1986. Cavigelli, M., M. Poulos, E. P. Lacey and G. Mellon. Sexual dimorphism in a temperate dioecious tree, Ilex montana (Aquifoliaceae). American Midland Naturalist 115(2): 397-406.
Made available courtesy of University of Notre Dame: http://nd.edu/~ammidnat/
***Reprinted with permission. No further reproduction is authorized without written permission from the University of Notre Dame.
This version of the document is not the version of record.
Figures and/or pictures may be missing from this format of the document.***

Sexual Dimorphism in a Temperate Dioecious Tree, Ilex montana (Aquifoliaceae)

MICHEL CAVIGELLI
Department of Biology, Oberlin College, Oberlin, Ohio 44074

MARGARET POULOS
Department of Biology, Depauw University, Greencastle, Indiana 46135

ELIZABETH P. LACEY[1]
Department of Biology, University of North Carolina, Greensboro 27412

and

GARNETT MELLON
Department of Religion, University of Virginia, Charlottesville 22903

ABSTRACT: A study of a population of *Ilex montana* mountain winterberry showed a strongly skewed age distribution with few individuals reaching reproductive maturity. Sexual differences of the reproductive adults were manifested in several ways. The tertiary sex ratio of 436 trees was significantly male-biased; males produced more flowers per tree than did females, and there was a slight spatial segregation between males and females. However, males and females did not differ in estimated age and size distributions, nor did the proportion of males vary with density. The data suggest that females flower less often than do males and that microenvironmental variation influences the spatial patterning of sexes within populations of this temperate dioecious tree.

INTRODUCTION

Sexual dimorphism in plants has recently received much attention from evolutionary biologists. These biologists have been motivated in part by Fisher (1930), who argued that selection would favor a 1:1 sex ratio in sexually reproducing organisms when the cost of producing a male offspring equalled that of producing a female. Workers have attempted to test Fisher's hypothesis by determining the sex ratio of different dioecious plant species. Thus far, sex ratios seem to vary greatly among species and in some cases even within species (*see* review by Willson, 1983). Most empirical data come from tropical trees and temperate herbs, groups of plants with quite different life forms growing in quite different environments.

Deviations from the expected 1:1 sex ratio have usually been attributed to the differential cost of reproduction between sexes (Bateman, 1948). Because females contribute more to fruit production and embryo development, the cost of producing an offspring is assumed to be greater for females. Sexual differences in secondary sex characteristics have been adduced as evidence for this differential cost. For example, females often grow larger than do males before flowering (*e.g.*, Bullock and Bawa, 1981; Gross and Soule, 1981; Meagher and Antonovics, 1982), produce larger leaves (Wallace and Rundel, 1979), flower later in the growing season (*e.g.*, Putwain and Harper, 1972; Opler and Bawa, 1978; Bullock and Bawa, 1981), produce fewer flowers (Opler and Bawa, 1978; Hancock and Bringhurst, 1980; Barrett and Helenurm, 1981; Gross and Soule, 1981) and produce less nectar (Bawa and Opler, 1977; Bullock and Bawa, 1981). Other studies, however, show opposing patterns (*see* review by Lloyd and Webb, 1977). Evidence for the differential cost also comes from spatial patterns of males and females.

[1]Send all correspondence and reprint requests to: Elizabeth P. Lacey

Males and females are often spatially segregated (*e.g.*, Lloyd and Webb, 1977; Grant and Mitton, 1979; Meagher, 1980), and a few studies have shown that females are more abundant in "higher quality" microsites (Freeman *et al.*, 1976; Lloyd and Webb, 1977). Other studies, however, show no spatial segregation (*e.g.*, Bawa and Opler, 1977; Melampy and Howe, 1977). Bawa and Opler (1975) postulated that sexual differences in microsite preference should be lower in trees than in herbs because trees allocate relatively less energy to reproduction than do herbs. Thus, habitat preferences of trees may be detectable only between, rather than within, populations (Meagher, 1980). Though present studies support this trend (*e.g.*, Melampy and Howe, 1977; Opler and Bawa, 1978; Grant and Mitton, 1979), no studies permit a comparison of species growing in similar habitats in which the spatial scale is the same for both trees and herbs.

The inability to make comparisons between life forms growing in similar habitats motivated our study of the dioecious mountain winterberry *Ilex montana* Torr. & Gray (Aquifoliaceae). Our objectives were to determine the sex ratio and spatial association of males and females and to compare male and female size and age distributions and four components of reproduction. Our study provides information about sexual differences in a temperate dioecious tree, very few of which have been studied in this regard. Additionally, the data permit at least a preliminary comparison of dioecious life forms that grow in temperate woodlands.

