Influence of Pecan Scab on Gas Exchange and Chlorophyll Content of Pecan Leaves

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ABSTRACT

Gould, A. B., Aldrich, J. H., and Andersen, P. C. 1996. Influence of pecan scab on gas exchange and chlorophyll content of pecan leaves. Plant Dis. 80:317-321.

The influence of pecan scab (*Cladosporium caryigenum*) on leaf physiology of summer-flush and spring-flush leaves of Choctaw and Cape Fear pecan (*Carya illinoensis*) was assessed in early October 1987 and 1989. In both years, net CO_2 assimilation, conductance to water vapor, transpiration rate, and chlorophyll content of summer-flush leaves were reduced in a linear or curvilinear manner with an increase in scab infection. Relatively low estimates of scab (5%) generally resulted in a 30 to 50% decline in the above physiological variables. The effect of scab on leaf gas exchange of summer-flush leaves was best described when scab severity on the entire leaflet, leaflet veins, or leaf petioles was considered rather than scab severity solely in the sector of leaflet tissue in which physiological variables were measured. In older spring-flush leaves, gas exchange was best correlated with scab severity on entire leaves. Both the disproportionate impact of scab on leaf physiology and the apparent influence of scab lesions in areas outside the sector in which dependent variables were quantified suggest that scab exerts a systemic effect on leaf tissue of pecan.

Pecan scab (caused by *Cladosporium caryigenum* (Ellis & Langl.) Gottwald [=*Fusicladium effusum* G. Wint.]) is often the most serious pest problem of pecan (*Carya illinoensis* (F.A. Wagenheim) K. Koch) culture in the southeastern United States (15). The fungus is aerially dispersed (7,8). Pecan scab affects the involucre (nut shuck), foliage, and young stem tissue and may result in fruit drop and foliage and stem dieback. Scab lesions on Schley pecan leaves consisted of dense, compact mats of mycelium with massive sporulation and resulted in a breakdown of spongy and palisade parenchyma cells (4). The recommended control of pecan scab entails the application of fungicides at 2- to 3-week intervals from budbreak until the beginning of September (6). Even with a rigorous spray program, however, chemical control is often not satisfactory, and crop losses may range from 50 to 100%. Moreover, nearly all pecan cultivars have manifested a continuous decline in resistance to scab over the last several decades (16). Biological control strategies for this disease are not currently available.

Pecan scab may interfere with physiological processes and inhibit leaf and nut growth. Gottwald and Wood (9) reported that pecan scab on leaves reduced leaf area of greenhouse-grown Wichita pecan seedlings at the rate of 22% per lesion per cm^2 of leaf surface and reduced net CO_2 assimilation of leaves at a rate proportional to the tissue colonized. However, the coefficients of determination relating net CO_2 assimilation to the density of scab lesions was relatively low ($r^2 = 0.32$). The authors suggested that this poor correlation may have been a function of the disproportionate influence of scab infection on leaf veins or petioles. Pecan scab on fruit also reduced fruit surface area; however, net CO_2 assimilation was reduced exponentially as the percentage of diseased surface area increased (9).

Pecan trees, when subjected to proper cultural practices and proper insect and disease control, have the potential to retain high photosynthetic rates into the fall (1,3). High photosynthetic rates during the fall facilitate the process of kernel filling (13,14,17–19). Moreover, the photosynthetic activity of pecan leaves during kernel development (July to October) influences the tendency of trees to bear light and heavy crops in alternate years (17–19). Therefore, the impact of scab on photosynthesis may extend well beyond the season of infection and may contribute to a tendency of pecan trees to set a high and a low number of fruit in alternate years (9). A delineation of the physiological impact of scab may thus have relevance to the production of pecans during the current and subsequent years.

This study was initiated to determine the influence of pecan scab density and lesion location on leaf gas exchange and chlorophyll content of Choctaw and Cape Fear pecan leaves under field conditions.

MATERIALS AND METHODS

Experimental plant material. Leaf gas exchange was measured in 1987 and 1989 on randomly chosen Cape Fear and Choctaw pecan trees situated in a 10-ha block at the University of Florida North Florida Research and Education Center in Monticello. The trees, planted in 1983, were in the second-leaf stage and received standard cultural management practices (6), although fungicides were not applied during the years of the study.

