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# PHOTOSYNTHETIC POTENTIAL OF LAUREL OAK SEEDLINGS FOLLOWING CANOPY MANIPULATION

**K.W. McLeod and M.K. Burke**[1]

**Abstract**—The theory of forest gap dynamics predicts that replacement individuals are those that can most fully use the light environment of a gap. Along the Coosawhatchie River in South Carolina, 12 canopy gaps were identified in a bottomland hardwood forest dominated by laurel oak (*Quercus laurifolia* Michaux). Each gap was enlarged to a uniform size by girdling large trees and removing smaller ones. In each gap, some plots were trenched, while some plots were left intact. Other plots, located in adjacent closed canopy forest, were treated identically. Photosynthetic light response curves of laurel oak seedlings were determined after gap enlargement. Seedling photosynthetic rates were significantly greater in gaps than under closed canopy for all light levels ≥ 150 µmol/m$^2$ per second. Maximum photosynthetic rates were approximately 50 percent of that for seedlings growing in full sunlight. Trenching, which eliminates root competition and increases availability to soil resources, did not affect photosynthesis. Based on these observations, laurel oak seedlings growing in gaps should have greater photosynthesis than those existing under full canopy.

## INTRODUCTION

It is difficult to regenerate bottomland hardwood forests with desirable tree species following clearcutting. We have a limited understanding of conditions that improve regeneration of desired tree species, although it is generally accepted that oak reproduction should be well established before the overstory is removed (Aust and others 1985). Opening of the canopy has also been suggested to encourage growth of advance regeneration (McKevlin 1992) particularly when fairly large (≥ 1.3 cm diameter at ground level) seedlings exist (Sander 1971). However, large oak seedlings are rare in bottomland hardwood forests due to decreasing shade tolerance of developing oak seedlings (Carvell and Tyron 1961). As well, canopy openings stimulate growth of potentially competing plant species, such as intolerant trees, grasses, sedges, and forbs (Billups and Burke 1999). As a result, gaps that provide sufficient sunlight for seedling establishment and survival may be necessary to ensure sufficient oak regeneration prior to harvest.

Exacerbating difficulties in bottomland regeneration is this system's typically unpredictable hydrology. Bottomland tree species produce a mast seed crop only every few years, and when seed is abundant the site hydrology must be favorable for seed germination and seedling establishment, the occurrence of which is rare in nature. These factors combined with low light levels typical of a bottomland hardwood forest floor result in very limited growth of advance regeneration. Conversely, light is not a factor in clearcut habitats, but a rise in the water table may be expected due to a reduction in evapotranspiration demand (Sun and others 2001). Even if an adequate number of tree seedlings are established, young plants of even flood tolerant species are highly susceptible to stresses associated with flooding (Kozlowski 1997). For these reasons, advance regeneration stock may be inadequate, may not be tall enough to compete with less desirable plant species that are favored under cleared conditions, or may not be tall enough to withstand site flooding. Due to heterogeneity of environmental conditions, it is very difficult to schedule harvesting to coincide with years where site conditions are conducive to regeneration of desirable slow and intermediate tree species prior to harvest.

Although regeneration of woody plants in floodplain forests has received some attention in the literature (DeSteven and Sharitz 1997, Jones and others 1994, Streng and others 1989), little is known about the influence of canopy density on the relative success of seedlings of bottomland hardwood tree species. For example, gap theory suggests that breaks in the forest canopy may allow advance regeneration to develop at an accelerated rate due to enhanced light conditions. Gaps can either form slowly from trees dying or rapidly from stem breakage or tree fall. The extent and persistence of the gap is regulated by the size of the original canopy tree, the amount of damage inflicted upon adjacent trees, and the lateral growth rate of neighboring canopy trees into the gap. Species that can acclimate and most fully use the new light environment of a gap will have a competitive advantage and become replacement individuals in the canopy.

