Light availability and soil flooding regulate photosynthesis of an imperiled shrub in lowland forests of the Mississippi Alluvial Valley, USA

B.R. LOCKHART[+], E.S. GARDINER, T.D. LEININGER, M.S. DEVALL, A.D. WILSON,
K.F. CONNOR, P.B. HAMEL, and N.M. SCHIFF

USDA Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research, P.O. Box 227,
432 Stoneville Road, Stoneville, MS 38776, USA

Abstract

Physiological responses to light availability and soil flooding on *Lindera melissifolia* (Walt.) Blume were studied. Shrubs were grown under 70, 37 or 5% of full sunlight with either 0, 45, or 90 d of soil flooding. We measured leaf photosynthetic rate (P_N) to test the hypothesis that soil flooding reduces P_N in *L. melissifolia* following shrub acclimation to low light availability. Results showed that light availability and soil flooding interacted to affect P_N. In the 0 d and 45 d flooding regimes (flood water removed 36–39 d prior to measurement), P_N was similar between shrubs receiving 70% or 37% light, and these shrubs had 147% greater P_N than shrubs receiving 5% light. Shrubs receiving 90 d of soil flooding had similar low rates of area-based P_N regardless of light level. Similar P_N between 0 d and 45 d flooded shrubs indicated physiological recovery following removal of flood water.

Additional key words: blade area; blade mass; interaction; plasticity; pondberry.

Introduction

Lowland forests in the Mississippi Alluvial Valley (MAV) of the southern United States are described as temperate deciduous forests that receive seasonal soil flooding from precipitation and overbank flow from adjacent streams (Bedinger 1981). Woody plants that reside in the understory of lowland forests are subject to two primary stress factors: (*1*) low light availability from overstory canopy cover; and, (*2*) anaerobic conditions in the rhizosphere from soil flooding. How plants respond to these stress factors largely determines understory woody species composition and structure in lowland forests. Therefore, information on plant response to low light availability and soil flooding informs forest managers to develop strategies to manipulate species composition and stand structure necessary to meet desired forest management goals that involve understory woody plants.

Lowland forests typically have multi-layered canopies that intercept much of the sunlight reaching the top of the forest canopy. Consequently, little sunlight is available for understory plants. For example, Lhotka and Loewenstein (2006) found that PAR reaching the understory of mature lowland forests is often <5% of that measured in full sunlight. Understory plants exhibit a range of acclimations to capture and utilize available sunlight in these low light environments (Givnish 1988). For example, understory plants develop shade leaves that are large, thin, and oriented horizontally relative to the stem with minimal leaf overlap. Shade leaves also have a lower light-saturation point and a lower light-compensation point at low light levels than sun leaves. These acclimations allow understory plants to maximize the interception of available sunlight and more efficiently utilize this light during photosynthesis (Boardman 1977).

Lowland forests also are subject to seasonal soil flooding. Excess water in the soil matrix due to flooding displaces air from pore space thereby reducing the amount of O_2 available for plant root metabolism. Hypoxia develops as competition for available O_2 between roots

---

Received 5 February 2016, *accepted* 15 July 2016, *published as online-first* 6 September 2016.

[+]Corresponding author; e-mail: blockhart@fs.fed.us

Abbreviations: B_{area} – blade area; B_{mass} – blade mass; $B_{m/a}$ – blade mass per unit area; B_{temp} – blade temperature; C_a – ambient CO_2 concentration; C_i – intercellular CO_2 concentration; FRF – Flooding Research Facility; g_s – stomatal conductance; MAV – Mississippi Alluvial Valley; N_{area} – N content per unit area; N_{mass} – N concentration; P_N – photosynthetic rate.

Acknowledgments: We thank two anonymous reviewers for their constructive comments that improved this manuscript. Support for this research was provided by the U.S. Army Corp of Engineers, Vicksburg District, Agreement Number SRS 01-IA-11330127-527; USDI, Fish and Wildlife Service Endangered-Threatened Species Subpermit SA0142-Amendment 3; and the USDA, Forest Service, Southern Research Station.

and microorganisms, followed by anoxia when all available O_2 has been consumed and anaerobic soil conditions develop (Fukao and Bailey-Serres 2004). Plant species that inhabit these forests, through anatomical and morphological acclimations, can survive in conditions where the rooting zone becomes anaerobic during part of the growing season (Kozlowski 1997). These acclimations allow plants to maintain physiological function, such as photosynthesis, until aerobic soil conditions return (Pezeshki and Anderson 1997).

Low light availability under multi-layered forest canopies, along with anaerobic soil conditions from flooding, creates a complex environment of stress for understory plants in lowland forests. Lenssen *et al.* (2003) outlined three general ways plants may respond to shaded and flooded environments. First, these two stress factors may affect plant response independent of each other. For example, plant response to soil flooding is not conditioned by the light environment. Second, the interaction of these two stress factors results in an amplified response. The interacting effects draw a greater response than each individual effect – plant response to soil flooding is conditioned by the light environment. Third, a plant response to the first stress factor (*e.g.*, low light availability) may be so strong that no further plant response (static response) is made with the addition of the second stress factor (*e.g.*, soil flooding). Plant responses to these stress factors involve species-specific traits of the plant to acclimate to the new environment and thus to maintain physiological function (Blom *et al.* 1990).

Lindera melissifolia (Walt.) Blume (pondberry) is a deciduous, dioecious woody shrub of the Lauraceae. It is endemic to lowland forests across the southeastern United States (Wiggers 2014). In the MAV, *L. melissifolia* is subject to periodic flooding during late winter or spring months (Hawkins *et al.* 2009c). It initiates leaf development and anthesis in February and March, often when soils are flooded (Hawkins *et al.* 2010). *L. melissifolia* habitat in the MAV has been reduced by changes in land use, primarily the conversion of lowland forests to row-crop agriculture. In this region, *L. melissifolia* is found in disjunct colonies within isolated forest patches (Hawkins *et al.* 2009c). Therefore, *L. melissifolia* was listed as an endangered species by the U.S. Fish and Wildlife Service in 1986 (Currie 1986). Subsequent recovery plans indicated the need for more information on *L. melissifolia* biology to inform strategies to conserve and restore this species (DeLay *et al.* 1993, Wiggers 2014).

We studied net photosynthetic rate (P_N) to determine the ecophysiological response of *L. melissifolia* to different light levels and soil flooding regimes. Previous research of *L. melissifolia* P_N indicates that this species has high morphological leaf plasticity to a range of light levels (Wright 1990, Aleric and Kirkman 2005). However, no studies have addressed possible interactive effects of defined combinations of light availability and soil flooding on P_N, especially in MAV populations. We hypothesized that soil flooding will detrimentally impact *L. melissifolia* P_N, and this response will be amplified when shrubs are grown under low light availability. Therefore, we addressed the following three research questions. (*1*) What is the P_N response of *L. melissifolia* along a gradient of light availability? (*2*) How does extended soil flooding affect *L. melissifolia* P_N? (*3*) Does exposure to soil flooding result in an independent, amplified or static response in *L. melissifolia* P_N based on shrub acclimation to low light availability? Understanding how light availability and soil flooding affect P_N will inform managers of the environmental conditions necessary to conserve and restore *L. melissifolia* in the lowland forests of the MAV.

