD for Agent decreased after inoculation with pathotype 2SA100. This may indicate that background germ plasm can independently modify the expression of these two resistance components.

Cultivars Kinko and Palmiet had LP and UD values similar to that of Agent, with SST25, which was the longest LP and lowest UD of all cultivars tested.

DISCUSSION

Comparative seedling and adult-plant evaluations with two *P. g.* f. sp. *tritici* pathotypes, 2SA100 and 2SA101, isolated during 1984 in South Africa from the cultivars SST44 and Gamka, clearly showed that the pathogen was virulent on cultivars carrying the *Sr24* gene. The frequent incidence of pathotype 2SA100, 58% of all isolates in 1984 and 55% in 1985, suggests that it may have been prevalent in the population some time before detection and gone undetected as a result of the preceding drought. Similar important changes in the rust flora, which remained undetected for at least a year, have also occurred elsewhere (7,10).

Comparative infection type studies between pre- and post-1984 pathotypes suggest that 2SA100 and 2SA101 were single-locus mutations from 2SA48 and 2SA52, respectively. Pathotype 2SA48 predominated in the South African virulence surveys until 1981, with 2SA52 constituting 6% of isolations from the western Cape during 1981 (J. Le Roux, *unpublished*). Alternatively, there may have been a mutation with respect to *Sr24*, with a second event affecting the gene corresponding to *Sr9g*, considering the high mutation rate documented for this pathogen gene (6). Because the first alternative involves only a single-step mutation, it is the favored explanation.

P. g. f. sp. *tritici* pathotypes 2SA100 and 2SA101 constituted 64% of all survey collections for 1985 (J. Le Roux, *unpublished*). Pathotype 2SA100 has been isolated from every major wheat-producing area in South Africa, whereas 2SA101 has been restricted to the south-western Cape and Transvaal. The wide virulence range of both pathotypes, with respect to both current and older cultivars, could explain the rapid increase in prevalence, especially during 1984. Moreover, pathotypes 2SA100 and 2SA101 appear to combine their increased virulences with aggressiveness and good survival abilities.

At present, *P. g.* f. sp. *tritici* pathotypes with virulence for *Sr24* constitute a threat to wheat production in the winter rainfall and irrigation areas of South Africa, because three of the seven recommended cultivars for these areas are susceptible to both pathotypes. Nine of the 23 cultivars currently recommended in South Africa possess *Sr24* either alone or in combination with other resistance factors.

Susceptibility of cultivated wheats in terms of LP and UD separated cultivars into three distinct response classes, viz., fully compatible SST44 and Gamka; moderately susceptible Kinko, Palmiet; and moderately resistant SST25.

When the presence of *Sr24*-virulent pathotypes was demonstrated during 1984, SST44 and Gamka were removed from the list of recommended cultivars in high-risk areas. However, rapid replacement of a prominent cultivar such as SST44 presents major logistical problems. Meanwhile, SST44 and other susceptible cultivars continue to be

