Interaction Between Flooding Stress and Phytophthora Root Rot Among Alfalfa Cultivars

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ABSTRACT

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The association between resistance to *Phytophthora megasperma* f. sp. *medicaginis* (*P. m. medicaginis*) and flooding injury was determined in greenhouse studies using 18 alfalfa cultivars and genotypes with various levels of resistance to *P. m. medicaginis*. Flooding stress applied for 3 days after zoospore inoculation resulted in as much plant damage as flooding stress applied for 6 days before inoculation. Increased secondary production of zoospores during postinoculation flooding may contribute to this response. Relative responses of cultivars to *P. m. medicaginis* were very similar when inoculated at either the vegetative (3-wk-old) or flowering (10-wk-old) stage of growth. Significant differences were found in both flood tolerance and *P. m. medicaginis* resistance among the cultivars. Cultivars resistant to *P. m. medicaginis* were generally more resistant to flooding stress in the absence of *P. m. medicaginis*; however, not all flood-tolerant cultivars displayed increased *P. m. medicaginis* resistance. Because the interaction among genotypes between *P. m. medicaginis* resistance and flood tolerance was significant, the two stress responses probably are not closely coupled. Ten-week-old plants with shoots removed just before treatment showed significantly more flooding injury and Phytophthora root rot damage than 3-wk-old plants. The stress of shoot removal may predispose the plant to injury from either physical or biological stress.

Additional key words: *Medicago sativa*, waterlogging injury

Phytophthora root rot (PRR) of alfalfa (*Medicago sativa* L.), first described by Erwin (5), is a widely distributed disease associated with poorly drained or periodically waterlogged soils. The fungus can kill seedlings or it can affect established mature plants, causing much of the taproot to rot and slough off (18). The affected plants are more vulnerable to environmental stress, especially drought. Because alfalfa is used extensively in long-term forage systems, persistence is an important attribute in cultivar selection.

Because both injury by flooding and damage by *Phytophthora megasperma* Drechs. f. sp. *medicaginis* (*P. m. medicaginis*) to alfalfa require a waterlogged soil, these physical and biological responses may be closely associated. The susceptibility of alfalfa to extended flooding is well known (3,7), as is the fact that some root rot diseases are favored by waterlogged soils (24). Preinoculation flooding stress predisposes plants, including alfalfa, to enhanced *Phytophthora* (2,4,14) disease.

Development of *P. m. medicaginis*-resistant alfalfa cultivars has progressed rapidly since the development of Agate alfalfa (9), which is moderately resistant to PRR. *Phytophthora*-resistant alfalfa cultivars produce greater dry-matter yield under wet soil conditions (8,17) than susceptible cultivars. Tolerance of alfalfa to flooding injury has also been reported because several cultivars (i.e., Iroquois, Lahontan, and Mich 80-16) have greater persistence in waterlogged soils (3,8,20).

The potential genetic interaction between flooding tolerance and *P. m. medicaginis* resistance in alfalfa has been alluded to several times in the literature. In a study on inheritance of *P. m. medicaginis*, deviation from expected segregation of alfalfa populations led Lu et al (16) to suggest that modifying genes may influence expression of *P. m. medicaginis* resistance. Lueschen et al (17) observed that PRR-resistant cultivars performed better than PRR-susceptible cultivars on wet, uninfested soils, which implied that greater flood tolerance was present in *P. m. medicaginis*-resistant cultivars. Also, Kuan and Erwin (14) suggested that flooding injury may have a corresponding effect on PRR resistance and that the comparative effect of flooding on cultivars with different levels of resistance to *P. m. medicaginis* should be examined.

The objective of this study was to investigate the responses of alfalfa cultivars and genotypes to flooding stress and *P. m. medicaginis* infection and characterize the interaction between flooding injury and PRR damage. Because both flood tolerance and PRR resistance vary with plant maturity, treatments were imposed at the seedling and flowering stages of growth.

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MATERIALS AND METHODS

Plant growth. All plants were grown in vermiculite in either 475-ml (3-wk-old plants) or 950-ml (10-wk-old plants) disposable pots. Ten plants were established from seed in each pot and watered as needed with complete nutrient solution. The experiment was conducted in a glasshouse set to maintain daytime temperatures of 28–29 C and night temperatures of 24–25 C; however, maximum daytime temperatures of 33–34 C were achieved for short periods on several days. Plants were either 3 wk old (seedling-vegetative stage) or 10–11 wk old and in the bud to early bloom stage of growth.

