The Influence of Compost Amendment or Straw Mulch on the Reduction of Gas Exchange in Potato by *Verticillium dahliae* and *Pratylenchus penetrans*

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ABSTRACT

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Single potato plants (*Solanum tuberosum* cv. Superior) were grown in microplots in soil that was fumigated and then infested with *Verticillium dahliae, Pratylenchus penetrans,* or both to evaluate the effects of these pathogens and of cultural treatments with spent mushroom compost or straw mulch on gas exchange of potato leaves. Photosynthesis and transpiration of terminal leaflets of a cohort of similar-aged leaves were measured once a week from the time of expansion until they senesced. Over all measurements, gas exchange per unit leaf area was less for plants in microplots infested with *V. dahliae* or *P. penetrans* than for those in uninfested plots. For leaves that expanded in early June, gas exchange was similar immediately after leaf expansion but declined more quickly when microplots were infested with one or both pathogens compared to no infestation. Overall, leaf gas exchange was increased by compost amendment but not affected by straw mulch. Compost amendment prevented some of the decline in gas exchange due to infestation by one or both pathogens. For leaves that expanded in July, compost increased the gas exchange immediately after expansion in both infested and non-infested plots.

Additional keywords: lesion nematode, photosynthesis, *Solanum tuberosum*, transpiration, Verticillium wilt

The early dying disease of potato (*Solanum tuberosum* L.) is caused primarily by *Verticillium dahliae* Kleb., but coinfection of potato by *V. dahliae* and *Pratylenchus penetrans* (Cobb) Filipjev & Schuur.-Stek. increases vascular infection by *V. dahliae* and the severity of disease (2,6,13,14,17,20). This disease results in premature vine senescence and can reduce tuber yield by 30 to 50% (19,20).

The loss of yield due to early dying is ascribed to a decrease in photosynthesis and the supply of assimilates required for tuber growth (3,4). Two mechanisms may lower photosynthesis on a whole-plant basis. One mechanism is loss of leaf area via stunting and defoliation or senescence. Due to leaf abscission or death, the plant would intercept less radiation and photosynthesis would be reduced in proportion to the loss in leaf area (10). Based on gas exchange measurements of entire eggplants grown in the field, the predominant effect of *V. dahliae* was to reduce leaf area rather than to lower the rate of photosynthesis per unit area (7). However, closing of stomata or increasing mesophyll resistance due to disruption in metabolic pathways could reduce photosynthesis per unit area or radiation-use-efficiency (RUE) of infected plants. *V. dahliae* can decrease RUE of potato in the absence of visual disease symptoms (5), and gas exchange in the field as early as 1 month after emergence of the plants (9). After onset of senescence, the decline in radiation interception is likely to be a more significant factor. *V. dahliae* may reduce potato photosynthesis through both mechanisms. From gas exchange measurements of individual leaves on field-grown potato plants, Bowden and Rouse (3,4) estimated that 33% of yield reduction was due to a reduction in RUE, and the remaining 67% was due to a reduction in leaf area. *V. dahliae* infection reduced transpiration, stomatal conductance, and photosynthesis of these field-grown plants (3,4).

The interaction of the effect of different pathogens on gas exchange had not been examined until recently. Saeed et al (22,23) examined the effects of *V. dahliae* and *P. penetrans* on gas exchange of cv. Russet Burbank potato grown in a controlled environment. When inoculated at low densities, gas exchange was reduced only when plants were infested with both pathogens. They concluded that there was a linear relation between stomatal conductance and leaf photosynthesis, but that biochemical factors reduced photosynthesis more than transpiration with concomitant infection (23).

Our objectives were to determine how *V. dahliae* and *P. penetrans* interact under field microplot conditions to affect gas exchange of cv. Superior potatoes, and whether compost soil amendment or straw mulch can ameliorate the effect of disease on photosynthesis and transpiration. A companion paper describes the effect of these cultural amendments on the development of potato early dying symptoms and tuber yield (15).