Leaf gas exchange measurements. Leaves were selected for gas exchange measurement on the basis of cultivar, age, and the presence or absence of pecan scab. (Note that pecan trees have compound leaves normally composed of 11 to 15 leaflets.) Leaves were categorized on the basis of age as expanded summer-flush or expanded spring-flush leaves. Gas exchange was measured on pecan leaflets in the field on a 6.25 cm^2 sector of leaf tissue. Leaflets were oriented perpendicular to sunlight and were still attached to the tree during measurement of leaf gas exchange. During 1 to 13 October 1987, gas exchange was measured between 10 A.M. and 2 P.M. on two to 14 sun-exposed leaflets on each of 14 trees. Dew often precluded accurate measurement of gas exchange prior to 10 A.M. In 1989, approximately 15 to 20 leaflets on each of 14 trees were measured in a similar manner between 2 and 11 October. Care was taken to eliminate from consideration leaves that showed symptoms of any leaf diseases other than scab.

CO_2 and H_2O vapor exchange were measured under ambient conditions of light, temperature, and relative humidity. In 1987, air temperature, leaf temperature, relative humidity, and photosynthetic photon flux varied between 19 and 28°C, 20 and 29°C, 10 and 46%, and 1,300 and 1,700 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. In 1989, the above climatic conditions varied between 26 and 35°C, 23 and 35°C, 12 and 54%, and 1,300 and 2,000 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively.

Ambient and leaf chamber CO_2 and H_2O vapor concentration, ambient air and

Florida Agricultural Experiment Station Journal Series R-04484.

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Accepted for publication 14 November 1995.