When gaps are formed in the forest canopy, gaps also are created in living root systems, thereby enhancing availability of soil moisture and nutrients, in addition to light. Of course, these flushes of resources may enhance growth of other plants, such as grasses, forbs and less desirable tree seedlings (Billups and Burke 1999), which can compete with seedlings of more slow-growing shade tolerant tree species. Therefore, moderately shade tolerant species would need to be released within several years if they are to survive (Johnson and Shropshire 1983) and grow to a competitive size. Under closed canopy conditions, advance regeneration can be released by removing undesirable midstory and understory vegetation (McKevlin 1992). With

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this release, advance regeneration may have a better chance of competing with fast growing shade-intolerant species that tend to quickly become established after harvest.

After gaps are formed, leaf morphology and physiology of advanced regeneration will likely change since the light environment will be drastically altered from closed canopy conditions (< 10 percent of full sunlight) towards full light conditions (2000 µmol/$m^2$ per second). In some species these morphological and physiological changes can occur very rapidly (days to weeks), while for other species with more fixed growth patterns may require production of new leaves (Kramer and Kozlowski 1979, Logan 1970, Patterson 1975). Logan (1970) suggests that those species that can change rapidly would have a competitive advantage in a wide range of habitats differing in light intensity.

The present study was designed to address the following questions: (1) Do laurel oak seedlings in larger canopy gaps, such as those occurring in more mature bottomland hardwood forests, have different ability to use light than those seedlings under an intact canopy? If so, then what physiological mechanism enhances their ability to use the higher light intensity? and (2) Do belowground resources, altered by gap creation and/or trenching, affect the photosynthetic response of laurel oak seedlings?

## Description of Study Site

The Coosawhatchie Bottomland Ecosystem Study site is located near Coosawhatchie in Jasper County, SC, USA (32° 40' N and 80° 55' W) and is approximately 320 ha of bottomland hardwood and swamp forest along the Coosawhatchie River. The site is owned and managed by Westvaco Corporation. The Coosawhatchie River is a fourth-order, anastomosing blackwater river that flows into the estuarine Broad River near Point South, SC. Geomorphology, soils, hydroperiod, vegetation, and vegetation dynamics of the site have been described in detail by Burke and Eisenbies (2000) and Burke and others (2003). The laurel oak community has a basal area of 40.7 ± 1.4 $m^2$/ha (mean ± 1 S.E.) (Burke and others 2000) and was logged as recently as 1950 (King and others 2000). Naturally-formed gaps on the site were small, with a mean of 216.1 $m^2$ with a median gap size of 187.8 $m^2$, about half to two-thirds of the natural gap size in bottomland hardwood forests of the Cache River in Arkansas (King and others 2000). In addition, total area of newly formed gaps on the Coosawhatchie site (0.02 percent) was less than the 0.5 to 1.3 percent reported for previous studies of similar forest types (King and others 2000, Qinghong and Hytteborn 1991, Runckle 1985, Van der Meer and Bongers 1996).

Few laurel oak *(Quercus laurifolia* Michaux) seedlings were found during summer of 1995. However, 1995 was a good mast year and 1996 was a dry summer, which resulted in abundant establishment of oak seedlings (Billups and Burke 1999). Seedlings were relatively more abundant in gap habitats (≥ 25/$m^2$), but about the same size in both habitats, probably because naturally formed gaps did not significantly increase light levels (Billups and Burke 1999).

## MATERIALS AND METHODS

In July 1998, all natural gaps in the study site were geo-located, length of their axes measured, orientation of the long axis documented, and abundance of seedlings and percent cover of other vegetation was estimated.

Due to the relatively small size of gaps, it was decided for this study that these gaps must be enlarged to get more light penetration to the forest floor. Using twice tree height as the minimum gap size needed for a ground vegetation response (Collins and Pickett 1987), 12 gaps, 6 in each of 2 stands, were selected for enlarging. In late July, a 30 m line running east-west was established with the original gap-making tree in the center. Using this tree as center and the established line, a half circle with a 15 m radius south of the line was marked as the area in which to kill/remove the remaining midstory and overstory. Midstory trees were cut off at ground level and removed, while canopy trees (d.b.h. ≤ 30 cm) were girdled twice each. Gap size was now approximately 350 $m^2$. Enlarging the gap to the south allowed for the maximum light penetration due to the solar angle.

