

United States
Department of
Agriculture

Forest Service



**Southern
Research Station**

Research Paper
SRS-45

Leaf Gas Exchange of Mature Bottomland Oak Trees

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July 2009
Southern Research Station
200 W.T. Weaver Blvd.
Asheville, NC 28804

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Abstract

We determined how changes in environmental moisture affected leaf gas exchange in Nuttall (*Quercus texana* Buckley), overcup (*Q. lyrata* Walt.), and dominant and codominant swamp chestnut (*Q. michauxii* Nutt.) oak trees in Mississippi and Louisiana. We used canopy access towers to measure leaf level gas exchange rates, e.g., photosynthesis, transpiration, stomatal conductance, on the upper crowns. Leaf gas exchange rates of the dominant swamp chestnut oak tree increased in response to summer precipitation. Nuttall and overcup oak trees exhibited constant gas exchange rates throughout the measurement periods. Dominant swamp chestnut oak also maintained high water use efficiency during periods of low soil moisture. These responses and access to water sources during soil drying may buffer extreme fluctuations in leaf gas exchange rates in mature canopy oak trees. Seasonal fluxes in water use and transpiration among individual oak trees of various sizes and other bottomland hardwood species need to be determined to assess their physiological and ecological contributions on the water balance of southeastern bottomland hardwood forests.

Keywords: Drought, leaf water potential, photosynthesis, *Quercus* spp., stomatal conductance, water use efficiency.

Introduction

Bottomland hardwood forests in the floodplains of the Southeastern United States make up a highly diverse and productive ecosystem. This complex ecosystem is subjected to extreme fluctuations in soil and climate conditions throughout the year (Kellison and others 1998). Most of these sites are flooded for several days or weeks in winter and spring and have experienced extremely dry soil conditions in summer (Hodges 1998). Oak (*Quercus*) species dominate the bottomland forests, and their distributions depend on their tolerance to extreme fluctuations in edaphic, hydrologic, and climatic conditions (Hodges 1998). Oak species of bottomland forests coexist by differing means of adaptation, including anatomical and morphological structure as well as physiological response to the environment (McKevlin and others 1998).

The physiological responses of several bottomland oak species to flooding have been studied under nursery and

field conditions (Gardiner 1994, McKevlin and others 1998, Oren and others 2001, Pereira and Kozlowski 1977, Pezeshki and Chambers 1985). These studies revealed both morphological and physiological responses of bottomland oak seedlings to flooding. However, the responses of bottomland oak trees to drought have not been studied, and little is known about how they sustain productivity under extremely dry conditions in the growing season, and about the differential access of trees to water sources during drought (Dawson 1996, Teskey and Sheriff 1996).

Overcup (*Quercus lyrata* Walt.) and Nuttall (*Q. texana* Buckley) oak are considered flood-tolerant species and are most commonly found on poorly drained soil in the major floodplains of the Mississippi River. Swamp chestnut oak (*Q. michauxii* Nutt.) and other oak species, such as cherrybark oak (*Q. pagoda* Raf.) and water oak (*Q. nigra* L.), are classified as less flood-tolerant species and occur on bottomland sites where soil conditions range from poorly drained to well drained (Hodges 1998). These species, differing in tolerance to soil drainage and flooding, also may have unique responses to soil drought. High vapor pressure deficit (VPD) and substantial soil moisture reductions may greatly affect their water consumption and loss during summer drought (Bassow and Bazzaz 1998, Giuliani and others 1997, Oren and others 2001, Pataki and others 1998). This study was conducted to characterize the diurnal variations of leaf gas exchange and water relations among mature oak trees in response to changes in environmental moisture (soil and atmosphere).

