Deviation from the Regression of Infection on Heading and Height as a Measure of Resistance to Septoria tritici Blotch in Wheat

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ABSTRACT

van Beuningen, L. T., and Kohli, M. M. 1990. Deviation from the regression of infection on heading and height as a measure of resistance to Septoria tritici blotch in wheat. Plant Dis. 74:488-493.

Data acquired over three years (1984–1986) on Septoria tritici blotch reported from the Advanced Lines of the Southern Cone (LACOS) wheat nursery, were analyzed and an average relative coefficient of infection was calculated for each entry in each year. In all three years, a significant negative correlation was found between Septoria tritici blotch and days to heading and height, which accounted for nearly half the variance in infection by Septoria tritici. A resistance parameter, deviation from the regression of the infection on heading and height, was defined by eliminating the linear effect of escape mechanisms through late heading or tall stature. This parameter is considered the best measure of true genetic resistance, which is of most interest to breeders. It facilitated identification of the most resistant germ plasm, using disease notes taken at a single critical moment. Germ plasm that originated in areas prone to epidemics by S. tritici, all of which are under strong maritime influence or are in the Parana River Basin, generally had higher levels of true resistance as well as escape mechanisms, resulting in reduced field infection. For breeding value, however, some earlier, shorter lines showing intermediate infection levels are thought to be superior.

Additional keywords: Triticum aestivum, Mycosphaerella graminicola, South America

Septoria tritici blotch, caused by Septoria tritici Rob. in Desm., (teleomorph, Mycosphaerella graminicola (Fuckel) Schröt.), constitutes a major disease problem of wheat (Triticum aestivum L.) throughout the Southern Cone region of South America, consisting of Argentina, Bolivia, Brazil, Chile, Paraguay, and Uruguay, and in other wheat-growing areas of the world. One of the areas in South America known to be most severely affected is the Argentinian pampa humeda, the humid rainfed plains of this country, where maximum disease pressure is found in areas along the Parana river, e.g., Pergamino (1). Southern Uruguay,

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Accepted for publication 3 January 1990 (submitted for electronic processing).

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considered a continuation of this area, is also commonly affected by the disease (5,19). Further north, in the Brazilian state of Rio Grande do Sul, wheat commonly sustains severe blotch problems, but here S. tritici is second in importance to Leptosphaeria nodorum Müller (anamorph: Septoria nodorum (Berk.) Cast. & Germ.) (11). In Chile, Septoria tritici blotch affects the major part of the wheat-growing area, the central-southern wheat areas and the rainfed coastal plains, where the early-planted facultative and spring wheats are especially affected (6).

Host resistance is the most effective and economic means to reduce yield losses from this disease. Avoidance of early seeding, especially when using short-cycle spring wheats, is often an effective measure by which to escape disease (5,6). Farmers in areas with high disease pressure and a low ratio of fungicide price to wheat price, such as Southern Brazil and some areas in Chile, generally complement host resistance with chemical control, mostly using systemic fungicides from the triazole group of ergosterol biosynthesis-inhibiting compounds (10). However, the most recent trend of decreasing wheat prices and stable or increasing fungicide prices in the region has resulted in greater emphasis on host resistance.

In 1981, the Southern Cone countries of South America established a network for exchange and evaluation of wheat germ plasm, through the yearly distribution of the Advanced Lines of the Southern Cone (LACOS) nursery. This nursery is commonly sown at 40 locations, and most newly released wheat cultivars from Southern Cone breeding programs, whether resulting from local crosses or being direct introductions, have been included in this nursery.

Yearly visits of the authors and their colleagues have contributed to standardization of evaluation criteria. Sufficient data has been received from all LACOS nurseries to allow reliable and precise conclusions to be drawn on resistance of the germ plasm to the most prevalent wheat diseases of the region, including leaf, stem, and stripe rusts and also Septoria tritici blotch. Furthermore, observations on plant height, days to heading, local adaptability, etc., have been important in interpreting the adaptation of the entries at each site.

