

Growth and competitive abilities of the federally endangered *Lindera melissifolia* and the potentially invasive *Brunnichia ovata* in varying densities, hydrologic regimes, and light availabilities

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Abstract: *Brunnichia ovata* (Walter) Shinners is a native, perennial, woody vine with the potential to become an aggressive competitor of the federally endangered shrub *Lindera melissifolia* (Walt.) Blume. Our study simulated habitat disturbances to hydrologic regime and light availability that may occur naturally, or through active management practices aimed at ensuring the sustainability of *L. melissifolia*, and we determined the species responses to these changes. First-year plants of *L. melissifolia* and *B. ovata* were grown at varying densities, in flooding or nonflooding treatments, and receiving 100%, 47%, or 21% light availabilities. For both species, density effects, in combination with light availability and flooding regime influenced total biomass accumulation. *Brannichia ovata* exhibited a high degree of plasticity with respect to biomass allocated between above- and below-ground tissues in response to flooding, whereas biomass allocation in *L. melissifolia* was relatively unaffected. Interspecific competition occurred primarily in nonflooding treatments. Our study highlighted the complexity of the relationship of *L. melissifolia* and *B. ovata* with regard to functional trait responses to changes in abiotic and biotic factors, and indicated that it will be necessary to consider entire plant community responses to mitigate increased competitive interactions and ensure the survival of *L. melissifolia* populations.

Key words: plant competition, endangered species, invasive species, pondberry, redvine.

Résumé : *Brannichia ovata* (Walter) Shinnner est une plante grimpante ligneuse indigène vivace qui peut devenir un compétiteur agressif de l'arbuste *Lindera melissifolia* (Walt.) Blume, déclaré par l'état en voie de disparition. Dans cette étude, les auteurs ont simulé des perturbations de l'habitat quant au régime hydrologique et à la luminosité disponible qui peuvent survenir de façon naturelle, ou à la suite de pratiques de gestion actives visant à assurer la viabilité de *L. melissifolia*, et déterminé les réponses des espèces à ces changements. Des plants de première année de *L. melissifolia* et de *B. ovata* ont été cultivés à différentes densités et soumis ou non à des inondations et une luminosité de 100, 47 et 21%. Chez les deux espèces, les effets de la densité combinés à la luminosité et le régime de crues influençaient l'accumulation de la biomasse totale. En réponse aux inondations, *B. ovata* présentait un plus haut degré de plasticité quant à la biomasse attribuée aux tissus aériens ou souterrains, alors que l'attribution de la biomasse chez *L. melissifolia* n'était relativement pas affectée. La compétition interspécifique survenait principalement en absence d'inondation. Les résultats des auteurs ont souligné la complexité de la relation des réponses fonctionnelles de *L. melissifolia* et *B. ovata* aux changements de facteurs abiotiques et biotiques, et indiqué qu'il sera nécessaire de considérer la réponse de la communauté dans son entier afin d'atténuer la compétition et assurer la survie des populations de *L. melissifolia*. [Traduit par la Rédaction]

Mots-clés : compétition entre plantes, espèce en voie de disparition, espèce envahissante, *Lindera melissifolia*, *Brannichia ovata*.

Introduction

The Endangered Species Act of 1973 ([U.S. Fish and Wildlife Service 1988](#)) contains three principal components. First, it outlines a process for determining

whether a species should be listed as threatened or endangered, and second, it provides legal protection of a listed species and its respective habitat. The third component requires development of a recovery plan. This

Received 14 September 2015. Accepted 11 December 2015.

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task is generally the responsibility of biologists and (or) ecologists appointed by the lead agency (e.g., U.S. Fish and Wildlife Service). The recovery plan must contain estimates of the current size and health of populations of the listed species, analyses of the causes that led to population decrease, and strategies required to promote population recovery (Foin et al. 1998). Criteria for downlisting and (or) delisting of the species are also included. Therefore, should a species meet these criteria and downlisting or delisting of the species occurs, this would be a reflection of the success of the recovery plan.