MATERIALS AND METHODS

Treatments. Experiments were conducted in field microplots established in Windsor, Connecticut. A total of 12 treatments consisting of four pathogen combinations (no pathogens, *V. dahliae* alone, *P. penetrans* alone, and both *V. dahliae* and *P. penetrans*) and three cultural treatments (compost, straw, or conventional) were applied in a factorial design that was replicated 5 times in 1993 and 10 times in 1994 and 1995. Microsclerotial inoculum of *V. dahliae* from a bran-soil culture or a sterile bran-soil mix (control) was added at 11.5 g/plot, and a *P. penetrans* inoculum extracted from monoxenic carrot disk culture or the suspension resulting from a similar extraction from carrot disks without nematodes (control) was added at 20,000 eggs, juveniles, and adults per plot, as described previously (15). Spent mushroom compost (Franklin Mushroom Farms, Franklin, CT) was added and incorporated into appropriate microplots at 2.7 liters/plot, approximately 2.5 cm in depth. Rye straw mulch was applied to an 8-cm depth around plants after side-dressing and hilling.

Certified B-sized seed potatoes (*Solanum tuberosum* L. cv. Superior) were planted at one tuber per microplot, between each microplot within rows, and in border rows at a 20-cm spacing. All plots were fertilized before planting and side-dressed

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to equalize nutrients and pH. Colorado potato beetles and foliar diseases such as early or late blight were controlled by weekly applications of insecticides and fungicides as necessary. The dates of cultural and experimental procedures are described elsewhere (15).

Measurements. The terminal leaflet of the fourth leaf on one stem in each microplot was tagged as it expanded in early June of 1993, 1994, and 1995. The size and gas exchange of this leaflet was measured repeatedly at weekly intervals until it senesced. On 7 July 1995, a leaflet on a higher node was selected as it expanded and both sets of leaflets were measured on 20 and 27 July. When it was selected and first measured, the area of each leaflet had expanded to 40 to 90% of its final size.

Gas exchange was measured in an open system by using an infrared gas analyzer (IRGA) operating in the differential mode to compare the gas concentration returned from a leaf chamber to that from a reference flow of air. In 1993, the IRGA was a CO_2 analyzer (Model 865, Beckman Instruments, Norwalk, CT), and in 1994 and 1995 the IRGA was both a CO_2 and H_2O analyzer (Model 6262, LiCor, Lincoln NE). Thus, transpiration was not measured in 1993. Ambient air was passed through a 20-liter reservoir to buffer short-term fluctuations in composition. A portion of this air flowed at 15 ml s^{-1} through the reference channel of the IRGA. The rest of the air flowed to the leaf chamber at approximately 40 ml s^{-1}, with the flow monitored by a calibrated tube flow meter. A diaphragm pump returned the air from the leaf chamber to the IRGA at a flow of about 30 ml s^{-1}. The leaf chamber consisted of two identical frames of acrylic covered with polypropylene film, held closed with a spring clamp, and sealed with 0.3-cm-thick closed-cell foam rubber. The chamber enclosing the leaf had inner dimensions of 5 by 10 by 2 cm. A manifold of tiny holes created a laminar flow across upper and lower surfaces of the leaf. A leaf was placed in the chamber so that the petiole was clamped on one side and the tip was clamped on the other. Thus, a 5-cm length of leaf and the full width of the leaf was inside the chamber. The chamber was oriented so that the upper surface of the leaf was perpendicular to solar radiation. The leaf was held in this position in unobstructed sunlight for approximately 1 min, until the IRGA reading stabilized. Measurements were taken at 5-s intervals for 30 s, averaged, and recorded along with the flow rate, temperature, and sunlight intensity. One leaf was measured from each plant (microplot). The concentration of CO_2 and H_2O in the ambient air was measured at hourly intervals by comparison with air scrubbed with NaOH and $MgSO_4$. These ambient concentrations were used to refine the IRGA response. Leaf areas were measured with a portable leaf area meter. The leaf gas exchange rates per unit area were calculated from the difference in concentration of CO_2 or H_2O between ambient and chamber air streams, multiplied by the air flow rate, and divided by the leaf area in the chamber.

