

Effect of Temperature on Adult-Plant Resistance to Leaf Rust in Wheat

Kalpana Kaul and Gregory Shaner

Former graduate research assistant and professor, Department of Botany and Plant Pathology, Purdue University, West Lafayette, IN 47907. Present address of first author: Department of Plant Pathology, Pennsylvania State University, University Park 16802. Portion of a Ph.D. thesis submitted by the first author to the Graduate School, Purdue University. This work was supported in part by Public Varieties of Indiana. Purdue Agricultural Experiment Station Journal Article 11,684. Accepted for publication 10 October 1988 (submitted for electronic processing).

ABSTRACT

Kaul, K., and Shaner, G. 1989. Effect of temperature on adult-plant resistance to leaf rust in wheat. *Phytopathology* 79:391-394.

Adult-plant resistance provides an important type of protection against leaf rust for soft red winter wheat in the northern part of its range in the United States. In breeding for this resistance and studying its inheritance, we noted that its expression seemed to be influenced by temperature. Experiments were conducted under controlled temperature conditions to examine this phenomenon in greater detail. Several wheat breeding lines and three cultivars were vernalized and then grown in the greenhouse or in growth chambers programmed for various diurnal temperature regimes, ranging from 15/12 to 30/21 C (day/night). Plants were inoculated with a pure culture of *Puccinia recondita* after flag leaves had emerged. The cultivar Morocco, the susceptible control, was consistently susceptible, of infection type (IT) 3⁺. Temperature induced major differences in ITs in all

but three lines with adult-plant resistance: P75438, P76603, and P69195, which were of IT 0 or IT 0c at all temperatures. None of the lines developed a susceptible reaction (IT 3⁺) at the lowest temperature regime, whereas all temperature-sensitive lines developed at least a few IT 3⁺ uredinia at the highest temperature regime. P77121 showed a sudden loss of resistance at high temperature. Coker 79-14, P751909, P76905, and P76779 showed a gradual shift to higher ITs as temperature increased. P751915 remained resistant only over a narrow range of temperature. P74140-6 and P74140-7 showed a higher IT at both high and low temperatures than at intermediate temperatures. The cultivar Compton showed a few IT 3⁺ when grown continuously at 30/21 C, but not when reared at a lower temperature until inoculation.

Additional keywords: environmental effect, *Triticum aestivum*.

The expression of resistance in wheat, *Triticum aestivum* L., to *Puccinia recondita* Rob. ex Desm. is in many cases sensitive to environment. As early as 1926 Mains and Jackson noted the difference in the resistance of the cultivar Hussar to some physiologic races of *P. recondita* after inoculation in autumn or winter compared to inoculation in late spring (18). Since then considerable research has been done on the effect of environment, mainly temperature, on leaf rust resistance in wheat. Browder's review includes information about the relative environmental sensitivity of 35 *Lr* genes, which he categorized as having low,

moderate, or high sensitivity (3). All known *Lr* genes are sensitive to postinfection temperatures, and of these, *Lr* 12, *Lr* 13, *Lr* 22a, *Lr* 22b, and *Lr* 26 can be detected only by inoculation of adult plants.

Adult-plant resistance to leaf rust has been extensively used in the Purdue-USDA wheat-breeding program. Nearly all of the cultivars developed in this program have adult-plant resistance, expressed as a low infection type (IT). Because leaf rust rarely develops in the northern part of the soft red winter wheat region until after the stem elongation stage of growth, this adult-plant resistance provides effective control of the disease. In a study of the inheritance of adult-plant resistance to *P. recondita*, we observed temperature sensitivity of resistance in some of the wheat lines. We

therefore believed it was important to study the effect of temperature on the expression of resistance more thoroughly, in order to improve the efficiency of breeding for this type of resistance. Temperature sensitivity may also assist in identifying certain genes that are masked in combination with other genes. Thus, temperature sensitivity may be a tool that can be used in combining several resistance genes in one cultivar (7). In this paper we report the results of tests on the stability of resistance under different temperatures in a group of diverse Purdue wheat breeding lines and the cultivars Compton and Coker 79-14 (Table 1). We present evidence that the sensitivity of resistance to temperature varies among lines.

