Induction of Resistance to *Erysiphe graminis* f. sp. *hordei* in Near-Isogenic Barley Lines

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ABSTRACT

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Inoculation of barley leaves with compatible or incompatible races of *Erysiphe graminis* f. sp. *hordei* protected leaves against subsequent infection by compatible races. When either compatible or incompatible inducer races were inoculated onto barley leaves and then removed at intervals, less than 1 hr of exposure to the inducer race provided significant protection against the challenge race. The resistance further intensified as the exposure time of the inducer race was increased to 6 or 9 hr. This early host response suggests that induction of resistance is initiated prior to appressorial penetration which occurs 6–8 hr after inoculation. Resistance was expressed as reduced numbers of colonies of the challenge race. Hence 6–9 hr of exposure to either a compatible or an incompatible inducer race reduced the number of mildew colonies produced by a compatible challenge race by 71–77%. There was no change in infection type. The protection increased with increasing inoculum density of the inducer race and lasted for at least 72 hr. Incompatible inducer races, which were not removed from the leaf prior to challenge inoculation, caused almost total protection against a compatible challenge race.

Additional key words: barley powdery mildew, induced resistance.

Induction of resistance, by which host plants are protected against pathogens by prior inoculation with the same or other pathogens, has attracted much attention in recent years. According to Kuć and co-workers (9) distinction can be made between two functionally different forms of induced resistance, systemic and local. Induced systemic protection against a pathogen can be elicited by previous inoculation of the host with either avirulent or virulent races of the same pathogen or with nonhost pathogens. The resistance-inducing factor is translocated from the site of induction to other, usually younger, plant parts, where it conditions the host tissue to respond in a resistant fashion upon subsequent challenge by a pathogen (2,5,7,10). In contrast to the systemic protection, induced local resistance is restricted to the site of inducer inoculation, and so far, only avirulent races of a pathogen and nonhost pathogens have been shown to act as inducers (6,9,14,15).

In the interaction between barley and *Erysiphe graminis* DC ex Mérat f. sp. *hordei* Marchal, induced systemic resistance to powdery mildew has recently been demonstrated by Hwang and Heitefuss (7), who found that inoculation of the lower leaves with either a compatible or an incompatible race of barley mildew caused partial resistance of the upper leaves to an otherwise compatible race. Ouchi et al (14,15) found that inoculation of barley leaves with avirulent races of *E. g.* f. sp. *hordei* elicited local resistance to subsequent infection by virulent races. The resistance was strictly localized, and establishment of resistance by the avirulent race required 6 hr. Only avirulent races were shown to act as inducers.

This paper shows, by the use of near-isogenic barley lines and a refined leaf inoculation technique, that not only avirulent but also virulent races of *E. g.* f. sp. *hordei* provide local protection against a subsequent application of a virulent race to the same leaf, and that the time needed by an inducer race to provide resistance is less than 1 hr. It was further investigated how the exposure time and inoculum concentration of the inducer races influence the degree of protection provided.

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MATERIALS AND METHODS

Barley lines. Two near-isogenic lines of barley (*Hordeum vulgare* L., 011301 and 112405) were used. The former line possesses the resistance gene *Ml*a; the latter possesses the resistance gene *Ml*a13 and possibly the gene *Ml*(Ru3) (L. Munk, *personal communication*). The genes *Ml*a and *Ml*a13 confer high resistance against races of *E. g.* f. sp. *hordei*. Both near-isogenic lines were selected from a backcrossing program in which the susceptible cultivar Pallas was used as the recurrent parent (L. Munk, *personal communication*).

Barley seedlings were grown in nutrient soil in 8-cm rectangular pots placed in a greenhouse which was maintained at approximately 20 C and had supplemental light (400 W/m^2) from standard, white, fluorescent tubes for 14 hr/day.

Isolates of *E. graminis*. Races A6 and H21 of *E. g.* f. sp. *hordei* were used. The isolates reacted differently with the two barley lines according to the compatibility pattern shown in Table 1. Isolates were maintained on the susceptible cultivar Pallas in a separate greenhouse under the same environmental conditions as those described above.

