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Growth and intraspecific competitive abilities of the dioecious *Lindera melissifolia* (Lauraceae) in varied flooding regimes[1]

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HAWKINS, T. S., N. M. SCHIFF, T. D. LEININGER, E. S. GARDINER, M. S. DEVALL, P. B. HAMEL, A. D. WILSON, AND K. F. CONNOR (USDA Forest Service, Southern Research Station, Stoneville, MS 38776). Growth and intraspecific competitive abilities of the dioecious *Lindera melissifolia* (Lauraceae) in varied flooding regimes. J. Torrey Bot. Soc. 136: 91–101. 2009.—The contribution of sexual dimorphism to male-biased colony ratios observed in field populations of the federally endangered *Lindera melissifolia* was investigated. Growth characteristics and intraspecific relative competitive abilities were determined for first-year male and female *L. melissifolia* plants grown at varied densities and receiving three flooding treatments. In the no-flooding and 30-day-flooding treatments, stem height, stem diameter, and total leaf area for male plants were significantly greater than that of higher density male plantings and of female plants without respect to density. In both male and female plants, stem growth ceased and leaves were abscised in response to flooding. Although density effects in combination with hydrologic regime influenced intersexual competition, male-bias from competitive exclusion was not indicated. Growth characteristics for male plants grown alone suggest potential for greater interspecific competitive abilities than that of female plants. Therefore, male plants may be better adapted for colonizing suitable habitat, thus contributing to male-biased colony ratios observed in naturally occurring populations.

Key words: competition, endangered, growth characteristics, hydrologic regime, pondberry.

In dioecious angiosperms, male and female plants may differ in morphology (Meagher 1980, Kohorn 1994), physiological response to environment (Gehring and Monson 1994, Nicotra 1999, Nicotra et al. 2003), or life history traits (Bullock and Bawa 1981, Hoffman and Alliende 1984, Thomas and LaFrankie 1993, Cipollini and Whigham 1994, Geber et al. 1999, Rocheleau and Houle 2001). These intersexual differences are often considered inherently linked to differential costs of reproduction of male and female plants. Numerous investigations of dioecious species have shown that females allocate more resources to reproduction than do males (Korpelainen 1992, Nicotra 1999, Rocheleau and Houle 2001, Ueno et al. 2006), and as a consequence (i.e., trade-off), allocate less toward vegetative growth and maintenance (Harper 1967, Harper and Ogden 1970, Ågren 1988). Further, intersexual differences in reproductive costs may incur sex-bias within dioecious plant populations (Harris 1968, Lloyd 1973, Lloyd and Webb 1977, Meagher 1980, Sakai and Oden 1983, Ågren 1988, Allen and Antos 1988, Bertiller et al. 2002, Eppley 2006). With greater investment of resources to vegetative growth and maintenance, male plants tend to have higher survival rates (Lloyd and Webb 1977, Lovett Doust and Lovett Doust 1988, Allen and Antos 1993) and greater tolerance to low resource environments (Grant and Mitton 1979, Freeman and McArthur 1982, Ågren 1988, Allen and Antos 1988, Popp and Reinartz 1988, Dawson and Bliss 1989) than do female plants. Therefore, within a population, sex-biased ratios and spatial segregation of sexes along environmental gradients are often observed (Grant and Mitton 1979, Ågren 1988, Bertiller et al. 2002, Eppley 2006).

Literature describing sexual dimorphism and how it relates to population structure of dioecious species is extensive; although, it most often involves investigations of plants at the reproductive stage of the life cycle. In

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part, this is due to an inability to distinguish sexes prior to a reproductive event. In most dioecious species, determining gender based on morphology prior to reproductive maturity is difficult, if not impossible (Dawson and Geber 1999). As a result, few studies have investigated sexual dimorphism in pre-reproductive dioecious species, and how it may influence sex ratio variation within a population.

The focus of our study is *Lindera melissifolia* (Walt.) Blume, a federally endangered (U.S. Fish and Wildlife Service 1986), dioecious shrub endemic to periodically flooded forests in the southeastern United States (Radford et al. 1968, Saucier 1978, Devall et al. 2001). Relatively small, disjunct populations are sparsely distributed throughout its range which extends from the Lower Mississippi Alluvial Valley (LMAV), east to North and South Carolina. *Lindera melissifolia* populations are composed of spatially segregated, unisexual colonies (Hawkins pers. obs.). Populations tend to be male-biased (Wright 1994, Hawkins et al. 2007), with male to female colony ratios ranging from 7:1 (Wright 1994) to 19:1 (Hawkins et al. 2007). In both male and female *L. melissifolia* plants, anthesis generally occurs during flooded conditions (late spring) and precedes leafing out. Reproduction is both sexual (seeds) and asexual (rhizomes). However, seedlings are rarely observed in naturally occurring populations (Wright 1994, Devall et al. 2001), and vegetative propagation of ramets appears to be the predominant form of reproduction (Wright 1994).