Materials and Methods

Field Site and Plant Material

This research was conducted at two sites: the bottomland hardwood forests of the Delta National Forest in Mississippi and the Kisatchie National Forest in Louisiana. The Delta National Forest site (Delta: 32.81° N, 90.78° E) is a major

floodplain about 2 km from the Mississippi River. The Delta site is dominated by sweetgum (*Liquidambar styraciflua* L.), Nuttall oak, and overcup oak. Sharkey (Chromic Epiaquerts) is the dominant soil series on the site, characterized by very deep, poorly drained, and very slowly permeable soils formed in clayey alluvium (Natural Resources Conservation Service 2001, Pettry and Switzer 1996). Flooding in major bottoms is usually seasonal with long duration (Hodges 1998). The Kisatchie National Forest site (Iatt: 31.73° N 92.64° W) is a 345-ha minor alluvial floodplain of Iatt Creek dominated by sweetgum, cherrybark oak, and water oak. The site was characterized in detail by Meier and others (1999). Soils are Typic Glossaqualfs of the Guyton soil series, consisting of very deep, poorly drained soils formed in thick loamy sediments (Broadfoot 1976, Natural Resources Conservation Service 2001). Flooding in minor floodplains is frequent and associated with local rainfall (Hodges 1998). The average annual precipitation (50-year period) is 1300 mm at the Delta site and 1450 mm at the Iatt Creek site (Unified Climate Analysis Network 2001). Mean maximum and minimum temperature (July and August 2000) at both sites were similar [Delta site: 31 and 5 °C, respectively; and Iatt Creek site: 31 and 3 °C, respectively (Unified Climate Analysis Network 2001)].

Each site has a canopy tower that provides access to the crowns of mature canopy oak trees. The access canopy tower at the Delta site (26 m) is within reach of the crowns of a Nuttall oak (height 31 m, d.b.h. 57 cm) and an overcup oak (height 28 m, d.b.h. 83 cm). The tower at the Iatt Creek site (29 m) is accessible to the crowns of dominant (height 27 m, d.b.h. 70 cm) and codominant (height 21 m, d.b.h. 31 cm) swamp chestnut oak trees.

Leaf Gas Exchange Measurements

Leaf gas exchange and water relations variables were measured using a portable leaf gas exchange system (PP Systems model, CIRAS-I, Hertfordshire, UK) on July 20 and August 9, 2000, at the Delta site, and July 12 and August 2, 2000, at the Iatt Creek site. Photosynthetic carbon assimilation rate (A), stomatal conductance (g_s), and transpiration rate (E) were measured on three to five fully expanded leaves randomly selected on each of two branches per tree. Leaf water potential (Ψ) was determined with a pressure chamber (PMS Instrument Company, Corvallis, OR). All measurements were conducted during relatively cloud-free days from 0700 to 1800 hours under ambient light and temperature conditions. Predawn leaf water potential (Ψ_{pd}) was determined at 0500 hours. On

each leaf gas exchange measurement day, four soil samples were collected at four cardinal directions within the drip line of each tree, using 20-cm deep soil cores for water content analysis. Soil water content was determined by the gravimetric method (oven-dried at 105 °C for 48 hours).

Meteorological Measurements

The topmost portion of each tower site was instrumented with an array of meteorological instruments (Delta: 26 m, Iatt: 29 m). Air temperature and humidity (Vaisala model HMP45A, Columbus, OH), photosynthetically active radiation (LI-COR model LI-190SZ, Lincoln, NE), and wind speed and direction (Windset model MET One 034A-L Windset, Logan, UT) were continuously monitored throughout the study using a data logger (Campbell Scientific model CR10x, Logan, UT). Rainfall and other meteorological data of each site were taken from the nearest weather stations (< 1 km from the project sites) maintained by U.S. Department of Agriculture World Agricultural Outlook Board and the Forest Service.

Statistical Analysis

Gas exchange variables and meteorological data were compared by one-way analysis of variance using Statistical Analysis System (SAS Institute 2001). Within a site, each species and sampling date combination served as a separate treatment. Fisher's least significant difference was used to compare responses between species within a site and measurement periods. Because only one tree per species was accessible from the towers, inferences can be drawn only for these trees and locations. However, common patterns of response may be suggestive and indicative of bottomland oak species in general.