Materials and methods

Location: The study was conducted 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 site is the location of the Flooding Research Facility (FRF). The FRF contains 12 0.4-ha impoundments that can be flooded independently to desired depths, providing for large-scale experimentation on plant responses to the timing and duration of soil flooding. Three shade houses (25.6 m long, 7.3 m wide and 2.4 m tall) were constructed in each impoundment to control light availability. A complete description on the design and operation of the FRF appeared in Lockhart *et al.* (2006).

Climate at the FRF is humid subtropical with hot, humid summers and mild winters. Average daily temperature is 17.3°C with a range from 27.3°C in July to 5.6°C in January (WorldClimate 2015). Precipitation averages 1,350 mm per year, with 57% falling between March and September (WorldClimate 2015). The clay alluvium at the FRF is representative of the Sharkey series, a common soil in the MAV. It is classified as a very-fine, smectitic, thermic Chromic Epiaquerts. *L. melissifolia* in the MAV is typically found on Sharkey soil (Hawkins *et al.* 2009c).

Plant material: A description of steckling propagation is listed in Lockhart *et al.* (2013). Ninety-six, single-stemmed stecklings, representing 20 MAV clones, were outplanted in April 2005 on a 1.2 m by 1.2 m spacing in each of the 36 shade houses at the FRF (3,456 plants for the total experiment). Stecklings were raised in their respective shade houses without soil flooding for the 2005 growing season to allow for acclimation to the field environment and assigned levels of light availability. Each shade house was maintained free of weed competition by hand hoeing and spot application of appropriate herbicides.

Treatments: Each of the 12 impoundments was randomly assigned one of three soil flooding regimes (0 d, 45 d or 90 d) selected to represent a linear increase in flood duration. Soil flooding was started on 1 March for the 2006 and 2007 growing seasons. Shrub leaf and flower bud expansion occurred during soil flooding in both years. Floodwater depth was maintained near 12 cm in 2006 and 19 cm in 2007 by monitoring staff gauges located in each impoundment to inform either draining or adding water as necessary. At the end of each scheduled soil flooding regime, flood water was drained from respective impoundments and ambient rainfall was the only source of soil moisture for the remainder of each growing season.

Three light levels [70% (high light availability), 37% (intermediate light availability) and 5% (low light availability) of ambient sunlight] were randomly assigned to the three shade houses in each impoundment. Light availability was controlled using neutral density shade cloth (*PAK Unlimited, Inc.*, Cornelia, GA, USA). Average diurnal PAR during physiology sampling, measured with quantum sensors (*LI-COR, Inc.*, Lincoln, NE, USA) located in each shade house of a soil flooding replicate, was 798.1 μmol(photon) m^{-2} s^{-1} (84.2% of full sunlight) for the 70% light level, 378.3 μmol(photon) m^{-2} s^{-1} (39.9% of full sunlight) for the 37% light level and 24.7 μmol(photon) m^{-2} s^{-1} (2.6% of full sunlight) for the 5% light level. Diurnal PAR in an open environment at the FRF was 947.6 μmol(photon) m^{-2} s^{-1}.

Measurements: P_N measurements were conducted in May 2007 when shrubs receiving the 45 d soil flooding regime had floodwater removed 36–39 d prior to measurements, and shrubs receiving the 90 d soil flooding regime were still flooded. P_N was measured on one leaf blade from six randomly selected shrubs per light level replicate in one randomly selected replicate of each soil flooding regime (6 shrubs × 3 light levels × 3 soil flooding regimes = 54 shrubs). P_N was conducted at 12:00 h solar time, ranging ± 20 min. Nine shrubs, three from each shade house in a soil flooding regime, were measured on a given day.

Blade P_N was measured with a *Cirus-2* portable photosynthesis system (*PP Systems, Inc.*, Amesbury, MA, USA). Measurements were conducted during cloud-free days on leaves that were free of damage and within a predetermined range of nodes sufficiently distant from the shoot apex to ensure full leaf blade expansion and maturation. Additional variables measured or calculated during sampling included PAR, blade temperature (B_{temp}), ambient CO_2 concentration (C_a), intercellular CO_2 concentration (C_i) and stomatal conductance (g_s).

After measurement, leaves were harvested and brought to the laboratory for processing. Blade area (B_{area}) was calculated by averaging three measurements collected on each blade with a *LI-COR LI-3100* leaf area meter (*LI-COR, Inc.*, Lincoln, NE, USA). Leaves were then oven-dried at 70°C until completely desiccated, and blade mass (B_{mass}) was determined with an analytical balance. N concentration (N_{mass}) was quantified using a *PE 2400 Series II* CHNS/O analyzer (*Perkin Elmer Corporation*, Waltham, MA, USA).

Statistical analyses: One randomly chosen replicate of each soil flooding regime and light level combination from the larger planting was used during P_N measurements. This conforms to a split-plot design with the soil flooding regime representing the whole-plot treatment and light level representing the split-plot treatment. Analyses were conducted using *PROC* analysis of variance (*ANOVA*) in *SAS 9.4* (*SAS Institute, Inc.*, Cary, NC, USA). Variables analyzed included B_{area}, B_{mass}, blade mass per unit area ($B_{m/a}$), N content per unit area (N_{area}), N_{mass}, PAR, B_{temp}, P_N, C_i/C_a ratio and g_s. Transformations were applied to variables as needed to normalize model residual errors. Untransformed values were displayed in all tables and figures. Least significant difference tests were used to separate treatment means. Statistical significance for all tests was determined at $p \leq 0.05$.

Results

Experimental treatments influenced PAR incipient on leaves and B_{temp} during P_N measurements. Leaf-level PAR averaged 1,460 μmol(photon) m^{-2} s^{-1} for shrubs measured in the 70% light environment. These measurements averaged 569 μmol(photon) m^{-2} s^{-1} greater than leaf-level measurements in the 37% light environment and 1,408 μmol(photon) m^{-2} s^{-1} greater than leaf-level measurements in the 5% light environment (Fig. 1). Soil flooding had no effect on PAR within respective light levels. Temperature of *L. melissifolia* leaves increased with increasing light availability and decreased with increasing duration of soil flooding. During P_N measurements, B_{temp} for shrubs in the 5% light environment averaged 31.8°C. The average B_{temp} increased 1.2°C for shrubs receiving 37% light, and 2.5°C for shrubs receiving 70% light (Fig. 2). B_{temp} was measured 1.8°C higher for shrubs receiving 0 d of soil flooding than for shrubs receiving 45 d or 90 d of soil flooding (Fig. 3).

