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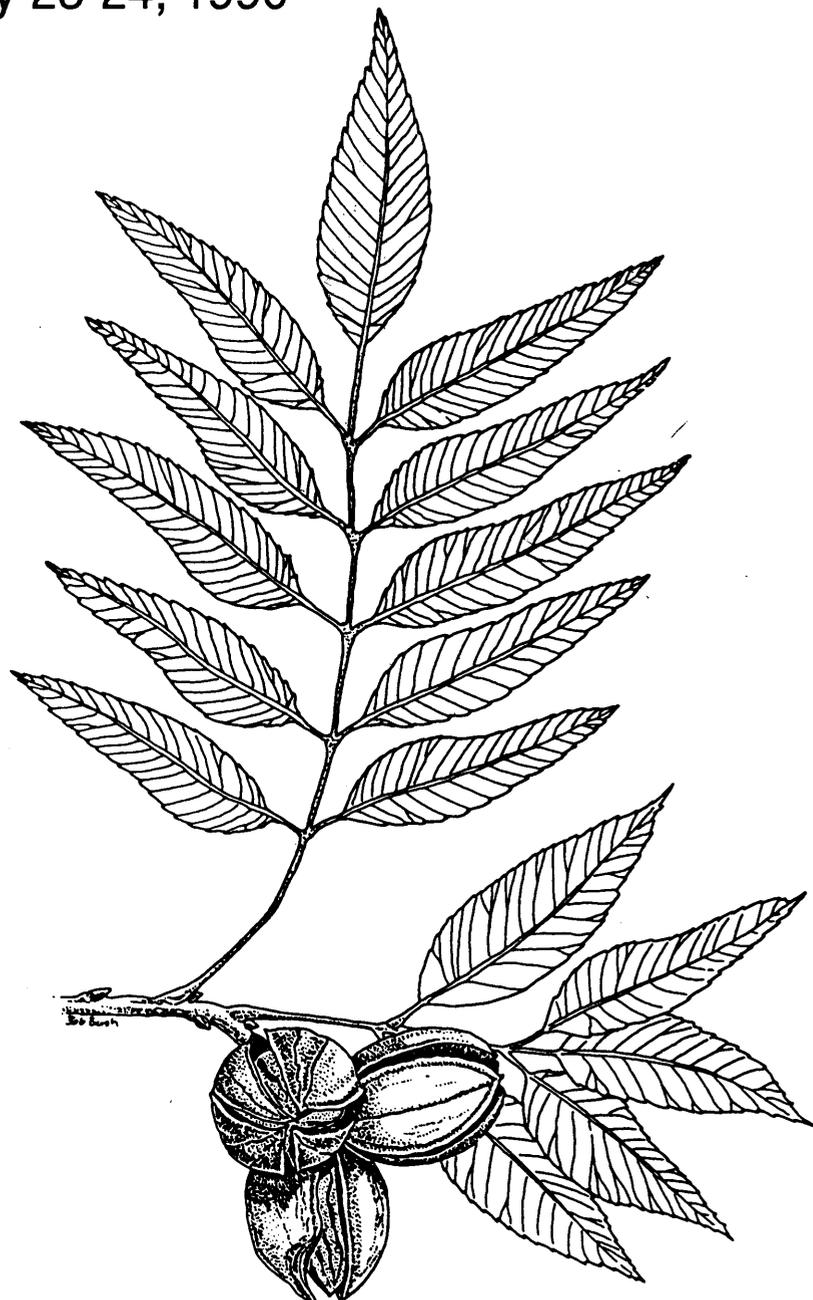
December 1991

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Pecan Husbandry: Challenges and Opportunities

First National Pecan Workshop Proceedings

Unicor State Park, Georgia
July 23-24, 1990



PHOTOSYNTHETIC CHARACTERISTICS OF PECAN AND TEN SPECIES OF FRUIT CROPS WITH EMPHASIS ON SUN TRACKING/NON-SUN TRACKING RESPONSES