METHODS

Ilex montana, commonly called mountain winterberry (Little, 1953), mountain holly or large-leaved holly, is a deciduous dioecious tree or shrub that grows on rich wooded mountainsides from New York to Louisiana (Small, 1933; Fernald, 1950; Little, 1953). Composed of tightly clumped ramets (usually 1-3, pers. observ. of the authors) radiating outward from a central axis, the tree can grow to $\cong$ 12 m tall. Plants flower in June, producing easily identifiable staminate or pistillate white flowers. Flowers either are clumped in axillary positions at the end of spur shoots produced the previous year or are found singly on new branches (Peattie, 1950). Insects probably pollinate the flowers because anthesis occurs after leaf expansion, making wind pollination unlikely. Also, flowers produce a pleasant fragrance. Casual observations detected no size differences between male and female flowers.

The *Ilex montana* population sampled was located at the University of Virginia's Mountain Lake Biological Station (elevation 1185 m) at the top of Salt Pond Mountain, near Pembroke, Giles Co., Va. Our experimental plot was a 0.77-ha trapezoidal area bordered on three sides by woodland paths and on the fourth side by a shallow drainage ditch connecting two ponds. All trees more than 20 cm tall within the plot were marked and sexed by flower type and were called adults. Though we decided to map all trees more than 20 cm tall, all trees were, in fact, at least several meters tall.

To examine the spatial association of males and females, we mapped the position of each individual. First, we divided the plot into 30 triangles and used 23 trees other than *Ilex* as aspices of the triangles. Then we measured the distances between adjacent apices and the distances between each winterberry and two neighboring apices. After transferring the map to graph paper we determined the Cartesian coordinates of each tree relative to the whole sample population. The map showed a strong gradient in tree density across the longer axis of the plot. Density dropped from approximately 38 trees to 0 trees per 0.1 ha in 130 m.

We used the map to test for spatial segregation of males and females. First, we divided the map into different quadrat sizes: 10 m x 10 m, 20 m x 20 m and 40 m x 40 m. The G^2 (log-likelihood ratio) test (Bishop *et. al.*, 1975) was used to test for heterogeneity of proportion of males at each quadrat scale. Because the plot was not rectangular, a few plants fell outside all quadrats and therefore were not included in the analysis; for example, 16 were not included in any 10 m by 10 m quadrat. Second, we performed a

nearest-neighbor analysis using the Monte Carlo simulation technique described by Meagher and Burdock (1980). One thousand trials of randomly assigning sexes to the mapped trees produced the (null) frequency distribution of G^2 needed to test whether sexes were positively or negatively associated with each other. We compared the observed G^2 with this null distribution. Third, we computed the distance between each nearest-neighbor pair. An analysis of variance tested whether sex of base plant and of neighbor influenced these distances. For all tests of spatial segregation, we considered only the reproductive adults.

To compare the size distributions of males, females and nonreproductive adults we recorded the diameter (at 20 cm) of each ramet of each adult at the time of mapping. These diameters were converted to cross-sectional areas, which were then summed over ramets for each plant. We did not measure ramets less than 40 cm tall because they constituted a miniscule portion of total plant biomass. Analysis of variance was used to determine whether sexes and reproductives vs. nonreproductives differed in cross-sectional area, our relative estimate of plant size.

For male and female reproductive output we focused on the trees rooted within a 134 m x 4 m belt transect that spanned the long axis of the plot. Number of flowers per fascicle and number of fascicles per branch were recorded for the lowest reproductive branch for each ramet of each tree. Using these data we calculated the number of flowers per lowest reproductive branch for each ramet and then summed over ramets within a tree. We also recorded the total number of flowering branches per ramet and tree. We defined a reproductive branch as a branch bearing one or more flowers. Twenty-seven flowering trees (16 males and 11 females) were measured, and all grew in the denser half of the transect.

Flower production was measured only on the lowest reproductive branch because higher branches were often beyond our reach. Although the lowest branch did not always reflect flower production on higher branches (pers. observ.) we did not believe that selection of the lowest branch would bias our results in favor of one sex. Both sexes have the same life form, and light seems to influence flower production of males and females similarly. For example, where the upper canopy was dense, *Ilex* trees formed a monolayer of branches, arising from reclining ramets. Branches and ramets in light gaps grew more vertically and seemed to produce many more flowers. Light gaps in the upper canopy most probably form independently of the *Ilex* beneath.

