

Photosynthesis, Transpiration, and Carbohydrate Content of Apple Leaves Infected by *Podosphaera leucotricha*

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ABSTRACT

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Powdery mildew infection significantly reduced photosynthesis and transpiration of apple leaves. Inhibition was more severe in leaves infected during early stages of development than in mature, fully expanded leaves. For mature leaves the percentage of leaf area covered by mycelia exceeded the percent reduction of photosynthesis and transpiration. Nine days after inoculation, leaf area covered by mycelia was 20% for mature leaves, with no reduction of photosynthesis or transpiration. At 30 days after inoculation, 90% of the leaf was covered and percentage reduction of photosynthesis and transpiration was 54 and 46%, respectively. Young

leaves infected during emergence from the bud were 90% covered by mycelia when they were 11 days old and their mean rates of photosynthesis and transpiration were reduced 85 and 55%, respectively. Infected young leaves were severely distorted; mature leaves appeared normal, except for surface mycelia. Reductions in photosynthesis and transpiration were accompanied by a corresponding reduction of leaf carbohydrate content. Infected leaves did not recover from inhibition of photosynthesis and transpiration after treatment with a combination fungicide and removal of the surface mycelia.

Podosphaera leucotricha (Ell. & Ev.) Salm. causes powdery mildew of apple, pear, and quince. On apple, this fungus affects twigs, foliage, blossoms, and fruits of current season growth. Infected twigs often are stunted and may die back. When young leaves are infected, they tend to increase in length but not in width, to be stunted, and to become folded longitudinally (2). The effects of powdery mildew infection on net photosynthesis, transpiration, and carbohydrate content of apple leaves have not been reported.

Several plant diseases have been reported to reduce the rate of photosynthesis: powdery mildew of barley (3,10,25,28), bean (23,26), beet (20), wheat (1,26), and soybean (21); rust of bean and safflower (18) and wheat (18,28); downy spot of pecan (19); anthracnose of bean (23); and apple scab (30). In some cases, photosynthesis was stimulated during the early stages of infection (1,3,18,26,34) or not affected (23) but later decreased.

Many plant diseases also have been reported to affect transpiration. Pear scab (22), downy mildew of tobacco (8), and rust of bean (13), *Rubus* (5) and wheat (32) increased the rate of transpiration. Decreased rates were reported for apple rust (24), grape downy mildew (22), powdery mildew of soybean (21), and pecan downy spot (19). Apple scab has had no effect on transpiration (22,30).

Plant pathogens that are capable of decreasing the rate of photosynthesis in apple could become increasingly important to modern apple production. In modern, high-density apple production systems, smaller trees have been shown to be more light efficient (16) and are capable of higher yields, as compared to standard size trees (7). In smaller trees, each leaf is of greater relative importance than a leaf on a standard-size tree in terms of absorption and utilization of light (11). Any reduction of leaf surface area or photosynthetic capability of trees in high-density production systems may have greater adverse effects on yield.

This study evaluated the effects of powdery mildew infection on photosynthesis, transpiration, and carbohydrate content of mature, fully expanded apple leaves, of young leaves that were infected in early stages of development, and of infected leaves before and after treatment with a combination fungicide.

MATERIALS AND METHODS

Apple (*Malus domestica* (Borkh.) 'McIntosh') seeds were germinated in wooden flats containing vermiculite. Two-week-old seedlings were transplanted in 15-cm-diameter polystyrene pots containing a mixture of peat, perlite, and sand (2:1:1, v/v). Mixture pH was adjusted to 6.5 with hydrated lime and the mix was amended with 1.4 gm of treble superphosphate (0-46-0), 0.1 gm of fritted trace elements, and 10 gm of Osmacote fertilizer (14-14-14, N-P-K) per liter. Pots were watered weekly with 500 ml of 200 µg/ml fertilizer (20-20-20, N-P-K) solution. Pots were maintained in a greenhouse with no artificial lighting and were watered daily to leaching. Insects were controlled as needed with an insecticide (E-Z Flo pyrethrin 6%).

