Plant Ecol (2013) 214:893–905
DOI 10.1007/s11258-013-0211-0

Lindera melissifolia responses to flood durations and light regimes suggest strategies for recovery and conservation

Brian Roy Lockhart · Emile S. Gardiner · Theodor D. Leininger ·
Paul B. Hamel · Kristina F. Connor · Margaret S. Devall ·
Nathan M. Schiff · A. Dan Wilson

Received: 20 July 2012 / Accepted: 6 May 2013 / Published online: 21 June 2013

Abstract Passive management to preserve endangered plant species involves measures to avoid anthropogenic disturbance of natural populations, but this approach may not sustain plants that require disturbance-maintained habitats. Active management is often necessary to maintain existing habitats or provide new habitats for endangered species recovery. Our objective was to examine the effects of two disturbances in floodplain forests, soil flooding and light availability, on survival, stem length, stem diameter and ramet production of endangered *Lindera melissifolia* (Walt.) Blume. We used a water impoundment facility to control the timing and duration of flooding (0, 45 or 90 days) and shade houses to vary light availability (70, 63 or 5 % ambient light). Hydroperiod had little direct effect on steckling survival, stem length growth and stem diameter growth, supporting indications that soil flooding may be important for reduction of interspecific competition in *L. melissifolia* habitat. Greater ramet production by stecklings receiving no soil flooding likely resulted from longer periods of favorable soil conditions during each growing season. Positive stem length growth and stem diameter growth under all light levels demonstrates the plasticity of this species to acclimate to a range of light environments, though, greatest survival and stem length growth occurred when *L. melissifolia* received 37 % light, and stem diameter growth was greatest beneath 70 % light. Further, female clones produced more ramets as light availability increased. These results indicate that passive management absent natural disturbance could jeopardize sustainability of extant *L. melissifolia* populations, and this species would respond favorably to active management practices that create canopy openings to increase understory light availability.

Keywords Active restoration · Gender · Lauraceae · Pondberry · Shade · Understory

Introduction

Plant species endemic to temperate floodplain forests are adapted to unique physicochemical environments derived from the interaction of periodic inundation and other abiotic and biotic factors (Junk et al. 1989). Sunlight availability is a prominent abiotic factor likely to interact with floodplain inundation to control

B. R. Lockhart (✉) · E. S. Gardiner ·
T. D. Leininger · P. B. Hamel · M. S. Devall ·
N. M. Schiff · A. D. Wilson
USDA Forest Service, Southern Research Station, Center
for Bottomland Hardwoods Research, P.O. Box 227,
Stoneville, MS 38776, USA
e-mail: blockhart@fs.fed.us

K. F. Connor
USDA Forest Service, Southern Research Station,
Restoring and Managing Longleaf Pine Ecosystems,
521 Devall Drive, Auburn, AL 36849, USA

plant structure of floodplain forests (Hall and Harcombe 1998; Niinemets 2010). Environmental stresses resulting from the interaction of floodplain inundation and light availability may be most influential on survival, growth and regeneration of understory plants. While understory plants, typically small trees, woody shrubs, vines and herbaceous plants, can comprise more than 50 % of vascular plant richness in floodplain forests (Schnitzler et al. 2005), little is known about how particular species respond to the stresses imposed by interacting factors such as floodplain inundation and light availability.

The hydrologic regime, or the timing, duration and depth of floodwater, distinguishes floodplain environments from upland and aquatic systems (Junk et al. 1989), and is a primary determinant of understory species structure in floodplain forests. Plants endemic to floodplain forests may exhibit a range of adaptations to tolerate or avoid soil flooding. Morphological modifications include development of hypertrophied lenticels, adventitious roots and stem buttressing; physiological processes include rhizosphere oxidation and anaerobic respiration. These adaptations are well known among floodplain tree species (Kozlowski 1984), while less is known about the influence of soil flooding on understory woody species.

The high tree species richness of some floodplain forests promotes development of densely stratified overstory and midstory canopies that intercept sunlight, leaving little light available to understory plants. Workers in the southeastern USA, for example, commonly observed light levels less than 5 % of full sunlight in floodplain forest understories (Lhotka and Loewenstein 2006). To compete in shaded environments, understory woody plants exhibit a range of adaptations to more efficiently utilize available sunlight. Adaptations include the ability to develop thin, large leaf blades presented horizontally with minimal blade overlap. Changes in leaf blade morphology and physiology lead to a lower light saturation point, lower light compensation point, and greater quantum yield at low light than sun leaf blades (Givnish 1988). In conditions of low light, carbon photosynthate distribution favors shoot development for light gathering purposes (Gardiner and Hodges 1998).

Researchers have shown that multiple environmental stresses can be more influential to floodplain understory plants than single stresses. For example, Hall and Harcombe (1998) proposed a soil flooding—shade tradeoff hypothesis where shade-tolerant but flood-intolerant species may be restricted to high light environments when soil flooding is present. The combination of soil flooding and low light availability may be too stressful for most species to tolerate; therefore, shade-tolerant species may only survive in high light environments where they can grow fast enough to escape soil flooding. They also hypothesized that flood-tolerant species may persist in light levels that are lower than expected. Battaglia and Sharitz (2006) tested the soil flooding—shade tradeoff hypothesis for common tree species in the Congaree National Park in South Carolina, USA. Their results were mixed as some species (e.g., *Fraxinus pennsylvanica* Marsh., *Quercus* spp. and *Ulmus americana* L.) followed the soil flooding—shade tradeoff hypothesis while *Acer rubrum* L. did not. Further, Mielke and Schaffer (2010) found soil flooding and light availability each affected photosynthetic rates and growth of *Eugenia uniflora* L., a small tropic shrub native to South American, but the interaction of these two factors had little influence on plant photosynthesis and growth. These results indicate plant responses to soil flooding, light availability and the interaction of soil flooding and light availability is species specific. Greater knowledge of how plants are affected by interacting environmental factors in an understory floodplain environment could be vital to informing active management strategies aimed at species conservation.

Lindera melissifolia (Walt.) Blume (Lauraceae) is a deciduous, woody shrub endemic to low-lying forests of the southeastern USA (USFWS 1986). It is dioecious, rhizomatous and grows on sites subject to seasonal flooding that can last for several days to several months between January and June. Impacts of deforestation and degradation of floodplain forests in the Lower Mississippi Alluvial Valley (LMAV) have reduced potential *L. melissifolia* habitat, and its current distribution in this region is maintained in isolated colonies within scattered forest patches (Hawkins et al. 2010). Consequently, the U.S. Fish and Wildlife Service listed this species as endangered in 1986 (USFWS 1986). Information on the functional biology of *L. melissifolia* is sparse. Unknown are the effects of soil flooding in concert with light availability on the survival, length, diameter and ramet production of this species. This report presents results from large-scale experimental impoundments designed to determine the influence of hydroperiod (timing and duration of soil flooding) and light availability on survival, stem length, stem diameter and number of ramets of *L. melissifolia* stecklings (rooted cuttings) over a two-year period. Our research questions included: (1) Does hydroperiod affect *L. melissifolia* survival, stem length, stem diameter or ramet production?; (2) Does an intermediate light level result in best *L. melissifolia* survival, stem length, stem diameter and ramet production?; (3) Does the interaction of hydroperiod and light availability influence *L. melissifolia* survival, stem length, stem diameter and ramet production?; and (4) Do male *L. melissifolia* plants exhibit greater survival, stem length, stem diameter and ramet production than female *L. melissifolia* plants?