Publication no. D-1996-0117-04R

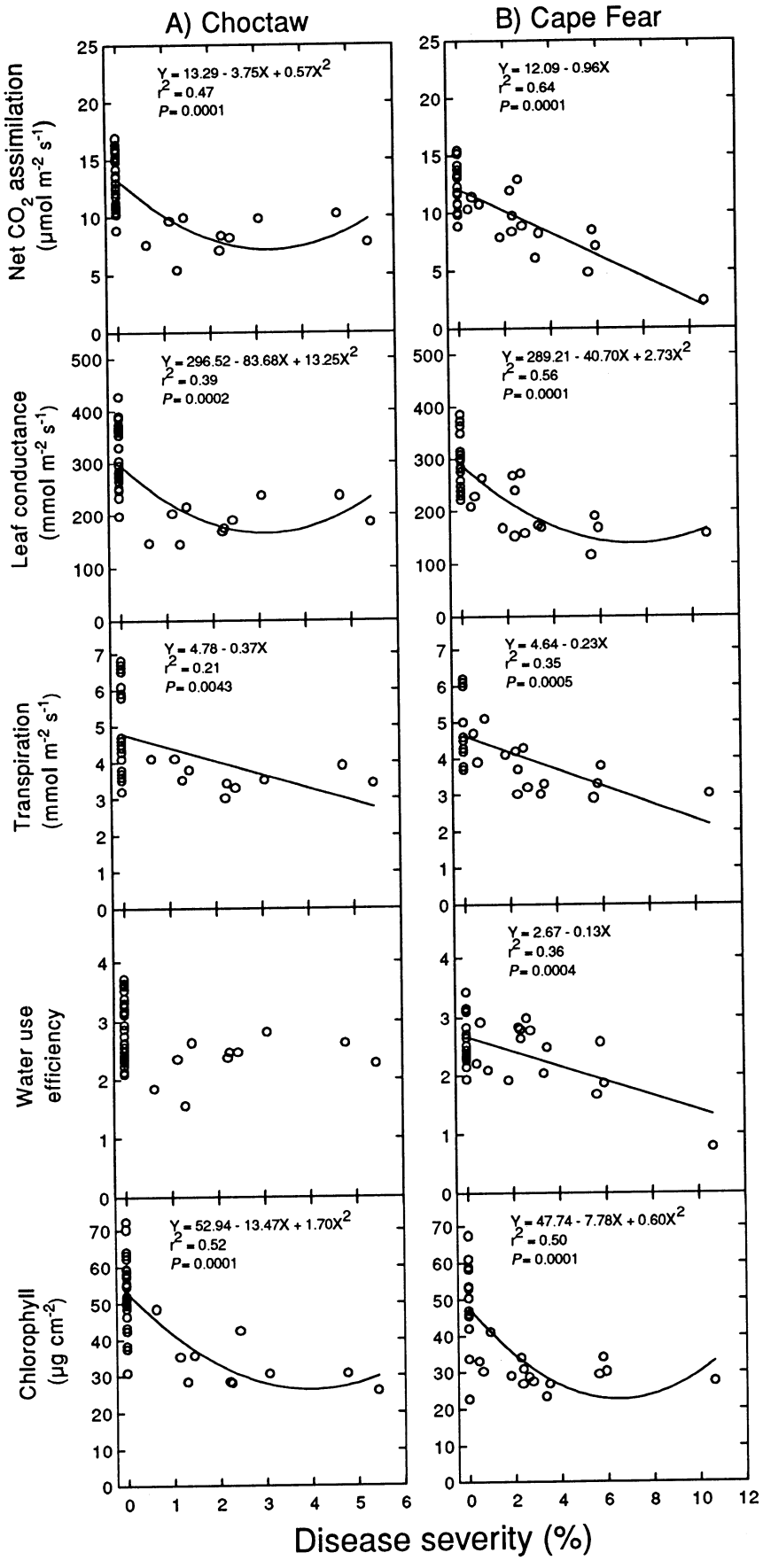

Fig. 1. Influence of pecan scab severity on net CO_2 assimilation, leaf conductance to water vapor, transpiration rate, water use efficiency, and leaf chlorophyll concentration in **(A)** Choctaw (n = 37) and **(B)** Cape Fear (n = 31) summer-flush leaves evaluated in 1987. The relationship of water use efficiency to disease severity for Choctaw pecan was not significant ($P < 0.05$).

leaf chamber temperature, and photosynthetic photon flux were measured as previously reported (2). Briefly, an ADC Model LCA-2 infrared CO_2 analyzer with an air supply unit and a Parkinson broadleaf leaf chamber (Analytical Development Corp., Hoddesdon, United Kingdom) were used. Net CO_2 assimilation rate, leaf conductance to water vapor, and transpiration rate were calculated with a DL2 Datalogger. Leaf conductance to CO_2 was calculated as leaf conductance to water vapor × 0.625, based on the ratio of water vapor and CO_2 diffusion coefficients in air. Water use efficiency was calculated by the mole fraction of CO_2 vapor uptake divided by H_2O vapor loss and multiplied by 1,000.

After field measurements were completed, the sector of the leaflet used for gas exchange measurement was outlined with a felt-tip pen. Entire leaves were then detached and transported to the laboratory in a cooler with ice for assessment of disease severity (described below) and measurement of leaf chlorophyll content. Following assessment of disease severity, the leaflet sector was cut from the leaflet using a sharp scalpel. Leaf chlorophyll (a + b) was extracted by placing the tissue in *N,N*-dimethylformamide in darkness for 24 h (11). Chlorophyll concentration was calculated from absorbance at 646 and 664 nm by the following equation: μg chl/ml = 27.45 A_{646nm} + 60.81 A_{664nm} (11).

Determination of disease severity. Disease severity, based on the percentage of leaf surface visually occupied by scab lesions, was determined in 1987 and 1989 on the 6.25-cm^2 leaflet sectors previously measured for gas exchange. Since pecan scab lesions were somewhat circular in shape, the area of each lesion on the adaxial leaf surface was calculated as the area of a circle. The total percent of diseased area within the 6.25-cm^2 sector was then calculated. In 1987, no attempt was made to quantify disease incidence outside the sector. In 1989, however, the area of pecan scab lesions was also estimated on the entire leaflet, leaflet petiolule, and leaf. Percent diseased tissue was visually assessed on each tissue by two independent evaluators, and the estimates were averaged. In addition, the percentage of area occupied by lesions on the adaxial plus abaxial surfaces of the midrib within the 6.25-cm^2 sector was measured. Finally, the total lesion area on the leaf petiole was calculated by assuming a circular shape for each lesion.

Statistical analysis. The relationships between percent disease (independent variable) and the measured physiological variables (dependent variables) for each cultivar and leaf age were quantified using regression analysis. Cape Fear and Choctaw were analyzed separately because the slopes of regression lines were often significantly different (from analysis of heterogeneity of slopes). For 1989 data, dis-

ease estimates expressed as a percent were subjected to arcsine–square root transformation to achieve a normal distribution prior to analysis. In addition, the total lesion area occupied by scab on the leaf petiole was log-transformed. Statistical Analysis Systems (SAS) software was used in all data analyses (10).