Inoculation procedure. The first inoculation, termed the inducer inoculation, was made when the first or second leaves of the barley plants were fully expanded. By the use of rubber bands, eight attached leaves of the same age from each pot were fixed with the adaxial side upward in a horizontal position on a polyacrylamide plate (Fig. 1). The inducer conidia, obtained from susceptible plants 8 days after inoculation, were inoculated onto the leaves by the aid of a 50-cm-high rectangular inoculation tower positioned over the fixed leaves. The tower was kept in position for 30 min until all spores had settled.

The use of the inoculation tower ensured that only a limited, well-defined area of the horizontally fixed leaves was inoculated with the inducer race and that all other plant parts remained free of inducer inoculum. For all inducer inoculations, two spore concentrations were used, either approximately 20 or 200 conidia per square millimeter of leaf area.

The removal of inducer inoculum was performed by gently rubbing the inoculated leaves in an upward direction with wet cotton, and afterwards the challenge inoculation of entire plants was accomplished by shaking infected leaves 2 m above the plants in an air-tight room. The conidia used for challenge inoculation were obtained from susceptible infected plants 6 days after inoculation. The use of young conidia prevented the formation of spore clumps landing on the plants, and the procedure ensured even and reproducible deposition of single conidia of the challenge race on the fixed plant surfaces.

Assessment of induced resistance. A quantitative estimation of induced resistance was obtained by counting the number of mildew colonies per 20 cm^2 of leaf area 7 days after the challenge inoculation. Plants that were inoculated only with the compatible challenge race served as controls. Changes in the infection types of challenge races were read 9 days after inoculation, according to the 0 to 4 scale of Mains and Dietz (13), in which 0 = no visible symptoms and 4 = strong development of mycelium and spores.

TABLE 1. Interactions of two near-isogenic barley lines and two races of *Erysiphe graminis* f. sp. *hordei* used in the experiment

Near-isogenic barley lines	Resistance genes	Infection types[a] produced by races	
		A6	H21
011301	*Ml*a	4	0, ln
112405	*Ml*a13	0	4

[a] Infection types: 4 = fully compatible interaction; 0 = incompatible interaction, no visible symptoms; and ln = weakly developed mycelium and necrotic lesions, no sporulation.

TABLE 2. The efficiency with which inoculum of the compatible race H21 of *Erysiphe graminis* f. sp. *hordei* was removed from leaves of near-isogenic barley line 112405

Removal of inoculum (hr) after inoculation[y]	Number of colonies per 20 cm^2 leaf area at two inoculum densities[z]	
	20 conidia/mm^2	200 conidia/mm^2
Control	>500	>500
0.5	5 a	10 a
3	5 a	9 a
6	6 a	9 a
9	4 a	10 a
12	7 a	27 b
15	58 b	150 c
18	156 c	242 d

[y] At the indicated hours after inoculation, conidia were removed by gently rubbing the leaf surfaces with wet cotton.

[z] Data are averages of three replicates, each replicate consisting of eight leaves. Means followed by the same letter within a column are not significantly different ($P = 0.05$).

RESULTS

Removal of mildew conidia from inoculated leaves. One of the aims of the work was to determine whether or not a virulent race of *E. g.* f. sp. *hordei* can protect barley against subsequent infection by the same race. To achieve this goal, it was necessary to employ a technique by which the inducer inoculum could be removed from the inoculated leaves before challenge inoculation was performed and before the inducer race became established in the tissue.

The efficiency by which conidia of the compatible race H21 could be removed from the adaxial leaf surface of near-isogenic barley line 112405 can be interpreted from Table 2 and Fig. 2. Only very few mildew colonies were produced if inoculum was removed within 9–12 hr after inoculation. Hence, at an inoculum density of 20 conidia per square millimeter, only four colonies developed per 20 cm^2 of leaf area if inoculum was removed 9 hr after inoculation (Table 2). In comparison, the numbers of mildew colonies that developed on the control leaves from which conidia had not been removed exceeded 500 colonies per 20 cm^2 (Fig. 2).

