Photosynthesis, Transpiration, and Water Potential of Apple Leaves Infected by *Venturia inaequalis*

R. A. Spotts and D. C. Ferree

Assistant professor, Department of Plant Pathology and associate professor, Department of Horticulture, respectively, The Ohio State University, Columbus, 43210, and the Ohio Agricultural Research and Development Center, Wooster, OH 44691. Present address of first author: Oregon State University, Mid-Columbia Experiment Station, 3005 Experiment Station Drive, Hood River, 97031.

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ABSTRACT

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Experiments were conducted with attached McIntosh and Delicious apple leaves to evaluate the effects of *Venturia inaequalis* infection on photosynthesis, transpiration, and water potential. Scab infection caused significant reduction of photosynthesis in Delicious leaves 14 days after inoculation and in Delicious and McIntosh leaves 28 days after. Percentage of total leaf area diseased exceeded percentage reduction of photosynthesis for both cultivars. Reduced CO_2 assimilation was detected in scab-infected leaves only after visible symptoms had appeared. Scab infection did not affect transpiration of apple leaves but caused a decrease in water potential of McIntosh leaves.

Additional key words: apple scab, *Malus domestica*, net CO_2 assimilation.

In modern, high-density apple production systems, smaller trees are more light efficient (17) and are capable of higher yields, compared to standard-size trees (5). Each leaf in the high-density orchard assumes greater importance than leaves on standard-size trees in terms of absorption and utilization of light. Thus, reduction of foliage by a disease such as apple scab, which could affect photosynthetic capability, could be important. However, no information is available on the effect of scab infection on photosynthesis or water potential, and information is limited on scab infection-related alterations of transpiration.

Several plant diseases decrease the rate of photosynthesis: powdery mildew of barley (2,9,28,31), bean (25,29), beet (22), and wheat (1,29); rust of bean and safflower (19) and wheat (19,31); downy spot of pecan (20); and anthracnose of bean (25). Photosynthesis was stimulated initially (1,2,19,29) or not affected (25) but later decreased; the decline often was coincident with visible chlorosis of diseased leaves.

Several effects of disease on transpiration have been reported. Decreased rates were reported for rust of apple (27), *Xanthium*, *Helianthus*, and *Dianthus* (32); grape downy mildew (23); and pecan downy spot (20). Increased rates of transpiration were associated with pear scab (23) and rust of Rubus (4) and wheat (33). Apple scab did not affect transpiration (23).

This study evaluated the effects of apple scab infection on: photosynthesis and transpiration of inoculated, and adjacent noninoculated, leaves before and after appearance of visible symptoms, and water potential of inoculated leaves after symptom appearance.

MATERIALS AND METHODS

Apple (*Malus domestica* [Borkh.] 'Delicious') trees on Malling (M) 9 rootstocks and McIntosh trees on M 7 rootstocks, trained to single shoots, were grown in 25-cm diameter polystyrene pots containing a mixture of loam soil, peat, and perlite (3:1:1, v/v). Trees were fertilized initially with 25 gm of slow-release fertilizer (14.0-6.0-11.6, N-P-K) placed on the soil surface, then with 500 ml of 200 μg/ml fertilizer (20.0-8.6-16.6, N-P-K) every 2 wk. Trees were watered daily to leaching. Insects were controlled as needed with an insecticide (E-Z Flo Pyrethrin 6%) which is known to have little influence on photosynthesis.