Materials and methods

Location

The study was conducted in Sharkey County, MS, USA on the Theodore Roosevelt National Wildlife Refuge Complex (32°58′N, 90°44′W). Temperatures average 17.3 °C daily with a range from 27.3 °C in July to 5.6 °C in January, and annual precipitation averages 1,350 mm (WorldClimate 2008). The experimental site was deforested for agriculture production prior to the 1970s. Row crop production continued on the site until 1994 when it was acquired by the Refuge Complex. The heavy clay alluvial soil at the experimental site is representative of the Sharkey series, a common soil in the LMAV, and is classified as a very-fine, smectitic and thermic Chromic Epiaquerts.

Treatments

The study was conducted in the Flooding Research Facility (FRF), which is comprised of 12, 0.4-ha rectangular impoundments that can be flooded to desired depths for controlled time periods (see Lockhart et al. 2006). Each of the 12 impoundments was randomly assigned one of three hydroperiod regimes: no soil flooding (0 days), 45 days of soil flooding, or 90 days of soil flooding. These hydroperiods were selected to represent a linear increase in flooding duration. Soil flooding was initiated on 1 March for the 2006 and 2007 growing seasons. Ground water was used to flood each impoundment. Water depth was maintained near 12 cm in 2006 and 19 cm in 2007. Greater water depth, relative to steckling lengths, was maintained in 2007 to reduce pump operations. At the end of each scheduled hydroperiod, water was drained from respective impoundments and ambient rainfall was the only source of soil moisture for the remainder of each growing season.

Three rectangular shade houses (25.6 m long by 7.3 m wide by 2.4 m tall) were constructed in each impoundment. Three light levels, 70, 37 and 5 % of full sunlight, were randomly assigned to houses in each impoundment. Light availability was controlled using neutral density shade cloth (PAK Unlimited, Inc., Cornelia, GA, USA).

Plant material

Lindera melissifolia planting stock was produced by Knight Hollow Nursery, Inc., Middleton, WI, USA. Parent plants representing different genotypes and gender were randomly chosen from colonies in the LMAV. About 300 stecklings were propagated from each of 20 genotypes, 9 male and 11 female. These stecklings were repotted into 0.98 L Deepot™ tubes (Stuewe and Sons, Inc., Tangent, OR, USA) containing a 2 parts peat to 1 part sand medium supplemented with superphosphate, 10:10:10 NPK and Milorganite® (Milwaukee Metropolitan Sewage District, Milwaukee, WI, USA). This material was grown for 5 months in a climate-controlled greenhouse supplemented with artificial light.

Ninety-six single-stemmed stecklings were planted on a 1.2 m by 1.2 m spacing in each shade house at the FRF during April 2005. Planting material was randomly assigned within each shade house so that each genotype was well represented. Transplants were raised without soil flooding for the 2005 growing season to allow for acclimation to the field environment. Plants were maintained free of competing vegetation for the duration of the experiment by hand hoeing and directed applications of herbicides to remove weeds.

Environmental monitoring and steckling measurements

Environmental sensors and data recorders were located in each shade house of one hydroperiod replicate. Sensors included two LI-190 quantum sensors (Li-Cor Biosciences, Lincoln, NE, USA) that measured photosynthetic photon flux density (μmol m^{-2} s^{-1}) and one relative humidity (%)-air temperature (°C) sensor. These sensors were connected to LI-1400 dataloggers that recorded averaged observations every 15 min. Additionally, these same variables were measured with another meteorological station positioned in an open area in the center of the FRF. Recordings were initiated on 22 March 2005 and continued through the duration of the study.

Stecklings were measured immediately after planting and following the 2005, 2006, and 2007 growing seasons. Stem length was measured from the ground to the base of the terminal bud. Stem diameter was measured with dial calipers 2 cm above the ground in two directions perpendicular to each other to compute an average diameter. The original stem was measured in 2005, along with a count of associated ramets. Length and diameter of the original stem and all ramets were measured in 2006 and 2007.

Design and analyses

A 3 × 3 × 2 factorial design was used to evaluate three hydroperiod levels, three light levels and two gender levels in 2006 and 2007. These fixed-effect treatments were evaluated in a completely randomized split–split plot design with hydroperiod representing the whole-plot treatment, light level representing the split-plot treatment and gender representing the split–split plot treatment. Data analysis for initial steckling measurements at the time of planting involved *t* tests to compare height and diameter. Because hydroperiod was not implemented until 2006, the 2005 growing season analysis consisted of a split-plot design with light level representing the whole-plot treatment (with 12 replicates) and gender representing the split-plot treatment.

Analyses were conducted using the GLM procedure in SAS 9.2 (SAS Institute, Inc., Cary, NC, USA) with adjustments in error terms for hydroperiod. Variables analyzed included survival (%), original stem length (cm), original stem diameter (mm), stem length growth (cm), stem diameter growth (mm) and number of ramets. Stem length growth and stem diameter growth were calculated as the difference in stem length or stem diameter between two consecutive growing seasons. Vapor pressure deficit (VPD; kPa) was calculated from measured air temperature and relative humidity using equations of Snyder and Paw (2002). Environmental data were pooled by light availability ($n = 3$). Duncan's Multiple Range Test was used for mean separation. Statistical significance among treatment means for each response variable was determined at $\alpha = 0.05$.

Results

Growing environment

Ambient light under the 70 and 37 % light levels was 71.5 and 32.6 %, respectively, in 2006. Ambient light for the 5 % light level was 2.2 % of ambient light. Diurnal patterns of light showed a typical bell-shaped pattern on cloud-free days with progressively increasing light to a peak around 12:00, followed by decreasing light until dusk (Fig. 1a–c). Light differed between treatment levels with $70 > 37 > 5$ % between 06:00 and 18:30 (P for 15-min readings was <0.01).