In the present article, an innovative analysis of the data on Septoria tritici blotch from three recent (1984, 1985, and 1986) LACOS nurseries is described, aimed at improving the interpretation of the data reported in the yearly publications of LACOS results (7,8,20). Along with the characterization of the germ plasm in terms of reaction to Septoria tritici blotch, the relationships between disease reaction and plant stature, days to heading (decimal growth stage 57 [22]), and site of selection of each entry were analyzed.

MATERIALS AND METHODS

Most collaborators used the recommended double-digit (DD) scale for assessment of leaf blotch diseases (4), which was accepted as the standard during a Latin American workshop on leaf blotch diseases of wheat, held at Passo Fundo, Brazil, in October 1983. The DD scale has found wide acceptance throughout the region because of its advantages over the Rosielle (12) and Saari-Prescott (15) scales. Relative height of disease on the plant (first digit) and average severity of necrotic leaf area (second digit), each registered on a linear 0-9 scale, constitute important parameters for explaining yield losses caused by this disease. Disease assessment using this scale can be fast and reasonably accurate, and its linearity facilitates processing and comparison. For sites where the DD scale was used, a coefficient of infection was derived by multiplying the two digits. The Saari-Prescott scale (15), still widely used, is reported for some sites. Only sites where the infection score of the most susceptible entry reached at least 60% of the maximum of the evaluation scale, and where the frequency of "zero-disease" was low, were included in the analysis. Low inoculum levels would allow entries to escape from disease and thus lead to erroneous conclusions as to resistance.

To calculate a balanced average, original disease scores were converted into relative values, expressed as a percentage of the maximum reading at the same site and referred to as the relative coefficient of infection (RCI). The RCI proved to be a far more important indicator of germ plasm performance than the original disease readings. For instance, a reading of 5/5 is high when the maximum reading is 6/6 (RCI = 69%) but is low when the maximum is 9/9 (RCI = 31%).

For the three years' data that were analyzed, the following parameters were calculated: 1) Pearson's linear correlation coefficients between disease readings from different locations, to assess the representativity of different evaluation sites; 2) differential performance (average RCI values) of entries from different origins, distinguishing the following zones on the basis of agroclimatic conditions and origin of germ plasm: a) Argentina b) Southern Brazil (Rio Grande do Sul and southern Parana) and Uruguay, c) Central Brazil (northern Parana, Sao Paulo) and Paraguay, and d) Chile; 3) linear regression of the RCI for Septoria tritici blotch (average over locations) on days to heading (average over locations); 4) linear regression of the RCI for Septoria tritici blotch (average over locations) on plant height (average over locations); 5) multiple linear regression of the RCI for Septoria tritici blotch (average over locations) on days to heading and plant height (average over locations); and 6) for each entry, the deviation from the multiple linear regression of the RCI on days to heading and plant height, expressed in units of the standard error of regression. The observed RCI (Y) is expressed as a linear function of days to heading (X_1) and plant height (X_2) , giving the equation: $Y = \alpha + (\beta_1 \times X_1) + (\beta_2 \times X_2) + e.$ The error term e constitutes an improved approximation of the true genetic resistance, here defined as those components of resistance that do not depend on days to heading and plant height, although it also includes nonlinear effects of days to heading and height and environmental error. Expressing e in units of the standard error of regression allows an immediate relative interpretation of the resistance. This value is referred to as the deviation from the regression of the infection on heading and height (DRIHH). A value of -2.0for an entry implies that it would be situated two units of the standard error below the regression plane and indicates that it has considerably less infection than can be explained by the linear effects of its heading and height.

RESULTS AND DISCUSSION

The locations that reported Septoria tritici blotch for the years 1984-1986 used two different evaluation scales and showed different degrees of infection (Table 1). Days from seeding to heading (Fig. 1) represent an average of six reporting sites in 1984 and 1985 and five sites in 1986. These sites were, for 1984: Bethlehem (R. S. Africa), Cd. Obregon (Mexico), Corvallis (U.S.A.), Londrina (Brazil), Santiago (Chile), and Toluca (Mexico); for 1985: Chillan (Chile), Hidango (Chile), Londrina (Brazil), Roque Saenz Peña (Argentina), Santiago (Chile), and Toluca (Mexico); and for 1986: Cd. Obregon (Mexico), Cochabamba (Bolivia), Hidango (Chile), Sta. Catalina (Ecuador), and Sta. Cruz (Bolivia). The value for plant height is an average of 10, eight, and six locations respectively for the 1984, 1985, and 1986 nurseries, mostly the same locations that reported days to heading.