Surface area of *L. melissifolia* leaves decreased with increasing light availability and duration of soil flooding. Shrubs grown under 5% light developed leaves with 124% greater B_{area} than shrubs grown under 70% light, and 30% greater B_{area} than shrubs receiving 37% light (Table 1). Ninety days of soil flooding reduced B_{area} by one-third relative to 0 d and 45 d floods. Among light environments, B_{mass} was the greatest for *L. melissifolia* raised under intermediate light availability. Shrubs raised under 37% light produced leaves with more mass than those receiving 5% light (Table 1). Ninety days of soil flooding led to a 22%

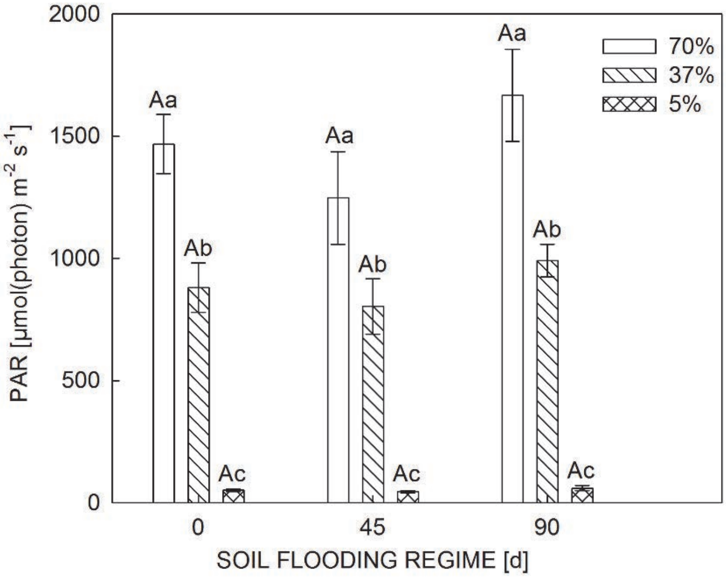

Fig. 1. Effect of light level and soil flooding regime on PAR measured at leaf-level during May 2007 photosynthesis (P_N) measurements at the Flooding Research Facility, Sharkey County, MS, USA. Bars are means ± SE ($n = 6$), and significance of all tests was determined at $p \leq 0.05$. Different *uppercase letters* note differences among soil flooding regime means at a given light level. Different *lowercase letters* note differences among light level means at a given soil flooding regime.

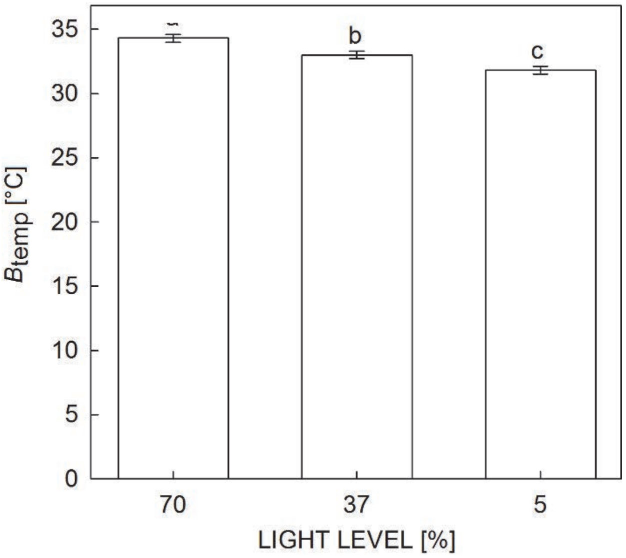

Fig. 2. Effect of light level on *Lindera melissifolia* blade temperature (B_{temp}) during May 2007 photosynthesis (P_N) measurements at the Flooding Research Facility, Sharkey County, MS, USA. Bars are means ± SE ($n = 6$), and significance of all tests was determined at $p \leq 0.05$. Different *lowercase letters* note differences among light level means.

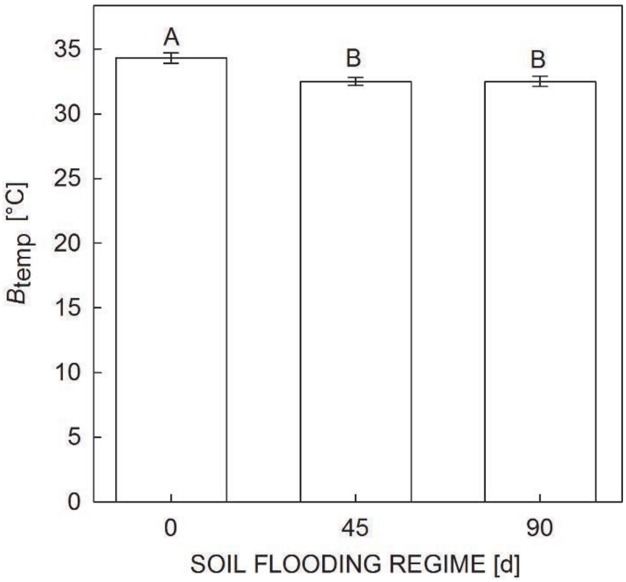

Fig. 3. Effect of soil flooding regime on *Lindera melissifolia* blade temperature (B_{temp}) during May 2007 photosynthesis (P_N) measurements at the Flooding Research Facility, Sharkey County, MS, USA. Bars are means ± SE ($n = 6$), and significance of all tests was determined at $p \leq 0.05$. Different *uppercase letters* note differences among soil flooding regime means.

reduction in B_{mass} compared to leaves from plants established in unflooded soils. Light availability and soil flooding interacted to influence *L. melissifolia* $B_{m/a}$ such that shrubs grown under 70% light and receiving 90 d of soil flooding produced leaves with the greatest $B_{m/a}$ (Table 1). The lowest $B_{m/a}$ was observed for leaves receiving 5% light regardless of soil flooding regime.

Foliar N content (N_{area}) increased with increasing light availability and decreased with increasing flood duration. Shrubs grown under 70% light maintained leaf blades with 38% greater N_{area} than shrubs grown under 37% light, and shrubs raised under 37% light maintained leaf blades with 31% greater N_{area} than shrubs raised under 5% light (Table 1). Ninety days of soil flooding reduced N_{area} relative to 0 d and 45 d of soil flooding. Foliar N concentration (N_{mass}) decreased with increasing light availability and flood duration. Within a given flood regime, shrubs grown under 5% light developed leaves with more than twice the N_{mass} of leaves from the other light environments (Table 1). The lowest N_{mass} in each light regime occurred when shrubs received 90 d of soil flooding.

The effects of light availability and soil flooding interacted to influence *L. melissifolia* P_N. The lowest P_N

Table 1. Effect of light level and soil flooding regime on blade area (B_{area}), blade mass (B_{mass}), blade mass per unit area ($B_{\text{m/a}}$), N content per unit area (N_{area}) and N concentration (N_{mass}) during photosynthesis (P_N) measurements at the Flooding Research Facility, Sharkey County, MS, USA, May 2007. Values are means ± SE ($n = 6$), and significance of all tests was determined at $p \leq 05$. Different *uppercase letters* note differences among soil flooding regime means. Different *lowercase letters* note differences among light level means. In the case of significant interaction, separation of treatment combination means are for within a level of each main effect.

