

Leaf acclimation to soil flooding and light availability underlies photosynthetic capacity of *Lindera melissifolia*, an endangered shrub of bottomland forests in the Mississippi Alluvial Valley, USA

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Lindera melissifolia is an endangered shrub indigenous to the broadleaf forest of the Mississippi Alluvial Valley (MAV). In this region, extant colonies of the species are found in periodically ponded habitats where a diversity of broadleaf trees can form well-developed overstory and sub-canopies—these habitat characteristics suggest that soil flooding and light availability are primary drivers of *L. melissifolia* ecophysiology. To understand how these two factors affect its photosynthetic capacity, we quantified leaf characteristics and photosynthetic response of plants grown in a large-scaled, field setting of three distinct soil flooding levels (no flood, 0 day; short-term flood, 45 days; and extended flood, 90 days) each containing three distinct light availability levels (high light, 30% shade cloth; intermediate light, 63% shade cloth; and low light, 95% shade cloth). *Lindera melissifolia* leaves showed marked plasticity to interacting effects of flooding and light with lamina mass per unit area ($L_{m/a}$) varying 78% and total nitrogen content per unit area (N_a) varying 63% from the maximum. Photosynthetic capacity (A_{1800-a}) ranged 123% increasing linearly with N_a from low to high light. Extended flooding decreased the slope of this relationship 99% through a reduction in N availability and metabolic depression of A_{1800-a} relative to N_a . However, neither soil flooding nor light imposed an additive limitation on photosynthetic capacity when the other factor was at its most stressful level, and the A_{1800-a} – N_a relationship for plants that experienced short-term flooding suggested post-flood acclimation in photosynthetic capacity was approaching the maximal level under respective light environments. Our findings provide evidence for wide plasticity and acclimation potential of *L. melissifolia* photosynthetic capacity, which supports active habitat management, such as manipulation of stand structure for improved understory light environments, to benefit long-term conservation of the species in the MAV.

Key words: Leaf mass per area, light acclimation, nitrogen, photosynthesis, shade, waterlogging

Editor: Kevin Hultine

Received 14 March 2023; Revised 21 June 2023; Editorial Decision 1 July 2023; Accepted 11 July 2023

Cite as: Gardiner ES, Leininger TD, Connor KF, Devall MS, Hamel PB, Schiff NM, Wilson AD (2023) Leaf acclimation to soil flooding and light availability underlies photosynthetic capacity of *Lindera melissifolia*, an endangered shrub of bottomland forests in the Mississippi Alluvial Valley, USA. *Conserv Physiol* 11(1): coad051; doi:10.1093/conphys/coad051.

Introduction

The Mississippi Alluvial Valley (MAV), a 10-million-ha geographic region surrounding the lower Mississippi River in the south-central United States, holds global significance for ecologically sustainable management and conservation of natural resources (Stanturf *et al.*, 2000). The fertile alluvial soils and temperate climate of the region support species-rich, deciduous broadleaf forests that are foundational to terrestrial and aquatic systems extending well beyond the margins of the MAV (Gardiner, 2014; Miranda *et al.*, 2021). The region, ideal for row crop production, has historically supported a robust, globally prominent agricultural economy (USDA Economic Research Service, 2015; Olson and Speidel, 2021). Successes in developing and protecting the MAV for agricultural production, however, have been at the expense of forest conservation such that indigenous bottomland forest extent has declined 70% (Gardiner, 2014).

Agricultural development and the subsequent forest lost in the MAV have produced consequences spanning several environmental and ecological fronts. Degradation of soil quality by cultivation and the resulting impacts of agricultural runoff to water quality have been found in local floodplain catchments (Bhattacharya *et al.*, 2016) and downstream of the region into the Gulf of Mexico (Rabotyagov *et al.*, 2014). Groundwater extraction for crop irrigation has surpassed aquifer recharge rates thereby lowering water tables and altering seasonal dynamics of the hydrologic cycle (Dakhlalla *et al.*, 2016). Terrestrial carbon pools have been exhausted as contemporary land use practices continue to suppress carbon storage functions in the MAV (Hanberry *et al.*, 2015). Habitat available to native flora and fauna has been reduced and critically degraded—impacts most obvious for fauna requiring expansive tracts of particular forest environments (Buehler *et al.*, 2008) or habitats created by functionally connected river-floodplain systems (Dembkowski and Miranda, 2011). The extensive deforestation has predictably led to fragmentation of remaining MAV forests (Rudis, 1995). This fragmentation has increased vulnerability to external threats and exacerbated degradation of remnant forests through reduced diversity of plant communities across the landscape, increased influx of invasive plant species, elevated susceptibility to forest decline and dieback syndromes, and persistent application

of misguided and ineffective forest management activities (Rudis, 1995; Gardiner, 2014).

Deforestation, alteration of floodplain hydrologic regimes and forest degradation have been implicated in the imperilment of *L. melissifolia* Lauraceae (pondberry), a shrub indigenous to the MAV (US Fish and Wildlife Service, 1993; Devall, 2013). In this region, *L. melissifolia* forms clonal colonies in the understory of broadleaf forests, typically where floodplain geomorphology and subsurface soil characteristics lead to microsites of ponded water during winter and spring months (Devall *et al.*, 2001; Hawkins *et al.*, 2010). Botanists historically have noted *L. melissifolia* as a rare plant (Steyermark, 1949), so directly linking human activities to the current population status of this species is tenuous. However, it has been reasoned that MAV land use has limited the availability of suitable habitats (Carter *et al.*, 1990), contributed to colony isolation in fragmented forests (Devall, 2013), and heightened vulnerability of existing colonies to external threats, including the non-native fungal pathogen *Raffaelea lauricola* (Fraedrich *et al.*, 2011). Accordingly, the US Fish and Wildlife Service listed *L. melissifolia* as federally endangered to highlight the need to thwart risks of habitat loss and degradation that could further jeopardize the persistence of this species (US Fish and Wildlife Service, 1993; Devall, 2013).

Life history accounts of *L. melissifolia* in the MAV routinely have highlighted a clear association between colony occurrence and recognizable commonalities among site factors of habitats (Morgan, 1983; Devall, 2013). Environmental conditions associated with these common site factors have been interpreted to represent life cycle requirements of the species. In the MAV, for example, *L. melissifolia* colonies typically occur where surface depressions are underlain with soil that exhibits poor internal drainage (Priest and Wright, 1991; Devall, 2013). During winter and early spring periods of high precipitation and low evapotranspiration, rainfall accumulates to form a perched water table that maintains inundation or ponding within surface depressions (Priest and Wright, 1991). Some workers have viewed this ability of *L. melissifolia* to colonize and proliferate into colonies of several hundred stems on these seasonally flooded sites as evidence that soil flooding is a biological requisite of the species (US Fish and Wildlife Service, 1993). Others held that

this correlation with soil flooding may not be a biological requirement of the *L. melissifolia* life cycle but it likely allows the species to thrive in areas where other species cannot because they lack comparable flood tolerance (Wright, 1990; Devall, 2013; Lockhart *et al.*, 2013).

Another commonality among *L. melissifolia* colonies in the MAV is their occurrence in the understory of mature, structurally complex forests (Hawkins *et al.*, 2009). Because these forests characteristically have a closed overstory canopy and a developed midstory that heavily shade the understory, Tucker (1984) considered *L. melissifolia* a shade dependent species that flourishes best in environments of “considerable shade”. Tucker’s (1984) interpretation conflicts with physiological models of growth and reproductive performance for shade-tolerant woody plants and our broader field observations and experimentation (Lockhart *et al.*, 2013; Lockhart *et al.*, 2017; Lockhart *et al.*, 2018; Leininger *et al.*, 2021). Oliver *et al.* (2005) explained that stand development patterns in MAV bottomland forests naturally advance toward structural complexity and canopy closure. Thus, occurrence of *L. melissifolia* in heavily shaded environments is not biologically obligatory; rather, it reflects morphological and physiological plasticity to the light environment that confers acclimation and shade tolerance (Lockhart *et al.*, 2013; Lockhart *et al.*, 2017).

