

## ABSTRACT

UNKS, RYAN R. Environmental Controls of Reproduction and Early Growth of *Lindera melissifolia* (Lauraceae). (Under the direction of Dr. Theodore Shear.)

*Lindera melissifolia* (Walt.) Blume is a federally endangered southeastern endemic shrub that is declining due to land clearing and conversion. In addition, gene flow is reduced due to habitat fragmentation, and new populations are not establishing. Reproduction by seeds is rare, and many populations are becoming male-biased. The goal of this study was to determine favorable environmental conditions for reproduction via seeds (safe sites) as well as for sustaining equal sex-ratios under field conditions. Seedlings were grown under varied moisture and light conditions for varied lengths of time and then harvested to determine dry mass and leaf area. Growth rates were analyzed using a two-way factorial analysis of covariance (ANCOVA). Net assimilation rate and morphological ratios were calculated and compared using a two-way analysis of variance (ANOVA). Seedlings were clipped below and above root collars as a means of simulating two levels of disturbance and then assessed for mortality and relative growth rates. Treatments were compared to a control using a one-way ANOVA. Adult stems of both sexes of *Lindera melissifolia* and co-occurring vascular flora were surveyed for percent cover within non-random plots centered on the highest densities of flowering stems. Flowering stems were counted and compared to transmittance and stem density using regression analysis. Multi Response Permutation Procedure (MRPP) and Indicator Species Analysis Indicator Values (IV) were used to compare species composition within plots with females present or absent. Plants grown under the lowest transmittance (3%) had only 50.8—52.7% of the growth rates of all other light treatments, but plants grown

under the three higher levels did not differ from each other (Table 9,  $p < .0001$ ). Low moisture under the highest (40%) light treatment resulted in reduced growth rates of 87—90% ( $p = .032$ ). Net assimilation rates were different for light effects, but moisture effects were different only under the highest light level, using a t-test ( $p = .0495$ ). Morphological responses showed a higher amount of plasticity under varied light than under varied moisture. Clipping of seedlings below the root collar decreased survivorship to 31%, while clipping of seedlings above the root collar did not significantly increase mortality. Relative growth rates of both clipping treatments were lower than the control treatment ( $p < .001$ ). Percent cover of *Lindera melissifolia* explained 52% of the variation in male flowering stems, but explained only 14% of the variation in female stems. Percent transmittance did not have a significant effect on flowering stems. Overall compositional difference between plots with female presence or absence was weak (MRPP:  $A = .02$ ,  $p = .016$ ). Indicator species analysis revealed a strong association of male flowering stems with *Pinus taeda* (IV=59.8) and *Vaccinium corymbosum* sensu lato (IV=47.7), and a weak association of female flowering stems with *Taxodium ascendens* (IV=26.7). Results confirm that hydrology is more important than light in creating safe sites and maintaining sex-ratios, but also that increased light under dry conditions lowers competitive ability. Hydrological regime, rather than canopy cover, should be the primary concern of land managers. Infrequent, low intensity disturbance may prove to be a useful secondary management tool for limiting competition from coastal plain woody species.

Environmental Controls of Reproduction and Early Growth of *Lindera melissifolia*  
(Lauraceae)

by  
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## **BIOGRAPHY**

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## INTRODUCTION

*Lindera melissifolia* (Walt.) Blume, pondberry, is a globally imperiled southeastern endemic shrub (Natureserve 2011, G2 status). It is listed as federally endangered in the United States, and its range and dispersal ability have become decreased primarily due to clearing and drainage for agriculture or timber management (Wright 1989, U.S. Fish and Wildlife Service 1993). It is declining at present (North Carolina Natural Heritage Program 2011, Natureserve 2011), and more specific ecological knowledge is greatly needed for developing a clear management strategy (Devall 2001, Aleric and Kirkman 2005, Hawkins et al. 2009). By determining the specific environmental requirements for reproduction of *L. melissifolia*, strategies can become coordinated to achieve the twenty-five permanently protected, self-sustaining populations needed for delisting under the U.S. Fish and Wildlife Recovery Plan (USFWS 1993).

*Lindera melissifolia* has the ability to tolerate flooding due to lacunae for diffusion of oxygen to underwater parts, and is found in a variety of seasonally-flooded depressional wetlands. In Mississippi it is currently found in bottomland hardwood communities with very poorly drained, fine-textured clayey soils and canopies of primarily *Acer negundo* L., *Celtis laevigata* Willd., *Fraxinus pennsylvanica* Marshall, *Liquidambar styraciflua* L., *Quercus nigra* L., and *Ulmus americana* L. (Devall et al. 1992, Morris 1986). In Arkansas and Missouri it is found exclusively in temporary sandhill ponds between dunes within bottomland

hardwoods in poorly drained loams and fine sandy loams dominated by *Acer rubrum* L., *L. styraciflua*, *Quercus lyrata* Walter, *Quercus palustris* Münchh., and *Quercus phellos* Münchh (Wright 1991). The single Alabama population is under partially open canopies of *Ilex myrtifolia* Walter, *N. biflora*, and *Quercus laurifolia* Michx. (Shotz 2005), while in Georgia it is found along the borders of sphagnum bogs in association with *Acer rubrum*, *L. styraciflua*, *Litsea aestivalis* (L.) Fernald, and *Pinus taeda* L. (Devall 2001). In South Carolina it is found in limestone sinkhole areas typically surrounded by *Taxodium ascendens* Brongn. (Devall 2001) and in North Carolina it is found in Carolina Bays with primarily sandy soils and canopies of *T. ascendens*, *P. taeda*, *N. biflora*, and *A. rubrum* (Devall et al. 2001).

*Lindera melissifolia* can tolerate low moisture conditions (Wright 1990a) due to low levels of stomatal conductance and facultatively deciduous leaves (Wright 1990a). Although it can occur in areas completely lacking shade in North Carolina, South Carolina, and Georgia (Devall et al. 2001), photosynthetic efficiency decreases in these conditions (Aleric and Kirkman 2005). Studies on light availability and photosynthetic ability of adults under differing light levels have shown that while *L. melissifolia* is an effective competitor under flooded, low light conditions, it is probable that it will be outcompeted in disturbed, open areas (Wright 1990b). While being adapted to low-light environments, *L. melissifolia* may have low water use efficiency in high light environments and therefore has lower drought tolerance under these conditions, which both affects adults adversely and also hinders the establishment and persistence of seedlings (Wright 1990b).

*Lindera melissifolia* is stoloniferous, with runners occurring just below the soil surface. Clonal sprouting is currently its main means of reproduction within established areas, while the two other North American *Lindera* spp. (*L. benzoin* and *L. subcoriacea*) primarily establish themselves by seeds (Godt and Hamrick 1996). *Lindera melissifolia* has low genetic diversity probably due to its evolutionary history, as *L. subcoriacea* has similarly low genetic diversity, but also due to a lack of gene flow between isolated populations (Godt and Hamrick 1996). It occurs locally in abundances of up to 10,000 stems (Wright 1989) and adults have been observed resprouting following fire (Wright 1989), but little is known about its preferred historical fire regime or seedling resprouting abilities (USFWS 1993).