RESULTS

During 1987, summer-flush leaves of Choctaw and Cape Fear (Fig. 1) infected with scab manifested reduced net CO_2 assimilation, leaf conductance to water vapor, transpiration, and chlorophyll content. The percentage of scab within the sector of the leaflet used for leaf gas exchange and chlorophyll content varied from 0 to 11%. All the above physiological variables were related to disease severity in a linear or quadratic manner. Coefficients of determination for net CO_2 assimilation or chlorophyll content as a function of disease severity ranged from 0.47 to 0.64, whereas r^2 values for other dependent variables were generally lower. Water use efficiency of Cape Fear, but not of Choctaw, was also correlated with increasing disease severity. Older spring-flush leaf tissue was free of scab in 1987 and was not measured.

Dependent variables were statistically analyzed during 1989 as a function of disease severity of scab, both within the sector measured (as in 1987) and on entire leaflets, petiolules, leaves, petioles, or on both surfaces of the leaflet midrib within the 6.25-cm^2 sector. In 1989, the percentage of scab in the 6.25-cm^2 sector varied from 0 to 18% on leaflets of each age. Maximum disease severity rating on the midrib within the 6.25-cm^2 sector, entire leaflets, leaflet petiolules, and entire leaves were 11, 28, 30, and 25%, respectively; and average area occupied by scab on the leaf petiole ranged from 0 to 47 mm^2. For each physiological variable, regression equations are reported only for those independent measures of disease severity with the highest regression coefficients and, for comparison purposes, disease severity within the 6.25-cm^2 sector used for gas exchange measurement (Table 1).

Physiological measurements of summer-flush leaves of Choctaw and Cape Fear were correlated to most estimates of disease severity, although relationships with disease on leaflet petiolules or leaf petioles were often weak or not significant. For Choctaw summer-flush leaves, physiological variables were most highly correlated to disease severity on the leaflet and not to disease severity on the 6.25-cm^2 leaf sector used for gas exchange measurement (Table 1). Coefficients of determination were improved by 40% for CO_2 vapor exchange and by about 185% for H_2O vapor exchange when disease severity on the entire leaflet was used as the dependent variable rather than disease severity within the sector. Disease severity on the leaf petiole, leaflet, or on the sector plus that on the midrib within the sector were the best correlates to physiological variables on summer-flush leaves of Cape Fear, although coefficients of determination were generally lower (i.e., r^2 range 0.17 to 0.36) than those obtained for Choctaw.

For older flush leaves, physiological variables were best correlated with disease severity on the entire leaf (Table 1). Other measurements of disease limited to leaflet tissue (i.e., the 6.25-cm^2 sector used for gas exchange measurements, midrib in the sector, entire leaflets, or leaflet petiolule) were very weak or not significant. Although an increase in disease severity reduced net CO_2 assimilation, leaf conductance, and transpiration rate in Choctaw spring-flush leaves, the opposite was evident for water use efficiency and leaf chlorophyll (Table 1). Coefficients of determination were much higher for Choctaw than for Cape Fear leaves, and relationships between physiological variables and disease severity for older flush Cape Fear leaves were poor or not significant (Table 1).

Relatively low scab infection had a substantial effect on all variables of leaf

Table 1. Statistical relationships of physiological variables to severity of pecan scab[a] in summer-flush and spring-flush leaves for Choctaw and Cape Fear pecan evaluated in 1989

	Independent variable: disease severity in tissue with best relationship to dependent variable				Statistical significance for disease severity (%)[b]		
Dependent variable	**Tissue[c]**	r^2	P	**Equation**	r^2	P	**Order**
Summer-flush leaves							
Choctaw (n = 61)							
Net CO_2 assimilation	Leaflet	0.60	0.0001	$Y = 15.55 - 16.24X$	0.43	0.0001	Linear
Leaf conductance	Leaflet	0.37	0.0001	$Y = 809.49 - 2521.34X + 3259.01X^2$	0.13	0.0045	Linear
Transpiration rate	Leaflet	0.39	0.0001	$Y = 10.97 - 25.60X + 38.22X^2$	0.12	0.0221	Quadratic
Water use efficiency	Leaf petiole	0.38	0.0001	$Y = 1.63 - 0.35X$	0.34	0.0001	Linear
Leaf chlorophyll	Leaflet	0.31	0.0001	$Y = 45.52 - 33.01X$	0.26	0.0001	Linear
Cape Fear (n = 52)							
Net CO_2 assimilation	Sector + leaflet midrib	0.36	0.0001	$Y = 14.36 - 23.25X$	0.33	0.0001	Linear
Leaf conductance	Sector + leaflet midrib	0.31	0.0001	$Y = 528.78 - 1099.00X$	0.31	0.0002	Quadratic
Transpiration rate	Sector + leaflet midrib	0.24	0.0005	$Y = 8.61 - 12.33X$	...	NS[d]	...
Water use efficiency	Leaf petiole	0.17	0.0029	$Y = 1.67 - 0.44X$	0.11	0.0165	Linear
Leaf chlorophyll	Leaflet	0.22	0.0005	$Y = 47.57 - 31.88X$	0.08	0.0455	Linear
Spring-flush leaves							
Choctaw (n = 23)							
Net CO_2 assimilation	Leaf	0.40	0.0061	$Y = 14.22 - 66.80X + 129.97X^2$	...	NS	...
Leaf conductance	Leaf	0.50	0.0009	$Y = 655.48 - 3172.61X + 4651.72X^2$	...	NS	...
Transpiration rate	Leaf	0.58	0.0002	$Y = 11.81 - 47.06X + 69.47X^2$	...	NS	...
Water use efficiency	Leaf	0.23	0.0221	$Y = 0.89 + 1.55X$	...	NS	...
Leaf chlorophyll	Leaf	0.39	0.0013	$Y = 21.81 + 18.09X$	...	NS	...
Cape Fear (n = 32)							
Net CO_2 assimilation	...	...	NS	...	...	NS	...
Leaf conductance	...	...	NS	...	...	NS	...
Transpiration rate	Leaf	0.13	0.0399	$Y = 8.86 - 7.61X$	...	NS	...
Water use efficiency	Leaf	0.22	0.0067	$Y = 0.88 + 1.78X$	...	NS	...
Leaf chlorophyll	...	...	NS	...	...	NS	...