MATERIALS AND METHODS

Seeds of 10 Purdue wheat breeding lines and the cultivars Compton (22) and Coker 79-14 were planted in flats of soil, watered, and placed in a cold room at 3 C for 2 to 3 days to break dormancy and obtain uniform germination. The flats were then moved to a greenhouse bench, and when plants reached the one- to two-leaf stage (growth stages 11–12) (24), they were returned to the cold room. After 62 days of vernalization in the cold room the

TABLE 1. Abbreviated parentage of wheat cultivars and breeding lines used in the study of the response of adult-plant resistance to temperature

Cultivar or line	Pedigree ^a
Compton	Fulhio / Purkof /3/ Trumbull /2/ Hope / Hussar /5/ Fairfield /4/ P194587 /3/ Hungarian /2/ Fultz / Hungarian /8/ LaPorte /7/ Minhardi / Wabash /5/ Fultz / Hungarian /2/ Illinois No. 1, W38 /3/ Wabash /4/ Fairfield /6/ Redcoat / Wisconsin 245 / Afghanistan /9/ Knox *4 /8/ (Purdue 5127) Kawvale /5/ Fultz / Hungarian /2/ Illinois No. 1, W38 /3/ Wabash /4/ Fairfield /6/ Trumbull *3 /2/ Hope / Hussar /7/ Knox sib. /5/ Fairfield /4/ P194587 /2/ Fultz / Hungarian /3/ Fultz / Hungarian /10/ Knox *2 / Frex /2/ Riley sib.
Coker 79-14	Wheat cultivar from Coker Pedigreed Seed
P69195	Siete Cerros / Arthur // Purdue 6850 sel. /6/ Afghanistan sel. / Purdue 5374 sel. /4/ Knox *2 // Frontana / Exchange /3/ Riley sib. /5/ Arthur sib. / Agatha /3/ Purdue 6729 F ₁
P74140	Abe / 6117 ^b /5/ Benhur B /3/ Benhur /2/ Benhur / Beau sib.
P75438	Beau type /6/ Benhur B /5/ X 126-16-3r-3 / Trumbull /2/ Hope / Hussar /4/ Wabash /3/ Fairfield / Dular /2/ Fultz sel. / Hungarian
P751909	Doublecrop four-way crosses bulked; 1/4 = Doublecrop; 1/4 = 6850B5-48, 68283A1-11, or Beau; 1/4 = 66289-28-3-6; and 1/4 = Beau or 6851A11-60
P751915	Beau three-way crosses bulked; 1/2 = Beau, Beau sib., or Beau par.; 1/4 = Beau; and 1/4 = Key or 67115A6-16 ^c
P76603	Beau /4/ Acc. 1303 /3/ Riley /2/ Acc. 161-2 ^d / Riley 67
P76779	Beau /6/ Benhur sib. / dwarf Redcoat /4/ Benhur sib. / Knox /2/ Redcoat / Norin 10
P76905	Suwon 85 / 6028A2-5-9-6-1 ^e // Benhur B / Lovrin 11
P77121	Benhur /2/ 39120A4-2-1-1-2-3-1-1-4 ^f / Monon type

^a Pedigrees are written according to the notation of Purdy et al. (20).

^b 6117 is a Knox type with additional resistance to *Puccinia recondita* from Rio Negro.

^c 67115A6-16 is a source of Hessian fly resistance (*H5*).

^d Acc. 161-2, Stellenbosch B176-3-5, has stem rust resistance.

^e 6028A2 is a Knox type with additional resistance to Hessian fly.