Four 1 m x 1 m subplots were established at random distances along the east-west line in each gap, two subplots east of center and two west. Four additional subplots were established 50 m from the midpoint of the gap edge in a random direction to establish paired non-gap plots for each gap. Non-gap areas were under full canopy cover. One subplot on either side of the gap-making tree or non-gap location was randomly chosen for trenching to eliminate root activity of midstory and overstory trees. In August, 1998, using a power trencher, 30-cm-deep trenches were dug approximately 25 cm outside the actual 1 m x 1 m subplot to minimize edge disturbance. Aluminum flashing was inserted into the trench to a depth of 30 cm, and the trench was backfilled. A previous study had determined that almost no roots penetrated below 30 cm due to high bulk density of the lower soil. A schematic diagram of a gap with associated subplots in shown in figure 1.

Seedlings were left to acclimate to the new light conditions during the rest of the 1998 growing season. The relationship between light intensity and photosynthesis was determined for a selected laurel oak seedling in each subplot on July 7, 8, 9, or 27, 1999. Seedlings in all combinations of trench/no trench and gap/no gap, associated with an individual gap were measured on a single day, but four days were required to measure seedlings in all gaps. Photosynthesis, transpiration, stomatal conductance, and internal leaf $CO_2$ concentration were measured with a LI-COR 6400 Portable Photosynthesis System using the LightCurve automatic program at light intensities of 1200, 900, 600, 300, 150, and 75 µmol/$m^2$ per second provided by a supplemental red/blue light source at a constant $CO_2$ concentration of 400 µmol/mol and a leaf temperature of 30 °C. Photosynthesis was first measured at the highest light intensity, followed by the next highest, and so forth for an individual seedling.

Twelve pairs (trench/no trench) of seedlings in gap and non-gap plots, six in each stand were measured in 1999. In late 1999, one stand was clearcut and seedling plots were

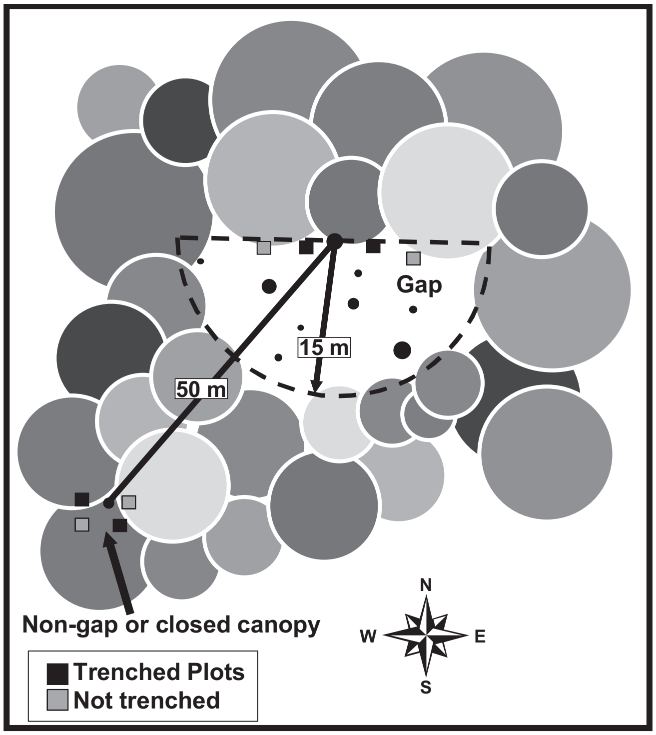

Figure 1—Schematic diagram of enlarged gap with associated subplots in the gap and intact canopy area.

destroyed and could not be relocated. In control or uncut forest stand, seedling photosynthesis was measured on October 3 and 4, 2000, but for only six pairs of plots in this one stand. Photosynthesis of four randomly selected laurel oak seedlings growing in full sunlight since the harvest in the clearcut site was also measured to determine potential maximum rates. We were unable to identify the precut light conditions of these seedlings, but they had been exposed to full sunlight for at least one growing season prior to measurement. For these open grown seedlings, photosynthesis was also measured at 1500 and 1800 μmol/m$^2$ per second.

