

GROWTH AND PHOTOSYNTHETIC RESPONSES OF THE FEDERALLY ENDANGERED SHRUB, *LINDERA MELISSIFOLIA* (LAURACEAE), TO VARIED LIGHT ENVIRONMENTS¹

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Photosynthetic, morphological, and growth responses to light environment can be useful measurements to determine favorable habitat conditions for the conservation of endangered species. For *Lindera melissifolia* (Walt.) Blume, we compared morphological and photosynthetic responses under natural and controlled light regimes, and growth under three light treatments: 100%, 42%, and 19% full sunlight. Typical sun–shade morphological responses to decreasing light levels included decreased stomatal density, increased specific leaf area, and increased leaf area ratio. Photosynthetic capacity ($3\text{--}6 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) was consistent with other shade-tolerant species. Light-saturated rates of photosynthesis of experimental plants increased with increasing light up to 42% sunlight, but declined at 100% sunlight. The 100% light treatment also resulted in lower plant biomass, primarily from a reduction in root biomass. Results indicate that canopy conditions at levels below 40% sunlight are optimal for plant growth and should be considered in management and reintroduction efforts for this species.

Key words: endangered species; Lauraceae; *Lindera melissifolia*; morphological plasticity; optimal habitat; photosynthetic light response; pondberry; shade tolerance.

Light is one of the major environmental factors influencing growth and distribution of plant species (Boardman, 1977; Lambers et al., 1998). Insufficient light levels may stress plants by limiting photosynthesis, resulting in reduced net carbon gain and plant growth. Conversely, high light levels may damage the photosynthetic apparatus (Lambers et al., 1998). Therefore, plants have developed various strategies to cope with these stresses, such as leaf plasticity for sun/shade acclimation, light avoidance, and photoprotective means to dissipate excess energy (Demmig-Adams and Adams, 1996). Differences in leaf morphology, anatomy, and physiology have been well documented for species adapted to sun or shade environments (Boardman, 1977; Björkman, 1981; Givnish, 1988).

Measuring photosynthetic and morphological responses can reveal information regarding tolerance and growth of a species to a range of light conditions and has been useful in agriculture, ecology, forestry, and horticulture (Loach, 1967; Boardman, 1977; Dean et al., 1982; Givnish, 1988; Walters et al., 1993; Baskauf and Eickmeier, 1994; Walters and Reich, 1996; Olsen et al., 2002; Valladares et al., 2002). This approach can also be useful in assessing optimal habitat conditions for the conservation of rare species found in only a few populations or in extremely varied conditions (Smith et al., 1993). *Lindera melissifolia* (Walt.) Blume, pondberry, is a good example of a federally endangered species (USFWS, 1986) that occurs across a wide range of light conditions from extreme shade to full sun, but the optimal conditions for growth remain unclear (Tucker, 1984; Devall et al., 2001).

Successfully managing populations of rare and endangered

species requires information regarding critical life history characteristics and habitat requirements (Brussard, 1991; Schemske et al., 1994). Unfortunately for most endangered species, little information is available on their biological and ecological requirements. Therefore, most active management has been based on untested field observations and not on experimental studies (Given, 1994). For example, inferences regarding the light requirements of *L. melissifolia* appear to depend on the light environment in which a population was observed (e.g., full sun or dense shade). Most populations have been observed under closed overstory canopies of bottomland forests, and consequently, *L. melissifolia* has been considered a shade-tolerant species (Klomps, 1980b; Devall et al., 2001). This species also occurs in an ecotonal habitat, adjacent to fire-maintained uplands and depression wetlands in the southeastern Coastal Plain. The frequency of fire (or absence of fire) in this ecotone influences the degree of canopy cover and thus the light availability. However, little information is available on how this species responds to canopy cover, or if light is an important factor influencing growth and distribution. Therefore, differences in observations have led to conflicting management recommendations (Klomps, 1980a; USFWS, 1993).

For active management of rare species to be most successful, it should be based on valid scientific data regarding their ecological requirements and species biology. The U.S. Fish and Wildlife Service Recovery Plan for Pondberry (1993) states a need for understanding the relationship between light exposure and colony vigor as one of the recovery objectives. Such information is useful in developing management strategies, particularly for determining if removal of competing vegetation will be necessary, and in identifying suitable sites to establish new populations. The purpose of this study was to determine the optimal light requirements for growth of the federally endangered shrub, *L. melissifolia*, by comparing growth, morphological, and photosynthetic responses of plants under natural and controlled light environments. The following questions were addressed: (1) How does *L. melissifolia* adjust photosynthetically to different light environments? (2) Do

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morphology, growth, and biomass differ for plants growing in varied light conditions?