From 12 hr after inducer inoculation, the infection pegs of the appressoria had penetrated the outer epidermal cell wall and the conidia became difficult to remove. Attempts to remove inoculum 18 hr after inoculation thus resulted in 156 and 242 mildew colonies per 20 cm^2 of leaf area when inoculum density was 20 and 200 conidia/mm^2, respectively (Table 2).

Similar results were obtained in time-course studies with the compatible interaction between race A6 and near-isogenic barley line 011301, demonstrating that the compatible inducer races under our experimental conditions should be removed, at the latest, 9 hr after inoculation to ensure that infection and subsequent production of mildew colonies did not occur.

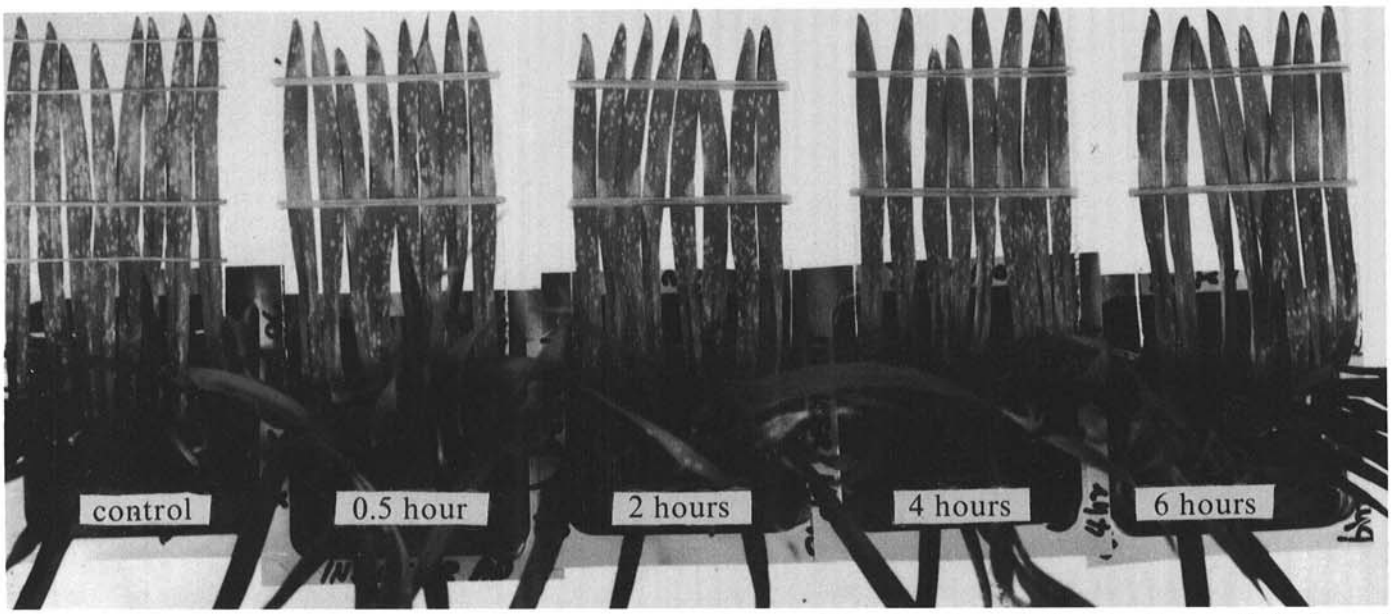

Fig. 1. Induced resistance in near-isogenic barley line 112405. The inducer race H21 (compatible) of *Erysiphe graminis* f. sp. *hordei* was applied by the use of an inoculation tower to the rectangular area between rubber bands. Inducer inoculum was removed after the number of hours indicated, and the entire plants were inoculated with challenge race H21 (compatible). Inoculum density of the inducer was approximately 200 conidia per square millimeter and that of the challenger approximately 20 conidia per square millimeter.