Since locations reporting data on Septoria tritici blotch did not always provide heading and height data, it was not possible to correct the Septoria tritici blotch assessments at individual locations. However, the high correlation that was found among different locations for plant height and also for days to heading $(0.7 \le r \le 0.8)$ suggests that averages of these traits across locations constitute reliable figures.

Correlation coefficients between locations for scores of Septoria tritici blotch were low but significant (Table 2). Colonia, Pergamino, Toluca (1 yr only), Cruz Alta (1 yr only), and possibly Hidango appear to be sites that are most representative of other locations, but data presented here do not provide sufficient support for selection of the best screening sites. Two factors that may have reduced the correlation coefficients among locations are genotype × environment interactions and variation in pathogenicity patterns (3) among locations.

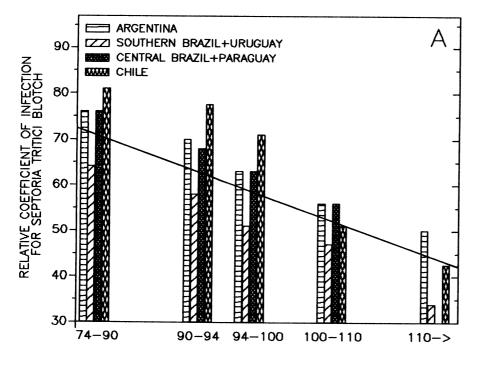
For the purpose of visualization, the entries were classified into five heading groups for each of the years 1984, 1985, and 1986, in such a way that each group represented at least 40 entries. Within each of these heading groups, important differences in disease scores were found among groups of germ plasm selected in different areas (Fig. 1). These results suggest that: 1) significant variation exists in the germ plasm under study for resistance to Septoria tritici blotch and this can be used for selection of more resistant entries, and 2) the level of resistance is closely related to the level of disease pressure. In effect, the consistently high disease pressure in Southern Brazil and Uruguay has made it possible for breeders to accumulate a higher level of resistance in entries from these areas, whereas the intermediate level of resistance found in wheats from

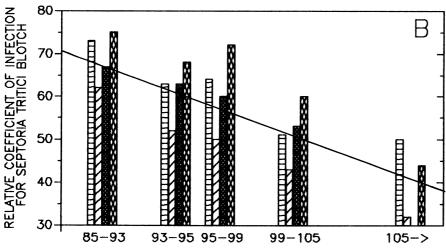
Table 1. Locations, evaluation scales used, and maximum disease ratings scored by collaborators reporting Septoria tritici blotch, 1984–1986

Year	Location	Country	Scale	Maximum rating		
1984	Balcarce	Argentina	0-9 ^y	8		
	Colonia	Uruguay	$0-9/0-9^{z}$	8/9		
	Pergamino	Argentina	0-9/0-9	9/9		
	Toluca	Mexico	0-9/0-9	8/7		
1985	Balcarce	Argentina	0-9/0-9	8/8		
	Colonia	Uruguay	0-9/0-9	8/9		
	Cruz Alta	Brazil	0-9/0-9	9/8		
	Hidango	Chile	0-9/0-9	8/8		
	Parana	Argentina	0-9/0-9	8/8		
	Pergamino	Argentina	0-9	8		
1986	Balcarce	Argentina	0-9	7		
	Colonia	Uruguay	0-9/0-9	8/7		
	Hidango	Chile	0-9/0-9	8/8		
	Patzcuaro	Mexico	0-9	9		
	Pergamino	Argentina	0-9	8		

^ySaari-Prescott scale (15).

^zDouble-digit scale (4).