MATERIALS AND METHODS

Study species—*Lindera melissifolia*, pondberry, is a federally endangered, deciduous, aromatic shrub in the Lauraceae. This species is found in seasonally flooded wetlands and is extant in only six states. The type of wetland habitat in which this species occurs varies regionally. In the southeastern Coastal Plain (Georgia, North and South Carolina), pondberry is found along the edges of limestone sinks, ponds, or other depressional wetlands, whereas populations in Arkansas, Missouri, and Mississippi are associated with bottomland hardwood forests. *Lindera melissifolia* is believed to be extirpated from Alabama, Florida, and Louisiana and has always been considered a rare species throughout its historical range (Steyermark, 1949). Currently, the major threats to this species include the loss or alteration of habitat through drainage modification, timber cutting, or the conversion of land for pine plantations, agriculture, and urban development (USFWS, 1993).

Lindera melissifolia is rhizomatous and predominately reproduces asexually. Plants are dioecious, with many populations consisting of one or two clones of a single sex, suggesting little potential for successful sexual reproduction or adaptation to environmental change (Wright, 1990a; USFWS, 1993; Wright, 1994; Godt and Hamrick, 1996). Flower and fruit production is sporadic, and seedling establishment is rarely observed in the wild (Morgan, 1983; Wright, 1990a; USFWS, 1993; Devall et al., 2001; Smith, 2003). Therefore, increasing the vigor of existing populations is critical for species persistence. In addition, the limited distribution and life history characteristics (e.g., dioecism and insufficient recruitment) suggest that reintroduction of new populations will also be necessary for species recovery (Godt and Hamrick, 1996; Devall et al., 2001).

Shade-house experiment—We compared photosynthetic and growth responses of rooted cuttings of *L. melissifolia* across a light gradient in a shade-house experiment. Plant material (90 cuttings), obtained from natural populations in North Carolina, South Carolina, and Missouri, was taken from multiple stems of approximately equal sexes. Cuttings were rooted and grown in pots for two years by Woodlanders Nursery (Aiken, South Carolina USA) in shade-house conditions prior to treatment. Greenhouse tables (230 cm × 90 cm) were arranged in a randomized complete block design of six blocks outdoors at the J. W. Jones Ecological Research Center (Newton, Georgia USA). Each block contained a row of three tables that were randomly assigned one of three light treatments (100%, 42%, and 19% full sunlight). Treatment light levels selected were within the range of the light conditions we measured in existing populations (although not necessarily the lowest light conditions observed). We used neutral density shade cloth over support frames attached to greenhouse tables to achieve desired light conditions. Shade cloth covered all four sides of the frame except for a 15-cm gap from the base of the table to permit air circulation and to help moderate temperature and relative humidity differences among treatments (Loach, 1967). Containerized plants were randomly assigned to tables before bud break on 3 February 2003. Each table contained five containerized plants, stratified according to source to control for locally adapted genotypes or size differences. Plants were watered to maintain field capacity, and all plants were fertilized biweekly using Peters 20–20–20 liquid fertilizer with micronutrients (Scotts Company, Marysville, Ohio USA) at a rate of 5 mL per 4 L of water. We applied Banrot fungicide (Scotts Company) at a rate of 3 g per 4 L of water every 4 wk. Each plant received 237 mL of the fertilizer and fungicide solution at each application.

Light availability of each treatment was determined with the LI-191SA line quantum sensor (Li-Cor, Inc., Lincoln, Nebraska USA). The average of three readings was recorded at plant height on a clear day in April at 1400 hours for each treatment. Photosynthetic photon flux density (PPFD) ± standard error for the three treatments was: 100% sunlight, 1728.67 ± 0.33 ; 42% sunlight, 717.77 ± 0.46 ; and 19% sunlight, $324.27 \pm 2.64 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$.

Light response curves were measured on a leaf area basis with the LI-6400 portable photosynthesis system (Li-Cor, Inc.) using the following irradiance levels: 1000, 700, 500, 300, 150, 80, 20, and $0 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Measure-

ments were made on three randomly selected, well-watered plants from each treatment from each block on separate days. Photosynthetic measurements were taken from approximately 1000 to 1430 hours under clear to partly cloudy skies in mid-May on the second or third fully expanded leaf from the apex (preliminary measurements indicated no evidence of midday stomatal closure). The order of treatments and plants used were randomly selected each day.

To quantify differences in growth response to light environment, a subset of three plants from each treatment replication was randomly selected for morphological and biomass measurements. At the beginning and end of the experiment, we measured final stem height, stem length as the total length of the main stem and all branches, and stem diameter at a marked point at the base of the stem (Montgomery and Chazdon, 2002). To determine mean stomatal density, we used the epidermal leaf peel technique (Winn, 1996). We applied clear nail polish to the abaxial surface of the leaf, allowed it to dry, then peeled the nail polish from the leaf and mounted the peel in distilled water on a microscope slide. We counted the number of stomata in a grid (0.0625 mm^2) under a compound 400× microscope and recorded the average number of stomata observed under three fields of view for each peel.