Variable	70% light	37% light	5% light	Soil flooding regime mean
B_{area} [cm^2]				
0 d flood	24.9 ± 2.6	47.4 ± 3.3	60.2 ± 6.3	44.2 ± 4.3^{A}
45 d flood	25.1 ± 2.4	36.6 ± 3.9	54.1 ± 8.4	38.6 ± 4.2^{A}
90 d flood	17.6 ± 2.1	32.6 ± 3.5	36.5 ± 5.6	28.9 ± 2.9^{B}
Light level mean	22.5 ± 1.5^{c}	38.8 ± 2.5^{b}	50.3 ± 4.5^{a}	
B_{mass} [g]				
0 d flood	0.17 ± 0.02	0.25 ± 0.01	0.11 ± 0.01	0.18 ± 0.02^{A}
45 d flood	0.18 ± 0.02	0.18 ± 0.02	0.10 ± 0.02	0.16 ± 0.01^{AB}
90 d flood	0.14 ± 0.02	0.20 ± 0.02	0.07 ± 0.01	0.14 ± 0.02^{B}
Light level mean	0.17 ± 0.01^{b}	0.21 ± 0.01^{a}	0.10 ± 0.01^{c}	
$B_{\text{m/a}}$ [mg cm^{-2}]				
0 d flood	6.9 ± 0.2^{Ba}	5.4 ± 0.2^{Bb}	$1.9 \pm <0.1^{Ac}$	4.7 ± 0.5
45 d flood	7.4 ± 0.1^{Ba}	4.9 ± 0.2^{Bb}	$1.9 \pm <0.1^{Ac}$	4.7 ± 0.6
90 d flood	8.2 ± 0.2^{Aa}	6.2 ± 0.2^{Ab}	$1.9 \pm <0.1^{Ac}$	5.4 ± 0.6
Light level mean	7.5 ± 0.2	5.5 ± 0.2	$1.9 \pm <0.1$	
N_{area} [mg cm^{-2}]				
0 d flood	0.157 ± 0.006	0.119 ± 0.007	0.087 ± 0.002	0.121 ± 0.008^{A}
45 d flood	0.165 ± 0.008	0.112 ± 0.004	0.093 ± 0.003	0.123 ± 0.008^{A}
90 d flood	0.135 ± 0.008	0.099 ± 0.003	0.073 ± 0.003	0.102 ± 0.007^{B}
Light level mean	0.152 ± 0.005^{a}	0.110 ± 0.004^{b}	0.084 ± 0.002^{c}	
N_{mass} [%]				
0 d flood	2.3 ± 0.1^{Ab}	2.2 ± 0.2^{Ab}	4.7 ± 0.1^{Aa}	3.1 ± 0.3
45 d flood	2.2 ± 0.1^{Ab}	2.3 ± 0.1^{Ab}	4.9 ± 0.1^{Aa}	3.1 ± 0.3
90 d flood	1.7 ± 0.1^{Bb}	1.6 ± 0.1^{Bb}	3.8 ± 0.1^{Ba}	2.3 ± 0.3
Light level mean	2.1 ± 0.1	2.0 ± 0.1	4.5 ± 0.1	

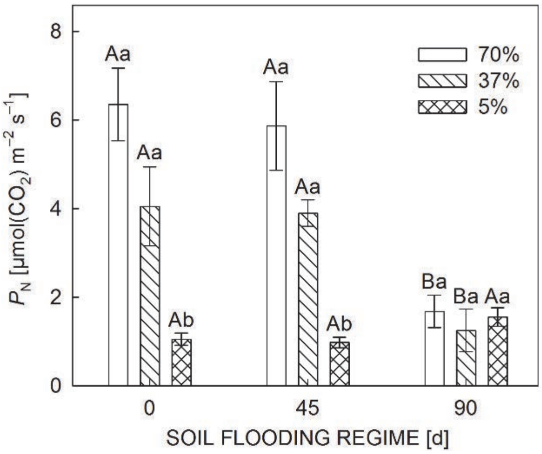

Fig. 4. Effect of light level and soil flooding regime on *Lindera melissifolia* net photosynthetic rate (P_N) during May 2007 measurements at the Flooding Research Facility, Sharkey County, MS, USA. Bars are means ± SE ($n = 6$), and significance of all tests was determined at $p \leq 0.05$. Different *uppercase letters* note differences among soil flooding regime means at a given light level. Different *lowercase letters* note differences among light level means at a given soil flooding regime.

occurred for shrubs raised under low light or 90 d of soil flooding (Fig. 4). Shrubs grown under 70% and 37% light (with 0 d or 45 d of soil flooding) had nearly 400% greater P_N than shrubs grown under 5% light (Fig. 4). P_N of shrubs receiving 0 d or 45 d of soil flooding (with 70% or 37% light) differed from shrubs receiving 90 d of soil flooding by more than 240% (Fig 4).

Based on the C_i/C_a ratio of *L. melissifolia* shrubs, the proportion of C_i to C_a tended to increase with decreasing light availability. For the 0 d and 45 d soil flooding regimes, the proportional C_i of shrubs receiving 5% light was more than 50% greater than shrubs receiving 70% or 37% light (Fig. 5). The C_i/C_a ratio did not differ among light environments for shrubs receiving 90 d of soil flooding. The proportion of C_i to C_a also tended to increase with increasing flood duration. For shrubs grown under 70% or 37% light, the proportional C_i of shrubs receiving 90 d of soil flooding was more than 26% greater than shrubs receiving 0 d or 45 d of soil flooding (Fig. 5). The C_i/C_a ratio did not differ among soil flooding regimes for shrubs receiving 5% light.

The g_s response of *L. melissifolia* shrubs to light availability and soil flooding was similar to the P_N response. In the absence of soil flooding, leaves grown under 70% light had 61% greater g_s than leaves grown under 37% or 5% light (Fig. 6). Shrub g_s was similar across light environments with 45 d or 90 d of soil flooding. For plants receiving 70% light, 90 d of soil flooding decreased g_s 57% compared to the other flooding regimes. A similar decrease (54%) was observed for shrubs raised under 37% light. Measured rates of g_s were not influenced by soil flooding when shrubs were raised under 5% light.

Discussion

What is the P_N response of *L. melissifolia* along a gradient of light availability? *Lindera melissifolia* inhabits forest understories that encompass a range of light environments including the low light environments beneath multi-layered lowland forest canopies, moderately shaded environments beneath forest canopy gaps, and high light environments near the periphery of sparsely-treed depressional wetlands (Wiggers 2014). The level of light environment heterogeneity observed among *L. melissifolia* habitats suggests this species possesses high plasticity to available PAR.

We found that *L. melissifolia* leaves acclimated to their light environment through changes in leaf morphology. B_{area} increased with decreasing light availability, thereby broadening the light-intercepting surface area of individual leaves. Lockhart *et al.* (2012) observed a similar pattern of B_{area} plasticity, noting that *L. melissifolia* raised in a growth chamber modified B_{area} relative to light availability. Further, Luken *et al.* (1997) reported a comparable finding for *L. benzoin*, a *L. melissifolia* congener found in the eastern United States, that expressed B_{area} plasticity to the light environment.