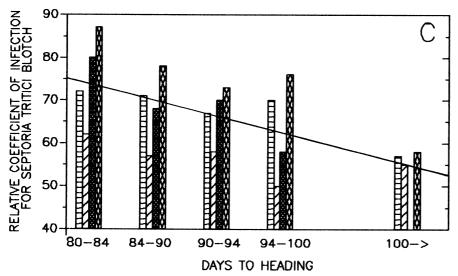


Fig. 1. Relationships between days to heading and Septoria tritici blotch, according to the origin of the entries, with corresponding linear regression lines, during three years. (A) 1984: 308 entries, Y = 136.6 - 0.80X, $r^2 = 0.41$. (B) 1985: 283 entries, Y = 176.6 - 1.23X, $r^2 = 0.32$. (C) 1986: 230 entries, Y = 130.9 - 0.70X, $r^2 = 0.23$. Heading groups are arranged to include at least 40 entries each. Values for days to heading represent means of six, six, and five locations for 1984, 1985, and 1986, respectively.

Argentina may be a reflection of the intermediate levels of disease pressure. Central Brazil and Paraguay also show an intermediate level of resistance, possibly because these areas introduced a high proportion of lines that possess resistance genes to leaf blotches, developed by CIMMYT from the winter wheat cultivars Kavkaz and Aurora. Disease pressure in Chile can be severe in the rainfed areas, but low virulence of isolates of S. tritici in Chile, compared to those from Uruguay and Argentina, may have contributed to the observed low levels of resistance in their wheat selections at a regional level (3).

The regression lines of the RCI on days to heading for the years 1984–1986 are included in Fig. 1. A significant negative linear relationship is shown between days to heading and Septoria tritici blotch in all three years. This is thought to be the combined effect of three independent causes, the first of which is an escape mechanism and the other two artifacts of the disease-screening methodology and analysis.

The later-maturing lines will sometimes remain relatively disease free because environmental conditions become progressively less favorable for disease, particularly in mediterranean climates that have dry summers. In the Southern Cone region, however, with the exception of Chile, periods of rain and high humidity are common even toward the end of the season. Therefore, the component of resistance that is independent of lateness plays an important role in that area.

It is customary to score disease infection in breeding nurseries at a single critical date for the entire nursery. Latematuring entries will very likely be found less infected, since their upper leaves have been exposed to the disease for a shorter time in comparison with early-maturing entries. A more correct evaluation requires that entries be scored at an identical growth stage, although this might result in underestimation of the resistance of late entries, which would be exposed to the higher inoculum built up on earlier entries.

In the late group of entries, lines from Uruguay and Southern Brazil were overrepresented. Since these areas contribute lines that seem to have a higher level of resistance, the average RCI of the late lines may have been reduced and have resulted in an underestimation of the breeding value of these lines.

Weaker but significant negative correlations were observed between plant height and Septoria tritici blotch. The taller entries, including mainly lines that represent traditional germ plasm from Brazil and Uruguay, tended to show lower infection levels, but the relation was weak enough to allow selection of semidwarf wheats with improved resistance. A possible explanation for this

negative correlation is that the tall entries present a physical barrier to the pathogen, since leaves are further apart, which may hinder upward spread by splash dispersal of conidia. The foliage on taller plants may also constitute a less favorable microclimate for the disease (18).

The combined effect of days to heading and plant height on the RCI for Septoria tritici blotch, using multiple linear regression analysis for the data of 1984, is shown in Fig. 2. When the observed RCI (Y) is plotted against the fitted RCI (\hat{Y}) , the distance to the "1:1 line" $(Y = \hat{Y})$ for each entry (i.e., the error term from the regression), expressed in units of the standard error of regression, represents the DRIHH value. By inverting the Xaxis scale, the "1:1 line" acquires a negative slope that reflects a decreasing RCI with increasing values for days to heading and plant height ($\alpha - \hat{Y}$, on the upper X-axis). DRIHH is negative if the observed RCI is less than the expected value. Also, it can be observed from these figures that the residues have a random distribution along the "1:1 lines," a condition for validation of the described procedure.

