Decreased Net Photosynthetic and Dark Respiration Rates of Pecan Fruit and Foliage in Response to Infection by *Cladosporium caryigenum*

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ABSTRACT

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Pecan fruit and foliage with various intensities of pecan scab were studied to determine the effect of scab on net photosynthetic rate and dark respiration. Low disease intensities (about 5–30% of fruit surface area infected) caused decreases of 83 and 49%, respectively, in net photosynthetic rate (NPR) and dark respiration rate (DRR). Additional disease increase (beyond 30% of fruit surface area infected) caused further reductions of 5 and 3%, respectively, in NPR and DRR. Nut surface area of fruit infected in mid-August decreased linearly with percent disease at a rate of 1:5.26 (percent disease in nut surface area:percent disease increase). Reduction in foliar NPR was roughly proportional to the amount of foliar surface area colonized. Thus, lesions covering 10% of the phylloplane caused about 10% reduction in NPR. Leaf area was also diminished by disease at a rate of 22% per lesion per square centimeter of leaf surface.

Pecan scab, caused by *Cladosporium caryigenum* (Ell. et Lang.) Gottwald (2), is the most serious disease of pecan throughout the southeastern pecan-growing states (4). The fungus is predominantly aerially dispersed (3,4,8) and attacks the involucre (nut shuck), foliage, and young stem tissues. It causes olivaceous to black spots that often coalesce to cover large areas of tissue. Severe infection causes abortion of fruit and dieback of foliage and twigs (1,8,10).

The effects of scab and time of infection on nut yield and quality have been investigated (5,7); however, the influence of scab on photosynthesis is unknown. Decreased net photosynthetic rate (NPR) may contribute to the reduction in yield and quality. Starch and hemicellulose have been found to decrease in pecan roots during early-season growth and during midseason kernel development (13). Carbohydrate accumulation during the previous season, therefore, may determine whether, and to what extent, a tree will bear fruit (12,16). Studies on foliage retention and leaf area per fruit support this work on carbohydrate accumulation and suggest that carbohydrate levels play a critical role in irregular bearing and possibly in differentiation and development of pistillate flower primordia (11,14–17). The major amount of photosynthate used during kernel development comes from subtending leaves on the same shoot as the fruit (11,12). The condition of the foliage, and possibly of the involucre, could have a potentially great influence on kernel development and quality. Therefore, diseases or insects inflicting significant foliar damage could possibly reduce tree productivity and nut quality (5). Downy spot of pecan, for instance, has been shown to dramatically decrease foliar photosynthetic rate as well as transpiration (9). Powdery mildew had no effect on net photosynthesis of pecan fruit or dark respiration of pecan fruit and foliage; however, net photosynthesis of severely mildewed foliage was reduced by as much as 42% (6).

The purpose of this study was to quantify the effects of scab at various disease intensity levels on the NPR and dark respiration rate (DRR) to better understand losses in nut productivity and quality associated with the disease.

MATERIALS AND METHODS

Effects of scab on pecan cultivar Wichita fruit were determined by measuring CO_2 exchange. In early September, fruit that had become infected in mid- to late August were sorted into four disease severity classes: 0–5, 20–30, 50–60, or 90–95% of shuck surface area naturally infected. Fruits were about 70–75% developed. Shoots supporting fruits were cut in the morning, immediately submerged in water, and recut under water several inches higher up the stem to avoid breaking the xylem water column. Fruits were transported immediately to the laboratory with their supporting branches still submerged, and CO_2 exchange was measured within 1 hr of collection. An aggregate CO_2 exchange of six fruits from each infection class was

