SIZE DIFFERENCES, SEX RATIO, AND SPATIAL DISTRIBUTION OF MALE AND FEMALE WATER TUPELO, NYSSA AQUATICA (NYSSACEAE)¹

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Many dioecious plant species show spatial segregation of the sexes along a gradient of habitat quality. This study explores the spatial distribution and size of male and female Nyssa aquatica (water tupelo) trees along a water depth gradient. Individuals were mapped to determine the spatial distribution of male and female trees and the relationship between distribution of males and females and water depth. Nearest neighbor analysis indicated that males and females were randomly distributed in space. Comparisons among plots, however, indicated that there were more male trees in the shallowest plot. Height and diameter at breast height were measured for each tree. Males were significantly larger in height and basal area than females. Coring of male and female trees indicated that size differences between the sexes cannot be attributed to age differences, suggesting that male water tupelo trees allocate more resources to growth than do female trees.

Studies of dioecious species reveal that male and female plants are distributed randomly in some species (e.g., Bawa and Opler, 1977; Melampy and Howe, 1977; Hancock and Brinthurst, 1980; Armstrong and Irvine, 1989), while in others, individuals of the same sex occur in clusters (Freeman, Killof, and Harper, 1976; Lovett Doust and Cavers, 1982; Sakai and Oden, 1983; Freeman and Vitale, 1985; Dawson and Bliss, 1989). A random distribution of males and females has been suggested to be optimal for distribution of pollen and dispersal of seeds (Bawa and Opler, 1977). This random distribution facilitates pollen reaching female flowers and reduces mass predation of concentrated seeds. Clustering of male and female individuals of a dioecious species into separate patches has been attributed to differences in resource requirements for fruit-producing and nonfruit-producing individuals. Many studies document that females contribute a greater amount of energy to sexual reproduction than males (Darwin, 1877; Schaffner, 1922; Puttwain and Harper, 1972; Lloyd, 1973; Onyekwelu and Harper, 1979; Wallace and Rundel, 1979; Conn and Blum, 1981; Gross and Soule, 1981; Bierzynchudek, 1982; Lovett Doust and Lovett Doust, 1983; Charlesworth and Charlesworth, 1987; Popp and Reintartz, 1988; Armstrong and Irving, 1989; Cipollini and Stiles, 1991). Thus, in cases where the sexes are found to be clustered in different habitat types, female individuals tend to be clustered in more resource-rich areas (Freeman, Killof, and Harper, 1976; Freeman, Harper, and Charnov, 1980; Dawson and Bliss, 1989).

Mechanisms that could result in clustering of same sex individuals include differential mortality of males and females in different habitats, the ability to switch sex based on environmental conditions, maternal adjustment of the sex ratios, active habitat selection, and different requirements of male and female seeds (Bierzynchudek and Eckhart, 1988).

Differences between the sexes in energy allocated to sexual reproduction may also be reflected in different sizes of equal-aged individuals. In numerous perennial dioecious plant species, males are significantly larger than females and the sex ratio is biased toward males (reviewed in Lloyd and Webb, 1977). Lower energy expenditures for reproduction in males would allow greater allocation to growth and result in competitive success over females. In one plant species, males have been shown to be more physiologically vigorous than females during early flowering (Tiedeman, McArthur, and Freeman, 1987). This superior competitive ability could result in males surviving longer than females; thus a larger proportion of males in the population.

The object of this study was to determine whether male and female water tupelo trees show different habitat preferences and whether the two sexes allocate different amounts of available resources to growth. We did this by examining sizes and spatial association of male and female tupelo along a water depth gradient in a southeastern tupelo-cypress floodplain forest.

MATERIALS AND METHODS

The study was conducted in a tupelo-cypress swamp forest in the floodplain of the Savannah River, Barnwell County, South Carolina. Water tupelo (Nyssa aquatica L.) is the most abundant and dominant species in this forest. It averages 900 stems per hectare and constitutes approximately 75% of the total basal area. Baldcypress (Taxodium distichum L. Rich.) averages 300 stems per hectare, and there is a sparse subcanopy of Carolina ash (Fraxinus caroliniana Mill.), Elm (Ulmus spp.) and red maple (Acer rubrum L.). The area was selectively logged for cypress at the turn of the century and possibly logged for tupelo in the early 1900s (John Hatcher, Aiken, SC, personal communication).

