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SEXUAL DIMORPHISM AND INTERSEXUAL DIFFERENCES IN RESOURCE ALLOCATIONS OF A DIOECIOUS SHRUB, *LINDERA MELISSIFOLIA* (WALT.) BLUME.

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ABSTRACT

Morphometric data were gathered to make intersexual comparisons on the morphology and reproductive resource allocation patterns of the rare, dioecious shrub, *Lindera melissifolia*. Females produced significantly fewer flowers and leaves than did males. No other significant differences could be detected in morphology. Female "clones" exhibit low area coverage and low stem density, which suggests higher costs of reproduction. If this is the case, the deficits produced in resource allocations directed toward sexual reproduction seem to result in increased mortality and/or reduced vegetative reproduction.

INTRODUCTION

In some dioecious plant species there may be marked differences between males and females due to their differential costs of reproduction (Lloyd and Webb, 1977; Meagher and Antonovics, 1982). Females tend to suffer more in normal vegetative growth when they sexually reproduce because it is more metabolically expensive (Putwain and Harper, 1972; Lloyd and Webb, 1977; Hoffmann, 1981; Meagher and Antonovics, 1982; Agren, 1988; Lovett Doust and Lovett Doust, 1988). One remarkable adjustment to the fact that females do have a greater cost in sexual reproduction was found in the case of *Simmondsia chinensis*. The females of this species have developed mechanisms for optimizing water, carbon, and nutrient use. They have allowed less resources to stem biomass but have developed larger leaves in order to maintain photosynthetic levels. They have developed a more open canopy than males with less vegetative biomass and have thickened their leaves for maximum water storage (Wallace and Rundel, 1979). This has allowed the sexes to remain relatively equal.

Another interesting adjustment exhibited by some species in response to reproductive resource allocations is the ability of individuals to switch in either direction between a male phase and female phase. Schlessman (1987) observed gender modification in *Panax trifolium* to be connected to the amount of stored resources available for the maturation of fruit. Policansky (1987) found that *Arisaema triphyllum* could "choose" their sex based on the size of the individual, with the larger individuals becoming females due to their greater reproductive potential.

The purpose of this study was to make intersexual comparisons on the morphology of the dioecious shrub, *Lindera melissifolia*, and to examine reproductive resource allocations within the species.

THE SPECIES

Lindera melissifolia (Walt.) Blume, is a low shrub, 0.6-2 m tall. Plants are stoloniferous and generally grow in putative "clones" of numerous stems that individually are not highly branched. Flowers are dioecious and small; the flowers of both sexes are pale yellow in color, but female flowers are less conspicuous than male (Steyermark, 1949). Fruits are approximately 1.25 cm long at maturity and are of brilliant scarlet color. The flowers appear in March in Arkansas, while mature fruits are present in October (Tucker, 1983; Steyermark, 1949).

Pondberry, listed as endangered by the U.S. Fish and Wildlife Service, occurs across the southeastern section of the country with reported occurrences in North Carolina, Georgia, Mississippi, Missouri, Tennessee, and Arkansas. It has apparently been extirpated from

Alabama, Florida, and Louisiana (Tucker, 1983). Locally, pondberry occurs in topographically isolated depressions in dunefields extended across eastern Arkansas and into southeastern Missouri (Wright, 1989b). Generally, these depressions are inundated in winter and early spring, with the water receding during the early portion of the growing season (Tucker, 1983). Wright (1989a) observed that the frequency and size of single-sex "clones" suggests that sexual reproduction may be ineffective.

STUDY SITE

The study site consists of a large undisturbed population of pondberry growing in a dunefield depression northeast of Swifton, Jackson County, Arkansas. The depression encompasses approximately 10,000 m² and contains 11 single-sex stands (hereafter termed "clones") of pondberry; 6 male and 5 female (Fig. 1). The male "clones" collectively cover an area of 3,262 m² with individual "clones" ranging in area from 21 m² to 1211 m². The female "clones" collectively cover an area of 155 m² with individual "clones" ranging in area from 1 m² to 95 m².