Air temperatures were greater under 5 % light compared to 70 and 37 % light, especially from mid-morning to mid-afternoon (Fig. 1d–f). Greater air temperature beneath 5 % light was indicative of radiant heat trapped beneath the shade cloth. No differences in air temperatures were found between 70 and 37 % light through the diurnal period. Relative humidity was similar through the diurnal period for all light levels except for brief periods when 5 % light had a lower relative humidity than 70 and 37 % light (Fig. 1g–i). Greater air temperatures and low relative humidity resulted in greater diurnal VPD under 5 % light, especially in July and September (Fig. 1j–l).

Survival

Lindera melissifolia steckling survival was highly influenced by light level and less so by hydroperiod (Table 1; Fig. 2). Following the 2007 growing season, survival was greater for stecklings receiving 37 % light (98.0 ± 0.5 standard error) than for stecklings receiving 70 % (89.8 ± 1.2) and 5 % light (75.2 ± 2.2). Female stecklings consistently showed a 2 % greater survival than male stecklings regardless of hydroperiod or light (Table 1; Fig. 2).

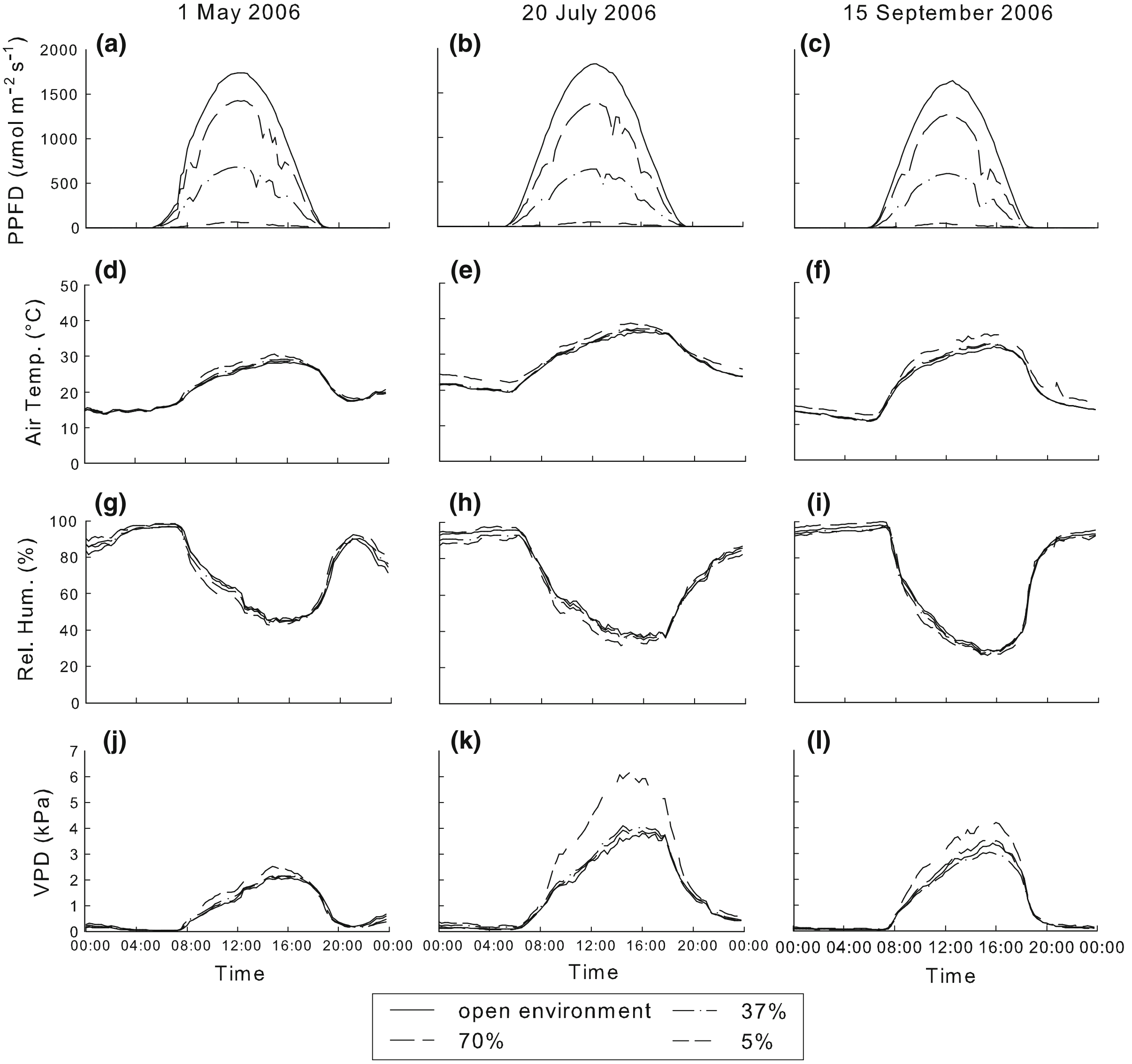

Fig. 1 Light (PPFD), air temperature, relative humidity and vapor pressure deficit (VPD) during 3 days (spring, mid-summer and late summer) under open conditions, 70, 37 and 5 % light

Stem length

Surviving stecklings exhibited increases in stem length each year (Table 1; Fig. 3). Stem length at the time of planting averaged 21.8 ± 1.7 cm, and increased to 115.9 ± 4.5 cm by the end of 2007. Stem length was not affected by hydroperiod within a year, but by 2007 a pattern of increasing stem length was beginning to emerge for stecklings that received no soil flooding or 45 days soil flooding. This pattern of increasing stem length over time is reflected in annual stem length growth. Steckling stem length growth was similar among hydroperiods in 2006, but stecklings with no soil flooding had 21 % greater stem length growth in 2007 than stecklings that received soil flooding (Table 2). Further, stecklings receiving 45 days soil flooding had 12 % greater stem length growth than stecklings receiving 90 days soil flooding.

Light level strongly influenced *L. melissifolia* stem length (Fig. 3). After the 2007 growing season, stecklings raised beneath 37 % light were 24 and 60 % longer than those raised beneath 70 and 5 %

Table 1 Summary of analysis of *L. melissifolia* stecklings response to hydroperiod, light availability and gender through three growing seasons