Gas exchange measurements were conducted at weekly intervals, between 0900 and 1500 h Eastern Standard Time. Leaves were measured in the same sequence based on plot number on each date. Irradiance was generally 1,200 to 1,700 µmol m^{-2} s^{-1} PPFD during measurements. When the data were analyzed within dates, no corrections were applied for irradiance or temperature. The data were also analyzed across all measurement dates within one year by repeated measures analysis, where each date was a repeated measure. The gas exchange was set to zero for dead or abscised leaves.

RESULTS

The average area of terminal leaflets used for gas exchange measurements was 19, 26, and 21 cm^2 in 1993, 1994, and 1995, respectively. Plants grown in microplots with compost amendment had larger leaves than those in non-amended plots. The increase in area was 20% in 1993 and 10% in 1994 and 1995 (data not shown). Covering the soil with straw mulch did not affect the area of terminal leaflets. Inoculation with *V. dahliae* decreased the leaf area only in 1995, by 15% compared to no inoculation. Inoculation with *P. penetrans* had little effect on leaflet area, except in the absence of *V. dahliae* in 1995, when *P. penetrans* infestation reduced the area by 13%.

The combined infestation with *V. dahliae* and *P. penetrans* resulted in the lowest ranking for photosynthesis on 10 out of 18 measurement dates over the three years of this study. However, combined infestation never lowered photosynthesis significantly more than one of the pests alone (Fig. 1). *V. dahliae* infestation lowered the rate of photosynthesis of terminal leaflets when averaged over all measurements in 1994 and 1995 (Table 1). Inoculation with *P. penetrans* also lowered the rate of photosynthesis significantly in 1994, but the effect was smaller than that for *V. dahliae*. *V. dahliae* infestation alone lowered photosynthesis more than *P. penetrans* in mid-July 1994, and on and after 22 June 1995. When a second set of leaflets was selected in 1995, *P. penetrans* infestation alone reduced gas exchange as much as in combination with *V. dahliae*, so that the effect of *P. penetrans* was rated as more significant than that of *V. dahliae* in the statistical analysis. The photosynthesis of the younger leaves was more rapid than that of the older leaves, when compared within dates.

Compost amendment increased photosynthesis in two of three years, but covering the soil surface with straw mulch did not affect gas exchange significantly in any year (Table 1). In early and mid-June but not in July 1993, terminal leaflets of plants grown in microplots amended with compost had greater photosynthesis per unit area than those without amendment (data not shown). Averaged over infestation levels in 1994, the cultural amendments had no effect on photosynthesis (Fig. 2). In 1995, compost amendment did not increase gas exchange during leaf expansion, but it slowed the decline in gas exchange of terminal leaflets that occurred as the leaves aged. Over all measurements in 1995, compost amendment increased photosynthesis by about 50% compared to no amendment.

In part, the effect of compost on leaf photosynthesis was due to a selective improvement in plots infested with *V. dahliae* or *P. penetrans*. In 1994, the decline in photosynthesis in the presence of both pathogens was greater in plots with no amendment than in plots with compost. Averaged over all dates in 1994, infestation with both pathogens reduced photosynthesis from 13.5 to 10.6 µmol m^{-2} s^{-1} (21%) in non-amended plots and from 13.5 to 12.2 µmol m^{-2} s^{-1} (10%) in compost-amended plots. For leaves that expanded in June 1995, the comparable reductions in photosynthesis were 40% in non-amended plots and 11% in compost-amended plots. The accelerated decline in photosynthesis of these leaves due to infestation, and the reversal of this decline due to compost amendment, resulted in a significant interaction between the effects of culture, pathogen, and time (Table 1). Leaves that expanded in July 1995 had a different response. Averaged over three dates, the decline in photosynthesis from 7.2 to 3.3 µmol m^{-2} s^{-1} (54%) due to infestation in non-amended plots, was similar to the decline from 11.9 to 6.4 µmol m^{-2} s^{-1} (44%) due to infestation in compost-amended plots.