To quantify ambient light conditions of the seedlings, photosynthetic active radiation (PAR) was measured at the time of each photosynthesis measurement. In August 1999, hemispherical photographs were taken 1 m above the ground at the center of the east-west line in the gap and centered among the four subplots outside the gap to determine openness of gap versus closed canopy plots. Photos were analyzed for percent canopy openness by GLA software (Frazer and others 1999). There was considerable variability of light conditions over each subplot within enlarged gaps, so on October 3, 2000 hemispherical photographs were taken at 1 m above the ground centered over each subplot.

Rates of photosynthesis, transpiration, stomatal conductance, and internal leaf CO$_2$ concentration were analyzed by analysis-of-variance for main effect [site (to be clearcut versus uncut), gap (in gap versus under full canopy cover), and trenching (trench versus not trenched)] and interaction effects by individual light level in each year (SAS 1999/2000).

## RESULTS AND DISCUSSION

Mean gap openness in both sites were similar after enlargement of the original gaps (14.0 vs. 13.7) (table 1), although the range in individual gap openness was quite large. The most open gap was 2.5x more open than the least open gap in summer of 1999 (19.8 vs. 7.1). Expanded gaps were about the same size as natural gap size in the Cache River system (King and others 2000). Some of the more open non-gap sites had more light than gaps that had not been opened very fully. In 1999, almost 2 years after the gaps were enlarged, some trees which were girdled still had not died or fully lost their leaves. With these highly variable light levels between sites and even between gap and non-gap, acclimation of photosynthesis may be difficult to observe.

Therefore, mean canopy openness was again measured in 2000 but measurements were centered over individual gap subplots of only the control (uncut) site. The other site had already been harvested. Variability among different gaps in the 2000 data was somewhat reduced from the 1999 data and showed a similar trend among gaps in the control stand (table 2). Values indicate that the amount of light penetrating to seedlings was less in 2000 than in 1999.

Ambient light intensity was measured external to the LICOR 6400 leaf chamber with a PAR sensor. These measures may vary due to instantaneous changes in cloud cover and shadowing caused by the daily path of the sun. These

**Table 1—Canopy openness[a] and light intensity in canopy gaps and in adjacent undisturbed intact canopy forest in 1999**

| | | Canopy openness[b] | | Light intensity[c] | |
|---|---|---|---|---|---|
| | | *mean* | *range* | *mean* | *range* |
| Uncut (control) | Gap | 14.0 | 7.8 – 19.8 | 130.3 | 35.6 – 225.4 |
| Uncut (control) | Nongap | 8.0 | 5.1 – 11.1 | 32.9 (73.5)[d] | 24.5 – 49.0 (276.3)[e] |
| To be clearcut | Gap | 13.7 | 7.1 – 19.6 | 141.5 (239.8)[d] | 65.2 – 287.6 (731.3)[e] |
| To be clearcut | Nongap | 11.3 | 9.7 – 12.6 | 61.8 | 31.8 – 134.8 |

[a] Openness values are percent of open sky visible.

[b] Determined by hemispherical photographs.

[c] Determined by a PAR quantum sensor (μmol/m$^2$/s).

[d] Mean with outlier included.

[e] Outlier value.

**Table 2—Openness of the canopy gaps of the uncut area in 1999 and 2000**

| | Canopy openness | | |
|---|---|---|---|
| Gap number | 1999[a] | 2000[b] | |
| | *mean* | | *range* |
| 1.2 | 10.6 | 8.8 | 7.4 – 10.7 |
| 2.3 | 16.8 | 9.6 | 7.7 – 9.9 |
| 3.3 | 7.8 | 6.8 | 6.1 – 7.5 |
| 3.5 | 15.8 | 8.5 | 7.8 – 9.6 |
| 4.2 | 13.2 | 9.3 | 7.3 – 11.0 |
| 4.4 | 19.8 | 1.6 | 7.5 – 13.8 |
| Mean ± 1 S.D. | 14.0 ± 4.4 | 9.1 ± 1.6 | — |

Openness values represent the relative amounts of open sky visible in hemispherical photographs.