Source	*df*	*F* value (*P* value)			
		Survival	Stem length	Stem diameter	No. ramets
2005 (planting)					
Gender	[a]	–[b]	(0.58)	(0.31)	–[b]
2005					
Light availability	2	23.45	284.64	1,351.08	93.71
		(<0.01)	(<0.01)	(<0.01)	(<0.01)
Gender	1	3.56	2.32	0.43	6.25
		(0.06)	(0.13)	(0.52)	(0.02)
Light availability × gender	2	1.48	9.17	2.41	2.59
		(0.24)	(<0.01)	(0.11)	(0.09)
2006					
Flood	2	4.58	1.23	0.91	1.90
		(0.06)	(0.36)	(0.45)	(0.23)
Light availability	2	121.13	3,479.94	4,594.22	1,080.09
		(<0.01)	(<0.01)	(<0.01)	(<0.01)
Gender	1	3.79	13.67	1.79	71.59
		(0.06)	(<0.01)	(0.19)	(<0.01)
Flood × light availability	4	2.56	1.13	3.52	1.29
		(0.07)	(0.37)	(0.03)	(0.31)
Flood × gender	2	0.34	1.80	3.28	0.29
		(0.71)	(0.19)	(0.05)	(0.56)
Light availability × gender	2	0.02	18.08	1.82	15.12
		(0.98)	(<0.01)	(0.18)	(<0.01)
Flood × light availability × gender	4	0.11	0.24	1.75	1.80
		(0.98)	(0.91)	(0.17)	(0.16)
2007					
Flood	2	4.29	2.25	1.52	5.14
		(0.07)	(0.19)	(0.29)	(0.05)
Light availability	2	117.63	3,968.69	3,410.83	1,078.89
		(<0.01)	(<0.01)	(<0.01)	(<0.01)
Gender	1	4.25	9.29	0.11	31.85
		(0.05)	(0.01)	(0.74)	(<0.01)
Flood × light availability	4	1.59	1.40	2.81	3.87
		(0.22)	(0.27)	(0.06)	(0.02)
Flood × gender	2	0.00	0.38	2.20	1.06
		(0.99)	(0.69)	(0.14)	(0.36)
Light availability × gender	2	0.06	8.21	1.08	7.40
		(0.94)	(<0.01)	(0.35)	(<0.01)
Flood × light availability × gender	4	0.12	0.27	0.60	0.70
		(0.97)	(0.90)	(0.67)	(0.60)

[a] *t* test degrees of freedom was 1,454 for male plants and 1,994 for female plants

[b] Survival and number of ramets not available

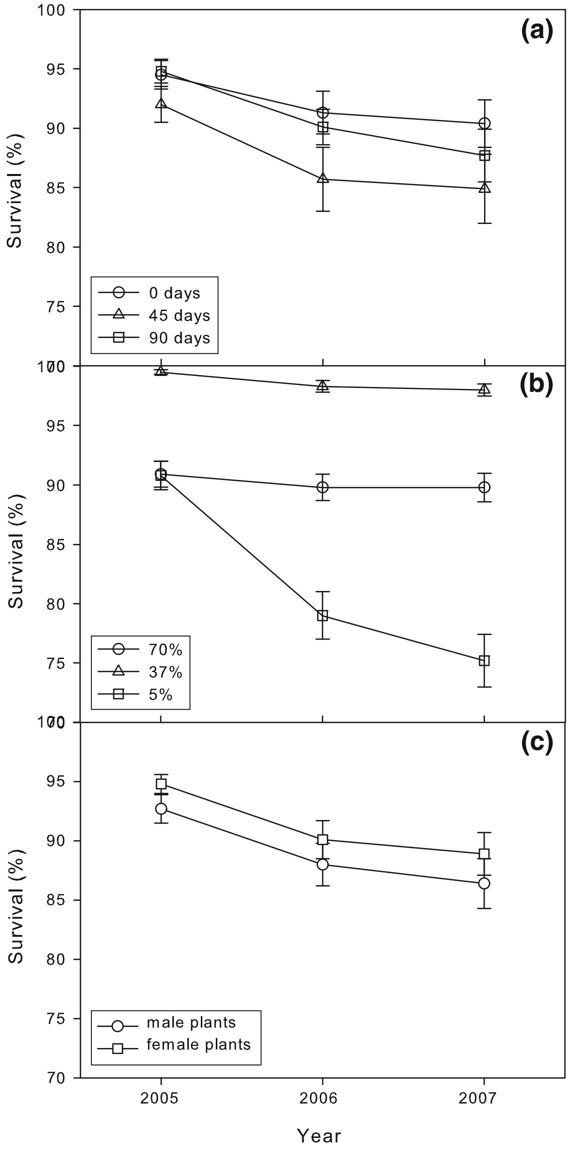

Fig. 2 *L. melissifolia* steckling survival by **a** hydroperiod, **b** light and **c** gender. Hydroperiod was not implemented in 2005; therefore, steckling survival for 2005 is for information purposes

light, respectively. A light level by gender interaction existed in 2006 and 2007 (Table 1) because male stecklings raised beneath 70 and 37 % light had slightly longer stem lengths than female stecklings.

Stem diameter

Lindera melissifolia steckling diameter across all treatment combinations at the time of planting averaged 1.8 ± 0.1 mm, and increased 506 % to 10.9 ± 1.0 mm by the end of 2007. Unlike stem length, hydroperiod and light level interacted to affect stem diameter (Table 1; Fig. 4). The hydroperiod by light availability interaction in 2006 was due to stecklings receiving the 45 day flood/70 % light combination being 2 % larger in diameter than stecklings receiving the 45 day flood/37 % light combination. Stecklings receiving the no flood/37 % light and the 90 day flood/37 % light combinations were 3 and 7 % larger in diameter than stecklings receiving the no flood/70 % light and the 90 day flood/70 % light combination, respectively. In 2007, stecklings receiving the no flood/70 % light and 45 day flood/70 % light combinations were 5 and 10 % larger in diameter than stecklings receiving the no flood/37 % light and 45 day flood/37 % light combinations, respectively, while no difference existed between stecklings receiving the 90 day flood/70 % light and 45 day flood/37 % light combination (Fig. 4). Male and female *L. melissifolia* did not differ in stem diameter (Table 1). Stecklings beneath 70 and 37 % light had greater stem diameter growth than stecklings beneath 5 % light after each growing season (Table 3). Further, after the 2007 growing season, stecklings receiving 70 % light had 18 % more stem diameter growth than stecklings receiving 37 % light (Table 3).

