

Prehaustorial and Posthaustorial Resistance to Wheat Leaf Rust in Diploid Wheat Seedlings

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ABSTRACT

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The histological reaction of 13 diploid wheat accessions (*Triticum monococcum* s.l.) to two isolates of wheat leaf rust (*Puccinia recondita* f. sp. *tritici*) was investigated and compared with the nonhost reactions to rye and barley leaf rust. The resistance of diploid wheat to wheat leaf rust ranged from almost completely prehaustorial without necrosis to almost completely posthaustorial with frequent necrosis. This variation depended on the diploid wheat accession rather than on the wheat leaf

rust isolate. The nonhost reaction to rye leaf rust was predominantly prehaustorial. The nonhost reaction of the rye cultivar Rogo to barley leaf rust was predominantly posthaustorial with necrosis. In the diploid wheats the barley leaf rust formed haustoria rather frequently (with necrosis induction). The diploid wheat accessions with high prehaustorial resistance to wheat leaf rust may be valuable sources for nonhypersensitive (and perhaps durable) resistance in cultivated wheat to this fungus.

Additional keywords: early abortion, histology, nonhost reaction.

Histological studies on interactions between plants and rust fungi demonstrated that several mechanisms of resistance can be discerned (9,11). Two commonly occurring types of resistance are the prehaustorial and the posthaustorial resistance. Prehaustorial resistance implies that sporeling development is arrested before the formation of haustoria. Usually the sporelings develop normal haustorial mother cells, but at the site of cell wall penetration a papilla is induced. This type of resistance is very common in nonhost interactions (7,9,11,17), such as when barley is inoculated with rye leaf rust (23), and also in the presumably durable partial resistance sensu Parlevliet (26) of barley cultivars to barley leaf rust (18,20).

Posthaustorial resistance means that the fungus is arrested after the formation of at least one haustorium. With this type of resistance, the cells that contain haustoria usually die. This plant cell necrosis is called *hypersensitivity*. Major genic race-specific resistance to rust fungi is almost always posthaustorial (9,11,16). Such a race-specific hypersensitivity resistance to rust fungi often turns out to be ephemeral, since the pathogen is able to develop races to which the resistance is not effective.

It has been argued that prehaustorial resistance is caused by general defense mechanisms in the plant (4,11,12). There is no basic compatibility between the plant and the fungus. The presumably durable character of nonhost resistance and of the partial resistance of barley to barley leaf rust suggests that prehaustorial resistance may be difficult to overcome by rust fungi (10,11,12).

Cases of uncertain nonhost status occur (e.g., where very few genotypes of a plant species allow only some reproduction of a normally inappropriate pathogen [22]). Examples of cases with such an unclear status are the combinations of barley and wheat leaf rust (19) and rye and wheat leaf rust (24). In these cases the predominant mechanisms of resistance may be prehaustorial, as in barley (13), or posthaustorial, as in rye (24). A further uncertainty is the possibility put forward by Heath (12) that plants with resistance to inappropriate formae speciales should not be considered typical nonhosts. This opinion may or may not be relevant in the case of *Puccinia recondita* Roberge ex Desmaz., where the species concept is debatable. Savile (30) and Urban (33) consider the wheat and rye leaf rust fungi as two separate species. It is common practice, however, to treat these rust fungi as formae speciales of one species, *P. recondita*.

The present paper reports on the relationship between diploid wheat and wheat leaf rust. Diploid wheat (originally *Triticum monococcum* L., *T. boeoticum* Boiss., and *T. urartu* Tum., but also known as *T. monococcum* sensu lato) is believed to have contributed the major part of the A-genome in the cultivated tetraploid and hexaploid wheats. Despite this close relationship with cultivated wheat, diploid wheat has a very high level of resistance to wheat leaf rust (*P. recondita* Roberge ex Desmaz. f. sp. *tritici* (Eriks. & E. Henn.) D. M. Henderson). Dhaliwal et al (6), The (32), Zitelli (37), and others each inoculated more than 120 accessions of diploid wheat with one or two isolates of wheat leaf rust. They classified over 99% of the accessions as resistant or, at most, medium resistant (infection type 2 on a 0-4 scale; 32). This low frequency of susceptibility suggests that the combination of plant and rust species takes an intermediate position between host and nonhost status. Histological examination of the plant-fungus interaction would reveal whether incompatibility is due to prehaustorial or posthaustorial mechanisms.