*Lindera melissifolia* is dioecious (U.S. Fish and Wildlife Service 1993) or very rarely polygamodioecious (Taylor 2007) and produces viable seeds in several populations. Production varies in quantity from year to year (Morgan 1983). Some populations currently have very few females; the reason for this is not well understood (Hawkins 2009). Female clones are shorter (Wright 1994), produce fewer numbers of flowers (Richardson 1990), allocate thirty-five times the resources to reproduction (Wright 1994), and have lower growth rates than males (Hawkins et al. 2009). Males may be favored under instances of disturbance or stress (Wright 1989) in addition to possibly being more vigorous at apomictic reproduction (Wright 1990a, Hawkins et al. 2009), especially following dieback at six to seven years of age, which may affect females at a higher rate (Wright 1994).

## OBJECTIVES

It was the goal of this study to determine conditions which favor the establishment and persistence of *L. melissifolia* seedlings and to inform management aspirations suited to both maintenance of current population densities and continued sexual reproduction. The environmental and ecological conditions of two North Carolina field study sites containing both seedling and adult *L. melissifolia* individuals were assessed in relation to the plant's known ecological characteristics followed by three studies designed to address specific research objectives: 1. To determine the role of light and hydrology in *L. melissifolia* establishment and to test the hypothesis that relative growth rate of seedlings is more impacted by water availability under high light conditions than under low light conditions (seedling establishment controls). 2. To determine the resprouting ability of first year seedlings in response to two simulated intensities of disturbance (resprouting ability). 3. To analyze patterns of vegetational composition and environmental variation within current *L. melissifolia* populations and the relationships between these factors, density of stems, and adult stem sex (male-bias).

## FIELD STUDY SITES AND INITIAL OBSERVATIONS

*Lindera melissifolia* is currently found in two locations in North Carolina, Pondberry Bay and Big Pond Bay, both of which are located in Small Depression

Pocosin community types (Schafale and Weakley 1990). In both cases, the depressions are Carolina Bays, a common geological feature of the southeastern Coastal Plain. Aerial photographs taken in the 1930s revealed the curious alignment and elliptical shape of bays, and their origin is still controversial (Eyton and Parkhurst 1975). It has been estimated that 97% of Carolina Bays in South Carolina have been disturbed by ditching, soil disturbance, and vegetation clearing (Bennett and Nelson 1991). Small Depression Pocosins that have experienced unsuppressed fire regimes are extremely rare (Schafale and Weakley 1990).

Pondberry Bay is located in Sampson county (34.985355,-78.472645) and is owned by the Plant Conservation Program of the North Carolina Department of Agriculture and Consumer Services. Approximately 1,000 *L. melissifolia* stems occur here (North Carolina Natural Heritage Program 2010). The soil series is Lynn Haven sand, a typic Alaquod (Soil Survey Staff 2011). Most of the bay is dominated by even-aged *P. taeda* of ca. thirty-four years, and was formerly managed by a timber company. Remnant cypress knees throughout the site indicate that it was formerly dominated by *T. ascendens* before being managed for pine. Under the areas of densest canopy, *L. melissifolia* is one of the few understory species present. *Taxodium ascendens*, *N. biflora*, and a number of other species associated with the Small Depression Pocosin (Schafale and Weakley 1990) community type occur sporadically. The highest stem densities of *L. melissifolia* occur in conditions of varying canopy cover along the edge of a small clearing in the northern half of the bay. Here a number of *P. taeda* trees were recently killed in a location of the bay

where a higher density of *T. ascendens* and *N. biflora* individuals occur, most likely during a three to four month flooding event following Hurricane Floyd in 1999. Observations in early 2009 and 2010 showed standing water only in close proximity to a small ditch at the southeast corner of the clearing in Pondberry Bay that is surrounded by extremely dense numbers of *L. melissifolia* stems (Krings 2010). This ditch is one of many in a network of ditches presumably installed during timber management, and a large number of female stems occur in close proximity to it. Aerial photos indicate that a road which passes within 50 m of the eastern edge of the bay was built between 1951 and 1958, possibly altering the hydrology. The bay was last observed completely flooded in 1995 (Leonard 1995).

Big Pond Bay is located in Cumberland county (34.917115,-78.58577), and approximately 4,000 *L. melissifolia* stems occur here (North Carolina Natural Heritage Program 2010). The northern half of the bay is owned by the Plant Conservation Program of the North Carolina Department of Agriculture and Consumer Services and was seed-tree cut within the last ten years, before being acquired. In areas where *L. melissifolia* is present, the soils are Rains sandy loam, a typic paleaquult (Soil Survey Staff 2011) and *A. rubrum*, *P. taeda*, *Lyonia lucida*, *Ilex glabra*, and *Smilax laurifolia* are the most common species. The uncut portion of the bay has a mixed canopy of *T. ascendens*, *N. biflora*, *A. rubrum*, and *P. taeda*. Many areas of both the cut and uncut areas within Big Pond Bay were submerged in >20 cm of water in April 2010 as well as Winter 2010/11.

*Lindera melissifolia* adults were observed under a variety of overstory conditions at both sites ranging from 5.5—86.6% transmittance, and to co-occur with both sun and shade species. Leaves of adults present in the areas of highest transmittance had a curled form, similar to those described by Aleric and Kirkman (2005) under high light and presumed stress. Thirty-five seedlings were observed under conditions of 1.5—6.5% transmittance. Seedlings were all growing in a 2.5—5 cm thick layer of pine and deciduous leaf litter, indicating that leaf litter is not preventing germination. No clear patterns of hydrological or microtopographical affinity were indicated by a cursory survey.

In November 2009, seeds at Pondberry Bay were covered with a black mold, which was later determined by North Carolina State University Plant Disease and Insect Clinic to be *Colletotrichum gloeosporioides* (Dr. Alexander Krings, pers. comm. 2009). Germination success of these seeds (N=123) was compared to uninfected seeds (N=549), and the negative effect of *C. gloeosporioides* on seedling germination was significant, with only 32.5% of infected seeds germinated compared to 91.3% of uninfected seeds  $\chi^2(1, N = 672) = 220.89, p = <.0001$ ). However, *C. gloeosporioides* is a ubiquitous organism and is primarily an agricultural pest (Burger 1920) that is also present in populations in Mississippi with no adverse effects (Devall et al. 2001). Additionally, as less than 10% of the 7000+ seeds present this late in the year appeared to be infected, and as the mold did not seem to be present at other times of year, its effects on the reproductive ecology of *L. melissifolia* were not further investigated.



## METHODS

### 1. Seedling establishment controls

Seeds were collected from Pondberry Bay under permit through the Plant Conservation Program of the North Carolina Department of Agriculture and Consumer Services in November 2009 (permit identification number 196). Seeds were de-pulped and the drupes were stratified for 5 months in moist peat at 5° C. In May 2010 seeds were planted in peat pots and watered daily under greenhouse conditions at North Carolina State University. Following germination and two weeks of growth, seedlings were transplanted into pots containing a mixture of 50% sand and 50% peat.

Seedlings were randomly assigned to 1 of 3 moisture levels (~50%, ~30%, and ~15% soil moisture, table 2) and 4 light levels (approx. 40%, 30%, 10% and 3% transmittance, table 3) and grown from June to September 2010. Dry soil (~15% moisture content) treatment conditions were achieved by utilizing pots with bottom drain holes situated in a tub filled with standardized depths of water. Field capacity (~30% moisture content) soil conditions were created by watering from above once daily and allowing excess water to escape through bottom drain holes. Wet (~50% moisture content) soil conditions were achieved by watering from above daily as well as by immersion of pots in standardized depths of water. Shade treatments were achieved by using various density shade cloth approximately 1 meter above pots. The moisture treatments were combined independently under each light treatment in

a three by four factorial design with thirty-six seedlings in each of the 12 resulting treatments. Moisture percentage was monitored weekly using a time domain reflectometry (TDR) unit with a three inch attachment probe (Table 1).

