Interactions of Temperature and Time with Some *Puccinia recondita*:*Triticum* Corresponding Gene Pairs

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Lines LR1(TC), RL6003; LR16(TC), RL6005; and LR17(TC), RL6008 can be obtained from P. L. Dyck and D. J. Samborski, Agriculture Canada Research Station, Winnipeg, Manitoba; USDA Small Grains Collection; or first author. Culture PRTUS21 also available from first author.

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ABSTRACT

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Three near-isogenic lines of *Triticum aestivum*, each with *Lr1*, *Lr16*, or *Lr17*, and their recurrent parent, Thatcher, were inoculated with two *Puccinia recondita* cultures, one known to be avirulent and the other virulent to the near-isogenic lines. Both cultures were virulent to Thatcher. The cultures were known to be avirulent and virulent from previous tests at continuous 20 C. These materials were exposed to four temperature regimes consisting of a varying initial period at 20 C followed by a period at 5 C for the remainder of the postinfection period. Exposures of 0, 2, 4, and 8 days at 20 C were made before transfer to 5 C. This experimental design provided a check system for the effects of host genotype, parasite genotype, temperature, and time at temperature on infection type. The data obtained indicated that *Lp1*/*Lr1* functions during the first 2 days at 20 C, *Lp17*/*Lr17* functions during the period from 2 to 4 days at 20 C, and *Lp16*/*Lr16* functions during the period from 4 to 8 days after infection at 20 C. Under continuous 5 C, none of the three corresponding gene pairs functioned optimally to produce their characteristic low infection types. These data indicate that different corresponding gene pairs have different temperature ranges in which they function optimally to produce the characteristic low infection type and that different corresponding gene pairs function in different time periods.

Additional key words: disease resistance, environment, genetics, leaf rust, specificity, wheat.

The effect of temperature higher than the commonly used test temperature (20 C) on resistance mechanisms in the cereal rusts has been well documented (2,8,10,16). In the wheat leaf rust system, the most notable examples of this are the International Standard differential cultivar Hussar, which has the gene *Lr11* (14,15), and the cultivar Africa 43, which has *Lr18* (1,7). In these cases, the *Lr* genes can be detected with avirulent cultures at 15–20 C, but their detection is difficult or impossible at higher temperatures. In the wheat stem rust system, *Sr6* can be detected at midrange temperatures (18–24 C) with avirulent cultures but not at higher temperatures (2,8). In the rust literature, this phenomenon commonly has been termed "high-temperature-sensitive" or "temperature-sensitive" resistance. In these studies, the focus has been on the influence of temperature on the expression of the host gene per se. We will focus on the expression of parasite:host interactions in differing environments.

Few studies have been made on the effect of lower than optimum temperature on the development of specific parasite:host interactions. Very early in the history of specificity studies of *P. recondita* and *Triticum*, however, Gassner and Straib (9) reported that the cultivar Malakof and certain *P. recondita* genotypes produced high infection types when grown at 6 C but produced a nonsporulating infection type at 20 C. The cultivar Rumkers Sommerdickkopf and certain *P. recondita* genotypes produced high infection type at 6 C but produced an intermediate infection type at 20 C. Excellent color photographs were published to substantiate the results they obtained. Hyde (11) recently reported that lower infection types occurred when wheat cultivar Maris Fundin inoculated with an avirulent *P. recondita* culture was grown at 15 C than when grown at 9 C. Both Gassner and Straib's data (9) and Hyde's results (11) are consistent with an hypothesis that low temperature was the causal factor in the change from lower to higher infection type. We have observed that Malakof and cultures known to be avirulent at 20 C produced high infection types when grown at 5 C during the winter wheat vernalization process (L. E. Browder and M. G. Eversmeyer, *unpublished*).

We approached this study from the viewpoint of temperature as a factor in parasite:host:environment specificity (4). In this paper, we show results of varying temperature between 20 and 5 C for varying periods of time during the postinfection period, varying parasite genotypes, and varying host genotypes with regard to three sets of corresponding gene pairs (5).

MATERIALS AND METHODS

Four lines of wheat (*Triticum aestivum* L.) were inoculated with two cultures of *Puccinia recondita* Rob. ex Desm. and exposed to four temperature-regime environments after infection had been ensured by an overnight period with free moisture at 16 ± 2 C.