Results

Microsite and Soil Moisture Conditions

For much of the Southeastern United States, 2000 was a relatively dry year (Drought monitor 2002). In 2000, the Delta site's rainfall accumulation was 1147 mm, constituting 88 percent of the site's 50-year mean of 1300 mm. The Iatt Creek site's rainfall total that year was 1194 mm, or 82 percent of its yearly mean of 1450 mm.

During the leaf gas exchange measurement period in July (July 20) at the Delta site, the highest daily temperature

was 38 °C and the mean daylight VPD was 1.59 (± 0.26) kilopascal (kPa). In August (August 9), the highest daily temperature was 36 °C and the mean daylight VPD was 1.60 (± 0.28) kPa. The Iatt Creek site, on the other hand, had a maximum temperature of 34 and 35 °C in July (July 12) and August (August 2), respectively, and a mean daylight VPD of 1.56 (± 0.26) kPa in July and 1.63 (± 0.29) kPa in August. Amount of soil moisture at the Delta site did not vary significantly between July and August (28 percent ± 0.5 and 27 percent ± 0.5 , respectively). Significantly lower soil moisture at the Iatt site was observed in July (12 percent ± 0.6) compared to August (17 percent ± 0.6). The increase in soil moisture in August at the Iatt Creek site was due to rainfall 3 days before soil sample collection and leaf gas exchange measurements. The soils of the Delta site are rich in clay while those of the Iatt Creek site are rich in sand (Natural Resources Conservation Service 2001).

Predawn Leaf Water Potential and Diurnal Physiology

At the Delta site, the Ψ_{pd} of Nuttall oak and overcup oak differed in July but were not significantly different between July and August (table 1). The differences between the species disappeared in August. The Ψ_{pd} of dominant and codominant swamp chestnut oak trees at the Iatt Creek site significantly increased (became less negative) by 47 and 50 percent, respectively, from July to August. The increase in Ψ_{pd} coincided with an increase in soil moisture in August. g_s and E of Nuttall oak and overcup oak at the Delta site did not differ significantly in both July and August measurement periods (table 1). At the Iatt Creek site, g_s in July was significantly lower in the dominant swamp chestnut oak tree compared to the codominant tree. The g_s and E of the dominant swamp chestnut oak tree in August were significantly higher than in July. Water use efficiency (WUE) (A/E) of the dominant swamp chestnut oak tree significantly declined in August when precipitation created an increase in soil moisture. The codominant swamp chestnut oak tree had significantly lower g_s and E in August than in July.

In July and August, gas exchange rates of the overcup oak tree increased between 0700 and 1200 hours and then declined throughout the afternoon (fig. 1). On the other hand, the Nuttall oak tree had low but almost constant leaf gas exchange rates throughout the day in July. In August, however, leaf gas exchange of Nuttall oak increased between 0700 and 1200 hours and then gradually declined throughout the day. Leaf gas exchange patterns for both species were related to photosynthetically active radiation

(PAR) values that increased between 0700 and 1200 hours and then declined the rest of the day. The Ψ of both trees declined between 0700 and 1200 hours and then recovered in the afternoon (fig. 1I). The codominant swamp chestnut oak tree started with a high g_s and E during early morning to midafternoon of the July and August measurement periods (fig. 2). In July, g_s and E of the codominant swamp chestnut oak tree started to decline at 1200 hours and continued to decrease the rest of the afternoon (figs. 2C and 2E). The increase in leaf gas exchange rates by the codominant tree in the morning to midafternoon was related to an increase in mean daylight PAR values from 0700 to 1200 hours in July. In dominant swamp chestnut oak, gas exchange rates remained the same throughout the day (figs. 2C, 2E, and 2G). In July and August, the Ψ of dominant and codominant swamp chestnut oak declined from early morning to midafternoon and then increased the rest of the afternoon (figs. 2I and 2J). Gas exchange rates and Ψ of both dominant and codominant swamp chestnut oak trees in August were similar throughout the day.