The aforementioned habitat characteristics suggest that soil flooding and light availability interact as primary drivers of *L. melissifolia* ecophysiology and persistence in MAV bottomland environments. The purpose of this work was to assess through controlled experimentation the interaction of soil flooding and light availability as regulators of photosynthetic acclimation of *L. melissifolia*, particularly acclimation of photosynthetic capacity. We quantified leaf characteristics and photosynthetic response of *L. melissifolia* shrubs that were subjected to imposed gradients of soil flooding and light availability. Quantifying acclimation of the *L. melissifolia* photosynthetic mechanism to these environmental factors revealed information directly relevant to management of forest stand structure to benefit growth and reproduction of this plant. Thus, we interpret the implications of findings from our research to inform development of improved management approaches that target progressive conservation of this imperiled species.

Materials and Methods

Experiment establishment

This research was established at a field site within the MAV on the Theodore Roosevelt National Wildlife Refuge in Sharkey County, Mississippi, USA (32° 58'N, 90° 44'W). The site has soils developed from alluvium (Sharkey series: very-fine, smectitic, thermic, chromic EPIAQUERTS), and a mild temperate climate (humid, subtropical: mean annual rainfall of 1394 mm and mean annual temperature of 17.8°C) (NOAA, 2010). In 2005, we established an experimental population of

Table 1: Soil flooding and light availability treatment levels assigned to experimental units planted in *L. melissifolia*

Factor	Treatment level
Soil flooding ^a	No flood = 0 days of soil flooding
	Short-term flood = 45 days of soil flooding
	Extended flood = 90 days of soil flooding
Light availability ^b	High light = 30% shade cloth
	Intermediate light = 63% shade cloth
	Low light = 95% shade cloth

^aImpoundments assigned short-term or extended flood were inundated to 12 cm above the soil surface for the duration of the assigned regime.

^bQuantum sensors maintained in shade houses indicated the high light regime received an annual (2006) photosynthetic photon flux density (PPFD) that was 71.5% of ambient sunlight; the intermediate light regime received an annual PPFD that was 32.6% of ambient sunlight; and the low light regime received an annual PPFD that was 2.2% of ambient sunlight (Lockhart *et al.*, 2013).

L. melissifolia in a complex of 12, 0.4-ha earthen impoundments known as the Flooding Research Facility (FRF) (Lockhart *et al.*, 2006). The FRF was designed to permit random assignment of independent flooding and draining regimes to individual, replicate units on native soil. Additionally, three, 187-m² shade houses—wooden-frames covered with neutral density shade cloth—constructed in each impoundment permitted random assignment and independent control of light availability (Lockhart *et al.*, 2006).

L. melissifolia planting stock was generated with micro-propagation techniques (Hawkins *et al.*, 2007) from 20 genotypes collected from MAV populations growing within 2.5 to 100 km of the FRF. Single-stemmed stecklings produced by rooting shoot cuttings from micropropagated plants (Hawkins *et al.*, 2007) were raised for 5 months in 0.98-L containers in a climate-controlled greenhouse (Lockhart *et al.*, 2013). In April 2005, 3456 stecklings were outplanted into native soil within FRF shade houses. Each shade house received 96 stecklings that were randomly assigned a planting position on a 6 × 16 rectangular grid with positions spaced 1.2-m apart (Lockhart *et al.*, 2013). Stecklings averaged 22 cm tall at outplanting (Lockhart *et al.*, 2013). Competition from other plants was eliminated from within shade houses for the duration of the study by hoeing and directed application of glyphosate herbicide.

The FRF was configured according to a split-plot design with three levels of the whole plot factor (soil flooding regime), and three levels of the split-plot factor (light availability regime) (Table 1). Impoundments were randomly assigned a soil flooding level (no flood, short-term flood or extended flood) and shade houses in an impoundment were randomly assigned a light availability level (high light, intermediate light or low light) resulting in nine soil flooding and light availability treatment combinations, which were



Figure 1: Partial view of the Flooding Research Facility capturing a worker preparing to measure photosynthetic light response of *L. melissifolia* growing in an experimental unit assigned extended flood and high light and showing the arrangement of shade houses within impoundments in the left background (Photo credit USFS files, Brian Lockhart).

replicated four times. Outplanted seedlings were established and acclimated to their respective light environments for one growing season before we initiated soil flooding treatment in advance of leaf-out on 1 March 2006.

Plant sampling

Measurements to quantify the photosynthetic light response (A/PFD) of established *L. melissifolia* plants were conducted in May 2006 (Figure 1.). This timing allowed for sampling of plants established in soil that did not receive flooding (no flooding), plants established in soil recently drained of floodwater (short-term flooding), and plants established in soil that was presently flooded (extended flooding). Sample plants were chosen from one randomly selected replicate of each whole plot level (soil flooding regime). In each selected whole plot, six plants were randomly selected from each split-plot (light availability regime). Thus, we selected six plants from each of the nine treatment combinations for a total of 54 sample plants.

The evening before each selected plant was measured it was covered with opaque cloth to limit light incident on the crown for the duration of the measurement; and, in plots absent of floodwater, soil within the dripline of the crown was irrigated to field capacity. These methods ensured sample leaves were hydrated and photosynthetically inactive prior to initiation of A/PFD measurements. We chose sample leaves that were mature, without visible damage, and positioned in the upper crown of the sample plant. CO₂ exchange of sample leaves was measured with a Cirrus-2 infrared gas analyzer fitted with an automatic leaf cuvette and programmable light attachment (PP Systems, Amesbury, MA, USA). For each sample leaf, net photosynthesis (A_{net}) was recorded when CO₂ exchange stabilized at five fixed levels of PFD (0, 1800, 800, 200 and 50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). Reference gas was maintained at 375 ppm of CO₂ and temperature within the leaf cuvette averaged 30°C during sampling.

Each sample leaf was harvested for laboratory processing immediately upon completion of respective CO₂ exchange measurements. In the laboratory, lamina area (L_a) was measured with a LI-3100 Area Meter (LI-COR Biosciences, Inc., Lincoln, NE, USA), then leaves were dried to constant mass at 70°C before dry mass was measured with an analytical balance. Dried sample leaves were pulverized with a ball mill to pass a 100-mesh sieve (150 μm nominal sieve opening), and total nitrogen (N) concentration of each sample was quantified with a PE 2400 Series II CHNS/O Analyzer (PerkinElmer, Waltham, MA, USA).

Data analysis

Variables of morphology and N composition resulting from sample leaf processing included L_a , lamina mass (L_m), lamina mass per unit area ($L_{m/a}$), total N content (N_a : area basis) and total N concentration (N_m : mass basis). We modeled A/PFD and estimated key physiological variables for each sample leaf with Photosyn Assistant software (Dundee Scientific Ltd, Dundee, Scotland, UK), which fits photosynthetic response curves according to methods described by Prioul and Chartier (1977). Variables quantified through A/PFD modeling included dark respiration (R_d), light compensation point (I_c), apparent quantum yield (ϕ), maximum photosynthesis at light saturation (A_{max}) and saturating light intensity (I_s). Photosynthesis variables were scaled relative to L_a and L_m where appropriate.

Effects of soil flooding, light availability, and their interaction on response variables were determined with Analysis of Variance (ANOVA) for a completely random factorial experiment arranged in a split-plot design. The analysis was structured to handle each sample leaf as an independent sample. Thus, sample size for each of the nine soil flooding and light availability treatment combinations totaled six observations. The ANOVA model held 53 total degrees of freedom (df); 10 df were partitioned in the whole plot error term and 30 df were partitioned in the split-plot error term.