Since physical influences on leaves, including wounding, may result in wound repair responses which influence susceptibility (1), we examined whether the physical removal of the inducer race with wet cotton could alter the susceptibility of barley plants. From Table 3 it is seen that treatment of barley leaves with wet cotton did not affect the number of mildew colonies compared with the untreated control.

Time required for induction of resistance by incompatible and compatible inducer races. To determine the time needed to induce resistance, leaves of the two near-isogenic barley lines were inoculated at certain time intervals with either an incompatible or a compatible inducer race of *E. g.* f. sp. *hordei* and incubated at 20 C. The inducer inoculum was then removed and the entire plants were challenge inoculated with conidia of a compatible race.

Both incompatible and compatible inducer races conferred a high degree of resistance, measured as a reduction in number of mildew colonies produced by compatible challenge races (Tables 4 and 5). The degree of resistance achieved depended on the length of time the leaves were exposed to the inducer race. When either incompatible or compatible races were used as inducers it was found that less than 1 hr of exposure to the inducer provided significant protection against the challenge races. The degree of resistance increased as the exposure time of the inducer race was increased to 6 or 9 hr (Fig. 1, Tables 4 and 5).

Studies on the durability of resistance conferred by the incompatible inducer race A6 on near-isogenic barley line 112405 appear in Fig. 3. It is seen, that 6 hr of exposure to the inducer inoculum provided almost full protection of the leaves for at least 72 hr against infection by the compatible race H21.

Characteristically, resistance was expressed as a reduction in the number of mildew colonies, whereas there was no change in infection types. Hence, 6 or 9 hr of exposure to either a compatible or an incompatible inducer race reduced the number of mildew colonies produced by a compatible challenge race by 71–77% (Tables 4 and 5). There were no essential differences in results obtained with first or second developed leaves.

Induction of resistance with and without removal of the inducer race. In the previous experiments, the inducer race was always removed from the leaves immediately prior to challenge inoculation. Table 6 compares the resistance elicited by an incompatible inducer race with and without removal of the inducer inoculum before challenge inoculation.

In one group of seedlings, the inducer inoculum was removed 1 hr after inoculation, and the leaves then immediately challenge inoculated. In another group, the inducer inoculum remained on the leaves during challenge inoculation. In agreement with previous results, 1 hr of leaf exposure to the inducer resulted in moderate, but significant, reduction in the number of mildew colonies produced by the challenge race, and there was no change in infection types. However, when the inducer inoculum remained on the leaves virtually no colonies were produced by the challenger,

TABLE 3. The effect of rubbing leaves of near-isogenic barley lines with wet cotton on their susceptibility to *Erysiphe graminis* f. sp. *hordei*

Rubbing time (hr) before inoculation[x]	Mildew colonies per 20 cm²[y] of leaf area for barley line/race:	
	011301/A6[z]	112405/H21[z]
Control	305 a	338 a
0	311 a	325 a
48	297 a	335 a
96	307 a	328 a

[x]The adaxial leaf surfaces were rubbed with wet cotton at the indicated time intervals before inoculation.

[y]Data are averages of three replicates, each replicate consisting of eight leaves. Means followed by the same letter within a column are not significantly different ($P = 0.05$).

[z]Fully compatible interactions between near-isogenic barley lines and races A6 and H21 of *E. g.* f. sp. *hordei*.

TABLE 4. Time required for an incompatible inducer race (A6) of *Erysiphe graminis* f. sp. *hordei* to elicit resistance against a subsequent compatible challenge race (H21) in near-isogenic barley line 112405

Time (hr) between 1st and 2nd inoculation	Mildew colonies per 20 cm² leaf area[z]					
	1st developed leaves			2nd developed leaves		
	Number	Reduction (%)	Infection type	Number	Reduction (%)	Infection type
Control	348 a	0	4	359 a	0	4
0.5	299 b	14.1	4	291 b	18.9	4
2	278 b	20.1	4	...	...	...
3	...	...	...	176 c	51.0	4
4	122 c	64.9	4	...	...	...
6	87 d	75.0	4	104 d	71.0	4
9	91 d	73.9	4	101 d	71.9	4

[z]Data are averages of three replicates, each replicate consisting of eight leaves. Means followed by the same letter within a column are not significantly different ($P = 0.05$). Both inducer and challenger inoculations were on the adaxial leaf surface. Inducer inoculum was removed immediately prior to challenge inoculation. Inoculum density of inducer race was approximately 200 conidia per square millimeter, and of the challenge race approximately 20 conidia per square centimeter. Rating of infection type was according to Mains and Dietz (13): 0 = no visible symptoms, and 4 = strong development of mycelium and sporulation.