Discussion

Relatively dry conditions in the summer of 2000 allowed the investigation of the water relations characteristics of four bottomland oak trees in response to soil drying in two bottomland forest sites that differ in hydrology and soil conditions. Different physiological responses of oak trees to summer precipitation were also observed in this study.

High Ψ_{pd} has been linked with the deep root systems of several species (Abrams 1990, Abrams and Knapp 1986, Hinckley and others 1983, Whitehouse and others 1983). However, in bottomland forests where soil oxygen is limiting due to regular flooding, roots of most trees do not grow beyond a certain soil depth (Hodges 1998). A similar study in a mature bottomland deciduous forest revealed that average rooting depth was ~40 cm (Pataki and Oren 2003). Consequently, the bottomland oak trees appear to have access to soil moisture despite their shallow root systems. Further, bottomland trees would have the same root depth and access to ground water but, depending on the species and size, these trees would vary in their root distribution and hence water extraction capabilities. The increase in Ψ_{pd} (became less negative) from July to August in swamp chestnut oak trees was in response to precipitation. Deeper and more extensive root systems are in contact with moist soil layers and can establish water potential equilibrium with soil at night (Hinckley and others 1983). Therefore,

Table 1—Response of leaf gas exchange of mature Nuttall oak (*Quercus texana* Buckley) and overcup oak (*Q. lyrata* Walt.) trees in the Delta National Forest, Mississippi, and dominant and codominant swamp chestnut oak (*Q. michauxii* Nutt.) trees in the Kisatchie National Forest (Iatt Creek), Louisiana, at different measurement dates and daylight mean photosynthetically active radiation in summer 2000

Parameters	Delta site				Iatt Creek site			
	July 20		August 9		July 12		August 2	
	Nuttall oak	Overcup oak	Nuttall oak	Overcup oak	Dominant swamp chestnut oak	Codominant swamp chestnut oak	Dominant swamp chestnut oak	Codominant swamp chestnut oak
g_s	87.4 A	98.7 A	91.3 A	95.4 A	59.5 C	161.9 A	100.7 B	119.2 B
se	5.0	8.1	7.7	9.6	7.0	19.7	5.6	5.3
E	3.2 A	3.7 A	3.4 A	3.6 A	2.2 A	4.5 A	3.2 B	3.6 B
se	0.2	0.3	0.3	0.3	0.2	0.4	0.1	0.1
A	1.4 B	3.0 A	2.4 AB	2.7 A	2.2 A	2.1 A	1.4	1.7 A
se	0.3	0.5	0.4	0.5	0.8	0.7	0.2	0.2
Ψ	-1.13 A	-1.49 B	-1.50 B	-1.32 AB	-1.15 A	-1.34 A	-1.35 A	-1.23 A
se	0.11	0.15	0.10	0.13	0.22	0.12	0.11	0.09
Ψ_{pd}	-0.36 B	-0.21 A	-0.31 AB	-0.22 A	-0.28 BC	-0.33 C	-0.19 A	-0.22 AB
se	0.08	0.04	0.02	0.02	0.01	0.04	0.04	0.03
WUE	0.57 A	0.71 A	0.47 A	0.49 A	0.79 A	0.41 B	0.41 B	0.46 B
se	0.07	0.09	0.09	0.09	0.29	0.11	0.06	0.05
PAR	84.4 C	377.56 AB	260.8 BC	510.8 A	85.46 A	158.79 A	87.79 A	110.88 A
se	12.5	74.8	40.0	93.0	30.9	63.6	14.9	22.0

g_s = stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$); E = transpiration rate ($\text{mmol m}^{-2} \text{s}^{-1}$); A = photosynthesis rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); Ψ (MPa) = leaf water potential; Ψ_{pd} (MPa) = predawn leaf water potential; WUE = water use efficiency (A/E); PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$) = photosynthetically active radiation. In a row (each site), means with the same letter are not significantly different ($P > 0.05$).

Ψ_{pd} is considered a good measure of how soil drying affects plant water status during the day (Nadezhdina 1999). It is an indirect measure of the “effective rooting depth” at which trees extract the bulk of their water requirements (Abrams and Knapp 1986).