In the present study, the histological reaction of diploid wheat to wheat leaf rust was compared with the nonhost reaction to nonpathogenic (inappropriate) leaf rust fungi. If the predominant mechanism of resistance would be prehaustorial, *T. monococcum* could be a valuable source of nonhypersensitive (and possibly durable) resistance in cultivated wheat to wheat leaf rust.

MATERIALS AND METHODS

Plant material. The first experiment consisted of seven accessions of diploid wheat (*T. urartu* Tu6735, *T. boeoticum* Tb1-1082, *T. monococcum* Tm2126/5, Tm2-1500, Tm1509/2, Tm1990/7, and TmEinkorn 1,3) provided by Dr. J. Valkoun of the Research Institute for Crop Production, Prague, and six *T. monococcum* accessions (Tm10909, Tm10910, Tm10913, Tm10597, Tm10594, and Tm10592) provided by Dr. M. Pasquini of the Istituto Sperimentale per la Cerealcoltura, Rome. We added bread wheat (*T. aestivum* L.) cultivars Chinese Spring and Little Club and rye (*Secale cereale* L.) inbred line R9 as checks. Three sets of these accessions were sown. Each set consisted of two plant boxes 37 × 39 cm. In each box Little Club was sown together with seven or eight of the remaining 15 accessions. Each accession was represented by four to seven seedlings per set.

In a second experiment, four diploid wheat accessions were studied in more detail. This study was performed in two consecu-

tive series and consisted of four sets each of the accessions Tb1-1082, Tm2-1500, TmEinkorn 1,3, and Tm2126/5, and Little Club, rye cultivar Rogo and line R9, and barley (*Hordeum vulgare* L.) line L94. Each accession was represented by six to eight seedlings per set. In series I of this second experiment, however, Tb1-1082 and TmEinkorn 1,3 had fewer seedlings per set. In these cases only leaf segments were available for fluorescence microscopy (see below). The seedlings were grown in a greenhouse compartment.

Inoculum. The three plant sets were inoculated with wheat leaf rust isolates Felix and Flamingo (both *P. r. tritici*) (3,35) and our standard rye leaf rust isolate (*P. r. recondita*), respectively. In the second experiment the fourth set was inoculated with barley leaf rust (*P. hordei* G. Oth, isolate 121).

Inoculation. About 15 days after sowing, the primary leaves were fixed in a horizontal position and inoculated in a settling tower. Each plant box received about 4 mg of urediospores mixed with about ten times as much the volume of spores of *Lycopodium* (18). An inoculum dose of 4 mg results in about 230 spores per square centimeter.

Sampling. In the first experiment, central parts of all primary leaves were collected at 6 days postinoculation (d.p.i.). In the second experiment, the seedlings were sampled twice. The first sampling was around noon 42 hours postinoculation (h.p.i.) and consisted of two leaf segments per combination of plant accession and rust. The second sampling was at 6 d.p.i. for all remaining primary leaves.

Macroscopic observations. At about 10 d.p.i. the infection types (IT) on the leaf stubs in the plant boxes were determined according to the 0 to 9 scale of McNeal et al. (15).

Microscopic observations. The leaf segments collected at 6 d.p.i. were prepared as whole mounts for fluorescence microscopy (29), using Uvitex 2B (Ciba-Geigy Corp., Ardsley, NY) instead of Calcofluor. All infection units in each leaf segment were classified according to phase of development (19,25). Also, the presence of plant cell necrosis, recognized by autofluorescence, was noted. This components analysis (18,36) was carried out with a Nikon Fluophot epifluorescence microscope at $\times 100$ (at $\times 400$ for details). The percentage of early abortion was calculated as the

number of early aborted sporelings divided by the number of early aborted and established sporelings per leaf segment. Sporelings were considered early-aborted when they had formed at least one, but not more than six, haustorial mother cells (19). The percentage of early abortion was averaged over the leaf segments per plant accession-isolate combination.