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Three arbitrarily chosen 50-m × 50-m plots were established in the swamp forest. Height, measured by a hypsometer, and diameter at breast height (dbh) were recorded for individual trees within the plots. Each 50-m × 50-m plot was divided into quarters, and the position of each tree with dbh greater than 5 cm was mapped by compass and tape from the center of each subplot. Water depth was measured at each point on a 5-m × 5-m grid in each 50-m × 50-m plot. Sex of trees was determined by observing spring flowering. A small number of individuals did not flower; they were classified as juveniles. Analyses were run with and without juveniles. Results were similar; only those without juveniles will be presented. Analysis of variance was used to compare height and basal area (BA) of males and females (SAS Institute, Inc., 1989).

Large-scale spatial segregation between males and females was assessed in three ways. First, a chi-square test was used to compare the sex ratios between the plots with the shallowest and the deepest water depth. Second, an ordered chi-square test (Bartholomew, 1959) was used to test for a consistent trend in sex ratio with increasing water depth across the three plots. Third, the correlation between average water depth and proportion of males was computed at three spatial scales. The largest scale was the three 50-m × 50-m plots; smaller scales were constructed by dividing the large plots into 12, 25-m × 25-m subplots and 75, 10-m × 10-m subplots. At the largest scale, the three plots were independent, so the hypothesis that there was no correlation could be tested using standard tests. At smaller scales, plots were not independent, so there were no simple significance tests. Even so, the estimated correlation coefficient still measured the association between the two variables.

Small scale patchiness was tested using a modified version of Pielou's test of spatial segregation (Pielou, 1961). Pielou's test determines whether two species (in this instance sexes) are randomly located with respect to each other. Given the locations of all individuals in a plot, the nearest neighbor of each individual is determined. For our test, a 2 × 2 contingency table was constructed by classifying each individual by its sex and the sex of its nearest neighbor. If the two sexes were spatially segregated, the number of males with male nearest neighbors would be higher than expected, as would the number of females with female nearest neighbors.

Departure from spatial randomness was tested using P. Dixon's modified test (Dixon, 1992). Pielou's original test was not appropriate when all trees in a stand are mapped (Meagher and Burdick, 1980), while the modified test had the appropriate statistical properties (Dixon, 1992). In the modified test, the expected number of neighbors and their variances were calculated differently. If \( N_m \) and \( N_f \) were the number of males and females in the plot, respectively, then: the expected number of males with male neighbors was \( (N_m)(N_m - 1)/(N_m + N_f - 1) \); the expected number of males with female neighbors was \( (N_m)(N_f)/(N_m + N_f - 1) \); the expected number of females with male neighbors was \( (N_f)(N_m)/(N_m + N_f - 1) \); and the expected number of females with female neighbors was \( (N_f)(N_f - 1)/(N_m + N_f - 1) \). These expected frequencies could be used to calculate separate tests of the association of males with males and the association of females with females or to compute a 2 df test of overall association. The modified Pielou test was more informative biologically and had better statistical properties than the original test (see Dixon, 1992, for further discussion).

RESULTS

While the overall ratio of males to females in the total sampled area was 1:1, the proportion of males varied among the plots (Table 1). The sex ratio in plot 1, the deepest plot, had a significantly smaller proportion of males than plot 2, the shallowest plot (\( \chi^2 = 4.18, 1 \text{ df}, P = 0.041 \)). There was also a significant trend: the pro-
portion of males increased with decreasing water depth (Bartholomew test of trend in proportions, \( \chi^2 = 4.43, 1 \text{ df}, P = 0.037 \)). In all three plots, male trees had significantly greater BA (\( P < 0.001 \)) and were significantly taller than females (\( P < 0.01 \)) (Table 1).