The combination of both independent agronomic characteristics accounted for close to half of the variance in Septoria tritici blotch infection (Table 3). The estimates for the regression coefficients of the RCI on days to heading (β_1) and height (β_2) indicate that for every 10 days of delay in heading, a reduction of 8% is expected for the RCI, and for every 10-cm increase in plant height, the RCI is reduced by approximately 5%, in this wide range of Southern Cone advanced lines.

Saari (14) described the relationships found between days to heading, plant height, and Septoria tritici blotch in a nursery consisting of 1,100 entries that was evaluated at a single critical date. The trend reported in that study, represented by linear regression coefficients of -1.16 for Septoria tritici blotch with days to heading and -0.89 with height, corresponds remarkably well with the relationships described above. The smaller values associated with plant height reported here, in comparison with the results of Saari, are possibly due to the recent successful incorporation of resistance into semidwarf wheats (9).

The associations observed between shortness, earliness, and susceptibility may be due to chance coincidence of these traits in parental lines, to pleiotropic effects, or to genetic linkage (17). Chance may have played an important role in the past, when early semidwarf wheats from CIMMYT with increased yield potential were selected in the absence of adequate pressure by Septoria tritici blotch. When these wheats were compared with traditional, tall, late wheats that had been selected under natural pressure by Septoria tritici

blotch, they appeared highly susceptible.

The artifact created by the single-date evaluation, the possible escape mechanisms offered by the more difficult upward spread of disease in tall plants, and the lower infection due to the drier

conditions encountered by late entries would all be perceived as pleiotropic effects. In the case of Septoria nodorum blotch, part of these pleiotropic effects could be separated from escape mechanisms, as evidenced by detecting

Table 2. Averages for the values of the Pearson's linear correlation coefficient (r) of Septoria tritici blotch scores of each location with scores of all other locations

Location	Country	1984 ^x	1985	1986	Mean
Colonia	Uruguay	0.44 ^z	0.39	0.39	0.41
Toluca	Mexico	0.40	•••	•••	0.40
Cruz Alta	Brazil	•••	0.35	•••	0.35
Pergamino	Argentina	0.39	0.30	0.29	0.33
Hidango	Chile	•••	0.43	0.19	0.31
Patzcuaro	Mexico	•••	•••	0.30	0.30
Parana	Argentina	•••	0.29	•••	0.29
Balcarce	Argentina	0.32	0.22	0.28	0.27

^xMean correlation coefficient over location combinations: 1984, n = 3; 1985, n = 5; 1986, n = 4.

^zAll values for correlation coefficients were significant (P = 0.01).

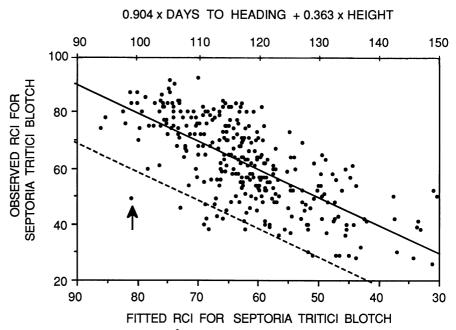


Fig. 2. Relationship between fitted (\hat{Y}) and observed (Y) relative coefficient of infection (RCI) for Septoria tritici blotch for 1984 data. A scale showing the fitted combination (Table 3) of days to heading and plant height is given on the upper axis $(-\hat{Y} + \alpha)$. Included are the 1:1 line (solid), where $Y = \hat{Y}$, and the broken line, where DRIHH = -2.0, positioned two standard errors of regression below it. The entry considered most resistant according to the DRIHH criterion is marked with an arrow.