Plants were inoculated by atomizing an aqueous conidial suspension at an air pressure of 1.4 kg/cm² with an artist's airbrush onto all leaves of either 5- or 12-wk-old seedlings. Control plants were sprayed with sterile distilled water. Conidial suspensions were prepared by collecting conidia from naturally infected leaves of McIntosh apple seedlings in the greenhouse. Conidia were washed from leaves with sterile distilled water and the suspension was adjusted to 50,000 conidia per milliliter by using a hemocytometer. Inoculated plants were allowed to air-dry, then were placed in a growth chamber at 21 C, 21.6 klux at bench level (12-hr photoperiod), and RH at saturation. After 1 wk, plants were moved back to the greenhouse and maintained under ambient conditions (temperature ranging 20-30 C) with no artificial light for the duration of the experiments. Throughout all experiments, pots containing mildew-infected apple seedlings were placed among pots with inoculated plants to serve as an additional source of inoculum. Due to the omnipresence of windblown conidia, control plants were sprayed to runoff at weekly intervals with a mixture of benomyl (methyl 1-butylcarbamoyl)-2-benzimidazolecarbamate) plus dinocap (2,4-dinitro-6-octyl phenyl crotonate, 2,6-dinitro-4-octyl phenyl crotonate, and nitrooctyl phenols [principally dinitro]—a mixture of 1-methylheptyl, 1-ethylhexyl, and 1-propylpentyl isomers) at the rate of 200 µg + 100 µg a.i./ml, respectively, beginning at time of inoculation.

Photosynthesis of attached apple leaves was measured with an infrared gas analyzer (MSA Model 200 Lira, Pittsburgh, PA

15235) with techniques similar to those of Ferree and Barden (12) and Sharma (27), as modified by Hall and Ferree (15). Sylvania phosphorous-coated metal-arc lamps provided a light intensity of 48.4 klux inside the Plexiglas leaf chambers. This exceeds the light saturation of apple (4). Air temperature inside the chamber was 24 ± 1 C.

Transpiration of attached leaves was measured with a dew-point hygrometer (EGG Model 880, EGG International Inc., Waltham, MA 02154) by determination of the dew point of air before and after it passed over the leaf while inside the Plexiglas chamber. Air-flow through the chamber was maintained at 3 L per min and temperature was measured by using a thermocouple in contact with the lower leaf surface. Leaf area was measured with a portable area meter (Lambda Instrument Co., Lincoln, NE 68504). Plants were returned to the greenhouse immediately after measurements were taken.

Carbohydrate concentrations of leaves were determined by collecting leaf samples immediately after the last measurements of photosynthesis and transpiration were taken. Leaves were quick-frozen and held at -18 C. Samples from each replication and treatment were then lyophilized and ground. Nonstructural carbohydrates were analyzed by using the takadiastase method as described by Smith (29) for extraction and the ferricyanide method of Hoffman (17) for determining glucose in the extract.

To study the effects of infection by *P. leucotricha* and fungicide treatment on mature leaves, the following treatments were established on 12-wk-old seedlings: (i) uninoculated plants sprayed with fungicide; (ii) inoculated plants treated at 16 days after inoculation by washing leaves (using a cotton swab) with the previously described fungicide combination, then spraying plants to runoff at weekly intervals; (iii) same as (i) only treated at 30 days after inoculation; and (iv) inoculated and nontreated. Measurements of photosynthesis and transpiration were taken on the 10th leaf above the cotyledonary node of each plant. Leaves were fully expanded and approximately 6 wk old at the time of inoculation. The first measurements were taken just prior to inoculation and then at 7-day intervals for 4 wk, beginning 9 days after inoculation. Disease severity was estimated visually at each reading as percent leaf area covered by mycelia. There were eight replications (plants) per treatment in a completely randomized block design.

To study the effect of mildew infection and fungicide treatment on leaves infected during early stages of development, the following treatments were established on 5-wk-old seedlings: (i) uninoculated plants sprayed with fungicide; (ii) inoculated plants treated with fungicide as previously described at 24 days after inoculation; and (iii) inoculated and nontreated. Measurements of photosynthesis and transpiration were made on the ninth leaf above the cotyledonary node. At the time of inoculation, the seventh leaf was fully expanded and the ninth leaf was still in the bud. Mycelia appeared on inoculated leaves after 10 days. At approximately 13

days after inoculation, mycelia were visible on the ninth leaf as it emerged from the bud. The ninth leaf was approximately 11 days old and fully expanded at the time of the first reading. The following growth measurements were recorded 45 days after inoculation: top fresh weight; root fresh weight; plant height; and number of leaves. There were eight replications in a completely randomized design.