Finally, we estimated the age structure of the *Ilex* population from a 30-m portion (the denser end) of the belt transect. We counted all trees (even those less than 20 cm tall) rooted in this portion and counted the number of terminal bud scars on each individual less than 20 cm tall. Scar number served as our measure of age for these individuals. We also cored (approx. 15 cm aboveground) the largest ramet of 13 adults and used the number of growth rings as our estimate of minimum age for these adults. A regression of age on diameter using 10 seedlings and these 13 adults (Fig. 1) provided age estimates for adults too small to core and, in general, for all uncored adults in the whole experimental plot. We examined the total population age distribution for the 30-m portion of the transect and using analysis of variance compared the age distribution of males, females and nonreproductives for all adults in the experimental plot.

RESULTS

Four hundred and thirty-six adult *Ilex* trees were mapped. These adults represented a very small portion of the total population as evidenced by the age distribution of individuals in the 30-m portion of the belt transect (Fig. 2). In that portion, 656 of 668 plants (98%) were seedlings (Fig. 2). This skewed distribution seemed to typify the whole area.

Among the adults, there were 217 males, 161 females and 58 nonreproductives. The 1.35:1 male to female sex ratio showed a significantly higher proportion of males than females ($G^2 = 4.17$, $df = 1$, $p < 0.05$). Although males and females significantly sur-

passed nonreproductives in cross-sectional area, male size did not differ from female size (Fig. 3). Likewise, reproductives were significantly older than nonreproductives (mean age = 26 years), but males (mean = 37 years) and females (mean 34 years) did not differ significantly in estimated age (Fig. 4).

Males and females did show different reproductive patterns (Table 1). Females produced significantly fewer flowers than did males, and this difference is explained by a difference in flower number per fascicle. Female fascicles on average comprised only one flower whereas males comprised 2-3. Also, females produced one half as many fascicles as did males. Though this difference in fascicle number was not significant at the 0.05 level, the data plus casual observations suggest that a larger sample size would show that females also produce significantly fewer fascicles. Males and females did not differ in total number of reproductive branches per plant.

An analysis of the spatial association of reproductive adults showed a slight segregation of males and females. First, the proportion of males varied significantly among the

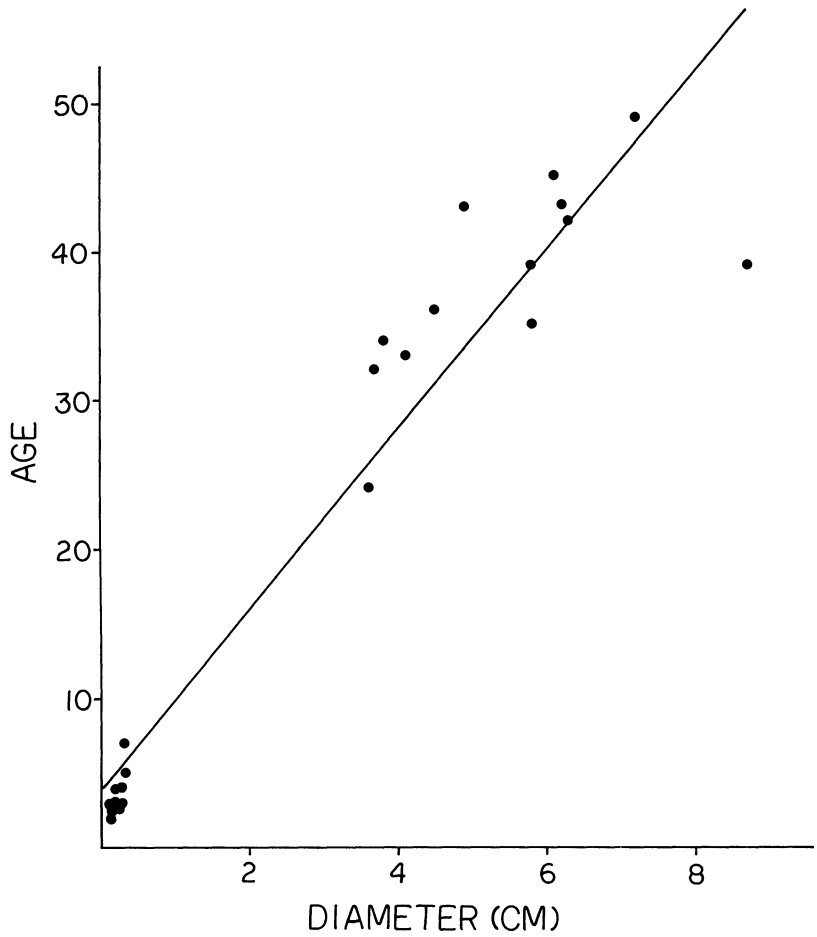

Fig. 1.—Correlation between age and diameter at 20 cm (or 2 cm for seedlings) of largest ramet per individual *I. montana* for 10 seedlings and 13 adults; y = 6.01 x + 4.06, r = .96. Age = no. of terminal bud scars for seedlings and no. of growth rings in tree cores and adults