Photosynthetically active radiation (PAR) was recorded using a quantum line sensor in tandem with temperature and relative humidity measurements within light treatments over the course of one day (Table 2). High and low temperatures within the greenhouse were logged daily. A temperature spike was recorded in the greenhouse, where maximum temperatures reached 46 °C consistently for a week, resulting in the transmittance levels not being appropriate for direct comparison to field conditions.

Beginning at six weeks of age, six individuals from each treatment were harvested once every two weeks for twelve weeks. Leaves were removed from harvested plants and scanned using a digital scanner, and leaf area was determined using Image J software (Rasband 2011). Plant material was oven-dried at 60° C for two days and then weighed to determine root, stem and leaf mass. The 'functional' approach (Hughes 1967), where a polynomial is fitted through ln-transformed total plant mass over time, was then utilized to compare relative growth rate throughout the experiment. This was accomplished by performing a two-way analysis of covariance (ANCOVA) of ln-transformed total plant mass with a continuous variable of time, and discrete variables of moisture and light category. This was followed by a one-way ANCOVA of moisture treatments by light treatments and a one-way ANCOVA of light treatments by moisture treatments. Specific leaf area (SLA=leaf

area/leaf mass), leaf area ratio (LAR=leaf area/total plant mass), leaf mass ratio (LMR=leaf mass/total plant mass), stem mass ratio (SMR=stem mass/total plant mass), and root mass ratio (RMR=root mass/total plant mass) were then calculated. A two-way ANOVA of morphological ratios was performed for each dependent variable of SLA, LAR, LMR, SMR and RMR, with independent variables of moisture and light. Relative growth rate was calculated for each individual plant using the 'classical' method ( $RGR = (\ln(\text{total plant mass}_2) - \ln(\text{total plant mass}_1)) / (\text{time}_2 - \text{time}_1)$ ), where initial plant mass at transplanting (total plant mass<sub>1</sub>) was determined by an allometric relationship between height and mass. Net assimilation rate (NAR=RGR/leaf area) was subsequently calculated for each individual plant. A two-way ANOVA of NAR as dependent variable and soil moisture and light transmittance as independent variables was then performed, followed by a one-way ANOVA of NAR of moisture grouped by light treatment. Tukey's Honestly Significant Difference method was used to determine significantly different levels for all ANOVA and ANCOVA models with a significance level of  $\alpha=.05$ . If an effect was found significant but the Tukey HSD did not distinguish between levels, a t-test was utilized to distinguish which treatment levels were different, and the possibility of Type I error was calculated. All statistical analyses were performed using JMP software (JMP Version 9).

## 2. Resprouting ability

In March of 2011, forty-eight seedlings of *Lindera melissifolia* were measured for total plant height and stem diameter and then randomly assigned treatments of clipping 1 cm above the root collar, clipping 1 cm below the root collar, and control (no clipping). Following treatment, all seedlings were grown for six weeks, at which point mortality was assessed and measurements were made of total plant height and stem diameter. Plant volume was estimated by squaring the diameter and multiplying this by the height. Relative growth rate was calculated by dividing the difference in ln-transformed plant volume by time. A one-way ANOVA and Tukey test were used to determine differences in survival between treatments; the same procedure was utilized to test differences in relative growth rate between treatments.

## 3. Male-bias

During March to April of 2011, both Pondberry Bay and Big Pond Bay were surveyed for female and male flowering stems of *L. melissifolia* and associated vascular plant species within 9-meter-squared vegetation plots. Fifty-five plots were non-randomly placed centered on the greatest densities of flowering *L. melissifolia* stems found. Flowering stems were counted by sex, and percent cover was determined for all vascular species present. Hemispherical canopy photos were taken at a height of 1.4 meters in mid-April, and the photos were analyzed using Gap Light Analyzer (GLA) to determine total transmittance for the growing season following the procedure of Frazer et al. (1999). Regression analysis of stem sex

related to stem density and percent transmittance was performed using JMP (JMP Version 9). Multiple response permutation procedure (MRPP) of composition data grouped by female presence/absence was performed using PC-ORD software (McCune and Mefford 2011) in two separate models which differed in *L. melissifolia* percent cover included or excluded, to avoid bias. Indicator species analysis (Dufrene and Legendre 1997) was performed by calculating an indicator value (IV) of female presence or absence where an IV of 100 equals complete fidelity of the species to either presence or absence. PC-ORD software (McCune and Mefford 2011) was used to calculate this value and perform a Monte Carlo test of significance with *L. melissifolia* percent cover included or excluded. P values of  $\alpha < .05$  were accepted in this analysis unless otherwise stated.

## RESULTS

### 1. Seedling establishment controls

The effect test of light\*week in the factorial ANCOVA model was significant ( $p < .001$ , table 3), showing that the assumptions were violated in homogeneity of regression slopes, and that plants under different light treatments had responded differently to time. The assumptions were similarly violated when grouped by dry and field capacity moisture (light\*week  $p = .02$ ,  $p = .001$ , respectively), but were not violated within wet treatments (Table 8,  $p = .134$ ). All tests of moisture when grouped by light were suitable for analysis (Tables 4,5, Figure 1). Mean growth was 29.9%

greater in wet treatments than dry treatments under the highest level of transmittance (40%, Table 6,  $p=.032$ ) and did not differ by moisture treatment within other light groups (Table 6, ns). Growth rates were not different at 40%, 30% and 10% transmittance levels within the wet treatment group (Table 7), but plants grown at the lowest transmittance (3%) had only 50.8—52.7% of the growth rates of all other light treatments (Table 9,  $p<.0001$ ).

Specific leaf area varied by moisture and light treatments (Tables 10,11), generally increasing with decreasing percent transmittance, and those grown under 40% transmittance were 91.9% greater than under 3% transmittance (Table 12,  $p<.0001$ ). Individuals grown in field capacity treatments had slightly (7.0%) greater specific leaf area than individuals grown in dry treatments, and those grown in wet treatments were not different from either (Table 12,  $p=.048$ ). Leaf area ratio became greater with decreasing transmittance and was 175% greater when grown under the lowest transmittance (3%) compared to those grown under 40% transmittance (Table 12,  $p<.001$ ), but was not different for moisture. Leaf mass ratio was slightly (9.5%) greater in dry conditions than in field capacity conditions ( $p=.041$ ), and was 44% greater under lowest (3%) transmittance compared to the highest transmittance (Tables 11,12,  $p<.0001$ ). Stem mass ratios were 21% greater in wet conditions compared to dry conditions (Table 12,  $p<.0001$ ), but were not different under varying light (Table 11). Root mass ratio was different for light ( $p<.0001$ ), but not for moisture (Tables 10,11). The 3% transmittance level fostered the lowest root mass

ratio, and the highest (40%) transmittance had a 47% greater ratio compared to this (Table 12,  $p < .0001$ ).