RESULTS

Mature leaves. Mean percent leaf area covered by mycelia on inoculated-untreated mature leaves was 20, 45, 70, 90, and 90% at 9, 16, 23, 30, and 37 days after inoculation, respectively. Mycelia were not observed on uninoculated control plants. There were no significant differences ($P = 0.05$) in photosynthesis or transpiration between treatments 9 days after inoculation (Tables 1 and 2), but after 16 days photosynthesis and transpiration of inoculated leaves were significantly lower than uninoculated controls. When infected leaves were washed with fungicides 16 days after inoculation, mycelia were removed and the leaves appeared normal and remained free of mycelia for the duration of the experiment. However, photosynthesis and transpiration of these leaves always remained significantly lower than the rates measured in uninoculated leaves. At 23 days after inoculation, photosynthesis and transpiration of inoculated, nontreated leaves were significantly lower than those treated at 16 days, and remained significantly lower for the duration of the experiment.

When inoculated leaves were washed with fungicide at 30 days after inoculation, mycelia were removed and the leaves appeared normal. However, no significant fungicide treatment effect was observed for leaves treated at 30 days after inoculation.

Nonstructural carbohydrate content of leaves decreased with a decrease in photosynthesis and transpiration. At 37 days after inoculation, mean carbohydrate content of uninoculated leaves was significantly higher than that of all other treatments (Table 1). Leaves treated at 16 days had significantly more carbohydrate than leaves treated for 30 days or inoculated, nontreated leaves. There was no significant difference between leaves treated at 30 days and inoculated nontreated leaves.

Young leaves. The seventh leaf of 5-wk-old seedlings was 85% covered by mycelia at 10 days after inoculation. The ninth leaf apparently was infected when it emerged from the terminal bud. Mildew mycelia were visible on young leaves that were less than 1 cm long. At 24 days after inoculation the ninth leaf was approximately 11 days old, and over 90% of the upper surface was covered with mycelia. Leaves that were infected during early stages of development were severely distorted compared to uninoculated leaves. Photosynthesis and transpiration of inoculated leaves were significantly lower than those of uninoculated leaves at 24 days after inoculation (Table 3). Photosynthesis and transpiration of

TABLE 1. Effect of powdery mildew infection and fungicide treatment on photosynthesis and carbohydrate content of mature apple leaves^w

Treatment ^x	Photosynthesis at days after inoculation ^y						Nonstructural carbohydrates ^z
	0	9	16	23	30	37	
Uninoculated control	19.94 a	19.57 a	19.16 a	16.79 a	14.47 a	13.28 a	3.1 a
Inoculated and treated after 16 days	20.02 a	19.16 a	14.27 b	12.58 b	10.86 b	9.66 b	2.7 b
Inoculated and treated after 30 days	19.38 a	19.73 a	13.90 b	9.35 c	6.64 c	5.28 c	2.4 c
Inoculated and nontreated	19.47 a	20.46 a	13.64 b	8.95 c	6.35 c	4.85 c	2.3 c

^wTenth leaf above the cotyledonary node; fully expanded and approximately 6 wk old at time of inoculation.

^xInoculated = plants sprayed to runoff with a 50,000 conidia/per milliliter suspension of *Podosphaera leucotricha*. Treated = leaves washed with a solution of benomyl + karathane (200 μ g + 100 μ g a.i./ml, respectively), then sprayed to runoff at weekly intervals with the same fungicide mixture. Uninoculated control plants were sprayed with fungicide weekly.

^yPhotosynthesis = (mg CO₂ dm⁻² · hr⁻¹). Based on eight replications per treatment. Numbers followed by the same letter within columns are not significantly different at $P = 0.05$ according to Duncan's new multiple range test.

^zTotal nonstructural carbohydrate (percent dry weight) of leaves at 37 days after inoculation.

infected leaves increased between the first and second readings, but always remained significantly lower than uninfected leaves. Differences in plant height and leaf number were obvious among treatments at 24 days after inoculation. Plant growth (production of new leaves and internode elongation) of inoculated plants appeared to have stopped or was greatly decreased compared to that of uninoculated plants. After treatment with fungicide, mycelia were no longer present and leaves were normal in color. Treated leaves did not recover from inhibition of photosynthesis and transpiration or from distortion; however, inoculated plants resumed growth within a few days after treatment. New leaves produced on treated plants appeared normal. Mean photosynthesis and transpiration of the 12th leaf (new leaf produced after treatment) was 18.81 and 1.93, respectively, and 4.18 and 0.95 for the ninth leaf on the same plant 45 days after inoculation. Inoculated nontreated plants remained infected and stunted.