Inoculum production. The original isolate used for this work was obtained from D. C. Erwin. This isolate infected more plants and resulted in larger root lesions than Ohio isolates. Eight single-zoospore isolates from this mass isolate were compared on Vernal alfalfa, and the two that produced the most and largest lesions were used throughout this investigation. The isolates were maintained on dilute V-8 juice modified by mixing with 5 g of Celite 545 filter aid (Johns Mansville) and filtration through a 1-cm-thick pad of Celite 545 on Whatman No. 1 filter paper before use (23).

Lima bean extract agar (20 frozen lima beans per liter autoclaved and passed through a household sieve and filtered with Celite 545 as described before with 20 g agar per liter) was used for zoospore production. Zoospores were produced in two ways. The first involved sequentially washing lima bean agar (LBA) cultures of *P. m. medicaginis*. LBA cultures were started with four 0.5-cm-diameter plugs of mycelium from V-8 juice agar. After 7 days of incubation at room temperature (25–28 C), the cultures were washed four times with sterile distilled water (15 ml per wash) replaced after 20 min. The plates then were flooded with 15 ml of water and incubated at room temperature for 4–5 hr for zoospore release. Zoospore suspensions were carefully poured into a beaker, counted with a hemacytometer, and used immediately.

The second method, used in the latter

part of the work, also used dilute LBA (20 ml per 125-ml Erlenmeyer flask). Flasks were started with one 0.5-cm-diameter plug from a V-8 juice agar culture. After 1 wk, the flasks were flooded with 25 ml of deionized water passed through a Milli-Q filter system (Millipore Corp.) and placed in a lighted (cool-white fluorescent bulbs) incubator at 19–20 C for 16 hr. Spores were counted by placing 10 ml of the pooled zoospore suspension in a polystyrene petri plate, adding three drops of 0.1% trypan blue in lactophenol, and counting four fields of 1 mm each after 20 min to allow the stained spores to settle on the bottom. Zoospores per milliliter were calculated from zoospores per square millimeter assuming all zoospores had sedimented.

Flooding and inoculation treatments. Flooding stress was initiated by transferring the plants to new pots without drainage holes and filling each pot with water to 1–1.5 cm above the surface of the vermiculite. This level was maintained with periodic additions of water. Pots flooded before inoculation with zoospores were drained 1 hr before inoculation by transferring the plants into pots with drainage holes. Pots with plants subjected to postinoculation flooding stress had a water level 1–1.5 cm above the vermiculite for 3 days after inoculation with zoospores.

Plants were inoculated with *P. m. medicaginis* by adding about 50,000 zoospores to each pot and washing them into the rooting medium with water until free water was visible at the surface. Nonflooding and preinoculation flooding stress treatments were drained 6 hr after inoculation and were watered daily with nutrient solution until harvest. Postinoculation flooding treatments were drained after the desired flooding period and were then watered daily with nutrient solution.

Experimental treatments. Experiment 1 was a preliminary experiment to determine the effects of duration of flooding stress on PRR damage using cultivars Vernal, Agate, and Trident. Treatments that resulted in large differences among cultivars were selected for further experiments. Main treatments were 2 and 6 days of preinoculation flooding stress and 1 or 3 days of postinoculation flooding stress. In experiments 2 and 3, 18 alfalfa cultivars (Table 1) representing a wide range of reported resistance to *Phytophthora* were compared. Several pairs of cultivars were included that varied widely in their level of PRR resistance but had a similar genetic background. For example, Mich 80-16P is a PRR-resistant genotype derived from Mich 80-16, and both Mich 80-16 and Oneida are selections derived from PRR-susceptible Iroquois (M. Tesar, *personal communication*). In experiment 2, 3-wk-old plants were subjected to 0 and 6 days of preinoculation flooding or 3 days of postinoculation flooding and either inoculated with *P. m. medicaginis* or not inoculated. The experiment with 3-wk-old plants was repeated twice in 1984.

In experiment 3, shoots of 10- to 11-wk-old plants were clipped to leave a 5-cm stubble and the same treatments as in experiment 2 were imposed. Only a single experiment was done in 1984. Several preliminary experiments were conducted in 1983, but only 14 cultivars were used.