Currently, knowledge of the ecology of this species is extremely limited and there is no correlative evidence, published or observed, linking population sex-bias with abiotic factors. Further, there has been a long-standing hypothesis that flooding is not a physiological requirement for plants of *Lindera melissifolia*, and that it serves only to minimize interspecific competition (Wright 1990). Our paper presents a large-scale study that addresses growth response to flooding in first-year, metabolically active male and female *L. melissifolia*. The objectives of our research were 1) to determine if first-year (pre-reproductive) male and female plants of *L. melissifolia* differ in growth and morphology and 2) to determine if differential responses to hydrologic regime exist within competitive and density dependent contexts. Few studies of dioecious species have addressed these aspects of dimorphism; although, Eppley (2006) recently provided evidence that differential competitive abilities between male and female *Distichlis spicata* seedlings can generate population sex-ratio variation. We hypothesize that if variation between genders occurs, male-biased ratios observed in naturally occurring populations of *L. melissifolia* are due, at least in part, to competitive exclusion incurred at pre-reproductive growth stages of the species' life cycle. Information of this nature would improve our understanding of how dimorphism in pre-adult plants may generate skewed population sex-ratios not only in *L. melissifolia*, but other dioecious species, as well. Further, we believe it is necessary to understand intraspecific competition in this dioecious shrub prior to interpreting results of studies conducted on interspecific competition.

Material and Methods. GENERAL EXPERIMENTAL DESIGN. Source plants used in this study included 11 (six male and five female) different genotypes of male and female *Lindera melissifolia* plants originating from micropropagation of stock plants collected from selected bottomland forests in the Lower Mississippi Alluvial Valley (Hawkins et al. 2007). To ensure no significant difference in plant size among genotypes prior to transplanting, 10 plants were randomly selected from each genotype. Plants were harvested, placed in paper bags, dried until desiccated, and weighed to the nearest 0.001 g.

On 22 December 2003, randomly selected male and female plants of approximately the same height (8–9 cm) and total weight (0.08 ± 0.01 g) were transplanted into ~31 cm (height) × 35 cm (diameter) pots containing a 2 peat:1 sand medium supplemented with superphosphate (467 $g \cdot m^{-3}$), 10:10:10 (N:P:K, 1130 $g \cdot m^{-3}$), and Milorganite® (2267 $g \cdot m^{-3}$). 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; plant is placed in the center of the container). Placement of plants into pots followed an addition series design [additive series (Hassel and Comins 1976) + replacement series (de Wit 1960)], thus incorporating variation in both total densities and gender ratios. One addition series contained a total of eight monogender (same sex)

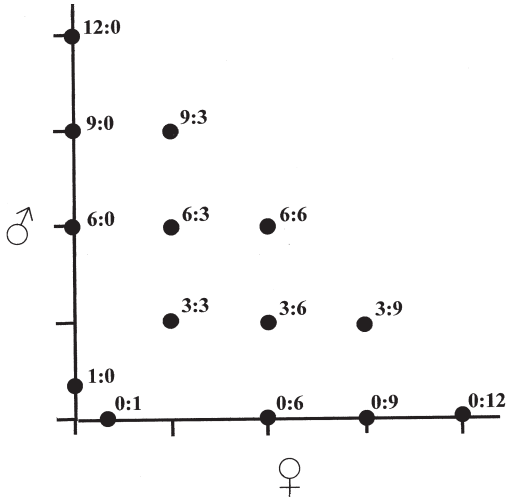

FIG. 1. Densities and gender proportions for *Lindera melissifolia* plants used in the addition series experimental design.

plantings and six mixtures (both sexes; Fig. 1). Plants that died within the first two weeks following transplanting were replaced by plants of comparable size.

Each addition series was placed in random sequence, in a single circle in one of nine 1135 L aquaculture tanks. Aquaculture tanks were positioned in a climate-controlled greenhouse in a randomized complete block design with three blocks of three addition series. Three replicates (one replicate per block) of each addition series received one of three flooding treatments: no-flooding (potting medium maintained at field capacity), 30-day-flooding (treatment initiated 17 wk after transplanting), and 60-day-flooding (treatment initiated 13 wk after transplanting). Potting medium was watered to field capacity when not flooded and, during flooding conditions, water was maintained ~2.54 cm above the potting medium surface. Throughout the study (21 wk), which approximated one growing season, diurnal temperatures were maintained at 23.3 ± 2.0°C (day)/18.9 ± 2.0°C (night), and plants received a 14 hr (light)/ 10 hr (uninterrupted dark) photoperiod. During the light period, plants received artificial light when ambient photosynthetic photon flux density (PPFD) dropped below 300 $\mu mol \cdot m^{-2} \cdot sec^{-1}$. During flooding treatments, mean water temperature was 22.3 ± 0.1°C and mean dissolved oxygen content was 7.7 ± 0.2 mg^{-1}.