All growth measurements were significantly higher for uninoculated plants than any other treatment (Table 4). Plants treated at 24 days had significantly higher growth measurements than did inoculated nontreated plants.

DISCUSSION

Powdery mildew infection significantly reduced photosynthesis and transpiration of young and mature apple leaves. Effects of

TABLE 2. Effect of powdery mildew infection and fungicide treatment on transpiration of mature apple leaves^a

Treatment ^y	Transpiration at days after inoculation ^z					
	0	9	16	23	30	37
Uninoculated control	1.66 a	1.34 a	1.38 a	1.10 a	0.92 a	0.83 a
Inoculated and treated after 16 days	1.72 a	1.24 a	1.04 b	0.83 b	0.66 b	0.62 b
Inoculated and treated after 30 days	1.75 a	1.26 a	1.01 b	0.62 c	0.49 c	0.33 c
Inoculated and nontreated	1.60 a	1.30 a	0.94 b	0.59 c	0.45 c	0.30 c

^aTenth leaf above the cotyledonary node; fully expanded and approximately 6 wk old at time of inoculation.

^yInoculated = plants sprayed to runoff with a 50,000 conidia per milliliter suspension of *Podosphaera leucotricha*. Treated = leaves washed with a solution of benomyl + karathane (200 µg + 100 µg a.i./ml, respectively), then sprayed to runoff at weekly intervals with the same fungicide mixture. Uninoculated control plants were sprayed with fungicide weekly.

^zTranspiration = (g H₂O dm⁻² · hr⁻¹). Based on eight replications per treatment. Numbers followed by the same letter within columns are not significantly different at *P* = 0.05 according to Duncan's new multiple range test.

infection were much more severe in young leaves than in mature leaves. Young leaves (infected in early stages of development) had over 90% of their leaf surface covered by mycelia when they were approximately 11 days old, and their mean rates of photosynthesis and transpiration were reduced 85 and 55%, respectively. It was 30 days after inoculation before mature leaves were 90% covered by mycelia, with a reduction in photosynthesis and transpiration of 54 and 46%, respectively.

When photosynthesis and transpiration of infected young leaves were severely reduced, plants appeared to stop growing and the production of new leaves practically ceased. No tissue necrosis was observed; thus, infected plants appeared to be living at or near the compensation point. In addition, leaves infected early in development were severely distorted. Infected mature leaves had no visible change in physical appearance, except for the presence of mycelia.

As with mature leaves, the inhibition of photosynthesis and transpiration in young leaves was not reversed following fungicide treatment and removal of mycelia; however, after eradication of the fungus, plants appeared to resume normal growth. Whereas individual leaves did not recover from the effects of powdery mildew infection, individual plants did appear to recover.

Nonstructural carbohydrate content of leaves appeared to be directly related to the rate of photosynthesis and transpiration. Infected leaves with significantly lower rates of photosynthesis and transpiration had a corresponding significant reduction in carbohydrate content. Whereas the method used for determining nonstructural carbohydrate content gives a good estimation, it should be noted that sorbitol (an important mobile component of the carbohydrate pool in apple) was not measured.

Shaw and Samborski (28) reported that barley powdery mildew reduces CO₂ fixation at the infection site and increases CO₂ fixation in adjacent tissue. The initial disease-induced increase of photosynthesis reported for several other diseases (1,3,18,26,34) was not observed in this study; however, photosynthesis of specific leaf areas was not determined.

Removal of mycelia did not reverse the inhibition of photosynthesis in infected leaves. This suggests that reduction of light penetration by mycelia was not a factor in photosynthesis inhibition. Because *P. leucotricha* does not penetrate leaf mesophyll cells and no chlorosis was observed in infected leaves, some translocatable factor may be related to inhibition of chloroplast activity (20). Mignucci and Boyer (21) theorized that this factor may be released by the pathogen or produced by the host in response to the pathogen. Several metabolic alternations have been observed in mildew-affected leaves (6,33,34).