We determined above- and belowground patterns of biomass allocation by harvesting plants the first week of September 2003 and separating them into leaves (including petioles), stems, and roots. Plant material was dried at 70°C and weighed. We measured leaf area with the LI-3100 area meter (Li-Cor, Inc.) prior to drying. The following measures were calculated for each plant sampled: specific leaf area (SLA) = total leaf area divided by total leaf mass, leaf area ratio (LAR) = total leaf area divided by total plant mass, leaf mass ratio (LMR) = total leaf mass divided by total plant mass, stem mass ratio (SMR) = total stem mass divided by total plant mass, and root mass ratio (RMR) = total root mass divided by total plant mass. Photosynthesis on a leaf mass basis was calculated from SLA values. Response variables used in data analyses were the means of photosynthetic and growth measurements made on three plants.

Field study—Four naturally occurring populations of *L. melissifolia* in the southeastern Coastal Plain were selected for field studies because they occur in habitats that represent the range of light conditions in which this species is found. Populations were located in Baker County, Georgia (Ichauway), Worth County, Georgia (Aultman Forest), and Berkeley County, South Carolina (Francis Marion National Forest; FMNF). Each of these populations occurred along the margin of a seasonally flooded depressional wetland dominated by *Nyssa sylvatica* var. *biflora* (Walt.) Sarg. and *Taxodium ascendens* Brongn. One population was at Ichauway (I-Shade) in the dense shade of *Quercus laurifolia* Michx., *Acer rubrum* L., and *Liquidambar styraciflua* L. Two populations occurred in the Aultman Forest; one (A-Sun) in an herbaceous zone with little canopy cover adjacent to a cypress dome surrounded by pine plantations, and the other (A-Shade) beneath a canopy of *A. rubrum*, *N. sylvatica*, and *T. ascendens*. The fourth population in the FMNF occurred across a gradient of canopy cover including full sun (FM-Sun), intermediate shade (FM-Int), and full shade (FM-Shade). The margin of this wetland is dominated by species such as *Ilex glabra* (L.) Gray, *Persea palustris* (Raf.) Sarg., *Cyrilla racemiflora* L., *Lyonia lucida* (Lam.) K. Koch, *Myrica cerifera* L., *A. rubrum*, *Magnolia virginiana* L., and *Liquidambar styraciflua*. When measurements were taken in June and July 2003, all study populations in Georgia and South Carolina were inundated with water levels ranging from 5.9 to 31.3 cm.

To determine differences in stem and leaf morphology among populations as a response to light conditions, we measured a minimum of 20 plants in each population. All plants within randomly placed 1-m² frames were selected for measurements until the minimum number of plants was sampled. For each plant, we measured stem height and diameter (base of the stem), and two leaves (second or third fully expanded leaf from the apex) were collected for specific leaf area and stomatal density measurements made in the lab using the same procedures mentioned earlier.

To compare photosynthetic responses of plants growing in different light conditions, we generated light response curves using the same light levels and conditions as those in the shade-house experiment. To compare the Georgia populations, a light curve was taken at each site on each of 4 d, alternating

TABLE 1. Biomass and growth variables for *Lindera melissifolia* grown under three light treatments. Values (mean \pm SE, $N = 6$) followed by different letters indicate significant differences (Tukey test, $P < 0.05$).

Variable	Treatment (% full sunlight)		
	19	42	100
Leaf biomass (g)	11.21 \pm 0.94 ^A	12.04 \pm 1.1 ^A	8.43 \pm 0.81 ^A
Stem biomass (g)	10.03 \pm 0.93 ^A	9.03 \pm 0.56 ^A	6.74 \pm 0.93 ^A
Root biomass (g)	22.4 \pm 2.23 ^A	22.22 \pm 1.42 ^A	14.41 \pm 1.2 ^B
Total biomass (g)	43.64 \pm 3.61 ^A	43.29 \pm 2.9 ^A	29.59 \pm 2.68 ^B
Total leaf area (cm ²)	2200.38 \pm 144.12 ^A	1676.89 \pm 143.67 ^A	942.67 \pm 99.08 ^B
SLA (cm ² /g)	199.27 \pm 6.49 ^A	139.74 \pm 4.28 ^B	110.86 \pm 1.53 ^C
LAR (cm ² /g)	52.95 \pm 1.30 ^A	39.11 \pm 1.69 ^B	32.28 \pm 1.81 ^B
LMR	0.27 \pm 0.01 ^A	0.28 \pm 0.01 ^A	0.29 \pm 0.01 ^A
SMR	0.23 \pm 0.01 ^A	0.21 \pm 0.01 ^A	0.22 \pm 0.01 ^A
RMR	0.5 \pm 0.01 ^A	0.51 \pm 0.01 ^A	0.49 \pm 0.02 ^A
Stomata #/0.0625 mm ²	26.94 \pm 1.14 ^B	33.94 \pm 1.30 ^A	37.28 \pm 1.98 ^A
Stem height (cm)	62.44 \pm 3.71 ^A	53.88 \pm 3.37 ^{AB}	45.60 \pm 3.97 ^B
Stem growth (cm)	181.26 \pm 15.78 ^A	176.82 \pm 13.86 ^A	144.32 \pm 30.38 ^A
Stem diameter growth (mm)	2.28 \pm 0.24 ^A	2.09 \pm 0.22 ^{AB}	1.56 \pm 0.29 ^B

Note: SLA = specific leaf area; LAR = leaf area ratio; LMR = leaf mass ratio; SMR = stem mass ratio; RMR = root mass ratio.

the site order each day. This method was also used at the South Carolina population (three sites along a light gradient), except that two light curves were taken at each site on each day (6 light curves per day) for 4 d. By measuring light response curves on separate days, we were able to account for any daily factors potentially influencing photosynthetic measurements.