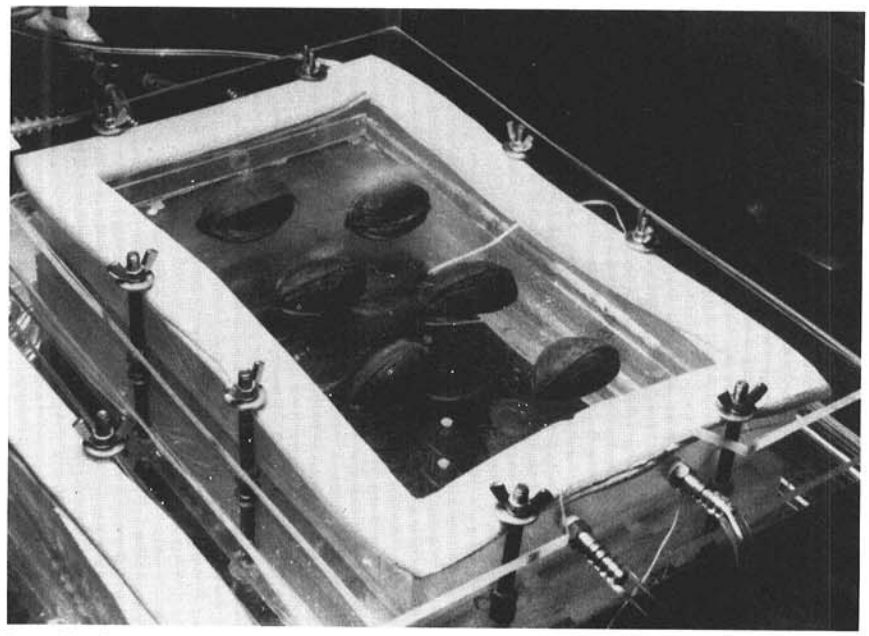

Fig. 1. Plexiglas photosynthetic chamber used for measuring CO_2 flux of diseased pecan fruit (shown) and diseased pecan foliage.

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estimated. Each class was replicated five times and measured in random sequence. Fruits remained attached to the shoot until measured. After CO_2 exchange measurements, the length and diameter of each fruit was measured and its surface area estimated by the formula for a prolate spheroid.

The influence of scab on foliar CO_2 exchange and leaf surface area of foliage was determined on attached, naturally infected leaves of greenhouse-grown Wichita seedlings. Seedlings were inoculated when about 2–3 wk old with conidia harvested from 6-wk-old sporulating oatmeal agar cultures of *C. caryigenum*. All cultures were of a monoconidial isolate (81-1f) obtained from Wichita pecan and were grown at 25 C with a 12-hr light/12-hr dark regime. Light was provided by fluorescent lights (Westinghouse F40/Agro-Life) about 30 cm above the petri dishes that provided a photon flux density of 1,050 $\mu E\ m^{-2}\ s^{-1}$ at the colony surface. Five milliliters of water was spread onto the surface of each plate, and the colony surface was brushed thoroughly with a stiff artist's brush to dislodge and suspend conidia. Possible culture nutrients were washed from spores by centrifuging the conidial suspension three times at 10,000 rpm for 5 min, decanting the supernatant, and resuspending the conidia in sterile, deionized water. Final conidial concentration was adjusted with a hemacytometer to 2.5×10^5 conidia per milliliter, and a dilution series of 2.5×10^6, 2.5×10^5, 2.5

Fig. 2. Leaf of greenhouse-grown Wichita pecan seedling showing multiple scab lesions.

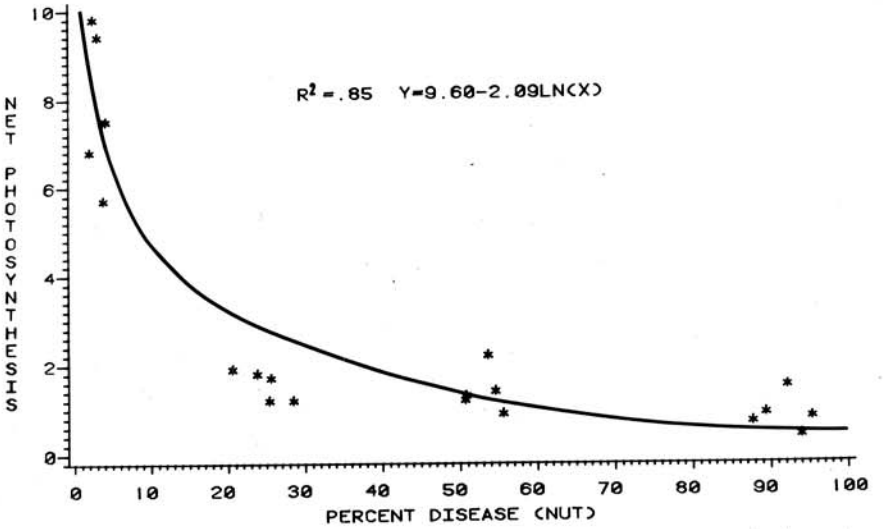

Fig. 3. Effect of scab intensity ($\log_e$ percent of fruit surface diseased) on net photosynthetic rate (mg $CO_2\ dm^{-2}\ hr^{-1}$) of pecan fruit.