Variable effects of disease on transpiration have been reported (5,8,13,19,21,22,24,31,32). These are often associated with morphological alterations of host tissues. Accelerated

TABLE 3. Effect of powdery mildew infection and fungicide treatment on photosynthesis transpiration and carbohydrate content of young apple leaves^a

Treatment ^w	Photosynthesis ^x (days after inoculation)			Transpiration ^y (days after inoculation)			Nonstructural carbohydrate ^z
	24	31	45	24	31	45	
Uninoculated control	18.73 a	21.43 a	20.33 a	1.85 a	2.20 a	2.04 a	3.4 a
Inoculated and treated after 24 days	2.70 b	5.56 b	4.18 b	0.83 b	1.05 b	0.95 b	2.8 b
Inoculated and nontreated	2.66 b	5.35 b	4.04 b	0.79 b	1.12 b	1.02 b	2.8 b

^aNinth leaf above the cotyledonary node. Leaves were infected as they emerged from the terminal bud and were approximately 11 days old and fully expanded at the first reading.

^wInoculated = plants sprayed to runoff with a 50,000 conidia per milliliter suspension of *Podosphaera leucotricha*. Treated = leaves washed with a solution of benomyl + karathane (200 µg + 100 µg a.i./ml, respectively), then sprayed to runoff at weekly intervals with the same fungicide mixture. Noninoculated control plants were sprayed weekly with fungicide.

^xPhotosynthesis = (mg CO₂ dm⁻² · hr⁻¹). Based on eight replications per treatment. Numbers followed by the same letter within columns are not significantly different at *P* = 0.05 according to Duncan's new multiple range test.

^yTranspiration = (g H₂O dm⁻² · hr⁻¹). Based on eight replications per treatment. Numbers followed by the same letter within columns are not significantly different at *P* = 0.05 according to Duncan's new multiple range test.

^zTotal nonstructural carbohydrate (percent dry weight) of leaves at 45 days after inoculation.

TABLE 4. Effect of powdery mildew infection and fungicide treatment on top fresh weight, root fresh weight, plant height, and number of leaves of apple seedlings

Treatment ^y	Mean ^z			
	Top fresh weight (g)	Root fresh weight (g)	Plant height (cm)	Number of leaves
Uninoculated control	11.8 a	6.4 a	38.0 a	26 a
Inoculated and treated after 24 days	7.3 b	3.4 b	24.0 b	17 b
Inoculated and nontreated	3.5 c	1.4 c	14.5 c	11 c

^yInoculated = plants sprayed to runoff with a 50,000 conidia per milliliter suspension of *Podosphaera leucotricha*. Treated = leaves washed with a solution of benomyl + karathane (200 µg + 100 µg a.i./ml, respectively), then sprayed to runoff at weekly intervals with the same fungicide mixture. Uninoculated control plants were sprayed weekly with fungicide.

^zBased on eight replications per treatment at 45 days after inoculation. Numbers followed by the same letter within columns are not significantly different at $P = 0.01$ according to Duncan's new multiple range test.

transpiration is associated with pathogens that rupture protective host tissues (5,8,9,32). Pathogens associated with a reduction in transpiration have been associated with hypertrophy of chlorenchyma, reduction of air spaces, or obstruction of conductive tissue and stomata (22,24).

The factors that caused reduction of photosynthesis and transpiration in mildew-infected apple leaves were not ascertained in this study. However, Mignucci and Boyer (21) observed similar decreases in photosynthesis and transpiration in mildew-infected soybean leaves, and reported that reduced rates of photosynthesis and transpiration are not caused by secondary effects of cell mortality or senescence. They also reported that neither stomatal closure nor cuticular alteration could account for the decrease in transpiration, and assumed that the effect was caused by some other change in the transpiration path within the leaf.

The construction of apple fruit production models to establish economic injury level values (14) for specific pests is important to the continued development of intensive apple management systems. Results of this study demonstrate several important considerations in the development of such a model for apple powdery mildew. Leaf age at time of infection and timing of fungicide applications after infection appear to be important factors. Leaves infected early in development will never attain full photosynthetic capability; however, timely application of a fungicide to eradicate the fungus may allow the normal development of new leaves. Leaves develop some form of resistance to mildew as they mature; therefore, the rate of infection and subsequent reduction in photosynthesis is greatly reduced with age. When mature leaves are infected, timely application of fungicide that will eradicate the fungus appears to stop further reduction of photosynthesis and transpiration.

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