None of the oak trees in this study exhibited midday depressions in leaf gas exchange rates (g_s , E, and A; figs. 1 and 2). The decline in leaf gas exchange rates followed the decline in maximum rates at noon and the decline in PAR as the day progressed. This result was consistent with a study by Bassow and Bazzaz (1998) of four deciduous

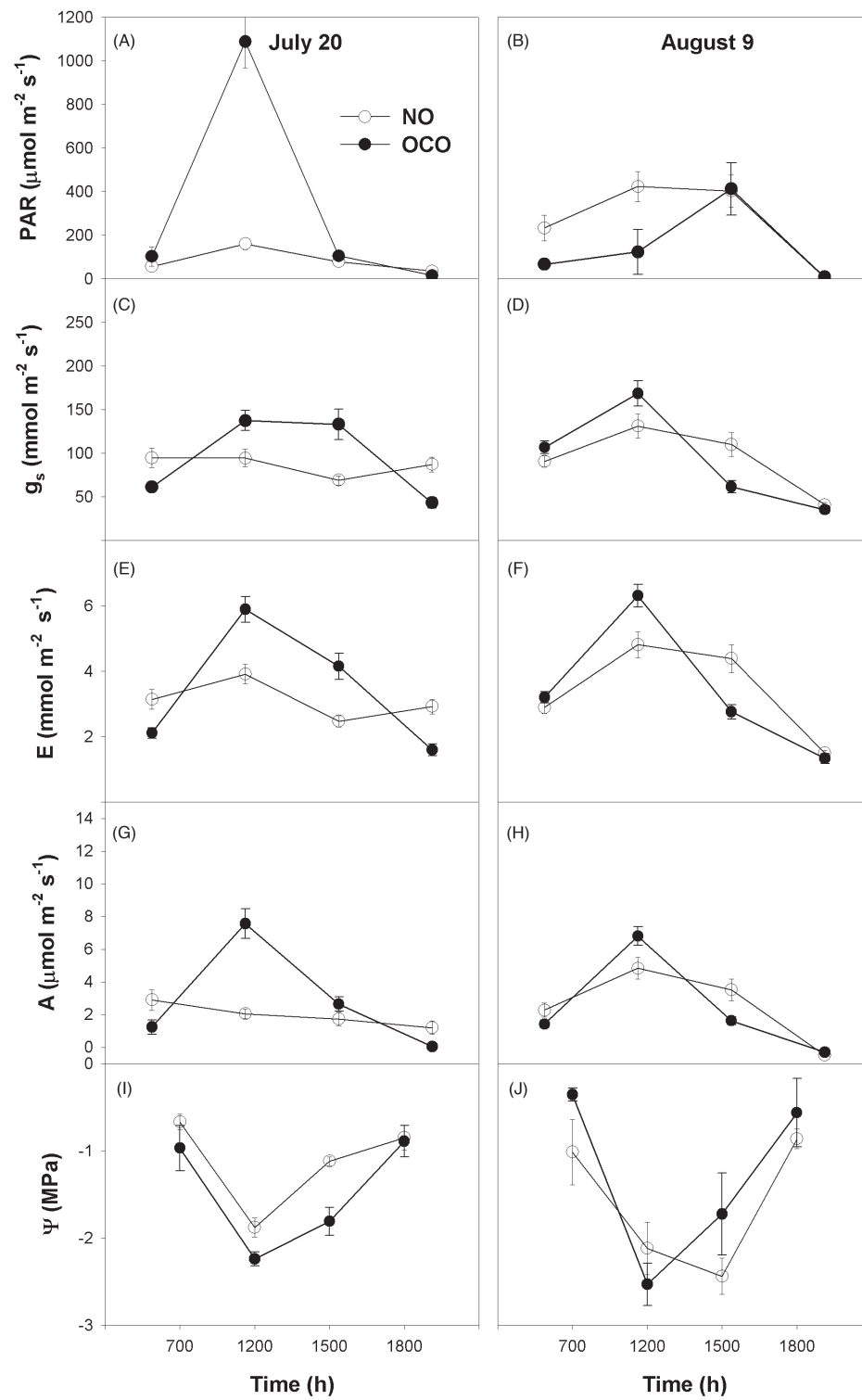


Figure 1—Diurnal response of Nuttall oak (NO) and overcup oak (OCO) on Delta National Forest (Delta site), Mississippi, on July 20, 2000 [PAR (A), g_s (C), E (E), A (G), and Ψ (I)] and on August 9, 2000 [PAR (B), g_s (D), E (F), A (H), and Ψ (J)].