The leaf segments collected at 42 h.p.i. were fixed, cleared, and stained with a mixture of trypan blue, lactophenol, and ethanol and with chloral hydrate as described before (method A in ref. 21). For 30 or 35 infection units per leaf section, the presence or absence of haustoria, and also possible necrosis of plant cells at the infection site, was recorded. Plant cells that had taken up excessive stain were considered necrotic (20). These observations were carried out with a Nikon Optiphot phase contrast microscope at $\times 1000$.

RESULTS

The observations on the interactions of rye and barley with wheat leaf rust and of barley with rye leaf rust were very similar to those reported earlier (19,24). They are not presented and discussed here.

Macroscopic observations. One accession of the diploid wheats (Tu6735) was as susceptible to the wheat leaf rust (IT 9) as the bread wheat controls (Table 1). The remaining diploid wheat accessions ranged from highly resistant (IT 0) to medium resistant (Tables 1 and 2). TmEinkorn 1,3 tended to have somewhat higher infection types than the other resistant diploid wheat accessions. There were no obvious differences between the Felix and Flamingo isolates with regard to the ITs.

The rye leaf rust fungus was only pathogenic on rye (IT 9) (Tables 1 and 2) and did not cause symptoms on the bread wheat and diploid wheat accessions.

The barley leaf rust was only pathogenic on barley line L94 and did not cause significant symptoms on the other accessions (Table 2).

Early abortion. As in previous experiments (e.g., 24), there were no apparent genotype effects on proportion of unsuccessful

TABLE 1. Infection types and percentage of early-aborted infection units determined on 2 bread wheat cultivars, 13 diploid wheat accessions, and 1 rye accession inoculated with wheat leaf rust fungus and rye leaf rust fungus

Accession	Wheat leaf rust ^a				Rye leaf rust	
	IT ^b		Early-aborted infection units (%) ^c		IT	Early-aborted infection units (%) ^{c,f}
	Fe	Fl	Fe ^d	Fl ^e		
Bread wheat						
Little Club	9	9	3 (27)	8 (3)	0	100 (53)
Chinese Spring	9	9	31 (8)	10 (6)	0	100 (4)
Diploid wheat						
Tu6735	9	9	4 (0)	9 (23)	0	99 (42)
Tb1-1082	0	1	89 (87)	100 (90)	0	99 (70)
Tm2-1500	2	1	91 (100)	63 (90)	0	100 (52)
TmEinkorn 1,3	5-6	6-7	97 (31)	88 (23)	0	100 (51)
Tm2126/5	0	0	100 (42)	96 (36)	0	99 (37)
Tm1509/2	0-2	0-2	84 (50)	75 (64)	0	99 (57)
Tm1990/7	2-4	2-4	49 (56)	48 (46)	0	100 (52)
Tm10909	3-4	4	18 (17)	23 (32)	0	99 (58)
Tm10910	2-4	1-2	42 (50)	35 (41)	0	99 (56)
Tm10913	2	2-4	37 (43)	35 (23)	0	98 (55)
Tm10597	2-4	2-3	30 (100)	13 (32)	0	100 (66)
Tm10594	3-5	5	94 (31)	19 (13)	0	99 (51)
Tm10592	0	1-2	29 (33)	37 (38)	2	99 (63)
Rye						
R9	9	1 (0)

^a Isolates Felix (Fe) and Flamingo (Fl).

^b Infection type, according to the 0 to 9 scale of McNeal et al (15).

^c Figures in parentheses are percentages of early-aborted infection units associated with plant cell necrosis.

^d Average based on 107 infection units per accession.

^e Average based on 486 infection units per accession.

^f Average based on 440 infection units per accession.

stoma penetration nor on substomatal vesicle abortion (*data not presented*).