[a] Value from a single measurement in the center of the linear portion of the semicircular plot.

[b] Values from the four subplots in each semicircular plot.

external changes would not affect photosynthesis since these measurements were made with artificial illumination. PAR measurements generally confirmed the light environments shown in hemispherical photographs. Mean light intensity in non-gap plots was 67 µmol/m$^2$ per second, while that in gaps was 185 µmol/m$^2$ per second (table 1).

Enlarged gaps were 7 times larger than gaps created in lodgepole pine forest that led to altered nutrient cycling patterns in the soil (Parsons and others 1994a, 1994b). Thus, gap enlargement and subsequent trenching should have created environments where significantly altered belowground processes were occurring.

In 1999, photosynthetic rates for laurel oak seedlings were significantly greater in gaps than under closed canopy at all light levels except for 75 µmol/m$^2$ per second (table 3 and fig. 2). During that same year, photosynthetic rates differed between controls, and the stand to be clearcut, except at the highest (1200 µmol/m$^2$ per second) light level. Difference between stands represent some differences in abiotic environment of the two stands that was not readily apparent. There was not a significant gap x site interaction, therefore main effects were not confounded.

Trenching had no effect on seedling photosynthetic rates in either year (table 3). Evidently in this fertile bottomland site, competition for soil nutrients and water was not great. Trenching, which both decreases root competition from other trees and increases root mortality and nutrient release, did not stimulate seedling photosynthesis. This response may have been moderated by the relative drought during 1999 and 2000 during which time root production in the laurel oak forest type was very low (Burke and Chambers 2003). This lack of response to trenching was consistent with the conservative metabolic responses usually observed for well adapted, K-selected species, in contrast to the boom-or-bust response of species growing in habitats marginal for that species (Vaitkus and McLeod 1995). No interaction terms among these factors (gap, site, or trenching) were statistically significant in either year.

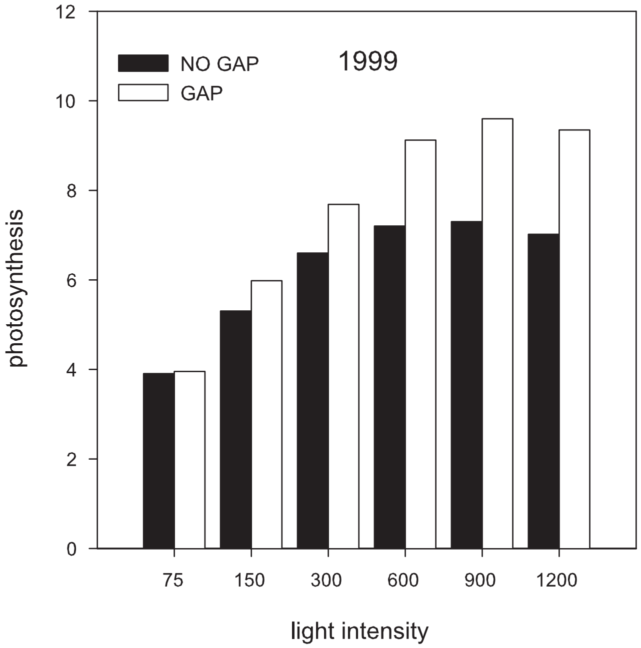

Figure 2—Net photosynthesis (µmol/m$^2$/s) of laurel oak seedlings at different light intensities (µmol/m$^2$ per second) in 1999. Seedlings had been growing in forest canopy gaps for at least 2 years (GAP), while other seedlings were growing under an intact canopy (NO GAP). Sample size was 24.

Other physiological parameters which are measured include the highly related conductance, transpiration and

**Table 3—Probability values for the effects of site, gap, and trenching on photosynthetic rate of laurel oak seedlings**

| | Light level | | | | | |
|---|---|---|---|---|---|---|
| | 75 | 150 | 300 | 600 | 900 | 1200 |
| | *µmol/m$^2$ per second* | | | | | |
| | | | **1999** | | | |
| Site | 0.0001 | 0.0002 | 0.0034 | 0.0106 | 0.0364 | NS |
| Gap | NS | 0.0314 | 0.0102 | 0.0001 | 0.0001 | 0.0001 |
| Trench | NS | NS | NS | NS | NS | NS |
| | | | **2000** | | | |
| Gap | NS | 0.0319 | 0.0099 | 0.0076 | 0.0053 | 0.0067 |
| Trench | NS | NS | NS | NS | NS | NS |

NS = nonsignificant.