GROWTH STUDY. Monogender plantings were used for the growth study. Stem heights and stem diameters (at root collar) were measured, and total plant leaf number was counted, at 3 wk intervals. On 18 May 2004, approximately 21 wk after transplanting, 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, and then oven-dried at 70°C until desiccated. Dried plant structures were weighed to the nearest 0.001 g. Prior to drying, leaves from each plant were measured using a LiCor LI-3100 leaf area meter. Specific leaf area (SLA; total leaf area of plant divided by plant total dry weight) and leaf area ratio (LAR; total leaf area of plant divided by total plant dry weight) were calculated for each harvested plant.

COMPETITION STUDY. Using total plant dry weights to represent yield, relative yield (RY) and relative yield total (RYT) were calculated for each gender:

$$RY = \frac{Y_m}{Y_p} \text{ and } RYT = RY_A + RY_B$$

where $Y_{m(p)}$ is total plant biomass of a gender grown in mixture (m) and monogender (p). Actual RYs of each gender were plotted against the respective planting proportion on de Wit (1960) diagrams. In this type of diagram, expected RYs (diagonal dashed lines) represent genders that grow equally well in mixture and in monogender. If the actual RY curve of one gender is concave, and that of the other is convex, competition is indicated. When actual RY curves for both genders are concave, mutual antagonism is occurring, and if actual RY curves for both genders are convex, niche differentiation is indicated. In accordance with plotted RYs, an RYT with a value of 1.0 implies competition, > 1.0 implies niche differentiation, and < 1.0 implies mutual antagonism (Harper 1977).

STATISTICAL ANALYSIS. In the growth study, repeated measures analysis of variance (ANOVA) was used to test for main effects and interactions for stem growth (height) and leaf number. Within treatments, a one-way ANOVA was used to compare stem diameter, biomass variables, and leaf variables among densities for each gender. If variables were not significant among a gender's plant densities within a treatment, the mean of combined density values were used for comparison between genders and among treatments. A one-way ANOVA was used for among treatment and between gender analyses and a Tukey (honestly significant difference) test was used as the multiple comparison procedure. Greenhouse-Geisser corrected probabilities are reported for the repeated measures ANOVA.

In the competition study, actual RYs were compared to their expected values at each proportion, and RYTs compared to the expected value of 1.0 by *t*-tests. The SAS procedure PROC GLM was used to perform statistical analyses (SAS Institute Inc. 2001).

Results. GROWTH STUDY. During weeks 1–12 (prior to flooding treatments) of the growth period, there was no significant difference in mean stem heights among densities within genders (time effect, $P < 0.0001$; density effect, $P \geq 0.6153$; time × density $P \geq 0.6219$; Figs. 2A–C), nor between genders ($P \geq 0.1315$). However, in weeks 15–21, mean stem height for male plants grown at a density of one in the no-flooding and 30-day-flooding treatments was significantly greater ($P \leq 0.0497$) than that of all other planting densities regardless of gender or treatment. Time × density interaction and time × flooding treatment interaction influenced male mean stem heights (Table 1), whereby time × flooding treatment interaction influenced female plant mean stem height (Table 2).

For plants receiving flooding treatments, negligible stem (height) growth occurred following initiation of flooding (Figs. 2B–C). Plants receiving no-flooding had significantly greater increase in stem height relative to those plants exposed to 30-day-flooding ($P = 0.0138$) and 60-day-flooding ($P < 0.0001$) treatments (Figs. 2A–C).