The association between occurrence of male tupelo trees and shallow water disappeared at smaller spatial scales (Table 2). Water depth and percent male tupelos were highly correlated in the 50-m × 50-m plots, but only weakly correlated in the 25-m × 25-m subplots. Almost no correlation was found in the 10-m × 10-m subplots.

No significant departures from random association were found at the smallest spatial scale, i.e., between nearest neighbors (Table 3). A positive test statistic in the nearest neighbor tests indicates that individuals have nearest neighbors of the same sex more frequently than expected if sexes are randomly associated. The only large test statistic is +1.77 (\( P = 0.076 \)) for males in plot 2 (Table 3), which had more male neighbors than expected, but not significantly so. Half of the test statistics were negative, indicating that association with the same sex was just as frequent as association with the other sex. The lack of statistically significant associations indicated there was no evidence to reject random spatial distribution of sexes at small spatial scales.

**DISCUSSION**

Results of this study indicate that male tupelo trees are significantly larger than females and that the sexes show some evidence of segregation in relation to water depth. These results may both be related to differences in resource requirements of the sexes.

The difference in size is consistent with Lloyd and Webb’s (1977) prediction for dioecious species. Two possible explanations for the larger size of male trees are that they have faster growth rates or that males have the same growth rates but males survive longer than females. If males survive longer, we would expect the mean age of males in this population to be greater than the mean age of females. When 21 male and 21 female trees were cored, no significant difference was found between the number of rings on male and female cores (M. Shea, unpublished data), suggesting that there was no age difference between the sexes. Tupelo trees are difficult to age due to the likely presence of false rings (Phipps, 1985). However, if the sexes produce false rings with the same frequency, then equal numbers of rings indicate equal ages. This leads us to conclude that the size difference between males and females may be the result of faster growth rates in males, which may be a result of male trees allocating less energy to reproduction.

The larger size of male tupelo trees seen in this population may enhance long-range pollen dispersal. When male trees are taller, wind- and gravity-dispersed pollen will be more likely to reach female trees. Evidence suggests

| Table 4. Dioecious species in which segregation of the sexes has been demonstrated. Sources in parentheses indicate source of information on pollinators if different than primary source |
|---|---|---|---|
| **Species** | **Pollination syndrome** | **Method** | **Source** |
| *Salix arctica* | Wind, bees | Plot | Dawson and Bliss, 1989 |
| *Thalictrum dioicum* | Wind | NN | Melampy, 1981 |
| *Thalictrum polygamum* | Wind, insect | NN | Melampy, 1981 |
| *Chamaeletrum luteum* | Insect | NN | Meagher, 1980 (Meagher, 1986) |
| *Ephedra viridis* | Wind | Plot | Freeman, Killof, and Harper, 1976 |
| *Acer negundo* | Wind | Plot | Freeman, Killof, and Harper, 1976 |
| *Thalictrum fendleri* | Wind | Plot | Freeman, Killof, and Harper, 1976 |
| *Sarcobatus vermiculatus* | Wind | Plot | Freeman, Killof, and Harper, 1976 |
| *Distichlis spicata* | Wind | Plot | Freeman, Killof, and Harper, 1976 |
| *Acer saccharinum* | Wind | NN | Sakai and Oden, 1983 |
| *Populus tremuloides* | Wind | Plot | Grant and Mitton, 1979 |
| *Spinacia oleracea L.* | Wind | Plot | Onyekwelu and Harper, 1979 |
| *Ariskaema triphyllum* | Fungus gnats | NN | Lovett-Doust and Cavers, 1982 (Bierzychudek, 1982) |
| *Spinacea oleracea* | Wind | Plot | Freeman and Vitale, 1985 (Onyekwelu and Harper, 1979) |
| *Scheidea globosa* | Wind | Plot | Sakai and Weller, 1991 |
Table 5. Dioecious species in which the sexes appear to be randomly distributed