Unfortunately, the outcomes of recovery plans are often less than successful, with few species recovering to the point of downlisting (Reffalt 1988; McMillan and Wilcove 1994). Shortcomings of recovery plans have been attributed to financial and time constraints on research (Foin et al. 1998) and limited availability of information for most listed species (Schemske et al. 1994). Further, if a recovery plan includes active management, we maintain that knowledge of all species within the plant community is necessary to determine how the community as a whole will respond to active management strategies. In other words, instead of focusing solely on the response of the species of concern, it is also necessary to have inherent understanding of the plant community response as a whole (Jensen and Meyer 2001). In light of this, the objectives of our study are (i) to investigate growth responses of a federally endangered plant species and a potential competitor by simulating disturbance through altered density, hydrologic regime, and along a gradient of light availabilities, and (ii) to determine whether these variables will influence interspecific competitive interactions.

Lindera melissifolia (Walt.) Blume, is a federally endangered (U.S. Fish and Wildlife Service 1986), deciduous, dioecious shrub that grows in periodically flooded forests in the southeastern United States (Radford et al. 1968). Disjunct populations are distributed throughout the Lower Mississippi Alluvial Valley (LMAV; Hawkins et al. 2009a) and Southeastern Coastal Plain (Beckley and Gramling 2013). Although *L. melissifolia* plants reproduce both sexually (seeds) and asexually (rhizomes), vegetative reproduction appears to be the predominant form of successful reproduction, given the lack of seedlings observed in extant populations (Wright 1994; Hawkins et al. 2010). Ramets produced from networks of rhizomes seemingly contribute to *L. melissifolia* populations, which are composed of spatially segregated unisexual colonies. Colony ratios within these populations tend to be male-biased (Hawkins et al. 2009b). Both Wright (1990) and Hawkins et al. (2010) acknowledged a strong presence of *B. ovata* within and around *L. melissifolia* colonies in the LMAV, and identified the species as having the potential to become an aggressive competitor.

Brunnichia ovata [(Walter) Shinners; Polygonaceae] is a native perennial, deciduous, woody vine distributed in

the southern United States from Florida to Texas and north to Kentucky, Missouri, and Oklahoma (Radford et al. 1968). Commonly known as redvine or American buckwheat vine, *B. ovata* has the potential to become weedy and (or) invasive (Southern Weed Science Society 1998), and is becoming increasingly prevalent in poorly drained soils under cultivation (Elmore 1984). Similarly, it is often a component of the groundcover in bottomland hardwood forests in the LMAV (Noble and Murphy 1975; Thompson 1980), and within the proximity of *L. melissifolia* colonies, its spatial presence often exceeds that of other competitors in the ground cover (Hawkins et al. 2010). However, aboveground competition between the two species is not evident. In theory, this is due to late winter and early spring flooding, which delays the emergence of *B. ovata* (Wright 1990; Hawkins et al. 2010). On the other hand, given its extensive root/rhizome system (Elmore et al. 1989; Shaw and Mack 1991), the potential for belowground competition exists.

Materials and methods

Based on results of a prior study investigating growth and intraspecific competitive abilities of *L. melissifolia* (Hawkins et al. 2009b), and given that male-biased colony ratios exist in naturally occurring *L. melissifolia* populations, male plants were used in our study. These plants originated from micropropagation of stock plants collected from selected bottomland hardwood forests in Sharkey County and Bolivar County (Mississippi) (Hawkins et al. 2007). Plants of *B. ovata* were propagated from 5–8 cm sections of rhizomes harvested in Bolivar County. To determine initial mean total dry mass for each species prior to transplanting, 20 plants were randomly selected each from *L. melissifolia* and *B. ovata*. Plants were harvested, placed in paper bags, dried until desiccated, and weighed to the nearest 0.001 g.