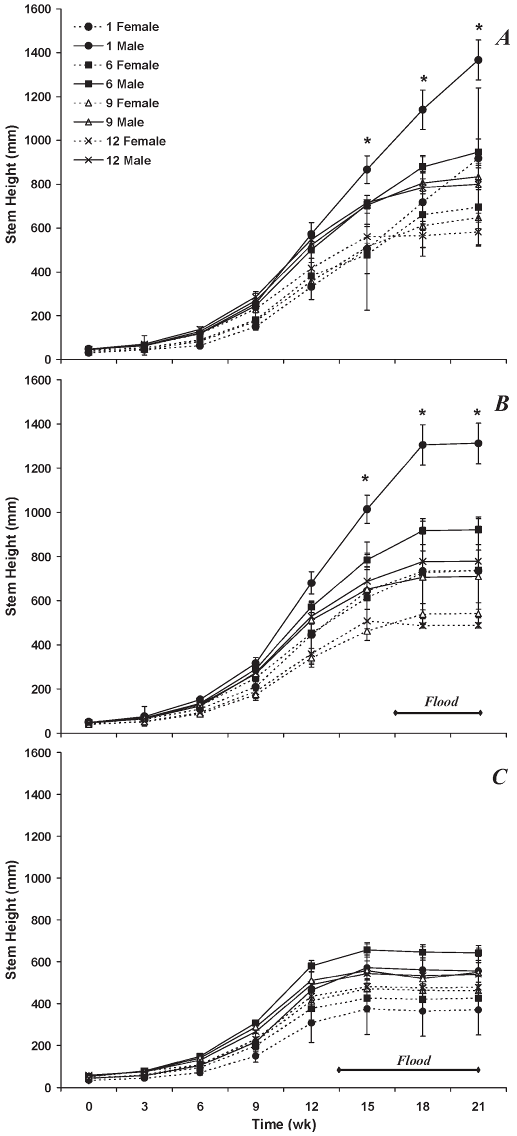

FIG. 2. Mean (± SE) stem heights for mono-gender plantings of male and female *Lindera melissifolia* plants grown at densities of 1, 6, 9, and 12 in (A) no-flooding, (B) 30-day-flooding, and (C) 60-day-flooding treatments. An asterisk indicates significantly greater stem height for male plants, density = 1 (ANOVA, $P \leq 0.05$).

Ten to 14 days following initiation of flooding treatments, plant leaf turgor declined, followed by some leaf abscission (Fig. 3B–C). In weeks 15–21, mean total leaf number (per plant) for male plants grown at a density of one was significantly greater than that of all other planting densities in the no-flooding and 30-day-flooding treatments ($P \leq 0.0102$; Figs. 3A–C). Interaction of time × density × treatment influenced leaf number for male plants (Table 1), and the interactions of time × density and time × treatment influenced leaf number for female plants (Table 2). At the end of the growth period (week 21), total leaf area for male plants grown at a density of one and receiving no-flooding was greater than male plants grown at higher densities, and female plants grown at all densities (Table 3). Mean leaf size was greatest for male plants receiving no-flooding, and SLA and LAR did

Table 1. Results of repeated measures ANOVA ($P = 0.05$) examining the effects of density, flooding regime, and time (plant age) on stem height and total leaf number for male *Lindera melissifolia*.

	Stem height			Leaf number		
Source	df	*F*	*P*	df	*F*	*P*
Block	2	0.58	0.1684	2	1.32	0.3176
Density	3	2.16	0.0932	3	6.50	0.0003
Treatment	2	7.32	0.0008	2	15.48	< 0.0001
Density × treatment	6	0.57	0.7508	6	1.75	0.1110
Time	7	680.94	< 0.0001	7	98.42	< 0.0001
Time × treatment	14	19.70	< 0.0001	14	33.44	< 0.0001
Time × density	21	5.86	0.0004	21	12.94	< 0.0001
Time × density × treatment	42	1.10	0.3625	42	3.93	< 0.0001

not differ between genders, nor among treatments ($P > 0.05$; Table 3).

Stem diameter growth (time$_{21}$–time$_{0}$) for male plants was influenced by density and treatment (density effect, $P = 0.0113$, treatment effect, $P < 0.0001$; density × treatment, $P = 0.6804$). Increase in stem diameter for male plants grown at a density of one and receiving the no-flooding treatment was significantly greater ($P < 0.0001$) than that of male plants grown at higher densities, and that of female plants regardless of planting density (Fig. 4). Change in stem diameter for female plants was influenced only by treatment (density effect, $P = 0.7513$; treatment effect, $P = 0.0003$; density × treatment, $P = 0.6804$).

Biomass variables for male plants grown at a density of one in the no-flooding treatment were greater than higher density male plantings within this treatment, and of all densities in the 30-day and 60-day-flooding treatments (Table 4). Leaf biomass for female plants grown at a density of one in the no-flooding treatment was greater than that of female plants receiving no- flooding and grown at higher densities, and that of all densities in the 30- and 60-day-flooding treatments (Table 4). Within treatments, there was no significant difference in mean biomass variables between male and female plants (Table 4).

Competition study. In the absence of flooding, actual RY for female *Lindera melissifolia* was significantly greater than the expected value when grown in equal proportion with male plants at a density of six ($P = 0.0281$; Fig. 5A). Actual RYs for male plants were significantly greater than expected values in the 30-day-flooding treatment at proportions of 6♂:3♀ ($P = 0.0143$; Fig. 5E) and 6♂:6♀ ($P = 0.0111$; Fig 5F). On the other hand, actual RYs for male plants were significantly lower than expected values at a 6♂:3♀ proportion ($P = 0.0279$) in the 60-day flooding treatment (Fig. 5H) and at a 6♂:6♀ proportion ($P = 0.0032$) in the no-flooding treatment (Fig. 5C). At a planting density of six, RYTs were significantly greater than the expected value of 1.0 for plants receiving no-flooding ($P = 0.0373$; Fig. 5A), but significantly lower in the 30-day-flooding ($P = 0.0207$; Fig. 5D) treatment. RYT for a density of nine in the 30-day-flooding treatment (Fig. 5E) was significantly higher ($P = 0.0141$) than the expected value of 1.0.