^f 39120A4-2-1-1-2-3-1-1-4 has stem rust resistance.

seedlings were individually transplanted in a standard greenhouse soil mixture in plastic pots 10 cm in diameter. The seedlings of each line were randomly assigned to six different groups. The largest group was grown in the greenhouse until the preboot to early heading stage. Natural daylight was supplemented by fluorescent lamps, to provide 20,000 ergs · cm⁻² · sec⁻¹ of light for 16 hr per day. The greenhouse temperature fluctuated between 16 and 29 C (mean 23 C). The plants of the other five groups were grown in growth chambers under different temperature regimes. The day/night temperatures (0600–2000 and 2000–0600 hours, respectively) were 15/12, 18/15, 21/19, 25/23, or 30/21 C. Within each experiment there were five to 10 plants in each temperature treatment, and the entire experiment was repeated twice. All of the lines were also grown in the field to evaluate their rust reaction under normal growing conditions. Plants of the spring wheat cultivar Morocco were included as a fully susceptible control.

Plants from each temperature regime as well as those growing in the field were inoculated at the preboot to early heading stages (growth stages 41 to 51) with a minimum of 1.2 mg of urediniospores of *P. recondita* f. sp. *tritici* isolate 7434-1-1T per plant, suspended in 0.6 ml of deionized water with one drop of the surfactant Tween 20 per 100 ml. This isolate is virulent on plants with *Lr* genes 2b, 2c, 2d, 3a, 3bg, and 9; it is avirulent on plants with *Lr* genes 1, 2a, 3ka, 10, 11, 12, 13, 16, 17, 18, 19, 24, 25, and 26. It is representative of races of *P. recondita* in Indiana. After inoculation, plants were kept moist by enclosing them in polyethylene bags for 16 hr. On the 14th and 21st days after inoculation, ITs were recorded, on a modified version of the IT scale of Stakman et al. (23). When two ITs were evident on the same leaf, both were recorded, with the more frequent type listed first. For example, IT 30 indicates that type 3 uredinia and type 0 flecks were both present on the leaf, with the type 3 uredinia predominating.

Plants that had been grown in the greenhouse were transferred to growth chambers and incubated at the five temperature ranges described above after the moist period.

RESULTS

All of the Purdue wheat breeding lines and the cultivars Compton and Coker 79-14 displayed IT 0 to *P. recondita* in the field (Table 2). All but P77121 showed lesions of mainly IT 0, with some IT 1⁺, when tested as adult plants in the greenhouse. A few P77121 plants also had a mixture of IT 0 and IT 1 reactions (Table 2). The cultivar Morocco was consistently susceptible both in the greenhouse and in the field. The cultivar Compton has a gene or genes for seedling resistance, as indicated by IT 03⁺; all other lines were susceptible as seedlings (Table 2).

The Purdue wheat breeding lines P69195, P75438, and P76603

TABLE 2. Leaf rust infection types on wheat lines inoculated as seedlings and in the preboot to early heading stages with *Puccinia recondita* and grown in the greenhouse, and from natural infection in the field

Wheat line	Experimental designation	Infection type ^a		
		Greenhouse		
		Seedling	Adult plant	Field
Morocco	Morocco	4	4	3 ⁺
69195C9-4-1-3-1-6	P69195	3 ⁺	01 ⁻	0
75438A1-9-1-9	P75438	3 ⁺	0	0
76603RC1-14-1	P76603	3 ⁺	0	0
Compton	Compton	03 ⁺	01 ⁻	0
77121RB1-3-6-7	P77121	3 ⁺	01	0
Coker 79-14-2	Coker 79	4	01 ⁻	0
751909CB1-31-1-5	P751909	3 ⁺	01 ⁻	0
76905A4-1-2-2	P76905	3 ⁺	0	0
76779A3-13-1	P76779	3 ⁺	01 ⁻	0
751915CB1-86-3-1-3	P751915	3 ⁺	01 ⁻	0
74140A11-1-1-2-2-6	P74140-6	3 ⁺	0	0
74140A11-1-1-2-2-7	P74140-7	4	0	0

^a When two infection types were evident on the same leaf, the more frequent type is recorded first.

were stable over the range of temperatures tested and consistently showed IT 0 or IT 0c when grown under controlled temperatures from the time of transplanting (Table 3). Morocco was consistently susceptible (IT 3⁺), though sporulation was decreased at 15/12 C. Some lines were less resistant at the higher temperatures: Coker 79-14, P751909, P76905, and P76779. Most plants of Coker 79-14 and P751909 were susceptible at 30/21 C, although a few plants showed IT 3 and IT 2⁺. P76905 was moderately susceptible at 30/21 C, and P76779 was moderately resistant.