[a] For each physiological variable, regression equations are reported only for those independent measures of disease severity with the highest regression coefficients and, for comparison purposes, disease severity within the 6.25-cm^2 sector used for gas exchange measurement.
[b] Measured in 6.25-cm^2 sector used for gas exchange measurements.
[c] Key: leaflet = % scab visually estimated on leaflet; leaf = % scab visually estimated on leaf; sector + leaflet midrib = % scab measured within sector tissue, including the midrib; and leaf petiole = total area (mm^2) occupied by scab on leaf petiole.
[d] Not significant ($P < 0.05$).

gas exchange. For example, a 5% disease severity rating (approximately 50% of the maximum disease observed in 1987) for summer-flush Choctaw and Cape Fear leaves was associated with a 34 and 40% reduction in net CO_2 assimilation, respectively, and a 24 and 37% reduction, respectively, in 1989 (Table 2). Scab infection was also associated with a reduction in leaf conductance and transpiration rate (Tables 1 and 2, and Fig. 1). Leaf chlorophyll concentration of summer-flush, but not spring-flush, leaves was also reduced by scab infection (Tables 1 and 2, and Fig. 1). Pecan scab had an inconsistent effect on water use efficiency of Choctaw and Cape Fear leaves. For Choctaw leaflets evaluated in 1987, however, the decline in CO_2 and H_2O vapor flux was similar, and water use efficiency essentially remained unchanged (Fig. 1). In 1989, CO_2 and H_2O vapor exchanges were reduced 59 and 73% for a 5% disease severity rating on Choctaw spring-flush leaves; however, the influence of scab on these physiological variables for Cape Fear leaves was nonsignificant ($P < 0.05$) (Table 2).

DISCUSSION

Summer-flush pecan leaves infected with scab had drastically reduced CO_2 and H_2O vapor exchange rates and leaf chlorophyll content (Tables 1 and 2, and Fig. 1). A relatively low disease severity rating often resulted in a disproportionate decline in physiological variables. For example, when only 5% of the leaf surface area of Choctaw and Cape Fear was infected with scab, net CO_2 assimilation of summer-flush leaves declined by an average of 37% in 1987 and 31% in 1989 (Table 2). Thus, net CO_2 assimilation was reduced six times more than the area occupied by scab lesions. Other variables of leaf gas exchange and chlorophyll content were reduced in a similar fashion. Gottwald and Wood (9) showed that net CO_2 assimilation of Wichita nuts decreased sevenfold more than the surface area occupied by scab lesions, and a reanalysis of their data in Figure 6 (9) also indicates that a 5% disease severity rating of scab on leaves induced a 20% decline in net CO_2 assimilation (i.e., fourfold reduction).

These data (Tables 1 and 2, Fig. 1, and Gottwald and Wood [9]) support the concept that scab lesions impact leaf physiology beyond the area of their physical presence. This is not surprising in light of the fact that scab can stunt and deform leaf tissue. Natural infection by downy spot (*Mycosphaerella caryigena* Demaree & J.R. Cole) (12) and leaf blotch *Mycosphaerella dendroides* (Cooke) Demaree & J.R. Cole) (2) has also reduced leaf gas exchange of pecan at a rate up to two or more times the percentage of leaf surface infected by the respective diseases.