Table 3. Regression models describing the relations between days to heading (X_1) , plant height (X_2) , and the relative coefficient of infection (RCI) for Septoria tritici blotch (Y) for 1984–1986

Year	Independent variables	Regression equation	r^2	Sx
1984	Heading ^y	$Y = 136.6 - 0.80 X_1$	0.41	7.8
	Heightz	$Y = 100.9 - 0.49 X_2$	0.17	9.3
	Heading, height	$Y = 179.8 - 0.90 X_1 - 0.36 X_2$	0.48	10.8
1985	Heading	$Y = 176.6 - 1.23 X_1$	0.32	11.6
	Height	$Y = 110.9 - 0.58 X_2$	0.25	12.2
	Heading, height	$Y = 182.0 - 0.79 X_1 - 0.50 X_2$	0.47	10.3
1986	Heading	$Y = 130.9 - 0.70 X_1$	0.23	11.0
	Height	$Y = 118.0 - 0.55 X_2$	0.18	11.3
	Heading, height	$Y = 172.6 - 0.65 X_1 - 0.49 X_2$	0.37	9.9

^{*}Standard error of regression, used for calculation of the resistance parameter, deviation from the regression of the infection on heading and height (DRIHH).

^y Mean correlation coefficient over location combinations and over years.

^yDays from seeding to heading, average of five to six locations.

² Height in centimeters, average of six to 10 locations.

the same relationship between resistance, heading, and height under artificial inoculation at heading stage (16,17). Height would partly be a reflection of genetic vigor, and more vigor may be related to increased resistance to a weak pathogen (16,17). Also, in the case of S. tritici, pleiotropy seems the more plausible explanation for the associations, although some evidence for linkage has been found (13). Breeding efforts should therefore concentrate on the component of resistance that is independent of lateness and tall stature.

A summary characterization of the germ plasm under study is provided in Table 4, including means over locations and years for the explanatory variables days to heading and plant height and for the dependent resistance measures RCI and DRIHH. The more detailed geographical subdivision in Fig. 1 shows that entries from southern Chile are much later and show reduced infection, even after correction, in comparison to lines from central Chile, which can be explained from the higher precipitation and disease pressure that characterize

southern Chile. Southern Brazil and Uruguay contributed the most resistant germ plasm, but with somewhat different contributions of the escape mechanisms of late heading and tallness.

The regression coefficients allow the identification of the best entries, independent of heading and height effects: those entries that are positioned more than 2.0 standard errors under the regression plane, i.e., those with a DRIHH value lower than -2.0, represent the entire range of height and maturity classes (Table 5). Selection based on this criterion puts maximum pressure on the resistance component that is independent of linear effects of height and days to heading, e.g., those genes that determine resistance of the leaf tissue.

The output of this procedure shows a strong presence of resistance derived from cv. Bezostaya-1 (Aurora, Kavkaz), which has been shown to possess major gene resistance (2). Durability of this resistance has yet to be shown by observations of recently released sister lines of Bobwhite and KVZ/K4500L.A.4.

Table 4. Means and standard deviations over locations and years (1984–1986) for days to heading, plant height, relative coefficient of infection (RCI), and DRIHHz values for Septoria tritici blotch, according to geographical origin of entries

	No. of entries		Days to	Height	Septoria tritici blotch		
Origin	1984	1985	1986	heading	(cm)	RCI	DRIHH
Argentina	57	52	55	99 ± 11	87 ± 7	61 ± 11	0.14 ± 0.9
Central Brazil	74	55	51	91 ± 6	91 ± 9	66 ± 12	0.16 ± 1.1
Southern Brazil	58	77	43	95 ± 6	102 ± 7	52 ± 11	-0.47 ± 0.9
Central Chile	40	30	37	94 ± 6	83 ± 6	73 ± 10	0.66 ± 0.8
Southern Chile	26	9	7	115 ± 9	84 ± 5	50 ± 11	-0.04 ± 1.0
Paraguay	40	40	20	94 ± 3	85 ± 6	65 ± 10	-0.09 ± 1.0
Uruguay	13	20	17	105 ± 9	95 ± 9	44 ± 9	-0.60 ± 0.8

^zResistance parameter, corrected for differences in days to heading and height.