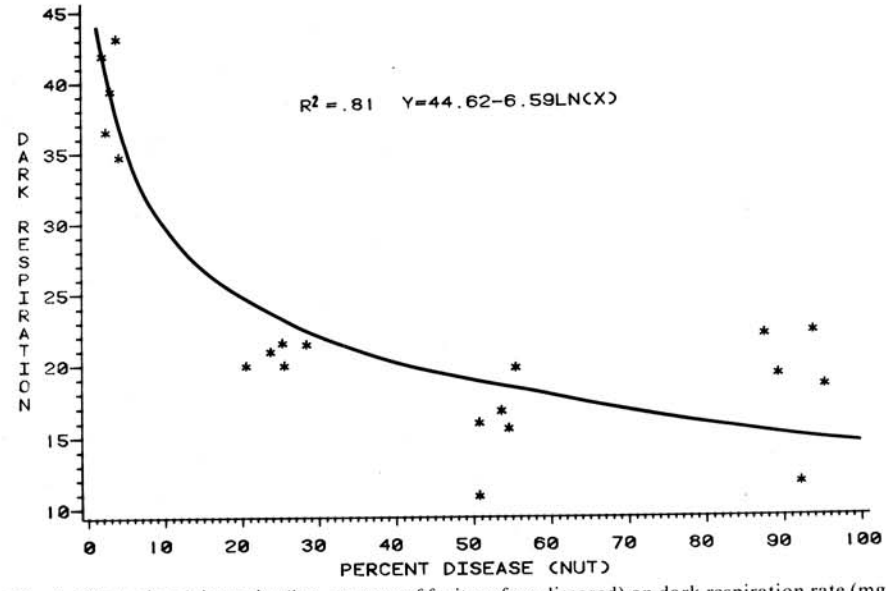

Fig. 4. Effect of scab intensity ($\log_e$ percent of fruit surface diseased) on dark respiration rate (mg $CO_2\ dm^{-2}\ hr^{-1}$) of pecan fruit.

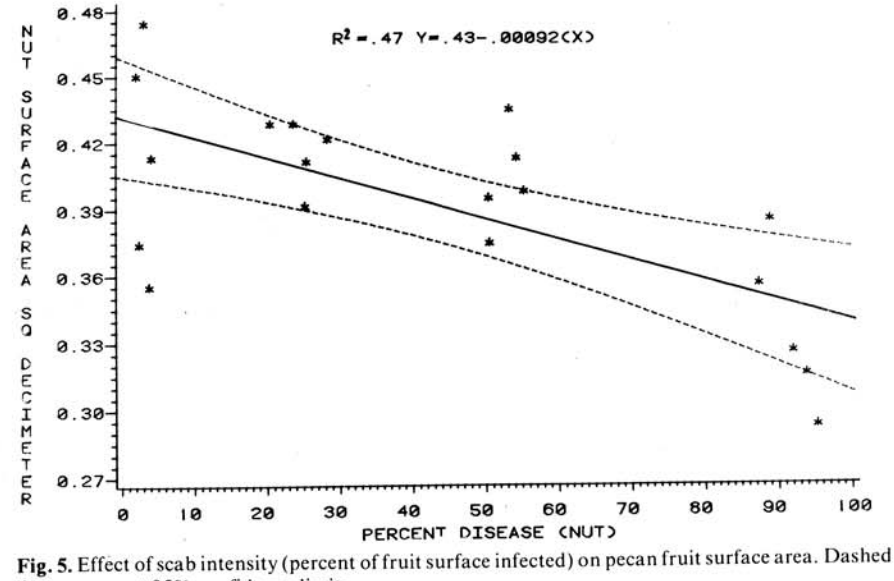

Fig. 5. Effect of scab intensity (percent of fruit surface infected) on pecan fruit surface area. Dashed lines represent 95% confidence limits.