Table 2: Source effect significance for leaf trait and photosynthesis variables measured on *L. melissifolia* established along gradients of soil flooding and light availability. F-values are noted with * if $P < 0.05$, ** if $P < 0.01$ and *** if $P < 0.001$

Variable	Source		
	Soil flooding (df = 2)	Light availability (df = 2)	Soil flooding x light availability (df = 4)
L_a	0.9	20.1***	1.3
L_m	1.9	11.5***	2.0
$L_{m/a}$	30.3***	365.9***	7.3***
N_a	11.9***	112.7***	4.8**
N_m	93.7***	164.9***	1.3
R_d	1.2	43.5***	0.3
ϕ	1.0	0.3	1.5
I_c	0.8	24.5***	0.5
I_s	11.0**	25.5***	6.0**
A_{max-a}	70.6***	97.4***	25.5***
A_{max-m}	56.7***	33.8***	15.3***

We separated means within significant source effects using Least Significant Difference. Simple linear regression was used to model relationships between A measured at a PFD of $1800 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (A_{1800-a} : L_a basis; A_{1800-m} : L_m basis) and $L_{m/a}$, N_a and N_m . All analyses were conducted with SAS software version 9.4 (SAS Institute, Inc., Cary, NC USA); an α of 0.05 determined significance of all tests.

Results

Leaf characteristics

Bud break and leaf development initiated about two weeks earlier in low light than in high light. Soil flooding did not appear to impact this process. Full leaf-out across all treatment combinations was completed more than a month in advance of photosynthesis measurements. Soil flooding was not a significant source of variation in *L. melissifolia* L_a or L_m , but light availability accounted for differences observed for each of these variables (Tables 2 and 3). L_a was inversely related to light availability such that leaves produced by plants in the high light environment were 46% as large as leaves of the low light environment (Tables 2 and 3). Conversely, L_m measured on plants from either high or intermediate light was twice that of plants receiving low light (Tables 2, 3).

Soil flooding and light availability interacted to affect $L_{m/a}$ of *L. melissifolia* leaves (Table 2). $L_{m/a}$ tended to increase with flood duration for plants grown under high or intermediate light, but not for plants grown under low light (Table 3). Soil flooding and light availability interacted also to influence N_a (Table 2). Extended flooding reduced N_a at least 27% in plants raised under high or intermediate light, while it did not affect N_a in plants raised under low light (Table 3). N_m of *L. melissifolia* was lowered 17% by short-term flooding,

and a further 30% by extended flooding (Tables 2, 3). Plants grown under low light produced leaves with the greatest N_m irrespective of flooding regime (Table 3).

Photosynthetic light response

R_d and I_c of *L. melissifolia* leaves were unchanged by soil flooding, but light availability produced a response in both variables (Tables 2, 4). Leaves that developed in the high light environment showed R_d rates 38% greater than those in intermediate light, while leaves that developed in the intermediate light environment showed R_d rates 150% greater than those in low light (Table 4). I_c exhibited a response to light availability like that observed for R_d . Neither soil flooding nor light availability influenced ϕ of *L. melissifolia* (Tables 2, 4). Interaction between treatment effects accounted for significant variation in I_s , A_{max-a} , and A_{max-m} (Table 2). I_s was generally lowest for plants experiencing the extended flood, or for plants grown in low light (Table 4). *Lindera melissifolia* leaves showed the greatest rates of A_{max-a} when plants were raised under high light in the absence of soil flooding (Table 4). The extended flood reduced A_{max-a} by more than 63% for plants in environments of high or intermediate light, but did not influence A_{max-a} of plants in low light (Table 4). Consistent with the response observed for A_{max-a} , soil flooding inhibited A_{max-m} when *L. melissifolia* was grown under high or intermediate light, and this effect was most pronounced under extended flooding (Tables 2, 4). Soil flooding did not impact A_{max-m} of plants raised under low light (Table 4).

Photosynthetic capacity

N_a of *L. melissifolia* leaves increased with increasing $L_{m/a}$ (Fig. 2a). Extended flooding depressed the slope in this rela-

Table 3: Leaf traits (mean $\pm$ standard error)^a of *L. melissifolia* established along gradients of soil flooding and light availability

Variable	Soil flooding regime			
	0 days	45 days	90 days	Light regime mean
L _a (cm ²)				
High light	18.6 ± 2.1	32.3 ± 4.9	17.9 ± 1.9	22.9 ± 2.4 ^c
Inter. light	39.6 ± 3.3	35.9 ± 7.8	29.5 ± 4.1	34.9 ± 3.1 ^b
Low light	49.8 ± 7.1	47.7 ± 7.9	50.4 ± 4.5	49.3 ± 3.6 ^a
Flooding regime mean	36.0 ± 4.0 ^A	38.6 ± 4.1 ^A	32.6 ± 3.8 ^A	
L _m (g)				
High light	0.10 ± 0.02	0.22 ± 0.03	0.15 ± 0.02	0.16 ± 0.02 ^a
Inter. light	0.16 ± 0.02	0.17 ± 0.04	0.19 ± 0.03	0.17 ± 0.02 ^a
Low light	0.07 ± 0.01	0.07 ± 0.01	0.09 ± 0.01	0.08 ± 0.01 ^b
Flooding regime mean	0.11 ± 0.01 ^A	0.15 ± 0.02 ^A	0.14 ± 0.01 ^A	
L _{m/a} (g m ^{−2})				
High light	52.8 ± 4.9 ^{C,a}	67.4 ± 2.1 ^{B,a}	81.4 ± 2.9 ^{A,a}	67.2 ± 3.4
Inter. light	39.4 ± 3.2 ^{B,b}	45.2 ± 2.1 ^{B,b}	62.1 ± 2.3 ^{A,b}	48.9 ± 2.7
Low light	14.2 ± 1.0 ^{A,c}	14.8 ± 0.9 ^{A,c}	19.3 ± 0.9 ^{A,c}	16.1 ± 0.8
Flooding regime mean	35.5 ± 4.3	42.5 ± 5.3	54.3 ± 6.4	
N _a (g m ^{−2})				
High light	1.80 ± 0.09 ^{A,a}	1.86 ± 0.05 ^{A,a}	1.32 ± 0.06 ^{B,a}	1.67 ± 0.07
Inter. light	1.38 ± 0.10 ^{A,b}	1.27 ± 0.11 ^{A,b}	1.01 ± 0.07 ^{B,b}	1.22 ± 0.06
Low light	0.74 ± 0.07 ^{A,c}	0.68 ± 0.06 ^{A,c}	0.75 ± 0.03 ^{A,c}	0.73 ± 0.03
Flooding regime mean	1.31 ± 0.12	1.27 ± 0.12	1.03 ± 0.06	
N _m (mg g ^{−1})				
High light	34.9 ± 2.4	27.8 ± 1.3	16.2 ± 0.4	26.3 ± 2.1 ^b
Inter. light	35.1 ± 0.9	27.9 ± 1.8	16.4 ± 1.1	26.5 ± 2.0 ^b
Low light	52.3 ± 1.5	46.3 ± 2.0	39.2 ± 0.9	45.9 ± 1.6 ^a
Flooding regime mean	40.8 ± 2.2 ^A	34.0 ± 2.3 ^B	23.9 ± 2.6 ^C	

^aUppercase letters indicate difference among soil flooding regime means in a row, while lowercase letters indicate difference among light regime means in a column ($\alpha = 0.05$).

tionship because leaves with relatively high values for $L_{m/a}$, i.e. those in high and intermediate light, showed reduced N_a under this flood regime. In contrast to N_a , N_m decreased with increasing $L_{m/a}$ (Fig. 2b). Slopes of curves fit to this relationship were similar for each of the three flood regimes, illustrating a decrease in N_m of about 12% for a 10 g m⁻² increase in $L_{m/a}$.