In general, the rate of transpiration per unit area of terminal leaflets was affected by pathogen infestation in a manner similar to that for photosynthesis (compare Figs. 1 and 3). The combined infestation with *V. dahliae* and *P. penetrans* resulted in the lowest ranking for transpiration on 9 out of 15 measurement dates in 1994 and 1995 (Fig. 3). Averaged over all dates in 1994, neither *V. dahliae* nor *P. penetrans* alone slowed the rate of transpiration, compared to uninfested plants (Table 2). However, the combined infestation did decrease transpiration significantly on four of six measurement dates. In 1995, transpiration of leaves that expanded in June was decreased by *V. dahliae* infestation and transpiration of leaves that expanded in July was decreased by *P. penetrans* infestation, compared to uninfested plants. The cultural amendments also had similar effects on the rates of transpiration and photosynthesis (compare Figs. 2 and 4). Compost amendment slowed the decline in transpiration

and infestation accelerated the decline in leaves that expanded in June 1995, leading to interactions between effects of these factors and time (Table 2). Transpiration of the second set of leaves selected in 1995 was increased by compost amendment as much as was photosynthesis (Fig. 4).

In part, the effect of compost on transpiration was due to a selective improvement in plots infested with *V. dahliae* or *P. penetrans*. Averaged over measurements in 1994, this interaction between effects of culture and pathogen was marginally significant at $P = 0.10$ (Table 2). Infestation with both pathogens reduced transpiration from 3.5 to 2.7 mmol m^{-2} s^{-1} (23%) in non-amended plots, and from 3.6 to 3.5 mmol m^{-2} s^{-1} (3%) in compost-amended plots. For leaves that expanded in June 1995, the comparable reductions in transpiration were 36% in non-amended plots and 15% in compost-amended plots. However, for leaves that expanded in July 1995, the decrease in transpiration due to combined infestation was similar in non-amended and compost-amended plots (34 and 29%, respectively).

As the leaves aged, transpiration did not decline as rapidly as photosynthesis did. Just after expansion in July 1995, the second set of leaves transpired as rapidly as did the first set of leaves when they expanded in June. However, photosynthesis of leaves just after expansion was slower in July than in June, 10 compared to 16 µmol m^{-2} s^{-1}, respectively.

A decline in leaf gas exchange due to pathogen infestation was apparent on 15 June 1994 and 22 June 1995. However, leaves did not show symptoms until after 5 July in these years (15). There was only a weak correlation between the time that gas exchange declined to half the maximum value and the time that 50% of the leaves of the plant showed symptoms of early dying. This interval between the decline in leaf photosynthesis and the appearance of disease symptoms was not related to cultural amendment or inoculation with *V. dahliae* and *P. penetrans*. Although the

Table 1. Repeated measures analysis of variance of effects of compost amendment, straw mulch, and infestation with *Verticillium dahliae*, *Pratylenchus penetrans*, or both on carbon exchange rate per unit leaf area of cv. Superior potatoes in field microplots

	Photosynthesis, µmol CO_2 m^{-2} s^{-1}			
Factor	**1993**	**1994**	**1995**	**1995, second set**
Culture[a]				
None	11.1	12.1	5.2	4.7
Compost	15.7	12.5	8.4	10.2
Straw	13.0	11.9	4.6	5.4
Pathogen[b]				
Vd– Pp–	13.4	13.6	7.4	9.8
Vd– Pp+	14.2	12.1	6.6	6.2
Vd+ Pp–	13.5	11.6	5.0	5.8
Vd+ Pp+	11.9	11.0	4.9	4.6
Factor (P =)				
Culture	0.012	NS	0.000	0.000
Pathogen	NS	0.003	0.000	0.000
Culture × pathogen	NS	NS	0.010	NS
Time	0.000	0.000	0.000	0.000
Time × culture	0.076	NS	0.017	0.005
Time × pathogen	NS	NS	0.000	0.087
Time × culture × pathogen	NS	NS	0.011	NS
Within pathogen				
Vd	NS	0.003	0.016	NS
Pp	NS	0.028	NS	0.001
Vd × Pp	NS	NS	NS	NS

[a] Mineral soil alone, amended with spent mushroom compost or straw applied as a mulch.
[b] With or without *Verticillium dahliae* (Vd) or *Pratylenchus penetrans* (Pp). NS = not significant.