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ABSTRACT

Leaf gas exchange characteristics of pecan leaves were compared to 10 species of fruit crops under field conditions in north Florida. In full sunlight [i.e., photosynthetic photon flux (PPF) ca. 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$] net CO_2 assimilation (A) and stomatal conductance to water vapor (g_s) were highest for pecan (A= 15.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$, g_s =452 $\text{mmol m}^{-2} \text{s}^{-1}$), intermediate to high for peach, apple pear, grape, blackberry and fig (A= 12.1 to 14.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$, g_s = 23 to 370 $\text{mmol m}^{-2} \text{s}^{-1}$) and low for satsuma, persimmon, blueberry and kiwi (A= 5.7 to 10.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$, g_s <220 $\text{mmol m}^{-2} \text{s}^{-1}$). The influence of non-steady state levels of irradiance was tested on gas exchange characteristics of pecan in more detail. In response to short-term (80 to 240 sec) reductions in irradiance, A declined rapidly, g_s was not altered, and transpiration (E) decreased very slightly. At low levels of irradiance water use efficiency (WUE) was near zero and intercellular CO_2 concentration (C_i) was near ambient levels. When leaves were exposed to 50 min of continuous shade A and g_s were reduced by 50 and 10%, respectively, and C_i remained increased by ca. 40 $\mu\text{mol mol}^{-1}$. In conclusion: 1) rates of gas exchange of pecan leaves are high for a C3 woody plant and; 2) pecan may be classified as non-sun tracking species with A and g_s not tightly coupled (i.e., non constant C_i).

INTRODUCTION

The influence of light intensity on carbon gain has been researched extensively under steady state conditions in the laboratory. Although providing useful physiologic information, these data often have little relevance to what is occurring under field conditions. In nature plants are often

exposed to numerous and drastic fluctuations in irradiance throughout the day as a result of intermittent cloud cover, wind-generated leaf movements and mutual leaf shading (Norman and Turner 1969, Knapp and Smith 1988, 1989, 1990).

Net CO_2 assimilation declines quickly with the onset of shade and increases rapidly with the occurrence of unobstructed sunlight; however, the stomatal response to fluctuating irradiance varies widely among species (Chazdon and Pearcy 1986, Knapp and Smith 1988, 1989, 1990, Pearcy 1988). Plants having a stomatal aperture strongly dependent on the level of irradiance are classified as "sun tracking", and those having stomatal (g_s) conductance essentially independent of short-term changes in irradiance are considered "non-sun tracking" (Knapp and Smith 1990). Little information concerning sun tracking/non-sun tracking responses is available for horticultural crops.

Rates of leaf gas exchange of pecan have been reported to be relatively high (Andersen and Brodbeck 1988, Wood 1988) or low (Crews et al. 1980, Reiger and Daniell 1988) for a C3 plant. However, leaf gas exchange of pecan in response to non steady state conditions of irradiance is not known. This information would increase our knowledge of whole tree carbon gain under field conditions.

The objectives of this study were to compare leaf gas exchange of pecan to 10 species of fruit crops and to investigate the influence of fluctuations in irradiance on gas exchange characteristics of pecan leaves.

MATERIALS AND METHODS

Experimental material. The experimental site was the University of Florida Agricultural Research and Education Center, Monticello, Florida located at 30.5 N latitude and 84 W longitude. Soil type was a Dothan loamy sand (Plinthic paleudults) containing 1% organic matter. All experiments were conducted on plants growing in the field.