We characterized the light environment at each site by leaf area index (total leaf area per unit area of ground; LAI) with the LAI-2000 plant canopy analyzer (Li-Cor, Inc.). LAI measurements were taken during overcast sky conditions for all Georgia populations and in the early morning for the South Carolina populations. In addition, we determined percentage light availability for each site with the LI-191SA line quantum sensor and LI-1000 dataloggers (Li-Cor, Inc.) by recording light levels at plant height and in an adjacent area located in full sunlight under clear sky conditions between 1100 to 1200 hours.

Statistical analyses—Light curves were fitted by nonlinear regression using the Mitscherlich model equation (Sigma Plot 8.0, SSPS Inc., Chicago, Illinois USA) (Potvin et al., 1990; Peek et al., 2002):

$$A = A_{\max} [1 - e^{-A_{\text{qe}} (\text{PPFD} - \text{LCP})}],$$

where A is net photosynthesis, A_{\max} refers to the asymptote of photosynthesis, A_{qe} represents the apparent quantum yield or initial slope of the curve, PPFD is the incident photosynthetic photon flux density, and the LCP refers to the

light compensation point that corresponds to the x -intercept (where photosynthetic uptake and respiratory CO_2 release are in equilibrium). This model was used to obtain the following parameters: light-saturated rate of photosynthesis (A_{\max}), light compensation point (LCP), and apparent quantum yield (A_{qe}). The rate of dark respiration (R_d) was calculated as the y -intercept of the curve. Using this equation, the light saturation point (LSP) was calculated as the PPFD where A_{\max} was reached (i.e., no further increase in photosynthesis with increasing light).

All shade-house experiment and photosynthetic data for field studies were analyzed using a randomized complete block analysis of variance (PROC GLM; SAS 9.0, SAS Institute Inc., Cary, North Carolina USA). Field studies were analyzed in two groups based on geographical location and sampling dates (i.e., A-Sun, A-Shade, I-Shade, and FM-Sun, FM-Int, FM-Shade). In this case, the block was the date photosynthetic data were collected. The morphological field data collected were analyzed using a one-way analysis of variance (PROC GLM; SAS Institute Inc.). Means comparisons were made using Tukey's honestly significant difference test ($P > 0.05$).

RESULTS

Shade-house experiment—Growth, as measured by total plant biomass, was 30% less in the full sun treatment than that of the other two light treatments ($F_{2,10} = 5.41$, $P = 0.03$), primarily from decreased root biomass associated with full sun conditions ($F_{2,10} = 5.95$, $P = 0.02$; Table 1, Fig. 1). Although not statistically significant, a trend for reduced stem and leaf biomass contributed to the lower total biomass in the full sun treatment ($F_{2,10} = 3.53$, $P = 0.07$ and $F_{2,10} = 3.10$, $P = 0.09$, respectively; Table 1, Fig. 1). Leaf mass ratio (LMR), stem mass ratio (SMR), and root mass ratio (RMR) did not differ among the three light treatments. Even though root biomass for the full sun treatment was significantly lower than the other two light treatments, plants did not differ in the partitioning of parts (i.e., leaves, stems, and roots) relative to total plant mass. Final stem height decreased with increasing light levels (Table 1). Total stem growth did not differ among the three light treatments, whereas stem diameter growth was significantly lower in the full sunlight treatment than in the low light treatment ($F_{2,10} = 4.30$, $P = 0.04$; Table 1).

Leaf morphology changed in response to light conditions. Total plant leaf area was greater in response to low and intermediate light treatments than to full sunlight ($F_{2,10} = 19.41$, $P < 0.001$; Table 1). Leaf area ratio (LAR) was greater at the lowest light treatment than in the other treatments ($F_{2,10} =$

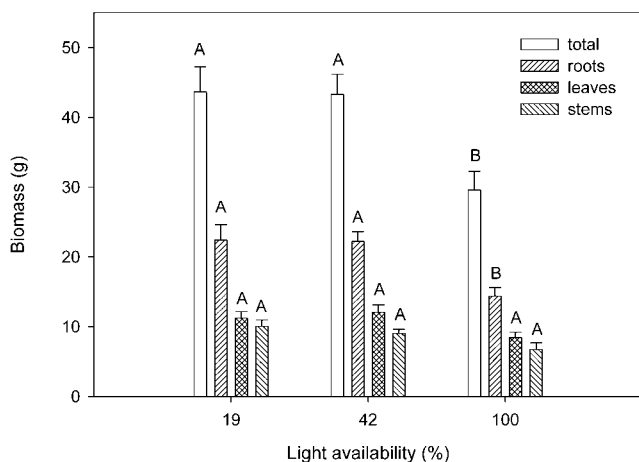


Fig. 1. Biomass components for *Lindera melissifolia* plants grown under three light treatments. Data are means with standard error bars ($N = 6$). Means with different letters indicate significant differences (Tukey test, $P > 0.05$).