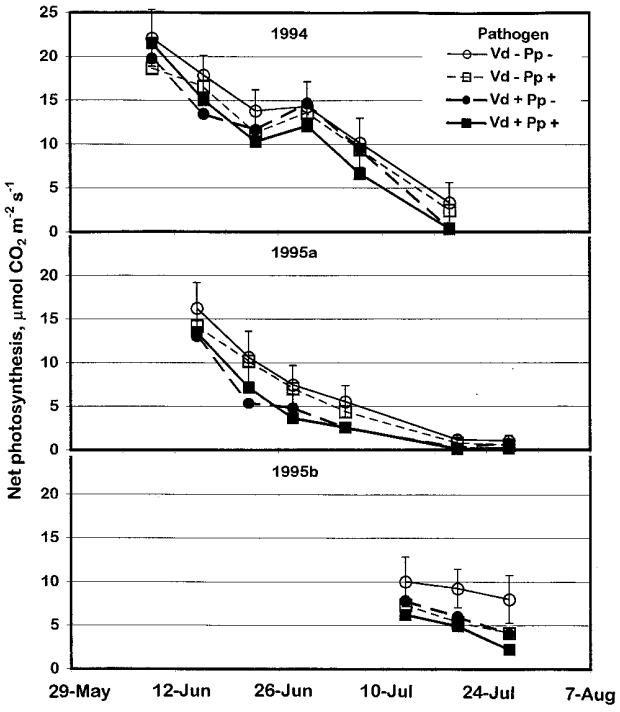

Fig. 1. Effect of infestation with *Verticillium dahliae*, *Pratylenchus penetrans*, or both on photosynthesis per unit leaf area of terminal leaflets of potato. The symbols represent weekly measurements averaged over cultural amendments. The error bars indicate the least significant difference within a weekly measurement. Results are separated for sets of leaves selected in 1994, and in June and July 1995.

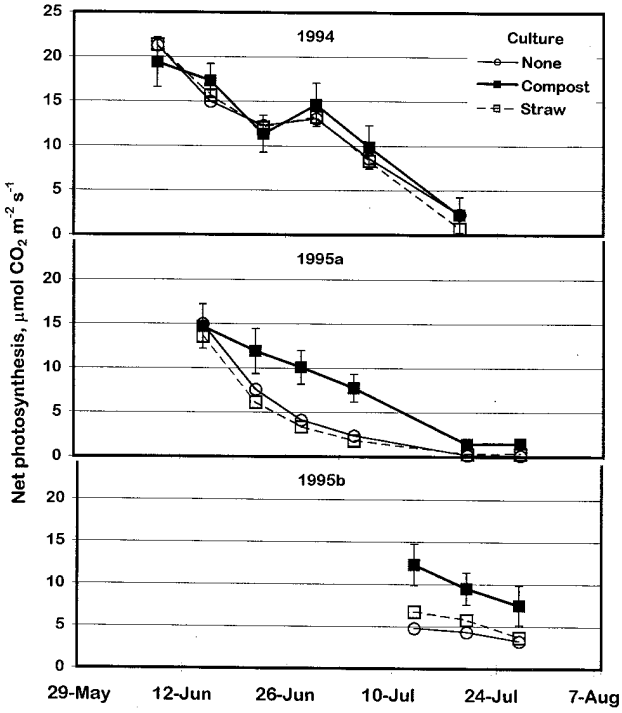

Fig. 2. Effect of the cultural amendments, compost, straw mulch, or none on photosynthesis per unit leaf area of terminal leaflets of potato. The symbols represent weekly measurements averaged over cultural amendments. The error bars indicate the least significant difference within a weekly measurement. Results are separated for sets of leaves selected in 1994, and in June and July 1995.

expression of disease symptoms and the decline in leaf gas exchange were both affected significantly by the treatments, some plants with poor gas exchange developed disease symptoms relatively late, while others had rapid gas exchange until symptoms started to appear.

