Interactions of Bean Yellow Mosaic Virus and an Aphid Vector with Phytophthora Root Diseases in Arrowleaf Clover

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ABSTRACT

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Arrowleaf clover was inoculated with bean yellow mosaic virus (BYMV), *Phytophthora erythroseptica,* and *P. megasperma* f. sp. *trifolii* individually and in dual virus-fungus combinations at 7 and 9 wk. Dual inoculations were accomplished simultaneously and sequentially. Severity of symptoms was evaluated by root disease scores, root volumes, and dry weights of foliage. Simultaneous dual inoculations, and prior inoculations with BYMV, greatly increased severity of symptoms as compared to those caused by the virus and *Phytophthora* species individually. These increases were often synergistic as determined by root disease scores. Subsequent inoculations of BYMV into plants infected with *Phytophthora* resulted in smaller increases in severity of symptoms. In alsike clover, a species tolerant to BYMV and resistant to the *Phytophthora* spp., dual inoculations with BYMV and *P. megasperma* f. sp. *trifolii* did not consistently give more severe symptoms than those caused by the pathogens individually. Plants of healthy and BYMV-infected arrowleaf clover were colonized more heavily by the pea aphid in the greenhouse than were plants infected by *P. erythroseptica* with or without BYMV. However, in assays repeated during three seasons in the field, no differences were observed in frequencies of natural infection by BYMV in healthy and Phytophthora-infected arrowleaf clover.

Additional key words: Acyrthosiphon pisum, Phytophthora erythroseptica, Phytophthora megasperma f. sp. *trifolii, Trifolium hybridum,* and *Trifolium vesiculosum.*

Viruses and fungal root diseases are important limiting factors for production of forage legumes. Clovers, alfalfa, and similar crops are infected by many aphid-transmitted viruses which often occur at high frequencies in stands (1,3,5,12,13,16,27). Most forage legumes are also damaged by one or more fungal root diseases that also may occur at high frequencies (7,12,14,17,24,29,30).

Few studies have evaluated the extent to which viruses and fungal root diseases occur together in forage legumes; their joint impact on symptom development, yield, and survival of plants; effects on vectors; or the likelihood that either type of disease may predispose plants to the other. Also, results described to date have not been consistent. Dual infection of alfalfa with alfalfa mosaic virus and *Phytophthora megasperma* Drechs. in the greenhouse caused greater damage than occurred with the pathogens individually during the winter in California, but not during the summer (10). Fusarium root rot and red clover vein mosaic virus (RCVMV) often infected the same plants of red clover in West Virginia, and this suggested that the virus predisposed plants to fungal root disease (7). Such predisposition by RCVMV in red clover did occur for *Fusarium oxysporum* Schlect. and *F. solani* (Mart.) Sacc., but not for *F. roseum* Link or *F. moniliforme* Sheldon (6). Infection of lupine by BYMV increased the severity of root and stem rot caused by *F. solani* (23), but infection of white clover by BYMV did not affect its interactions with *F. oxysporum, F. solani, Rhizoctonia solani* Kuhn, or *Macrophomina phaseolina* (Tassi) Goid (19). Clover yellow mosaic virus caused symptoms of root rot in red clover, similar to those observed in the field in Idaho, in the presence or absence of *F. oxysporum, F. roseum,* and *Tetracocosporium paxianum* Szabo (28).

Arrowleaf clover (*Trifolium vesiculosum* Savi) in Mississippi is damaged by a disease complex that involves both aphid-transmitted viruses and root-infecting fungi (15). The most severely affected plants usually show foliar symptoms of virus infection along with root rot and crown deterioration and are killed before seed is set. BYMV was the most frequent virus identified during five seasons, but clover yellow vein virus (CYVV), peanut stunt virus (PSV), and occasionally other viruses were also present (15; R. Pratt, W. Knight, and O. Barnett, *unpublished*). Incidences of virus

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infection often approach 100% near the end of the growing season (15). BYMV, CYVV, and PSV alone cause stunting, malformation of leaves, and occasional death of young plants (9).

Phytophthora species are thus far considered to be the principal causal organisms of root rot of arrowleaf clover in Mississippi. A species provisionally identified as *P. erythroseptica* Pethyb. is moderately virulent on arrowleaf clover and *P. megasperma* f. sp. *trifolii* is highly virulent (24).