A 10 g m⁻² rise in $L_{m/a}$ elevated A_{1800-a} about 19% for plants raised absent of soil flooding, and about 17% for plants that experienced the short-term flood (Fig. 3). A_{1800-a} was not responsive to $L_{m/a}$ if plants were subjected to the extended flood. A_{1800-a} showed strong response to N_a , except in plants subjected to the extended flood (Fig. 4a). Plants

receiving no flooding or short-term flooding exhibited an increase in A_{1800-a} of at least 47% per 0.5 g m⁻² rise in N_a . A_{1800-m} responded positively to N_m if plants experienced short-term soil flooding, and the steepest response (49% rise in A_{1800-m} for a 10 mg g⁻¹ increase in N_m) was marked by plants that experienced extended flooding (Fig. 4b).

Discussion

Photosynthetic function has been a focal point of *L. melissifolia* ecophysiology research since Wright (1990) initiated his field studies. Though few, investigations conducted before the current research provide important records of *L. melissifolia*

Table 4: Photosynthesis variables (mean $\pm$ standard error)^a of *L. melissifolia* established along gradients of soil flooding and light environment

Variable	Soil flooding regime			
	0 days	45 days	90 days	Light regime mean
R_d ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)				
High light	-1.02 ± 0.08	-0.85 ± 0.13	-0.95 ± 0.05	-0.94 ± 0.05^a
Inter. light	-0.76 ± 0.11	-0.63 ± 0.14	-0.66 ± 0.04	-0.68 ± 0.06^b
Low light	-0.27 ± 0.07	-0.23 ± 0.07	-0.32 ± 0.04	-0.27 ± 0.03^c
Flooding regime mean	-0.68 ± 0.09^A	-0.57 ± 0.09^A	-0.64 ± 0.07^A	
ϕ ($\mu\text{mol CO}_2 (\mu\text{mol photons})^{-1}$)				
High light	0.043 ± 0.004	0.033 ± 0.003	0.037 ± 0.004	0.038 ± 0.002^a
Inter. light	0.037 ± 0.002	0.048 ± 0.008	0.029 ± 0.002	0.038 ± 0.003^a
Low light	0.025 ± 0.012	0.042 ± 0.012	0.034 ± 0.001	0.034 ± 0.006^a
Flooding regime mean	0.035 ± 0.004^A	0.041 ± 0.005^A	0.033 ± 0.002^A	
I_c ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)				
High light	24.8 ± 3.3	28.5 ± 6.2	27.4 ± 2.9	26.9 ± 2.4^a
Inter. light	20.3 ± 2.9	16.4 ± 5.7	23.7 ± 2.6	20.2 ± 2.3^b
Low light	7.4 ± 0.9	5.7 ± 0.9	9.2 ± 0.8	7.4 ± 0.6^c
Flooding regime mean	17.5 ± 2.3^A	16.8 ± 3.5^A	20.1 ± 2.3^A	
I_s ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)				
High light	$379.0 \pm 20.2^{A,a}$	$447.8 \pm 60.7^{A,a}$	$192.2 \pm 23.2^{B,a}$	339.7 ± 33.8
Inter. light	$358.7 \pm 29.3^{A,a}$	$275.0 \pm 61.2^{AB,b}$	$179.0 \pm 12.2^{B,a}$	270.9 ± 27.9
Low light	$147.6 \pm 14.8^{A,b}$	$129.2 \pm 19.9^{A,c}$	$164.8 \pm 9.3^{A,a}$	147.2 ± 9.0
Flooding regime mean	295.1 ± 28.1	284.0 ± 42.0	178.7 ± 9.1	
$A_{\text{max-a}}$ ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)				
High light	$15.2 \pm 0.9^{A,a}$	$12.9 \pm 0.4^{B,a}$	$5.6 \pm 0.3^{C,a}$	11.2 ± 1.0
Inter. light	$12.4 \pm 0.7^{A,b}$	$10.9 \pm 1.2^{A,b}$	$4.4 \pm 0.3^{B,a}$	9.2 ± 0.9
Low light	$4.4 \pm 0.3^{A,c}$	$4.1 \pm 0.2^{A,c}$	$5.3 \pm 0.3^{A,a}$	4.6 ± 0.2
Flooding regime mean	10.6 ± 1.2	9.3 ± 0.9	5.1 ± 0.2	
$A_{\text{max-m}}$ ($\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$)				
High light	$299.3 \pm 30.2^{A,a}$	$194.5 \pm 9.2^{B,b}$	$69.0 \pm 3.4^{C,b}$	187.6 ± 24.9
Inter. light	$322.7 \pm 21.1^{A,a}$	$241.0 \pm 24.8^{B,a}$	$70.5 \pm 3.9^{C,b}$	211.4 ± 27.5
Low light	$312.5 \pm 17.9^{A,a}$	$278.7 \pm 12.4^{A,a}$	$274.3 \pm 11.4^{A,a}$	288.5 ± 8.7
Flooding regime mean	311.5 ± 13.0	238.0 ± 12.4	137.9 ± 23.7	

^aUppercase letters indicate difference among soil flooding regime means in a row, while lowercase letters indicate difference among light regime means in a column ($\alpha = 0.05$).

photosynthesis across the range of the species (Wright, 1990; Aleric and Kirkman, 2005; Lockhart *et al.*, 2017), contributing elemental information on variability of leaf function under a variety of plant and site conditions. But experimental data useful to inform active management to sustain species conservation are lacking, e.g. evaluation of plasticity of the photosynthetic mechanism to important environmental factors, and

available research findings appear confounded or conflicting (Aleric and Kirkman, 2005; Lockhart *et al.*, 2017). Our work provides fundamental insight into the *L. melissifolia* photosynthetic mechanism by showing how photosynthetic capacity acclimates to two interacting environmental factors, soil flooding and light availability, prominent in alluvial floodplain habitats occupied by this species.

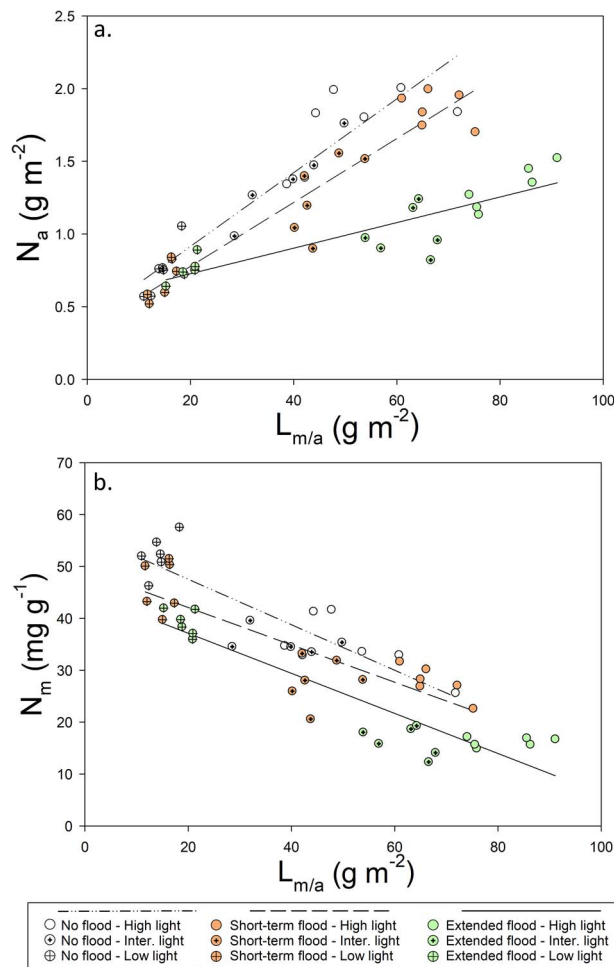


Figure 2: Response of leaf nitrogen to lamina mass per unit area in *L. melissifolia*. Data are plotted by soil flood and light availability treatment combinations with regression lines fit by soil flooding regime. (a) Relationship between N_a and $L_{m/a}$ (no flood: $r^2 = 0.88$, $P < 0.0001$; short-term flood: $r^2 = 0.90$, $P < 0.0001$; extended flood: $r^2 = 0.78$, $P < 0.0001$). (b) Relationship between N_m and $L_{m/a}$ (no flood: $r^2 = 0.74$, $P < 0.0001$; short-term flood: $r^2 = 0.69$, $P < 0.0001$; extended flood: $r^2 = 0.86$, $P < 0.0001$).

