

physiology

Biomass Accumulation in the Endangered Shrub *Lindera melissifolia* as Affected by Gradients of Light Availability and Soil Flooding

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We studied the impacts of light availability and soil flooding on biomass accumulation and tissue biomass fractions in *Lindera melissifolia* (Walt.) Blume, an endangered woody shrub of the southeastern United States. Our experiment was located in a large-scale flooding research facility where plants were established and grown for three years while receiving combinations of 70%, 37%, or 5% of full sunlight with either 0, 45, or 90 days of soil flooding. We hypothesized that biomass accumulation would decrease with decreasing light availability and that soil flooding would further reduce plant mass. In the absence of soil flooding, shrubs receiving 37% light accumulated the greatest biomass (972 g), shrubs receiving 70% light were intermediate in biomass accumulation (737 g), and shrubs receiving 5% light accumulated the least biomass (14 g). Shrubs raised beneath 37% light had root biomass fractions less indicative of water stress than shrubs raised beneath 70% light, and leaf and stem biomass fractions less indicative of light deprivation than shrubs raised beneath 5% light. The light environment also influenced how soil flooding affected *L. melissifolia* biomass accumulation. Soil flooding had no detectable effect on the amount of biomass accumulated by shrubs acclimated to 5% light. However, shrubs acclimated to 70% or 37% light showed a 26% decrease in biomass accumulation after 90 days of soil flooding. Our findings demonstrate a responsive plasticity of *L. melissifolia* biomass accumulation relative to light availability and soil flooding, and this plasticity was driven by shifts among leaf, stem, and root biomass fractions. This plasticity supports development of silvicultural options for active management of this endangered species in floodplain forests of the Mississippi Alluvial Valley.

Keywords: environmental interactions, Flooding Research Facility, growth stress factors, phenotypic plasticity, pondberry, shade houses, tissue fractions.

Plants growing in their natural environment experience a multitude of stresses that fluctuate in intensity at temporal and spatial scales (Gaspar et al. 2002, Niinemets and Valladares 2006, Valladares et al. 2007). Ecophysiological research that investigates plant response to stress often involves establishing a gradient of intensity for one stress factor of interest, for example, a range of light availability, while holding constant other environmental conditions (Blackman and Wilson 1951, Jarvis 1964, Gottschalk 1994). More complex experiments may be constructed to test plant response to two or more stress factors that occur simultaneously or partially overlap each other (Walters and Reich 1996, Gardiner and Krauss 2001, Lenssen et al. 2003). Of particular interest to plant ecophysiologicals studying stress response is how multiple stresses interact to influence

plant function (Chapin et al. 1987, Alexieva et al. 2003, Atkinson and Urwin 2012). Specifically, when a plant is subjected to a stress that negatively affects its function, how does a second stress impact plant function? Experiments that address the effects of multiple stresses and their interactions on plants may be more complex in design and interpretation of results, but may also provide more detailed insight into how plants function in their natural environment (Grime 1977, Hall and Harcombe 1998, Lenssen et al. 2003, Niinemets 2010).

Plasticity in photosynthate allocation, especially to different tissue fractions, in response to environmental stresses is an important determinant in the survival and growth of plants (Sultan 2000). Biomass accumulation, particularly among leaf, stem, and root tissues, provides a key metric for assessing plant response to

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environmental stressors (Chapin 1991, Poorter and Nagel 2000, Niinemets 2010). When observed along a gradient of environmental stress, biomass accumulation within the various tissue fractions can illustrate phenotypic plasticity associated with plant acclimation to stress. For example, plants growing in a low-light environment may prioritize photosynthate allocation to leaf and stem tissues to improve exposure to and capture of available sunlight (Poorter and Nagel 2000). Likewise, plants growing in a high-light environment tend to experience diurnal water stress and, therefore, often prioritize photosynthate allocation to root tissues for increased water gathering function (Kolb and Steiner 1990, Canham et al. 1996, Poorter et al. 2012). For plants experiencing two significant stresses, the physiological and (or) morphological response to the initial stress may alter response to the second stress. An example of this interaction was provided by Lavinsky et al. (2007), who demonstrated that soil flooding altered biomass accumulation by *Genipa americana* seedlings relative to their light environment.

Lindera melissifolia (Walt.) Blume (pondberry) is a rhizomatous, woody shrub that is found in the understory of floodplain forests and other wet sites across the southeastern United States (Hawkins et al. 2010, Beckley and Gramling 2013). Despite its fairly large range, *L. melissifolia* is found in only a few disjunct colonies and was given endangered species status in 1986 (U.S. Fish and Wildlife Service 1986). The U.S. Fish and Wildlife Service has subsequently called for information that reveals the basic species biology and ecology of *L. melissifolia* to inform the development of management strategies for its conservation and recovery (U.S. Fish and Wildlife Service 1993, 2014).