The four lines of wheat were the cultivar Thatcher and three backcross-derived, near-isogenic lines in a Thatcher background. The lines were: Thatcher, CI 10003, abbreviated as TC; LR1(TC), RL6003; LR16(TC), RL6005; and LR17(TC), RL6008. These near-isogenic lines were developed by P. L. Dyck and D. J. Samborski of the Agriculture Canada Research Station, Winnipeg, Manitoba. From previous studies, these lines are known to have the following genotypes: TC—*Hr1Hr16Hr17*, LR1(TC)—*Lr1Hr16Hr17*, LR16(TC)—*Hr1Lr16Hr17*, and LR17(TC)—*Hr1Hr16Lr17*, where *Lr* indicates the presence of the gene for low reaction and *Hr* indicates the absence of the *Lr* gene. The two *P. recondita* cultures used were PRTUS3 and PRTUS21. Culture PRTUS3 was known to be avirulent to lines with *Lr1*, *Lr16*, or *Lr17* when grown at continuous 20 C (3). Culture PRTUS3 has been deposited in the American Type Culture Collection Plant Rust Collection as PR3. Culture PRTUS21 was

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known to be virulent to lines with *Lr1*, *Lr16*, or *Lr17* when grown at continuous 20 C (L. E. Browder and M. G. Eversmeyer, *unpublished*).

The four environments used were varying sequences of 20 and 5 C after removing the materials from the moist chamber. We used varying periods in a growth chamber at 20 C followed by exposure to 5 C in another growth chamber for the remainder of the postinfection period. One group of infected plants was exposed for 0 days at 20 C before transfer (Env. 0), another group was exposed for 2 days at 20 C before transfer (Env. 2), another group was exposed to 4 days at 20 C before transfer (Env. 4), and a fourth group was exposed for 8 days at 20 C before transfer (Env. 8).

Eight to 10 seeds of each of the four wheat lines were planted separately in 7.5-cm plastic pots. Order of host lines within pots, plants to be inoculated with the different cultures, and pots to be placed in the different environments were selected according to a randomized plan. Four plantings of each set of lines inoculated with each culture were grown in each environment during one replication of the experiment; four observations of each treatment were made in each replicate. The experiment was replicated three times. Replicates were grown in different time periods. Seedling plants were grown in a vermiculite growth medium and supplied with Hoagland's solution at watering intervals.

Infection type, coded in the system proposed by Browder and Young (6), were recorded at intervals during the postinfection period, and color slide photographs were made of representative observations of the materials; these slides were used to determine consistency of results between replicates.

RESULTS AND DISCUSSION

Observations of infection type were made at 2- to 3-day intervals after sporulation began with the PRTUS21:Thatcher association until the plants began to deteriorate, usually about 40 days. We will present, however, typical data from one replicate near the end of the postinfection period (Table 1). These results were typical of all replicates, although slight variations in infection type occurred between replicates of the same parasite:host:environment treatment.

The low infection types produced in Env. 8 by PRTUS3 and LR1(TC), PRTUS3 and LR17(TC), and by PRTUS3 and LR16(TC) were very similar to the characteristic low infection types expected 10–12 days after infection at continuous 20 C (3). From the Env. 8 data, we can confirm that PRTUS3 was avirulent to the three near-isogenic lines and PRTUS21 was virulent to the three lines. Thus, we can assign the putative genotype *Lp1Lp16Lp17* to PRTUS3 and *Hp1Hp16Hp17* to PRTUS21, where *Lp* indicates an allele for low pathogenicity and *Hp* indicates the absence of such an allele. In Env. 0, LR1(TC) and PRTUS3, LR17(TC) and PRTUS3, or LR16(TC) and PRTUS3 did not produce the characteristic low infection type of their putative corresponding gene pairs. Only slight reductions in sporulation were observed in associations of the three near-isogenic lines and PRTUS3 relative to the sporulaton of the Thatcher recurrent parent and PRTUS3. In Env. 2, Env. 4, and Env. 8, LR1(TC) and PRTUS3 produced the characteristic low infection type for *Lp1*/*Lr1* (3). In Env. 4 and Env. 8, LR17(TC) and PRTUS3 produced an infection type similar to the characteristic low infection type for *Lp17*/*Lr17* (3). Only in Env. 8 did LR16(TC) and PRTUS3 produce the approximate characteristic low infection type of *Lp16*/*Lr16* (3).