Forested floodplains are characteristically dynamic environments with high spatial and temporal variability in abiotic site factors. Many woody plants of temperate floodplains possess plasticity of leaf response that enables acclimation to these dynamic environments. Leaf plasticity is clearly expressed along a light availability gradient by deciduous trees and shrubs of temperate floodplains (McMillen and McClendon, 1983; Niinemets, 1997; Granata *et al.*, 2020), including *L. melissifolia* (Aleric and Kirkman, 2005; Lockhart *et al.*, 2017). Anatomical, morphological, and physiological acclimation support optimization of photosynthetic capacity under the “chronic” stress of the ambient light environment. Leaf plasticity and acclimation of the photosynthetic mechanism are also evident when edaphic or hydrologic factors

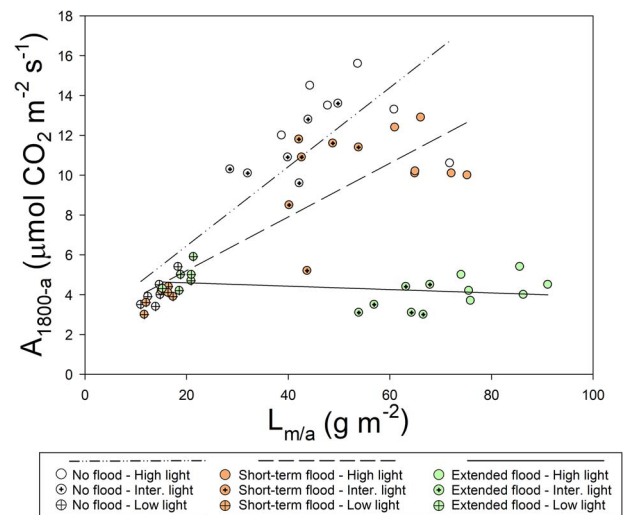


Figure 3: Response of photosynthesis to lamina mass per unit area in *L. melissifolia*. Data are plotted by soil flood and light availability treatment combinations with regression lines fit by soil flooding regime. Relationship between A_{1800-a} and $L_{m/a}$ (no flood: $r^2 = 0.73$, $P < 0.0001$; short-term flood: $r^2 = 0.72$, $P < 0.0001$; extended flood: $r^2 = 0.08$, slope not different from 0, $P = 0.26$).

impose stress on some woody plants of floodplains (Angelov *et al.*, 1996; Gardiner and Krauss, 2001; Niinemets and Kull, 2003). In cases of flooded or waterlogged soil, which for river floodplains is typically a temporary but “acute” stress that is most deleterious during the growing season, leaf acclimation is primarily physiological (Tatin-Froux *et al.*, 2014). Some well-adapted floodplain species exhibit resilience by maintaining sub-optimal photosynthetic function while soil is waterlogged, then appear to recover to full photosynthetic capacity when aerobic conditions return to the soil environment (Angelov *et al.*, 1996; Anderson and Pezeshki, 2000; Rodríguez *et al.*, 2015). Observations across soil flooding and light availability gradients established in this study reveal that *L. melissifolia* expresses leaf plasticity through structural and physiological mechanisms that foster photosynthetic acclimation and regulate its photosynthetic capacity.

Plasticity in leaf morphology and N-status

Soil flooding has been linked to a reduction in leaf lamina area and mass of some broadleaf trees and shrubs, including *L. melissifolia* (Liu and Dickmann, 1992; Lockhart *et al.*, 2017), but observation of these morphological responses for species endemic to temperate floodplains is seldom reported. Reduced lamina size is viewed as indicative of root hypoxia stress and likely results from limitations on cell wall extensibility that inhibit complete lamina expansion (Smit *et al.*, 1989). Observations noted in this report are inconsistent with those previously reported by Lockhart *et al.* (2017), who found that 90 days of soil flooding reduced *L. melissifolia* lamina area 35% and reduced lamina mass 22%. Our study shows soil

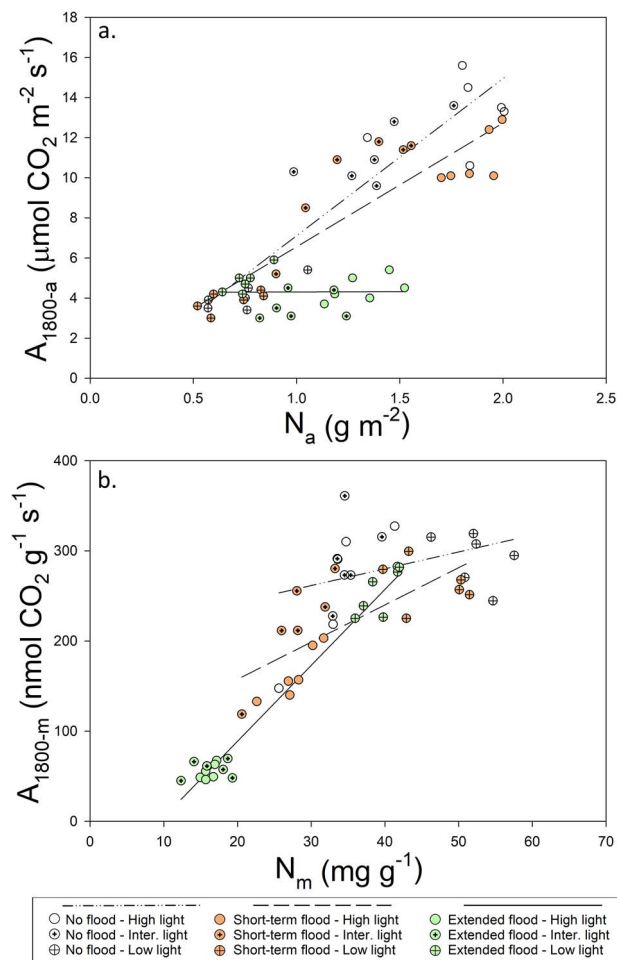


Figure 4: Response of photosynthesis to leaf nitrogen in *L. melissifolia*. Data are plotted by soil flood and light availability treatment combinations with regression lines fit by soil flooding regime. (a) Relationship between A_{1800-a} and N_a (no flood: $r^2 = 0.83$, $P < 0.0001$; short-term flood: $r^2 = 0.81$, $P < 0.0001$; extended flood: $r^2 = 0.0001$, slope not different from 0, $P = 0.96$). (b) Relationship between A_{1800-m} and N_m (no flood: $r^2 = 0.12$, slope not different from 0, $P = 0.15$; short-term flood: $r^2 = 0.52$, $P = 0.0007$; extended flood: $r^2 = 0.97$, $P < 0.0001$).

flooding of a similar duration imposed by Lockhart *et al.* (2017) did not affect *L. melissifolia* lamina area or mass, and when viewed together with Lockhart *et al.* (2017) reveals interannual variation in leaf size that may have contributed to the differing responses.

The light environment imposes a more influential role in leaf development of floodplain trees and shrubs than does soil flooding. Like other temperate broadleaves (Koike *et al.*, 2001; Muraoka and Koizumi, 2005; Sack *et al.*, 2006; Granata *et al.*, 2020), *L. melissifolia* lamina area was inversely related to light availability, while lamina mass showed a positive relationship to the gradient. This plasticity in lamina morphology is associated with acclimation that generally sup-

ports efficiencies in light harvesting and CO_2 uptake across the irradiance gradient. Our findings verify other published examinations of *L. melissifolia* leaf morphology relative to light availability—phenotypic variation in lamina area, particularly, ranges greatly ($> 115\%$ from high to low light in the current study) across a gradient of light availability (Lockhart *et al.*, 2012; Lockhart *et al.*, 2017). Thus, the species exhibits wide plasticity for acclimation of gross leaf morphology in simulated understory environments of markedly different light availability.