TABLE 2. Leaf-level photosynthetic parameters for *Lindera melissifolia* grown under three light treatments. Values (mean ± SE, N = 6) followed by different letters indicate significant differences (Tukey test, P < 0.05).

Parameter	Treatment (% full sunlight)		
	19	42	100
A_{max} ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	4.39 ± 0.20 ^B	6.07 ± 0.65 ^A	3.31 ± 0.31 ^B
A_{max} ($\text{nmol CO}_2 \cdot \text{g}^{-1} \cdot \text{s}^{-1}$)	87.23 ± 3.84 ^A	85.80 ± 11.48 ^A	36.86 ± 3.83 ^B
A_{qe} ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)/($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	0.0087 ± 0.0003 ^B	0.0091 ± 0.001 ^{AB}	0.0142 ± 0.0023 ^A
R_d ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	-1.03 ± 0.08 ^A	-1.79 ± 0.09 ^B	-2.51 ± 0.24 ^C
LCP ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	27.46 ± 2.30 ^B	30.74 ± 1.97 ^B	47.03 ± 6.14 ^A
LSP ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	861.29 ± 40.47 ^{AB}	890.83 ± 100.85 ^A	578.68 ± 74.38 ^B

Note: A_{max} = light-saturated rate of photosynthesis; A_{qe} = apparent quantum yield; R_d = rate of dark respiration; LCP = light compensation point; LSP = light saturation point.

33.82, $P < 0.0001$). Specific leaf area (SLA) decreased with increasing light levels, indicating that shade leaves were thinner than sun leaves ($F_{2,10} = 127.38$, $P < 0.0001$). Stomatal density was significantly lower only in the lowest light environment ($F_{2,10} = 12.68$, $P = 0.0018$).

Light-saturated rates of photosynthesis (A_{max}) on a leaf area basis increased as light levels increased from 19 to 42% full sunlight, but decreased as light levels increased from 42 to 100% full sunlight ($F_{2,10} = 16.50$, $P < 0.001$). Maximum rates of photosynthesis on a leaf area basis of plants grown in intermediate light (42% full sunlight) were 28–48% greater than either of the extreme light treatments (Table 2, Fig. 2). These plants also had greater light saturation points than plants grown under full sun. Light-saturated rates of photosynthesis on a leaf mass basis were similar for the 19 and 42% light treatments, and were higher than the 100% light treatment. The apparent quantum yield differed among treatments; mean values for plants in full sun were greater than those in the lowest light (19% sunlight; $F_{2,10} = 5.05$, $P = 0.03$). Plants in the 100% light treatment had significantly greater light compensation points and rates of dark respiration than the other two light treatments ($F_{2,10} = 11.30$, $P = 0.003$ and $F_{2,10} = 38.44$, $P < 0.0001$, respectively; Table 2, Fig. 2). No significant block effect was observed for any of the response variables analyzed ($P > 0.05$).

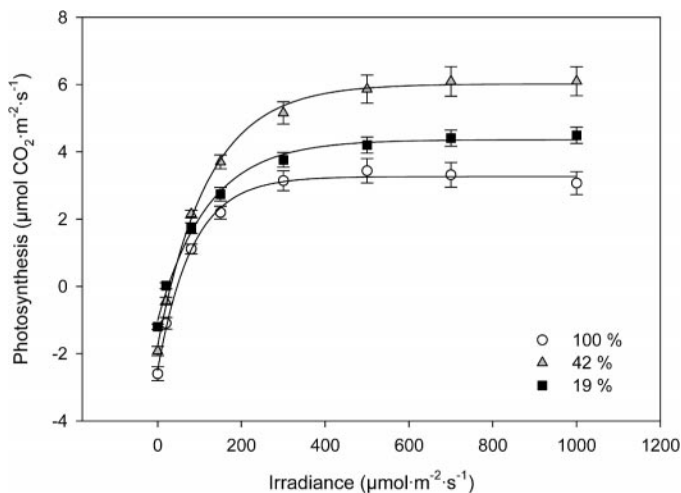


Fig. 2. Light response curve of photosynthesis as a function of irradiance for *Lindera melissifolia* plants grown under three light treatments. Data points represent means ± standard errors (N = 6). Light curves were fitted by non-linear regression using the Mitscherlich model equation.