Plant material. Plant material was as follows: 7-year old pecan *Carya illinoensis* (Wagenh.) C. Koch cv. Elliot], 10-year-old peach [*Prunus persica* (L.) Batsch cv. Flordaking], 9-year-old apple (*Malus domestica* Borkh. cv. Anna), 2-year-old pear (*Pyrus communis* L. cv. Flordahome), 2-year-old satsuma, (*Citrus reticulata* L. cv. Owari), 3-year-old persimmon (*Diospyros kaki* L. cv. Fuyu), 6-year-old rabbiteye blueberry, (*Vaccinium ashei* Reade

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cv. Bluegem), 4-year-old grapevine, (*Vitis* sp. cv. Suwannee), 2-year-old blackberry (*Rubus* sp. cv. Shawnee), 2-year-old fig, (*Ficus carica* L. cv. Alma), and 2-year-old kiwi, [*Actinidia deliciosa* (A. Chev) cv. Hayward]. Pecan, peach, apple, grape, blueberry, blackberry and kiwi were supplied with drip irrigation at least 3 times weekly. Satsuma and fig were supplied with overhead sprinkler irrigation at least 3 times weekly. Pear and persimmon were not irrigated; however, leaf gas exchange measurements were performed after abundant rainfall.

Leaf gas exchange of pecan and 10 species of fruit crops. Ambient and leaf chamber CO₂ and H₂O vapor concentration, air temperature (AT) and photosynthetic photon flux (PPF) were measured in the field with an Analytical Development Corporation (ADC) Model LCA-2 infrared gas analyzer, an air supply unit, and a Parkinson broadleaf leaf chamber (Analytical Development Corp Ltd., Hoddesdon, Herts., England) as described previously (Andersen and Brodbeck 1988). Calculations of net CO₂ assimilation rate (A), stomatal conductance to water vapor (g_s), vapor pressure deficit (VPD), leaf temperature (LT), transpiration (E) and intercellular CO₂ concentration (Ci) were accomplished with an ADC DL2 Datalogger and appropriate software. Leaf gas exchange was measured on recently expanded leaves from 1000 to 1400 HR on selected sunny days during late May, June or July 1988 under the following conditions: PPF = 2163 ± 30 μmol m⁻² s⁻¹, air temperature 31.3 ± 0.9°C and vapor pressure deficits, VPD = 3.5 ± 0.3 kPa (means ± SE).

Influence of short-term fluctuations in irradiance on pecan. Gas exchange was measured on 11 June 1988, on 'Stuart' leaves exposed to fluctuations in irradiance in the following sequence: 100, 66, 33, 10 and 100% sun with each measurement sequence lasting ca. 80 sec. Different levels of PPF were achieved by placing polyethylene shade cloth of varying light transmittance over the leaf chamber with the leaf remaining in the chamber for the entire measurement sequence. Preliminary experiments of continuous measurements on leaves in 100% sun showed that gas exchange of leaves in the chamber was not altered for at least 10 min. Leaf gas exchange was also measured on interior canopy leaves (naturally shaded) under ambient levels of PPF (ca. 483 ± 21 μmol m⁻² s⁻¹). Each measurement was replicated ten times (10 trees). Means ± SE are presented.

Influence of moderate-term fluctuations in irradiance. The effects of moderate durations of shading were tested on 'Stuart' leaves from 1000 to 1200 hr on 12 June 1988. Gas exchange was measured periodically on sun-exposed leaves for 20 min, then for 50 min after polyethylene shade cloth (30% light transmittance) was placed over the leaf. Shade cloth was then removed and measurements were continued in 100% sun for 50 min. Leaf gas exchange was determined by inserting a leaflet from each of four trees into the leaf chamber every 4 to 6 min. Values of A, g_s and Ci were grouped for each time interval. Means ± se are reported.

RESULTS

Leaf gas exchange of pecan and 10 species of fruit crops. Ambient conditions of PPF (2050 to 2340 μmol m⁻² s⁻¹), VPD (3.1 to 4.2 kPa) and AT (28 to 34°C) were relatively similar during gas exchange measurements of all species except blueberry (VPD = 5.5 kPa, AT = 36.8°C) (Tables 1, 2). Leaf temperatures varied from 28 to 33°C with the exception of blueberry (37°C). Leaf temperature minus AT for pecan was most negative for pecan (-1.8°C), followed by grape (-1.6°C), peach (-1.5°C) and fig (0.2°C). Species manifesting positive LT-AT differentials include apple (0.9°C), pear (0.1°C), satsuma (0.5°C), persimmon (0.1°C), blueberry (0.1°C), blackberry (0.1°C) and kiwi (2.1°C). Leaf gas exchange on adaxial leaf surfaces was negligible for all broadleaf species; hence, the stomatal pathway accounted for essentially all CO₂ depletion and water vapor loss.