Our research was established to gain an understanding of biomass accumulation plasticity in *L. melissifolia* relative to two environmental factors common to its habitat in the Mississippi Alluvial Valley (MAV), USA. Plants were established in native soil and raised for three years under a gradient of light availability and subjected to a range of soil flooding regimes to test our hypotheses. We hypothesized that the total biomass accumulated by this species would decrease with decreasing light availability, and that soil flooding will impose additional reductions in biomass accumulation. Also, the proportional accumulation of biomass in leaf, stem, and root tissues (biomass fractions) will be influenced by light availability and soil flooding such that the greatest proportional accumulation of biomass in leaf and stem tissues would occur in shrubs acclimated to a low-light environment and receiving a relatively long period of soil flooding. We expected the greatest proportional accumulation of biomass in root tissues would be observed in shrubs acclimated to a high-light environment and receiving no soil flooding. Results from this experiment will contribute to our basic knowledge of plant stress response in floodplain forests, and provide a foundation to inform forest management strategies that target development of stand and environmental conditions conducive to growth of the endangered *L. melissifolia*.

Materials and Methods

Study Site

The study was established at the Flooding Research Facility (FRF), an outdoor site designed for large-scale experimentation on plant responses to soil flooding (Lockhart et al. 2006). The FRF is located at the Sharkey Restoration Research and Demonstration Site on the Theodore Roosevelt National Wildlife Refuge Complex, Sharkey County, MS, USA (32°58' N, 90°44' W) (Gardiner et al. 2008). This

area is in the Subtropical Division of the Humid Temperate Domain with hot, humid summers and mild winters (Bailey 1980). Average daily temperature is 17.3°C with a range from 5.6°C in January to 27.3°C in July (WorldClimate 2016). Precipitation averages 1366 mm per year (WorldClimate 2016). The Sharkey series, a common soil in the MAV, is the native soil at the FRF. It is classified as a very fine, smectitic, thermic Chromic Epiaquerts (NRCS 2016). Samples from the FRF indicate that the texture of this alluvial soil ranges from 2 to 3% sand, 27 to 31% silt, and 66 to 71% clay (Wood 1998). *L. melissifolia* colonies in the MAV are often found on Sharkey soil (Hawkins et al. 2009b), and the closest natural colonies of this species are located about 2.5 km south of the FRF on the Delta National Forest.

Treatments

The FRF contains 12, 0.4-ha rectangular (201.2 m long and 18.3 m wide) impoundments that can be independently flooded to desired depths. Each impoundment was randomly assigned one of three soil flooding regimes: 0 days (0 d), 45 days (45 d), or 90 days (90 d). The assignment of soil flooding regimes to impoundments established four replicates for each of the three regimes.

Soil flooding was initiated on March 1 for the 2006 and 2007 growing seasons using groundwater stored in a catchment adjacent to the impoundments. The imposed hydroperiods were not necessarily designed to strictly mimic natural flooding regimes, but were representative of hydroperiods observed at *L. melissifolia* sites in the MAV (Devall et al. 2001, Hawkins et al. 2010). We targeted a floodwater depth that would inundate all plants in each shade house without flooding the lower leaves of these plants. Staff gauges located in each impoundment informed when water was to be added or withdrawn to maintain the floodwater depth. Mean floodwater depth in the impoundments was 11.7 ± 0.4 cm (mean ± standard error) in 2006 and 19.1 ± 1.2 cm in 2007. Growth of *L. melissifolia* in 2006 allowed for the increased flooding depth in 2007, which reduced the frequency of pump operation. Water was drained from designated impoundments at the end of each scheduled soil flooding regime. Rainfall provided the only source of water to impoundments receiving the 0 d soil flooding regime. Annual precipitation totaled 1215 mm and 1373 mm in 2005 and 2006, respectively, but deviated from the long-term average of 1366 mm in 2007 when it totaled 789 mm (based on the Yazoo City, MS, weather station located about 35 km from the FRF; NOAA 2017).

Three wooden-framed, rectangular shade houses (25.6 m long, 7.3 m wide, and 2.4 m tall) were constructed in each impoundment (36 total shade houses). Light availability was controlled by covering the frame of each shade house with neutral density shade cloth (PAK Unlimited, Inc., Cornelia, GA). Shade houses in an impoundment were randomly assigned 70% of ambient sunlight, 37% of ambient

Management and Policy Implications

We found that *Lindera melissifolia* (pondberry), an endangered shrub in the southeastern United States, has plasticity to a variety of light environments and soil flooding regimes. This plasticity suggests wide flexibility in the development and application of forest stand treatment options that facilitate colony growth. That is, managers of *L. melissifolia* habitat could implement silvicultural treatments of various intensities or stand density targets to promote stand structure conducive to colony vigor and growth.

sunlight, or 5% of ambient sunlight; corresponding to a gradient of relatively high, intermediate, and low light availability, respectively. Lockhart et al. (2013) indicated that the diurnal pattern of ambient light available for each light level was 71.5% of full sunlight for the 70% light level, 32.6% of full sunlight for the 37% light level, and 2.2% of full sunlight for the 5% light level. Soil flooding regimes and light availability levels resulted in nine treatment combinations replicated four times across the experiment. Additional reporting of the environmental variables measured in impoundments and shade houses is reported in Lockhart et al. (2013).