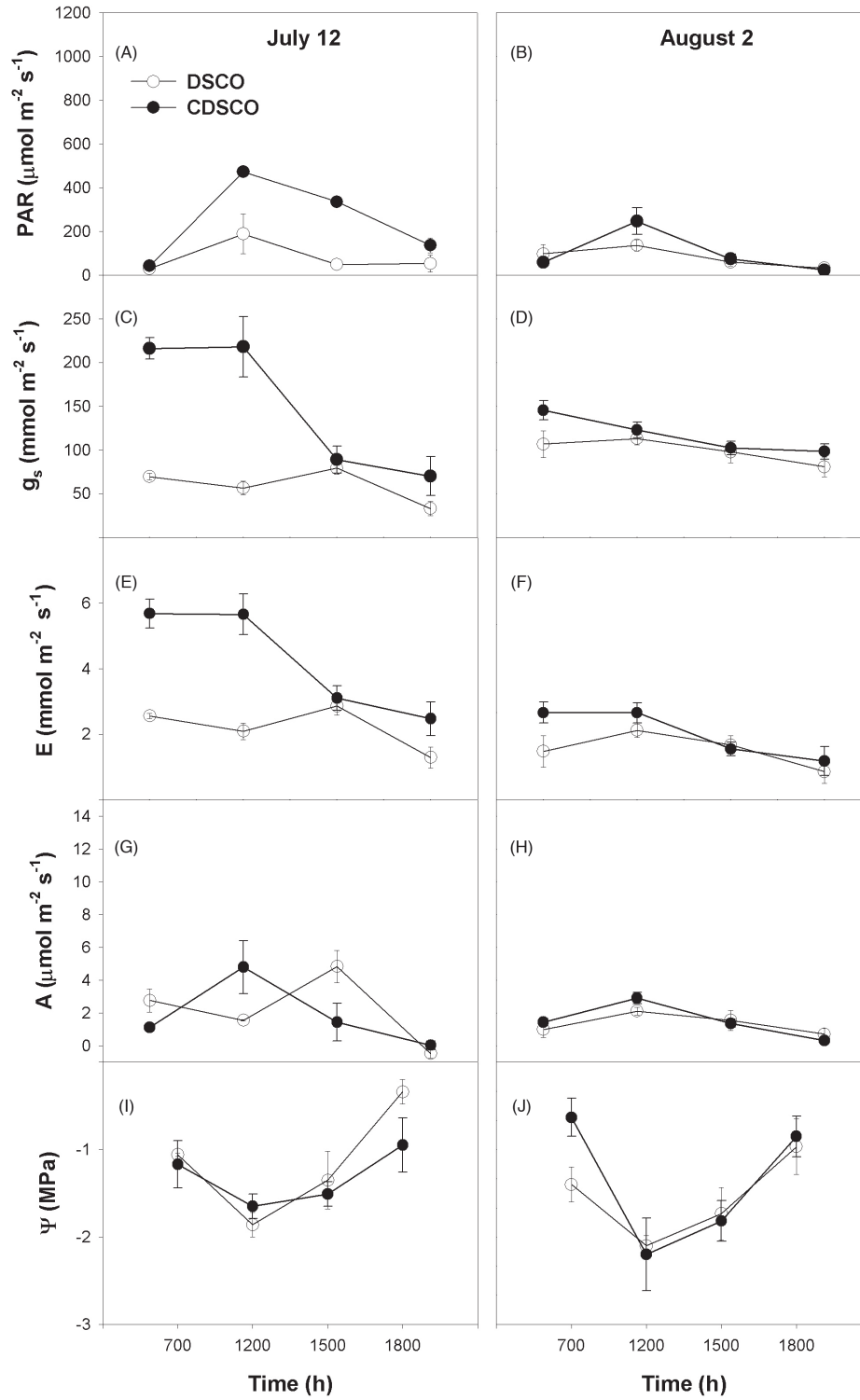


Figure 2—Diurnal response of dominant (DSCO) and codominant swamp chestnut oak (CDSCO) on Kisatchie National Forest (Iatt Creek), Louisiana, on July 12, 2000 [PAR (A), g_s (C), E (E), A (G), and Ψ (I)] and on August 2, 2000 [PAR (B), g_s (D), E (F), A (H), and Ψ (J)].

species that exhibited no midday depressions in diurnal patterns of photosynthesis and that showed photosynthesis rates affected by canopy light intensity, leaf and air temperature, and VPD. Bassow and Bazzaz (1998) argued that the drought conditions when measurements were taken might not have been extreme enough for the trees to exhibit stomatal closure at midday. In this study, the relatively high values of Ψ_{pd} (−0.19 to −0.36 megapascal [MPa]) of the four oak trees suggest the ability of the roots of these trees to reach ground water. However, differences in their water utilization patterns during daylight hours triggered different responses of these trees to summer drought.

Stomata conductance of several species also has been observed to decline as soil dries out (Hogg and Hurdle 1997, Hogg and others 2000, Martin and others 1997, Pataki and others 1998). In this study, g_s and E of codominant swamp chestnut oak declined in response to high VPD in August. The high VPD also caused decline in A and g_s in a number of species such as red maple (*Acer rubrum* L.), trembling aspen (*Populus tremuloides* Michx.), eucalypts (*Eucalyptus tetradonta* F. Muell.), and hazelnut (*Corylus cornuta* Marsh.) (Hogg and others 2000, O'Grady and others 1999). In contrast, there was no change in g_s , E, and daily water use for both Nuttall and overcup oak trees from July to August. The constant leaf gas exchange rates can be attributed to constant soil moisture content and VPD in July and August.