Prior to inoculation, trees were washed thoroughly with tap water for 2 hr. *Venturia inaequalis* conidia (isolate VE1770-8 obtained from E. B. Williams, Purdue University) were harvested from 14-day-old 2.5% malt extract wick cultures (18), suspended in distilled water to give a concentration of 1.0×10^5 conidia per milliliter and atomized at 1.4 kg/cm^2 with an artist's airbrush onto the four terminal leaves of seven Delicious trees (youngest leaf was designated leaf 1, oldest as leaf 4). Conidia also were harvested from active lesions in an unsprayed McIntosh orchard, adjusted in aqueous supension to 8.7×10^4 conidia per milliliter, and atomized onto the four terminal leaves of seven McIntosh trees. Conidial germination after 24 hr at 18 C was 85% for isolate VE 1770-8 and 60% for the McIntosh isolate. Control trees were sprayed with distilled water. All trees were maintained in the dark at 18 C in a saturated atmosphere during the 24-hr infection period, then held in a growth chamber at 21 ± 1 C, 70 ± 5% RH. Maximum light intensity in the chamber at median plant height was 21.6 klux with lights programmed for 18 hr of light per day.

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 (10) and Sharma (30), as modified by Hall and Ferree (13). Sylvania phosphorus-coated metal-arc lamps provided a light intensity of 48.4 klux inside the Plexiglas leaf chambers which is above light saturation for apple (3). Air temperature inside the chambers was 24 ± 1 C.

Transpiration of attached leaves was measured with a dew point hygrometer (EGG Model 880, EGG International Incorp., Waltham, MA 02154) by determination of the dew point of air before and after entering the leaf chamber. Water potential was measured with a pressure bomb (Model 1000, PMS Instrument Co., Corvallis, OR 97330). Leaf area was measured with a portable area meter (Lambda Instrument Co., Lincoln, NE 68504). Trees were returned to the growth chamber immediately after measurements were made.

To study the effect of scab on photosynthesis and transpiration before the appearance of visible symptoms, measurements were made on leaf 1 and 2 of McIntosh trees 7 days after inoculation. The effect of scab on photosynthesis and transpiration after visible symptoms appeared was determined on leaves 1 to 4 of McIntosh

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and Delicious 14 and 28 days after inoculation. Percentage of diseased leaf area was estimated visually 14 days after inoculation and calculated from leaf area measurements 28 days after inoculation by excising diseased areas and subtracting healthy from total area values. To determine the effect of scab on photosynthesis and transpiration of healthy leaves above and below diseased leaves, measurements were made on the leaf above leaf 1 and below leaf 4 of McIntosh and Delicious 15 and 29 days after inoculation. The effect of scab on water potential of leaves 1 to 3 was measured on McIntosh and Delicious 29 days after inoculation.

The experimental design was a randomized complete block and a split plot treatment with disease as the whole plot and leaf position as the split plots.

TABLE 1. Effect of infection by *Venturia inaequalis* on net photosynthesis and transpiration of McIntosh and Delicious leaves

	Days after inoculation				
	7	14		28	
Treatment[a]	McIntosh	McIntosh	Delicious	McIntosh	Delicious
Net photosynthesis (mg CO_2 $dm^{-2} \cdot hr^{-1}$)[b]					
Control	21.9 x	22.6 x	28.2 x	15.5 x	23.9 x
V. inaequalis	23.6 x	24.4 x	25.3 y	10.2 y	19.8 y
Transpiration (g H_2O $dm^{-2} \cdot hr^{-1}$)[b]					
Control	2.61 x	2.63 x	2.22 x	1.20 x	1.70 x
V. inaequalis	3.19 x	2.52 x	2.18 x	1.44 x	1.50 x

[a] McIntosh leaves inoculated with 8.7×10^4 conidia per ml and Delicious with 1.0×10^5. Control leaves sprayed with distilled water.
[b] Numbers followed by the same letter within columns are not significantly different at $P = 0.05$ according to Duncan's new multiple range test. Each value represents the mean of 20 leaves.

RESULTS

Chlorotic lesions appeared on inoculated apple leaves 12–13 days after inoculation, and lesion development appeared complete after 28 days. On McIntosh, average diseased leaf area 28 days after inoculation was 53, 58, 56, and 11% on leaves 1, 2, 3, and 4, respectively. On Delicious, average diseased leaf area 28 days after inoculation was 46, 25, 0, and 0% on leaves 1, 2, 3, and 4, respectively.