Plant Material

L. melissifolia planting stock consisted of 20 genotypes (11 female and 9 male) secured from colonies growing in the MAV. Micropropagation techniques described in Hawkins et al. (2007) were used at Knight Hollow Nursery (Middleton, WI) to replicate clones of each genotype. This process ensured stecklings (rooted cuttings) were genetically identical to parent plants and provided planting stock of uniform physiological age. We received six-month-old stecklings from the nursery and transplanted them into 0.98 L Deepot™ tubes (Stuewe and Sons, Inc., Tangent, OR). Plants were raised in a climate-controlled greenhouse at the Southern Hardwoods Laboratory (Stoneville, MS) for five months prior to outplanting in the field.

In April 2005, 96 single-stemmed stecklings (shade house mean stem length was 21.6 ± 0.3 cm and mean basal diameter was 1.85 ± 0.01 mm) were outplanted on a 1.2 m by 1.2 m spacing in each shade house (3456 total plants). Planting spots in each shade house were assigned a randomly chosen steckling, but random selections were constrained to provide for 48 male and 48 female plants with representation from each clone. These plants were allowed to acclimate to the field environment under assigned light levels for the 2005 growing season. Plants that died during the first month after planting were replaced with plants of the same genet. Cultivation with hoes and careful application of chemicals (glyphosate) directly to weeds controlled all competition for the duration of this experiment. Plant survival following the 2007 growing season was $87.7 \pm 6.7\%$. Lockhart et al. (2013) reported that this survival varied by light availability with $89.8 \pm 1.2\%$, $98.0 \pm 0.5\%$, and $75.2 \pm 2.2\%$ survival in the 70%, 37%, and 5% light levels, respectively.

Biomass Sampling

Following the 2007 growing season, six shrubs were randomly sampled from each shade house to quantify aboveground biomass ($n = 216$). Shoots from each sample shrub were clipped at the groundline and separated into stem and leaf tissues. Length (cm) and basal diameter (mm) of all stems were recorded, and all shoot tissues were stored at 2°C for later processing. All leaves were measured twice with a LI-COR LI-3100 leaf area meter (LI-COR, Inc., Lincoln, NE); these measurements were averaged, and leaf averages were summed for a plant to calculate plant leaf area (m²). Stem and leaf tissues were dried to desiccation at 70°C before measuring biomass (g) with an analytical balance.

A subset of these plants were also sampled for belowground biomass (roots and rhizomes). Six sample plants were chosen from one randomly selected replication of each soil flooding regime and associated shade houses ($n = 54$). Soil constituting the rhizosphere

of sampled plants was excavated with shovels and stored in 120-l plastic containers under refrigeration at 2°C. Excavations tracked roots from the root-collar to their terminus. Ample soil around each primary root was collected to ensure capture of all fine roots. Roots and rhizomes were extracted from the soil matrix by gleaning these tissues from individual soil peds. Due to the volume of soil collected for this sampling procedure (about 26 m³), root extraction lasted about 36 months. We did not observe rot or any other visible change in roots held under refrigerated storage during this lengthy processing period. Extracted tissues were stored in 95% non-denatured ethanol until they were washed with distilled water, dried to desiccation at 70°C, and weighed.

Modeling and Statistical Analyses

Linear regression equations were developed to estimate belowground biomass of each plant sampled only for aboveground biomass (Table S1). These root biomass estimates were used in subsequent analyses of whole plant biomass and proportional accumulation among tissue types, as described below. Root biomass excavated during sampling, along with aboveground morphological variables listed above, was subject to stepwise regression (PROC REG; SAS 9.4, SAS Institute, Inc., Cary, NC) to identify an independent variable that accurately estimated plant root biomass. Plant leaf area was found to be the best predictor of root biomass for plants of each light level ($r^2 = 0.95$ to 0.96). Rhizomes that had yet to form a ramet constituted 0.3% of belowground biomass, so these tissues were pooled with root biomass for construction of these equations and all other analyses.

Response variables included in the data analyses were: stem length; maximum stem length; stem diameter; maximum stem diameter; number of ramets; plant leaf area; leaf biomass; stem biomass; root biomass; plant biomass (plant biomass = leaf + stem + root biomass); and leaf biomass fraction (LBF = leaf biomass / plant biomass), stem biomass fraction (SBF = stem biomass / plant biomass), and root biomass fraction (RBF = root biomass / plant biomass) (g g⁻¹). Means were calculated for analysis of each response variable. Shade house means for stem length and stem diameter were calculated from length and diameter values averaged for each plant, as most plants were multi-stemmed. Shade house means for maximum stem length and maximum stem diameter were calculated based on the mean of the longest stem and largest diameter, respectively.

Response variable means were analyzed according to a completely random, split-plot design with soil flooding regime representing the main plot treatment and light level representing the subplot treatment. Analyses were conducted using PROC GLIMMIX. Prior to analysis, data normality was tested using PROC UNIVARIATE and transformations were applied to variables as needed to normalize model residual errors. We tested whether shrub size had any effect on plant biomass distribution among biomass fractions. Linear regressions between the log₁₀ transformation of plant biomass and LBF, SBF, or RBF showed only a weak effect (Durbin-Watson values ranged from 1.21 to 1.44, $P < 0.01$); therefore, transformation of these response variables was deemed unnecessary to account for the possible influence of shrub size on treatment effects (Poorter et al. 2012). Untransformed values of all response variables are displayed in all tables and figures. The least significant difference (LSD) test was

used to separate means of significant effects. When a significant interaction occurred between soil flooding regime and light level, separations were conducted for light-level means in each soil flooding regime, and soil flooding regime means for each light level. Statistical significance for all tests was determined at $P \leq 0.05$.