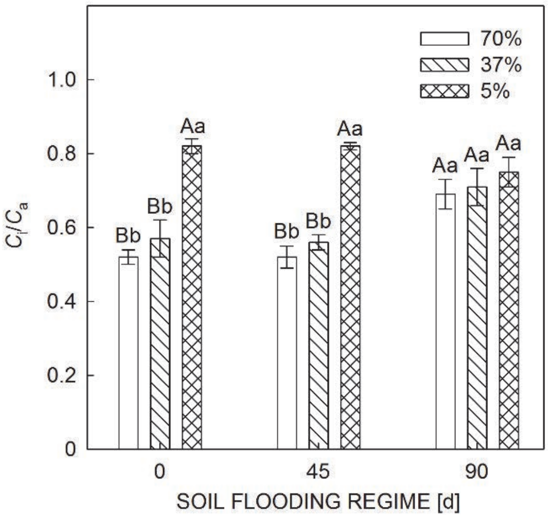

Fig. 5. Effect of light level and soil flooding regime on the ratio of intercellular and atmospheric CO_2 concentration (C_i/C_a) during May 2007 photosynthesis (P_N) measurements on *Lindera melissifolia* at the Flooding Research Facility, Sharkey County, MS, USA. Bars are means ± SE ($n = 6$), and significance of all tests was determined at $p \le 0.05$. Different *uppercase letters* note differences among soil flooding regime means at a given light level. Different *lowercase letters* note differences among light level means at a given soil flooding regime.

Concurrent with increases in B_{area}, $B_{m/a}$ decreased with decreasing light availability in respective soil flooding regimes. Aleric and Kirkman (2005) and Lockhart *et al.* (2012) also found lower $B_{m/a}$ with decreasing light availability in *L. melissifolia*, and Luken *et al.* (1997) reported a similar $B_{m/a}$–light availability relationship in *L. benzoin*. Further, Yasumura *et al.* (2006) observed a lower $B_{m/a}$ with decreasing light availability for *L. umbellata*, a *L. melissifolia* congener found in eastern Asia. The lower $B_{m/a}$ of leaves acclimated to low light availability has been associated with a decrease in blade cuticle thickness, a reduction in palisade cell length, an absence of palisade cell stacking, and a decrease in mesophyll cell volume (Boardman 1977, Chabot *et al.* 1979).

Light availability also affected the foliar N status of *L. melissifolia*. N_{mass} was greatest at low light availability and declined with increasing light availability. A similar N_{mass}–light availability relationship was found for *L. umbellata* (Yasumura *et al.* 2005) and *Acer saccharum* seedlings (Ellsworth and Reich 1992), but not for *Quercus pagoda* seedlings (Gardiner and Krauss 2001). The greater N_{mass} for *L. melissifolia* shrubs raised under low light was accompanied by a greater B_{area} for these shrubs. Conversely, N_{area} was the greatest at high light availability and

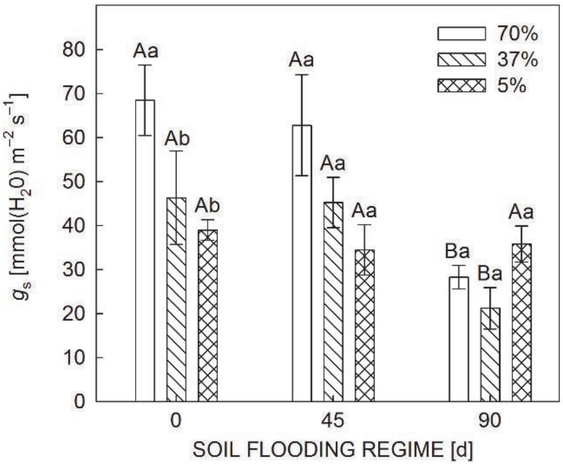

Fig. 6. Effect of light level and soil flooding regime on *Lindera melissifolia* stomatal conductance (g_s) during May 2007 photosynthesis (P_N) measurements at the Flooding Research Facility, Sharkey County, MS, USA. Bars are means ± SE ($n = 6$), and significance of all tests was determined at $p \le 0.05$. Different *uppercase letters* note differences among soil flooding regime means at a given light level. Different *lowercase letters* note differences among light level means at a given soil flooding regime.

declined with decreasing light availability. Yasumura *et al.* (2005) reported a similar trend for N_{area} and light availability in *Fagus crenata*, *Magnolia salicifolia* and *L. umbellata*. Rosati *et al.* (2000) ascribed the positive relationship between N_{area} and light availability to the same mechanisms driving the previously described relationship between $B_{m/a}$ and light availability.

Leaf acclimation, such as lower $B_{m/a}$, higher N_{mass}, and a greater chlorophyll concentration (Hawkins *et al.* 2009a), supported positive rates of P_N for *L. melissifolia* in the low light environment. We expected this result because native colonies are often found under similar light levels in natural forests, and others have reported leaf-level light-compensation points for this species below PAR of 10 μmol(photon) m^{-2} s^{-1} (Wright 1990, Aleric and Kirkman 2005). The lower B_{temp} and g_s observed for shrubs that received 5% light relative to those that received more light suggests that water stress had minimal impact on *L. melissifolia* P_N under heavy shade. This finding is further supported by the relatively balanced C_i/C_a ratio of shrubs raised in the low light environment.

In this experiment, intermediate and high light environments led to leaf acclimation, such as a greater $B_{m/a}$ and N_{area}, that increased leaf-level P_N. Our finding is consistent with Aleric and Kirkman (2005) who reported P_N acclimation in *L. melissifolia* growing in a range of light environments in South Carolina. With the increase in PAR and the concomitant increase in P_N we also observed an increase in the gradient between C_i and C_a. The lower proportion of C_i for shrubs raised under intermediate light indicated that PAR was not a limit on P_N as observed for the lowest light level. The greater N_{area} observed for these shrubs, as is generally observed to increase with increasing light, suggests a greater allocation of N to carbon fixation relative to light gathering (Evans 1989).

In contrast to the rise in P_N we observed with the increase in light from the low light to the intermediate light environment, the increase in light availability from the intermediate light to the high light environment did not raise P_N. Previous research demonstrated that *L. melissifolia* showed little P_N acclimation to increases in PAR above intermediate light availability (Wright 1990, Aleric and Kirkman 2005). For example, Aleric and Kirkman (2005) reported similar maximum P_N when the light environment was 28% or 95% of full sunlight in a South Carolina colony. This finding is not consistent with other published literature on P_N acclimation – published light-response curves demonstrate that high light environments support acclimation that builds P_N capacity (Gardiner and Krauss 2001, Niinemets and Valladares 2004, Jensen *et al.* 2012).

The apparent saturation of P_N capacity above intermediate PAR may be attributed to environmental factors associated with increased radiant energy. The high light environment in our study resulted in greater air temperature, as noted by the increase in B_{temp} and a lower relative humidity, than in the intermediate light environment. Therefore, shrubs growing in the high light environment experienced a greater vapor pressure deficit (Lockhart *et al.* 2013), resulting in a more intense diurnal period of water stress. The higher leaf g_s for shrubs raised in the high light environment, especially for shrubs receiving 0 d of soil flooding, is further indication of water stress that may have limited P_N. For example, mid-day depressions in diurnal P_N due to water stress have been reported for many broadleaf species (Iio *et al.* 2004, Kamakura *et al.* 2012).