P77121 was the only line on which resistance was lost completely and suddenly at 30/21 C. Compton showed a few IT 3⁺ uredinia along with predominant flecking. Interestingly, these IT 3⁺ uredinia were not observed if the plants were first grown in the greenhouse and transferred to the growth chamber at 30/21 C only after inoculation (Table 3).

None of the lines tested showed complete loss of resistance at lower temperatures (Table 3). P751915, P74140-6, P74140-7, and P77121 were less resistant at 15/12 C. Only one plant of P77121 showed IT 1; all others were highly resistant (IT 0c). P751915 was highly resistant only within a narrow range of temperatures, being moderately resistant at 15/12 C and completely susceptible at 30/21 C.

The two selections from P74140 showed similar but not identical reactions to *P. recondita*. The reaction of P74140-6 was more strongly influenced by temperature, and this selection was generally less resistant than P74140-7. At 30/21 C, IT 0 was the predominant reaction of P74140-7, whereas IT 3⁺ predominated in P74140-6. Similarly, at 15/12 C most P74140-7 plants showed only

flecking, whereas P74140-6 was moderately susceptible.

The rust reactions of plants that were first grown in the greenhouse and transferred to growth chambers after inoculation were somewhat different from the reactions of plants grown at controlled temperatures immediately after vernalization (Table 3). The lines were generally more resistant when grown in the greenhouse prior to inoculation. P74140-6, P74140-7, P751909, and P751915 were more susceptible when grown in growth chambers immediately after vernalization. P74140-6 changed from a resistant reaction to a predominantly susceptible reaction at 30/21 C, whereas P74140-7 was still predominantly resistant.

The cultivars P76779 and P76905 were different from others in that they were more resistant when reared entirely under controlled conditions. P76905 produced both susceptible and moderately susceptible plants when reared in the greenhouse and then transferred to growth chambers after inoculation, as opposed to all moderately susceptible plants when grown in the growth chamber right from transplanting. Similarly P76779 produced some susceptible plants when the incubation temperature was 30/21 C, whereas only IT 2⁺ types were observed when plants were grown continuously at 30/21 C. When grown in the greenhouse until inoculation, all the lines showed a resistant to moderately resistant reaction at 15/12 C, except P74140-6, on which IT 2⁺ pustules were also observed. As noted before, P74140-7 differed from P74140-6 in that no moderately susceptible plants of P74140-7 were observed.

DISCUSSION

In the present study, genetically diverse Purdue wheat breeding lines were somewhat more resistant in the field than in the greenhouse (Table 2). This result is similar to other observations of wheats with adult-plant resistance (8). The reduced sporulation on the susceptible cultivar Morocco at 15/12 C supports other reports of temperature sensitivity of rust reaction types (6,14). Because of this relationship between temperature and latent period, we recorded ITs at both 14 and 21 days after inoculation.

Major differences in ITs were observed over the temperature regimes from 15/12 to 30/21 C, except for those of three lines: P75438, P76603, and P69195, which showed IT 0 or IT 0c at all temperatures, and Morocco, which was consistently susceptible (IT 3⁺). None of the resistant lines showed IT 3⁺ at the lower extreme (15/12 C), whereas at least a few IT 3⁺ were observed at the upper extreme (30/21 C) in all temperature-sensitive lines (Table 3). This implies that leaf rust resistance in these Purdue wheat lines is more stable at lower temperatures than at higher temperatures.