$\times 10^4$, and 2.5×10^2 conidia per milliliter was prepared. Twenty potted seedlings were inoculated to runoff on both upper and lower leaf surfaces with each concentration of conidial suspension using an artist's airbrush sprayer (Paasche Airbrush Co., Chicago, IL) at about 1,406 g/cm^2 (20 psi). Plants were immediately placed in a Percival dew chamber in darkness for 48 hr at 25 C (100% RH), and foliage was kept wet to promote infection. Plants were then moved to the greenhouse and incubated 3 wk in a polyethylene plastic chamber at 22–28 C (80–95% RH) to allow lesions to achieve maximum size and infected leaves to mature. At the end of this incubation period, 33 of the 80 trees were selected so that the fifth simple leaves from the bottom represented a continuous gradient of disease from zero to the most severe infection.

CO_2 measurements were made on each of the 33 trees selected at random. All CO_2 measurements were by the standard differential analysis method, measuring the flux in CO_2 entering and exiting a photosynthesis chamber, with a Beckman 865 IR CO_2 analyzer (Beckman Instruments, Inc., Berkeley, CA). The rectangular Plexiglas photosynthesis chamber (about 280-ml volume) was sealed gastight with a rubber O-ring and an Ensolite foam gasket (Fig. 1). Chambers were supplied with ambient air at a flow rate of 2 L min^{-1}. Energy was provided from a color-improved mercury-vapor lamp suspended perpendicular to the leaf surface. Photon flux density at the leaf or fruit surface was 700 μE m^{-2} s^{-1} as measured by a Li-Cor 185 quantum sensor (Li-Cor, Inc., Lincoln, NE). Leaf temperature was maintained at 27 ± 1 C, and monitored with a leaf thermistor. DRR was measured by covering the chamber with an opaque shroud.

After CO_2 measurements, the fifth leaf (from seedling base) was excised from each plant (Fig. 2). The numbers of lesions per leaf and individual leaf surface areas were determined with a LI-300 leaf area meter (Li-Cor).

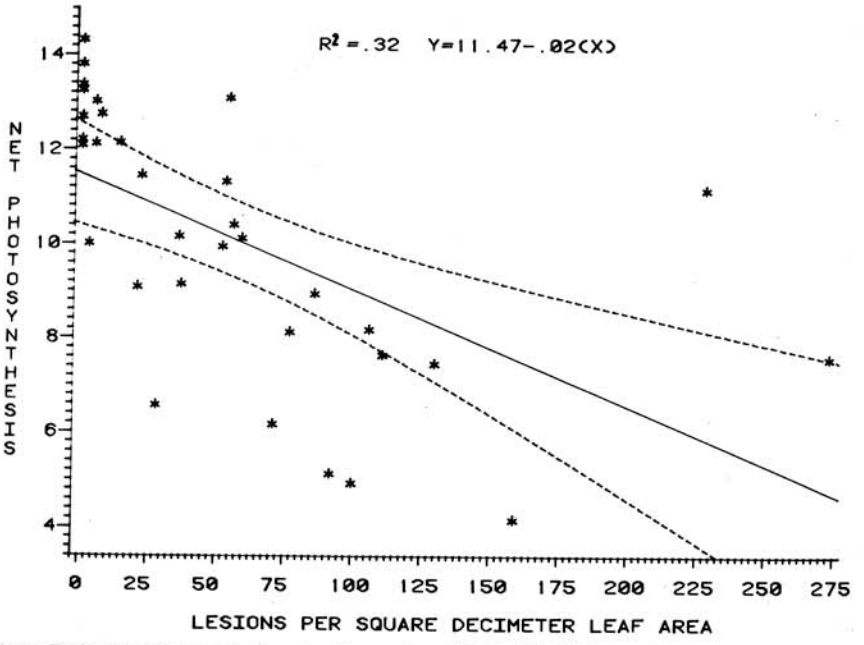

Fig. 6. Foliar net photosynthetic rate of pecan (mg CO_2 dm^{-2} hr^{-1}) in relation to frequency of scab lesions. Dashed lines represent 95% confidence limits.