The percentage of early abortion of wheat leaf rust in diploid wheat ranged from 4% in the susceptible Tu6735 to 100% in the highly resistant Tb1-1082 and Tm2126/5 (Table 1, first experiment). In several of the resistant diploid wheats (Tm10909, Tm10597, Tm10592), the percentage of early abortion was rather low. In general, the results for the Felix and the Flamingo isolates with regard to early abortion in diploid wheat were similar. On Tm10594, however, Felix had a much higher percentage of early abortion than Flamingo (Table 1). The amount of necrosis that was associated with the early abortion could vary from low to high (Table 1).

On the basis of the results presented in Table 1, we selected the accessions Tb1-1082 and Tm2-1500 for their high proportion of early abortion and high incidence of necrosis. TmEinkorn 1,3 and Tm2126/5 were selected for their high proportion of early abortion with relatively infrequent necrosis. These four diploid wheat accessions were studied in more detail in the second experiment (Table 3).

The high percentage of early abortion of wheat leaf rust in the four diploid wheat accessions, and also the respectively high and low incidence of necrosis associated with it, was confirmed. The agreement between series I and II was good; the percentage of early abortion did not differ by more than 15%. The data are presented, therefore, as averages over the two series.

The infection attempts by the rye leaf rust on the diploid wheats and bread wheat resulted in early abortion of almost all sporelings with rather frequent (Table 1, first experiment) or infrequent (Table 3, second experiment, both series) necrosis.

The barley leaf rust fungus aborted early in bread wheat, in the diploid wheats, and in rye (Table 3). In series I this early abortion tended to be associated with less frequent necrosis than in series II (Table 3). In rye the large majority of early-aborted barley leaf rust sporelings were associated with necrosis.

Established colonies. The complements of the percentages of early abortion in Tables 1 and 3 are the percentages of established colonies. In the host combinations of bread wheat and wheat leaf rust, rye and rye leaf rust, and barley and barley leaf rust, these percentages were high. Such colonies were large (typically more than 600 μm in diameter), and many had formed at least sporogenic tissue. This was also true for the susceptible Tu6735 with wheat leaf rust (Table 1).

The established colonies of wheat leaf rust in the resistant diploid wheats (Tables 1 and 3) were small (typically less than 500 μm in diameter) and in most cases associated with necrosis.

Haustorium formation. The sporelings in the leaf segments of the second experiment that were collected 42 h.p.i. could be

classified into three categories (Table 4):

1. Sporelings that did not have a haustorium and also had not induced plant cell necrosis. On the site of contact between haustorial mother cell and plant cell, a cell wall apposition (papilla) could very often be seen.

2. Those that had formed at least one haustorium, not associated with necrosis.

3. Those in which at least one haustorial mother cell was associated with necrotic (excessively stained) plant cell(s). Because of the cell disintegration and dark staining it was not always possible to be sure whether or not the cell contained a haustorium. Possible other haustorial mother cells of the sporelings in this category could have formed a haustorium without necrosis or could have failed to produce a haustorium. The results for the two wheat leaf rust isolates were very similar, so the results are presented in Table 4 as averages over both isolates.

The diploid wheats differed in resistance mechanism to the wheat leaf rust fungus. The two accessions with high early abortion and infrequent necrosis (TmEinkorn 1,3 and Tm2126/5, Tables 1 and 3) allowed very little haustorium formation by the wheat leaf rust (Table 4). In the two accessions that were studied because of their high early abortion with frequent necrosis (Tb1-1082 and Tm2-1500, Tables 1 and 3), the wheat leaf rust had induced frequent cell necrosis at the time of sampling (Table 4). In Tm2-1500 the large majority of these necrotic cells contained visible haustoria. Many sporelings had formed haustoria in cells that did not show signs of necrosis at 42 h.p.i. With Tb1-1082, a haustorium could rarely be detected in the frequently occurring necrotic cells. Probably the cell necrosis occurred during the cell wall penetration by the fungus. Necrotic cells in this accession often contained structures that suggested degenerated haustorial necks or very young haustoria. The diploid wheats did not differ convincingly in their reaction to the rye leaf rust fungus. In all four accessions the rye leaf rust aborted most frequently without having formed haustoria and without induction of necrosis. Some sporelings succeeded in the formation of a haustorium in an epidermal cell. In this regard the diploid wheats behaved similarly to the bread wheat cultivar. The nonhost reaction of the diploid wheats to the barley leaf rust varied from predominantly pre-haustorial (Tm2-1500, series I, Tm2126/5) to partly posthaustorial with frequent cell necrosis (Tb1-1082 and Tm2-1500, series II). In rye, the barley leaf rust sporelings had frequently induced necrosis. In the necrotic cells haustoria were usually visible.