Field study—The South Carolina study sites comprised a single population that was distributed across a wide gradient of light conditions. FM-Sun occurred under little canopy cover with a leaf area index (LAI) of 0.71 and 95% light availability. FM-Intermediate, with an LAI of 2.19 and 28% light availability, occurred along the margin of the wetland. FM-Shade was located under a dense shrub thicket with an LAI of 4.42 and only 3% light availability (Table 3A). Plant height did not differ among populations in South Carolina; however, stem diameter was nearly 50% less under dense shade than in the more open habitats (Table 3A). The Georgia populations represented only the extreme light conditions (i.e., no intermediate condition). A-Sun was located in an herbaceous region of a wetland with an LAI of 0.12 and 93% light availability. A-Shade and I-Shade had similar tree canopies with LAIs of 2.93 and 3.32 and 7% and 6% light availabilities, respectively (Table 3B). Basal stem diameter did not differ among the three Georgia populations (Table 3B), although mean plant height in the A-Sun population was less than that of other two shaded sites. Specific leaf area decreased and stomatal density increased with increasing light, regardless of geographic location (Table 3A, B).

Patterns of photosynthetic responses to varied light conditions in field sites were generally similar to those of plants grown under experimental light treatments. In the South Carolina sites, the light-saturated photosynthetic rate (A_{max}) in FM-Intermediate exceeded that of FM-Shade by 45%, but did not differ from FM-Sun (Table 4A). The apparent quantum yield was greatest for FM-Shade plants compared to the intermediate and sun sites ($F_{2,6} = 16.90$, $P = 0.003$). Although light-saturated photosynthetic rates were similar for plants in two of the Aultman forest sites (i.e., A-Sun and A-Shade; Table 4B), the Ichauway population (I-Shade) had greater A_{max} rates than A-Sun. Apparent quantum yields were similar for the three Georgia populations (Table 4B). Light compensation points and rates of dark respiration increased with increasing light for all sites. As in the shade-house experiment, no significant block effect was observed for any of the photosynthetic parameters ($P > 0.05$).

DISCUSSION

Our results indicate that *L. melissifolia* is capable of acclimating to varied light conditions through plasticity in leaf morphology and physiology. Plants showed the typical sun-shade morphological responses that have been reported in numerous other studies, including decreased stomatal densities, increased specific leaf area, and increased leaf area ratio with decreasing light levels (Dean et al., 1982; Midgley et al., 1992; Holmes

TABLE 3. A. Light environment and morphological characteristics (mean \pm SE, $N = 20-33$) for *Lindera melissifolia* growing under natural light regimes in the Francis Marion National Forest, South Carolina, USA. B. Light environment and morphological characteristics (mean \pm SE, $N = 22-33$) for *L. melissifolia* growing under natural light regimes in three southwestern Georgia populations. Values followed by different letters indicate significant differences (Tukey test, $P < 0.05$).

A.			
Characteristic	Site		
	FM-Sun	FM-Int	FM-Shade
Light availability (%)	95	28	3
LAI	0.71 \pm 0.03	2.19 \pm 0.06	4.42 \pm 0.13
Stem height (cm)	41.89 \pm 1.46 ^A	40.82 \pm 2.13 ^A	36.56 \pm 3.19 ^A
Stem diameter (mm)	4.07 \pm 0.18 ^A	4.09 \pm 0.25 ^A	2.13 \pm 0.16 ^B
SLA (cm ² /g)	178.10 \pm 3.90 ^C	288.56 \pm 15.25 ^B	382.83 \pm 9.02 ^A
Stomata #/0.0625 mm ²	32.73 \pm 0.63 ^A	25.43 \pm 0.96 ^B	14.20 \pm 0.40 ^C
B.			
Characteristic	Site		
	A-Sun	A-Shade	I-Shade
Light availability (%)	93	7	6
LAI	0.12 \pm 0.02	2.93 \pm 0.16	3.32 \pm 0.26
Stem height (cm)	41.70 \pm 2.47 ^B	55.83 \pm 5.76 ^A	58.14 \pm 2.8 ^A
Stem diameter (mm)	4.01 \pm 0.34 ^A	4.28 \pm 0.48 ^A	4.20 \pm 0.21 ^A
SLA (cm ² /g)	130.33 \pm 4.30 ^B	397.13 \pm 10.72 ^A	408.30 \pm 13.65 ^A
Stomata #/0.0625 mm ²	36.72 \pm 0.56 ^A	15.24 \pm 0.41 ^C	19.35 \pm 0.36 ^B

Note: LAI = leaf area index; SLA = specific leaf area.

and Cowling, 1993; Groninger et al., 1996; Beaudet and Messier, 1998; Sack and Grubb, 2002). Similar to responses of other shade-tolerant species, leaves of *L. melissifolia* adjusted physiologically to shading by lower light compensation points and rates of dark respiration (Sims and Pearcy, 1991; Midgley et al., 1992; Hamerlynck and Knapp, 1994; Groninger et al., 1996; Olsen et al., 2002). Maximum rates of photosynthesis for populations ranged between 3 and 6 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, a response consistent with shade-tolerant trees and shrubs from temperate regions, but less than the typical rates of 10–15 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ reported for sun leaves (Loach, 1967; Larcher, 1995). Differences in photosynthetic rates based on area and mass suggest that changes in both leaf area and biochemistry may be influencing photosynthetic response to light intensity. However, adjustment in leaf morphology appears to be the primary control on photosynthesis based on response

differences between the 19 and 42% light treatments on a per-unit leaf area and no difference on per-unit tissue mass (Hamerlynck and Knapp, 1994).