Net assimilation rates varied by moisture ( $p = .045$ ) and by light ( $p < .0001$ , Table 13). A Tukey test showed no significant difference between those grown under 30 and 40% transmittance, or between moisture treatments overall (Table 14). When grouped by light, moisture effects were different for the highest (40%) category alone (Table 15,  $p = .0495$ ). The subsequent Tukey test did not reveal any differences, despite the wet treatment having 44.1% higher mean net assimilation rate ( $23011 \text{ (ln}(\mu\text{g)/wk)/cm}^2$  compared to  $15964 \text{ (ln}(\mu\text{g)/wk)/cm}^2$ ). Due to the significance of the ANOVA test, a subsequent t-test comparison of means showed dry treatments to have lower net assimilation rates than both field capacity and wet treatments ( $p = .0295$ , field capacity vs. dry,  $p = .0380$ , wet vs. dry). The possibility of a type-I error with this t-test was calculated to be 14.27%.

## 2. Resprouting ability

Seedlings had the ability to resprout from both roots and stems. Percent survival after clipping above the root collar was not significantly different from the control, at 68.8% compared to 87.5%, respectively. Clipping below the root collar lowered survival to 31.3% ( $F = 6.85$ ,  $p = .003$ ). The control (no clipping) treatment had 71.4% higher mean relative growth rate than those clipped above the root collar, and had 147.6% higher mean relative growth rate compared to those clipped below the

root collar ( $F=15.35$ ,  $p<.001$ ). The clipped treatments were not significantly different from each other in relative growth rate (Table 17).

### 3. Male-bias

Number of male flowering stems was explained by percent cover of *L. melissifolia* ( $R^2=0.53$ ,  $p<.001$ , Figure 2) to a much greater degree than the number of female flowering stems was ( $R^2=.14$ ,  $p=0.023$ , Figure 2). There was no direct relationship between the number of female flowering stems to transmittance ( $R^2=.03$ ,  $p=.31$ ), or of the number of male flowering stems to transmittance ( $R^2=.04$ ,  $P=.307$ ). There was a weak, but significant (MRPP:  $A=.02$ ,  $p=.016$ ) division between plots with female presence versus female absence when *L. melissifolia* percent cover was included as a factor, but this division was not significant when *L. melissifolia* percent cover was excluded (MRPP:  $A=.01$ ,  $p=.14$ ). Plots which were exclusively male were indicated strongly by *P. taeda* ( $IV=59.8$ ,  $p=.041$ ). A less rigorous threshold of  $p<.10$  included *T. ascendens* as indicator of female presence ( $IV=26.7$ ,  $p=.098$ ) (Table 18). Indicator analysis excluding *L. melissifolia* percent cover (Table 20), with an acceptability threshold of  $p<.10$  included *P. taeda* ( $IV=59.8$ ,  $p=0.041$ ) and *Vaccinium corymbosum* sensu lato ( $IV=47.7$ ,  $p=.098$ ) as indicators of female absence, and *T. ascendens* ( $IV=26.7$ ,  $p=.099$ ) as an indicator of female presence (Table 19). Additionally, it was noted that *T. ascendens* and *N. biflora* were found almost exclusively in female plots (Table 17), though *T. ascendens* had a relatively



low IV value (26.7) and *N. biflora* was excluded as an indicator ( $p=.155$ ) (Table 19).

## DISCUSSION AND CONCLUSIONS

While Aleric and Kirkman (2005) showed that *L. melissifolia* has decreased photosynthetic efficiency under conditions of higher light, this may be exacerbated under conditions of low soil moisture leading to it having decreased competitive ability in open areas with low moisture (Wright 1990b). Despite a lack of analysis of light and moisture interaction using a two-way ANCOVA, the results of the greenhouse relative growth rate study clearly indicate that higher levels of light transmittance in the absence of adequate moisture are not favorable for establishment of *L. melissifolia* seedlings. When grown in dry soil (~15% moisture), the highest (40%) transmittance level clearly had negative results, but did not have a demonstrably negative effect under other soil moisture conditions. This finding was confirmed in net assimilation rate comparisons by light, albeit with a less rigorous t-test, where there was a large difference in assimilation rates between wet and dry treatments under 40% transmittance alone. Additionally, that wet treatment-grouped results alone had similar regression slopes after ln-correction and were appropriate for light provides indirect evidence that water use is a factor in light effects.

Morphological ratios followed patterns of allocation that are expected in plants with plasticity under varied light regimes, further showing that *L. melissifolia* is highly shade tolerant, as noted by Wright (1990b) and Aleric and Kirkman (2005). Water

effects on specific leaf area were slight, indicating lowered plasticity in response to varied water levels. Poor performance of individuals grown in 3% transmittance in all moisture conditions indicates that conditions of extremely heavy shade are not preferable for establishment. Though the greenhouse transmittance levels may not be directly compared to field conditions due to the greenhouse temperature spike, which potentially affected water use, all seedlings observed at Pondberry Bay occurred under very low light levels of approximately 4% transmittance. It is likely that these heavily shaded areas beneath adults were the only places where seeds were able to disperse and successfully germinate, but are too heavily shaded for optimal growth. Unfortunately, the short time period of this study made analysis of the growth of these individuals impossible, but they were observed to be less than 10 cm tall after one year, while plants grown in adequate light in greenhouse conditions reached similar heights after only one month.

Analysis of field transmittance data showed no evidence of a direct relationship between adult stems or male-bias and transmittance, and indicates that light as a factor in itself probably does not determine adult plant persistence. The highest numbers of male flowers were observed in the densest clusters of *L. melissifolia*, confirming that males sprout more vigorously and are better suited to colonizing new sites by this means (Wright 1990b). The lack of relation of sex to transmittance is compounded by Wright's (1990b) observation of lowered stomatal conductance in females, which would likely favor females under drought conditions, and argues that a lack of periodic inundation is favoring males rather than drought

stress limiting females. Analysis of compositional data from Pondberry Bay and Big Pond Bay in North Carolina indicates a weak association of *L. melissifolia* females with *T. ascendens* and *N. biflora*, which are both obligate wetland species (USDA 2011). The very strong association of males with *P. taeda* and somewhat weaker association with *I. opaca*, which are facultative and facultative- species (USDA 2011), respectively, provides evidence for a subtly different hydrologic regime ultimately favoring males. The lowered significance threshold ( $p < .10$ ) included *V. corymbosum* s.l. and *L. lucida* as indicators of females, and both of these are facultative wetland species (USDA 2011).

The evidence from the compositional component of this study combined with greenhouse results ultimately indicates that environmental factors, rather than biological factors, may be influencing male-bias. There are no records of hydrological regimes currently available for the study sites, but it seems probable that changes in seasonal water fluctuations are favoring male establishment, likely by a mechanism of decreased female sprouting when competitors are not excluded by hydrologic regime. Change of hydrologic regime is especially of concern at Pondberry Bay, where it seems likely that the road, the accompanying ditch, and a network of smaller ditches within the Bay have altered the hydrological regime from its historical state.

The two North Carolina populations of *L. melissifolia* include sexually reproductive females and males, whose seeds are viable in the greenhouse and the field, further emphasizing the extremely high conservation value of these sites.