Randomly selected juvenile *L. melissifolia* plants of similar size (0.14 ± 0.02 g) and *B. ovata* plants of similar size (0.12 ± 0.01 g) were transplanted into ~ 31 cm (height) \times 35 cm (diameter) pots containing a 2:1 v/v peat–sand medium supplemented with superphosphate ($467 \text{ g} \cdot \text{m}^{-3}$), 10:10:10 (N–P–K, $1130 \text{ g} \cdot \text{m}^{-3}$), and Milorganite ($2267 \text{ g} \cdot \text{m}^{-3}$). Plants were placed in a single circle, ~ 3 cm from the edge of the container, with individual plants equidistant from neighboring plants (exception is density = 1, which means that the plant was placed in the center of the container). For densities >1 , and in mixed plantings, species were alternated in the circle. Placement of plants into pots followed an addition series design [additive series (Hassell and Comins 1976) + replacement series (de Wit 1960)], which incorporates variation in both total densities and plant ratios. One addition series contained a total of six monocultures (single species at densities of 1, 6, and 9) and three mixtures ($3_{L.m.} : 3_{B.o.}$, $3_{L.m.} : 6_{B.o.}$, and $6_{L.m.} : 3_{B.o.}$). Plants that died within the first 2 weeks following

Table 1. Results of three-way analysis of variance (ANOVA, $p = 0.05$) testing main effects and interactions of density, flooding regime, and light availability on total biomass, and percent biomass allocated to roots, stems, and leaves for first-year plants of *Lindera melissifolia* grown in monoculture.

Source	df	Total biomass		Biomass allocation (%)					
		F	P	Roots	P	Stem	P	Leaves	P
(1) Density	2	0.14	0.8717	4.42	0.0211	0.02	0.9791	1.98	0.1562
(2) Flooding	1	35.31	<0.0001	55.44	<0.0001	5.63	0.0245	8.97	0.0056
(3) Light	2	3.98	0.0298	6.93	0.0035	2.32	0.1164	7.10	0.0031
1x2	2	0.54	0.5894	0.15	0.8585	0.35	0.7064	0.10	0.9067
1x3	4	1.75	0.1654	0.38	0.8233	1.47	0.2357	0.61	0.6615
2x3	2	0.46	0.6381	5.36	0.0104	1.50	0.2393	0.37	0.6952
1x2x3	4	3.13	0.0295	1.62	0.1948	0.25	0.9071	0.82	0.5224

transplanting were replaced with plants of comparable size.

Each addition series was placed in a random sequence, in a single circle, in one of 18–1135 L aquaculture tanks. Tanks were positioned in a climate-controlled greenhouse in a randomized complete block design with three blocks of six tanks each containing an addition series (i.e., 9 pots per tank). Three replicates (one replicate per block) received one of two flooding treatments (no flooding or 21 days of flooding initiated 30 days after transplanting) and one of three light availabilities (100%, 47%, or 21%). Light availability was maintained by suspending neutral density shade cloth over and around PVC structures attached to the rim of tanks receiving 47% and 21% light availability. Tanks randomly selected to receive 100% light availability had the PVC structure attached to the rim without shade cloth. The potting medium was watered to field capacity when not flooded, and during flooding, water was maintained ~2.54 cm above the medium surface. Throughout the study, diurnal temperatures were maintained at 23.0 ± 3.0 °C (day) and 19.0 ± 2.0 °C (night). Thermographs were used to monitor temperatures in shade structures, and no significant differences were found among shade structures or between shade structures and open tanks. Plants received a 14 h (light): 10 h (dark) photoperiod. During the light period, plants received artificial light when ambient photosynthetic photon flux density (PPFD) dropped below $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

After 8 weeks of growth, water was removed from aquaculture tanks containing the addition series that received flooding treatments. All plants were harvested, the roots washed free of soil, and each plant separated into roots, leaves (blade + petiole), and stems. Individual structures for each plant were placed in separate paper bags, labeled with the respective plant number, and then oven-dried at 70 °C until desiccated. Dried plant structures were weighed to the nearest 0.001 g. Final total plant dry mass (i.e., biomass) represented yield (Y). Relative yield (RY) and relative yield total (RYT) were calculated for each species (*L.m.*, *Lindera melissifolia*; *B.o.*, *Brunnichia ovata*):

$$\text{RY}_{(\text{L.m. or B.o.})} = \frac{Y_m}{Y_p} \text{ and RYT} = \text{RY}_{(\text{L.m.})} + \text{RY}_{(\text{B.o.})}$$

where actual RYs for a species were the quotient derived by dividing total plant biomass of a species grown in mixture (Y_m) by total plant biomass of that species grown in monoculture (Y_p). Actual RYs were compared with their expected values (0.50 for $3_{\text{L.m.}}:3_{\text{B.o.}}$; 0.33 or 0.66 for $3_{\text{L.m.}}:6_{\text{B.o.}}$ and $6_{\text{L.m.}}:3_{\text{B.o.}}$).