All two and three way interactions were not statistically significant.

internal leaf $CO_2$ concentration. As conductance increases, photosynthesis and transpiration usually increase since conductance is a measure of gas exchange rates of $CO_2$ and water vapor into and out of a leaf. As the rate of photosynthesis increases, internal leaf $CO_2$ concentration decreases since diffusion of $CO_2$ into the leaf can not keep up with depletion of $CO_2$ as it is fixed at higher photosynthesis rates. Significant differences in stomatal conductance, transpiration and internal leaf $CO_2$ concentration were consistent with those observed for photosynthesis (table 4).

Photosynthesis was similarly affected by seedling location within or outside of a gap in 2000 (fig. 3 and table 3). Transpiration, stomatal conductance, and internal leaf $CO_2$ concentration were rarely affected by seedling location in 2000 (data not shown). Absolute rates of photosynthesis between years were also similar, but these rates were approximately 50 percent of maximum photosynthesis of seedlings growing in full sun in the adjacent clearcut site (fig. 3). Trenching and the interaction of trenching with gap did not have statistically significant effects on seedling photosynthetic rates in 2000 (table 3).

Low photosynthesis rates have been linked to decreased root production and decreased survival during drought (Bourdeau and Laverick 1958, Kramer and Decker 1944). Drought in 1999 and 2000 and resultant low river water levels would have made adequate root production a necessity. Higher photosynthetic rates of seedlings in a gap would allow greater root production and greater ability to acquire water precisely at a time when water was most needed. These differences may be responsible for lower survival rate of seedlings under the closed canopy. (personal observation. M.K. Burke).

Light response curves illustrate several important general characteristics of photosynthesis. Maximum rates of photosynthesis increased as the light environment in which seedlings acclimated was greater. With this, the light levels at which light saturated photosynthesis occurred also increased (e.g., from 227 to 379 μmol/m$^2$ per second for non-gap and gap seedlings in 2000, respectively, (table 5). However, light saturation for gap seedlings was still much lower than for seedlings growing in full sun (1189 μmol/m$^2$ per second). Quantum use efficiency (determined as the slope of the increase in photosynthesis between 75 and 150 μmol/m$^2$ per second light) also increased from non-gap to gap- to full-sun-grown seedlings (table 5).

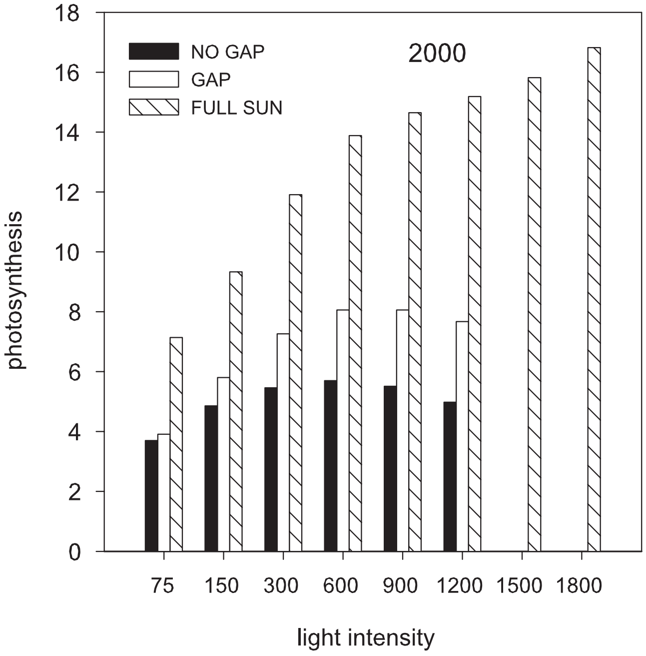

Figure 3—Net photosynthesis (μmol/m$^2$ per second) of laurel oak seedlings at different light intensities (μmol/m$^2$ per second) in 2000. Seedlings had been growing in forest canopy gaps for at least 2 years (GAP) while other seedlings were growing under an intact canopy (NO GAP). FULL SUN seedlings had been growing in a clearcut site following the 1999 growing season. Sample size was 12 for gap and no gap seedlings and 4 for seedlings in full sun. Seedlings in full sun were not compared statistically to those in gaps or under full canopy.