Though this study only included North Carolina genotypes and habitats, it provides evidence that safe sites for *L. melissifolia* seedlings, as well as exclusion of competitors and female stem persistence, are likely highly influenced by hydrological regime. It is advised that extensive overstory removal be avoided as other species better adapted for full sun will likely outcompete *L. melissifolia*. The results of this study point to hydrological conditions which create disturbance and limit competitors. Further quantitative study of precise cyclical soil moisture conditions and microtopography in relation to male bias should be of highest priority for informing management of sexually reproducing *L. melissifolia* populations. Study of the hydrological regimes of depressional wetlands which favor sexually reproducing *L. melissifolia* may also provide specific, quantitative standards for Carolina Bays and other wetlands where it currently occurs, or may have occurred historically. *L. melissifolia* co-occurs with *L. aestaevalis*, another Lauraceae species of concern, in Georgia, South Carolina, and North Carolina, and future research should focus on their overlapping habitat requirements, as well as other co-occurring wetland obligates. Analysis of this type is needed in order to better understand current conditions of populations, and whether these conditions may be producing stress which will result in further decline of depressional wetland communities.

Absence of fire from North Carolina populations is also likely favoring competing species like *P. taeda* and *V. corymbosum* s.l.. This study has shown quantitatively that *L. melissifolia* resprouts readily from roots and stems, but does so with lowered rates of growth. Though clipping does not directly simulate fire, and a

greater understanding of historical fire regime is required, it indicates that infrequent, low intensity fire may prove to be a useful management tool in the future.

Decreased survivorship during high intensity fires is an expected outcome for a species adapted to the areas within and along the edges of depressional wetlands which probably burned less frequently than surrounding areas in the past. Higher intensity fires and soil disturbance should be avoided, and fire in North Carolina populations remains problematic due to the thick, predominantly *P. taeda* leaf litter layer present.

It is thought that for the species to persist, diverse genotypes of *L. melissifolia* must either be planted or otherwise disperse into existing populations (Wright 1989). Seeds at Pondberry Bay are probably not being animal dispersed within the site, and suitable nearby habitat is scarce. Big Pond Bay has much higher diversity of bird species than Pondberry Bay (under casual observation), and seeds do not persist on plants as late in the year (pers. obs.). Seeds are known to be dispersed short distances during winter by hermit thrushes in Mississippi (Smith et al. 2004) and may have been dispersed in the past by flooding regimes in bottomlands which are now strictly controlled (Devall et al. 2001). Future studies should further assess past and present animal dispersal in conjunction with habitat fragmentation in North Carolina. Future studies at Big Pond Bay may reveal currently unknown animal species which consume seeds in addition to the few noted by Ridley (1930) and others (Smith et al. 2004).

While many state that *L. melissifolia* has been historically rare due to conclusions drawn by Steyermark (1949) from the low number of collections before 1900, it is possible that habitat destruction is responsible for this low number of collections, as a large amount of possible habitat had already been logged or drained for agriculture even by the time Walter described it in 1788 (Lilly 1981).

Clearing certainly occurred in most North Carolina areas with cypress canopies due to the valuable, rot-resistant wood (Lilly 1981). Numerous authors have cited Steyermark (Aleric and Kirkman 2005, Devall et al. 2001, USFWS 1993), without perhaps considering the incompatibility of *L. melissifolia*'s reproductive ecology with the rapid, widespread clearing and draining of its coastal plain habitat following European colonization. *Lindera melissifolia*'s weak reproduction by seeds and decreased competitive ability under full sun probably leaves it unable to reproduce effectively under rapid clearing and fragmentation of suitable habitat, especially under conditions of vigorous competition from coastal plain woody species. Its local abundance, variable habitat, and widespread distribution through the entire southeastern United States implies that it may have been more abundant at one time, unlike many rare species with small, localized populations.

In conclusion, the findings of this study along with *L. melissifolia*'s requirement of wetland area and the highly varied co-occurring species composition throughout its range argues that seedling and adult success is most closely tied with hydrology and exclusion of interspecific competitors. Restoration of hydrological regime should be of utmost importance for managers attempting to avoid the

continued losses of populations as witnessed even since *L. melissifolia*'s listing as federally endangered (United States Fish and Wildlife Service 1993, North Carolina Natural Heritage Program 2010, Natureserve 2011).

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## APPENDIX

Table 1. Average percent soil moisture in greenhouse experiment moisture treatments of *Lindera melissifolia*

Treatment	Average percent soil moisture	Standard deviation
3%-dry	13.86	2.53
10%-dry	10.16	1.96
30%-dry	12.46	3.43
40%-dry	15.84	3.88
3%-field	37.34	2.78
10%-field	33.84	2.83
30%-field	33.11	3.66
40%-field	31.09	4.25
3%-wet	47.71	1.65
10%-wet	47.54	1.24
30%-wet	44.31	2.01
40%-wet	44.29	2.58

Table 2. Values of photosynthetically active radiation (PAR), temperature, and humidity within greenhouse light treatments of *Lindera melissifolia*, including standard deviations (standard deviations are in parentheses)

Treatment, % transmittance	Average PAR $\mu$ moles / m <sup>2</sup> s	Actual Transmittance	Average temperature (C°)	Average % humidity
100%	699 (59)	n/a	n/a	n/a
40%	272.8 (103.86)	0.39	29.17 (1.48)	58.03 (8.52)
30%	208.5 (82.252)	0.30	28.91 (1.26)	58.89 (8.45)
10%	91.5 (48.413)	0.13	28.78(1.6)	57.62 (8.51)
3%	19.8 (6.123)	0.03	29.57 (1.49)	57.49 (6.88)

Table 3. Effect test results of *Lindera melissifolia* relative growth rate factorial ANCOVA

Source of variation	N	Degrees of Freedom	Sum of Squares	F ratio	Probability > F
light	3	3	34.35	89.60	<.0001
moisture	2	2	0.34	1.32	0.269
light*moisture	6	6	1.57	2.05	0.058
week	1	1	60.82	475.92	<.0001
light*week	3	3	3.24	8.46	<.0001
moisture*week	2	2	0.21	0.83	0.437
light*moisture*week	6	6	0.42	0.55	0.77

Table 4. ANCOVA model test results of effects of moisture of *Lindera melissifolia* relative growth rate ANCOVA by light treatment

Treatment, % transmittance	Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio	Probability > F
10	Model	5	18.49	3.7	46.3	<.0001
	Error	102	8.15	0.08		
	C. Total	107	26.63			
3	Model	5	9.01	1.8	22.88	<.0001
	Error	103	8.11	0.08		
	C. Total	108	17.13			
30	Model	5	10.18	2.04	11.62	<.0001
	Error	102	17.88	0.18		
	C. Total	107	28.06			
40	Model	5	29.35	5.87	33.38	<.0001
	Error	106	18.64	0.18		
	C. Total	111	47.99			

Table 5. Effect test results of *Lindera melissifolia* relative growth rate ANCOVA by light treatment

% transmittance	Source of variation	N	Degrees of Freedom	Sum of Squares	F ratio	Probability > F
3	moisture*week	2	2	0.03	0.18	0.832
	moisture	2	2	0.23	1.47	0.234
	week	1	1	8.70	110.45	<.0001
10	moisture*week	2	2	0.44	2.73	0.07
	moisture	2	2	0.36	2.28	0.108
	week	1	1	17.79	222.7	<.0001
30	moisture*week	2	2	0.08	0.23	0.796
	moisture	2	2	0.04	0.12	0.887
	week	1	1	10.06	57.4	<.0001
40	moisture*week	2	2	0.086	0.25	0.783
	moisture	2	2	1.26	3.57	0.032
	week	1	1	27.94	158.93	<.0001