Results

Our analyses of third-year biomass accumulation indicated that whole plants and tissue fractions of *L. melissifolia* were affected to various degrees by the interactions of soil flooding and light availability (Table 1, Figure 1). Shrubs acclimated to high light and receiving the 90 d soil flooding regime showed reduced biomass accumulation compared to shrubs receiving the 0 d or the 45 d soil flooding regime (Figure 1A). The shorter, 45 d flood resulted in a decrease in biomass when shrubs were raised beneath intermediate light availability. Soil flooding had no apparent effect on biomass accumulation when *L. melissifolia* was raised in low light. Results parallel to those for whole plants were observed when biomass accumulation was analyzed separately by leaf, stem, and root tissues (Table 1, Figures 1B–D).

The greatest biomass accumulation by *L. melissifolia* was observed when shrubs were raised under conditions of intermediate light in the absence of annual soil flooding (0 d) (Figure 1A). Shrubs receiving low light accumulated the least amount of biomass regardless of soil flooding regime (Figure 1A). These results were in general agreement with measured variables of stem and leaf morphology (Tables 1, 2, and S2).

Soil flooding and light availability interacted to influence LBF in *L. melissifolia* but not SBF or RBF (Table 1, Figure 2). Shrubs acclimated to high or intermediate light and receiving the 0 d or 45 d soil flooding regime showed reduced LBF compared to shrubs acclimated to the same light availabilities and receiving the 90 d soil flooding regime (Figure 2A). Further, within the 0 d or 45 d soil flooding regimes, shrubs acclimated to low light had greater LBF than shrubs acclimated to high or intermediate light. Soil flooding regime had no effect on the proportional accumulation of biomass in stem tissues (SBF) (Table 1), but this variable increased with decreasing light availability (Figure 2B). Finally, RBF decreased with increasing flood duration and independently with decreasing light availability (Figures 2C and D).

Discussion

Three years after establishment, we demonstrated that light availability and soil flooding (two annual floods) interacted to affect biomass accumulation of *L. melissifolia*. In the absence of annual soil flooding, biomass accumulation exhibited a quadratic response in which the greatest accumulation was observed in shrubs acclimated to intermediate light. Shrubs acclimated to high or low light produced lesser amounts of plant mass. This pattern of biomass accumulation differed from our hypothesized linear pattern of decreasing biomass with decreasing light availability. We speculate that water stress from higher vapor pressure deficits was a primary contributor to the reduced plant mass observed under the high-light environment (Lockhart et al. 2013). Plants exposed to rising vapor pressure deficits respond by reducing stomatal aperture to curtail water vapor loss (Pallardy and Kozlowski 1979). However, this physiological response of reduced stomatal aperture to a high light environment also limits CO₂ diffusion through stomata leading to lower rates of photosynthesis and reduced photosynthate production (Chaves 1991, Osakabe et al. 2014), ultimately resulting in reduced biomass accumulation (Lendzion and Leuschner 2008). Our findings are supported by other research conducted on various shrubs (Valladares et al. 2000) and tree seedlings (Gottschalk 1987, Canham et al. 1996, Gardiner and Hodges 1998, Montgomery 2004), indicating that this is not an uncommon biomass accumulation pattern for understory woody plants.

Our analysis of the proportional accumulation of root biomass by *L. melissifolia* plants receiving high light provides further evidence of shrub water stress. Shrubs acclimated to the high-light environment developed a larger RBF than shrubs in the other light environments. We speculate that the transpiration rate of shrubs in this high-light environment exceeded water uptake by roots during episodes of high vapor pressure deficit in the diurnal period (Hodges 1967, González-Rodríguez et al. 2001). Plants often respond to water stress by shifting photosynthate allocation to root tissues—a strategy to increase soil moisture uptake (Walters et al. 1993, Gardiner and Hodges 1998, Poorter 1999, Poorter et al. 2012). This plasticity in photosynthate allocation has been described by the functional equilibrium concept (e.g., optimal partitioning theory) whereby plants allocate photosynthates to tissues that can acquire resources most limiting to growth (Bloom et al. 1985, Poorter et al. 2012).

Table 1. Summary of analyses of *L. melissifolia* response variables to soil flooding regime, light level, and the interaction of light level and soil flooding regime following the 2007 growing season at the Flooding Research Facility, Sharkey County, MS, USA. Numbers in bold indicate statistical significance at $P \leq 0.05$ according to conventional order of hypothesis testing.