Net CO₂ assimilation rate (A) varied approximately 3-fold among species (Tables 1, 2). Highest values were recorded for pecan (A = 15.9 μmol m⁻² s⁻¹) and grape (14.6 μmol m⁻² s⁻¹). Net CO₂ assimilation rates of apple, pear, blackberry and fig leaves were intermediate (11.6 to 13.3 μmol m⁻² s⁻¹); and rates of satsuma, persimmon, blueberry and kiwi were relatively low (5.2 to 9.7 μmol m⁻² s⁻¹). Values of E also varied about 3-fold among species (3.1 to 9.7 μmol m⁻² s⁻¹), and followed a similar pattern to that of g_s. Water use efficiency was in the range of 1.4 to 2.2 for all species except blueberry (0.9) and grape (1.1).

Pecan also manifested the highest g_s of any species (452 mmol m⁻² s⁻¹). Moderately high rates of g_s were recorded for pear, grape and apple (g_s = 338 to 368 mmol m⁻² s⁻¹), intermediate rates (198 to 245 mmol m⁻² s⁻¹)

for pear, satsuma, persimmon, blackberry and fig and low rates (91 to 130 $\mu\text{mol m}^{-2} \text{s}^{-1}$) for blueberry and kiwi.

Intercellular CO_2 concentration varied less between species than other measurements of leaf gas exchange. The values of C_i varied from 198 to 234 $\mu\text{mol m}^{-2} \text{s}^{-1} \text{CO}_2$. Values of A were neither directly nor inversely proportional to values of C_i .

Influence of short-term fluctuations in irradiance on leaf gas exchange of pecan.

Stepwise alterations in light intensity, in the sequence 100, 66, 33, 10 and 100% sun, greatly influenced CO_2 uptake, while g_s and E remained essentially constant (Fig. 1). Consequently, A and WUE were much lower, and C_i was higher at reduced levels of irradiance. Net CO_2 assimilation and WUE were near zero at 10% sun (PPF ca. 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$), and C_i was near ambient CO_2 concentration. (Leaf temperature was ca. 1.6°C higher in 100% than in 10% sun and was not likely to be a major contributing factor). Net CO_2 assimilation, WUE and C_i quickly returned to initial values when leaves were re-exposed to 100% sun. Net CO_2 assimilation was also reduced more than g_s or E in leaves exposed to prolonged shade in the canopy interior (ca. 23% sun, PPF= 474 $\mu\text{mol m}^{-2} \text{s}^{-1}$; hence WUE was less and C_i was higher in shaded interior leaves compared to sun-exposed exterior leaves.

Influence of moderate-term fluctuations in irradiance on leaf gas exchange of pecan.

Net CO_2 assimilation, g_s and C_i were stable for 20 min when leaves were exposed to 100% sun (Fig. 2). Shortly after the onset of shading (30% sun) A was rapidly reduced, g_s declined slightly and C_i increased. After 50 min of exposure to 30% sun (i.e., 70 min after initial measurements) A remained stable at 50% of initial values, and g_s and C_i declined gradually. With a return to full sun (i.e., 75 min) gradual increases in A and g_s , and decreases in C_i were noted. However, values of A and g_s failed to return to initial values perhaps due to increases in leaf temperature and vapor pressure deficits after return to 100% sun (See Fig. 2).

DISCUSSION

Leaf gas exchange of pecan varies considerably depending upon the nature of the plant material. Field measurements have indicated that pecan leaves have relatively high rates of leaf gas exchange. Andersen and Brodbeck (1988) reported that 'Stuart' and 'Choctaw' manifested a maximum A and $g\text{H}_2\text{O}$ of 18 to 22 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and

700 to 800 $\text{mmol m}^{-2} \text{s}^{-1}$, respectively.