Table 5. Southern Cone advanced lines with superior resistance to Septoria tritici blotch

		Origin ^v	Height ^w (cm)	Days to ^x heading	S. tritici	
Year	Cultivar or cross				RCI	DRIHH*
1984	U.S.A. A IV A/GTA"S"	ARG	66	83	49	-2.9
	MRS//KAL/BB/3/AZ	PARY	71	95	38	-2.8
	MRS//KAL/BB/3/AZ	PARY	69	95	40	-2.7
	RABI"S"/FG"S"	ARG	71	90	46	-2.5
	ALD"S"/2*BH1146	BRS	85	89	42	-2.4
	ALDAN"S"/PF70354	BRS	80	94	42	-2.2
1985	TRAP"S"	BRS	92	94	36	-2.4
	BOBWHITE"S"	BRS	84	97	38	-2.4
	KVZ/CJ71	ARG	94	105	27	-2.4
	BOBWHITE"S"	PARY	82	99	38	-2.3
	KVZ/K4500L.A.4	URUY	91	98	37	-2.1
	KVZ/K4500L.A.4	BRS	97	98	34	-2.1
1986	KVZ/K4500L.A.4	BRS	90	88 .	40	-3.2
	BB/GLL//CJ71/3/T AEST//KAL/BB	BRS	100	96	33	-2.9
	IAS58/E7408//ALD"S"/PF7326	BRS	93	82	47	-2.7
	ALD/CNT7/PF70354/3/PAT24//BB/KAL	BRS	96	85	47	-2.4
	IAS20/TP//PF70100	BRS	113	86	42	-1.9
	NS19.92/3/CC/INIA66//CAL	CHILE	80	92	56	-1.8

^vARG = Argentina, BRS = Brazil, PARY = Paraguay, URUY = Uruguay.

Virulence for Aurora (parent of Bobwhite) and, in lower frequencies, for Kavkaz has already been reported from Israel (2). To widen the diversity of resistance genes, resistant lines that are not related to Bezostaya-1 by descent should receive extra attention.

The nurseries in 1984 included some durum wheat entries, which appeared to be among the most resistant material throughout the region, especially after correction for their earliness and short stature. Although this phenomenon may be due to the very limited presence of durum wheats in commercial production in the region, their apparent resistance deserves further evaluation.

The DRIHH parameter is close to the methodology used by collaborators of the Australian Septoria Nursery (21). However, it has the advantage of giving a continuous distribution rather than a discrete classification in heading and height groups. A disadvantage may be its relative complexity, but available standardized computer procedures may facilitate its application.

The same analytical procedure leading to a DRIHH parameter can be applied to other leaf blotch diseases, such as spot blotch caused by Cochliobolus sativus (Ito & Kurib.) Drechs. ex Dastur (anamorph: Bipolaris sorokiniana (Sacc. in Sorok.) Shoem.), tan spot caused by Pyrenophora tritici-repentis (Died.) Drechs. (anamorph: Drechslera triticirepentis (Died.) Shoem.), Septoria nodorum blotch, caused by L. nodorum (anamorph: S. nodorum), and even for Fusarium head blight caused by Gibberella zeae (Schw.) Petch (anamorph: Fusarium graminearum Schwabe). Scores for leaf rust caused by Puccinia recondita Rob. ex Desm. f. sp. tritici, were also found to show a negative association with days to heading as a result of evaluation at a single critical date, and so a correction procedure should also be considered for this disease.

A DRIHH analysis is considered especially useful to take full advantage of results reported from general germ plasm nurseries with wide distribution. For practical reasons, evaluation of each disease is commonly done for the entire nursery at a single critical date. If collaborators can report accompanying data on height and days to heading, correction of readings using the described procedure will be a good way to facilitate improved interpretation of the results.

For nurseries that specifically evaluate resistance to Septoria tritici blotch, the above procedure could be used. Here it would be preferable, however, to take notes at identical growth stages for each entry, preferably at several times, to plant susceptible checks of differing maturity, or to divide the nursery into subnurseries of similar maturity, planted at different dates (4).

^{*}Average of six to 10 locations.

^{*}Average of five to six locations.

y Relative coefficient of infection for Septoria tritici blotch, average of four to six locations.

² Resistance parameter, corrected for differences in days to heading and height.

ACKNOWLEDGMENTS

We are grateful to all collaborators in the joint LACOS nursery effort, and to CIMMYT colleagues, for their valuable suggestions.

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