TABLE 5. Time required for a compatible inducer race (A6) of *Erysiphe graminis* f. sp. *hordei* to elicit resistance against a subsequent compatible challenge race (A6) in near-isogenic barley line 011301

Time (hr) between 1st and 2nd inoculation	Mildew colonies per 20 cm² leaf area[z]					
	1st developed leaves			2nd developed leaves		
	Number	Reduction (%)	Infection type	Number	Reduction (%)	Infection type
Control	397 a	0	4	415 a	0	4
0.5	330 b	19.3	4	344 b	19.4	4
2	306 b	25.3	4	...	...	...
3	...	...	...	187 c	57.2	4
4	161 c	61.8	4	...	...	...
6	109 d	74.9	4	125 d	72.2	4
9	121 d	71.9	4	104 d	77.2	4

[z]Data are averages of three replicates, each replicate consisting of eight leaves. Means followed by the same letter within a column are not significantly different ($P = 0.05$). Both inducer and challenger inoculations were on the adaxial leaf surface. Inducer inoculum was removed immediately prior to challenge inoculation. Inoculum density of inducer race was approximately 200 conidia per square millimeter, and of the challenge race approximately 20 conidia per square millimeter. Rating of infection type was according to Mains and Dietz (13): 0 = no visible symptoms, and 4 = strong development of mycelium and sporulation.

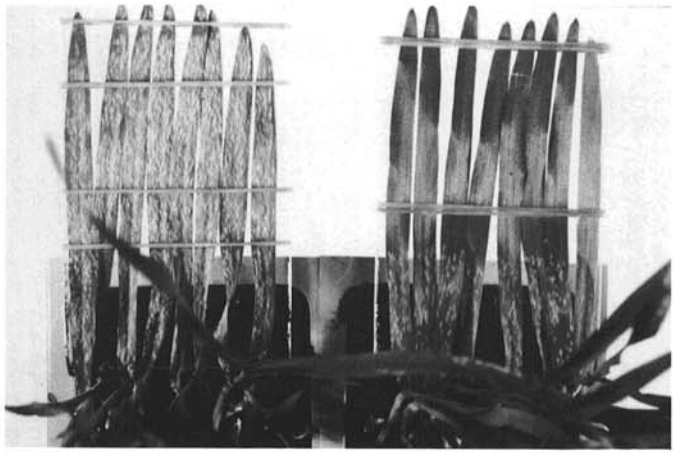

Fig. 2. Efficiency with which compatible conidia of *Erysiphe graminis* f. sp. *hordei* race H21 were removed from leaves of near-isogenic barley line 112405 with wet cotton. **Left,** Control leaves 9 days after inoculation. **Right,** Conidia were removed 9 hr after inoculation.

and the few colonies that did develop produced either no, or usually only a few, conidia. Typically, a fairly large number of necrotic spots developed.

The effect of inducer race inoculum density on the induction of resistance. The degree of induced resistance increased with increasing inoculum density of the inducer race, regardless of whether the inducer race was incompatible (Fig. 4A) or compatible (Fig. 4B). Thus, Fig. 4B shows that inoculation with 20 conidia per square millimeter of leaf area with the compatible inducer race H21 caused a 50% reduction in the number of mildew colonies produced by challenge inoculation with the same race. When 200 conidia per square millimeter of leaf area were applied in the inducer inoculation, the reduction in number of mildew colonies was about 75%. Again, the highest degree of protection was obtained by allowing a time interval of 6 hr between the first and second inoculation.