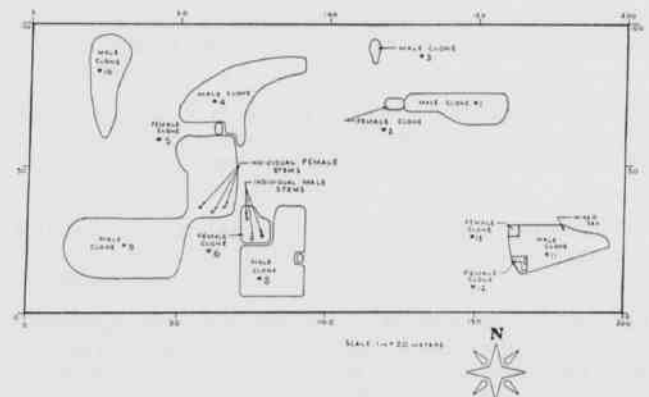


Figure 1. Map of study site.

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MATERIALS AND METHODS

FIELD MORPHOLOGICAL MEASUREMENTS AND OBSERVATIONS

On March 18, 1989, morphological measurements were taken from 397 individual stems. Six 1 x 1 m quadrats were randomly constructed within each "clone". Nine of the 11 "clones" were sampled; "clones" 10 and 11 were censused due to their small size. Measurements were taken from 4 flowering and 4 vegetative stems from each quadrat. Vegetative stems in "clones" where all flowering stems were of one sex were presumed to be one of the same sex, a procedure followed by Agren (1988) in a study of *Rubus chamaemorus*. The process of stem selection was randomized by selecting the flowering and vegetative stems nearest each corner of the quadrat. In the same quadrats, all stems were counted to determine stem density.

The height of each stem was measured from the ground to the tip of the tallest terminal branch. The living height of each stem was measured from the ground to the beginning of winter dieback (stems can experience some dieback but resume growth in spring) (Steyermark, 1963). The number of terminal branches was determined for each stem, as well as the number of flowers.

On May 6, 1989, morphological measurements were taken from the leaves of 162 individual stems; 81 male and 81 female. Stems were randomly selected from male "clones" 4, 8, and 9 and female "clones" 13, 5, and 6 at fixed intervals along a randomly constructed transect through each "clone". The number of leaves from the lowest terminal branch of the lowest main branch of each stem was counted. The length from the base of the blade to the apex, width at the widest point, and petiole length of the third fully expanded leaf of the lowest terminal branch of the lowest main branch on each stem were measured.

On May 23, 1989 fifty female stems, from within the population, were marked in order to determine if *Lindera melissifolia* possesses the capability to change sexual state from female to male.

DESTRUCTIVE HARVESTS

On March 18, 1989 a random sample was made of 40 stems, 23 male and 17 female, from widely distributed areas of the population. The stems were detached at ground level and brought back to the laboratory intact. Stems were dried for 24 hours at 75 °C, then weighed to obtain total biomass. The number of annual growth rings was counted and base diameter measured for each stem.

RESULTS

SEX CHANGE DATA

On March 16, 1990 the 50 marked female stems were examined and all flowering stems were determined to be female.

STEM DENSITY, TOTAL HEIGHT, LIVING HEIGHT, NUMBER OF BRANCHES, AND FLOWER NUMBER

In order to examine intersexual differences only, the data from all male "clones" were pooled, as were the data from female "clones". Mean stem density of all male "clones" was 14.11 ± 0.87 SE/m². For all female "clones" mean stem density was 8.80 ± 1.45 SE/m² ($P < .01$, t-test).

Multivariate tests of significance conducted between flowering and vegetative stems among total height, living height, and number of branches using the SPSS-X MANOVA procedure (SPSS, 1983) reflected a significant difference in the 2 groups ($P < .001$). Univariate F-tests reflected significant differences ($P < .001$) for each character measured between flowering and vegetative stems.

In order to determine if there were any intersexual differences in vegetative and flowering stems, multivariate tests of significance for sex by status (flowering and vegetative) among total height, living height, and number of branches were conducted using the SPSS-X MANOVA

procedure. No significant differences were detected. Since there were no significant differences between sexes among flowering and vegetative stems, the 2 groups were pooled and the population was examined only for intersexual differences.