100 m^2 quadrats but not among larger quadrats (Table 2). Second, the nearest-neighbor results showed that males were slightly more often found next to males than to females ($G^2 = 3.518$, df = 1, $p = 0.064$). Third, though males and females showed no difference in mean distance to their nearest neighbor, the distance did differ when the neighbor's sex was also considered (Fig. 5; Table 3). Female nearest-neighbor pairs were closer together than were male or male-female pairs. Thus males were more often found next to males but were farther apart than were neighboring females. Density was not a factor in determining this spatial pattern as evidenced by the absence of any correlation between the proportion of males in each 100 m^2 quadrat and quadrat density. Males and females were equally likely to be found in high or low density quadrats (Pearson product-moment correlation coef. = −0.045, $p = 0.75$, N = 53).

DISCUSSION

Our data show that *Ilex montana* populations can be quite dense and, as evidenced by the age distribution, suffer high mortality at young ages. Most individuals were 3-4 years old, and few survived past 10 years. Browsing, probably by white-tailed deer, *Odocoileus virginianus*, is likely contributing to this early mortality.

Of the 378 marked reproductive adults, 58% were males and 42% females. Male-biased sex ratios such as this one have been explained in several ways. Gametic and zygotic selection could both produce biased ratios (Opler and Bawa, 1978), though empirical studies more strongly support zygotic selective mechanisms. Skewed seedling (primary) sex ratios have not been detected in either *Chamaelirium luteum* (Meagher, 1981) or *Ilex opaca* (Clark and Orton, 1967). Several zygotic selective mechanisms exist. First, differential prereproductive mortality of the two sexes would produce a skewed adult (secondary) sex ratio. Females could suffer higher prereproductive mortality if they re-

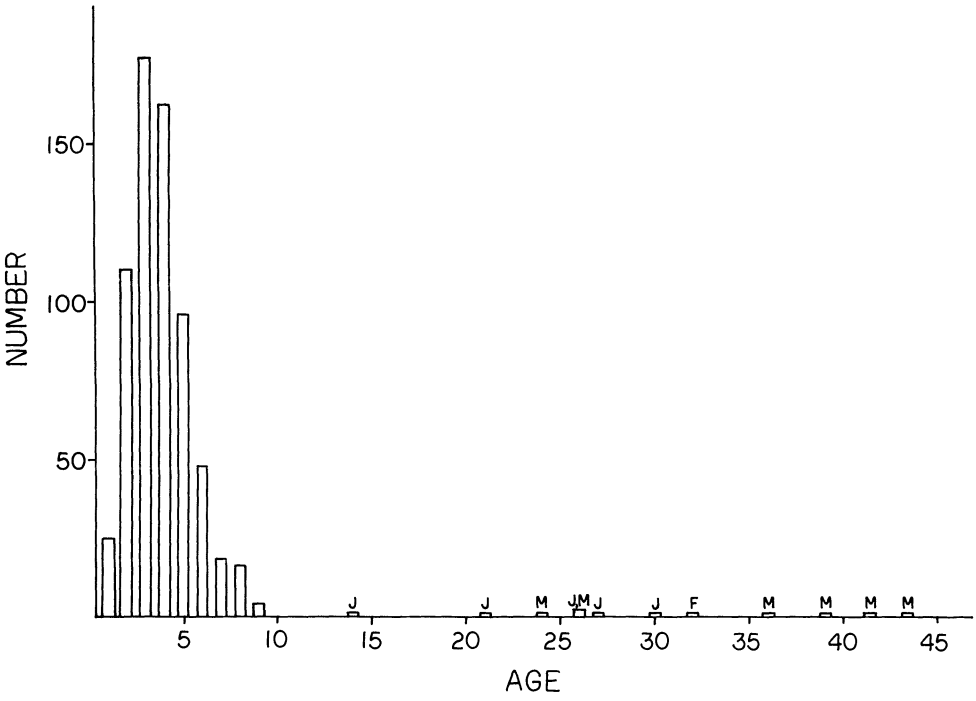

Fig. 2.—Age distribution of *I. montana* in 30 m x 4 m area. Seedlings were 1-9 years old. Adult sex is indicated above each tree: M = male, F = female, J = nonreproductive