Response Variable	Soil Flooding Regime		Light Level		Soil Flooding Regime x Light Level Interaction	
	$F_{(2, 19)}$	P	$F_{(2, 9)}$	P	$F_{(4, 18)}$	P
stem length (cm)	0.80	0.48	46.28	<0.01	0.59	0.67
maximum stem length (cm)	1.49	0.28	248.74	<0.01	2.80	0.06
stem diameter (mm)	0.95	0.42	25.98	<0.01	0.59	0.67
maximum stem diameter (mm)	2.04	0.19	201.80	<0.01	2.21	0.11
number of ramets	2.78	0.12	64.03	<0.01	0.71	0.59
plant leaf area (m ²)	3.64	0.07	167.57	<0.01	6.55	<0.01
plant biomass (g)	5.08	0.03	86.46	<0.01	7.50	<0.01
leaf biomass (g)	2.02	0.19	85.26	<0.01	5.05	0.01
stem biomass (g)	3.06	0.10	146.47	<0.01	5.46	0.01
root biomass (g)	8.17	0.01	93.31	<0.01	9.91	<0.01
leaf biomass fraction (g g ⁻¹)	2.91	0.11	14.24	<0.01	7.32	<0.01
stem biomass fraction (g g ⁻¹)	3.45	0.08	50.85	<0.01	1.19	0.35
root biomass fraction (g g ⁻¹)	4.31	0.05	49.88	<0.01	0.65	0.64

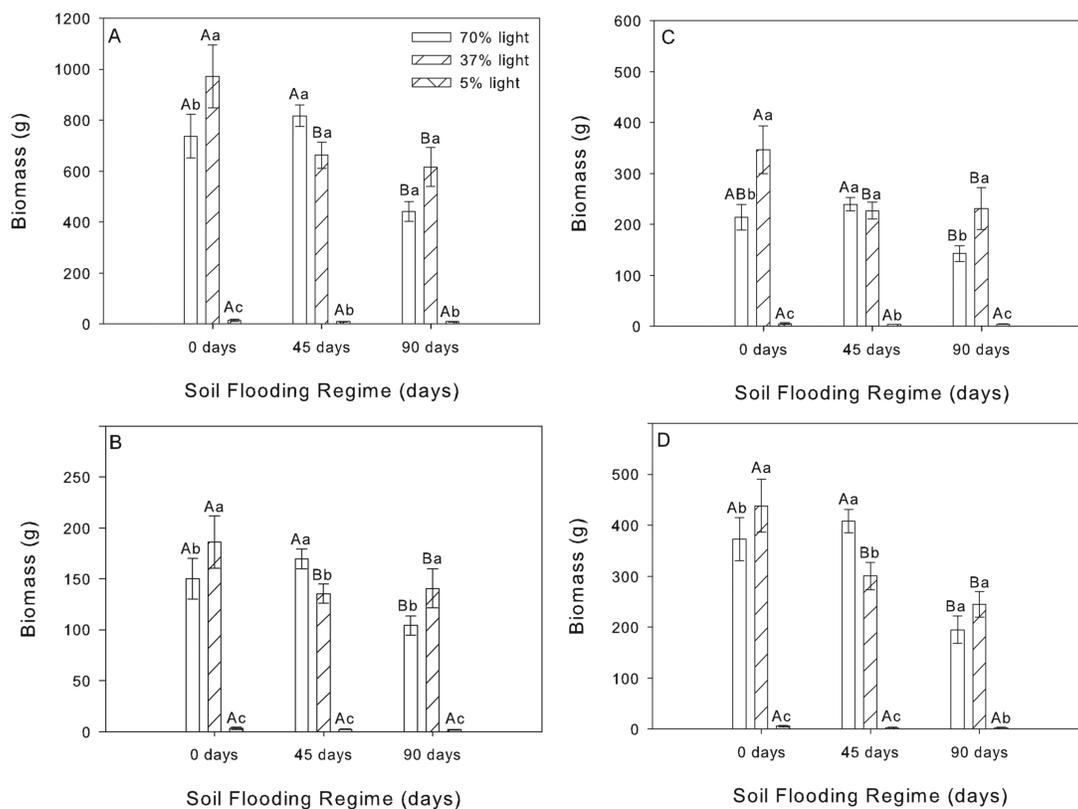


Figure 1. Effect of light level and soil flooding regime on *L. melissifolia* biomass for plants sampled following the 2007 growing season at the Flooding Research Facility, Sharkey County, MS, USA. (A) Plant, (B) leaf, (C) stem and (D) root biomass. Bars are means with \pm SE noted with the vertical line at the top of each bar, and significance of all tests was determined at $P \leq 0.05$. Different uppercase letters indicate differences among soil flooding regime means for a given light level. Different lowercase letters indicate differences among light-level means for a soil flooding regime.

Table 2. Effect of light level on *L. melissifolia* stem variables for plants sampled for biomass distribution following the 2007 growing season at the Flooding Research Facility, Sharkey County, MS, USA. Values are means \pm SE, and significance of all tests was determined at $P \leq 0.05$. Different letters within a row indicate differences among light-level means.