The fact that aphid-transmitted viruses and fungal root diseases are both frequently associated with decline and premature death of arrowleaf clover suggests that these diseases may interact to promote symptom development, or that their occurrence may be related. Both of these possibilities were investigated in this study. Effects of viral and fungal infection on colonization of arrowleaf clover by an aphid vector of BYMV were also evaluated.

MATERIALS AND METHODS

Single and dual inoculations of arrowleaf and alsike clovers with BYMV and *Phytophthora* species. Effects of single and dual virus-fungus inoculations of arrowleaf and alsike clovers were determined in the greenhouse. Alsike clover was also evaluated because, unlike arrowleaf, it is tolerant to BYMV and resistant to the *Phytophthora* species (24). Germinated seeds of arrowleaf cultivar Meechee and of alsike clover were planted near the rims of 10.5-cm-diameter clay pots containing a steamed soil mixture, and a compatible inoculum of *Rhizobium* was added after 7 days (24). Inoculum of BYMV and the *Phytophthora* species was applied at 7 and 9 wk. Mixtures of cornmeal and sand, infested with two isolates of each *Phytophthora* species, were composited for each species and added center wells of pots (24). An isolate of BYMV (9) was mechanically inoculated onto three leaves of each plant using sap from infected alsike clover. Twenty plants (two per pot) were utilized in each treatment. One set of controls received no inoculations and one set received stimulated inoculations with noninfested cornmeal-sand and leaf sap at 7 wk. All pots were flooded for 2 days at 4-day intervals for 2 wk after inoculation to promote root infection by *Phytophthora*.

BYMV and each *Phytophthora* species were individually and simultaneously inoculated onto arrowleaf clover at both 7 and 9 wk. They were also inoculated sequentially at the same times in all virus-fungus combinations. Alsike clover was inoculated only with BYMV and *P. megasperma* individually and simultaneously at 7 wk. Both experiments were repeated once with daylengths of 11–13 hr and temperatures usually 20–25 C.

At 13 wk of age, plants were removed from pots, washed free of soil, and evaluated by measuring three parameters. Dry weights of non-necrotic foliage were determined after air-drying in the greenhouse for several days and subsequent oven-drying at 50 C for 24 hr. Root volumes were determined by immersing roots in graduated cylinders and measuring the displacement of water. Root disease scores (0–4) were assigned according to the extent of visible rotting and discoloration of roots, with 0 = none, 1 = slight, and 4 = most severe (24). Inverses of root disease scores were designated "root health scores" and were expressed as percentages of controls. Differences between treatments ($P<0.05$) were determined by analysis of variance and use of the Student-Newman-Keuls test (26). Virus-fungus interactions ($P<0.05$) were determined by factorial analyses.

Assays for BYMV in healthy and Phytophthora-infected arrowleaf clover. Arrowleaf clover plants, healthy and infected with *P. erythroseptica,* were grown in the greenhouse, transported to the field, and assayed for BYMV after 0, 2, 3, and 4 wk. The experiment was repeated during three seasons. Seventy-two plants were grown individually in 10.5-cm-diameter pots during each season, and half were inoculated with the fungus at 6–7 wk. During the first season, plants were taken to the field immediately after inoculation; during the second and third seasons, plants were maintained in the greenhouse for an additional 2–3 wk to allow development of foliar symptoms. In each season, 24 potted plants, 12 healthy and 12 infected with *Phytophthora,* were randomly arranged and buried to the rims at 60-cm intervals in a 4 × 6 arrangement at each of three locations within an arrowleaf clover nursery. Pots were watered daily. Three young leaves from each plant were assayed at each sampling. Sap was expressed by grinding with phosphate-buffered saline and added to wells in enzyme-linked immunosorbent assay (ELISA) plates previously sensitized with BYMV antiserum (20). Plates were incubated at 4 C for 12 hr, washed free of sap, and mailed to Clemson University, where ELISAs were done as previously described (20,21).

Colonization of healthy and diseased arrowleaf clover by an aphid vector. Colonization of arrowleaf clover by the pea aphid, *Acyrthosiphon pisum* (Harris), a vector of BYMV (11,18), was compared for healthy plants and plants infected with BYMV, *P. erythroseptica,* and BYMV plus *P. erythroseptica* simultaneously. Inoculations were made at 7 wk and plants were utilized at 11 wk. Sixteen plants of each disease class, one plant per pot, were randomized in an 8 × 8 arrangement at 30-cm intervals on a greenhouse bench. Eight pots containing six to eight broadbean (*Vicia faba* L.) plants infested with mature colonies of primarily alate pea aphids were placed at equidistant points around the perimeter. Populations of aphids on clover plants were scored visually since exact counts would have required disruptive or destructive sampling which might have affected behavior and reproduction of aphids. Scores were taken from each plant at 10, 20, and 30 days after introduction of aphids as follows: score 1 = no aphids, 2 = 1–5 aphids, 3 = 6–20, 4 = 21–50, 5 = 51–100, and 6 = 100+. Scores of populations were subjected to analyses of variance, and the LSD ($P<0.05$) between treatment means was determined.

