PHOTOSYNTHETIC CHARACTERISTICS OF FIVE HARDWOOD SPECIES IN A MIXED STAND[1]

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Abstract-In 1998, photosynthesis (Pn) was measured on cherrybark oak, green ash. swamp chestnut oak, sweetgum, and water hickory in a mixed stand established in February 1994. Based on the apparent quantum yield Obtained from light response curves, cherrybark oak had the lowest Pn in August whereas sweetgum, green ash and water hickory were squally active in Pn. Daily August Pn of sweetgum and green ash peaked before 10 am and decreased sharply thereafter. Between 3 and 5 pm, sweetgum and green ash Pn were about 40 percent of their peak Pn. Daily September Pn did not show such sharp decreases in the afternoon for any species. Sweetgum had the highest chlorophyll level and the largest specific leaf weight in August. The ability of cherrybark oak and swamp chestnut oak to maintain leaves with adequate chlorophyll contents contributed to their active Pn in mid-December.

INTRODUCTION

Multiple species coniferous stands are generally unsuccessful because a tingle species usually becomes dominant in ths stand due to differences in seedling growth rates. Stands with multiple hardwood species characteristically coexist in the forest with species distributions ranging from random to clumped. These mixed species stands can be invaluable for providing forest products and for providing food for wildlife.

One wmmon and central aspect of tree physiology is that survival and growth of transplanted seedling stocks are dependent upon the availability and metabolism of sucrose (Sung and others 1994, 1995, 1998a, b). For most plants, the product of photosynthesis (Pn) is translocated in the form of sucrose to all carbon sinks such as stems and roots for growth and storage (Shiroya and others 1962). We report the photosynthetic characteristics of five hardwood species in a mixed stand 4 years after establishment. Details on the establishment of this five-hardwood species study and results of survival and growth of individual species are reported by Kormanik and others (this proceedings).

MATERIAL8 AND METHODS

All seedlings in this study were grown at the Georgia Forestry Commission's Flint River Nursery (Montezuma, GA) using a single hardwood nursery protocol developed by Kormanik and others (1994). Prior to sowing, soil levels of Ca, K, P, Mg, Cu, Zn, and B were adjusted to 500, 80, 80, 50, 2, 6, and 1.2 ppm, respectively. Nitrogen was applied as NH_4NO_3 at an annual rate equivalent to 1322 kg per ha. Seedling bed density for all species was 54-57 per m^2. In February 1994, two hundred 1-0 seedlings from each of the five hardwood species—cherrybark oak (CBO, *Quercus pagoda* Raf.), green ash (GA, *Fraxinus pennsylvanica* Marsh.), swamp chestnut oak (SCO, *Q. michauxii* Nutt.), sweetgum (SG, *Liquidambar styraciflua* L.), and water hickory (WH, *Carya aquatica* Nutt.)—were selected from the top 50 percent of the crops based on first-order lateral root number, root collar diameter, and height (Kormanik and others, this proceedings). These seedlings were randomly planted at a 3.3 x 3.3 *m* spacing on a cleared 2.5-ha site at the National Environmental Research Park (Savannah River Natural Resource Management and Research Institute, New Ellenton, SC). Soil series on this sit8 is mainly Rembert sandy loam with Hornsville fine sandy loam, Neeses loamy sand, Norfolk loamy sand, Ailey sand, and Albany loamy sand in some areas. Fertilization and vegetation control on this stand is reported in detail by Kormanik and others (this proceedings).