The wheat lines and *P. recondita* cultures used in these experiments were known to represent three gene-for-gene relationships in which wheat genes for low reaction (*Lr* genes) function together with genes for low pathogenicity (*Lp* genes) to produce a low infection type that is characteristic for each corresponding gene pair (3). Thus, the data obtained from these experiments indicate the corresponding gene pairs, *Lp1*/*Lr1*, *Lp17*/*Lr17*, and *Lp16*/*Lr16* do function at 20 C but not at 5 C to produce the characteristic low infection type. This agrees with the findings of Gassner and Straib (9) and Hyde (11). A large amount of data indicates that other corresponding gene pairs function at relatively low temperatures (10–20 C) but not at relatively high temperatures (2,6,7,9,15). Although the studies of Gassner and Straib (9), Hyde (11), and our present study seem to contradict the other studies (2,6,7,9,15), they can be reconciled by the concept that specific corresponding gene pairs function optimally in specific environments (4).

The data from the present experiment also indicate either that the different sets of corresponding gene pairs function at different times after infection is established or that the three sets of corresponding gene pairs require different amounts of time to function. The 01C infection type (Table 1) of LR1(TC) and PRTUS3 occurred in Env. 2, Env. 4, and Env. 8; the major effect of *Lp1*/*Lr1* occurred during the first 2 days at 20 C, and this effect was not markedly changed by more time at 20 C. In one replicate, slight sporulation occurred in Env. 2. The function of *Lp1*/*Lr1* in LR1(TC) and PRTUS3, may have occurred even earlier than the second day without being detected in our experiments. Low infection types occurred when the LR17(TC):PRTUS3 treatment was exposed to Env. 4 and Env. 8. At least 4 days at 20 C were required to detect the function of *Lp17*/*Lr17* by observation of infection type. Further function of *Lp17*/*Lr17* occurred between 4 and 8 days at 20 C as indicated by the lower infection type in Env. 8 than in Env. 4. Four to 8 days at 20 C were required to detect the function of *Lp16*/*Lr16* by observation of infection type differences. The biochemical function of a given corresponding gene pair may occur very quickly at a given point of parasite:host development, or it may occur over a longer period of time. Our present data do not resolve this question. They do, however, clearly show that different sets of corresponding gene pairs function, or complete their function, at different times in the parasite:host development period (12).

Specificity of *Lp1*/*Lr1* in the *P. recondita*:*Triticum* system to 20

TABLE 1. Interactions of temperature and time with three sets of corresponding gene pairs of *Puccinia recondita:Triticum* as manifested by infection type data

	Infection type[a] observed with environment and culture							
	Env. 0[b]		Env. 2		Env. 4		Env. 8	
Host line	PRTUS3[c]	PRTUS21	PRTUS3	PRTUS21	PRTUS3	PRTUS21	PRTUS3	PRTUS21
Thatcher	99P	99P	88P	88P	88P	88P	88P	88P
LR1(TC)	88P	88P	01C	88P	01C	88P	01C	88P
LR17(TC)	88P	88P	88P	88P	23X	88P	14N	88P
LR16(TC)	88P	88P	88P	88P	88P	88P	34N	88P

[a] Infection types coded in a system where the first code represents a relative amount of sporulation, where 0 = no sporulation and 9 = most sporulation observed; the second code represents a relative lesion size, where 0 = no lesion and 9 = largest lesion observed. The third (alphabetic) code is a mnemonic descriptor of tissue damage surrounding the sporulating area of the lesions: P = pale, C = chlorotic, and N = necrotic, and X = a mosaic pattern of varying sized lesions.

[b] Environments are coded as number of postinfection days at 20 C before transfer to 5 C for remainder of postinfection period, e.g., Env. 2 = 2 days of growth at 20 C and 32 days at 5 C. All plants were exposed to the same environment until infections were established.

[c] Putative genotypes: PRTUS3 = *Lp1Lp17Lp16*, PRTUS21 = *Hp1Hp17Hp16*, Thatcher = *Hr1Hr17Hr16*, LR1(TC) = *Lr1Hr17Hr16*, LR17(TC) = *Hr1Lr17Hr16*, and LR16(TC) = *Hr1Hr17Lr16*.

C was indicated by Modawi et al (13). In that study, other sets of corresponding gene pairs were detected when *Lp1*/*Lr1* was negated by exposure to continuous 5 C.

The data from this study are consistent with the concepts that genotypes are expressed in specific environments and that parasite and host genotypes function together to effect the phenotype of the parasite-host association. The data from this study, however, indicate that timing of environments during development of parasite-host associations with specific genotypes also is important. There are four determinants of infection type in the *P. recondita*:*Triticum* system: parasite genotype, host genotype, environment, and time in environment.

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