quire more resources for survival. If such were the case in *Ilex*, we would expect to find males and females segregated spatially with females occupying "higher quality" microsites. In addition or instead, we would expect to find that males predominate in denser quadrats or that the distances between female nearest-neighbor pairs surpass those of male pairs. The data for *Ilex montana* do show slight spatial segregation between the sexes, but the males are not more abundant than females in denser quadrats, and distances between males surpass those between females. Therefore, the data do not support this hypothesis. Conversely, the data do not suggest higher prereproductive mortality for males.

Alternatively, females could delay reproduction until a later age (Opler and Bawa, 1978; Meagher and Antonovics, 1982), as in *Ilex opaca* (Clark and Orton, 1967), or females could suffer higher mortality after reproduction because they expend more energy producing offspring (Harris, 1968; Lloyd, 1973). Both possibilities would bias the

TABLE 1.—Reproductive traits and associated F statistics for 16 males and 11 females sampled from an *Ilex montana* population. Flower and fascicle number are based on data from the lowest reproductive branches for all ramets per tree. Statistics for mean flowers per fascicle were obtained by first averaging flower number for all fascicles counted per tree and then averaging these means over trees

Variable	Sex	Mean ± SE	Range	Coefficient of variation	F statistic	p
Flowers	M	233 ± 66	1-895	114	4.57	0.0426
	F	58 ± 19	1-171	107		
Fascicles	M	80 ± 20	1-247	97	2.41	0.1333
	F	40 ± 13	1-117	107		
Flowers Per fascicle	M	2.5 ± 0.2	1-3.6	34	16.42	0.0004
	F	1.4 ± 0.1	1-2.0	21		
Reproductive Branches Per tree	M	16 ± 3	1-46	82	0.85	0.3650
	F	12 ± 3	1-25	77		

TABLE 2.—G^2 values for proportion of males in different sized quadrats: N = number of quadrats in each test; NS = $p > .10$, *** = $p < 0.005$ (significant heterogeneity); df = N-1

Quadrat size	N	Plants per quadrat (Range)	G^2
10m × 10m	53	1-19	86.65^{***}
20m × 20m	12	2-49	15.63^{NS}
40m × 40m	2	54-130	0.09^{NS}

TABLE 3.—Distances between nearest-neighbors summarized in Figure 5: two-way ANOVA

Source	$F_{1,372}$	p
Sex of base plant	0.13	0.72
Sex of neighbor	2.12	0.15
Interaction	9.08	0.003

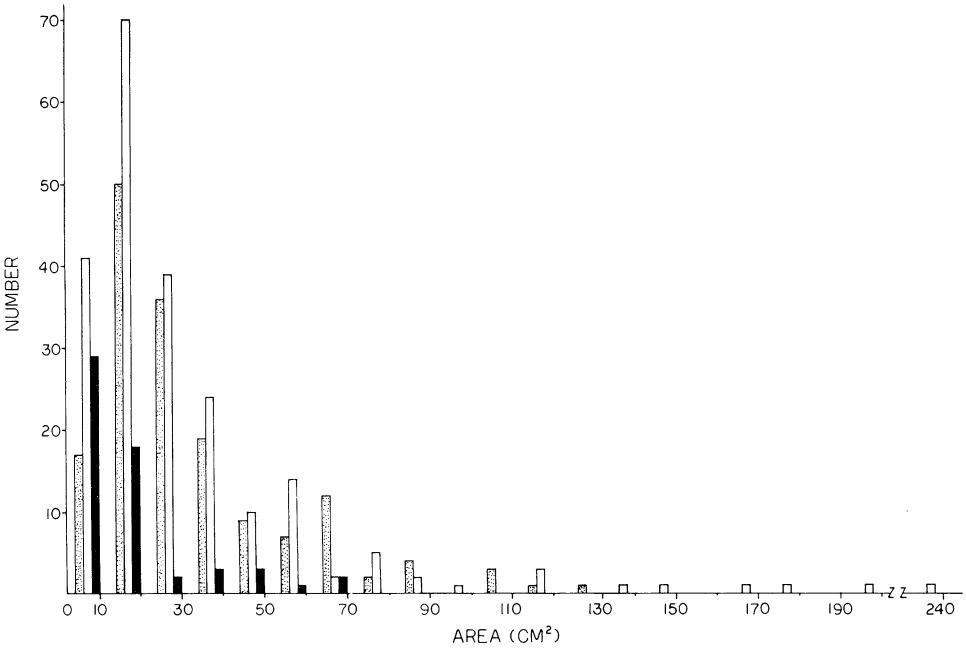

Fig. 3.—Size distribution of nonreproductive (solid), male (open) and female (hatched) adults in the experimental plot (.77 ha). Size is shown in terms of total cross-sectional area of all ramets per tree at 20 cm aboveground