**Table 4—Statistically significant effects on physiological parameters measured in 1999**

| Light intensity | Photosynthesis | Conductance | Transpiration | Internal leaf $CO_2$ concentration |
|---|---|---|---|---|
| *μmol/m$^2$/s* | *μmol/m$^2$/s* | - - - - - - - - - -*mol/m$^2$/s*- - - - - - - - - - | | *μmol/mol* |
| 75 | Site (UN > CC) | Site (UN > CC) | Site (UN > CC) | None |
| 150 | Site (UN > CC)<br>Gap (G > NG) | None | Site (UN > CC) | None |
| 300 | Site (UN > CC)<br>Gap (G > NG) | None | Site (UN > CC) | Gap (NG > G) |
| 600 | Site (UN > CC)<br>Gap (G > NG) | GAP (G > NG) | Gap (G > NG) | Gap (NG > G) |
| 900 | Site (UN > CC)<br>Gap (G > NG) | GAP (G > NG) | Gap (G > NG) | Site (CC > UN)<br>Gap (NG > G) |
| 1200 | Gap (G > NG) | None | None | Site (CC > UN)<br>Gap (NG > G) |

UN = site to be left uncut; CC = site to be clearcut; G = Gap; NG = no-gap.

Differences were determined by three-way ANOVA for sites, gap vs. no-gap, trench vs. no trench and for all two- and three-way interactions. Only site and gap vs. no-gap significantly affected these variables.

**Table 5—Summary of characteristics derived from light response curves for laurel oak seedlings**

| Year | Site | Light condition | Light saturation | Quantum efficiency |
|---|---|---|---|---|
| | | | *μmol/m² per second* | *mol $CO_2$/mol PAR* |
| 1999 | Both sites combined | Nongap | 341 A | 0.019 A |
| | | Gap | 491 B | 0.027 B |
| 2000 | Control (uncut) | Nongap | 227 A | 0.016 A |
| | | Gap | 379 B | 0.025 B |
| | Clearcut | Full sun | 1,189 | 0.029 |

Different upper case letters within a year and characteristic indicate significant differences at the 5 percent level between seedlings in gap verses nongaps.

As the relationship between conductance and photosynthesis changes, photosynthetic capacity of seedlings will be altered. At low conductance values, photosynthesis and conductance are linearly related: photosynthesis is limited by the stomatal conductance and photosynthesis is said to be stomatal-limited. Once stomata are fully open, the rate of photosynthesis is regulated by the ability of chloroplast to fix $CO_2$. In this study, higher maximum photosynthesis values at similar stomatal conductances implies internal leaf modifications. Leaves of the full sun seedlings were most modified, and leaves of non-gap-grown seedlings were least modified (figs. 4 and 5). The relationship between photosynthesis and stomatal conductance for seedlings in gaps and under intact canopy were similar during the two years. At comparable conductances, photosynthesis of full-sun seedlings in 2000 was 1.7 and 1.5 times that of seedlings growing under a full canopy or in a canopy gap, respectively (fig. 5), suggesting that the ability of laurel oak to acclimate to light may be substantially greater than that documented here in experimentally enlarged gaps.

## CONCLUSIONS

Exposure to higher light levels in gaps led to greater photosynthesis rates of seedlings at light levels ≥150 μmol/m² per second with apparent changes in the relationship between photosynthesis and conductance. Laurel oak seedlings, previously exposed to high light levels in canopy gaps, would have greater photosynthetic rates than seedlings from under an intact canopy and hence probably have greater size before any harvesting operations. Elimination of root competition in trenched plots did not increase seedling photosynthetic response in gaps. The initial advantage in size and photosynthetic potential could provide a competitive advantage for these seedlings following canopy disturbances that drastically change the light environment.