Table 6. Tukey test results of *Lindera melissifolia* relative growth rate ANCOVA by light (levels within each light treatment connected by the same letter are not significantly different)

Treatment, % transmittance	Moisture treatment		Least squared mean total plant mass mg
40	wet	A	187.56
	field capacity	AB	161.07
	dry	B	144.39

Table 7. ANCOVA model test results of effects of light on *Lindera melissifolia* relative growth rate by moisture

Treatment	Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio	Probability > F
dry	Model	7	29.27	4.18	28.68	<.0001
	Error	137	19.97	0.15		
	C. Total	144	49.24			
field capacity	Model	7	35.65	5.09	71.12	<.0001
	Error	140	10.02	0.07		
	C. Total	147	45.67			
wet	Model	7	35.82	5.12	30.55	<.0001
	Error	136	22.78	0.17		
	C. Total	143	58.60			

Table 8. Effect test results of *Lindera melissifolia* relative growth rate ANCOVA by moisture

Treatment	Source	N	Degrees of Freedom	Sum of Squares	F ratio	Probability > F
dry	light	3	3	9.01	20.61	<.0001
	week	1	1	18.7	128.26	<.0001
	light*week	3	3	1.56	3.56	0.016
field capacity	light	3	3	15.05	70.08	<.0001
	week	1	1	18.73	261.63	<.0001
	light*week	3	3	1.17	5.47	0.001
wet	light	3	3	11.91	23.7	<.0001
	week	1	1	23.56	140.65	<.0001
	light*week	3	3	0.95	1.89	0.134

Table 9. Tukey test results of *Lindera melissifolia* relative growth rate ANCOVA by moisture (levels connected by the same letter are not significantly different)

Moisture Treatment	Light treatment, % transmittance				Least squared mean total plant mass mg
wet	40	A			184.95
	30	A			181.10
	10	A			178.08
	3		B		93.97

Table 10. Model results from *Lindera melissifolia* morphological ratio analysis ANOVA

Morphological ratio	Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio	Probability > F
specific leaf area	Model	11	3.41E-06	3.10E-07	44.01	<.0001
	Error	425	2.99E-06	7.04E-09		
	C. Total	436	6.40E-06			
leaf area ratio	Model	11	1.06E-06	9.68E-08	50.53	<.0001
	Error	425	8.14E-07	1.92E-09		
	C. Total	436	1.88E-06			
leaf mass ratio	Model	11	1.34	0.12	9.97	<.0001
	Error	425	5.2	0.012		
	C. Total	436	6.54			
stem mass ratio	Model	11	0.20	0.02	7.62	<.0001
	Error	425	1.04	0.002		
	C. Total	436	1.24			
root mass ratio	Model	11	1.53	0.14	12.65	<.0001
	Error	425	4.67	0.011		
	C. Total	436	6.20			



Table 11. Effect tests from *Lindera melissifolia* morphological ratio analysis ANOVA

Morphological ratio	Source of Variation	N	Degrees Of freedom	Sum of Squares	F ratio	Probability > F
specific leaf area	light	3	3	3.29E-06	155.62	<.0001
	moisture	2	2	4.32E-08	3.07	0.048
	light*moisture	6	6	7.21E-08	1.70	0.118
leaf area ratio	light	3	3	1.05E-06	182.48	<.0001
	moisture	2	2	1.16E-09	0.30	0.739
	light*moisture	6	6	1.31E-08	1.14	0.338
leaf mass ratio	light	3	3	1.21	33.03	<.0001
	moisture	2	2	0.08	3.22	0.041
	light*moisture	6	6	0.05	0.65	0.692
stem mass ratio	light	3	3	0.01	1.92	0.126
	moisture	2	2	0.18	36.65	<.0001
	light*moisture	6	6	0.01	0.74	0.616
root mass ratio	light	3	3	1.4	42.39	<.0001
	moisture	2	2	0.05	2.34	0.098
	light*moisture	6	6	0.07	1.1	0.362

Table 12. Tukey test results from *Lindera melissifolia* morphological ratio analysis ANOVA (levels connected by the same letter are not significantly different)

Morphological ratio test	Treatment		Least square means
specific leaf area	3 % transmittance	A	476 cm <sup>2</sup> /g
	10 % transmittance	B	362 cm <sup>2</sup> /g
	30 % transmittance	C	288 cm <sup>2</sup> /g
	40 % transmittance	D	248 cm <sup>2</sup> /g
specific leaf area	field capacity	A	353 cm <sup>2</sup> /g
	wet	AB	347 cm <sup>2</sup> /g
	dry	B	330 cm <sup>2</sup> /g
leaf area ratio	3 % transmittance	A	198 cm <sup>2</sup> /g
	10 % transmittance	B	118 cm <sup>2</sup> /g
	30 % transmittance	C	85 cm <sup>2</sup> /g
	40 % transmittance	C	72 cm <sup>2</sup> /g
leaf mass ratio	3 % transmittance	A	0.427
	10 % transmittance	B	0.33
	30 % transmittance	B	0.299
	40 % transmittance	B	0.298
leaf mass ratio	dry	A	0.357
	wet	AB	0.331
	field capacity	B	0.327
stem mass ratio	wet	A	0.28
	field capacity	B	0.261
	dry	C	0.23
root mass ratio	40 % transmittance	A	0.454
	30 % transmittance	AB	0.44
	10 % transmittance	B	0.414
	3 % transmittance	C	0.31

Table 13. Effect tests of *Lindera melissifolia* net assimilation rate ANOVA

Source of Variation	N	Degrees of Freedom	Sum of Squares	F ratio	Probability > F
moisture	2	2	800898514.61	3.11	0.045
light	3	3	12255502602	31.8	<.0001
light*moisture	6	6	633113687.97	0.82	0.554

Table 14. ANOVA Tukey test of *Lindera melissifolia* net assimilation rates (levels connected by the same letter are not significantly different)

Treatment, moisture	Tukey-test	Mean net assimilation rate (Ln( $\mu$ g)/wk)/cm <sup>2</sup>	Standard deviation
field capacity	A	16334.0	932.14
wet	A	16017.4	944.68
dry	A	13282.2	941.3
Treatment, % transmittance			
40	A	20755.5	1071.55
30	A	19004.2	1090.61
10	B	13832.1	1090.89
3	C	7146.1	1085.69

Table 15. Model results from *Lindera melissifolia* net assimilation rate ANOVA by light

Treatment, % transmittance	Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio	Probability > F
10	Model	2	93250281.95	46625140.98	0.51	0.604
	Error	105	9675429576.4	92146948.35		
	C. Total	107	9768679858.4			
3	Model	2	27733209.571	13866604.79	0.39	0.68
	Error	106	3800178056.3	35850736.38		
	C. Total	108	3827911265.9			
30	Model	2	62193243.856	31096621.93	0.17	0.84
	Error	105	18741326589	178488824.66		
	C. Total	107	18803519833			
40	Model	2	1269275824	634637912.02	3.09	0.0495
	Error	109	22377782653	205300758.28		
	C. Total	111	23647058477			

Table 16. ANOVA Tukey test of *Lindera melissifolia* net assimilation rates under varied moisture within 40% transmittance (levels connected by the same letter are not significantly different)

Treatment	Tukey test	Mean net assimilation rate (Ln( $\mu$ g)/wk)/cm <sup>2</sup>	Standard deviation
field capacity	A	23219.0	2294.3675
wet	A	23011.1	2388.0534
dry	A	15964.1	2355.5613

Table 17. ANOVA Tukey test of clipped *Lindera melissifolia* seedling volume relative growth rates

Treatment		Least squared means (ln(mm <sup>3</sup> )/day)
control	A	5.29
above	B	3.08
below	B	2.14

Table 18. Species list of vascular plant species co-occurring with *Lindera melissifolia* male and female stems. Taxon concepts follow those in Weakley (2011).