In 1998, three areas within the stand were systematically selected so that five species were located within a radius of IO m of each other. These areas were at least 30 m apart. One tree from each species was tagged within each area. In August 1998, Pn light response curves were determined from each tagged tree in the three areas using a portable open-system infra-red gas analyzer (LiCor 6400) equipped with an internal red-blue light source and a CO, mixer. Measurements were made between 8 am and 11 am (Eastern Standard Time) on one fully expanded, attached leaf from the outside canopy of each tagged tree. The same leaf was measured over a range of different levels of photosynthetic photon flux density (PPFD, 400 - 700 nm) levels. During Pn measurements, selected PPFD levels were used randomly with a 3- to 5-min adjustment period between measurements. The reference chamber CO_2 was set at 350 ppm for all measurements. Individual values of Pn obtained from three CBO, three SCO, two GA, two SG, and two WH were pooled to construct a light response curve for each species using the model of Long and Hällgren (1993):

$$Pn = \frac{Pmax \cdot PPFD}{Km + PPFD} - Rd, \qquad (1)$$

where

Pmax = the maximal Pn,
Rd = the dark respiration rate, and
Km = the PPFD at one-half of Pmax.

tight compensation point (Γ, PPFD at which Pn equals zero) was calculated as

$$\frac{Rd \cdot Km}{Pmax - Rd}.$$

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[1] Paper presented at the Tenth Biennial Southern Silvicultural Research Conference, Shreveport, LA, February 16-18, 1999.

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The apparent quantum yield (the slope (derivative) evaluated at the midpoint between Γ and 100 μmol m^2 per s PPFD) was

$$\frac{Pmax \cdot Km}{\left(Km + \frac{\Gamma + 100}{2}\right)^2}.$$

Light response curves were fit to the individual photosynthesis observations using PROC NLIN (SAS Institute Inc. 1987). Parameter estimates and asymptotic standard errors were obtained for Pmax, Km, and Rd. Apparent quantum yield, Γ, and Pn at 2000 μmol per m^2 per s PPFD were calculated from the estimated parameters. Due to the complex mathematical nature of these quantities, no standard errors were computed.

The same tagged trees used to obtain light response curves were measured for daily Pn between 7 am and 5 pm (Eastern Standard Time) in August and September. One fully expanded leaf randomly selected from the outside canopy of each tree was measured throughout the day. Since the selected leaves may be shaded during measurement, Pn was measured at 1800 μmol m^2 per s. The reference chamber CO_2 was set at 350 ppm for all measurements. In November, because of leaf discoloration and abscission, different GA and SG trees that had adequate foliage and were in the vicinity of the previously tagged ones were measured. One GA and two SG were measured in November. By December, only CBO and SCO were measured.

Leaves were harvested at the end of the daily Pn measurements, stored on ice, transported back to the laboratory, and stored at -80 °C until chlorophyll analysis was performed. A leaf segment of 1 cm^2 was weighed, quickly placed in liquid N_2, and powdered with a pestle and mortar. Ethanol (95 percent) (30:1, volume : leaf fresh weight, ml:g) and $CaCO_3$ (1 :2, weight : leaf fresh weight) were used to extract chlorophyll. Immediately after centrifugation, supernatant OD's at 849,854, and 885 nm were determined using a Beckman DU-70 spectrophotometer.

RESULTS

Light response curves for all species are curvilinear with calculated Pmax ranging between 8.7 μmol per m^2 per s for CBO to 14.1 μmol per m^2 per s for WH (table I). Swamp chestnut oak and CBO had similar values of Pmax and Pn at 2000 μmol per m^2 per s (equivalent to full sunlight). These values were similar to and greater than greenhouse-grown second year SCO and CBO, respectively (Angelov and others 1998). Except for the apparent quantum yield, there were no statistical differences in other light response curve parameters among species. Based on the apparent quantum yield, CBO had the lowest Pn in August whereas SG, GA, and WH were equally active in Pn (table 1).

No significant differences due to time of day were observed for CBO in either August or September (fig. la). Based on the August through December data, the highest Pn was measured in November for CBO. Surprisingly, measurements taken on a cool December morning (ambient temperature l3 °C, leaf chamber temperature l8 °C) indicated that CBO photosynthesized as much as it did during the morning measurements in September (fig. la). In fact, December CBO Pn was comparable to that measured in September for GA, SG, and SCO (flg. l).