How does extended soil flooding affect *L. melissifolia* P_N? In addition to forest understory habitats, *L. melissifolia* also inhabits areas subject to seasonal soil flooding. Yet, little information exists on how soil flooding impacts *L. melissifolia* physiology. Flooding effects reported for this species have primarily noted impacts on biomass accumulation and distribution among plant tissues (Hawkins *et al.* 2009b, Unks *et al.* 2014, Hawkins *et al.* 2016). Hawkins *et al.* (2009b), who studied first-year plants raised in a greenhouse, noted that 30 d of soil flooding halted stem growth, limited total biomass accumulation, and promoted leaf abscission of plants raised free of competition. These observations led the authors to conclude that juvenile and metabolically-active *L. melissifolia* holds limited tolerance to soil flooding (Hawkins *et al.* 2009b). Additional work by Hawkins *et al.* (2016), however, found few differences in the amount of biomass distributed between above and belowground tissues when plants were grown in flooded *vs.* non-flooded soil. Further, Lockhart *et al.* (2013), who studied four-year-old shrubs growing in native soil, found that a 90 d flood repeated over two consecutive years had minimal effect on shrub survival or growth.

We found that soil flooding imparted several changes to *L. melissifolia* leaf blades, including decreases in B_{area}, N_{mass} and N_{area}, and an increase in $B_{m/a}$. A reduction in B_{area} is commonly observed when leaves develop during periods of soil inundation (Liu and Dickmann 1992, Anderson and Pezeshki 1999), and is likely due to constraints in cell wall extensibility that limit leaf cell expansion and division (Smit *et al.* 1989). Increased $B_{m/a}$ during soil flooding has been reported for several woody plant species (Harrington 1987, Liu and Dickmann 1992, Gardiner and Krauss 2001, Mielke and Schaffer 2010). This response has been attributed to the accumulation of starch in leaves that results from a reduction in photosynthate translocation mediated by root dysfunction (Vu and Yelenosky 1991, Angelov *et al.* 1996, Jaeger *et al.* 2009, Kreuzwieser *et al.* 2004). Foliar N characteristically decreases in plants subjected to soil flooding. Harrington (1987) attributed a lower N_{mass} in flooded *P. trichocarpa* seedlings to less N available for uptake by stressed roots due to the denitrification of NO_3 to gaseous N and N_2O. Decreased N uptake in flooded plants also may be due to root dysfunction (Kozlowski 1997, DeLaune *et al.* 1998). Further, Gardiner and Krauss (2001) speculated that observed reductions in N concentration could possibly result from the diluting effect of photosynthate accumulation in the leaves of plants stressed by flooded soil as described above.

In association with the previously described changes in leaf morphology, soil flooding led to a decline in *L. melissifolia* P_N, particularly in high and intermediate light environments. Photosynthetic impairment in woody plants is common when stressed by flooded soils (Pezeshki and Chambers 1985, Dreyer *et al.* 1991, Gravatt and Kirby 1998, Pezeshki 2001, Jaeger *et al.* 2009, Mielke and Schaffer 2010). We found that the P_N response in *L. melissifolia* coincided with a reduction in leaf g_s. Stomatal closure has been noted as a primary reaction by plants upon initiation of soil flooding (Kozlowski 1997). While this response reduces transpiration and thereby maintains cell turgor, stomatal closure is also implicated as the mechanism that reduces P_N during short-term soil flooding (Pezeshki 2001, Kozlowski 2002). We cannot speculate on the short-term stomatal conductance and P_N relationship of shrubs in our study because flood-stressed shrubs that we measured initiated leaf expansion and matured during periods of soil flooding. However, Herrera *et al.* (2008) reported that stomatal limitations to P_N decrease during prolonged soil inundation because stomata regain function; this shifts stress-induced limitations to P_N towards non-stomatal mechanisms during long-term soil flooding.

Evidence from this work indicates that soil flooding may impair *L. melissifolia* P_N through mechanisms in addition to stomatal closure. We observed a greater proportional C_i when shrubs raised in high or intermediate light environments endured 90 d of soil flooding. This rise in C_i appears to indicate a reduced photosynthetic demand for CO_2. Non-stomatal factors linked to photosynthetic declines in plants growing in flooded soils include lower leaf blade chlorophyll content (Pezeshki 2001), reduced Rubisco content and activation (Vu and Yelenosky 1991), and photosynthate accumulation in leaf blades (Goldschmidt and Huber 1992, Gardiner and Krauss 2001). The increase in $B_{m/a}$ that we observed during prolonged flooding supports speculation that photosynthate accumulation may be linked to the decline in P_N noted for shrubs receiving high or intermediate light. Goldschmidt and Huber (1992) illustrated that feedback inhibition of P_N associated with photosynthate accumulation is likely driven by down-regulation of the Calvin cycle.

The scheduling of our P_N measurements relative to timing of the 45 d soil flooding regime provided information on physiological recovery following recession of flood water (note that flood water was removed from the 45 d soil flooding regime 36 d before measurements began). We observed apparent recovery of physiological function following floodwater removal – leaf morphology and gas-exchange variables were similar for shrubs growing in high or intermediate light environments that received 0 d or 45 d floods. Physiological recovery from soil flooding has been reported for a range of floodplain species including *Populus deltoides* (Regehr *et al.* 1975), *A. saccharinum* (Peterson and Bazzaz 1984), *Q. nuttallii* (Anderson and Pezeshki 1999), *A. rubrum* (Anella and Whitlow 2000), *Alnus japonica* (Iwanaga and Yamamoto 2007), and *Distylium chinense* (Li *et al.* 2011). In agreement with our findings, scientists studying these species noted resumption of P_N at rates similar to nonstressed plants.

Does exposure to soil flooding result in an independent, amplified or static response in *L. melissifolia* P_N based on plant acclimation to low light availability? Research that addresses the effects of two or more stress factors operating simultaneously on woody plant physiology is inherently difficult to interpret because independent and interacting effects may obscure resolution of physiological response (Niinemets 2010). Lenssen *et al.* (2003) outlined a model to account for independent and interacting plant responses to light availability and flooding. Plants growing in a shaded environment may react to the addition of soil flooding with an independent, amplified or static P_N response.

In our study, *L. melissifolia* shrubs that were acclimated to the low light environment showed a static P_N response to prolonged soil flooding. The addition of soil flooding did not reduced P_N beyond the limitations imposed by low available PAR. Therefore, we reject our hypothesis that soil flooding would amplify *L. melissifolia* P_N response following acclimation to low light availability. We emphasize that our hypothesis was based on imposing a soil flood on plants acclimated to the stress of low light availability. A different conclusion may be reached if the hypothesis was applied to plants acclimated to higher light environments.

Our results differed from other studies that addressed the effects of soil flooding on woody plants acclimated to a low light environment. Mielke and Schaffer (2010) demonstrated an independent response in *Eugenia uniflora* P_N when seedlings acclimated to 25–30% of full sunlight were subjected to 14 days of flooding. Results presented by Gardiner and Krauss (2001) illustrated an amplified decrease in P_N response to soil flooding by *Q. pagoda* seedlings raised under 27% of full sunlight. Likewise, the decrease in P_N by *Genipa americana* seedlings acclimated to <10% of full sunlight was amplified when flooded for 100 d (Lavinsky *et al.* 2007). The range of P_N response observed among these various studies may be attributed to species-specific differences in plasticity to the light environment and tolerance to soil flooding. However, methodological differences in experimental design, treatment application or measurement protocols likely influenced interpretation of results.