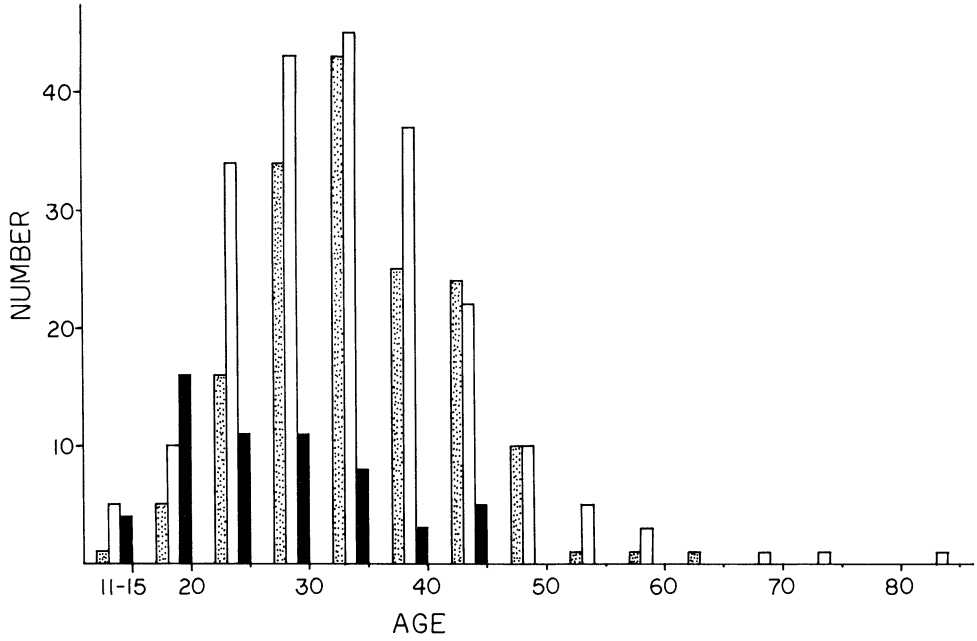

Fig. 4.—Estimated age distribution of nonreproductive (solid), male (open) and female (hatched) adults in the experimental plot. Age estimated from regression equation given in Figure 1

sex ratio in any one year toward males. Both, however, would also produce sexual differences in age or size distributions. If females delayed reproduction then the age or size distribution of females would lie to the right of the male distribution. Higher postreproductive mortality in females would narrow the female distribution and lower mean age or size of reproduction relative to mean age or size in males. No such differences were detected in our *Ilex* population; therefore, neither mechanism seems likely to have caused the observed male bias.

Finally because of the increased cost of reproduction, females may reproduce less often than do males (Bawa and Opler, 1978; Meagher and Antonovics, 1982). Meagher (1981) found that males of *Chamaelirium luteum* flower more often than do females, thus, the sex ratio in any year (*i.e.*, tertiary sex ratio) is more male-biased than the cumulative, or secondary sex ratio. Because this explanation predicts neither differences in age or size distributions nor spatial segregation between the sexes, it is best supported by our data. Thirteen percent of the adult *Ilex montana* in our plot did not flower in 1984. Their small size and age relative to flowering adults indicate that some are truly juveniles (*i.e.*, prereproductive). However, some may well be females that did not flower that year. If even half were female, then the male bias of the cumulative sex ratio would disappear. Thus, at this point, the data show a male-biased sex ratio for a single year (*i.e.*, skewed tertiary sex ratio), but do not rule out a 1:1 cumulative (secondary) sex ratio. We hypothesize that the tertiary bias will disappear over the years as nonflowering females eventually flower and that the primary and secondary sex ratios are, in fact, 1:1.