Photosynthesis in diseased leaves was not significantly less ($P = 0.05$) than that of control leaves until day 14 for Delicious and day 28 for McIntosh (Table 1). This reduction appeared related to disease severity. On McIntosh, CO_2 assimilation of diseased leaves 1 and 2 was significantly less ($P = 0.05$) than controls, and their average diseased area was 55%. Reduction of CO_2 assimilation in leaves 3 and 4 was not significant; their average diseased area was 33%. Similarly, on Delicious 28 days after inoculation, reduction of CO_2 assimilation was significant ($P = 0.05$) on leaf 1 but not leaf 2, and their average diseased area was 46 and 25%, respectively. Photosynthesis of leaves 3 and 4, which were not infected, was not different from that of control leaves 3 and 4. Average diseased leaf area for all inoculated leaves was 46 and 36%, and average reduction of photosynthesis was 30 and 25% for McIntosh and Delicious, respectively. No significant effect of scab on transpiration was measured before or after visible symptoms appeared (Table 1).

Scab had no effect on photosynthesis in McIntosh leaves above or below inoculated leaves on day 15 (Table 2) or in leaves of either cultivar above or below inoculated leaves on day 29 (Table 3). The reduction of CO_2 assimilation of the Delicious leaf below leaf 4 (Table 2) may be in error since no effect on photosynthesis of leaf 3 or 4 was measured, nor was this reduction evident 29 days after inoculation. The scab-induced reduction of CO_2 assimilation of leaf 2 of Delicious on day 15 (Table 2) and of both apple cultivars on day 29 (Table 3) corresponded to the main effect reported above

TABLE 2. Net photosynthesis and transpiration of McIntosh and Delicious leaves above and below inoculated leaves 15 days after inoculation

	Leaf position[a]					
	Above		Leaf 2		Below	
Treatment[b]	McIntosh	Delicious	McIntosh	Delicious	McIntosh	Delicious
Net photosynthesis (mgCO_2 $dm^{-2} \cdot hr^{-1}$)[c]						
Control	21.7 x	24.3 x	24.5 x	23.3 x	17.6 x	25.2 x
V. inaequalis	24.2 x	23.2 x	20.8 x	19.0 y	20.9 x	21.3 y
Transpiration (g H_2O $dm^{-2} \cdot hr^{-1}$)[c]						
Control	2.44 x	1.70 x	2.97 x	1.63 x	2.93 x	1.88 x
V. inaequalis	2.51 x	1.70 x	2.65 x	1.64 x	2.93 x	1.64 x

[a] Above = leaf immediately above leaf 1; below = leaf immediately below leaf 4.
[b] McIntosh leaves 1 to 4 inoculated with 8.7×10^4 conidia per milliliter and Delicious leaves 1 to 4 with 1.0×10^5. Control leaves 1 to 4 sprayed with distilled water.
[c] Numbers followed by the same letter within columns are not significantly different at $P = 0.05$ according to Duncan's new multiple range test. Each value represents the mean of five leaves.

TABLE 3. Net photosynthesis and transpiration of McIntosh and Delicious leaves above and below inoculated leaves 29 days after inoculation

	Leaf position[a]					
	Above		Leaf 2		Below	
Treatment[b]	McIntosh	Delicious	McIntosh	Delicious	McIntosh	Delicious
Net photosynthesis (mgCO_2 $dm^{-2} \cdot hr^{-1}$)[c]						
Control	16.7 x	23.1 x	17.1 x	25.2 x	18.3 x	25.5 x
V. inaequalis	17.5 x	22.8 x	12.2 y	22.4 y	15.0 x	25.6 x
Transpiration (g H_2O $dm^{-2} \cdot hr^{-1}$)[c]						
Control	1.87 x	2.12 x	1.74 x	2.08 x	1.93 x	2.16 x
V. inaequalis	1.53 x	2.05 x	1.65 x	2.16 x	1.92 x	2.04 x

[a] Above = leaf immediately above leaf 1; below = leaf immediately below leaf 4.
[b] McIntosh leaves 1 to 4 inoculated with 8.7×10^4 conidia per milliliter and Delicious leaves 1 to 4 with 1.0×10^5. Control leaves sprayed with distilled water.
[c] Numbers followed by the same letter within columns are not significantly different at $P = 0.05$ according to Duncan's new multiple range test. Each value represents the mean of five leaves.