DISCUSSION

Ouchi et al (14,15) found that inoculation of barley leaves with an avirulent race of *E. g.* f. sp. *hordei* protected against subsequent inoculations of the same leaves with virulent races. Recently Hwang and Heitefuss (7) found that inoculation of the lower leaves of barley plants with either a virulent or an avirulent race of barley powdery mildew systemically protected the upper leaves against infection by virulent races. However, local protection against *E. g.* f. sp. *hordei* conferred by sequential inoculations with a virulent race has to our knowledge not been noted before. A prerequisite for using virulent races of *E. graminis* as inducers was that the inducer inoculum could be effectively removed from the leaf surfaces before the challenge races were applied. Wiping with wet cotton was very effective in removing inducer inoculum from the leaves if it was done before the inducer became established in the host. Under our experimental conditions the virulent inducer races did not produce mildew colonies when inoculum was removed within 9 hr after inoculation.

Since cell injury may influence leaf susceptibility by stimulating wound repair responses of the host tissues (1), it is essential to note that the physical effect of rubbing the leaves with wet cotton did not alter the susceptibility of barley leaves to mildew infections.

Resistance was induced within one hour following inoculation with either a virulent or an avirulent inducer race, but the resistance intensified as the interval between the two inoculations was increased to 6 or 9 hr. This early host response suggests that induction of resistance is initiated prior to host penetration from appressoria which occurs, at the earliest, 6–8 hr after inoculation. Until recently, penetration was considered to constitute the first interaction between barley and *E. g.* f. sp. *hordei* (4,8). However, the results of recent studies of the early stages of host-pathogen interactions in powdery mildew of barley (3,11) show that short, nonappressorial germ tubes produced during the initial stage of conidial germination may penetrate the host cell wall and incite a host response as early as 1–2 hr after inoculation. This is before the

TABLE 6. Induction of resistance in barley leaves with and without removal of incompatible inducer race of *Erysiphe graminis* f. sp. *hordei*. Near-isogenic barley line 011301, inducer race H21, and challenge race A6

Inducer conidia applied (no./mm²)	Mildew colonies per 20 cm² leaf area[y]					
	Inducer removed after 1 hr			Inducer not removed		
	Number	Reduction (%)	Infection type	Number	Reduction (%)	Infection type
Control[z]	330 a	0	4	330 a	0	4
20	302 b	8.5	4	34 b	89.7	1-3 n
200	294 b	10.9	4	5 b	98.5	1-3 n

[y] Data are averages of three replications, each replicate consisting of eight leaves. Means followed by the same letter within a column are not significantly different ($P = 0.05$); the letter n after infection types indicates necrotic lesions.

[z] The inducer race not applied.

Fig. 3. Durability of induced resistance in near-isogenic barley line 112405 against *Erysiphe graminis* f. sp. *hordei*. **Left,** Control leaves 9 days after inoculation with race H21. **Right,** The rectangular leaf area between the two upper rubber bands was inoculated with incompatible inducer race A6, which was removed again after 6 hr. Challenge inoculation of entire leaves with race H21 was performed 72 hr after removal of the inducer race.