Table 2 *L. melissifolia* steckling stem length growth (original stems) by hydroperiod

Hydroperiod	2005 (cm)[a]	2006 (cm)	2007 (cm)
0 days	28.2 (2.9) a[b]	29.3 (3.2) a	42.6 (4.7) a
45 days	28.8 (2.8) a	26.4 (3.1) a	36.0 (4.3) b
90 days	27.5 (2.8) a	25.2 (2.9) a	31.6 (3.7) c
F value	0.13	1.73	12.09
(*P* value)	(0.88)	(0.25)	(0.01)

Values in parentheses are standard errors

[a] Hydroperiod was not implemented in 2005; therefore, steckling length growth for 2005 is for information purposes

[b] Different letters within a column represent a difference at $P \leq 0.05$

Ramet production

Following the end of the 2005 growing season, 46 % of surviving stecklings had produced ramets, with an average of 0.9 ± <0.1 ramets per plant. The number of ramets per steckling increased 961 % during the 2006 growing season, and increased an additional

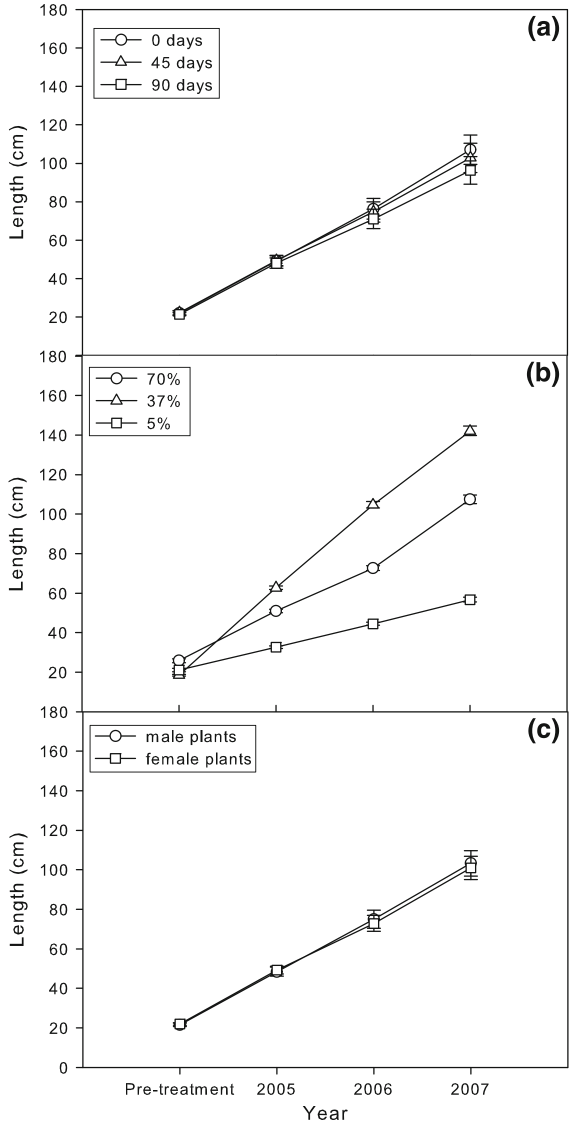

Fig. 3 *L. melissifolia* original stem length by **a** hydroperiod, **b** light and **c** gender. See Fig. 2 for explanation

99 % during the 2007 growing season. Hydroperiod and light level influenced ramet production (Table 1). Stecklings receiving 5 % light developed 2.6 ± 0.2 ramets during the 2007 growing season regardless of hydroperiod (Fig. 5). Concurrently, *L. melissifolia* stecklings raised without soil flooding under 70 and 37 % light produced 34.8 ± 1.8 ramets per plant. Stecklings assigned to either 70 or 37 % light along with soil flooding were intermediate in ramet production. Light level and gender also interacted to influence ramet production. Female stecklings grown beneath 70 and 37 % light produced 19 and 7 % more ramets than male stecklings at the end of the 2006 and 2007 growing seasons, respectively (Fig. 5).

Table 3 *L. melissifolia* steckling diameter growth (original stems) by light level

Light level	2005 mm	2006 mm	2007 mm
70 %	3.3 (0.1) a[a]	3.9 (0.1) a	5.2 (0.2) a
37 %	3.7 (0.1) b	3.9 (0.1) a	4.4 (0.1) b
5 %	1.3 (<0.1) c	0.6 (<0.1) b	0.4 (0.1) c
F value	1,324.07	2,341.43	2,982.12
(*P* value)	(<0.01)	(<0.01)	(<0.01)

Values in parentheses are standard errors

[a] Different letters within a column represent significant differences at $P \leq 0.05$

Discussion

Soil flooding

Our results indicate *L. melissifolia* was minimally affected by the soil flooding imposed in this experiment. Survival, stem length and stem diameter growth were similar between non-flooded and flooded stecklings in 2006 and 2007. Visual inspection of stecklings following flood water removal revealed no hypertrophied lenticels or adventitious root development.

Lindera melissifolia stecklings did, however, have lower stem length growth with increasing hydroperiod length during the 2007 growing season, but stem length growth in 2007 was greater than in 2006 for each hydroperiod. Also, non-flooded stecklings produced more ramets than flooded stecklings by the end of the 2007 growing season, but, as with stem length growth, ramet production in 2007 exceeded 2006 ramet production for all hydroperiods. Perhaps our strongest evidence that *L. melissifolia* is minimally stressed by soil flooding is our observation that stecklings which received soil flooding progressed through flowering and leaf-out while flood water was present. Our findings indicate that *L. melissifolia* stecklings acclimated to soil saturation through physiological mechanisms rather than morphological mechanisms. Acclimation to temporally saturated floodplain soil by altering physiological function has

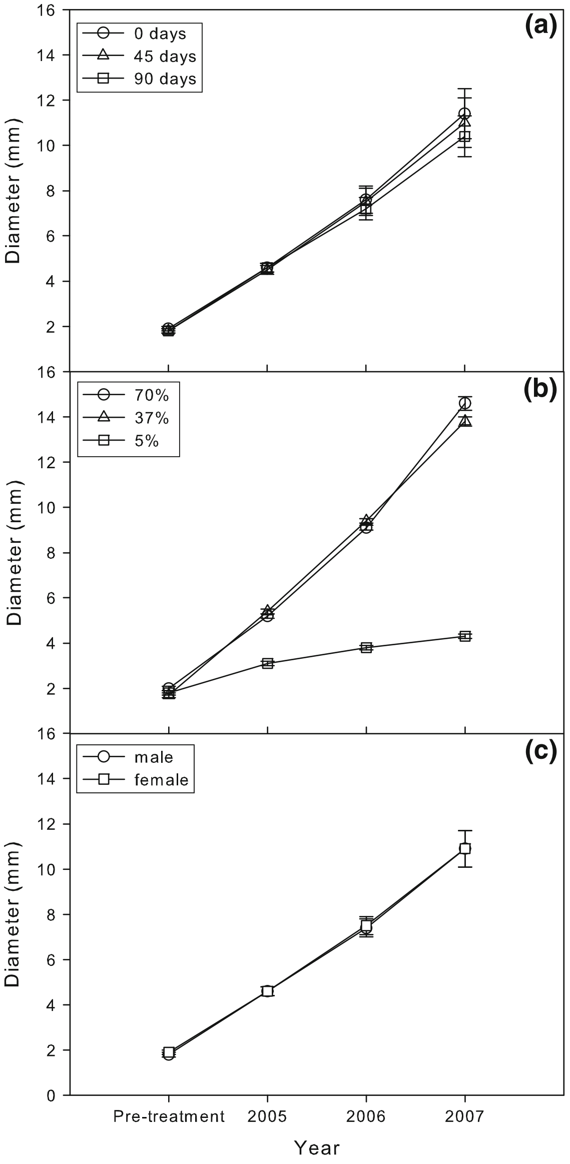

Fig. 4 *L. melissifolia* original stem diameter by **a** hydroperiod, **b** light and **c** gender. See Fig. 2 for explanation