Wood (1988) reported similar maximum rates ($A= 16$ to 18 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $g_s= 600$ to 900 $\text{mmol m}^{-2} \text{s}^{-1}$) on 'Desirable' trees. These results contrast sharply with data from excised 'Stuart', 'Mobile' and 'Brooks' branches in the laboratory (Crews et al. 1980) (maximum $A= 8.5 \mu\text{mol m}^{-2} \text{s}^{-1}$), and from a study of containerized 'Curtis' seedlings in the greenhouse (maximum $g_s = 160 \text{mmol m}^{-2} \text{s}^{-1}$) (Rieger and Daniell 1988). Previous work performed in the field has shown that pecan was not inhibited at $LT= 41.5^\circ\text{C}$, $PPF= 2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $VPD= 3\text{kPa}$ (Andersen and Brodbeck 1988). This was ascribed to a relatively high hydraulic conductance for pecan compared to most other woody species (Andersen and Brodbeck 1988, Steinberg et al. 1990). Transpiration rates and WUE reported in Table 1 are similar to previously published reports (Andersen and Brodbeck 1988, Wood 1989). The 10 remaining species of fruit crops manifested lower maximum rates of leaf gas exchange than pecan. A comparison to previously reported values appears elsewhere (Andersen 1989).

Although intermittent cloud cover invariably has a rapid effect on A , some plant species undergo rapid stomatal closure ("sun tracking") while other species maintain a relatively constant aperture in sun or shade ("non-sun tracking") (Mooney et al., 1983; Knapp and Smith 1987, 1988, 1989, 1990). Our data indicate that pecan with adequate soil moisture is a non-sun tracking species. Steady state measurements of g_s were lower in shade than in full sunlight (Fig. 3) indicating that the lack of stomatal closure short-term (Fig. 1) and moderate-term (Fig. 2) reductions in irradiance was due to slow guard cell adjustments, and not because g_s was at maximum values at low levels of PPF (Fig. 3).

A consequence of a non tracking response to intermittent cloud cover is a great reduction in WUE. A potential disadvantage of a non-tracking response includes a more rapid depletion of soil water which may eventually translate to increased plant moisture stress. Conversely, assuming adequate soil moisture levels, a non-tracking response maximizes carbon gain during the period of reduced irradiance and after a return of full sunlight as a consequence of elevated C_i (Mansfield et al. 1990). The low WUE occurring in interior canopy leaves is compounded by the fact that older leaves which are often located in the canopy interior gradually become insensitive (i.e., do not close) in response to a reduction in water potential (Andersen and Brodbeck 1988).

Disproportionate reductions in A compared to g_s in leaves exposed to short-term reductions in irradiance (Fig. 1), in naturally-shaded leaves located in the canopy interior (Fig. 1), and in leaves after 50 min exposure to 30% sun (Fig. 2) resulted in a 30 to 60 μmol^{-1} increase in C_i . Similar increases in C_i have been reported in leaves of *Helianthella quinquenervis* and *Senecio triangularis* exposed to simulated cloud cover (Knapp and Smith 1988). Thus, photochemical reactions in the chloroplast responded rapidly to changes in irradiance compared to turgor-mediated guard cell adjustments (Nobel 1983). While anatomical, physiological, and biochemical mechanisms involved in shade acclimation of pecan are complex and poorly understood, feedback inhibition from adjacent leaves did not play a major role in acclimation since there was no effect of shading or removal of adjacent leaves (data not shown). This suggests that acclimation to irradiance is solely based on the light microclimate of each individual leaf or leaflet.