Additional support for a systemic effect of scab on leaf physiology was obtained from 1989 data, where the best correlations were achieved when physiological variables were related to disease severity on leaflets, petioles, leaflet midribs, or entire leaves rather than to disease incidence within the measurement sector. The mechanism responsible for the disproportionate impact on leaf physiology may, in part, relate to reduced water/assimilate transport through leaves if lesions occur on leaf veins or petioles. This hypothesis is supported by the fact that the variation in three of the five physiological variables measured in summer-flush Cape Fear leaves as a function of disease severity was explained best when lesions on the leaflet midrib within the sector were considered in the regression equation (Table 1). In addition, Diehl et al. (5) found that scab-infected tissue contained greater concentrations of phenolic compounds than uninfected tissue, which may also contribute to a systemic effect. Thus, chemical changes associated with scab infection that spread outside the lesion may also be a partial explanation for the severe impact of scab on leaf physiology.

For older spring-flush leaves, the systemic effect appears to spread further, as scab incidence on the entire leaf was invariably the best correlate to physiological variables. In 1987, gas exchange of spring-flush leaves was not even significantly influenced by the percentage of scab in the measurement sector. The deleterious impact of scab is further accentuated when one considers that scab is also associated with a decline in leaf area (9), indicating that reduction in carbon gain on a leaf area basis is conservative compared to that occurring on a whole tree basis.

Although scab appeared to have a similar influence on the physiology of summer-flush leaves of both cultivars, older spring-flush leaves of Choctaw appeared to be more sensitive than Cape Fear. We have no explanation for this phenomenon, since by most accounts Cape Fear has been equally or more susceptible to scab than Choctaw (16).

In conclusion, scab had a strong negative impact on gas exchange and chlorophyll content of pecan leaves under field conditions. The percentage reduction in net CO_2 assimilation and other variables was often six or more times the percentage of leaf area occupied by scab lesions. Highest correlation coefficients for summer-flush leaves were always achieved when physiological variables were analyzed as a function of the percentage of scab infection on entire leaflets, leaflet veins, or leaf petioles rather than on disease severity solely in the 6.25-cm^2 sector used for physiological measurements. For older spring-flush leaves, variations in gas exchange or chlorophyll content were best explained by scab severity on entire leaves. These data indicate that scab can have a systemic effect outside the areas of scab lesions. Thus, in addition to reducing leaf areas and causing premature leaf and nut abscission, scab can greatly reduce carbon gain, leaf chlorophyll content, and plant water use at relatively low levels of infection. These data, plus the fact that scab infections can spread very rapidly, do not support a threshold concept for the control of pecan scab.

Table 2. The percent change in physiological variables associated with a pecan scab disease severity rating of 5% on summer-flush and spring-flush leaves of Choctaw and Cape Fear pecan[a]

	1987		1989	
Variable	**Choctaw (%)**	**Cape Fear (%)**	**Choctaw (%)**	**Cape Fear (%)**
Summer-flush leaves				
Net CO_2 assimilation	−34	−40	−24	−37
Leaf conductance	−29	−47	−50	−47
Transpiration rate	−39	−25	−35	−32
Water use efficiency	NS[b]	−24	−28	−34
Leaf chlorophyll	−47	−50	−16	−15
Spring-flush leaves[c]				
Net CO_2 assimilation	...	...	−59	NS
Leaf conductance	...	...	−73	NS
Transpiration rate	...	...	−60	−19
Water use efficiency	...	...	39	46
Leaf chlorophyll	...	...	19	NS

[a] Percent change was determined from the regression equations in Figure 1 (1987) and Table 1 (1989). During 1987, the independent variable is the percentage of 6.25-cm^2 sector of tissue that was occupied by scab lesions. During 1989, the independent variable was that specified in Table 1.
[b] Not significant ($P < 0.05$).
[c] Spring-flush leaves were free of scab in 1987, so physiological variables were not measured.

ACKNOWLEDGMENTS

We thank Paul Bertrand (University of Georgia, Tifton), the Division of Plant Industry, and the University of Florida Cooperative Extension Service Plant Disease Clinic, Gainesville, for assistance in verifying the identity of pecan scab. We also thank Brent Brodbeck, Phillip Crampton, Betty Collins, and Marlene Karasik for technical assistance.

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