TABLE 2. Infection types^a of isolates of the wheat leaf rust fungus, the rye leaf rust fungus, and the barley leaf rust fungus on bread wheat, diploid wheat, rye, and barley accessions in two series (I and II)

Accession	Wheat leaf rust ^b				Rye leaf rust		Barley leaf rust ^c	
	Fe		Fl		I	II	I	II
	I	II	I	II				
Bread wheat								
Little Club	9	9	9	9	0	0	0	0
Diploid wheat								
Tb1-1082	0	0	0	0	0	0	0	0
Tm2-1500	0	0	0	0	0	0	0	0-1
TmEinkorn 1,3	0	1	0	2-3	0	0	0	0
Tm2126-5	0	0	0	0	0	0	0	0-1
Rye								
Rogo	9	9	0	0
R9	9	9	0	0
Barley								
L94	0	0	9	9

^a According to the 0 to 9 scale of McNeal et al (15).

^b Isolates Felix (Fe) and Flamingo (Fl).

^c Isolate 121.

TABLE 3. Percentage of early abortion of sporelings of isolates of the wheat leaf rust fungus, the rye leaf rust fungus, and the barley leaf rust fungus on bread wheat, diploid wheat, rye, and barley accessions

Accession	Early-aborted sporelings (%) ^a			
	Wheat leaf rust		Rye leaf rust	Barley leaf rust isolate 121
	Felix	Flamingo		
Bread wheat				
Little Club	18 (16) ^b	11 (9)	100 (9)	100 (33, 63) ^c
Diploid wheat				
Tb1-1082	100 (88)	100 (76)	99 (14)	100 (41, 82)
Tm2-1500	94 (96)	86 (94)	98 (19)	98 (19, 52)
TmEinkorn 1,3	90 (16)	96 (19)	100 (10)	100 (13, 34)
Tm2126/5	100 (20)	100 (16)	98 (7)	100 (8, 23)
Rye				
Rogo	7 (16)	100 (79, 82)
R9	19 (16)	100 (100, 96)
Barley				
L94	100 (8)	6 (18, 62)

^a Percentages averaged over two consecutive series of the second experiment.

^b Figures in parentheses indicate percentage of early-aborted sporelings associated with plant cell necrosis.

^c Percentages of early-aborted sporelings associated with necrosis are presented for both series.

TABLE 4. Induction of necrosis and formation of haustoria by sporelings of wheat leaf rust, rye leaf rust, and barley leaf rust fungi in bread wheat, diploid wheat, rye, and barley accessions

Accession	Series ^a	Wheat leaf rust (%) ^{b,c}			Rye leaf rust (%)			Barley leaf rust (%)		
		-N		+N ^d	-N		+N ^d	-N		+N ^d
		0	≥1		0	≥1		0	≥1	
Bread wheat										
Little Club	I	29	69	2	97	3	0	80	0	20 ^e
	II	28	72	0	100	0	0	38	0	62 ^e
Diploid wheat										
Tb1-1082	II	14	2	84 ^e	91	0	9	48	2	50 ^e
Tm2-1500	I	11	42	46	81	4	14 ^e	84	5	10
	II	5	20	75	65	10 ^f	25 ^e	40	17	42
TmEinkorn 1,3	II	94	6	0	83	17 ^f	0	75	8	17
Tm2126/5	I	97	2 ^f	1 ^e	86	14 ^f	0	94	0	6 ^e
	II	96	2	3 ^e	83	13 ^f	3	77	8	15
Rye										
Rogo	I	30	69	1	20	7	73
	II	12	88	0	28	0	72
Barley										
L94	I	7	91	1
	II	3	95	2

^aTwo series of the second experiment.