Evaluation of damage by flooding and *Phytophthora*. Twelve days after inoculation, shoot fresh weight was determined by clipping regrowth above the stubble from 10-wk-old treated plants or all growth above 3 cm for 3-wk-old treated plants. Vermiculite was removed from roots by immersion in water and vigorous agitation. Lesions on the taproot were scored according to the following scale: 1 = no lesions, 2 = small lesions present, 3 = lesions greater than 1 cm but taproot intact, 4 = severe lesions with taproot rotted off >1 cm from crown, and 5 = root dead.

Fresh weight of shoots was used to estimate total plant injury caused by flooding stress and PRR damage. Data were subjected to analysis of variance to examine main effects and treatment interactions. Correlation analysis was also used to estimate the association of PRR damage with flooding stress. The experimental design was a split-split plot with four replicates (blocks).

RESULTS

Postinoculation flooding stress was much more injurious to plant growth than were equal periods of preinoculation flooding stress (Table 2) because flooding for 3 days postinoculation caused much greater PRR damage than flooding for 6 days preinoculation. Therefore, we used a 6-day preinoculation, a 3-day postinoculation, and a nonflooding treatment in subsequent experiments. The preinoculation treatment represents a flooding stress applied separately from the *P. m. medicaginis* stress, whereas the postinoculation treatment reflects response to both stresses applied concurrently.

Three-week-old, rapidly growing alfalfa was affected by application of flooding stress for 6 days before inoculation. Fresh weights of shoots from flooded plants for all cultivars for both experiments were reduced 28% relative to nonflooded controls. The 10-wk-old clipped plants were much more sensitive to flooding stress than nonclipped plants and averaged nearly a 50% reduction in shoot growth after flooding.

Fresh weights of shoots and root disease ratings in these experiments were consistently significantly correlated with $r > 0.90$. Because of this close association between root disease score and shoot growth, shoot fresh weight was used in experiments 2 and 3 to quantitate *Phytophthora* damage. Fresh weight of shoots also integrates total plant injury caused by flooding and PRR when plants were exposed to both stresses.

Experiment 2. Significant differences in PRR damage of 3-wk-old plants were attributable to cultivar and flooding treatments as expected, although the effects of flooding treatments were not great (Table 3). Cultivars with reported high levels of resistance to *P. m. medicaginis* (e.g., Trident and A77-B10)

Table 1. Alfalfa cultivars and genotypes and their resistance to *Phytophthora megasperma*

Cultivar	Seed source[a]	Disease resistance[b]
A77-10B	UCR	R
WI 79-43	UW	R
Oneida	C	R
79 PII-P	NAPB	R
Trident	C	R
Answer	C	R
OT 78/2	ORS	R
G7730	NAPB	R
Agate	C	R
Lahontan	C	MR
FAR 14/1	ORS	MR
PolySc 2	ORS	MR
Mich 80-16P	MSU	MR
African	C	S
Vernal	C	S
Iroquois	C	S
Anchor	C	S
Mich 80-16	MSU	S

[a] UCR = University of California, Riverside; UW = University of Wisconsin, Madison; NAPB = Nickerson American Plant Breeders, Inc.; ORS = Ottawa Research Station, Canada; MSU = Michigan State University, East Lansing; and C = commercial.
[b] R = resistant, MR = moderately resistant, and S = susceptible. Ratings determined from published report (25) and from D. K. Barnes, E. T. Bingham, A. M. Farris, J. B. Moutray, and M. B. Tesar (*personal communications*).

Table 2. Effect of flooding on Phytophthora root rot scores of 3-wk-old plants inoculated with *Phytophthora megasperma*

Flooding treatment	Phytophthora root rot score[a]		
	Vernal	Agate	Trident
Nonflooded	2.80[b]	2.05	2.18
2 Days before inoculation	2.48	2.09	2.02
6 Days before inoculation	3.80	2.60	2.58
1 Day after inoculation	3.52	2.43	1.88
3 Days after inoculation	4.30	3.10	3.02
LSD (0.05)	0.75	0.39	0.33

[a] Root rating: 1 = no root lesions, 5 = plants dead.
[b] Mean of four replicates of 10 plants each.

also showed high levels of resistance to *P. m. medicaginis* in this study. Although resistance to *P. m. medicaginis* was generally maintained across flooding stress treatments, the flooding treatment × cultivar interaction was highly significant. Many cultivars showed no or little additional PRR damage when severely stressed with 6-day preinoculation or 3-day postinoculation flooding (i.e., A77-10B and 79PII-P), whereas other cultivars showed a significant effect of preinoculation flooding on PRR damage (e.g., Trident and Mich 80-16P).