The observed plasticity in lamina area and mass relative to light availability would be expected to impact other key leaf traits more directly associated with photosynthetic capacity. The ratio of lamina mass to lamina area, i.e. $L_{m/a}$, reflects leaf tissue structure and cell composition (John *et al.*, 2017) and provides an informative index of acclimation strongly linked to photosynthetic capacity (Ellsworth and Reich, 1992; Ellsworth and Reich, 1993; Niinemets, 1997; Sack *et al.*, 2006; Niinemets, 2010). Within a species, relatively low $L_{m/a}$ indicates leaves structured to favor light absorbance in low light environments owing to its association with a thin epidermis, and low palisade and spongy mesophyll volumes (Niinemets, 2010; Villar *et al.*, 2013; Gratani, 2014). Relatively high $L_{m/a}$ indicates leaves structured to favor CO_2 fixation in high light environments because of its association with a high palisade density and volume and high spongy mesophyll volume (Poorter *et al.*, 2009; Niinemets, 2010; Villar *et al.*, 2013; Gratani, 2014). As such, $L_{m/a}$ of temperate broadleaf species characteristically decreases along gradients of high to low irradiance (Niinemets, 1997). By contrast, $L_{m/a}$ reportedly increases during periods of soil flooding (Liu and Dickmann, 1992; Gardiner and Krauss, 2001; Poorter *et al.*, 2009). This increase is not attributed to structural acclimation, but appears to be driven by an accumulation of non-structural carbohydrates caused by interruption of their translocation out of the leaf (Vu and Yelenosky, 1991; Gardiner and Krauss, 2001; Martínez-Alcántara *et al.*, 2012; Sloan *et al.*, 2016). $L_{m/a}$ of *L. melissifolia* examined in this study responded to the interacting effects of soil flooding and light availability. $L_{m/a}$ was greatest under the longest flood duration and highest light availability, but the effect of soil flooding was not evident where light availability was low. This observation appears consistent with the supposition that soil flooding led to an accumulation of non-structural carbohydrates that boosted $L_{m/a}$ where photosynthesis was not limited by light. Within a flood regime, $L_{m/a}$ of *L. melissifolia* leaves ranged more than 270% from low to high light, confirming that development of leaf structure exhibits strong plasticity to light availability (Aleric and Kirkman, 2005; Lockhart *et al.*, 2017), and suggesting this plasticity is a primary mechanism supporting photosynthetic acclimation to the light environment.

Coupled with the observed variation in morphology and structure, we found soil flooding and light availability to affect N content and concentration of *L. melissifolia* leaves.

Foliar N tends to drop, sometimes leading to leaf chlorosis, in woody plants experiencing waterlogged soil. The decline in leaf N results from root hypoxia which can inhibit N uptake and alter N translocation to foliage (DeLaune *et al.*, 1998; Martínez-Alcántara *et al.*, 2012). Additionally, the decline in leaf N is sometimes associated with an increase in $L_{m/a}$ as was the case in this study (Gardiner and Krauss, 2001). This suggests that it may also be linked, in part, to the previously discussed carbohydrate accumulation thought to have increased $L_{m/a}$ (Martínez-Alcántara *et al.*, 2012; Sloan *et al.*, 2016; Lockhart *et al.*, 2017). Leaf chlorosis was not evident in *L. melissifolia* studied in this experiment, even for plants that experienced extended flooding (personal observation by Gardiner). But, extended flooding led to a lower N_a in leaves of high and intermediate light environments, and N_m decreased with flood duration regardless of light regime suggesting that soil flooding likely limited N uptake, translocation to leaves, and/or the N:carbohydrate ratio in leaves.

Consistent with other reports (Ellsworth and Reich, 1992; Niinemets, 1997; Aranda *et al.*, 2004; Lockhart *et al.*, 2017), we found a positive relationship between N_a and light availability that bore a similar pattern to our findings for treatment effects on $L_{m/a}$ and N_m . Variation in N_a relative to the light environment has been linked to plasticity in lamina morphology and anatomy, and to plasticity in N partitioning that supports efficient photosynthesis under the prevailing light environment. Accordingly, a relatively high N_a is typical of leaves acclimated to light-rich environments and is associated with an increase in the fraction of N partitioned to RuBP carboxylase (rubisco) to sustain high carbon fixation. Respectively, a relatively low N_a is typical of leaves acclimated to light-poor environments and is associated with an increase in the fraction of N partitioned to chlorophyll to enhance light harvesting (Evans, 1989; Ellsworth and Reich, 1992; Niinemets, 1997). N_a status of *L. melissifolia* in this study varied with soil flooding and light availability consistent with other temperate broadleaves, and implies shifts in N partitioning between rubisco and chlorophyll fractions that support photosynthetic acclimation may have occurred with the environmentally driven variation in N_a and $L_{m/a}$.

Plasticity in photosynthetic traits

Variation in leaf traits due to soil flooding and light availability was accompanied by substantial variation in *L. melissifolia* photosynthesis as was expected from results of previous work (Wright, 1990; Aleric and Kirkman, 2005; Lockhart *et al.*, 2017). Analysis of A/PFD allowed us to partition variation in photosynthetic response to effects of soil flooding and light availability, and to identify which photosynthetic traits exhibit plasticity in response to these environmental factors. Unfortunately, we cannot compare our findings to those of Wright (1990) or Aleric and Kirkman (2005) because soil flooding, which was reportedly present at their respective study sites, was not accounted for in their sampling or analyses. Three traits, R_d , ϕ , and I_c , showed no variation

attributable to soil flooding. Reports detailing the impact of flooding stress on these traits are few, but reduced ϕ has been noted as a primary impairment to photosynthesis of flood-stressed, mesophytic shrubs and trees (Davies and Flore, 1986; Gardiner and Krauss, 2001). The ability to maintain ϕ during seasonal soil flooding events appears significant in the adaptiveness of *L. melissifolia* to floodplain habitats and warrants further ecophysiological investigation.

In contrast to soil flooding, light availability influenced R_d and I_c . Both traits ranged more than 70% and were least where leaves developed in low light. These observations are consistent with photosynthetic acclimation to light availability reported for some temperate broadleaf species (Ellsworth and Reich, 1993; Kubiske and Pregitzer, 1996; Oguchi *et al.*, 2005; Granata *et al.*, 2020). Ranges in R_d and I_c are often driven by the extent of adjustment in $L_{m/a}$ across the irradiance gradient (Mitchell *et al.*, 1999; Lusk and Reich, 2000).

Soil flooding and light availability effects on *L. melissifolia* were most impactful to photosynthetic traits indicative of leaves functioning at maximal CO_2 uptake and fixation capacity, i.e. I_s , A_{max-a} , and A_{max-m} . Calculation of a simple index (Valladares *et al.*, 2002) quantifies plasticity in A_{max-a} at 0.69 and 0.66 for the soil flooding and light availability effects, respectively. Though flooding obviously constrains photosynthesis in most temperate floodplain broadleaves, including *L. melissifolia*, (Dreyer, 1994; Anderson and Pezeshki, 2000; Li *et al.*, 2015; Lockhart *et al.*, 2017), the literature remains ambiguous concerning how this stress impacts photosynthetic traits derived from A/PFD response curves (Gardiner and Krauss, 2001). With respect to light availability, plasticity observed for A_{max-a} is within the range of plasticity reported for other temperate broadleaves (Valladares *et al.*, 2002). Broadleaf species for which light availability alters leaf morphology generally show comparatively low values for I_s and A_{max-a} under the stress of low light, while values for A_{max-m} tend to covary with shade tolerance and successional status (Bazzaz and Carlson, 1982; Walters *et al.*, 1993; Niinemets and Valladares, 2004). Much less is known about the combined effects of the two environmental stresses on expression of these photosynthetic traits in temperate trees and shrubs. We found variation in response by *L. melissifolia* for each of these traits to be attributable to interacting effects of the environmental factors, but the effects were not additive at the most stressful level for each factor, i.e. they did not appear amplified (*sensu* Lenssen *et al.*, 2003). In other words, soil flooding did not co-limit A_{max-a} if *L. melissifolia* was raised under low light, nor did light availability co-limit A_{max-a} if plants received extended flooding.