Response Variable	Light Level		
	70%	37%	5%
stem length (cm)	66.1 \pm 4.5 b	90.0 \pm 4.2 a	45.3 \pm 2.3 c
maximum stem length (cm)	125.2 \pm 3.3 b	170.6 \pm 5.8 a	57.4 \pm 2.6 c
stem diameter (mm)	5.70 \pm 0.37 a	6.19 \pm 0.36 a	3.49 \pm 0.17 b
maximum stem diameter (mm)	14.75 \pm 0.60 a	13.95 \pm 0.41 a	4.19 \pm 0.21 b
ramets (number)	14.2 \pm 1.4 a	13.3 \pm 1.2 a	1.0 \pm 0.2 b

In concurrence with our expectation, *L. melissifolia* shrubs acclimated to the low-light environment produced the least amount of biomass—this is consistent with the concept that with all other factors being equal, light is the primary limitation to plant growth (Luken et al. 1997, Gardiner and Hodges 1998, Poorter et al. 2012). Unks et al. (2014) projected that low-light availability would limit biomass accumulation in this species during the first year of seedling growth, and our results extend this conclusion through the third growing season at the FRF. In addition to limiting whole-plant biomass accumulation, the stress of low-light availability appeared to trigger a plastic response in photosynthate allocation among tissues. As we hypothesized, *L. melissifolia*

raised under low light favored biomass accumulation in leaf and stem tissues over biomass accumulation in root tissue. Others have reported a corresponding shift in proportional biomass accumulation by seedlings (<1 year old) of this species (Unks et al. 2014), but it is noteworthy that this response was confirmed in our study of plants with more advanced ontogeny. The plastic shift in photosynthate allocation to aboveground tissues is a strategy to increase light capture in low-light environments (Walters et al. 1993). Additional support for this strategy in *L. melissifolia* was reported by Lockhart et al. (2017), who found that low light availability prompted morphological acclimation in leaf blades consistent with improved light capture.

We indicate above that *L. melissifolia* exhibited greater plant mass when raised beneath intermediate light availability. This level of biomass accumulation was associated with intermediate responses in tissue biomass fraction plasticity. Plants raised beneath intermediate light developed an RBF less indicative of water stress than those of plants raised in high light, and an LBF and SBF less indicative of light deprivation compared to those of plants raised in low light. In this study, intermediate light, particularly in the absence of soil flooding, appears to have provided the least stressful growing environment for *L. melissifolia*.

A primary interest of this research was to examine how *L. melissifolia* grown along a gradient of light availability responds to the stress of annual soil flooding. We recognize numerous pathways in which plants may respond to these stress factors (Lenssen et al. 2003, Niinemets 2010, Najeeb et al. 2016), and these are indicated

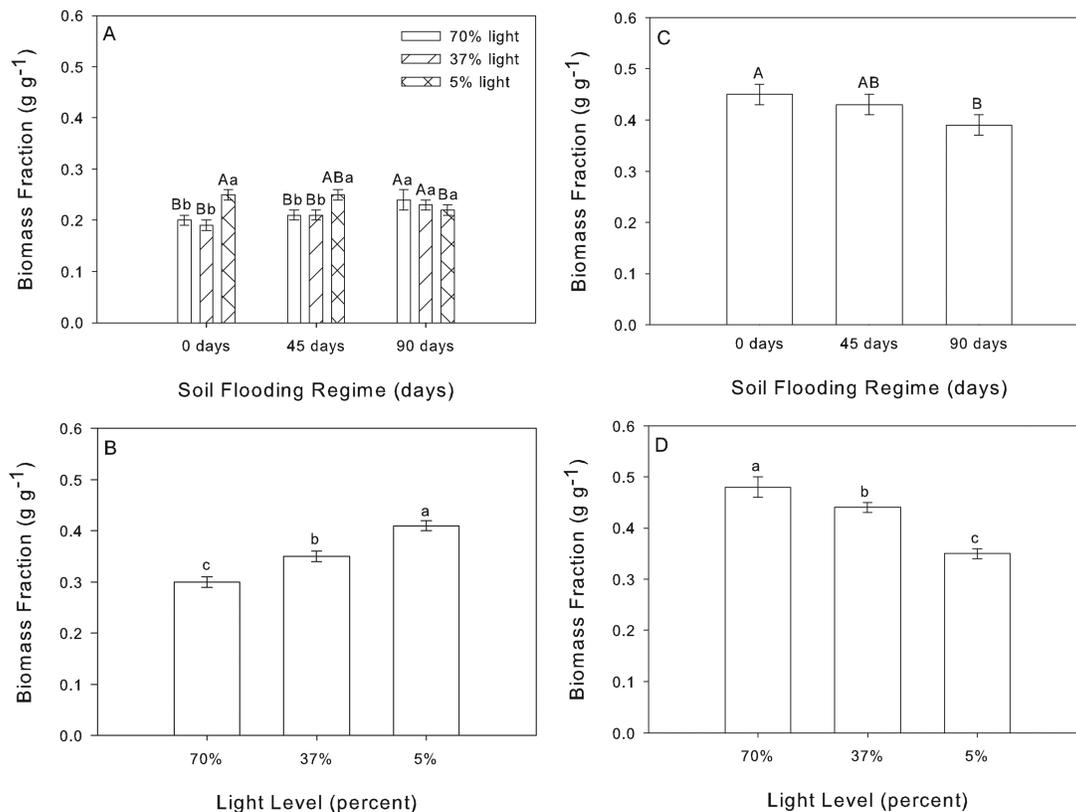


Figure 2. Effect of light level and soil flooding regime on *L. melissifolia* biomass fractions for plants sampled following the 2007 growing season at the Flooding Research Facility, Sharkey County, MS, USA. (A) Leaf biomass fraction, (B) stem biomass fraction, and (C) and (D) root biomass fraction. Bars are means with \pm SE noted with the vertical line at the top of each bar, and significance of all tests was determined at $P \leq 0.05$. Different uppercase letters indicate differences among soil flooding regime means for a given light level. Different lowercase letters indicate differences among light-level means for a soil flooding regime.