The sum of RYs for *L. melissifolia* and *B. ovata* equal actual RYT, and actual RYT were compared with the expected value of 1.0.

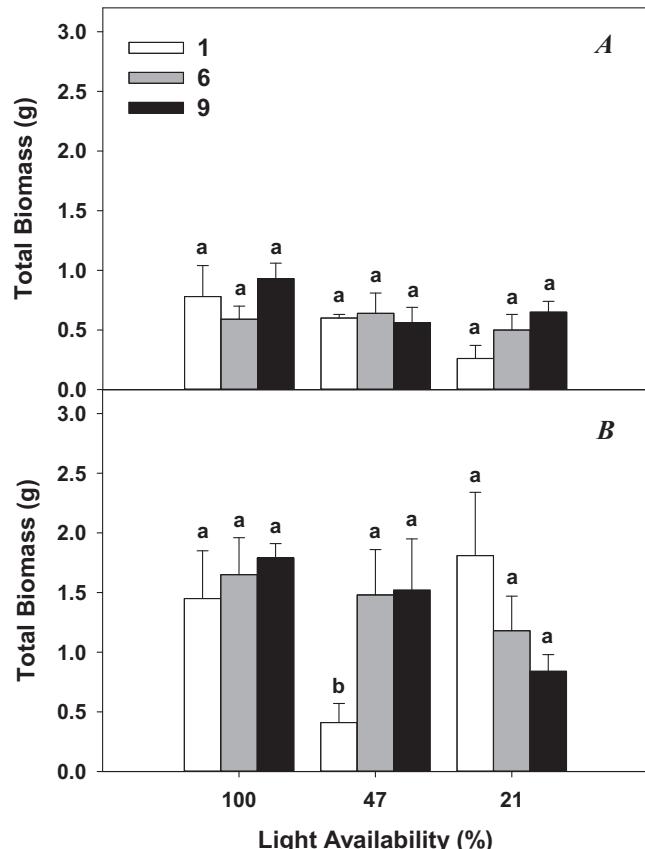
Statistical analyses

For plants grown in monoculture, three-way analysis of variance (ANOVA) was used to test for main effects and interactions for total plant biomass and percent biomass allocated to roots, stems, and leaves. The square root of biomass allocation percentages were arcsine-transformed for analysis. One-way ANOVA was used to compare values within and between treatments and species, and Tukey's HSD (honestly significant difference) test was used as the multiple comparison procedure (SAS Institute Inc. 2007; $\alpha = 0.05$).

Results

When grown in monoculture, total biomass accumulation in *L. melissifolia* plants was influenced independently by flooding and light availability, and the interaction of density, flooding, and light availability (Table 1). There was no difference in plant total biomass among plant densities within the flooding treatment (Fig. 1A). In the nonflooding treatment, *L. melissifolia* plants grown at a density of 1 and receiving 47% light availability accumulated less total biomass than all other plants within this treatment regardless of density or light availability (Fig. 1B). Between flooding treatments, plants grown at a density of 1 and receiving 21% light availability in the nonflooding treatment accumulated more total biomass than plants at densities of one or six and receiving 21% light availability in the flooding treatment ($p < 0.05$; Figs. 1A and 1B).

Fig. 1. Mean (\pm SE) total biomass (g) for first-year plants of *Lindera melissifolia* grown at densities of 1, 6, and 9, in (A) flooded and (B) nonflooded conditions, and in light availabilities of 100%, 47%, and 21%. Within a hydrologic treatment, values with different lowercase letters are significantly different (Tukey, $p < 0.05$).