Multivariate tests of significance conducted between sexes among total height, living height, number of branches, and flower number, using the SPSS-X MANOVA procedure, reflected a significant difference in the 2 groups ($P < .01$). Univariate F-tests reflected a significant intersexual difference ($P < .01$) in the number of flowers per stem. Female stems had significantly fewer flowers than did male stems (mean \pm SE: female 29.5 ± 4.3 , $n = 57$; male 623.0 ± 7.9 , $n = 96$; $P < .01$). No significant differences were found in total height, living height, or number of branches.

LEAF LENGTH, LEAF WIDTH, PETIOLE LENGTH, AND LEAF NUMBER

Multivariate tests of significance conducted between sexes among leaf length, leaf width, petiole length, and leaf number, using the SPSS-X MANOVA procedure, reflected a significant difference in the 2 groups ($P < .05$). Univariate F-tests reflected a significant intersexual difference ($P < .01$) in the number of leaves per branch. Female branches had significantly fewer leaves than did male branches (mean \pm SE: female 6.1 ± 0.1 , $n = 81$; male 6.6 ± 0.1 , $n = 81$; $P < .01$). No significant differences were found in leaf length, leaf width, or petiole length.

TOTAL BIOMASS, STEM DIAMETER, AND RING NUMBER

Descriptive statistics and t-tests were conducted for total biomass, stem diameter, and ring number using the StatPac Gold Statistical Analysis Package (1987).

The mean total biomass of stems harvested was (mean \pm SE): female 9.04 ± 1.06 g, $n = 17$; male 12.40 ± 1.7 g, $n = 23$. The mean stem diameter of stems harvested was: female 5.1 ± 0.3 cm, $n = 17$; male 5.7 ± 0.3 cm, $n = 23$. The mean ring number of stems harvested was: female 2.8 ± 0.2 , $n = 17$; male 3.3 ± 0.3 , $n = 23$. The descriptive statistics suggest that male stems have greater total biomass, greater ring number and larger stem diameter; however, multivariate tests of significance conducted between sexes among these characters, using the SPSS-X MANOVA procedure, found no significant differences. A one tailed t-test between sexes demonstrated male stems to have a significantly greater number of annual growth rings than female stems ($t = 1.93$, $P < .05$).

DISCUSSION

Female stems that were marked and re-examined in the subsequent season showed no evidence of sex change.

The only significant intersexual differences, among the morphometric characters measured, that might constitute sexual dimorphism in *Lindera melissifolia* were flower number and leaf number. Male stems in the population have over twice the number of flowers as females; in addition, females develop fewer leaves per branch than do males. What, if any, is the significance of these findings in relation to the phenology of reproductive resource allocations within the species?

Obviously, males will not incur any reproductive expenditure beyond flowering (Gross and Soule, 1981). Females, on the other hand, must endure the added reproductive costs of fruit production, making the total female reproductive effort potentially greater than that of males. This being the case, a male-biased floral sex ratio would be beneficial to the female, which has allocated a substantially greater amount of resources to each individual flower. Darwin (1877) and several later authors have suggested that in many species, females spend more resources on fruiting and flowering than males do on flowering (Barrett and Helenrum, 1981). Lloyd and Webb (1977) pointed out that selection could cause females to spend proportionately less of their resources on sexual reproduction by producing fewer flowers than males. In other words, differences between the sexes could adapt males and females to their distinct reproductive roles.

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Leaf number and size may reflect differences in resource allocations. Females of dioecious species could conceivably accommodate higher reproductive expenditures by allocating resources, possibly used by males to produce a greater number of flowers, to the production of leaves and other photosynthetic structures during the growing season (Gross and Soule, 1981; Lloyd and Webb, 1977). This is not the case with *Lindera melissifolia* in which females produced significantly fewer leaves per branch than did males, with no significant differences in leaf size or branch number. This would tend to place females at a disadvantage having less photosynthetic surface with which to meet higher reproductive expenditures. A similar situation is found in *Rubus chamaemorus* in which fruit-producing female ramets formed leaves that were 10-25% smaller than the leaves produced by male ramets and by female ramets whose flowers had been excised to prevent fruit development (Agren, 1988).