The response of pecan leaves to shading are at variance with the strong positive correlations between A and g_s (and constant C_i) that have been reported for many herbaceous species (Dubbe et al. 1978, Farquhar et al. 1978, Wong et al. 1979, 1985a, 1985b, 1985c). However, C_i has been altered in leaves as a function of: Nutrition in peach [*Prunus persica* (L.) Batsch] (DeJong 1982); ABA treatment in grapevine (*Vitis vinifera* L.) (Downton et al. 1987); VPD, leaf temperature and PPF in olive (*Olea europaea* L.) (Bongi et al. 1987), blueberry (*Vaccinium* spp.), (Moon et al. 1987) and grapevine (Downton et al. 1987). Downton et al. (1988) showed that patchy stomatal closure may result from exogenous ABA application which, may in turn, result in erroneous calculations of C_i . The amount of error is proportional to the degree of nonlinearity of A and g_s (Mansfield et al. 1990). Nevertheless, fluorescence data confirmed that C_i was more variable than previously assumed (Downton et al. 1988).

In conclusion, rates of leaf gas exchange of pecan are high for a C3 woody species. Net CO_2 assimilation and g_s were not strongly coupled in pecan leaves (i.e., a fixed level of C_i was not maintained) under conditions of non-limiting soil moisture, in response to fluctuations in irradiance, or in leaves exposed to prolonged periods of shade. A consequence of the weak coupling between A and g_s in pecan leaves is to maximize carbon gain at the expense of increased

water loss. With the development of plant moisture stress a tighter coupling of A and g_s may occur (Knapp and Smith 1990).

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Table 1. Leaf gas exchange characteristics of persimmon (cv. Fuyu), blackberry (cv. Bluegem) grape *Vitis* sp. (cv. Suwane), *Rubus* sp. (cv. Shawnee), fig (cv. Alma) and kiwi (cv. Hayward) under field conditions in north Florida.

Variable	Species					
	persimmon	blueberry	grape	blackberry	fig	kiwi
PPF ($\mu\text{mol m}^{-2} \text{s}^{-1}$) ^z	2106 ± 44 ^y	2305 ± 60	2114 ± 67	2120 ± 37	2165 ± 63	2200 ± 78
VPD (kPa)	3.7 ± 0.1	5.5 ± 0.1	3.6 ± 0.1	3.3 ± 0.1	3.3 ± 0.1	4.1 ± 0.1
AT (°C)	30.1 ± 0.1	36.8 ± 0.1	34.3 ± 0.3	29.0 ± 0.1	28.4 ± 0.3	28.1 ± 0.2
LT (°C)	30.2 ± 0.2	36.9 ± 0.2	32.7 ± 0.4	28.9 ± 0.1	28.6 ± 0.3	30.2 ± 0.2
A ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	7.6 ± 0.5	5.2 ± 0.4	14.6 ± 0.5	11.9 ± 0.6	12.1 ± 0.5	6.2 ± 0.4
E ($\text{mmol m}^{-2} \text{s}^{-1}$)	5.4 ± 0.2	6.0 ± 0.2	9.3 ± 0.2	5.7 ± 0.3	5.6 ± 0.3	3.1 ± 0.2
WUE ($\text{mmol CO}_2 \text{ mol H}_2$)	1.39 ± 0.05	0.86 ± 0.04	1.06 ± 0.04	2.08 ± 0.07	2.20 ± 0.11	2.00 ± 0.06
g_s ($\text{mmol m}^{-2} \text{s}^{-1}$)	201 ± 18	130 ± 3	361 ± 9	245 ± 21	243 ± 20	91 ± 7
Ci ($\mu\text{mol mol}^{-1}$)	236 ± 3	232 ± 4	215 ± 2	205 ± 6	198 ± 7	198 ± 4

^zAbbreviations: PPF=photosynthetic photon flux, VPD=vapor pressure deficit, AT=air temperature, LT=leaf temperature, A=net CO₂ assimilation rate, E=transpiration rate, WUE=water used efficiency, g_s =leaf conductance to water vapor, Ci=intercellular CO₂ concentration.