Acclimation of photosynthetic capacity to soil flooding and light availability

Development of photosynthetic capacity in temperate broadleaves is inextricably linked to leaf N status because leaf N is predominantly held in proteins supporting light

harvesting, electron transport, and carbon fixation functions (Evans, 1989; Reich *et al.*, 1995). Accordingly, photosynthetic capacity responds to variation in leaf N content and allocation brought about by leaf acclimation, particularly to the light environment, that affects leaf anatomy and structure, leaf N concentration, or N partitioning among light harvesting and carbon fixation functions (Niinemets, 1997; Aranda *et al.*, 2004; Kitaoka and Koike, 2005; Delagrangé, 2011). In this study, photosynthetic capacity (A_{1800-a}) of *L. melissifolia* showed significant acclimation to environmental gradients by ranging about 121% across soil flooding regimes (extended flood to no flood) and about 123% across light environments (low light to high light). This suggests the species is capable of acclimation across broader environmental gradients, particularly in respect to light availability, than what might be concluded from most observations of its natural occurrence in the MAV (Hawkins *et al.*, 2009; Devall, 2013). Obviously, natural occurrence of *L. melissifolia* is limited by several factors in addition to those affecting its ecophysiology but the potential for photosynthetic acclimation bares relevance to tolerance of soil flooding and the light environment. An understanding of the mechanisms that support this photosynthetic acclimation in *L. melissifolia* can be gained from relationships between photosynthetic capacity and indices of physiological plasticity, principally leaf N, and structural plasticity, principally $L_{m/a}$, established in the literature (Ellsworth and Reich, 1992; Reich *et al.*, 1995; Niinemets and Valladares, 2004; Kitaoka and Koike, 2005).

L. melissifolia developed greatest photosynthetic capacity (A_{1800-a}) in the absence of soil flooding and in the environment of highest light. A_{1800-a} decreased as light availability decreased; response along this gradient was linear to variation in N_a . Acclimation to open versus shaded environments observed for some temperate broadleaves, including *Quercus petraea* and *Acer saccharum*, suggests variation in N_a that drives the linear A_{1800-a} – N_a relationship arises exclusively from structural acclimation of the leaf, i.e. change in N_a is proportional to change in $L_{m/a}$ (Gardiner *et al.*, 2009; Delagrangé, 2011; except see Ellsworth and Reich, 1992). For those species, the preeminence of leaf structure in determining N_a was confirmed by observation of a corresponding relationship between photosynthetic capacity and $L_{m/a}$, or stable N_m across the light gradient or range of $L_{m/a}$. Yet, many species, including *L. melissifolia* in this study, show change in N_m accompanying change in $L_{m/a}$ in response to the light environment. As with this species, the relationship between N_m and $L_{m/a}$ most often is negative because structural change to the lamina that increases $L_{m/a}$ tends to move leaf chemical composition to a lower N fraction (Niinemets, 1997; Poorter *et al.*, 2009). The significance of this pattern is that the amounts of N partitioned to light harvesting versus carbon fixation functions varies with leaf N availability (Evans, 1989; Niinemets, 1997) and can impart a physiological impact on the A_{1800-a} – N_a relationship (Ellsworth and Reich, 1992; Delagrangé, 2011).

We expected to find an element of metabolic plasticity affecting the A_{1800-a} – N_a relationship that would substantiate a physiological component of acclimation of *L. melissifolia* photosynthetic capacity across the studied range of light environments after recording variation in N_m associated with $L_{m/a}$. This should be revealed through variation in A_{max-m} and the A_{1800-m} – N_m relationship. Reich *et al.* (1998) and Kaelke *et al.* (2001) illustrated the dependency of A_m upon N_m for a range of deciduous broadleaf tree species but noted the strength of this relationship varied between species and especially for intra-specific comparisons of photosynthetic acclimation across light environments. For example, Gardiner *et al.* (2009) demonstrated the importance of N availability to acclimation of photosynthetic capacity of *Fagus sylvatica* in contrasting understory environments, but *Quercus robur* photosynthetic acclimation showed much less reliance on N_m . In this study, A_{max-m} of *L. melissifolia* did not differ by light level (Table 3), and A_{1800-m} was unrelated to N_m for plants grown in the absence of soil flooding. While N_m differed between light environments, and this was likely accompanied with shifts in N partitioning among proteins of the photosynthetic process (Niinemets, 1997; Delagrangé, 2011), photosynthetic capacity lacked responsiveness to N availability. This finding suggests acclimation of photosynthetic capacity to the prevailing light environment is primarily accomplished through adjustment of leaf structure and the resulting impact on N_a rather than adjustment of metabolic efficiencies. This is consistent with analysis by Reich *et al.* (1998), who found the A_{1800-m} – N_m relationship often lacks prominence for species that express strong variation in leaf structure relative to light availability.

Soil flooding too had great impact on photosynthetic capacity of *L. melissifolia* but the effect arose physiologically and was expressed only if plants were raised under environments of intermediate or high light. Extended flooding flattened slope of the A_{1800-a} – N_a relationship 99% which appeared attributable to two sources: depression of A_{1800-a} for a given level of N_a and a reduction in the range of N_a . The depression of A_{1800-a} relative to N_a indicates metabolic impairment of photosynthetic capacity—confirmed by the substantial decline in A_{1800-m} relative to N_m . Because of the differential effect among light environments and the lack of an effect on ϕ , we suspect soil flooding reduced photosynthetic capacity of *L. melissifolia* primarily through impairment of carbon fixation functions (Gardiner and Krauss, 2001). Evidence of reduced N partitioning to rubisco or suppressed rubisco activity has been reported for other flood-stressed temperate broadleaves that exhibited decline in photosynthetic capacity (Davies and Flore, 1986; Gardiner and Hodges, 1996; Gardiner and Krauss, 2001; Kitao *et al.*, 2022). Vu and Yelenosky (1991), who worked with *Citrus* spp., reported direct evidence that suppressed carboxylation contributes to the metabolic decline by measuring decreased rubisco activation that ranged between 35% and 60% for two cultivars during 24 to 54 days of soil flooding. Though we cannot confirm soil flooding reduced rubisco activity in

L. melissifolia our observation of depressed A_{1800-a} for a given level of N_a indicates contributions of this factor to the metabolic reduction in photosynthetic capacity.

Soil flooding is suspected to also impact photosynthetic capacity by lowering the amount of N partitioned to carboxylation functions (Liao and Lin, 1996; Herrera *et al.*, 2008; De Pedro *et al.*, 2020; Kitao *et al.*, 2022). We recorded a reduction in the range of N_a relative to $L_{m/a}$ that accompanied a depressed A_{1800-a} with extended flooding in high and intermediate light environments. This pattern diminished the dependency of A_{1800-a} upon $L_{m/a}$ as observed for the light effect and shifted importance of N availability to the relationship, i.e. high A_{1800-m} was maintained through extended flooding in the low light environment where plants retained relatively high N_m . Given that *L. melissifolia* in high and intermediate light environments was unable to maintain N_m and consequently N_a under extended flooding, N partitioning may have receded away from carboxylation functions. Evans (1989) illustrated that the proportion of total leaf N partitioned to thylakoid proteins remains relatively stable across the range of N_a , while the proportion partitioned to Calvin Cycle proteins increases with increasing N_a .