Although not statistically significant, there appears to be a trend for male stems to have a greater total biomass, more annual growth rings, and a larger diameter. This trend of "male vigor" need not absolutely be attributed to intersexual reproductive resource allocations, since biomass is not necessarily distributed in equivalent ways in plants, and may often vary between the sexes among dioecious species (Agren, 1988; Abrahamson and Caswell, 1982; Wallace and Rundel, 1979).

Although morphological differences, aside from flower and leaf number, cannot be detected from the characters examined in this study, the female may still bear a heavier reproductive burden than the male. It appears that sexual reproduction in *Lindera melissifolia* is ineffective, evidenced by the presence of large single-sex "clones" (Wright, 1989a). The study population has a highly male-biased sex ratio, with male "clones" covering 95.55% of the total area and having a mean stem density 1.6 times that of the female "clones". This appears to be an extreme case in comparison with other dioecious species. Other male:female ratios reported in the literature include *Ilex montana*, 1.35:1 (Cavigelli *et al.*, 1986) and *Compsoeura sprucei*, 1.25:1 (Bullock, 1982). Bullock (1982) suggested that biased sex ratios may sometimes be the result of increased growth and vigor in males, and not increased mortality of females. Cavigelli *et al.* (1986) indicated that spatial segregation is a secondary implication of sexual dimorphism. Bawa and Opler (1977) pointed out that spatial segregation could be caused by vegetative multiplication, and that segregation of the sexes could diminish sexual reproduction because the probability of finding a mate is fixed by location. Taking these findings into consideration, it seems likely that, if indeed reproductive costs are greater for the females, the deficits are felt predominantly at the level of the "clone" rather than at the individual stem. The only case of deficits resulting from increased reproductive expenditures possibly being reflected at the level of the stem is that of leaf number. Since the time of leaf production coincides with the enlargement of fruit, females may produce fewer leaves as a result of competition for resources between the developing leaves and fruit. Greater reproductive expenditures by females may result in higher stem mortality and/or reduced vegetative stem production (Lovett Doust and Lovett Doust, 1988; Hancock and Bringham, 1980; Grant and Mitton, 1979). Elevated costs of reproduction are commonly expressed at the "clonal" level through male-biased sex ratios (Lovett Doust and Lovett Doust, 1988; Lloyd and Webb, 1977; Sohn and Policansky, 1977). Males can sometimes tolerate high densities better than females (Lovett Doust *et al.*, 1987).

If females allocate a greater proportion of their available energy to reproduction than do males, it stands to reason that females would have a smaller proportion of energy available for growth and maintenance (Gross and Soule, 1981; Harper and Ogden, 1970). This energy deficit would be compounded in *Lindera melissifolia* by decreased leaf production in females resulting in fewer photosynthetic structures which, if present, might help bear the cost of fruit production. If these energy deficits are not felt at the level of the stem, it follows that there could be reduced vegetative reproduction at the "clonal" level. In contrast, a lower reproductive effort on the part of males would leave more energy resources available for increased vegetative reproduction, thus widening the male-biased sex ratio (Lloyd and Webb, 1977).

Lovett Doust and Lovett Doust (1988) suggest that female stems may sequester resources from connected vegetative stems to pay the increased costs of reproduction, resulting in higher mortality and lower survivor-

ship within female "clones". Hancock and Bringham (1980) corroborate this, pointing out that since pistillate plants are devoting a higher proportion of their total biomass to sexual reproduction than males (at the expense of root and shoot production), they may suffer higher mortality. Our measurements of stem dieback, however, failed to reveal significant differences between sexes.

SUMMARY AND CONCLUSIONS

Females of the dioecious shrub, *Lindera melissifolia* produce significantly fewer flowers than do the males of the species. This probably entails a selective advantage, since females tend to have a higher resource expenditure per flower due to the energy required for fruit production. Females also produce fewer leaves than males, incurring an even greater disadvantage in the absence of photosynthetic structures that could help bear the additional costs of fruiting.

Aside from flower and leaf number, no sexually dimorphic characters were found in this study.

There is lower area coverage by and lower stem density within female "clones", as compared to males. If, indeed, the cost of reproduction is greater for the female than for the male, the deficit in reproductive resource allocation is reflected at the "clonal" level through increased mortality or decreased survivorship and/or reduced vegetative reproduction.

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