Discussion. In monogender plantings at densities of six, nine, and 12, we found no evidence of sexual dimorphism in growth variables for male and female *Lindera melissifolia*. At these densities, and within treatments,

Table 2. Results of repeated measures ANOVA ($P = 0.05$) examining the effects of density, flooding regime, and time (plant age) on stem height and total leaf number for female *Lindera melissifolia*.

	Stem height			Leaf number		
Source	df	*F*	*P*	df	*F*	*P*
Block	2	1.20	0.3085	2	0.98	0.3449
Density	3	0.37	0.7781	3	4.33	0.0054
Treatment	2	1.26	0.2848	2	7.74	0.0006
Density × treatment	6	0.65	0.6862	6	0.20	0.9754
Time	7	198.77	< 0.0001	7	95.49	< 0.0001
Time × treatment	14	4.49	0.0104	14	29.00	< 0.0001
Time × density	21	1.34	0.2617	21	8.72	< 0.0001
Time × density × treatment	42	0.80	0.5756	42	1.56	0.0603

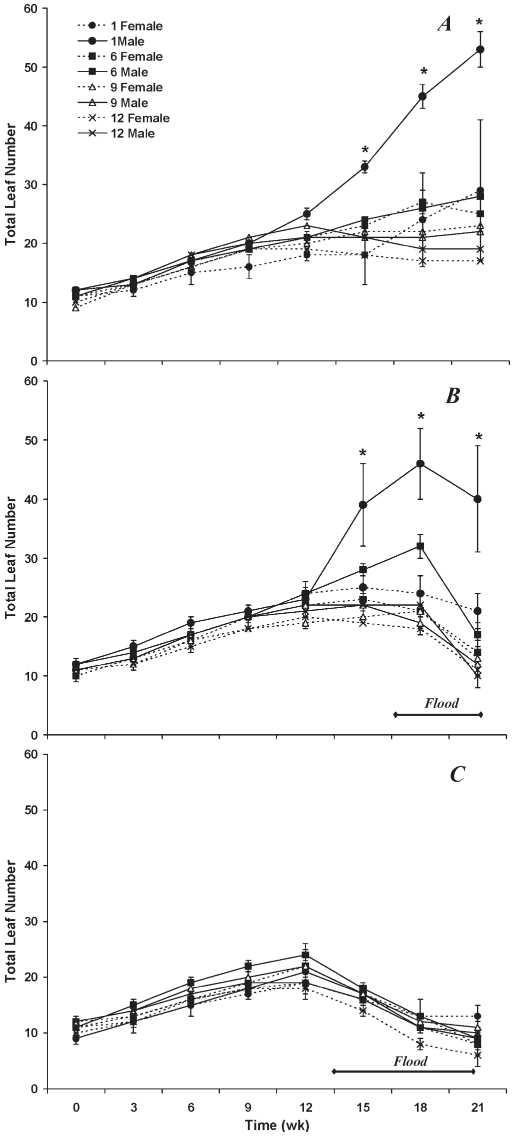

FIG. 3. Mean (± SE) plant total leaf number for monogender plantings of male and female *Lindera melissifolia* plants grown at densities of 1, 6, 9, and 12 in (A) no-flooding, (B) 30-day- flooding, and (C) 60-day-flooding treatments. An asterisk indicates significantly greater total leaf number for male plants, density = 1 (ANOVA, $P \leq 0.05$).

genders did not differ in biomass accumulation, leaf variables, stem height, or stem diameter. However, at the lowest planting density (one), stem height, stem diameter, and total leaf area for male plants significantly exceeded that of higher density male plantings, and of female plants without respect to density. Further, male plant stem height and stem diameter was influenced independently, or through interaction, by density effect. Density effect was insignificant for these growth variables in female plants. Although gender specific response to crowding in dioecious species has been shown to induce sex-biased population ratios through differential growth rates and disparities in mortality between sexes (Nanami et al. 2005, Eppley 2006), this is unlikely for *L. melissifolia*. Male plant sensitivity to crowding would, in theory, promote female-biased sex ratios, and naturally occurring populations are known to be strongly male-biased (Wright 1994, Hawkins et al. 2007).