Conclusions: *L. melissifolia* exposed to a gradient of light availability exhibited morphological plasticity that supported physiological acclimation to the light environment. B_{area} and $B_{m/a}$ were adjusted to increase light gathering capability for positive P_N in the low light environment. *L. melissifolia* increased P_N with increasing light availability up to intermediate light, but water stress in the high light environment impeded further increases in P_N.

P_N response of *L. melissifolia* to soil flooding was determined by the light environment. In environments of intermediate and high light, soil flooding impaired P_N through stomatal and non-stomatal factors. In these light environments, reduced g_s indicated that stomata limited P_N while soil was flooded, but a greater proportional C_i was indication that non-stomatal factors also limited P_N. Non-stomatal impairment of P_N appeared to be associated with an increase in $B_{m\text{-}a}$ – this may be indicative of feedback inhibition of P_N that resulted from flood-induced disruption to photosynthate translocation from leaves. Soil flooding did not appear to reduce P_N of shrubs acclimated to low light environments.

When flood water was drained from soil, *L. melissifolia* rapidly recovered P_N function to levels equivalent of shrubs that did not experience soil flooding. The capacity of this species to recover from acclimation to flooded soil may provide it a competitive advantage over species less able to respond (Hawkins *et al.* 2016), particularly in environments where light is not limiting. This research illustrated that the complexity of interacting environmental factors need to be considered in the development of conservation and recovery plans for this endangered species in the lowland forests of the MAV.

References

Aleric K.M., Kirkman L.K.: Growth and photosynthetic response of the federally endangered shrub, *Lindera melissifolia* (Lauraceae), to varied light environments. – Am. J. Bot. **92**: 682-689, 2005.

Anderson P.H., Pezeshki S.R.: The effects of intermittent flooding on seedlings of three forest species. – Photosynthetica **37**: 543-552, 1999.

Anella L.B., Whitlow T.H.: Photosynthetic response to flooding of *Acer rubrum* seedlings from wet and dry sites. – Am. Midl. Nat. **143**: 330-341, 2000.

Angelov M.N., Sung S.S., Doong R.L. *et al.*: Long- and short-term flooding effects on survival and sink-source relationships of swamp-adapted tree species. – Tree Physiol. **16**: 477-484, 1996.

Bedinger M.S.: Hydrology of bottomland hardwood forests of the Mississippi Embayment. – In: Clark J.R., Benforado J. (ed.): Wetlands of Bottomland Hardwood Forests. Pp. 161-176. Elsevier Sci. Publ. Co., New York 1981.

Blom C.W.P.M., Bögermann G.M., Laan P. *et al.*: Adaptations to flooding in plants from river areas. – Aquat. Bot. **38**: 29-47, 1990.

Boardman N.K.: Comparative photosynthesis of sun and shade plants. – Annu. Rev. Plant Physiol. **28**: 355-377, 1977.

Chabot B.F., Jurik T.W., Chabot J.F.: Influence of instantaneous light-flux density on leaf anatomy and photosynthesis. – Am. J. Bot. **66**: 940-945, 1979.

Currie R.R.: Endangered and threatened wildlife and plants; determination of endangered status for *Lindera melissifolia*. – Fed. Reg. **51**: 27495-27500, 1986.

DeLaune R.D., Pezeshki S.R., Lindau C.W.: Influence of soil redox potential on nitrogen uptake and growth of wetland oak seedlings. – J. Plant Nut. **21**: 757-768, 1998.

DeLay L., O'Conner R., Ryan J. *et al.*: Recovery plan for pondberry (*Lindera melissifolia*). Pp. 49. U.S. Fish and Wildlife Service, Southeast Region, Atlanta 1993.

Dreyer E., Colin-Belgrand M., Biron P.: Photosynthesis and shoot water status of seedlings from different oak species submitted to waterlogging. – Ann. Sci. For. **48**: 205-214, 1991.

Ellsworth D.S., Reich P.B.: Leaf mass per area, nitrogen content and photosynthetic carbon gain in *Acer saccharum* seedlings in contrasting forest light environments. – Funct. Ecol. **6**: 423-435, 1992.

Evans J.R.: Photosynthesis and nitrogen relationships in leaves of C_3 plants. – Oecologia **78**: 9-19, 1989.

Fukao T., Bailey-Serres J.: Plant responses to hypoxia – is survival a balancing act? – Trends Plant Sci. **9**: 449-456, 2004.

Gardiner E.S., Krauss K.W.: Photosynthetic light response of flooded cherrybark oak (*Quercus pagoda*) seedlings grown in two light regimes. – Tree Physiol. **21**: 1103-1111, 2001.

Gardiner E., Stanturf J., Leininger T. *et al.*: Establishing a research and demonstration area initiated by managers: the Sharkey Restoration Research and Demonstration Site. – J. For. **106**: 363-369, 2008.

Givnish T.J.: Adaptation to sun and shade: a whole-plant perspective. – Aust. J. Plant. Physiol. **15**: 63-92, 1988.

Goldschmidt E.E., Huber S.C.: Regulation of photosynthesis by end-product accumulation in leaves of plants storing starch, sucrose, and hexose sugars. – Plant Physiol. **99**: 1443-1448, 1992.

Gravatt D.A., Kirby C.J.: Patterns of photosynthesis and starch allocation in seedlings of four bottomland hardwood tree species subjected to flooding. – Tree Physiol. **18**: 411-417, 1998.

Harrington C.A.: Responses of red alder and black cottonwood seedlings to flooding. – Physiol. Plantarum **69**: 35-48, 1987.

Hawkins T.S., Gardiner E.S., Comer, G.S.: Modeling the relationship between extractable chlorophyll and SPAD-502 readings for endangered plant species research. – J. Nat. Conserv. **17**: 125-129, 2009a.

Hawkins T.S., Schiff N.M., Leininger T.D. *et al.*: Growth and intraspecific competitive abilities of the dioecious *Lindera melissifolia* (Lauraceae) in varied flooding regimes. – J. Torrey Bot. Soc. **136**: 91-101, 2009b.

Hawkins T.S., Skojac III D.A., Lockhart B.R. *et al.*: Bottomland forests in the Lower Mississippi Alluvial Valley associated with the endangered *Lindera melissifolia*. – Castanea **74**: 105-113, 2009c.

Hawkins T.S., Skojac, Jr., D.S., Schiff N.M. *et al.*: 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, 2010.

Hawkins T.S., Schiff N., Wilson A.D. *et al.*: Growth and competitive abilities of the federally endangered *Lindera melissifolia* and the potentially invasive *Brunnichia ovata* in varying densities, hydrologic regimes, and light availabilities. – Botany **94**: 269-276, 2016.

Herrera A., Tezara W., Marin O. *et al.*: Stomatal and non-stomatal limitations of photosynthesis in trees of a tropical seasonally flooded forest. – Physiol. Plantarum **134**: 41-48, 2008.