DISCUSSION

In these experiments, gas exchange of cv. Superior potato plants was reduced by infesting the soil in microplots with either *V. dahliae* or *P. penetrans* alone. Similar effects of *V. dahliae* alone on photosynthesis and transpiration of potato have been reported for experiments conducted in a controlled environment (3,5) or in the field (4,8). *V. dahliae* causes a decline in gas exchange as leaves age that is more rapid than the decline for leaves of non-infected plants. However, this is the first report that *P. penetrans* infestation alone reduces gas exchange. Our observations suggest the time course of the decline in gas exchange due to *P. penetrans* infestation was similar to that due to *V. dahliae* infestation. Root-knot and cyst nematodes were shown to decrease gas exchange of potato (24), soybean (11), and tomato (18). Growth, photosynthesis, and transpiration of potato were not affected until the population of cyst nematodes was greater or equal to 30/g of soil (24). In growth chamber experiments in which nematode inoculum levels were about 1 to 5/g, neither photosynthesis nor transpiration of 'Russet Burbank' potato was affected by *P. penetrans* infestation alone (23). In greenhouse experiments in which nematode inoculum levels were insufficient to affect growth of 'Superior' potato, *P. penetrans* infection affected neither transpiration nor leaf xylem potential, but it did reduce root hydraulic conductivity (12). However, the 'Superior' potato used in our experiments is reported

Table 2. Repeated measures analysis of variance of effects of compost amendment, straw mulch, and infestation with *Verticillium dahliae*, *Pratylenchus penetrans*, or both on transpiration per unit leaf area of cv. Superior potatoes in field microplots

	Transpiration, mmol H_2O m^{-2} s^{-1}		
Factor	**1994**	**1995**	**1995 second set**
Culture[a]			
None	3.2	1.7	2.9
Compost	3.2	2.6	4.8
Straw	3.2	1.6	3.3
Pathogen[b]			
Vd– Pp–	3.5	2.3	4.9
Vd– Pp+	3.2	2.1	3.6
Vd+ Pp–	3.2	1.7	3.3
Vd+ Pp+	2.9	1.6	2.7
Factor (*P* =)			
Culture	NS	0.000	0.000
Pathogen	NS	0.005	0.000
Culture × pathogen	0.100	NS	NS
Time	0.000	0.000	NS
Time × culture	NS	0.050	NS
Time × pathogen	NS	0.055	0.069
Time × culture × pathogen	NS	NS	NS
Within pathogen			
Vd	NS	0.041	NS
Pp	NS	NS	0.000
Vd × Pp	NS	NS	NS

[a] Mineral soil alone, amended with spent mushroom compost or straw applied as a mulch.
[b] With or without *Verticillium dahliae* (Vd) or *Pratylenchus penetrans* (Pp). NS = not significant.

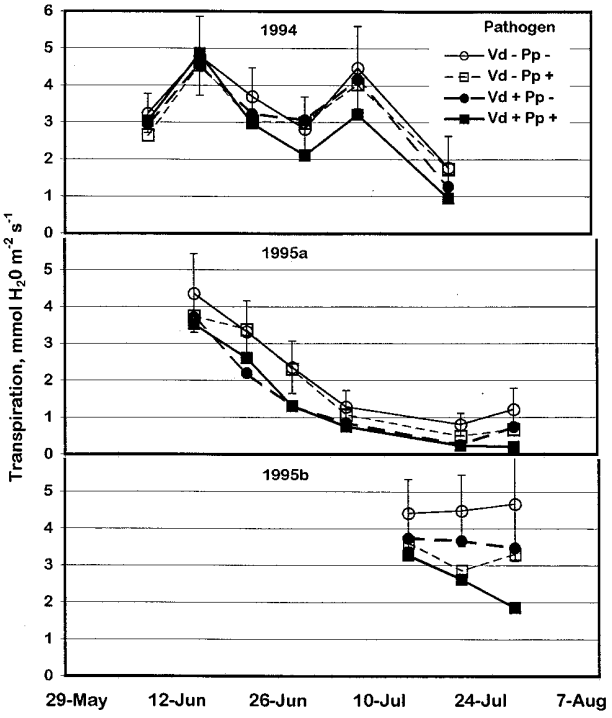

Fig. 3. Effect of infestation with *Verticillium dahliae*, *Pratylenchus penetrans* or both on transpiration per unit leaf area of terminal leaflets of potato. The symbols represent weekly measurements averaged over cultural amendments. The error bars indicate the least significant difference within a weekly measurement. Results are separated for sets of leaves selected in 1994, and in June and July 1995.