In August, GA Pn peaked before 9 am and then decreased 88 percent from 9 am to 3 pm (fig. l b). Peak daily Pn for GA occurred around noon in September and remained at the same level in the afternoon. Peak August and September Pn values for GA were similar to CBO Pn (fig. la, l b). In contrast to CBO, November Pn for GA was lower than peak Pn of August and September (fig. l b). August daily Pn for SCO was similar in trend to August CBO Pn measurements

Table 1—Estimates (and asymptotic standard errors) of August photosynthesis light response curve parameters for cherrybark oak (CBO), green ash (GA), swamp chestnut oak (SCO), sweetgum (SG), and water hickory (WH) in a mixed stand

Parameters	CBO	GA	SCO	SG	WH	P-value[a]
Pmax[b c]	8.7±0.9a[d]	10.9±0.3a	8.9±0.3a	13.5±0.3a	14.1±0.6a	0.0553
Pn at 2000 μmol m^{-2} s^{-1}	6.7a	9.8a	7.4a	11.0a	12.1a	.0366
Km	280 ±120a	121 ±13a	118 ±16a	115 ±10a	150 ±27a	.0310
Light compensation	32.4a	5.8a	15.4a	16.6a	11.1a	.4054
Apparent quantum yield	.0249b	.0820a	.0589ab	.0892a	.0810a	.0034
Dark respiration	.9±0.6a	.5±0.3a	1.0±0.3a	1.7±0.3a	1.0±0.5a	2718

[a] The P-value from an analysis of variance based on parameters fitted to each individual tree.
[b] Parameters for a given species were estimated with data pooled from all photosynthetic measurements collected from two or three trees for that species. Three CBO, three SCO, and two trees for the other species were measured.
[c] All parameters are in μmol m^{-2} s^{-1} except that apparent quantum yield is in mol C mol^{-1} quanta.
[d] Parameters in a row followed by the same letter are not significantly different at the α = 0.05 experimentwise error rate based on Bonferroni pairwise comparisons.