A response pattern of increasing maximum photosynthetic rates (per leaf area) with increasing light up to intermediate light levels, followed by a decline in A_{max} at high light levels, similar to that of our experimental observations, has been reported for other shade-tolerant species (Loach, 1967; Chabot and Chabot, 1977; Oberbauer and Strain, 1986; Tani et al., 2001). However, these results are inconsistent with those of Wright (1990b) in which the thicker sun leaves of *L. melissifolia* plants growing in large canopy gaps (photosynthetically active radiation [PAR] $> 970 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) had maximum rates of photosynthesis up to 56% greater than those of shade leaves. Photosynthetic responses of plants measured in the field study were also not in complete agreement with our ex-

TABLE 4. A. Leaf-level photosynthetic parameters (mean \pm SE, $N = 4$) for *Lindera melissifolia* growing under natural light regimes in the Francis Marion National Forest, South Carolina, USA. B. Leaf-level photosynthetic parameters (mean \pm SE, $N = 4$) for *L. melissifolia* growing under natural light regimes in three southwestern Georgia populations. Values followed by different letters indicate significant differences (Tukey test, $P < 0.05$).

A.			
Parameter	Site		
	FM-Sun	FM-Int	FM-Shade
A_{max} ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	4.99 \pm 0.582 ^{AB}	5.89 \pm 0.45 ^A	3.24 \pm 0.28 ^B
A_{qe} ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)/($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	0.0106 \pm 0.0018 ^B	0.0130 \pm 0.0009 ^B	0.0214 \pm 0.0009 ^A
R_d ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	-1.56 \pm 0.18 ^A	-1.03 \pm 0.04 ^B	-0.40 \pm 0.03 ^C
LCP ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	27.58 \pm 1.61 ^A	12.69 \pm 0.64 ^B	5.70 \pm 0.59 ^C
LSP ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	757.07 \pm 95.21 ^A	575.75 \pm 40.74 ^{AB}	318.67 \pm 12.89 ^B
B.			
Parameter	Site		
	A-Sun	A-Shade	I-Shade
A_{max} ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	3.48 \pm 1.17 ^B	4.11 \pm 0.39 ^{AB}	5.99 \pm 0.43 ^A
A_{qe} ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)/($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	0.0138 \pm 0.0016 ^A	0.0158 \pm 0.0009 ^A	0.0126 \pm 0.0021 ^A
R_d ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	-1.58 \pm 0.059 ^A	-0.43 \pm 0.02 ^B	-0.63 \pm 0.07 ^B
LCP ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	33.11 \pm 6.97 ^A	6.70 \pm 1.22 ^B	8.48 \pm 1.25 ^B
LSP ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	490.71 \pm 77.85 ^A	454.54 \pm 52.30 ^A	667.63 \pm 56.83 ^A

Note: A_{max} = light-saturated rate of photosynthesis; A_{qe} = apparent quantum yield; R_d = rate of dark respiration; LCP = light compensation point; LSP = light saturation point.

perimental observations. These discrepancies may be due to other environmental factors such as temperature, relative humidity, soil moisture, and nutrient availability, all of which influence photosynthesis under natural conditions (Thompson et al., 1988; Kozłowski et al., 1991). For example, inundated conditions have been shown to reduce photosynthesis, particularly for leaves in full sunlight, and may have been a confounding factor in our study (Gravatt and Kirby, 1998; Gardiner and Krauss, 2001). Consequently, comparisons between measurements of flooded field study plants and nonflooded experimental plants were difficult to interpret. Further studies will be necessary to understand the relationship between light environment and flooding on photosynthesis for this species.

Plants growing in high light environments were unable to increase their light-saturated photosynthetic rates, but had higher respiration rates than low light plants. Potentially, increased rates of respiration for sun leaves may have resulted from factors such as photoinhibitory costs, light environment, and/or carbon gain, and little was associated with the maintenance of photosynthetic capacity (Sims and Pearcy, 1991). No evidence for photoinhibition was observed in this study. Even though plants appeared to maintain efficient photosynthesis in high light environments, accurate apparent quantum yield measurements can be difficult to obtain and would require closer investigation (Singsaas et al., 2001). The low photosynthetic and high respiration rates observed for high light plants indicate that these plants were stressed and had unequal carbon balances, which may explain the reduction in biomass observed for plants growing in the high light treatment compared to lower light treatments. Additionally, we observed that leaves of *L. melissifolia* growing under extremely high light environments, in the field as well as under experimental conditions, tended to roll longitudinally. Leaf rolling is considered a light avoidance strategy used by plants to minimize leaf temperature and transpiration (Lambers et al., 1998). Thus, the leaf rolling habit that we observed may be an indicator of stress under high light conditions.