^yReported values are means ± 1 SE; persimmon n=12, blueberry n=13, grape n=14, blackberry n=13, fig n=12 and kiwi n=12.

Table 2. Leaf gas exchange characteristics of pecan (cv. Elliot), peach (cv. Flordaking), apple (cv. Anna), pear (cv. Flordahome) and satsuma (cv. Owari) under field conditions in north Florida.

Variable	Species				
	pecan	peach	apple	pear	satsuma
PPF ($\mu\text{mol m}^{-2} \text{s}^{-1}$) ^z	2083 ± 43 ^y	2251 ± 26	2243 ± 39	2049 ± 48	2053 ± 65
VPD (kPa)	3.1 ± 0.1	3.5 ± 0.1	3.6 ± 0.2	3.5 ± 0.1	3.2 ± 0.1
AT (°C)	33.4 ± 0.1	34.0 ± 0.2	32.9 ± 0.2	30.0 ± 0.3	27.6 ± 0.2
LT (°C)	31.6 ± 0.2	32.5 ± 0.3	32.0 ± 0.7	29.7 ± 0.3	28.1 ± 0.3
A ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	15.9 ± 0.3	13.3 ± 0.3	11.6 ± 0.6	11.8 ± 0.4	9.7 ± 0.6
E ($\text{mmol m}^{-2} \text{s}^{-1}$)	9.7 ± 0.1	9.3 ± 0.2	8.6 ± 0.2	5.7 ± 0.1	4.8 ± 0.3
WUE ($\text{mmol CO}_2 \text{ mol H}_2$)	1.63 ± 0.04	1.45 ± 0.04	1.35 ± 0.06	2.10 ± 0.04	2.02 ± 0.04
g_s ($\text{mmol m}^{-2} \text{s}^{-1}$)	452 ± 7	368 ± 12	338 ± 12	222 ± 8	198 ± 16
Ci ($\mu\text{mol mol}^{-1}$)	223 ± 2	227 ± 2	234 ± 4	200 ± 1	212 ± 3

^zAbbreviations: PPF=photosynthetic photon flux, VPD=vapor pressure deficit, AT=air temperature, LT=leaf temperature, A=net CO₂ assimilation rate, E=transpiration rate, WUE=water used efficiency, g_s =leaf conductance to water vapor, Ci=intercellular CO₂ concentration.

^yReported values are means ± 1 SE; pecan n=18, peach n=31, apple n=10, satsuma n=11.