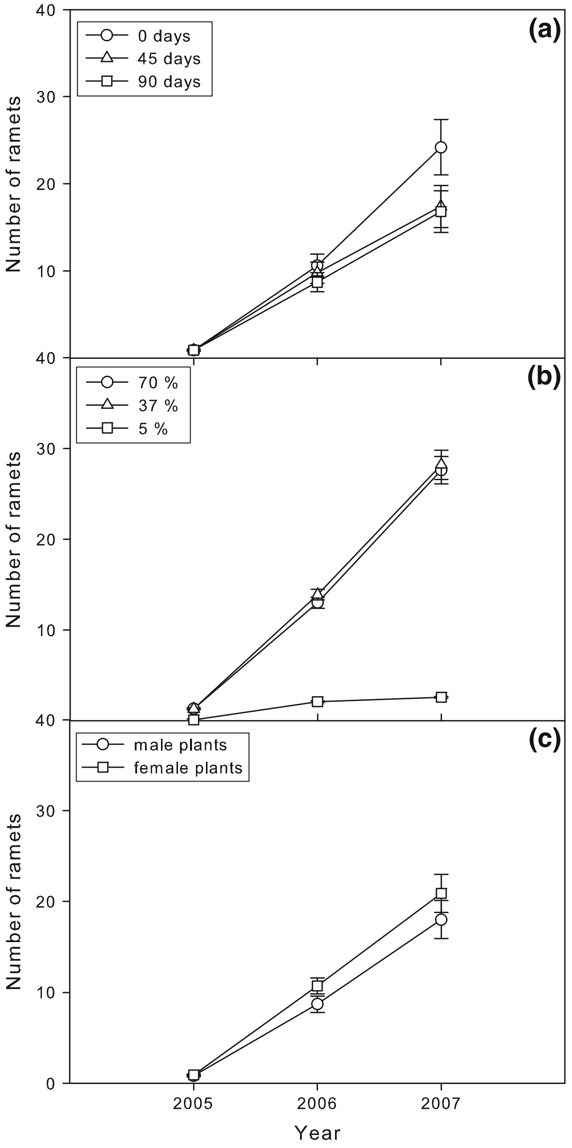

Fig. 5 *L. melissifolia* number of ramets per plant by **a** hydroperiod, **b** light and **c** gender. See Fig. 2 for explanations

been observed for many other floodplain species (Kozlowski 1984).

Following removal of flood water, stecklings grew well as indicated by the increases in stem length, stem diameter and ramet production in 2007. Our results indicate soil saturation primarily influenced *L. melissifolia* stecklings by reducing growing season length, rather than inflicting acute stress deleterious to long-term survival, stem length and stem diameter. *L. melissifolia* in this experiment grew best where soil flooding was absent, but the species also endured 90 days of soil flooding for two consecutive years with minimal consequences.

Light availability

Our results showed light availability had a strong effect on *L. melissifolia* survival, stem length and stem diameter. Stecklings grown in 5 % light had the lowest survival, and lowest stem length and diameter growth throughout the study period. These stecklings developed few new leaves following the initial spring flush of about five leaves per steckling. Aleric and Kirkman (2005) noted that *L. melissifolia* plants in low light (19 % full sunlight) maintained a lower light-saturated photosynthesis rate and light compensation point than plants receiving intermediate (42 % full sunlight) or full sunlight.

Lindera melissifolia stecklings receiving 70 % light experienced greater survival, stem length and stem diameter than stecklings receiving 5 % light, but lower survival and stem length than stecklings receiving 37 % light. Stecklings in high light appeared to be under moisture stress because leaf blades were consistently folded and at sharp angles of inclination. These morphological traits represent paraheliotropic mechanisms for avoidance of excessive light to reduce moisture stress or photoinhibition. Aleric and Kirkman (2005) and Lockhart et al. (2012) also observed *L. melissifolia* leaf blade folding by seedlings raised under high light.

Greater steckling diameter growth observed in 70 % light than 37 % light reflects a plastic response in carbon distribution probably driven by water stress. Stecklings receiving high light probably experienced diurnal periods of water stress which likely triggered carbon allocation to roots. Enhanced root growth would allow stecklings to increase water absorption to maintain stomatal guard cell turgor and thereby support photosynthesis. High light environments are characterized by greater air temperature and lower relative humidity than shaded environments. Leaf surface temperatures under high light were probably greater than for leaves exposed to intermediate light. Therefore, blades in high light would have experienced greater VPDs than leaves in low light, especially during the summer months. High VPDs reduce stomatal openings or completely close guard cells (Yong et al. 1997), subsequently reducing photosynthetsis.

Lindera melissifolia stecklings raised under 37 % light maintained greater survival and stem length growth than stecklings raised beneath 70 or 5 % light. It is possible that lower VPDs for stecklings beneath 37 % light produced a less stressful growing environment for stecklings. A lower VPD would have led to increased carbon assimilation by supporting a higher rate of diurnal photosynthesis. We observed *L. melissifolia* stecklings receiving 37 % light had larger leaves and longer internode lengths than stecklings receiving 70 % light. This concurs with earlier findings from *L. melissifolia* seedlings in a growth chamber experiment (Lockhart et al. 2012), and adds evidence that *L. melissifolia* exhibits morphological plasticity consistent with reducing light interception and moisture stress when raised under high sunlight.

Results from this study confirm that *L. melissifolia* can grow beneath a wide range of light availability, but appears to grow best when receiving intermediate light (Aleric and Kirkman 2005; Lockhart et al. 2012). *L. melissifolia* acclimates to high light by developing morphological features, such as folded sun leaves with angles of inclination to reduce exposure to high light. Further, this species acclimates to low light by developing shade leaves that are relatively large and displayed horizontally. *L. melissifolia* thus exhibits morphological plasticity to a range of light environments (Aleric and Kirkman 2005), and this plasticity could provide managers with flexibility in determining habitat management options for its recovery.

Soil flooding and light availability interaction

A key issue associated with plants growing in floodplain forest understory environments is the interaction of soil flooding and light availability (Niinemets 2010). Others have hypothesized that this interaction can determine spatial and temporal patterns of plant reproduction by influencing regeneration mechanisms, and differential survival and growth among plants in floodplains (Menges and Waller 1983; Lavinsky et al. 2007). Menges and Waller (1983), working with herbaceous species in Wisconsin floodplain forests, found light availability was important in differentiating plant guilds only when soil flooding was infrequent. Conversely, Lavinsky et al. (2007) indicated soil saturation and light availability had a synergistic effect on the establishment and growth of *Genipa americana* L., a small tree of South American floodplain forests. Undoubtedly, soil flooding and light availability can present a complex interaction fundamental to the survival, growth and regeneration of many floodplain forest plants.