Biomass allocated to *L. melissifolia* roots was affected by all treatments (Table 1; density, flooding, light, and flooding \times light). However, biomass allocated to stems was influenced only by flooding regime, and leaf biomass was influenced independently by flooding regime and light availability (Table 1). In high density plantings (density = 6 and 9), greater biomass was allocated to leaves ($p \leq 0.0419$; data not shown) and lower biomass was allocated to roots ($p < 0.0001$; data not shown) for plants receiving flooding and 21% light availability, than for those plants in the nonflooding treatment and receiving 100% light availability. This translated into significantly greater aboveground biomass accumulation in flooding treatments receiving 21% light availability than in nonflooding treatments at all light availabilities (Table 2). Alternatively, when grown at a density of 1, aboveground to belowground biomass ratios in *L. melissifolia* plants were unaffected by flooding regime (Table 2).

Total biomass in *B. ovata* plants grown in monoculture was influenced independently by density, flooding regime, light availability, and their interactions (Table 3). In both flooding and nonflooding treatments, total biomass was greatest for plants grown at a density of 1 and

receiving 100% light availability (Figs. 2A and 2B). Root biomass was influenced independently by all variables and their interactions (with the exception of density \times flooding; Table 3). Further, aboveground to belowground ratios were higher in flooding treatments when compared with those in nonflooding treatments across planting densities and light availabilities (Table 2). These differences resulted from greater biomass allocation to leaves ($p \leq 0.0022$; data not shown) and less biomass allocation to roots ($p \leq 0.0027$; data not shown). We observed adventitious root formation just above the surface of the water in *B. ovata* plants receiving the flooding treatment. Growth habit was trailing, and plant stems extended over the sides of the aquaculture tanks without shade cloth. Those plants receiving 47% and 21% light availability utilized axillary shoot tendrils to climb up the interior of the shade cloth structure.

When grown in mixture, deviations from expected relative yield (RY) occurred primarily in non-flooding treatments. In equal proportions ($3_{L.m.}:3_{B.o.}$) and in the nonflooding treatment, actual RY for *B. ovata* was greater than expected ($p = 0.0340$) in 100% light availability, and less than expected ($p = 0.0163$) at 21% light availability (Table 4). However, relative yield total (RYT) deviated significantly from the expected value of 1.0 in the mixture receiving 21% light availability ($p = 0.0461$; Table 4).

At the proportion of $3_{L.m.}:6_{B.o.}$ and in nonflooded conditions, actual RY for *L. melissifolia* was lower than expected ($p = 0.0119$) in 100% light availability, and was greater than expected ($p = 0.0043$) for *B. ovata* at 47% light availability (Table 4). In neither of these conditions did RYT deviate significantly from 1.0.

In mixtures of $6_{L.m.}:3_{B.o.}$, actual RYs for *L. melissifolia* were significantly lower than expected in the nonflooding treatment and at 21% light availability ($p = 0.0255$; Table 4), as well as in the flooding treatment at 100% light availability (0.45 ± 0.02 , $p = 0.0443$). Actual RYTs did not differ from the expected value of 1.0.

Discussion

Two key components determining species composition in floodplains and periodically flooded bottomland forests are hydrologic regime and light availability (Menges and Waller 1983; Klimas 1988; Gosselink and Lee 1989). Our study simulated changes in these variables that may occur naturally, or through management practices. In turn, our results revealed functional trait responses in both *L. melissifolia* and *B. ovata* to short-term flooding and changes in light availability.

When grown in monoculture, plant size (total biomass accumulation) of *L. melissifolia* was affected independently by flooding and light availability, as well as the interaction of density, flooding, and light availability. Plants receiving the lowest light availability, and growing at a density of 1 in the flooding treatment accumulated significantly lower total biomass than those grown

Table 2. Aboveground:belowground ratios for monoculture plantings of *Lindera melissifolia* and *Brunnichia ovata* grown in flooded and nonflooded conditions, three light availabilities, and at three planting densities.