The differences observed in rust reaction between plants grown in growth chambers immediately after transplanting and plants transferred to growth chambers after inoculation imply a preinoculation temperature effect. These differences were most pronounced at the two extreme temperature regimes. Mohamed (19) found that preinoculation temperatures affect the number of wheat stem rust infection centers and IT. More infection centers were produced and ITs were higher at a preinoculation temperature of 27.2 C than at 21.1 C. A similar effect was seen at 30/21 C in the present study, in which IT 3⁺ was observed more frequently if the plants were grown continuously at higher temperatures. This effect would also explain the observation of a few IT 3⁺ uredinia in the cultivar Compton when it was grown continuously at 30/21 C.

The effects of postinoculation temperature on the expression of resistance in wheat have been reported for leaf rust resistance. Most temperature-sensitive genes become ineffective at high rather than low temperatures (1,3,15,16), but the loss of resistance at low temperatures has also been reported (6,13). According to Hyde, a change of temperature during the early postpenetration phase can change the host-pathogen interaction; i.e., an increase in temperature decreases compatibility, and a decrease in temperature increases compatibility (13). Similar losses of resistance at low and high temperatures have been observed in response to *P. striiformis* West. (5,17,21) and *P. graminis* Pers. f. sp. *tritici* Erikss. & Henn. (10,11). Postinoculation temperature effects have also been reported for *P. coronata* (25). A complex additive

TABLE 3. Infection types^a produced by isolate 7434-1-IT of *Puccinia recondita* f. sp. *tritici* on the flag leaf of wheat lines inoculated at the preboot to early heading stages and incubated under various diurnal temperature regimes

Wheat line	Growth conditions ^b	Diurnal temperature regime (day/night)				
		15/12C	18/16C	21/19C	25/23C	30/21C
Morocco	GC	3 ⁺	3 ⁺	3 ⁺	3 ⁺	3 ⁺
	GH	3 ⁺	3 ⁺	3 ⁺	3 ⁺	3 ⁺
P69195	GC	0	0c	0c	0c	0c
	GH	0c	0c	0c	0c	0
P75438	GC	0	0c	0c	0c	0c
	GH	0c	0c	0c	0c	0c
P76603	GC	0	0c	0c	0c	0c
	GH	0c	0c	0c	0c	0c
Compton	GC	0c	0	0	0	03 ⁺
	GH	0	0	0	0	0
P77121	GC	0/1	0c	0c	0c	3 ⁺
	GH	0/01 ⁻	0c	0c	0c	3 ⁺
Coker 79	GC	0c	0c	01 ⁻ c	2 ⁺ /3 ⁻	3 ⁺ 3
	GH	0c	0c	0c	2/2 ⁺	3 ⁺ /2 ⁺
P751909	GC	0	0c	0c	1 ⁻	3 ⁺ /2 ⁺
	GH	0c	0c	0c	01 ⁻	3/2 ⁺
P76905	GC	0c	0c	0c	2 ⁺ /1 ⁻	3 ⁺ 3c
	GH	0	0c	0c	1 ⁻ /1 ⁻ 0c	3 ⁺ /2 ⁺
P76779	GC	0	0c1c ⁻	0/1c	0/1 ⁺ /2 ⁺	2 ⁺
	GH	0	0c	0c/1 ⁻	0/1 ⁺	0/3 ⁺
P751915	GC	20/2 ⁻ c	0c	0/02 ⁺	2/2 ⁻	3 ⁺
	GH	01 ⁺	0c	0c/0c1 ⁻	1/1 ⁺	3 ⁺ /2 ⁺
P74140-6	GC	2 ⁺ /3	0c	0c1 ⁻	0c	3 ⁺ 0
	GH	2 ⁺ /2 ⁺	0c	0c	0c	0/02 ⁺
P74140-7	GC	0/2 ⁺	0c	0c	0/0c1 ⁻	03 ⁺
	GH	0	0c	0c/0c1	0c1 ⁻	0/02 ⁺

^aIf more than one infection type occurred on a leaf, the most frequent is listed first. If a line is heterogeneous for infection type, the predominant type is given first, followed by a slash and then the less frequent infection type.