(Table 1). No significant effect of scab on transpiration was measured on leaves above or below inoculated leaves of either apple cultivar (Tables 2 and 3).

Scab infection significantly reduced ($P = 0.05$) the water potential of McIntosh leaves but did not affect that of Delicious leaves 29 days after inoculation. The water potential of control and infected McIntosh leaves was −6.2 and −9.3 bars, respectively. The water potential of control and infected Delicious leaves was −13.2 and −12.4 bars, respectively.

DISCUSSION

Scab infection caused a significant reduction of photosynthesis 28 days after infection. The average percentage of leaf area diseased exceeded percentage reduction in CO_2 assimilation for both cultivars. Because host tissue associated with well-developed scab lesions is usually necrotic (24), it is likely that CO_2 assimilation of remaining healthy tissue increased and partially compensated for the overall scab-induced reduction based on whole leaf measurements, but photosynthesis of specific leaf areas was not determined in this study. Shaw and Samborski (31) reported that barley powdery mildew and wheat rust reduced CO_2 fixation at the infection site, but CO_2 fixation of adjacent tissue increased. Livne (19) reported that photosynthesis of healthy bean trifoliolate leaves increased on plants with rust-infected unifoliolate leaves. In this study, reduction of photosynthesis was associated only with scab-infected leaves and only after visible symptoms appeared. In addition, the initial scab-induced increase of photosynthesis reported for several other diseases (1,2,19,29) was not observed.

Transpiration was not affected by scab infection in these studies. Variable effects of disease on transpiration have been reported and often can be associated with morphological alterations of host tissues. Pathogens that rupture protective host tissue often cause accelerated water loss (4,33). Alternatively, pathogens that cause hypertrophy of chlorenchyma, reduction of air spaces, or obstruction of conducting tissue and stomata usually cause decreased transpiration (23,27). Nusbaum (24), reported that even in very old scab infections, apple leaf cuticle remained intact, and as conidiophores expanded, perforated cuticle formed a closely fitting collar about the conidiophore neck. Also, *V. inaequalis* hyphae were subcuticular and in intimate contact with epidermal cells, and did not penetrate the vascular system during the parasitic phase. Under these conditions, little effect of scab infection on transpiration is likely. Müller-Thurgau (23), with the cobalt chloride paper method, reported no effect of apple scab on transpiration.

In addition to causing reduced photosynthesis, scab infection resulted in lowered (more negative) water potential of McIntosh leaves. Lower water potential indicates a foliar stress and may be related to decreased photosynthesis. Davenport et al (8) reported that during water potential increases, stomata may be open wider, resulting in increased CO_2 assimilation. The scab-induced decrease in water potential of McIntosh leaves was not observed in Delicious leaves, and it is not known if this is due to a difference in cultivars, isolates, or severity of infection.

Gutierrez et al (12) proposed the concept of economic injury levels (EIL), and Hall and Ferree (14) stressed the importance of establishing EIL values for intensive apple management systems. Direct relationships between leaf area and quality and growth of apple have been reported (15,16,21). Damage to apple foliage may result in reduced vegetative growth, fruiting, or fruit retention (6,7,11,26). The results of our investigation of apple scab-induced reduction in photosynthetic CO_2 assimilation as related to foliar disease severity provide important information for the construction of apple fruit production models to establish EIL values. However, much additional information is needed, including effects of disease, insect, and environmental stress agents, alone and in combination, on fruit tree physiology and production.

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