Light availability (%)	<i>Lindera melissifolia</i>			<i>Brunnichia ovata</i>		
	Density			Density		
	1	6	9	1	6	9
Flooded						
100	5.12±0.87Aa	4.67±0.36Aabc	4.54±0.55Aab	27.29±3.60Ba	21.82±1.67Ba	24.96±2.52Ba
47	5.19±0.49Aa	5.60±0.49Ab	4.85±0.43Ab	25.52±2.11Ba	24.93±1.02Ba	22.74±0.84Ba
21	7.10±1.00Aa	6.47±1.07Aa	6.45±0.40Aa	22.17±1.17Bab	21.88±0.38Ba	18.49±1.49Ba
Nonflooded						
100	4.05±0.54ABAa	2.92±0.13Ac	3.07±0.41ACb	6.72±0.45Bc	4.50±0.16Cc	3.42±0.34AcB
47	3.32±0.32Aa	3.73±0.29BCbc	3.81±0.06BCb	4.05±0.49BCc	5.41±0.37BCbc	6.46±1.16Bb
21	3.80±0.48Ba	3.81±0.20Bbc	3.70±0.20Bb	15.94±0.81Cb	9.55±0.98Ab	9.09±1.17Ab

Note: Means with dissimilar uppercase letters within rows or lowercase letters within columns are significantly different (Tukey's HSD, $p < 0.05$).

Table 3. Results of three-way analysis of variance (ANOVA, $p = 0.05$) testing main effects and interactions of density, flooding regime, and light availability on total biomass, and percent biomass allocated to roots, stems, and leaves for first-year plants of *Brunnichia ovata* grown in monoculture.

Source	df	Biomass allocation (%)							
		Total biomass		Roots		Stem		Leaves	
		F	P	F	P	F	P	F	P
(1) Density	2	40.19	<0.0001	3.92	0.0303	0.02	0.9842	0.85	0.4389
(2) Flooding	1	20.72	<0.0001	425.73	<0.0001	9.92	0.0036	42.33	<0.0001
(3) Light	2	84.48	<0.0001	19.71	<0.0001	1.13	0.3350	4.14	0.0255
1×2	2	9.65	0.0006	1.69	0.2019	4.09	0.0264	1.53	0.2314
1×3	4	22.28	<0.0001	5.54	0.0018	1.54	0.2142	0.86	0.4990
2×3	2	12.50	0.0001	26.89	0.0104	0.17	0.8456	5.07	0.0124
1×2×3	4	7.97	0.0002	5.17	0.0026	1.67	0.1824	0.22	0.9255

at the same density and light availability in the nonflooding treatment. However, in the nonflooding treatment, plants grown at a density of 9 and receiving 100% light availability achieved the same total biomass as those at a density of 1 and receiving 21% light availability. Significantly reduced total biomass for *L. melissifolia* grown at a density of 1 in nonflooding conditions and receiving 47% light availability seems somewhat anomalous, and may be an artifact of this study or genotypic influence born out of random plant selection. However, single (density = 1) *L. melissifolia* plants grown under these treatments bears repeating to determine whether this was a consequence of flooding regime and light availability interaction.

In a similar study investigating growth and competition in juvenile male and female *L. melissifolia*, Hawkins et al. (2009b) found density effects on plant size to be more pronounced, whereby male plants grown at a density of 1 and receiving a nonflooding treatment, accumulated total biomass almost three times greater than those plants grown at higher densities and (or) receiving flooding treatments (all plants received 100% light availability). However, in that study, the plant growth period (21 weeks) and flooding durations (30 and 60 days) were longer. Comparatively, this illustrates the dynamic nature of the interactions flood timing and duration, light

availability, and plant density as it influences growth response in *L. melissifolia*.

Lindera melissifolia plants exhibited very slight plasticity in biomass allocated between aboveground tissues (stems and leaves) and belowground tissues (roots) in response to treatments, and any significant differences were observed primarily between flooding and nonflooding treatments. For example, greater biomass was allocated to aboveground tissues only at the higher density plantings in flooded conditions and lowest light availability, than those same densities at all light availabilities in the nonflooding treatments. In contrast, Lockhart et al. (2013) described adult *L. melissifolia* as displaying a high level of plasticity across a light availability gradient, as well as being relatively unaffected by hydrologic regime. This suggests that functional trait responses of first-year *L. melissifolia* to abiotic factors may be constrained by ontogeny (Gedroc et al. 1996; Geng et al. 2007; Lockhart et al. 2012).