Rank correlation analysis of cultivar response comparing no preflooding stress (0 days) and 6-day preinoculation flooding stress were statistically significant ($r = 0.66$). Rank correlation of 6-day preinoculation flooding and 3-day postinoculation flooding treatments were also significant ($r = 0.76$).

Experiment 3. Plant injury caused by flooding stress after clipping was very severe, and many of the cultivars had few or no living plants when harvested (Table 4). However, many cultivars showed significantly higher levels of flood tolerance than the least flood-resistant cultivars (e.g., Vernal, Anchor, and Mich 80-16P). Significant genetic variability was present for this character as well as for *P. m. medicaginis* resistance.

The relative cultivar response of 10-wk-old plants to *P. m. medicaginis* infection (Table 4) was similar to that observed in 3-wk-old plants (Table 3). Because flooding 10-wk-old clipped plants for 6 days before inoculation severely injured many cultivars, it was not possible to accurately quantitate additional damage caused by *P. m. medicaginis* inoculation and infection. *Phytophthora* damage of 10-wk-old plants was severe when flooded for 3 days postinoculation. The best cultivars had reductions in shoot fresh weight of 50% relative to the uninoculated controls, and susceptible cultivars were completely killed by the disease. As was observed in 3-wk-old plants, A77-10B and 79PII-P were among the most *P. m. medicaginis*-resistant lines and Vernal and Anchor were among the least resistant.

Table 3. Injury of 3-wk-old alfalfa lines inoculated with zoospores of *Phytophthora megasperma* in response to various levels of flooding stress

	Plant injury (% of control)[a]		
Cultivar	Nonflooded	6 Days preinoculation flooding	3 Days postinoculation flooding
79 PII-P	98	93	92
A77-10B	97	90	91
WI 79-43	95	85	88
Trident	94	82	81
G7730	91	81	85
Agate	89	80	73
Oneida	89	81	94
Mich 80-16P	89	52	62
Answer	84	76	71
Lahontan	74	67	68
OT 78/2	66	73	73
FAR 14/11	57	72	67
Mich 80-16	57	41	53
PolySc	57	39	48
African	49	47	55
Vernal	46	41	36
Anchor	44	34	39
Iroquois	39	46	37
LSD (0.05)	7.2	9.2	7.3

[a] Inoculated plant shoot fresh weight/uninoculated plant shoot fresh weight × 100; mean of two experiments, four replicates per experiment. Differences between cultivars, treatments, and treatment × cultivar interactions were significant at $P = 0.01$ (ANOVA).

Table 4. Shoot regrowth of 10-wk-old clipped alfalfa in response to 6 days of flooding stress or *Phytophthora megasperma* damage after no flooding or 3 days of postinoculation flooding

	Phytophthora damage[a]		
Cultivar	Nonflooded	Flooded	Flooding injury[b]
79 PII-P	84	57	73
A77-10B	85	61	72
WI 79-43	85	33	69
Trident	65	19	61
G7730	76	19	38
Agate	86	18	33
Oneida	81	49	59
Mich 80-16P	55	7	28
Answer	68	29	79
Lahontan	77	16	61
QT 78/2	76	22	43
FAR 14/1	67	20	34
Mich 80-16	30	5	44
PolySc 2	35	5	75
African	32	10	40
Vernal	23	5	44
Anchor	30	5	17
Iroquois	37	14	59
LSD (0.05)	11.3	10.2	18

[a] Percentage shoot regrowth of inoculated plants relative to that of uninoculated plants.
[b] Percentage shoot regrowth of 6 day flooded plants relative to that of nonflooded plants in absence of *Phytophthora megasperma* (four observations).

DISCUSSION

PRR caused total loss of fine secondary roots and produced severe taproot lesions in susceptible alfalfa genotypes as has been previously reported (18). The relative PRR damage ratings among cultivars were consistent among experiments. The most *P. m. medicaginis*-resistant lines were A77-10B, 79PII-P, and WI79-43, and the least resistant cultivars were Vernal, Iroquois, and Anchor. More variability was noted in the relative rankings of cultivars with intermediate *P. m. medicaginis* resistance.

The disease index (in parentheses) reported by Vaziri et al (25) for six cultivars included in this study, A77-10B (2.10), Trident (3.10), Agate (3.56), Lahontan (3.66), Answer (3.79), and African (4.45), are nearly in the same relative ranking as was found for 3-wk-old nonflooded seedlings in Table 3. Thus, our methods resulted in cultivar rankings consistent with reported *P. m. medicaginis* resistance levels. For flood tolerance, no comprehensive comparison of cultivar resistance has been reported in the literature; however, Iroquois and Lahontan appear to have greater flooding tolerance under field conditions (6,19). Recently, Alva et al (1) found no difference in flood tolerance of Iroquois and Oneida, which is consistent with the responses of these cultivars in this study.