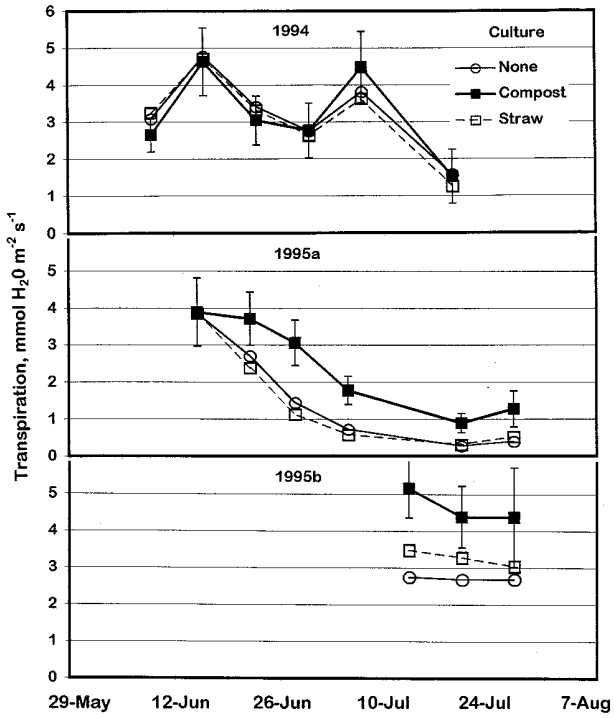

Fig. 4. Effect of the cultural amendments, compost, straw mulch, or none on transpiration per unit leaf area of terminal leaflets of potato. The symbols represent weekly measurements averaged over cultural amendments. The error bars indicate the least significance difference within a weekly measurement. Results are separated for sets of leaves selected in 1994, and in June and July 1995.

to be intolerant to *P. penetrans* infection under field conditions (1). In our microplots, *P. penetrans* infestation alone was at damaging levels, up to 300 nematodes/g of soil, and responsible for yield loss (15). The effect of *P. penetrans* alone may have been due to the high densities we achieved.

A combined infestation with *V. dahliae* and *P. penetrans* generally resulted in a faster or greater decline in photosynthesis than infestation with either pathogen alone. However, there was no synergistic effect between pathogens. In other studies where neither pathogen alone had a significant effect, there was an interaction of the effects of *V. dahliae* and *P. penetrans* that increased the vascular colonization by *V. dahliae* and the expression of disease symptoms and decreased tuber yield (6,16,21,22). This synergy was also observed when gas exchange was measured in a controlled environment (23). Under low light conditions or in a constant environment, the effect of *V. dahliae* on photosynthesis in asymptomatic leaves of potato was due to stomatal closure (5). However, in the presence of both pathogens, nonstomatal effects were responsible for some of the reduction in gas exchange as photosynthesis declined more than transpiration (23). In our study, the relative change in transpiration was slightly less than the change in photosynthesis. In 1994, either pathogen alone significantly decreased photosynthesis, but only the combination of both pathogens resulted in a significant decline in transpiration. In mid- to late July in 1994 and 1995, photosynthesis declined more rapidly than transpiration as the leaves aged. In part, these results may be due to increasing temperature as the season progressed. A warm temperature would promote transpiration but decrease photosynthesis. In the field, we found that transpiration was affected relatively less than photosynthesis, whether the effect was due to *V. dahliae* alone or in combination with *P. penetrans*.