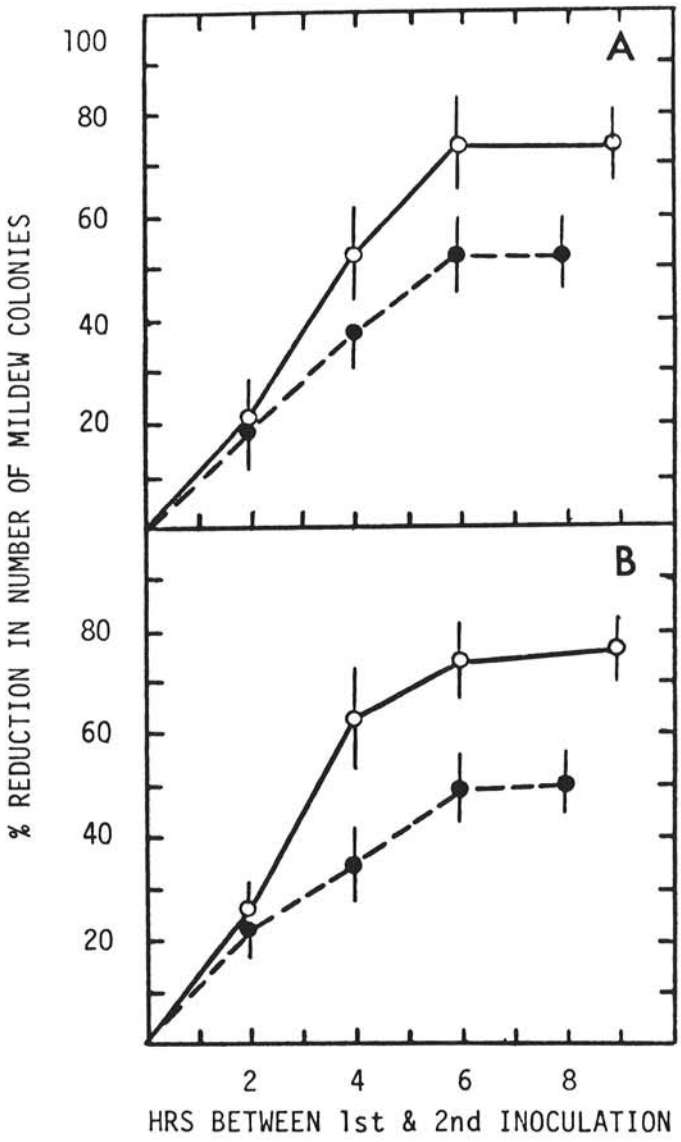

Fig. 4. The influence of inducer-inoculum density on the induction of resistance against subsequent infection by *Erysiphe graminis* f. sp. *hordei*. **A,** Near-isogenic barley line 011301, inducer race H21 (incompatible), challenge race A6 (compatible). **B,** Near-isogenic barley line 112405, inducer race H21 (compatible), challenge race H21 (compatible). Symbols: •------•, inoculum density 20 conidia per square millimeter: o——o, inoculum density 200 conidia per square millimeter. The inducer inocula were removed immediately before the challenge inoculations were made.

appressoria differentiate and establish interactions with the host. An early host-pathogen interaction at the pre-appressorial stage was also found by Littlefield (12) who demonstrated induction of resistance in flax 4 hr after inoculation with avirulent races of *Melampsora lini*.

Our findings that 1 hr of host exposure to an inducer race is enough to establish resistance against a subsequent challenge race, suggest that the early stage of induced resistance in these studies might result from interactions between the nonappressorial, primary germ tube and host cell. If so, induced resistance may be unrelated to natural race-specific resistance which seems to be established at the time of appressorial penetration (4). The finding that induced resistance reduces the number of mildew colonies without affecting infection type further suggests that protection might act at the level of host penetration and not during postpenetration development of the pathogen.

The fact that the degree of induced resistance was proportional to the amount of inducer inoculum might indicate a competition for infection sites on the leaves, as suggested by Littlefield (12) in the interaction between flax and *Melampsora lini*.

Our findings that a compatible race of *E. g.* f. sp. *hordei* induce resistance against the same or other compatible races are especially interesting in the light of the concept of induced susceptibility. Thus Ouchi et al (14,15) demonstrated that barley leaves exposed to a compatible race of *E. g.* f. sp. *hordei* became susceptible to incompatible races or nonpathogens. Induction of susceptibility required 15–18 hr to become established and was confined to cells with haustoria of the inducer race or adjacent cells. Induction of resistance, as shown by us, required only 1 hr of exposure to the compatible inducer race and was thus established far before appressorial penetration.

The results support the notion that plants in general recognize fungi, pathogens as well as nonpathogens, as incompatible organisms and therefore respond with a general defense against them. This is further emphasized by recent research (16) showing that barley plants respond to normal-occurring leaf saprophytes with rapid active defense reactions similar to those induced by avirulent races of *E. g.* f. sp. *hordei*. Susceptibility seems to occur only when these general defense reactions are suppressed or inactivated by some unknown mechanisms.

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