However, when grown at a density of one, male plants were taller and possessed greater leaf biomass than that of female plants. These attributes within nature could translate into better interspecific competitive abilities for male *Lindera melissifolia*. Plant height is one of the most important determinants in plant competitive abilities (Keddy and Shipley 1989, Hillis and Murphy 1996), whereby, taller plants can intercept more light than shorter plants, and are able to invest more resources in uptake of nutrients for conversion to biomass (Keddy 1989). In turn, larger species tend to suppress smaller species (Goldsmith 1978). Within this framework, male *L. melissifolia* are better adapted than female plants to colonize suitable habitat. This, followed by vegetative propagation as the predominant mode of reproduction, may be a contributing factor to male-bias in *L. melissifolia* populations. A similar mechanism for sex-bias has been described for *Thalictrum dioicum* L., a dioecious species similar in population structure to *L. melissifolia*. Melampy (1981) described *T. dioicum* populations as male-biased and composed of unisexual colonies. Skewed sex ratios in this species result from vegetative propagation, and not differential growth rates, or preference for microhabitat (Melampy 1981). Vegetative propagation also has been found to be an important underlying factor in sex-bias in populations of *Rumex acetosella* L. (Korpelainen 1991), *Clematis virginiana* L., *Salix exigua* Nutt., *Silene alba* (Mill.) Krause, *S. cucubalus* Wibel, and *T. pubescens* Pursh (Iglesias and Bell 1989).

Results of high density (≥ 6) plantings in the growth study are consistent with those reported for the ecologically widespread congener *Lindera benzoin* (L.) Blume, in that there was no difference in size or growth variables in

Table 3. Leaf variables (mean ± SE) for male and female *Lindera melissifolia* grown in three flooding regimes. Values within a row with different lowercase letters are significantly different (Tukey, $P < 0.05$). SLA = specific leaf area; LAR = leaf area ratio.

Variable	No-flooding		30-Day		60-Day	
	Male	Female	Male	Female	Male	Female
†Total leaf area (cm^2)	1088.3 ± 82.6^{a}	999.8 ± 151.3^{ab}	717.9 ± 169.3^{abc}	592.3 ± 109.2^{bc}	390.9 ± 21.3^{c}	309.9 ± 47.6^{c}
Leaf size (cm^2)	56.5 ± 4.8^{a}	45.0 ± 6.0^{ab}	23.9 ± 2.9^{c}	28.1 ± 3.9^{bc}	30.0 ± 2.3^{bc}	25.6 ± 2.8^{c}
SLA ($cm^2 \cdot g^{-1}$)	274.8 ± 10.3^{a}	259.5 ± 9.1^{a}	286.5 ± 10.6^{ab}	274.8 ± 17.5^{a}	321.8 ± 21.0^{ab}	356.5 ± 31.6^{b}
LAR ($cm^2 \cdot g^{-1}$)	83.9 ± 4.0^{a}	84.4 ± 4.3^{a}	67.1 ± 6.2^{a}	84.7 ± 10.1^{a}	91.8 ± 8.6^{a}	86.3 ± 11.9^{a}

† Mean total leaf area for male, density one, no-flooding (2741.2 ± 560.2 cm^2) was significant ($P = 0.0089$) and was not included in tabled male total leaf area calculation.

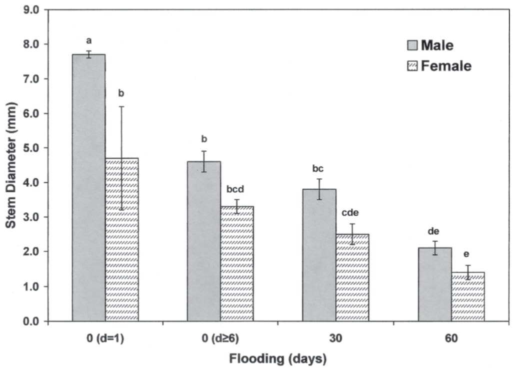

FIG. 4. Mean (± SE) change ($\Delta_{\text{final-initial}}$) in stem diameter for monogender plantings of male and female *Lindera melissifolia* plants receiving three flooding treatments (d = density). Values with different lowercase letters are significantly different (Tukey, $P \leq 0.05$).

male and female plants during pre-reproductive growth stages (Cipollini and Whigham 1994). Although Primack (1985) found similar growth rates for male and female *L. benzoin* in two Massachusetts populations, Cipollini and Whigham (1994) noted differential growth rates between genders of *L. benzoin* plants at reproductive maturity. Therefore, it is possible that sexual dimorphism in *L. melissifolia* also occurs in plants at more advanced growth stages than the plants included in our study, and this aspect of the species life cycle in relation to population sex-bias warrants further investigation.

Although density effects in combination with hydrologic regime exerted some influence on intersexual competition, we found no strong evidence to support our hypothesis that male-biased colony ratios found in naturally occurring populations of *Lindera melissifolia* are the result of competitive exclusion incurred during the first-year, pre-reproductive growth stage of this species' life cycle. When soil was maintained at field capacity, RY for female plants grown at a density of six significantly exceeded the expected value, and RYT was greater than 1.0. This planting density and level of water availability favored female competitors, and niche differentiation was indicated. On the other hand, when male and female plants were grown at this same density and received the 30-day-flooding treatment, RYs were lower (although not significant) than the expected values, and RYT was significantly lower than

Table 4. Biomass (mean ± SE) variables for male and female plants of *Lindera melissifolia* grown in three flooding regimes. Values with different lowercase letters are significantly different (Tukey, $P < 0.05$).