The effect of *V. dahliae* on gas exchange differed between the first and second cohort of leaves selected in 1995. This difference may be due to the progression of the disease from local to systemic infection. As defined by Bowden and Rouse (3,4), the interval during which gas exchange of new leaves is not affected is local infection, and a later period in which all leaves are affected is systemic infection. Photosynthesis of the youngest leaves near the top of a potato canopy can remain constant at approximately 20 μmol m^{-2} s^{-1} for up to 90 days after planting (4). In our experiments, the first set of leaves was selected during local infection. For the first set of leaves, photosynthesis was initially about 20 μmol m^{-2} s^{-1} for all treatments shortly after expansion, and fell below 10 μmol m^{-2} s^{-1} after a month or so. Photosynthesis fell below this mark more rapidly in plants grown in infested soil. Early in the season, *V. dahliae* infestation had a greater effect on photosynthesis than did *P. penetrans*. The second set of leaves was selected during systemic infestation. Photosynthesis of these leaves was only 10 μmol m^{-2} s^{-1} and infestation affected these leaves shortly after expansion. At this stage, *P. penetrans* infestation had as great an effect on photosynthesis as *V. dahliae*. We speculate that nematode infestation leads more quickly or more completely to systemic infection than infestation with *V. dahliae* alone.

One effect of compost amendment was to delay the decline with age of photosynthesis of leaves that expanded early in the season. In 1993, compost amendment increased the initial rate of photosynthesis in both infested and non-infested soil, but it maintained photosynthesis particularly for plants grown in infested soil. Compost did not increase photosynthesis at the time the first cohort of leaves expanded in June 1994 and 1995. A difference in photosynthesis between compost-amended and non-amended plots developed because the decline in photosynthesis in the presence of one or both pathogens was more rapid in non-amended plots than in compost-amended plots. Thus, in each year, the decline in photosynthesis due to aging of leaves in infested plots was delayed by compost amendment. Compost had a different effect on leaves that expanded in July 1995; it enhanced photosynthesis immediately after expansion of this second set of leaves and, at this stage in the infection cycle, compost amendment increased photosynthesis in both infested and non-infested plots. The duration of our study was not sufficient to determine if compost prevented the photosynthetic decline due to infection of these later developing leaves.

Compost amendment increased the concentration of nitrogen in potato leaves in a field study of the effect of fumigation and compost on early dying in potato (7). The decline in leaf nitrogen due to disease was prevented in part by compost amendment. Thus, the effect of compost on leaf nitrogen may be a factor that maintains photosynthesis under disease pressure. Another factor may be the decrease in population of nematodes associated with compost amendment (15). In one other study of effects of organic matter and nematodes, there was a greater decline in photosynthesis in soybean due to *Heterodera glycines* in sandy soils than in organic muck soils (11). As in our study, the decline in photosynthesis due to infection was greater in a sandy soil than in one with a greater fraction of organic matter. Amending the soil with spent mushroom compost may affect potato physiology through its effect on the physical properties of soil, or it may depress pathogen populations though changes in microbial ecology in soil, or it may alter the plant response to pathogen infection (25). The mechanism remains to be determined.

Our observations suggest that compost amendment prevents the decline in gas exchange due to infestation with *V. dahliae, P. penetrans*, or both, leading to an apparent interaction between disease and cultural amendments. Such an interaction was never observed when either symptom development, area under the disease progress curve, or tuber yield was measured for these same plants (15). Infection with *V. dahliae* can affect gas exchange in potato before visible symptoms develop (5). Symptoms were not seen until after 5 July in each year of our study (15), whereas a significant decline in gas exchange was seen on 15 June 1994 and 22 June 1995. Thus, compost suppressed the disease-related decline in gas exchange before leaves were visibly senescent. Compost increased gas exchange of later developing leaves independent of infestation. Compost increased yield in each year and, averaged over three years, the 105% increase in yield due to compost (15) was much greater than the 30% increase in gas exchange of the first cohort of leaves. Besides enhancing gas exchange per unit leaf area, compost increased other attributes, such as number of leaves and area per leaf. The effects of compost on these other aspects of plant growth resulted in a similar increase in yield in both infested and non-infested plots.

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