In contrast to *L. melissifolia*, plants of *B. ovata* showed a high degree of plasticity in response to flooded versus nonflooded conditions. In the two highest light availabilities and flooded conditions, *B. ovata* plants allocated four to seven times more biomass to aboveground tissues than plants in nonflooded conditions. However, at the low-

Fig. 2. Mean (\pm SE) total biomass (g) for first-year plants of *Brunnichia ovata* grown at densities of 1, 6, and 9, in (A) flooded and (B) non-flooded conditions, and in light availabilities of 100%, 47%, and 21%. Within a hydrologic treatment, values with different lowercase letters are significantly different (Tukey, $p < 0.05$).

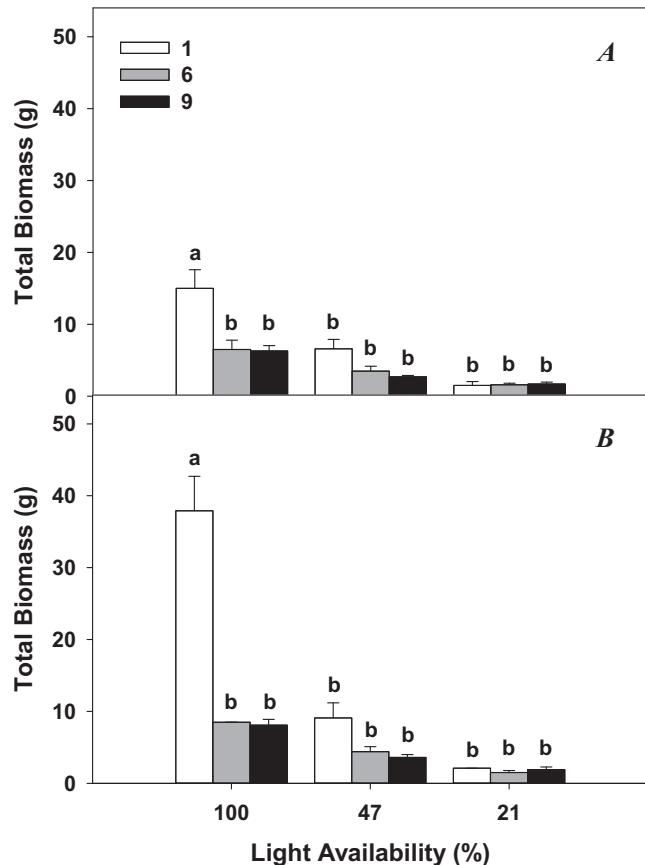


Table 4. Relative yield (RY) and relative yield total (RYT) for *Lindera melissifolia* (L.m.) and *Brunnichia ovata* (B.o.) grown in three planting ratios, two planting densities, and three light availabilities in nonflooded conditions.

Plant ratio	RY _{L.m.}	RY _{B.o.}	RYT	Light (%)
3 _{L.m.} :3 _{B.o.}	0.23	0.75 [†]	0.98	100
	0.74	0.49	1.20	47
	0.30	0.31*	0.66*	21
3 _{L.m.} :6 _{B.o.}	0.09*	0.80	0.89	100
	0.22	0.94 [†]	1.20	47
	0.45	0.65	1.10	21
6 _{L.m.} :3 _{B.o.}	0.60	0.42	1.02	100
	0.50	0.40	0.90	47
	0.29*	0.45	1.06	21

Note: *, Actual value significantly lower than the expected value ($p < 0.05$); †, actual value significantly higher than the expected value ($p < 0.05$).

est light availability and in flooded conditions, aboveground biomass was reduced to only two times that of plants grown in nonflooded conditions. Further, total biomass was affected by all variables independently, and through interactions, and was most pronounced when *B. ovata* was grown at a density of 1. Given this species

plasticity in biomass allocation and morphology (i.e., adventitious roots and axillary tendrils), as well as plant size, *B. ovata* plants possess functional traits that promote invasiveness (Claridge and Franklin 2003; van Kleunen et al. 2010).