^bGC = plants placed in growth chamber immediately after vernalization; GH = plants reared in greenhouse until inoculation, then placed in growth chamber.

resistance to *P. coronata* in oats becomes less effective as temperature increases (12).

Postinfection temperature affects all *Lr* genes, but *Lr* 11, *Lr* 12, *Lr* 13, *Lr* 14a, and *Lr* 18 are particularly sensitive to high temperature. In 1983, Dyck and Johnson found *Lr* 16 and *Lr* 17 to be temperature-sensitive also (6), although Browder had classified them as insensitive (3). This difference in sensitivity could be due to the use of different isolates of *P. recondita*. In our experiments a single isolate of *P. recondita*, 7434-1-1T, was used to test the leaf rust reaction. Dyck and Johnson found that the response of wheat lines having *Lr* 2a, *Lr* 2b, *Lr* 3, and *Lr* 3ka to temperature depends on the isolate of *P. recondita* with which they are tested (6). Chamberlain and Doodson found that the sensitivity of various *Yr* genes to temperature depends on the race of *P. striiformis* used (4). Bromfield, working with 87 cultivars of bread wheat (*T. aestivum*) and durum (*T. durum* L.), found that a cultivar that changes reaction to one race of *P. graminis* f. sp. *tritici* may not do so with another (2). These studies imply that a change in reaction may not be a direct response to temperature on the part of the host's resistance genes alone. Nor, apparently, is the alteration of reaction a direct response on the part of the parasite's pathogenicity genes alone, since the change in reaction occurs when a given rust race is growing in one host cultivar and not necessarily in another. Thus temperature most likely affects the host-parasite interaction.

Latent period, the time between inoculation and uredinial eruption, is an important parameter affecting the rate of disease progress of cereal rusts. The latent period of *P. recondita* in seedlings of *T. aestivum* decreases as the temperature rises from 10 to 26.5 C and then increases as it rises from 26.5 to 32.2 C (9). Generally, cultures more virulent, as judged by IT on a particular host line, have a shorter latent period than less virulent cultures at the same temperature. The latent period of *P. recondita* in wheat increases as the temperature decreases, and this rate of decrease is greater for slow-rusting lines than for fast-rusting lines (14). In the present study, other than increased sporulation of IT 3⁺ on the 21st day, no differences were seen between the ITs observed on the 14th day after inoculation and those on the 21st day.

These observations and the results of the present study demonstrate the importance of temperature during genetic studies of resistance to cereal rusts. Information on differences in the temperature response of Purdue lines is used in the breeding program. Resistance genes that become ineffective at high or low temperatures should not be used in the development of cultivars where such temperatures are common during the growing season. In genetic studies, failure to detect a gene in segregating populations may be because the material was grown under temperatures at which the expression of resistance is partially or completely inhibited. Obviously, extreme temperatures should be avoided in genetic studies. In wheat breeding, sensitivity to high or low temperature makes it possible to combine two genes that respond differently to temperature, and the combination leads to more stable and possibly more durable resistance.