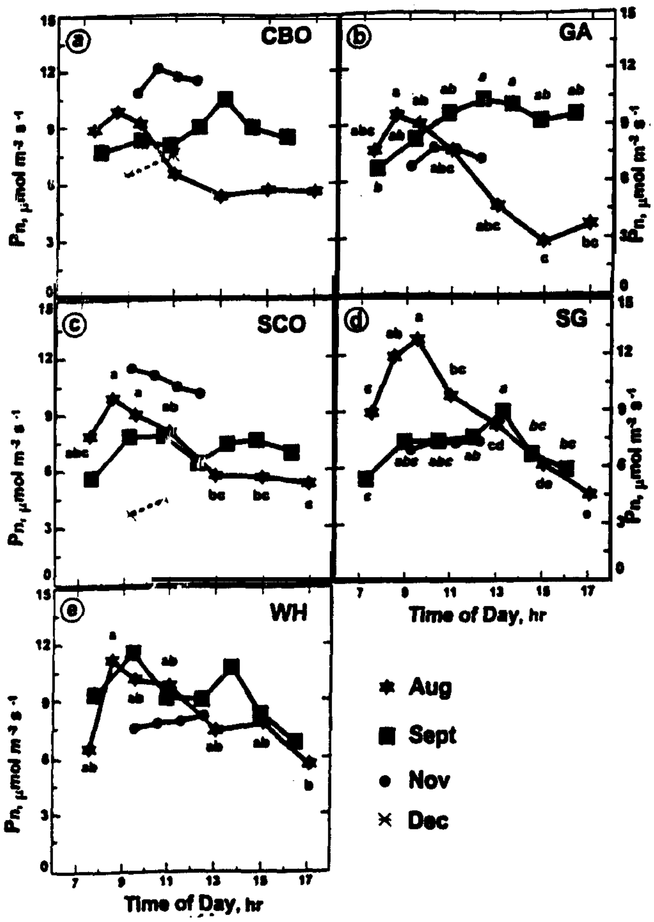

Figure 1—Daily photosynthesis (Pn) of five hardwood species in a mixed stand established in February 1994. Photosynthesis (Pn) measurements were made in 1998. The same leaves were measured throughout the day with a 1600 μmol per m^2 per s photosynthetic photon flux density. (a) cherrybark oak (CBO); (b) green ash (GA); (c) swamp chestnut oak (SCO); (d) sweetgum (SO): (e) water hickory (WH). Statistical analysis was performed on time of day for August and September within each species using a randomized block design where block was tree. Symbols without a letter were not significantly different at the a = 0.05 level.

(fig. la, 1c). Peak September SCO Pn was lower than that of CBO during this month. December SCO Pn was 50 percent lower than December CBO Pn (fig. la, 1c).

Of all species Pn measurements in August, SG had the most active Pn (fig. 1). its peak Pn occurred before 10 am. The 5 pm Pn then decreased to 33 percent of the peak (fig. 1d). By mid-September, the majority of SG in this stand began to discolor. its daily peak Pn decreased from 13 μmol per m^2 per s in August to 8.5 μmol per m^2 per s in September (fig. la, 1c). By mid-November, most SG and GA leaves in the stand have completely abscised. Values of November Pn for GA, SG, and WH that still had some leaves ranged between 7 and'9 μmol per m^2 per s (fig. 1 b, 1 d, 1 e). Unlike GA or SG, WH had similar Pn among the months.

Storage of GA leaves at -80 °C resulted in a dark discoloration. For this reason, the levels Of GA chl Presented in table 2 are probably under estimated. in August, SG leaves had the highest levels of chlorophyll (chl) per Unit area and the largest leaf specific fresh weight (LSW) among ail species (table 2). in September, chi contents increased for CBO and WH; remained the same for SCO; and decreased slightly for SG (table 2). Compared to September, November CBO and SCO chl contents increased whereas SG and WH chi decreased. The chi a to b ratios ranged from 2.07 to 3.15 and did not differ significantly among species (table 2). There were no changes in the LSW for all five species over the growing season (table 2).

DISCUSSION

To our best knowiedge, this study is the first to report Pn of these hardwood species in an artifidaiiy regenerated, mixed stand. Similarities among most parameters of the light response curves for each species indicated that ail five species are equally responsive to light photosynthetically. In this study all Pn measurements were conducted on leaves of the outside canopy. Light response curves might be different if leaves inside the canopy were also measured.

Ail species, except for CBO, had a dear daily Pn pattern in August (fig. 1). These patterns were similar among species. Furthermore, the August daiiy Pn patterns of all five species windded with the summer drought (fig. t). There was little precipitation in July and August of 1998. Low Pn in the afternoon was mainly caused by stomatal closure (data not shown). Apparently under drought conditions, these trees photosynthesize actively early in the morning and then conserve water in the afternoon by dosing the stomata. By mid-September, however, several major precipitation events were receded on this study site. No such drastic decreases in Pn (fig. 1) or stomatal conductance (date not shown) were observed in the afternoon. For most species, the daily peak Pn in September also occurred later in the morning as compared to August data.

in this study, each species had its characteristic seasonal Pn pattern. For example, WH photosynthesized similarly throughout the growing season. However, SG was most active in Pn in August but its Pn decreased the most among the five species in September, On one hand, high Pn values for SG in August were doseiy associated with its high chi contents. On the other hand, the summer drought of 1998 might have accelerated SG leaf discoloration thereby reducing chl contents in September. Sun9 and others (1994) reported 9-year-old SG trees grown in sludge treated soil still had green canopy and maintained active sucrose metabolism in stems toward mid-October. However, nonfertilized SC trees discolored and their sucrose metabolism decreased sharply after August, just as in the current study. Maintenance of green leaves and thus active sucrose metabolism late in the growing season was shown to increase volume growth for sludge-grown SG as compared to the control SG (Sung and others 1994). Thus, another component relating to competitive strategies of certain tree species may be the amount of photosynthetically active leaf retention late in the gmwing season.