Variable	Flooding (days)	Male	Female	*P*	*N*
Root biomass (g)	0 (density = 1)	12.8 ± 3.8^{a}	6.0 ± 2.7^{a}	0.1446	6
	0 (density = 6)	4.8 ± 0.3^{b}	4.2 ± 0.5^{a}	0.1670	18
	30	3.1 ± 0.4^{b}	2.2 ± 0.4^{b}	0.1292	24
	60	0.9 ± 0.1^{b}	0.7 ± 0.1^{b}	0.2733	24
Stem biomass (g)	0 (density = 1)	12.9 ± 2.7^{a}	5.6 ± 3.0^{a}	0.1446	6
	0 (density = 6)	4.0 ± 0.3^{b}	3.4 ± 0.3^{ab}	0.4123	18
	30	5.5 ± 1.1^{b}	3.2 ± 0.6^{ab}	0.2350	24
	60	2.0 ± 0.2^{b}	1.8 ± 0.2^{b}	0.3757	24
Leaf biomass (g)	0 (density = 1)	11.8 ± 0.3^{a}	8.7 ± 0.2^{a}	0.2666	6
	0 (density = 6)	3.8 ± 0.3^{b}	3.5 ± 0.3^{b}	0.4787	18
	30	2.4 ± 0.7^{b}	2.0 ± 0.4^{bc}	0.5733	24
	60	1.0 ± 0.2^{b}	0.7 ± 0.2^{c}	0.2696	24
Total biomass (g)	0 (density = 1)	37.5 ± 9.5^{a}	18.0 ± 8.7^{a}	0.2024	6
	0 (density = 6)	12.6 ± 0.8^{b}	10.3 ± 1.2^{a}	0.1381	18
	30	11.1 ± 2.2^{b}	7.2 ± 1.3^{b}	0.1398	24
	60	3.8 ± 0.3^{b}	3.1 ± 0.3^{b}	0.1095	24

1.0, suggesting mutual antagonism. Although male plants showed significant deviation from expected RY in three other mixture combinations, this was not countered by deviation from expected RY for female plants (or values of RYT) indicating that, in general, male and female *L. melissifolia* plants grew equally well regardless of density, gender ratio, or hydrologic regime. On the other hand, equivalent intersexual competitive abilities during flooding should be interpreted as the state of relative male-female competition pre-treatment, and thereafter, of growth stasis in both genders during flooded conditions with equal rates of plant tissue decline with increased flood duration. Based on these results and within the contexts of density or competitive exclusion, it is unlikely that within a population, a shift in male colony to female colony ratios would be precipitated by a gender specific response to change in hydrologic regime in first-year *L. melissifolia* plants.

Plant response to flooding did not differ between genders and was characteristic of plant species sensitive to submersion (Hook 1984, Jackson and Drew 1984). Cessation of stem growth and extent of leaf loss resulted in significantly reduced biomass components for plants receiving the 30-day and 60-day-flooding treatments relative to plants that did not receive a flooding treatment. We did not monitor below ground response to flooding at timed intervals during our study, so it is impossible to know whether lower root biomass with increased flood duration resulted simply from cessation of root growth, degradation of roots, or a combination of the two. However, in many woody plant species, decreases in root biomass is a common response to flooding, and appears to be related to low metabolic activity, followed by decreases in the root turnover and growth under anaerobic conditions (Kozlowski 1997).

The ability of a plant species to establish and persist in a floodplain environment is affected by the timing, duration, and frequency of the flooding event (Ernst 1990). Further, plant response to flooding may depend on the stage of a plant's ontogenetical development (Salo 1989, Ernst 1990, Klimešová 1994), and changes in the timing of a flooding event are more dangerous to juvenile plants than mature plants (Whigham et al. 1979, Klimešová 1994). The most numerous, and perhaps the largest populations of *Lindera melissifolia*, occur in periodically flooded bottomland forests in the LMAV. Flooding at these sites generally begins in late winter and subsides in early spring (Hawkins unpubl.), with no apparent detrimental effects to the health of reproductively mature *L. melissifolia* (Wright 1990, Hawkins pers. obs.). This suggests that persistence of *L. melissifolia* in these forests relies, at least in part, on an ecological adaptation to flooding through coincidence of periods of water logging with periods of plant dormancy or low metabolic activity (McAlpine 1961). Although we cannot speculate on the response of metabolically active, reproductively mature *L. melissifolia* plants to alteration of time and