Water use efficiency (A/E) in the dominant swamp chestnut oak tree was significantly higher in July than in August. This suggests that the dominant tree was conserving more water in July, when soil water was limiting. Apparently, the dominant swamp chestnut oak tree tended to conserve water by restricting water loss during the driest measurement day in July. Thus, low g_s and E and high A were observed in July in the dominant tree. In August, however, an increase in soil moisture due to precipitation increased g_s and E in the dominant swamp chestnut oak tree. In another study, the increase in WUE during soil drying was attributed to the stomatal control of water loss at the beginning of the stress (Arndt and others 2000). Swanson (1994) explained that high canopy g_s on moist soils contributes greatly to total stand water loss during soil drying between rain events. Thus, dominant oak trees that can consume considerably large amounts of water on a daily basis have a great impact on the overall water balance in bottomland forests.

In summary, the increase in leaf gas exchange and Ψ_{pd} of the dominant and codominant swamp chestnut oak trees

was related to summer precipitation in August. Differential access of oak trees to water sources was evident with the relatively constant leaf gas exchange despite substantial environmental variation between July and August measurements. Long-term measurements of sap flow of oaks and other bottomland species are necessary to determine the seasonal fluxes in water use and their physiological and ecological consequences in water balance of bottomland forests.

Acknowledgments

This study was supported by the Forest Service, Southern Global Change Program and the Mississippi State University, Department of Forestry. Milan Vavrek and Diomides Zamora provided valuable reviews of the manuscript.

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Gazal, Rico M.; Kubiske, Mark E.; Connor, Kristina F. 2009. Leaf gas exchange of mature bottomland oak trees. Res. Pap. SRS-45. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 8 p.

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