Sexual differences in energy allocation to reproduction in *Ilex* are reflected in ways other than through the life history traits just discussed (*i.e.*, mortality, time of reproduction). They are also reflected during reproduction through the partitioning of resources to various reproductive components. Bawa and Opler (1975) found that, for most dioecious trees in Costa Rica, flower number per fascicle, fascicle number per plant and sex ratio all contribute to an excess of staminate over pistillate flowers in a population for a given year. Female *Ilex montana* produce fewer flowers per fascicle and possible also fewer fascicles than do males. Thus, these data for a temperate tree are consistent with data from previous tropical studies. In *Chamaelirium luteum*, which grows in rich Eastern tem-

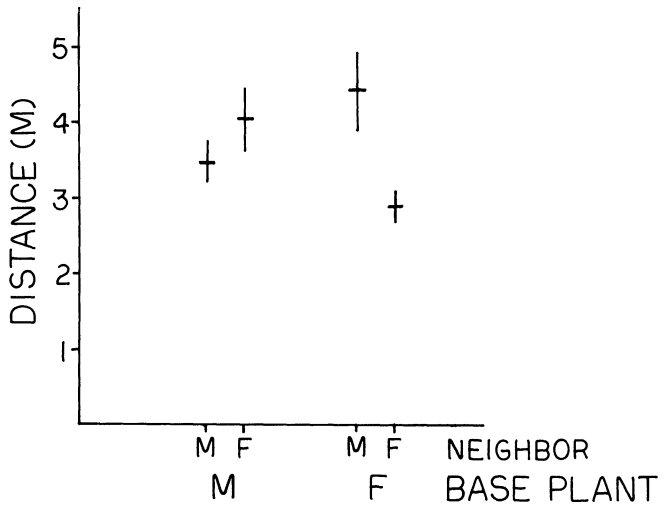

Fig. 5.—Mean distances between nearest-neighbor pairs shown by sex of base plant and sex of neighbor: horizontal line = mean, vertical bar = 1 SE

perate hardwood forests as does *Ilex montana,* females also produce fewer flowers per plant (Meagher and Antonovics, 1982). Thus, two different life forms growing in similar habitats show similar patterns of flower production.

Previous studies (Bawa and Opler, 1977; Melampy and Howe, 1977; Grant and Mitton, 1979) reported only random distributions of sexes within populations of woody perennials. In contrast, both the nearest-neighbor and spatial heterogeneity tests show a weak nonrandom distribution of sexes in a population of *Ilex montana.* Several factors may explain this difference. Small sample sizes and low tree density in tropical studies may make it hard to detect within-population segregation in the tropics (Bawa and Opler, 1977). Temperate clonal trees like aspen (Grant and Mitton, 1979) can spread over several hectares, preventing the detection of heterogeneity in small areas. In contrast, *Ilex montana* is a small understory tree which grows in dense enough populations for heterogeneity to be detected in 10 m x 10 m quadrats. Bawa and Opler (1975) predicted that the amount of detectable segregation in woody perennials would not be as great as that found in herbaceous perennials, and this is supported by the data. Meagher (1980) found spatial heterogenity of *Chamaelirium luteum* males and females in 5 x 5 m quadrats. We did not look for heterogeneity at this size because these quadrats contained so few plants. The reason for this difference in spatial pattern may have nothing to do with resource allocation, as was suggested by Bawa and Opler (1975), but may be merely a function of scale. The larger the plant, the more area one needs to cover to detect environmental changes actually influencing the plant.

A nonrandom distribution of sexes could be caused by sexual differences in environmental tolerances, vegetative propagation or competitive ability (Meagher, 1980). Intraspecific competition is probably not influencing the distribution of males and females. First, there was no correlation between tree density and the proportion of males in the 10 m x 10 m quadrats. Secondly, the higher cost of reproduction for females that underlies the differences in competitive ability is not supported because the distance between females is less than that between males. Since cloning has not been detected in *Ilex montana*, cloning is not a causal factor. Rather, the nonrandom distribution is best explained by sexes responding to undetected variations in the microenvironment.

Sexual differences in secondary sex characteristics can be expressed in many different ways, through survivorship patterns, reproductive timing, resource allocation to components of reproductive and vegetative growth and spatial segregation. One way of trying to understand the evolution of these differences is to compare similar life forms growing in different habitats. Another way, which has received little attention, is to compare different life forms growing in similar habitats. A preliminary comparison of *Ilex montana* and *Chamaelirium luteum* shows differences in scale of spatial patterning but similarities in resource allocation to reproductive components. These differences and similarities may reflect general constraints or lack thereof that the life form, itself, may place upon the evolution of sexual dimorphism. The study of *Ilex montana* suggests that additional comparative studies of life forms would be worthwhile.