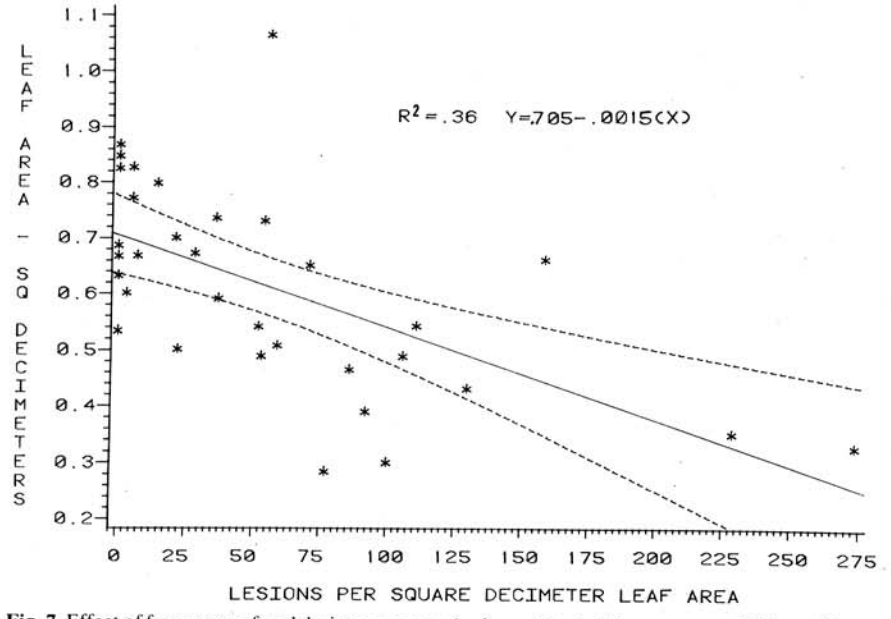

Fig. 7. Effect of frequency of scab lesions on pecan leaf area. Dashed lines represent 95% confidence limits.

RESULTS AND DISCUSSION

Both NPR and DRR of involucres decreased exponentially as percent diseased surface area increased (Figs. 3 and 4). About 95% of this decrease occurred between the 0–5 and 20–30% disease categories, resulting in 83 and 49% reductions in NPR and DRR, respectively. Disease more severe than the 20–30% category caused further reductions of 5 and 3%, respectively, in fruit NPR and DRR as estimated from the logarithmic regression curves (Figs. 3 and 4). Apparently, even a few lesions on the fruit surface can affect the production of photosynthate for fruit development.

Fruit surface area also decreased as disease increased (Fig. 5). Slight, moderate, and heavy disease levels (about 20–30, 50–60, and 90–95% of shuck surface area infected) caused average decreases of 4, 12, and 21%, respectively, in fruit surface area. Fruits all became diseased in mid- to late August. Therefore, the data presented here represent midseason to late-season disease effects only. Fruit that become diseased during the rapid growth phase (June and July), when photosynthate demand is high, have been shown to attain smaller final size and poorer quality than nondiseased fruits (5). Infection early in the season can cause fruit drop and severe stunting (5).

Foliar NPR and leaf area declined as disease increased (Figs. 6 and 7). Foliar lesions, however, reduced photosynthesis less than an equivalent proportion of diseased area on the involucre. Reductions in NPR appear to be roughly proportional to the surface area diseased (compare Figs. 6 and 7). The average lesion resulting from greenhouse inoculations is about 2–3 mm in diameter. Average surface area of a simple leaf from 3-wk-old greenhouse-grown pecan seedlings is about 70 cm^2. Thus, one lesion per square centimeter occupies 13–28% of the leaf surface area. Using the regression equation in Figure 6, this translates to about 22% decrease in NPR or roughly a 1:1 proportion of percent diseased surface area:percent NPR decrease. Exceptions to this may be infections of

the midrib and major leaf veins, which presumably would restrict or stop vascular transport including photosynthate transport from large portions of leaf blade. This may explain the inconstancy of the data represented in Figure 6 and the low coefficient of determination ($r^2 = 0.32$).

These results are similar to those found for downy spot of pecan, caused by *Mycosphaerella caryigena* Ell. & Ev. (9). *M. caryigena* appears to be more injurious than *C. caryigenum*. Downy spot resulted in a 20% leaf surface infection that caused a 40% reduction in CO_2 assimilation.

Since numerous scab lesions in the field occur on the leaf rachis or veins, it is likely that significant amounts of photosynthate are lost, thus reducing photosynthate required for kernel filling. Severe foliar scab infections may also reduce tree energy reserves for the next year's crop, which could contribute to reduced fruit set, poor nut quality, and irregular bearing.

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