In our study, significant hydroperiod by light interactions occurred with *L. melissifolia* steckling stem diameter in 2006 and 2007, and number of ramets in 2007. Stecklings receiving high light without soil flooding or with 45 days soil flooding developed stems with larger diameters than stecklings receiving 90 days soil flooding and stecklings receiving 37 % light.

Stecklings receiving no soil flooding and intermediate to high light produced more ramets in 2007 than stecklings in similar light levels that received soil flooding. Greater ramet production in the absence of soil flooding may affect future *L. melissifolia* regeneration and distribution, although stecklings receiving soil flooding with high and intermediate light produced 83 % more ramets in 2007 than in 2006. Stecklings in low light produced few ramets regardless of hydroperiod regime. As with other stem measurements, *L. melissifolia* ramet production appears to be a function of light availability, with soil flooding restricting growing season length for ramet production.

These results demonstrate that soil flooding is not a requirement for development of vigorous *L. melissifolia* plants. In contrast, stecklings receiving low light, regardless of hydroperiod, exhibited consistently poor stem length growth and stem diameter growth. Therefore, light availability appears to be the key factor responsible for maintaining *L. melissifolia* vigor. This finding is exemplified by stecklings that received 90 days of soil flooding and high or intermediate light. Stecklings receiving these treatment combinations showed high survival, stem length growth and stem diameter growth by the end of each growing season, demonstrating *L. melissifolia*'s resilience to flooding stress if given sufficient light during the growing season.

If soil flooding does not directly benefit *L. melissifolia* survival and growth, then why are natural colonies located on areas subject to soil flooding? We can only speculate that the answer may lie in the effects of soil flooding on other competing plant species. While *L. melissifolia* develops clonal colonies that casually appear to be free of interspecific competition, Hawkins et al. (2010) observed 69 vascular plant species growing in *L. melissifolia* colonies on three sites in Mississippi. It is possible that the flood tolerance exhibited by *L. melissifolia* enables it to colonize and dominate micro-sites with a flooding regime deleterious to species that are more competitive on drier micro-sites. If this is the case, soil flooding would be an important factor in the survival, stem length and stem diameter of *L. melissifolia* through its impact on interspecific competition.

Gender

Naturally occurring *L. melissifolia* colonies are strongly male biased (Wright 1994; Hawkins et al. 2007). For other plant species, female plants often allocate more photosynthate to sexual regeneration than do male plants, leading to possible greater competitive ability among male plants. Results from this study revealed few differences between male and female steckling survival, stem length and stem diameter. An important aspect of the current study was that stecklings were spaced to avoid intraspecific competition and the soil surface was kept free of other vegetation; therefore, neither gender had the opportunity to express differential competitive ability.

Differences observed between genders were related to interactions with light availability, and appeared to favor female stecklings. For example, female stecklings in 70 and 37 % light had slightly greater survival than male stecklings, while no differences occurred between genders in 5 % light. Likewise, female stecklings produced more ramets under these greater light availabilities. Assessment of survival, stem length and stem diameter of male and female *L. melissifolia* in this study yielded little insight into why native colonies in the LMAV are strongly male-biased.

Recovery and conservation of *L. melissifolia*

Recovery efforts for endangered plant species may entail a passive management strategy by allowing natural populations to develop without human influence to avoid risk of harming the species. This strategy is often adopted because of a lack of information on the biological requirements for survival, growth and regeneration of the imperiled species (Schemske et al. 1994), or because of a lack of information on active management practices to develop and maintain proper habitat (Mackenzie and Keith 2009). A passive approach, however, may be inappropriate for plants that inhabit disturbance maintained habitats, particularly those where the natural disturbance regime has been altered. For example, *L. melissifolia* is native to the 11 million ha LMAV where natural disturbance regimes promoted creation of forest canopy gaps and frequent saturation of the alluvial soils by floodwater. Today, only about 26 % of the LMAV is forested, and levees, drainage structures and roads have severely impacted natural hydrologic regimes. An active management approach could therefore provide habitat conditions previously created by natural disturbance regimes.

Management of *L. melissifolia* on federal land in the LMAV is currently passive, and intended to maintain natural forest structure. The USDA Forest Service Delta National Forest adheres to a policy of establishing a 30 m buffer around extant *L. melissifolia* colonies inside of which forest management practices are prohibited (Banker and Goetz 1989). While the buffer prevents anthropogenic disturbance within *L. melissifolia* colonies, stand development and successional processes inherent to floodplain forests promote development of multi-storied, closed canopy structure. Our research suggests the passive management approach could be detrimental to maintenance and growth of extant *L. melissifolia* colonies, and provides findings from which to model a strategy of active management that produces and sustains suitable *L. melissifolia* habitat.

Our findings are consistent with *L. melissifolia* being a stress tolerator with respect to soil flooding. Descriptions of *L. melissifolia* population locations include margins of depressional wetlands dominated by *Nyssa biflora* Walter and *Taxodium ascendens* Brongn. (Aleric and Kirkman 2005), floodplain forests (Hawkins et al. 2009) and edges of shallow ponds in old sand dune fields (Devall et al. 2001). These sites are indicative of areas subject to annual or near annual soil flooding. The high frequency of this disturbance creates stressful conditions for plants by reducing available soil oxygen, especially if the disturbance occurs after plants have initiated growth following winter dormancy. Our study shows *L. melissifolia* can tolerate up to 90 days of soil flooding with little effect on survival, stem length growth, stem diameter growth and ramet production. We even observed *L. melissifolia* flowering and leafing out in the presence of soil flooding. The mechanisms utilized by *L. melissifolia* to tolerate soil flooding are presently unknown, but these adaptations allow *L. melissifolia* to tolerate long periods of reduced soil oxygen whereas potential competitors may not be able to tolerate such conditions.

Our results illustrate that light availability is a strong determinant of *L. melissifolia* survival, stem length growth and stem diameter growth. The implication of this finding is that closed canopy, multi-storied forest structures will limit *L. melissifolia* survival, stem length and stem diameter. Active management practices developed to regulate stand density and crown cover to provide appropriate understory light environments would promote higher survival rates and increase stem length growth and stem diameter growth. For example, Lockhart et al. (2000) showed that removal of the midstory canopy in floodplain forests increased understory light to about 25 % of full sunlight. Other plant species will likely respond to an increase in understory light availability. Therefore, additional silvicultural practices to control competing vegetation following midstory canopy treatment may be needed to ensure *L. melissifolia* survival where hydrologic regimes are unfavorable for competing vegetation control.