TABLE 1. Responses of arrowleaf clover following individual and dual inoculations with bean yellow mosaic virus (BYMV) and *Phytophthora erythroseptica*[y]

Plant characteristics[z]	BYMV (+/−) and times	*P. erythroseptica* (+/−) and inoculation times		
		(−)	(+) 7 wk	(+) 9 wk
Foliar dry weights	(−)	100 a	41 c	61 b
	(+) 7 wk	54 b	8 f	17 ef
	(+) 9 wk	64 b	27 de	32 cd
Root volumes	(−)	100 a	51 bc	57 bc
	(+) 7 wk	48 c	9 e	17 de
	(+) 9 wk	72 b	36 cd	27 de
Root health	(−)	100 a	63 b	50 c
	(+) 7 wk	100 a	22 d *S*	22 d *S*
	(+) 9 wk	100 a	50 c *S*	18 d *S*

[y]Values are mean of 10 pots, two plants per pot, expressed as percentages of mean control values. All plants were evaluated at 13 wk. For each plant characteristic, values not followed by the same letter differ significantly ($P = 0.05$) according to the Student-Newman-Keuls test. *S* = synergism as indicated by significant ($P = 0.05$) factorial interactions.

[z]Foliar dry weights (grams) were determined after drying at 50 C for 24 hr. Root volumes (cubic centimeters) were determined from displacement of water by immersed roots. Root health values are inverses of root disease scores (24).

RESULTS

Single and dual infections of arrowleaf and alsike clovers with BYMV and *Phytophthora* species. Results of the two experiments with each clover species were similar; mean values of treatments from one experiment with each species are presented in Tables 1, 2, and 3.

BYMV reduced foliar dry weights and root volumes of arrowleaf clover, but it did not cause any symptoms of root rot. *P. erythroseptica* and *P. megasperma* caused disease according to all three parameters; symptoms were more severe with *P. megasperma* (Tables 1 and 2).

The most severe symptoms in arrowleaf clover occurred with simultaneous dual inoculations of BYMV and the two *Phytophthora* species at 7 and 9 wk, and with prior inoculations of BYMV (Tables 1 and 2). Foliar dry weights of plants in these

treatments were always less than for plants inoculated with the same pathogens individually. In the treatments involving *P. erythroseptica* and prior or simultaneous BYMV, root volumes were always less and severity of root disease was greater than with the pathogens individually. In the treatments involving *P. megasperma* and prior or simultaneous BYMV, root volumes and root disease scores did not always differ significantly from those obtained with *P. megasperma* alone. However, this fungus alone greatly reduced root volumes and caused severe root disease.

Symptoms were less severe when BYMV was inoculated onto arrowleaf clover plants subsequent to each *Phytophthora* species. For *P. erythroseptica,* root health was less with prior virus than with subsequent virus (Table 1); for *P. megasperma,* root health and foliar dry weights were less with prior virus than with subsequent virus (Table 2).

Increases in severity of root disease were synergistic for all treatments involving dual inoculations of BYMV and *P. erythroseptica,* and for one treatment involving dual inoculations of BYMV and *P. megasperma* (Tables 1 and 2).

In alsike clover, both BYMV and *P. megasperma* alone significantly reduced root volumes (Table 3). BYMV also significantly increased foliar dry weights. Dual inoculations at 7 wk gave slightly more severe root disease than that caused by *P. megasperma* alone. However, root volumes obtained with dual inoculations were not less than with the pathogens individually, and foliar dry weights were not less than with *P. megasperma* alone (Table 3).

Infection of healthy and Phytophthora-infected arrowleaf clover by BYMV in the field. Results of assays of plants in the field are presented in Table 4. No significant differences in acquisition of BYMV by healthy and Phytophthora-infected arrowleaf clover were detected at any sampling in spite of great differences in incidence of the virus during the three seasons.