by the presence or absence of a statistically significant interaction between light availability and soil flooding as they affect plant function. For example, Mielke and Schaffer (2010) found that light availability and soil flooding independently affected biomass accumulation of *Eugenia uniflora* seedlings. Other studies have found soil flooding to interact with light availability, resulting in a range of biomass accumulation responses depending on species differences in shade and flood tolerances, and plant ontogeny (Lavinsky et al. 2007, Jans et al. 2012, Branco et al. 2017). As discussed above, we hypothesized that biomass accumulation would decrease with decreasing light availability, and that annual soil flooding would impose additional reductions in plant mass. Our results confirm that annual soil flooding interacted with light availability to influence *L. melissifolia* plant mass, but not as we expected.

Annual soil flooding for 45 days imparted the greatest impact to shrubs raised in the intermediate-light environment. In this light environment (37% of available sunlight), shrubs receiving 45 days of soil flooding showed 32% less total plant mass than shrubs that did not receive soil flooding. Decreased biomass accumulation by terrestrial plants during episodes of soil flooding is commonly reported in the literature (Day 1987, Peterson and Bazzaz 1984, Mielke et al. 2005a, Chen and Xie 2009). The hypoxic condition of flooded soil generates physiological dysfunction that limits carbon gain (Kozlowski 1997). For example, stomatal closure is a commonly reported early response to soil flooding (Pezeshki 2001, Herrera et al. 2008). This stomatal closure decreases CO₂ diffusion into the leaf (Farquhar and Sharkey 1982), leading to a decline in

photosynthesis (Lavinsky et al. 2007, Mielke and Schaffer 2011, Pimentel et al. 2014, Oliveira and Gualtieri 2016), a decrease in photosynthate production, followed by a decline in biomass accumulation (Sena Gomes and Kozlowski 1980, Mielke et al. 2003, Mielke and Schaffer 2010, Branco et al. 2017).

Similar to our findings, Hawkins et al. (2009a) showed reduced biomass accumulation in first-year *L. melissifolia* seedlings raised in pots and subjected to 30 days of soil flooding. The decreased biomass accumulation they observed was associated with a decrease in the LBF that was attributed to leaf abscission (Hawkins et al. 2009a). In contrast to their study, our field experimentation did not elicit a change in the proportional distribution of biomass among leaf, stem, and root tissues when soil was flooded annually for 45 days. Additionally, soil flooding did not initiate leaf abscission by the ontogenetically advanced shrubs studied in our experiment.

While 45 days of annual soil flooding impacted *L. melissifolia* established beneath intermediate light, biomass accumulation of plants receiving high light was not affected by this treatment. This finding refuted our hypothesis that soil flooding stress would reduce plant biomass accumulation. We do not know why plants established under these respective light environments differed in their response to soil flooding. But, we speculate that acclimation to high light may have masked shrub response to relatively short-term soil flooding. We previously discussed how shrubs receiving high light (and no soil flooding) likely experienced diurnal water stress that led to extended periods of stomatal closure. The stomatal response of plants exposed to soil flooding (Kozlowski and Pallardy 1979,

Mielke 2005a, 2005b, Branco et al. 2017) may parallel stomatal acclimation to diurnal water stress (Hsiao 1973, Angelopoulos et al. 1996, Galmés et al. 2007). Thus, we would not observe additional reductions in biomass accumulation relative to soil flooding if the stomatal responses to these two stress factors were similar, and if stomatal function was the primary limitation to photosynthesis during short-term soil flooding (Lockhart et al. 2017).

As with plants grown in the high-light environment, annual 45-day soil floods had no effect on biomass accumulated by *L. melissifolia* shrubs established in the low-light environment. We previously reported that in the absence of soil flooding, shrubs receiving low light accumulated 98% less biomass than shrubs receiving high or intermediate light—this is indicative of the significant stress exerted by low light on understory *L. melissifolia*. While we expected soil flooding to further reduce biomass accumulation of shrubs receiving low light (Lensen et al. 2003), our findings are comparable to those reported for other species. Branco et al. (2017), who grew *Theobroma cacao* under 1% of available sunlight, found that 56 days of soil flooding had no further effect on plant mass. Likewise, *Genipa americana* seedlings receiving 8% of full sunlight accumulated equal amounts of biomass when raised with or without 100 days of flooding (Lavinsky et al. 2007). These results indicate that the apparent stress of light deprivation is sufficiently influential on plant function to prevent any further reduction in biomass accumulation due to additional days of soil flooding. Several authors have described this static response by suggesting the impact of one stress factor dominates plant function such that a second stress factor has little or no impact on plant growth (Lensen et al. 2003, Niinemets 2010, Najeeb et al. 2016).