Scientific Name	Common Name	Female Presence Average Cover	Female Presence Count	Female Presence Percent Frequency	Female Absence Average Cover	Female Absence Count	Female Absence Percent Frequency
<i>Acer rubrum</i>	Red Maple	0.12	27	71.05	0.064	9	64.29
<i>Andropogon sp.</i>	Unknown Andropogon	0.023	12	31.58	0.047	4	28.57
<i>Cyrilla racemiflora</i>	Ti-ti	0.001	1	2.63	0.014	1	7.14
<i>Gelsemium sempervirens</i>	Carolina Jessamine	0.012	10	26.32	0.005	3	21.43
<i>Ilex glabra</i>	Gallberry	0.037	20	52.63	0.026	5	35.71
<i>Ilex opaca</i>	American Holly	0.009	5	13.16	0.05	4	28.57
<i>Lindera melissifolia</i>	Pondberry	0.269	38	100	0.406	14	100
<i>Liquidambar styraciflua</i>	Sweetgum	0	0	0	0.007	1	7.14
<i>Litsea aestivalis</i>	Pondspice	0.003	2	5.26	0	0	0
<i>Lyonia lucida</i>	Fetterbush	0.016	1	2.63	0.03	3	21.43
<i>Magnolia virginiana</i>	Sweetbay	0.011	2	5.26	0.018	3	21.43
<i>Nyssa biflora</i>	Swamp Black Gum	0.027	16	42.11	0.009	2	14.29
<i>Persea palustris</i>	Swamp Bay	0.062	18	47.37	0.033	5	35.71
<i>Pinus taeda</i>	Loblolly Pine	0.054	27	71.05	0.125	12	85.71
<i>Quercus sp.</i>	Unknown Oak	0.002	4	10.53	0.001	1	7.14
<i>Rhexia sp.</i>	Unknown Rhexia	0	1	2.63	0	0	0
<i>Rubus sp.</i>	Unknown Rubus	0.001	2	5.26	0	0	0
<i>Smilax glauca</i>	Whiteleaf Greenbriar	0.018	20	52.63	0.037	9	64.29
<i>Smilax laurifolia</i>	Blaspheme-vine	0.006	8	21.05	0.026	4	28.57
<i>Smilax rotundifolia</i>	Common Greenbrier	0.048	21	55.26	0.047	4	28.57
<i>Taxodium ascendens</i>	Pond-cypress	0.033	11	28.95	0.003	1	7.14
<i>Toxicodendron radicans</i>	Poison-Ivy	0	1	2.63	0	0	0
Unknown Poaceae sp.	N/A	0.011	6	15.79	0.004	1	7.14
Unknown Cyperaceae sp.	N/A	0.001	1	2.63	0.006	1	7.14
<i>Vaccinium corymbosum sensu lato</i>	Smooth Highbush Blueberry	0.061	20	52.63	0.124	10	71.43
<i>Woodwardia virginica</i>	Virginia Chain Fern	0.033	7	18.42	0.048	6	42.86

Table 19. Indicator species of *Lindera melissifolia* female presence or absence (including *L. melissifolia* percent cover as a factor). Taxon concepts follow those in Weakley (2011).

Scientific Name	Presence or Absence	Indicator Value (IV)	Mean	Standard Deviation	p value
<i>Acer rubrum</i>	Presence	46.2	42.4	6.31	0.237
<i>Andropogon sp.</i>	Absence	19.2	23.3	6.52	0.7
<i>Cyrilla racemiflora</i>	Absence	6.8	5.5	2.82	0.265
<i>Gelsemium sempervirens</i>	Presence	18.5	19.8	6.12	0.545
<i>Ilex glabra</i>	Presence	30.8	32.7	7.02	0.531
<i>Ilex opaca</i>	Absence	24.1	14.8	5.4	0.046
<i>Lindera melissifolia</i>	Absence	60.1	54.3	3.23	0.054
<i>Liquidambar styraciflua</i>	Absence	7.1	3.8	2	0.269
<i>Litsae aestivalis</i>	Presence	5.3	5.6	2.92	0.802
<i>Lyonia lucida</i>	Absence	14	8.7	3.84	0.054
<i>Magnolia virginiana</i>	Absence	13.5	9.8	4.22	0.114
<i>Nyssa biflora</i>	Presence	31.4	24.9	6.5	0.153
<i>Persea palustris</i>	Presence	30.9	30.3	6.89	0.384
<i>Pinus taeda</i>	Absence	59.8	46.2	6.66	0.039
<i>Quercus sp.</i>	Presence	7.2	10	4.21	0.841
<i>Rhexia sp.</i>	Presence	2.6	3.9	2.02	1
<i>Rubus sp.</i>	Presence	5.3	5.8	2.22	0.602
<i>Smilax glauca</i>	Absence	43.4	36.5	6.89	0.162
<i>Smilax laurifolia</i>	Absence	23.5	18.7	6	0.171
<i>Smilax rotundifolia</i>	Presence	27.9	32.8	7.2	0.71
<i>Taxodium ascendens</i>	Presence	26.7	18.4	5.9	0.098
<i>Toxicodendron radicans</i>	Presence	2.6	3.8	1.99	1
<i>Unknown Poaceae sp.</i>	Presence	11.9	12.5	4.87	0.491
<i>Unknown Cyperaceae sp.</i>	Absence	6.5	5.7	2.62	0.264
<i>Vaccinium corymbosum sensu lato</i>	Absence	47.7	37.5	7.02	0.097
<i>Woodwardia virginica</i>	Absence	25.3	19.8	6.09	0.173

Table 20. Indicator species of *Lindera melissifolia* female presence or absence (without including *L. melissifolia* percent cover as a factor). Taxon concepts follow those in Weakley (2011).