A significant aspect of the physiological impairment discussed above is the apparent post-flood acclimation of *L. melissifolia* towards maximal photosynthetic capacity of the light environment. Other authors studying temperate broadleaf species emphasized that the ability to recover physiological function after floodwaters recede confers a level of fitness in floodplain environments (Wagner and Dreyer, 1997; Anderson and Pezeshki, 2000; Glenz *et al.*, 2006; Li *et al.*, 2015; Sample *et al.*, 2023). Measurements from plants assigned the short-term flood were collected 30–40 days after floodwater was drawn down and all relationships between A_{1800-a} , or A_{1800-m} , and $L_{m/a}$, N_a , and N_m held slopes intermediate to those for extended and no flooding. The slope of the A_{1800-a} – N_a relationship for plants that experienced short-term flooding was 79% of the slope held by plants that had experienced no flooding indicating that metabolic constraints to photosynthetic capacity during soil flooding were waning. Post-flood acclimation appeared to be driven by increased N_m , and subsequently N_a , relative to $L_{m/a}$ which shifted dependence of A_{1800-a} towards N_a as observed in the absence of flooding. However, the A_{1800-m} – N_m relationship remained significant, marking persistence of the flooding effect that depressed N_m and A_{1800-m} in high and intermediate light environments. Thus, post-flood acclimation of photosynthetic capacity appears to involve transition from the physiological factors predominant during soil flooding to the structural factors predominant in the absence of flooding.

Conservation Implications

Long-term conservation of *L. melissifolia* in the MAV could benefit from active management that improves size and vigor of existing colonies and promotes regeneration of

additional colonies on suitable, unoccupied sites within forests the species currently inhabits. This study shows how two prominent environmental factors in the MAV floodplain interact to govern acclimation of photosynthetic capacity in *L. melissifolia* and contributes important information towards developing silvicultural prescriptions that foster improved colony vigor, growth, and reproduction. Key findings from our work that hold conservation implications include: 1) photosynthetic capacity of *L. melissifolia* exhibited wide plasticity and acclimation to environmental factors; 2) the photosynthetic mechanism showed resistance amid co-occurring stresses; 3) physiological plasticity enabled acclimation of the photosynthetic mechanism after floodwater removal; and 4) the light environment was primal to development of *L. melissifolia* photosynthetic capacity.

Our research revealed that photosynthetic capacity of *L. melissifolia* acclimated to prevailing light and soil hydrologic regimes through structural and physiological mechanisms of considerable plasticity. The range of plasticity observed for this understory shrub was comparable to that expressed by other temperate broadleaf species of more common occurrence and wider range (Valladares *et al.*, 2002; Takahashi *et al.*, 2005; Villar *et al.*, 2013). We confirm *L. melissifolia* can adjust leaf structure and physiology to maintain a positive carbon balance under multiple stresses indicative of a wide range of alluvial floodplain habitats. This confirmation substantiates previous findings for growth and reproduction of *L. melissifolia* (Lockhart *et al.*, 2018; Leininger *et al.*, 2021) and dismisses concerns of narrow habitat suitability for this species relative to development of the photosynthetic mechanism. The plasticity and acclimation potential associated with the photosynthetic mechanism imparts an element of flexibility in design and implementation of silvicultural practices aimed at habitat improvement for the species. *Lindera melissifolia* is inherently capable of photosynthetic acclimation across the range of understory microsites that could be created by silvicultural practices of different intensities, and application of practices need not be restricted to sites of specific hydrologic regimes.

Following the first conservation implication, neither soil flooding or light imposed an additive limitation on *L. melissifolia* photosynthetic capacity when the other factor was at its most stressful level. This finding connotes a strong tolerance to soil flooding under the chronic stress of low light and implies a level of resistance inherent to the *L. melissifolia* photosynthetic mechanism. Niinemets (2010) stated that survival under a chronic stress like shade often depends on the capacity of a species to resist a second stress while structurally and physiologically acclimated to the first. Indeed, the ability to survive soil flooding in a shaded understory environment is not common among woody broadleaf shrubs in forests of the MAV (Hawkins *et al.*, 2009). The resistance exhibited by the *L. melissifolia* photosynthetic mechanism is likely fundamental to stress tolerance and persistence of this plant in habitats of marginal suitability or declining quality. This

characteristic affords conservationists the ability to prioritize effort on sites holding colonies in most need of active management.

Photosynthetic capacity of *L. melissifolia* is dynamic and not fixed by soil flooding regime when leaves develop under sufficient light at the onset of the growing season. The observed impairment to photosynthetic capacity by soil flooding was primarily physiological, and plants responded readily to removal of floodwater from soil through shifts in leaf N that supported increased photosynthesis. Thus, the effect of soil flooding appeared temporary as photosynthetic capacity of plants acclimated to fit their light environment after floodwater receded. The ability to respond photosynthetically to an improved soil environment is an attribute beneficial to other floodplain species (Pezeshki, 2001) and would also be important to active management for sustaining *L. melissifolia* in MAV floodplain habitats. The fact that leaf area develops while soil is flooded and photosynthetic capacity acclimates quickly after floodwater recedes would allow *L. melissifolia* to compete for site resources made available through active management. We speculate that the resistant and dynamic nature of its photosynthetic mechanism imparts a physiological component to the competitive adaptiveness of *L. melissifolia* in its floodplain habitats.

Our observations substantiate primacy of the light environment on development of photosynthetic capacity in *L. melissifolia* during and after soil flooding. The prevailing influence of light availability over photosynthetic capacity is consistent among temperate broadleaf species, including understory broadleaves, which require an ability to acclimate to understory light environments that range from heavily shaded to sunlit. The range of acclimation observed in *L. melissifolia* photosynthetic capacity relative to light establishes compatibility of the species with silvicultural manipulation of stand structure for improved habitat where overstory and midstory canopies create heavy shade. The importance of this characteristic cannot be understated for conservation of this species because forests of the MAV where *L. melissifolia* is endemic naturally develop multi-storied, dense canopies (Oliver *et al.*, 2005; Hawkins *et al.*, 2009). In forests of this condition, understory light availability is easy to quantify and monitor and light deficiencies can be alleviated through manipulation of forest stand structure. In application, though, we recognize that stand disturbance would release competing vegetation and alter competitor interactions with *L. melissifolia*, especially on sites or in years of short-duration surface inundation (Wright, 1990; Hawkins *et al.*, 2016). This underscores the need for applied research to support development of comprehensive silvicultural prescriptions that account for the environmental and ecological complexities inherent to natural *L. melissifolia* colonies. Still, active management of stand structure to improve understory light environments offers an approach, compatible with its ecophysiology, to bolster colony vigor, growth, and reproduction for sustained conservation of *L. melissifolia*.

Author contributions

ESG, TDL, KFC, MSD, PBH, ADW, and NMS conceived the idea and contributed to funding acquisition, which was led by TDL. TDL provided project administration. ESG and TDL co-supervised the work. ESG developed the methods, led the investigation, conducted the analysis, and archived data. ESG drafted the text, tables and figures. ESG, TDL, KFC, MSD, PBH, ADW and NMS evaluated results, reviewed findings, edited drafts and contributed to the final manuscript.

Conflicts of interest

None declared.

Funding

This work was supported by the US Army Corps of Engineers, Vicksburg District (grant/award no: SRS 01-IA-11330127-527) and by the US Forest Service (operating funds of the Southern Research Station).

Data Availability Statement

Data pertaining to this research are on file with the US Forest Service, Center for Bottomland Hardwoods Research and are available on request from the corresponding author.

Acknowledgements

We extend our thanks to Brian Lockhart for coordinating and managing field site establishment, maintenance, and measurement and to Tom Dell for statistical advice. We also appreciate technical support given by Bryce Burke, Brian LaBarre, David Murphy, John Nelson, and Chuck Walker. Plant material used in this research was collected under US Department of Interior, Fish and Wildlife Service permit number Endangered-Threatened Species Sub-permit SA0142-Amendment 3.

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