Colonization of healthy and diseased arrowleaf clover by an aphid vector. Pea aphids colonized healthy plants and those infected with BYMV more heavily than plants infected by *P. erythroseptica* with or without BYMV (Table 5). This trend was first evident at 10 days. Significant differences between mean scores for aphid populations on plants of the different treatments appeared at 20 days and were maintained at 30 days.

DISCUSSION

Results of this study demonstrate that BYMV and the *Phytophthora* species interact to cause severe root and foliar symptoms in arrowleaf clover. Increases in symptoms are related to

TABLE 2. Responses of arrowleaf clover following individual and dual inoculations with bean yellow mosaic virus (BYMV) and *Phytophthora megasperma* f. sp. *trifolii*[y]

Plant characteristics[z]	BYMV (+/−) and inoculation times	*P. megasperma* (+/−) and inoculation times		
		(−)	(+) 7 wk	(+) 9 wk
Foliar dry weights	(−)	100 a	35 c	39 c
	(+) 7 wk	54 b	5 d	5 d
	(+) 9 wk	64 b	26 c	2 d
Root volumes	(−)	100 a	30 d	10 e
	(+) 7 wk	48 c	2 e	2 e
	(+) 9 wk	72 b	13 e	2 e
Root health	(−)	100 a	10 b	5 c
	(+) 7 wk	100 a	5 c *S*	3 c
	(+) 9 wk	100 a	10 b	0 c

[y]Values are means of 10 pots, two plants per pot, expressed as percentages of mean control values. All plants were evaluated at 13 wk. For each plant characteristic, values not followed by the same letter differ significantly ($P = 0.05$) according to the Student-Newman-Keuls test. *S* = synergism as indicated by significant ($P = 0.05$) factorial interactions.

[z]Foliar dry weights (grams) were determined after drying at 50 C for 24 hr. Root volumes (cubic centimeters) were determined from displacement of water by immersed roots. Root health values are inverses of root disease scores (24).

TABLE 3. Responses of alsike clover following individual and dual inoculations with bean yellow mosaic virus (BYMV) and *Phytophthora megasperma* f. sp. *trifolii*[y]

Plant characteristics[z]	BYMV (+/−) and inoculation times	*P. megasperma* (+/−) and inoculation times	
		(−)	(+) 7 wk
Foliar dry weights	(−)	100 a	100 a
	(+) 7 wk	132 b	99 a
Root volumes	(−)	100 a	66 b
	(+) 7 wk	65 b	66 b
Root health	(−)	100 a	97 a
	(+) 7 wk	100 a	92 b

[y]Values are means of 10 pots, two plants per pot, expressed as percentages of mean control values. All plants were evaluated at 13 wk. For each plant characteristic, values not followed by the same letter differ significantly ($P = 0.05$) according to the Student-Newman-Keuls test.

[z]Foliar dry weights (grams) were determined after drying at 50 C for 24 hr. Root volumes (cubic centimeters) were determined from displacement of water by immersed roots. Root health values are inverses of root disease scores (24).

TABLE 4. Occurrence of bean yellow mosaic virus (BYMV) in healthy and *Phytophthora*-infected arrowleaf clover plants in the field during three seasons

Season	*Phytophthora* infection in roots[y]	Number of plants assayed positive for BYMV after being in the field[z]:			
		0 wk	2 wk	3 wk	4 wk
Spring 1979	(−)	···	···	33	21
	(+)	···	···	32	19
Fall 1979	(−)	0	0	0	1
	(+)	0	0	0	1
Spring 1980	(−)	0	0	19	34
	(+)	0	0	15	28

[y]Plants were infected with *Phytophthora erythroseptica* in the greenhouse at 6–7 wk and taken to the field immediately (spring, 1979) or after symptom development (fall, 1979; spring, 1980). Twenty-four plants (12 healthy and 12 Phytophthora-infected) were randomized at 60-cm intervals in each of three locations in an arrowleaf clover nursery.

[z]Leaf samples were taken from each plant at indicated times after placement in the field and assayed for BYMV by ELISA. Data indicate numbers of plants assayed positive out of 36 total. Differences in frequencies of virus in Phytophthora-infected and noninfected plants were not significant ($P < 0.05$) at any sampling time.