Table 2—Leaf chlorophyll a and b (chl) contents, chl a/b ratios, and leaf specific fresh weight (LSW) (and standard error) for cherrybark oak (CEO), green ash (GA), swamp chestnut oak (SCO), sweetgum (SG), and water hickory (WH) in a mixed stand

Parameters	CBO[a]	GA	SCO	SG	WH	P-value[b]
			August			
Chl, mg g^{-1}	2.13±0.07a[c]	1.46fo.21 a	1.95±0.11a	2.24±0.21a	2.23±0.16a	0.0331
Chl a/b	2.75±0.06a	2.69±0.15a	2.37±0.21a	2.07±0.28a	2.29±0.09a	.0985
Chl, mg m^{-2}	304.0±5bc	229.0±25c	296.0±26bc	472.0±12a	374.0±32ab	.0002
LSW, g m^{-2}	144.0±3b	158.0±9b	151.0±8b	213.0±14a	167.0±3b	.0010
			September			
Chl, mg g^{-1}	2.2[illegible]±0.24a	1.46±0.23a	2.23±0.69a	1.80±0.17a	2.71±0.17a	.2170
Chl a/b	3.1[illegible]±0.33a	3.05±0.09a	2.85±0.25a	2.29±0.27a	2.60±0.14a	.1367
Chl, mg m^{-2}	356.0±48a	249.0±53a	310.0±68a	432.0-a	498.0±111a	.1939
LSW, g m^{-2}	159.0±8ab	168.0±9ab	146.0±12b	239.0±17a	180.0±28ab	.0224
			November			
Chl, mg g^{-1}	2.30±0.21a	1.39a	2.29±0.30a	1.64±0.10a	2.09±0.21a	2204
Chl a/b	2.75±0.04a	2.58ab	3.07±0.12a	2.07±0.11b	2.30±0.02b	.0004
Chl, mg m^{-2}	471.0±59a	266a	405.0±53a	325.0±11a	392.0±41a	2712
LSW, g m^{-2}	203.0±11a	191a	177.0±4a	199.0±6a	190.0±17a	.5529
			December			
Chl, mg g^{-1}	1.78±0.31a	—	1.62±0.18a	—	—	.6890
Chl a/b	2.85±0.04a	—	2.93±0.03a	—		2109
Chl, mg m^{-2}	340.0±51a	—	274.0±25a	—	—	.3083
LSW, g m^{-2}	193.0±9a	—	171.0±16a	—		.3056

[a] 1-0 seedlings were transplanted in February 1994. Same leaves used for daily photosynthesis measurements were harvested at the end of the day for chl analysis. One GA and two SG trees were measured in November. Only CBO and SCO were measured in December.

[b] The P-value from an analysis of variance.

[c] Parameters in a row followed by the same letter are not significantly different at the a = 0.05 experimentwise error rate based on Bonferronipairwise comparisons.

Cherry bark oak and SC0 are two examples of late season Pn. In contrast to SG, CBO and SCO increased their Pn and chl contents from August to November. The ability of CBO to maintain green leaves and photosynthesize well into the winter may enable this species to be competitive in a mixed stand. It was reported that in December both stem and taproot cambial tissue of second year nursery-grown CBO seedlings had low activities of sucrose metabolizing enzymes (Sung and others 1995). Thus, with active Pn and almost no diameter growth occurring in CBO stem and taproot in December, photosynthates probably are used for food reserves in stems and taproots and possibly for continuous lateral root development. We will follow seasonal and daily Pn in 1999 beginning in the spring to confirm the results obtained in 1998.

ACKNOWLEDGMENTS

This research was funded by Department of Energy grant DE-AI09-76SR00870 via Savannah River Natural Resource Management and Research Institute.

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