<table>
<thead>
<tr>
<th>Species</th>
<th>Pollination syndrome</th>
<th>Method</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Silene alba</td>
<td>Insect</td>
<td>Plot</td>
<td>Lovett Doust, O'Brien, and Lovett Doust, 1987</td>
</tr>
<tr>
<td>Myristica insipida</td>
<td>Beetle</td>
<td>NN</td>
<td>Armstrong and Irvine, 1989</td>
</tr>
<tr>
<td>Simmondsia chinensis</td>
<td>Wind, bees</td>
<td>Plot</td>
<td>Wallace and Rundel, 1979 (Niklas and Buchman, 1985)</td>
</tr>
<tr>
<td>Oxyris quadripartita</td>
<td>Flies</td>
<td>NN</td>
<td>Herrera, 1988 (Herrera, 1984)</td>
</tr>
<tr>
<td>Thapsia americana</td>
<td>Insect</td>
<td>NN</td>
<td>Melampy and Howe, 1977</td>
</tr>
<tr>
<td>Fragaria chiloensis</td>
<td>Bees</td>
<td>Other</td>
<td>Hancock and Brighurst, 1980 (Shoemaker, 1977)</td>
</tr>
<tr>
<td>Guarea lucii</td>
<td>Insect</td>
<td>NN</td>
<td>Bawa and Opler, 1977</td>
</tr>
<tr>
<td>Randia spinosa</td>
<td>Insect</td>
<td>NN</td>
<td>Bawa and Opler, 1977</td>
</tr>
<tr>
<td>Triplaris americana</td>
<td>Insect</td>
<td>NN</td>
<td>Bawa and Opler, 1977</td>
</tr>
<tr>
<td>Zanthoxylum setuliforme</td>
<td>Insect</td>
<td>NN</td>
<td>Bawa and Opler, 1977</td>
</tr>
<tr>
<td>Nyssa aquatica</td>
<td>Insect, wind</td>
<td>Plot</td>
<td>This paper</td>
</tr>
</tbody>
</table>

that wind contributes to the dispersal of water tupelo pollen (M. Shea and R. Sharitz, unpublished data).

We did not observe an overall male-biased sex ratio as predicted by Lloyed and Webb (1977) for dioecious species. This absence of a male-biased sex ratio may be due to the young age of the population, which was logged at the turn of the century. Perhaps there has not been sufficient time for a differential survival of males and females to be expressed.

Males and females are segregated in relation to water depth, but this segregation is only detectable at large spatial scales. Comparisons between the plots indicate that the proportion of males is greater in shallow plots. Figure 1 illustrates the distribution of males and females in the shallowest plot. On a fine scale, using a nearest neighbor analysis, water tupelo trees do not exhibit spatial segregation of the sexes. This demonstrates the need to be very careful to define an appropriate spatial scale if only one spatial scale is studied.

Previous studies of spatial segregation of the sexes have used either a nearest neighbor analysis or a comparison of plots (Tables 4, 5). The choice of method may influence whether a study detects spatial segregation. Comparison of plots was more frequent (ten out of 15) among studies that found spatial segregation. Nearest-neighbor analysis was more common (seven out of 11) among studies that did not detect segregation. This pattern may be due to the different spatial scales, different sample sizes or statistical power, or other biological differences (e.g., pollinators, see below) between the two groups of studies.

No evidence indicates that spatial segregation of the sexes results from competition between the sexes or that it is adaptive (Bierzychudek and Eckhart, 1988). Spatial segregation may benefit a population if it results in each sex occupying its optimal habitat; however, segregation may reduce the efficiency of pollen dispersal. Bawa and Opler (1977) suggest that random distribution of the sexes is ideal for pollen dispersal. It is interesting to compare the pollination syndromes of species that show spatial segregation between sexes to species that do not (Tables 4, 5). With few exceptions, segregated species are wind pollinated while unsegregated species are insect pollinated. Insect pollinators usually move short distances between near neighbors while foraging, transporting pollen short distances; whereas wind-transported pollen usually travels greater distances from the source (Levin and Kerster, 1974). Thus spatial segregation of the sexes may be more difficult to maintain in insect-pollinated species. It will be interesting to see if this strong correlation between clumping of the sexes and pollination syndrome is found in future work on dioecious species.

LITERATURE CITED


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