Plastic responses to resource availability are often linked to competitiveness (Berendse and Elberse 1990). However, the morphological response of *B. ovata* to flooded conditions and lower light availability was a proportional increase in biomass allocated to aboveground tissues, resulting in lengthy vining via axillary tendrils away from flooding and toward higher light availabilities. In a natural environment this would allow for escape from unsuitable habitat and movement to favorable habitat, and potentially alleviate direct competition with *L. melissifolia*. On the other hand, increased biomass to belowground tissues in nonflooded conditions and across all light availabilities suggests occupation of suitable habitat, and belowground competition with *L. melissifolia* may come into play.

Our competition study presented 18 permutations of variables, and when utilizing relative yield (RY) to assess competitive interactions, deviation from expected RY was indicated in six of the 18 interspecific interactions. Of these six, five occurred in nonflooded conditions. When grown in equal proportions with *L. melissifolia*, and at the highest light availability, actual RY for *B. ovata* exceeded the expected value. This also occurred in the 3_{L.m.}:6_{B.o.} mixture grown at 47% light availability. These results suggest that within the assemblage of variables just described, growth of *B. ovata* benefited from the interspecific interaction, and *L. melissifolia* was relatively unaffected. In contrast, actual RYs for *L. melissifolia* in the nonflooding treatments were lower than expected at the highest and lowest light availability, and at proportions of 3_{L.m.}:6_{B.o.} and 6_{L.m.}:3_{B.o.}, respectively. When grown in monoculture, *B. ovata* allocated significantly more biomass to roots in nonflooding treatments, which suggests that belowground competition may be occurring (Casper and Jackson 1997) in mixed plantings with the same treatments. Our use of RY to assess competition illustrates how changes in biotic and abiotic parameters (i.e., hydrologic regime, plant proportion, and light availability) may affect growth and interspecific competitive abilities of both species.

When using relative yield total (RYT) to assess interspecific interactions, competition was indicated only when *L. melissifolia* and *B. ovata* were grown in equal proportions, in nonflooded conditions, and at 21% light availability. In this instance, RYT was <1.0 , indicating mutual antagonism (Harper 1977). The disparity between RY and RYT in identifying competition is not unusual, and the limitations of using a single index to assess competitive interactions has been the subject of past discussions (e.g., Gibson et al. 1999; Williams and McCarthy 2001; Weigelt and Jolliffe 2003). Our results indicated that RY identified

competitive interactions far better than RYT, which is consistent with results found by Williams and McCarthy (2001), and our assessment of competitive interactions was further enhanced by supplementing competition indices with growth analyses.

Based on field research and general observations, Wright (1990) and Hawkins et al. (2010) identified *B. ovata* as having the potential to become a strong competitor of *L. melissifolia*. However, low light availability typical of bottomland forests (Lhotka and Loewenstein 2006) and periodic flooding during winter and early spring delay the emergence of *B. ovata* and seemingly eliminate aboveground competition (Hawkins et al. 2010). On the other hand, our study suggests that in the absence of flooding and with higher light availability, belowground competition may occur and initiate direct interactions with *B. ovata* that place first year *L. melissifolia* at a competitive disadvantage.

One of the recommendations in the 5 year review of the status and recovery of *L. melissifolia* (U.S. Fish and Wildlife Service 2013) is further study of the effects of various types of disturbance on the species' survivorship and reproduction. Our study has shown that functional trait responses of *L. melissifolia* to abiotic and biotic changes would depend on numerous factors and their simultaneous interactions, as well as competitor responses. Further, while disturbance may aid survivorship of juvenile plants, it may not have the desired effect on plants at later reproductive growth stages. Although our study simulated disturbance by varying light and hydrologic regime, competitor response was limited to a single potential plant competitor. Indeed, Hawkins et al. (2010) identified 69 plant species growing within *L. melissifolia* colonies located in Mississippi, and thus it is necessary to consider entire plant community response prior to initiating disturbances or employing active management strategies aimed at ensuring survivorship of *L. melissifolia* populations.

Acknowledgements

The authors thank Charisse Oberle, Steven Hughes, Amy Abel, and Jim Gruhala for their assistance with data collection; the U.S. Army Corps of Engineers for underwriting the cost of this research; and Dr. Jeffrey Walck and Dr. Siti Hidayati for review of an earlier draft of this manuscript.

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