Even though measurements of leaf-level photosynthetic rates can be useful in determining how light influences a plant's photosynthetic response, these measures do not necessarily corroborate plant growth rates (Givnish, 1988; Körner, 1991; Lambers et al., 1998). For example, although plants in the 19% light treatment had lower maximum rates of photosynthesis than those in the intermediate light treatment, biomass and growth patterns did not differ. The fact that all experimental plants survived the duration of the study, but growth and photosynthesis were significantly reduced in full sun, indicates that *L. melissifolia* can persist in a range of light environments, but high light environments do not appear to be optimal for growth. This conclusion is consistent with previous anecdotal observations that growth of this species is often stunted under high light levels (Tucker, 1984) and that most populations of *L. melissifolia* have been observed in shade to partial shade. In addition, low root production could limit competition for below-ground resources under high light conditions. How this species would respond to more extreme shade conditions than those used in our experimental treatment is unclear.

Plants in light-limited environments often increase allocation to stems and leaves at the expense of roots or other storage organs (Boardman, 1977; Lentz and Cipollini, 1998; Niinemets, 1998; Van Hees and Clerkx, 2003). However, we did not observe the differences in biomass partitioning between

above- and belowground parts found in other studies (Groninger et al., 1996; Pattison et al., 1998). These inconsistencies could reflect species-specific responses in biomass partitioning to light environment. The degree of partitioning has been shown to differ among species and may change as a plant grows (Niinemets, 1998; Longbrake and McCarthy, 2001; Montgomery and Chazdon, 2002; Van Hees and Clerkx, 2003). Carbon allocation patterns may also reflect tolerance of the species to irradiance. Allocation to shoot development is a light-seeking strategy often observed for shade-intolerant species growing in low light environments (Walters et al., 1993; Beaudet and Messier, 1998; Lentz and Cipollini, 1998). Even though differences in stem height were not pronounced among natural populations of *L. melissifolia*, sun plants were typically shorter than shade plants for both the Georgia populations and the experimental plants. Stem height was likely overestimated for FM-Sun plants; shorter plants were submerged and could not be located.

Management implications—Although controlled experiments offer information regarding a particular resource, a suite of environmental factors interact to influence plant establishment and growth in natural environments. For example, plants growing under shade cloth do not experience the brief periods of direct solar radiation known as sunflecks that commonly occur under a forest canopy. Depending on the type of canopy, sunflecks can increase total daily irradiance, greatly affecting plant growth and survival (Chazdon and Pearcy, 1991). For instance, plants growing under dense shrub thickets similar to FM-Shade may receive fewer and lower-intensity sunflecks than populations growing under tree canopies with more diffuse cover. If this is the case, then removing dense shrub canopies may be beneficial to populations of *L. melissifolia*, whereas thinning mature tree canopies may not be effective and could be deleterious. Environmental factors not examined in this study—such as light quality, intensity and duration of sunflecks, or nutrient and moisture availability—need further investigation and should be considered when assessing optimal habitat requirements and developing management options for conserving rare and endangered plant populations such as *L. melissifolia*. In addition, the historical habitat of a rare species across its entire range should be evaluated when making management decisions. For example, this may be particularly important for *L. melissifolia* because it occurs in such distinctly different habitats within its range. In the Southern Coastal Plain, fire may have played a role in eliminating the dense shrub thickets found in areas such as the Francis Marion National Forest, whereas in populations along the Mississippi alluvial plains, more frequent flooding may have played a greater role in structuring the community composition.

In conclusion, *L. melissifolia* is a facultative shade species with the ability to adjust to a range of light environments. Light-saturated photosynthetic rates observed for this species were consistent with other shade-tolerant plants and were lower than typical rates for species adapted to high light environments. Even though plants can persist in full sun environments, these conditions do not appear to be optimal for growth. In addition, populations may be suppressed by competing vegetation that is favored in more open habitats (Wright, 1990a). Based on our results, we recommend maintaining canopy conditions at irradiance levels below 40% full sunlight for optimal plant growth. In addition, these light lev-

els should be considered when assessing the suitability of sites for reintroduction efforts.

To develop effective conservation measures for populations of rare and endangered species, observations of their natural history, distribution, and habitat characteristics are essential. However, active management of rare species often has been based on untested observations of patterns and not on experimental data that provide mechanistic explanations (Given, 1994). As human intervention has become increasingly necessary to prevent the further decline of rare plant populations, this lack of experimental data poses difficulties for resource managers in understanding how to manage certain components (Noon and Franklin, 2002). While this study addresses questions about the favorable conditions for a particular endangered species in the southeastern USA, the methodological framework for linking physiology to management of a rare species is applicable to rare species in general. Our approach illustrates how a combination of experimental manipulations and field observations can provide sound ecological data and causal models for the larger issues surrounding effective management and conservation of rare and endangered species, particularly for species that occur across a wide range of conditions and limited distribution. It also suggests how suitable habitat can be identified for reintroduction sites when such action is necessary for the recovery of the species.

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