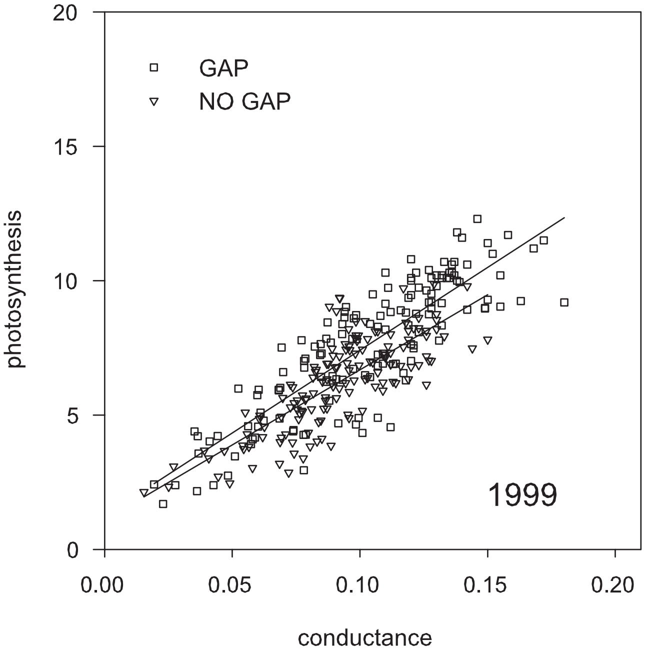

Figure 4—Relationship between net photosynthesis (μmol/m² per second) and stomatal conductance (mol/m² per second) in 1999 for seedlings that had been growing in enlarged canopy gaps for most of two growing seasons (gap) and those growing under an intact canopy (no gap).

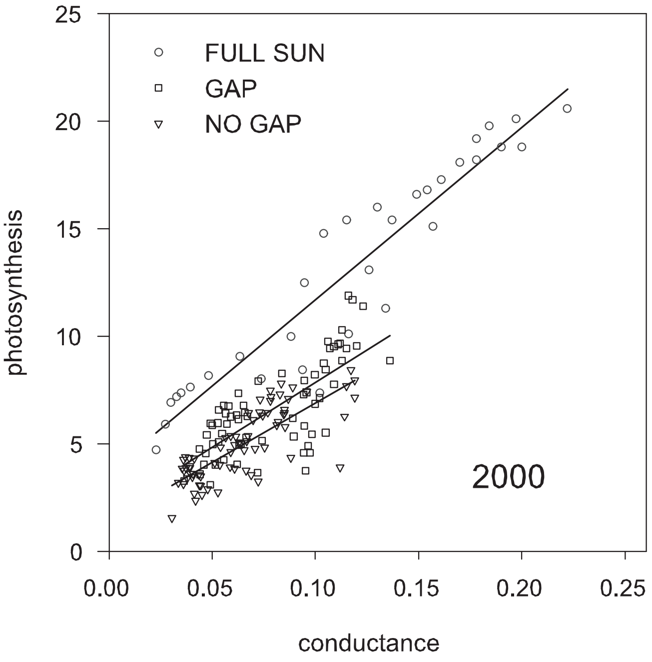

Figure 5—Relationship between net photosynthesis (μmol/m² per second) and stomatal conductance (mol/m² per second) in 2000 for seedlings growing under an intact canopy (no gap), in canopy gaps, and in full sun.

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**Description:** Ninety-two papers and thirty-six poster summaries address a range of issues affecting southern forests. Papers are grouped in 15 sessions that include wildlife ecology; fire ecology; natural pine management; forest health; growth and yield; upland hardwoods - natural regeneration; hardwood intermediate treatments; longleaf pine; pine plantation silviculture; site amelioration and productivity; pine nutrition; pine planting, stocking, spacing; ecophysiology; bottomland hardwoods - natural regeneration; and bottomland hardwoods—artificial regeneration.