Extending annual soil flooding to 90 days brought additional responses in biomass accumulation by *L. melissifolia*. In the high-light environment, extended soil flooding decreased shrub biomass accumulation by about 335 g (76%) relative to the 0 d or 45 d treatment levels. This flood-induced biomass reduction appears to be in contrast with responses observed when plants were grown under intermediate or low light. To explain these responses, we previously described how the high-light environment led to a 32% reduction in shrub biomass—this was attributed to water stress imparted by relatively high vapor pressure deficits associated with this light regime. While annual soil flooding for 45 days resulted in no observable consequence, lengthening the flooding regime to 90 days reduced biomass accumulation by 43%. Thus, we demonstrate that the treatment combination of high light and 90 days of soil flooding brought an interacting effect on *L. melissifolia* biomass accumulation.

Our understanding of the physiology leading to the decreased biomass accumulation noted above is incomplete, but our analysis of plant biomass fractions indicates that the plant shifted biomass away from the root fraction and toward the leaf fraction. Others studying how soil flooding influences plant morphology have reported this pattern of morphological plasticity (Mielke, de Almeida, et al. 2005, Branco et al. 2017). Though an environment of high light and 90 days of annual flooding favored biomass accumulation in the leaf fraction, we recognize that this treatment combination placed a substantial limitation on *L. melissifolia* photosynthesis. In earlier work from our FRF study site, Lockhart et al. (2017) demonstrated that net photosynthesis of shrubs acclimated to the high-light environment was reduced by 74% during soil flooding—90 days of soil flooding constituted about 25% of each

growing season. This significant loss of carbon gain via fixation during the early growing season would certainly constrain biomass accumulation relative to treatment combinations of lesser flood durations.

This research presents several relevant implications for managing *L. melissifolia* colonies in mature floodplain forests of the MAV. A central finding of this experiment is the plasticity in *L. melissifolia* whole-plant morphology that provided for satisfactory growth under a range of light environments and soil flooding regimes. Our results demonstrate that *L. melissifolia* shrubs can persist under stressful environmental conditions of low light availability and seasonal soil flooding through three years. This tolerance to prominent environmental stress factors in floodplain forests provides a window of opportunity to initiate active management of targeted colonies. A second implication drawn from this experiment is our suggestion that *L. melissifolia* colonies existing under heavy shade would likely respond to active management that provides favorable light availability regardless of the hydrological regime of the site. Others have indicated a positive growth response by this species when released from a heavily shaded environment (Glitzenstein 2007, Lockhart et al. 2015). Our findings support this observation for colonies established on sites representative of various soil flooding regimes. However, our research does not address the role of soil flooding in moderating the potential impact of competing vegetation on *L. melissifolia* survival and growth. A third implication from our research is drawn from the range of light availability (37% to 70% light availability) under which we observed robust biomass accumulation by this species. This finding suggests wide flexibility in the development and application of forest stand treatment options that facilitate colony growth. That is, managers of *L. melissifolia* habitat could implement silvicultural treatments of various intensities or stand density targets to promote stand structure conducive to colony vigor and growth.

Conclusions

We report on the plasticity of biomass accumulation by the endangered *L. melissifolia* relative to light availability and soil flooding. Light availability held the strongest effect on biomass accumulation during this three-year field study, but this effect was not consistent with our hypothesis that plant mass would decrease with decreasing light availability. Plant mass showed a non-linear response to light availability with the greatest biomass accumulation occurring under intermediate light. Plants raised in the high-light environment accumulated less biomass than plants receiving intermediate light—a relatively higher root biomass fraction suggests water stress limited plant growth in the high-light environment. *L. melissifolia* mass was least when plants were grown under low light. The relatively high leaf and stem biomass fractions of plants raised in low light is indicative of light deprivation that limited plant growth.

Our analysis illustrated interaction between light availability and soil flooding effects whereby biomass accumulation of *L. melissifolia* in response to soil flooding differed by light environment. This finding was inconsistent with our hypothesis that soil flooding would limit plant mass in all light environments. Annual soil flooding for 90 days had no impact on biomass accumulation of plants raised under low light—the predominance of light deprivation in this environment conditioned the apparent static response to soil flooding. A decrease in plant mass attributable to soil flooding was

apparent when shrubs raised in the intermediate-light environment received 45 days of annual soil flooding. The impact of flooding on biomass accumulation in this light environment was maintained when annual soil flooding was extended to 90 days. Plant mass was unaffected by 45 days of annual soil flooding when *L. melissifolia* was established in a high-light environment. But, extending soil flooding to 90 days substantially reduced plant mass and shifted accumulation away from root tissue to leaf tissue. These findings establish the influence of late dormant season/early growing season soil flooding to *L. melissifolia* growth and vigor. Plants established in this study withstood annual soil flooding and resumed positive and substantial biomass accumulation through two subsequent growing seasons, particularly in the intermediate- and high-light environments.

Supplementary Materials

Supplementary data are available at *Forest Science* online.

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