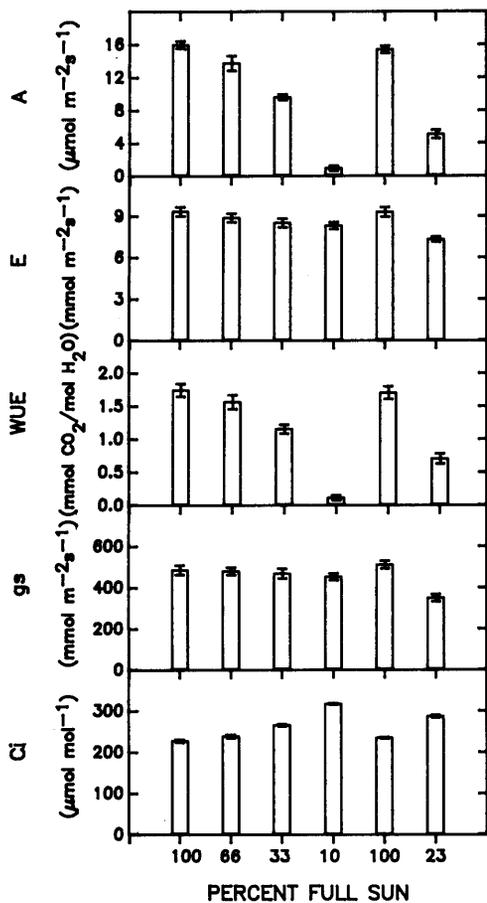


Figure 1. Net CO₂ assimilation (A), transpiration (E), water use efficiency (WUE), stomatal conductance (g_s) and intercellular CO₂ concentration (C_i) of 'Stuart' pecan leaves exposed to 100 (PPF = 2120 ± 14.5 μmol m⁻² s⁻¹), 66, 33, 10 and 100% sun with each sequence lasting ca. 80 sec. The last column (i.e., 23% fill sun; 483 ± 21 μmol m⁻² s⁻¹) represents the natural irradiance level of leaves measured in the canopy interior. Error bars correspond to mean ± SE, n = 10. Leaf temperatures were 30.4 ± 0.8, 29.5 ± 0.8, 29.0 ± 0.9, 28.8 ± 0.7, 29.8 ± 0.8 and 29.1 ± 0.6°C (mean ± SE) for the 100, 66, 33, 10, 100 and 23% sun treatments, respectively. Vapor pressure deficits were 1.9 ± 0.1, 1.7 ± 0.1, 1.6 ± 0.1, 1.5 ± 0.1, 1.9 ± 0.1 and 1.8 ± 0.1 kPa for the 100, 66, 33, 10, 100 and 23% full sun treatments, respectively.

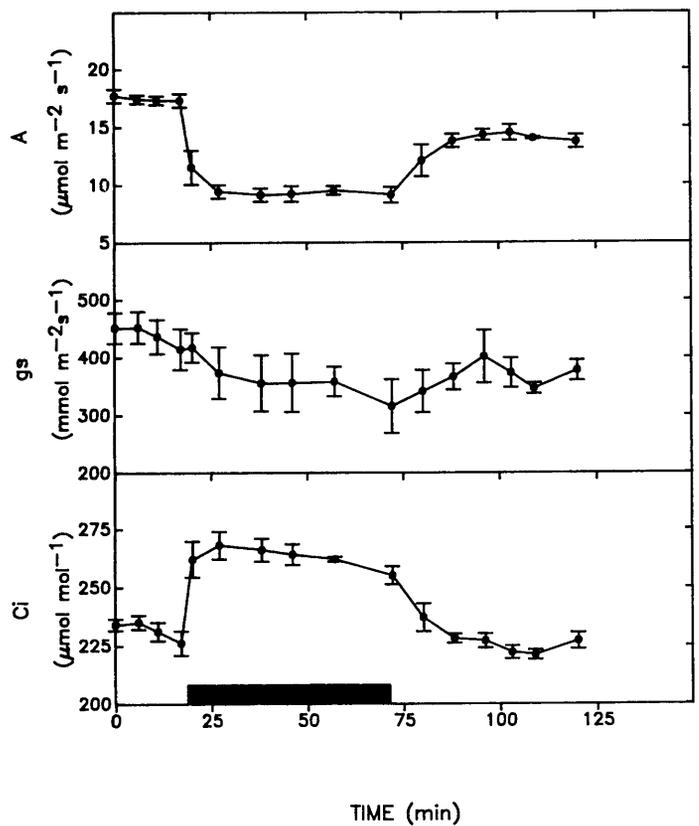


Figure 2. Effect of variable sunlight on net CO₂ assimilation (A), stomatal conductance (g_s) and intercellular CO₂ concentration (C_i) of 'Cape Fear' pecan leaves. Leaves were exposed to 20 min of 100% sun (PPF = 1924 ± 24 μmol m⁻² s⁻¹), then 50 min of 33% sun (PPF = 583 ± 10 μmol m⁻² s⁻¹) represented by the darkened horizontal bar, then 50 min of 100% sun. Circles and error bars represent means ± SE, n = 4. Leaf temperatures were 29.0 ± 0.2, 30.7 ± 0.3 and 35.1 ± 1°C (mean ± SE) for the 100, 30, and 100% sun period, respectively. Vapor pressure deficits were 2.2 ± 0.1, 2.2 ± 0.1 and 3.3 ± 0.1 kPa for the 100, 30 and 100% sun period, respectively.