LITERATURE CITED

1. Anderson, R. G. 1963. Studies on the inheritance of resistance to leaf rust of wheat. Proc. Int. Wheat Genet. Symp., 2nd. Hereditas (suppl.) 2:144-155.
2. Bromfield, K. R. 1961. The effect of postinoculation temperature on seedling reaction of selected wheat varieties to stem rust. Phytopathology 51:590-593.
3. Browder, L. E. 1980. A compendium of information about named genes for low reaction to *Puccinia recondita* in wheat. Crop Sci. 20:775-779.
4. Chamberlain, N. H., and Doodson, J. K. 1972. The influence of temperature on the reaction of wheat seedlings infected with yellow rust. Pages 69-77 in: Proc. Eur. Mediterr. Cereal Rusts Conf., 3rd, Prague.
5. Coakley, S. M., and Line, R. F. 1981. Quantitative relationships between climatic variables and stripe rust epidemics on winter wheat. Phytopathology 71:461-467.
6. Dyck, P. L., and Johnson, R. 1983. Temperature sensitivity of genes for resistance in wheat to *Puccinia recondita*. Can. J. Plant Pathol. 5:229-234.
7. Dyck, P. L., and Kerber, E. R. 1985. Resistance of the race-specific type. Pages 469-500 in: The Cereal Rusts, Vol. II. A. P. Roelfs and W. R. Bushnell, eds. Academic Press, Orlando, FL.
8. Dyck, P. L., and Samborski, D. J. 1982. The inheritance of resistance to *Puccinia recondita* in a group of common wheat cultivars. Can. J. Genet. Cytol. 24:273-283.
9. Eversmeyer, M. G., Kramer, C. L., and Browder, L. E. 1980. Effect of temperature and host-parasite combination on the latent period of *Puccinia recondita* in seedling wheat plants. Phytopathology 70:938-941.
10. Forsyth, F. R. 1956. Interaction of temperature and light on the seedling reaction of McMURACHY wheat to race 15B of stem rust. Can. J. Bot. 34:745-749.
11. Green, G. J., and Johnson, T. 1955. Specificity in the effect of high temperature on the adult plant reaction of wheat varieties to races of stem rust. Can. J. Bot. 33:197-201.
12. Harder, D. E., and McKenzie, R. I. H. 1984. Complex additive type of resistance to *Puccinia coronata* in *Avena sterilis*. Can. J. Plant Pathol. 6:135-138.
13. Hyde, P. M. 1982. Temperature-sensitive resistance of the wheat cultivar Maris Fundin to *Puccinia recondita*. Plant Pathol. 31:25-30.
14. Johnson, D. A. 1980. Effect of low temperature on the latent period of slow and fast rusting winter wheat genotypes. Plant Dis. 64:1006-1008.
15. Johnson, L. B., and Schafer, J. F. 1965. Identification of wheat leaf rust resistance combinations by differential temperature effects. Plant Dis. Rep. 49:222-224.
16. Jones, D. R., and Deverall, B. J. 1977. The effect of the *Lr* 20 resistance gene in wheat on the development of leaf rust, *Puccinia recondita*. Physiol. Plant Pathol. 10:275-285.
17. Lewellen, R. T., Sharp, E. L., and Hehn, E. R. 1967. Major and minor genes in wheat for resistance to *Puccinia striiformis* and their responses to temperature changes. Can. J. Bot. 45:2155-2172.
18. Mains, E. B., and Jackson, H. S. 1926. Physiologic specialization in the leaf rust of wheat, *Puccinia triticina* Erikss. Phytopathology 16:89-120.
19. Mohamed, H. A. 1960. Predisposition of wheat seedlings to stem rust infection and development. Phytopathology 50:339-340.
20. Purdy, L. H., Loegering, W. Z., Konzak, C. F., Peterson, C. J., and Allan, R. E. 1968. A proposed standard method for illustrating pedigrees of small grain varieties. Crop Sci. 8:405-406.
21. Qayoum, A., and Line, R. F. 1985. High-temperature, adult-plant resistance to stripe rust of wheat. Phytopathology 75:1121-1125.
22. Shaner, G. E., Ohm, H. W., Foster, J. E., Patterson, F. L., Gallun, R. L., and Buechley, G. C. 1985. Registration of 'Compton' wheat. Crop Sci. 25:712-713.
23. Stakman, E. C., Stewart, D. M., and Loegering, W. Q. 1962. Identification of physiologic races of *Puccinia graminis* var. *tritici*. U.S. Dep. Agric. Bull. E-617, rev.
24. Zadoks, J. C., Chang, T. T., and Konzak, C. F. 1974. A decimal code for the growth stages of cereals. Weed Res. 14:415-421.
25. Zimmer, D. E., and Schafer, J. F. 1961. Relation of temperature to reaction type of *Puccinia coronata* on certain oat varieties. Phytopathology 51:202-203.