Another significant finding from this research was that female stecklings responded differently than male stecklings in ramet production. Natural *L. melissifolia* populations are primarily populated with male colonies (Wright 1994; Hawkins et al. 2007). Greater ramet production by female stecklings than male stecklings with increasing light availability informs managers that active management practices as described above should provide micro-sites favorable to invigorate female ramet production. Increased asexual regeneration by female stecklings could lead to greater sexual regeneration due to growth of female colonies, with the advantage of greater dispersal of drupes to colonize new areas. Therefore, active management could potentially result in higher fecundity and a more balanced sex ratio in *L. melissifolia* populations.

Healthy populations of native understory plants are integral to the ecological structure and function of floodplain forests. Additional scientifically rigorous experiments should be done in suitable floodplain forests in the LMAV to develop silvicultural practices that meet the biological requirements of *L. melissifolia*. The testing of active management practices that restore and promote self-sustaining *L. melissifolia* populations are likely achievable and necessary to develop management tools for the full recovery of this rare species.

Acknowledgments Support for this research was provided by the U.S. Army Corp of Engineers, Vicksburg District, Agreement Number SRS 01-IA-11330127-527; U.S. Department of the Interior, Fish and Wildlife Service under permit number Endangered-Threatened Species Subpermit SA0142-Amendment 3; and the U.S. Department of Agriculture, Forest Service, Southern Research Station.

References

Aleric KM, Kirkman LK (2005) Seed germination observations of the federally listed *Lindera melissifolia*. Castanea 70:157–160

Banker B, Goetz EJ (1989) Biological evaluation for pondberry (*Lindera melissifolia*) on the Delta National Forest. U.S. Fish and Wildlife Service, Jackson

Battaglia LL, Sharitz RR (2006) Responses of floodplain forest species to spatially condensed gradients: a test of the flood-shade tolerance tradeoff hypothesis. Oecologia 147:108–118

Devall M, Schiff N, Boyette D (2001) Ecology and reproductive biology of the endangered pondberry, *Lindera melissifolia* (Walt) Blume. Nat Areas J 21:250–258

Gardiner ES, Hodges JD (1998) Growth and biomass distribution of cherrybark oak (*Quercus pagoda* Raf.) seedlings as influenced by light availability. For Ecol Manag 308:127–134

Givnish TJ (1988) Adaptation to sun and shade: a whole-plant perspective. Aust J Plant Phys 15:63–92

Hall RBW, Harcombe PA (1998) Flooding alters apparent position of floodplain saplings on a light gradient. Ecology 79:847–855

Hawkins TS, Schiff NM, Gardiner ES, Leininger T, Devall MS, Wilson D, Hamel P, McCown DD, Connor K (2007) Micropropagation of the endangered shrub pondberry (*Lindera melissifolia* [Walt.] Blume). HortScience 42:407–409

Hawkins TS, Skojac DS, Lockhart BR, Leininger TD, Devall MS, Schiff NM (2009) Bottomland forests in the Lower Mississippi Alluvial Valley associated with the endangered *Lindera melissifolia*. Castanea 74:105–113

Hawkins TS, Skojac DA, Schiff NM, Leininger TD (2010) Floristic composition and potential competitors in *Lindera melissifolia* (Lauraceae) colonies in Mississippi with reference to hydrologic regime. J Bot Res Inst Texas 4:381–390

Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems. In: Dodge DP (ed) Proceedings of the International Large River Symposium. Can Spec Pub Fish Aqu Sci 106, pp 110–127

Kozlowski TT (1984) Plant responses to flooding of soil. Bioscience 34:162–167

Lavinsky AO, De Souza Dant'Ana C, Mikelke MS, De Almeida AF, Gomes FP, França S, De Costa Silva D (2007) Effects of light availability and soil flooding on growth and photosynthetic characteristics of *Genipa americana* L. seedlings. New For 34:41–50

Lhotka JM, Loewenstein EF (2006) Indirect measures for characterizing light along a gradient of mixed-hardwood riparian forest canopy structures. For Ecol Manage 226:310–318

Lockhart BR, Hodges JD, Gardiner ES (2000) Response of advance cherrybark oak reproduction to midstory removal and shoot clipping. South J Appl For 24:45–50

Lockhart BR, Gardiner ES, Leininger TD, Connor KF, Hamel PB, Schiff NM, Wilson D, Devall M (2006) Flooding facility helps scientists examine the ecophysiology of floodplain species used in bottomland hardwood restorations. Ecol Rest 23:151–157

Lockhart BR, Gardiner ES, Stautz T, Leininger TD (2012) Development and plasticity of endangered shrub *Lindera melissifolia* (Lauraceae) seedlings under contrasting light regimes. Plant Species Biol 27:30–45

Mackenzie BD, Keith DA (2009) Adaptive management in practice: conservation of a threatened plant population. Ecol Manag Restor 10:S129–S135

Menges ES, Waller DM (1983) Plant strategies in relation to elevation and light in floodplain herbs. Am Nat 122:454–473

Mielke MS, Schaffer B (2010) Leaf gas exchange, chlorophyll fluorescence and pigment indexes of *Eugenia uniflora* L. in response to changes in light intensity and soil flooding. Tree Phys 30:45–55

Niinemets Ü (2010) Responses of forest trees to single and multiple environmental stresses from seedling to mature plants: past stress history, stress interactions, tolerance and acclimation. For Ecol Manag 260:1623–1639

Schemske DW, Husband BC, Ruckelshaus MH, Goodwillie C, Parker IM, Bishop JG (1994) Evaluating approaches to the conservation of rare and endangered plants. Ecology 75:584–606

Schnitzler A, Hale BW, Alsum E (2005) Biodiversity of floodplain forests in Europe and eastern North America: a comparative study of the Rhine and Mississippi Valleys. Biodivers Conserv 14:97–117

Snyder RL, Paw KT (2002) Measuring vapor pressure deficit in the field. http://biomet.ucdavis.edu/biomet/VPD/vpd.htm. Accessed 2 Feb 2009

USFWS (U.S. Fish and Wildlife Service) (1986) Endangered and threatened wildlife and plants: determination of endangered status for *Lindera melissifolia*. Fed Reg 51:27495–27500

WorldClimate (2008) Rolling Fork, Sharkey County, Mississippi USA. http://www.worldclimate.com. Accessed 6 Sep 2009

Wright RD (1994) Sex ratio and success, an assessment of *Lindera melissifolia* in Arkansas. Proc Ark Acad Sci 48:230–233

Yong JWH, Wong SC, Farquhar GD (1997) Stomatal responses to changes in vapour pressure differences between leaf and air. Plant, Cell Environ 20:1213–1216