TABLE 5. Aphid colonization of arrowleaf clover plants noninfected and infected individually and in combination with bean yellow mosaic virus (BYMV) and *Phytophthora erythroseptica*

Infection treatments[x]	Mean scores of aphid populations on plants 10–30 days after exposure[y,z]		
	10 days	20 days	30 days
0 (healthy)	2.13 a	4.31 a	5.25 a
BYMV	1.75 a	3.75 a	4.50 a
P. erythroseptica	1.31 a	2.06 b	2.69 b
BYMV + *P. erythroseptica*	1.38 a	2.13 b	2.75 b

[x]Plants were grown individually in pots, inoculated, and exposed to the pea aphid (*Acyrthosiphon pisum*) after symptoms were well developed. Sixteen plants of each treatment were randomly arranged on a greenhouse bench.

[y]Values are means of 16 plants scored as follows: 1 = no aphids, 2 = 1–5 aphids, 3 = 6–20 aphids, 4 = 21–50 aphids, 5 = 51–100 aphids, and 6 = 100+ aphids.

[z]Means within a column not followed by the same letter differ significantly. Values of LSD ($P < 0.05$) were 0.95, 0.69, and 0.78 for mean scores at 10, 20, and 30 days after exposure, respectively.

the sequence of inoculation of the pathogens and often represent synergistic interactions. This appears to be the first detailed report of interactions between a virus and *Phytophthora* spp. which lead to increased severity of disease. Similar interactions were previously reported with *Aphanomyces* and *Pythium* (8,22).

The results of the greenhouse study correspond well to situations observed in the field, where severely diseased arrowleaf clover plants, which die prematurely, often manifest symptoms of both virus and Phytophthora infection. The interactions demonstrated experimentally, therefore, appear to be important limiting factors for production and survival of plants in the field. Results suggest that development of resistance to either BYMV or the *Phytophthora* species in arrowleaf clover might greatly alleviate total disease losses by preventing the highly destructive virus-fungus interactions.

Diseases caused by viruses and root-infecting fungi are not the only factors that limit productivity and survival of arrowleaf clover in Mississippi. Deterioration of crown tissue is also frequently observed. This appears similar to the condition described as "internal breakdown" in red clover, which has been considered a physiogenic disorder (7). No fungal pathogens have been consistently isolated from internally necrotic crowns (R. Pratt, *unpublished*). Such crown deterioration, when present, undoubtedly contributes significantly to decline and premature death of arrowleaf clover.

Results obtained with alsike clover, a species tolerant to BYMV and resistant to *P. megasperma* (24), were very different from those obtained with arrowleaf. No strong effects on symptom development occurred with dual inoculations of the two pathogens. This suggests that strong interaction effects with viruses and fungi can occur only if one or both of the pathogens cause significant damage alone. BYMV and *P. megasperma* both cause moderate to severe disease symptoms on arrowleaf clover individually and, therefore, their combined effects are significant and often synergistic. The same pathogens cause only slight damage on alsike clover and, therefore, their combined effects are also slight or insignificant. The interactions of viruses and root-infecting fungi described on other forage legumes do not appear to have been as strong as those observed on arrowleaf clover in this study (6,10,19,28). These viruses or fungi or both may not have been as virulent or damaging individually as the pathogens of arrowleaf clover. Strong virus-fungus interactions have been described on other crops where one or both pathogens caused severe symptoms alone (4,8,22,25).

Results of this study also suggest that diseases caused by BYMV and the *Phytophthora* species on arrowleaf clover are likely to occur together. The much greater severity of root rot in plants infected with BYMV indicates that the virus increases their susceptibility to the fungi or promotes greater infection by increasing root exudates (2). For either reason, it appears likely that the occurrence, spread, and severity of diseases caused by *Phytophthora* in the field would be increased in the presence of widespread BYMV infection.

Potential effects of parasitization by *Phytophthora* species on the frequency and spread of viruses in arrowleaf clover are less clear. Infection of individual plants by *P. erythroseptica* did not influence frequency of natural infection by BYMV in the field. However, pea aphids colonized healthy and BYMV-infected plants more heavily than plants infected with *P. erythroseptica* in the greenhouse. Lower initial scores for aphid populations on plants infected by *Phytophthora* at 10 days postinfestation, and less increase in scores by 30 days, suggests that both host preference and reproduction of pea aphids may be affected by Phytophthora root rot. If aphids are preferentially attracted to healthy and virus-infected plants, or repelled from fungus-infected plants, then movement of viruliferous aphids to plants not infected by *Phytophthora* would be favored. This would serve to predispose additional plants to severe Phytophthora disease and thus increase total damage caused by both diseases. Additional studies are needed to determine how movement and feeding activity of aphids, as they relate to virus epidemiology, may be affected by occurrence of root rot and associated foliar symptoms in arrowleaf clover.

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