Scientific Name	Presence or Absence	Indicator Value (IV)	Mean	Standard Deviation	p value
<i>Acer rubrum</i>	Presence	46.2	42.5	6.43	0.251
<i>Andropogon sp.</i>	Absence	19.2	23.3	6.52	0.694
<i>Cyrilla racemiflora</i>	Absence	6.8	5.5	2.77	0.262
<i>Gelsemium sempervirens</i>	Presence	18.5	19.6	5.93	0.539
<i>Ilex glabra</i>	Presence	30.8	32.6	7.05	0.511
<i>Ilex opaca</i>	Absence	24.1	14.9	5.35	0.045
<i>Liquidambar styraciflua</i>	Absence	7.1	3.9	2.01	0.272
<i>Litsae aestivalis</i>	Presence	5.3	5.5	2.77	0.795
<i>Lyonia lucida</i>	Absence	14	8.7	3.82	0.056
<i>Magnolia virginiana</i>	Absence	13.5	9.9	4.25	0.115
<i>Nyssa biflora</i>	Presence	31.4	24.9	6.44	0.155
<i>Persea palustris</i>	Presence	30.9	30.4	6.89	0.393
<i>Pinus taeda</i>	Absence	59.8	46	6.73	0.041
<i>Quercus sp.</i>	Presence	7.2	10	4.21	0.834
<i>Rhexia sp.</i>	Presence	2.6	3.8	1.96	1
<i>Rubus sp.</i>	Presence	5.3	5.9	2.28	0.584
<i>Smilax glauca</i>	Absence	43.4	36.5	6.95	0.163
<i>Smilax laurifolia</i>	Absence	23.5	18.6	5.81	0.16
<i>Smilax rotundifolia</i>	Presence	27.9	33	7.22	0.725
<i>Taxodium ascendens</i>	Presence	26.7	18.4	5.75	0.099
<i>Toxicodendron radicans</i>	Presence	2.6	3.8	1.99	1
<i>Unknown Poaceae sp.</i>	Presence	11.9	12.5	4.91	0.496
<i>Unknown Cyperaceae sp.</i>	Absence	6.5	5.7	2.66	0.27
<i>Vaccinium corymbosum sensu lato</i>	Absence	47.7	37.5	7.2	0.098
<i>Woodwardia virginica</i>	Absence	25.3	19.8	6.35	0.182

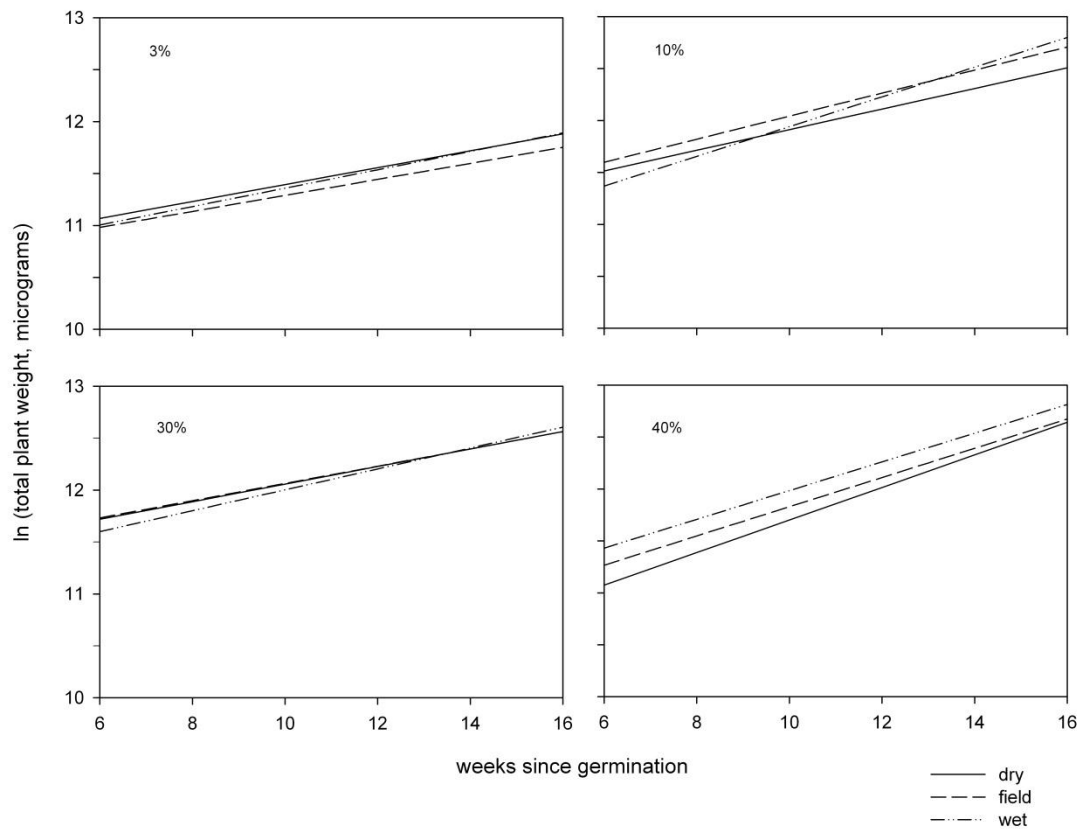


Figure 1. Within-light treatment effects of soil moisture on *Lindera melissifolia* ln-transformed plant mass ( $\mu\text{g}$ ) over time.



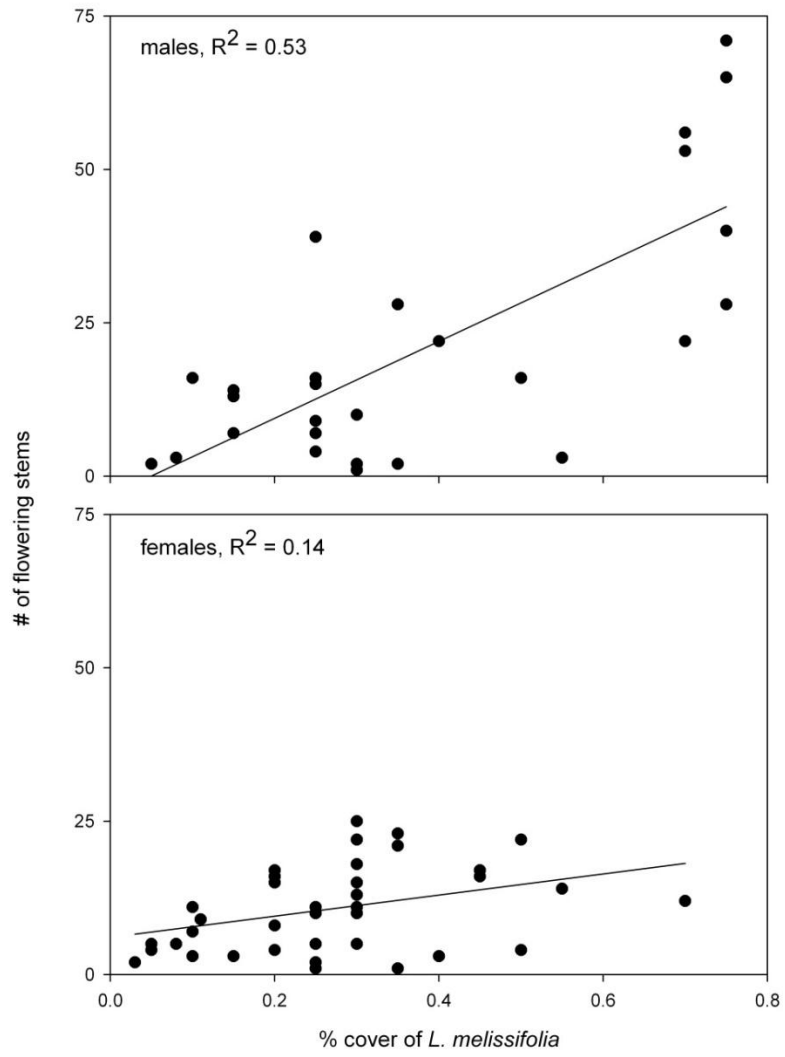


Figure 2. Relation of male and female flowering stems of *Lindera melissifolia* to percent cover