The significant interaction between cultivar response to *P. m. medicaginis* infection and flooding stress is important because in some cultivars, PRR damage was not increased by flooding (Table 3). Although correlation coefficients relating cultivar PRR damage in the presence and absence of flooding stress were always significant, the r values were not high ($r = 0.65$ for comparison of 0- and 6-day flooding stress). Although there was an overall relationship between degree of resistance to *P. m. medicaginis* (damage) and tolerance to flooding stress, many cultivars did not show a close association

of these factors. Because improvement of PRR resistance has been accomplished by recurrent selection of resistant phenotypes growing on *P. m. medicaginis*-infested and waterlogged soil (9), both characters may be selected in breeding programs. Genetic resistance to *P. m. medicaginis* is very complex in alfalfa (11,16), and these data suggest flooding tolerance is not a prerequisite for *P. m. medicaginis* resistance.

Kuan and Erwin (14) suggested that preflooding predisposes alfalfa to *P. m. medicaginis* infection by causing root injury and increasing exudation of nutrients. They reported increased zoospore accumulation on preflooded roots but did not relate zoospore accumulation to subsequent plant damage. If *P. m. medicaginis* damage was closely associated with preinoculation flooding stress in this study, cultivars with reported flooding tolerance (i.e., Iroquois, Lahonton, and Mich 80-16) should have less PRR damage in response to preinoculation flooding than non-flood-tolerant cultivars such as Vernal and Anchor. However, there were no significant differential responses to flooding stress among these cultivars.

Because postinoculation flooding treatments were much more effective than preinoculation flooding in increasing disease, flooding either increases the production and dispersion of inoculum (13) or negatively affects root metabolism, thus facilitating *P. m. medicaginis* growth within the diseased root tissue. Because significant changes occur in alfalfa root metabolism, membrane permeability, and energy status, within 3 days of alfalfa root anaerobiosis (A. L. Barta, *unpublished*), the tissue may be more susceptible to disease. Levitt (15) has indicated that flooding stress, though not directly injurious, can cause secondary O_2 deficiency stress in the tissue. In separate experiments, we have also observed an increase in zoospores present in the flood water 2 days after inoculation of roots. This inoculum increase could have a major effect on increasing plant damage because inoculum concentration directly affects disease resistance in seedlings (12). However, there was a greater effect of flooding for 3 days postinoculation on clipped plants (Table 4) than on 3-wk-old vegetative plants (Table 3), suggesting that inoculum level cannot be the only factor responsible for this increased disease level.

In contrast to the marked effect of 3-day postinoculation flooding stress on *P. m. medicaginis* damage, only the 6-day preinoculation flooding treatment caused greater PRR damage. The 6-day flooding stress also caused measurable plant flooding injury, which suggests that flooding stress affects PRR damage in two ways: 1) Flooding causes root injury that predisposes the plant to increased PRR damage (4,14) and 2) O_2-deficiency stress negatively alters root physiology or *P. m. medicaginis* resistance of the infected root.

Ten-week-old plants that were clipped were more susceptible to PRR damage and flooding injury than were 3-wk-old plants even though it has been documented that older alfalfa plants are more resistant to *P. m. medicaginis* (21). Clipping alfalfa may increase PRR damage (22) and flooding injury (3,7). The additional stress of shoot removal may have been critical in this response because even nonflooded but clipped, inoculated plants showed greater injury than nonclipped 3-wk-old plants.

It must be emphasized that the results of this study were obtained by flooding and inoculating roots totally flooded in vermiculite under controlled conditions in the greenhouse. Flooding in the field may expose plants to stresses additional to anaerobiosis (i.e., excessive Mn^{+2} and Al^{+3} uptake and soil ethylene accumulation [15]), thus relative flood response of these cultivars could differ. Also, cultivars with a more shallow root system, as Mich 80-16, which show improved persistence on poorly drained soils (M. Tesar, *personal communication*), may not have shown higher flood tolerance because the entire root system was waterlogged. However, *P. m. medicaginis* resistance of greenhouse-grown plants has been shown to correlate with field resistance tests (9,10). Additional studies are needed to describe the interaction of physical and biological stress under field conditions.

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