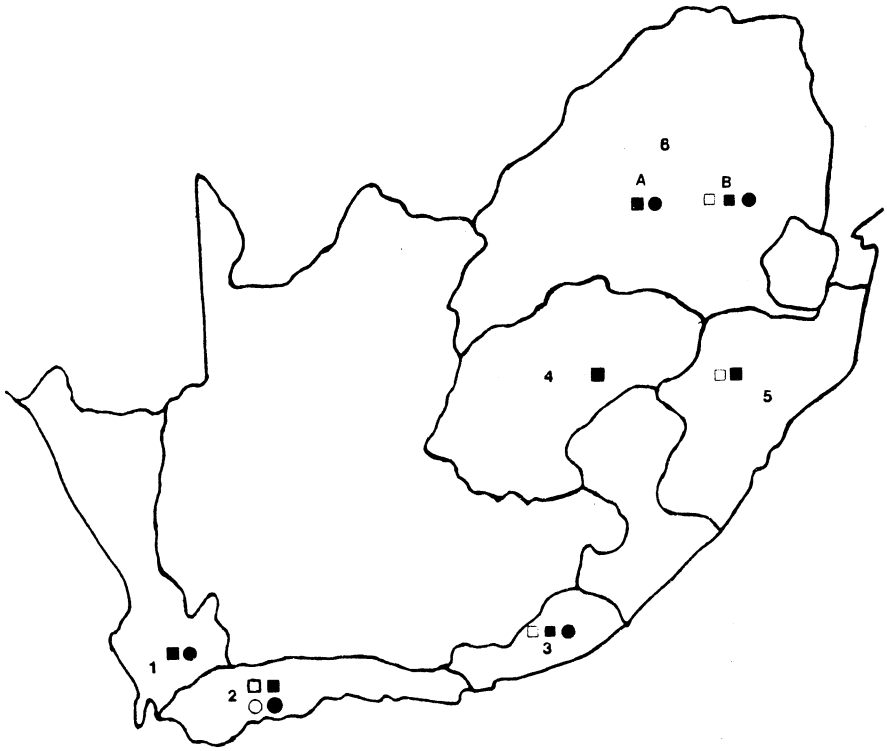

Fig. 1. Ecological areas for wheat production and the occurrence of *Puccinia graminis* f. sp. *tritici* pathotypes 2SA100 and 2SA101 in South Africa. Area 1: western Cape Province, hard red spring wheats, winter rainfall region, dryland; area 2: southern Cape Province, hard red spring wheats, winter rainfall region with limited summer rains, dryland; area 3: eastern Cape Province, hard red spring wheats, winter rainfall region, dryland; area 4: Orange Free State, hard red winter wheats, summer rainfall region, dryland; area 5: Natal, hard red spring wheats, summer rainfall region, predominantly under irrigation; and area 6: Transvaal, hard red spring wheats, summer rainfall region: A = Springbokvlakte, dryland, and B = Groblersdal, irrigated. □ = 2SA100, 1984; ■ = 2SA100, 1985; o = 2SA101, 1984; and • = 2SA101, 1985.

Table 5. Mean latent period for various host-pathogen combinations resulting from inoculation of adult plants with *Puccinia graminis* f. sp. *tritici* pathotypes virulent (2SA100) and avirulent (2SA48) for *Sr24*

	Latent period (hr)[y]				
Pathotype	Morocco	Agent	SST44	Gamka	Pathotype mean
2SA48	153.23 a[z]	343.94 d	241.05 bc	253.36 c	247.89 h
2SA100	138.56 a	213.49 b	160.76 a	158.38 a	167.80 i
Cultivar mean	145.89 e	278.72 g	200.90 f	205.87 f	

[y] Latent period expressed as number of hours from inoculation to 40% uredinia formed.
[z] Values are means of 12 replicates. Means followed by the same letter are not significantly different ($P = 0.05$) according to Tukey's procedure.

Table 6. Mean uredinium density values for various host-pathogen combinations resulting from inoculations of adult plants with *Puccinia graminis* f. sp. *tritici* pathotypes virulent (2SA100) and avirulent (2SA48) for *Sr24*

	Uredinium density[y]				
Pathotype	Morocco	Agent	SST44	Gamka	Pathotype mean
2SA48	9.83 a[z]	7.90 b	5.67 d	6.99 bc	7.60 f
2SA100	9.61 a	6.25 cd	8.35 b	9.72 a	8.48 e
Cultivar mean	9.72 g	7.07 i	7.01 i	8.36 h	

[y] Uredinium density values are expressed as the number of uredinia per centimeter of stem length.
[z] Values are means of 12 replicates. Means followed by the same letter are not significantly different ($P = 0.05$) according to Tukey's procedure.

cultivated on alarmingly large areas.

Differences in susceptibility among host lines having *Sr24* were evident in both seedling and adult plant stages. Bt*Sr24*Ag, 3Ag#1, and 3Ag#3 were fully susceptible to pathotypes 2SA100 and 2SA101, whereas Agent was moderately susceptible. The lower seedling response of Agent to these pathotypes was obvious when compared with the fully susceptible SST44 and Gamka. These differences were further supported by the significantly longer LP and lower UD values obtained with adult plants. Nevertheless, Agent must be regarded as susceptible in terms of size and type of pustules as well as LP and UD. In inheritance studies of Agent, Gough and Merkle (2) and McIntosh et al (9) demonstrated the presence of additional genes for resistance to certain pathotypes. The presence of such additional resistance factors, as well as differences in genetic background, may explain the lower seedling and adult plant reactions of Agent compared with those of SST44 and Gamka.

In the development of commercial wheat cultivars resistant to the prevailing pathotypes of *P. g.* f. sp. *tritici* in southern Africa, wheat breeders have exploited a number of resistance genes. These genes, including *Sr9e, Sr36, Sr24,* and *Sr31,* mostly derived from species related (12) to *T. aestivum*, were used on an individual basis to broaden the genetic diversity between cultivars rather than in the enhancement of resistance reserves within the same cultivar. The present study, as well as that of Lombard (4), clearly shows that the incorporation of single resistance genes has placed the rust resistance of South African cultivars on a very narrow genetic base. Furthermore, there is no evidence that resistance transferred from species such as tetraploid (*T. timopheevi, Sr36*; *T. turgidum, Sr9e; T. elongatum, Sr24*) or diploid (*T. monococcum, Sr21*) species will prove durable when used individually. Therefore, care must be taken to accumulate, within the same cultivar, newly found resistance to the complete virulence spectrum of stem rust in proven combinations.

To expedite this, carefully selected pathotypes, such as the *Sr24*-virulent pathotypes identified in this study, must be used. In addition, international cooperative testing, making use of critical pathogen genotypes available in other countries, will need to be conducted on a much broader basis than is the case at present.

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