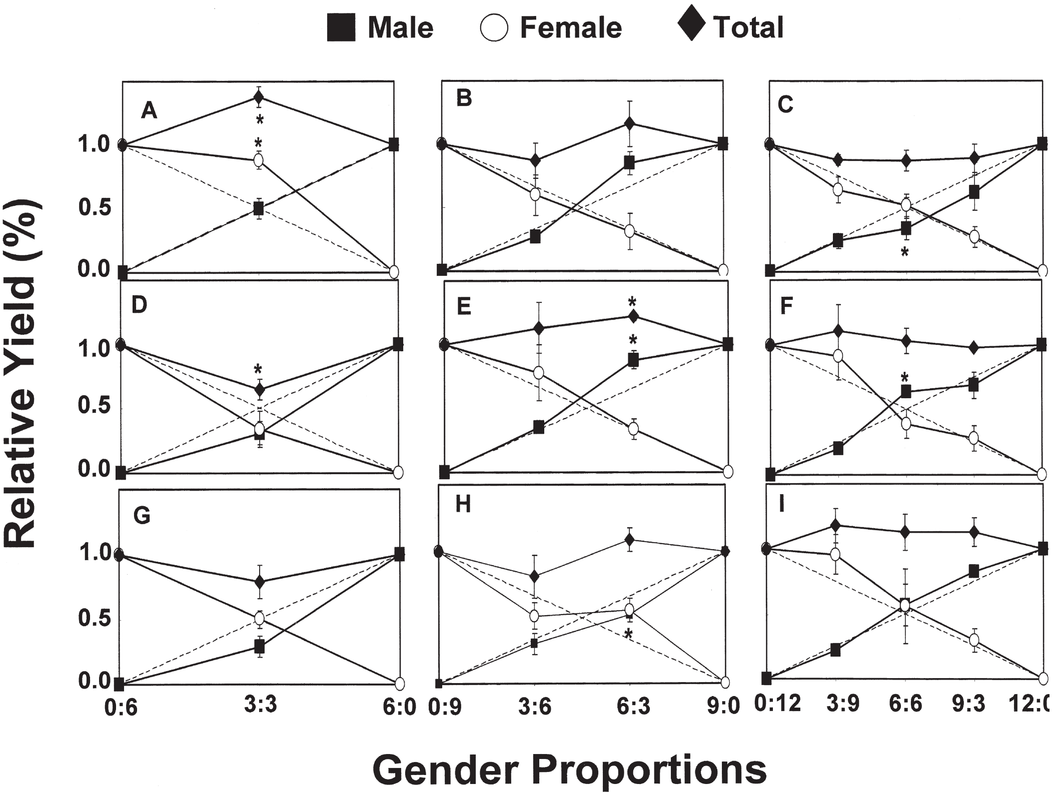

FIG. 5. DeWit diagrams illustrating mean (± SE) relative yield (RY) and relative yield total (RYT) as a function of male and female *Lindera melissifolia* proportions for (A) no-flooding, density = 6; (B) no-flooding, density = 9; (C) no-flooding, density = 12; (D) 30-day-flood, density = 6; (E) 30-day-flood, density = 9; (F) 30-day-flood, density = 12; (G) 60-day-flood, density = 6; (H) 60-day-flood, density = 9; (I) 60-day-flood, density = 12. Diagonal dashed lines are the expected RY when plants grow equally well in mixture and monoculture. An asterisk indicates a significant difference (*t*-test; $P \leq 0.05$) in RY or RYT from the expected value.

duration of flooding, our study has shown that during high metabolic activity, first-year *L. melissifolia* plants are not adapted to tolerate extended flooding conditions.

MANAGEMENT IMPLICATIONS. The Recovery Plan for Pondberry requires permanent protection of 15 self-sustaining *Lindera melissifolia* populations for down-listing the species, and delisting requires permanent protection of 25 self-sustaining populations (U.S. Fish and Wildlife Service 1993). Management plans aimed at achieving these criteria should strongly consider the influence of time and duration of site flooding events on *L. melissifolia* plants at all stages of ontogenetic development. There is no indication that flooding regime promotes colony sex-bias within an *L. melissifolia* population, and growth response of reproductively mature plants to alteration in hydrologic regime is not known. However, we have shown the potential for detrimental effects on the health of young plants should alteration in hydrologic regime result in occurrence of an extended flooding event during periods of high metabolic activity. On the other hand, disturbance has been shown to promote ramet production (Wright 1990); therefore, short-term flooding (7–10 days) during the growing season may promote asexual reproduction and encourage colony expansion.

Aleric and Kirkman (2005) recommended that when reintroducing *Lindera melissifolia* to its natural habitat, canopy conditions should be maintained at irradiance levels below 40% full sunlight for optimal plant growth. These irradiance levels in combination with flooding restricted to the dormant season would not only provide optimum growing conditions for young *L. melissifolia*, but also suppress interspecific competition. The latter is of particular importance for first-year female *L. melissifolia* given their slower growth relative to that of male *L. melissifolia* plants.

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