Iio A., Fukawawa H., Nose Y. *et al.*: Stomatal closure induced by high vapor pressure deficit limited midday photosynthesis at the canopy tops of *Fagus crenata* Blume on Naeba mountain in Japan. – Trees **18**: 510-517, 2004.

Iwanaga F., Yamamoto F.: Growth, morphology and photosynthetic activity in flooded *Alnus japonica* seedlings. – J. For. Res. **12**: 243-246, 2007.

Jaeger C., Gessler A., Biller S. *et al.*: Differences in C metabolism of ash species and provenances as a consequence of root oxygen deprivation by waterlogging. – J. Exp. Bot. **60**: 4335-4345, 2009.

Jensen A.M., Gardiner E.S., Vaughn K.C.: High-light acclimation in *Quercus robur* L. seedlings upon over-topping a shaded environment. – Environ. Exp. Bot. **78**: 25-32, 2012.

Kamakura M., Kosugi Y., Muramatsu K. *et al.*: Simulations and observations of patchy stomatal behavior in leaves of *Quercus crispula*, a cool-temperate deciduous broad-leaved tree species. – J. Plant Res. **125**: 339-349, 2012.

Kozlowski T.T.: Responses of woody plants to flooding and salinity. – Tree Physiol. Monograph No. 1, 1997.

Kozlowski T.T.: Physiological-ecological impacts of flooding on riparian forest ecosystems. – Wetlands **22**: 550-561, 2002.

Kreuzwieser J., Papadopoulou E., Rennenberg H.: Interaction of flooding with carbon metabolism of forest trees. – Plant Biol. **6**: 299-306, 2004.

Lavinsky A.O., De Sonza Sant'Ana C., Mielke M.S. *et al.*: Effects of light availability and soil flooding on growth and photosynthetic characteristics of *Genipa americana* L. seedlings. – New Forest. **34**: 41-50, 2007.

Lenssen J.P.M., Menting F.B.J., Van der Putten W.H.: Plant responses to simultaneous stress of waterlogging and shade: amplified or hierarchical effects? – New Phytol. **157**: 281-290, 2003.

Lhotka J.M., Loewenstein E.F.: Indirect measures for characterizing light along a gradient of mixed-hardwood riparian forest canopy structures. – Forest Ecol. Manag. **226**: 310-318, 2006.

Li X.L., Li N., Jin Y. *et al.*: Morphological and photosynthetic responses of riparian plant *Distylium chinense* seedlings to simulated Autumn and Winter flooding in Three Gorges Reservoir Region of the Yangtze River, China. – Acta Ecol. Sin. **31**: 31-39, 2011.

Liu A., Dickmann D.I.: Responses of two hybrid *Populus* clones to flooding, drought, and nitrogen availability. I. Morphology and growth. – Can. J. Bot. **70**: 2265-2270, 1992.

Lockhart B.R., Gardiner E.S., Leininger T.D. *et al.*: Flooding facility helps scientists examine the ecophysiology of floodplain species used in bottomland hardwood restorations. – Ecol. Restor. **24**: 151-157, 2006.

Lockhart B.R., Gardiner E.S., Stautz T. *et al.*: Development and plasticity of endangered shrub *Lindera melissifolia* (Lauraceae) seedlings under contrasting light regimes. – Plant Spec. Biol. **27**: 30-45, 2012.

Lockhart B.R., Gardiner E.S., Leininger T.D. *et al.*: *Lindera melissifolia* responses to flood duration and light regimes suggest strategies for recovery and conservation. – Plant Ecol. **214**: 893-905, 2013.

Luken J.O., Kuddes L.M., Tholemeier T.C. *et al.*: Comparative response of *Lonicera maackii* (Amur honeysuckle) and *Lindera benzoin* (spicebush) to increased light. – Am. Midl. Nat. **138**: 331-343, 1997.

Mielke M.S., Schaffer B.: Photosynthetic and growth responses of *Eugenia uniflora* L. seedlings to soil flooding and light intensity. – Environ. Exp. Bot. **68**: 113-121, 2010.

Niinemets Ü., Valladares F.: Photosynthetic acclimation to simultaneous and interacting environmental stresses along natural light gradients: optimality and constraints. – Plant Biol. **6**: 254-268, 2004.

Niinemets Ü.: Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. – Forest Ecol. Manag. **260**: 1623-1639, 2010.

Peterson D.L., Bazzaz F.A.: Photosynthetic and growth responses of silver maple (*Acer saccharinum* L.) seedlings to flooding. – Am. Mid. Nat. **112**: 261-272, 1984.

Pezeshki S.R., Chambers J.L.: Stomatal and photosynthetic response of sweetgum (*Liquidambar styraciflua*) to flooding. – Can. J. Forest Res. **15**: 371-375, 1985.

Pezeshki S.R., Anderson P.H.: Response of three bottomland species with different flood tolerance capabilities to various flooding regimes. – Wetl. Ecol. Manag. **4**: 245-256, 1997.

Pezeshki S.R.: Wetland plant responses to soil flooding. – Environ. Exp. Bot. **46**: 299-312, 2001.

Regehr D.L., Bazzaz F.A., Boggess W.R.: Photosynthesis, transpiration and leaf conductance of *Populus deltoides* in relation to flooding and drought. – Photosynthetica **9**: 52-61, 1975.

Rosati A., Day K.R., DeJong T.M.: Distribution of leaf mass per unit area and leaf nitrogen concentration determine partitioning of leaf nitrogen within tree canopies. – Tree Physiol. **20**: 271-276, 2000.

Smit B., Stachowiak M., Van Volkenburgh E.: Cellular processes limiting leaf growth in plants under hypoxic root stress. – J. Exp. Bot. **40**: 89-94, 1989.

Unks R.R., Shear T.H., Krings A. *et al.*: Environmental controls of reproduction and early growth of *Lindera melissifolia* (Lauraceae). – Castanea **79**: 266-277, 2014.

Vu J.V.C., Yelenosky G.: Photosynthetic responses of citrus trees to soil flooding. – Physiol. Plantarum **81**: 7-14, 1991.

Wiggers M.S.: Pondberry (*Lindera melissifolia*) 5-year review: Summary and Evaluation. Pp. 42. U.S. Fish and Wildlife Service, Southeast Region, Mississippi Field Office, Jackson, 2014.

WorldClimate: Rolling Fork, Sharkey County, Mississippi USA. – Available from http://www.worldclimate.com (accessed December 9, 2015).

Wright R.D.: Photosynthetic competence of an endangered shrub, *Lindera melissifolia*. – Proc. Ark. Acad. Sci. **44**: 118-120, 1990.

Yasumura Y., Onoda Y., Hikosaka K. *et al.*: Nitrogen resorption from leaves under different growth irradiance in three deciduous species. – Plant Ecol. **178**: 29-37, 2005.

Yasumura Y., Hikosaka K., Hirose T.: Seasonal changes in photosynthesis, nitrogen content and nitrogen partitioning in *Lindera umbellate* leaves grown in high and low irradiance. – Tree Physiol. **26**: 1315-1323, 2006.