^bAverage of two isolates.

^c-N = did not induce necrosis; +N = induced necrosis; 0 = without formation of at least one haustorium 42 h postinoculation; ≥ = with formation of at least one haustorium 42 h postinoculation.

^dPresence of haustoria was not always certain.

^eIn the necrotic plant cell, a haustorium was rarely found.

^fAlmost all haustoria were formed in epidermal cells.

DISCUSSION

The very low infection types of the diploid wheat accessions are in accordance with the literature (34). The cultivar Einkorn has been reported to have a somewhat higher IT than most of the other accessions (34), which is confirmed by our observations. The susceptibility of the *T. urartu* accession Tu6735 has also been reported by Valkoun et al (34). Raupp et al (27) and Gill et al (8) reported a rather high frequency of susceptibility in accessions of *T. boeoticum* and *T. urartu*. Belea (2), however, claims that the subspecies *boeoticum* is resistant to leaf rust, whereas *T. urartu* is "sensitive."

In the present experiments the resistance expression was studied by two methods: the histological components analysis by means of fluorescence microscopy and the observation of haustoria by phase contrast microscopy. A comparison of Tables 3 and 4 indicates that a high percentage of early-aborted sporelings with infrequent necrosis (Table 3, components analysis) is explained by a high incidence of prehaustorial abortion (Table 4). A high frequency of early abortion with necrosis or a low frequency of early abortion is explained by a high frequency of haustorium formation (or at least, as with Tb1-1082 combined with wheat leaf rust and barley leaf rust, haustorium initials). This suggests that early abortion without necrosis indicates prehaustorial resistance, and early abortion with necrosis indicates posthaustorial resistance.

The results demonstrate that in certain plant-rust combinations nonhost resistance may be posthaustorial and associated with hypersensitivity. An example for this is the rye cultivar Rogo with barley leaf rust (Tables 3 and 4). Rye is not known to be a host of barley leaf rust (1,5). We conclude that there is either a resistance-avirulence system superimposed on an established basic compatibility between rye and barley leaf rust or an absence of basic compatibility that is expressed not before but after formation of the first haustoria. It may be relevant that cv. Rogo shows a completely prehaustorial reaction to another nonpathogenic grass rust species, *Uromyces dactylidis* G. Oth (L. J. M. Hendrickx and R. E. Niks, unpublished data). In that case, the absence of basic compatibility apparently leads to failure in haustorium formation.

It is not possible to generalize about the mechanism of resistance of diploid wheat to the wheat leaf rust fungus. Some accessions

(TmEinkorn 1,3 and Tm2126/5) caused almost complete early abortion of sporelings before the formation of haustoria. This reaction is also found in such combinations as bread wheat and rye leaf rust (Table 4) and bread wheat and barley leaf rust (20). In other accessions (Tb1-1082 and Tm2-1500) the fungus is arrested usually after at least the initiation of haustorium formation, or even after some colonization of the plant tissue (e.g., Tm10909 and Tm10592 in Table 1). This resistance is associated with plant cell necrosis. This posthaustorial hypersensitive resistance is similar to the host resistance of wheat to wheat leaf rust (14,31) or barley to barley leaf rust (20,25), and also to the nonhost reaction of the rye cv. Rogo to barley leaf rust (Table 4).

Breeding studies have shown that wild grasses may contain major (*Lr*) genes for resistance to wheat leaf rust. Such genes have been introduced into wheat (28) from a source like *Aegilops speltoides*, which is about as resistant to wheat leaf rust as *T. monococcum*. Such resistance due to *Lr* genes is typically of the hypersensitive type and in most cases not durable. It is tempting to assume that the hypersensitive posthaustorial resistance in the diploid wheats is also caused by *Lr*-like genes. The nonhypersensitive prehaustorial resistance to the rust in TmEinkorn 1,3 and Tm2126/5, however, may be due to the presumably more durable general defense mechanism.

We have started experiments to study the genetics of the prehaustorial and posthaustorial resistance of diploid wheats and the possibility of transferring either type to cultivated tetraploid and hexaploid wheat.

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