Acknowledgments.—We thank Tom Meagher for offering helpful comments on an early draft of this manuscript and for making available his computer programs for some of the data analyses; Lisa Harper, Todd Herman, Susan Suby and Carol Witherspoon for help in gathering the data; and Jerry Wolff, director of the University of Virginia Mountain Lake Biological Station, for providing us with the opportunity to conduct this study. This paper was written while EPL was on leave at Duke University, and we thank Duke University for providing secretarial assistance and computer facilities.

LITERATURE CITED

BARRETT, S. C. H. AND K. HELENURM. 1981. Floral sex ratios and life history in *Aralia nudicaulis* (Araliaceae). *Evolution,* **35**:752-762.

BATEMAN, A. J. 1948. Intrasexual selection in *Drosophila. Heredity,* **2**:349-368.

BAWA, K. S. AND P. A. OPLER. 1975. Dioecism in tropical forest trees. *Evolution*, **29**:167-179.
_____ AND _____. 1977. Spatial relationships between staminate and pistillate plants of dioecious tropical forest trees. *Ibid.*, **31**:64-68.
BISHOP, Y. M., S. E. FEINBERG AND P. W. HOLLAND. 1975. Discrete multivariate analysis: Theory and practice. Massachusetts Institute of Technology Press, Cambridge, Mass. 557 p.
BULLOCK, S. H. AND K. S. BAWA. 1981. Sexual dimorphism and the annual flowering pattern in *Jacaratia dolichaula* (D. Smith) Woodson (Caricaceae) in a Costa Rican rain forest. *Ecology*, **62**:1494-1504.
CLARK, R. B. AND E. R. ORTON. 1967. Sex ratio in *Ilex opaca* Ait. *Hortscience*, **2**:115.
FERNALD, M. L. 1950. Gray's manual of botany. American Book Company, New York. 1632 p.
FISHER, R. A. 1930. The genetical theory of natural selection. Oxford University Press, Oxford. 291 p.
FREEMAN, D. C., L. G. KLICKOFF AND K. T. HARPER. 1976. Differential resource utilization by the sexes of dioecious plants. *Science*, **193**:597-99.
GRANT, M. C. AND J. B. MITTON. 1979. Elevational gradients in adult sex ratios and sexual differentiation in vegetative growth rates of *Populus tremuloides* Michx. *Evolution*, **33**:914-918.
GROSS, K. L. AND J. D. SOULE. 1981. Differences in biomass allocation to reproductive and vegetative structures of male and female plants of a dioecious, perennial herb, *Silene alba* (Miller) Krause. *Am. J. Bot.*, **68**:801-807.
HANCOCK, J. F., JR. AND R. S. BRINGHURST. 1980. Sexual dimorphism in the strawberry *Fragaria chiloenis*. *Evolution*, **34**:762-768.
HARRIS, W. 1968. Environmental effects on the sex ratio of *Rumex acetosella* L. *N. Z. Ecol. Soc. Proc.*, **15**:151-154.
LITTLE, E. L., JR. 1953. Checklist of native and naturalized trees of the United States (including Alaska). *Agric. Handb. No. 41*. Washington, D.C. 472 p.
LLOYD, D. G. 1973. Sex ratios in sexually dimorphic Umbelliferae. *Heredity*, **31**:239-249.
_____ AND C. J. WEBB. 1977. Secondary sex characters in plants. *Bot. Rev.*, **43**:177-216.
MEAGHER, T. R. 1980. The population biology of *Chamaelirium luteum*, a dioecious lily. I. Spatial distributions of males and females. *Evolution*, **34**:1127-1137.
_____. 1981. The population biology of *Chamaelirium luteum*, a dioecious lily. II. Mechanisms governing sex ratios. *Ibid.*, **35**:557-567.
_____ AND J. ANTONOVICS. 1982. The population biology of *Chamaelirium luteum*, a dioecious member of the lily family: Life history studies. *Ecology*, **63**:1690-1700.
_____ AND D. BURDOCK. 1980. On the use of the nearest-neighbor frequency analyses in studies of association between species. *Ibid.*, **61**:1253-1255.
MELAMPY, M. N. AND H. F. HOWE. 1977. Sex ratio in the tropical tree *Triplaris americana* (Polygonaceae). *Evolution*, **31**:867-872.
OPLER, P. A. AND K. S. BAWA. 1978. Sex ratios in tropical forest trees. *Ibid.*, **32**:812-821.
PEATTIE, D. C. 1950. A natural history of Eastern and Central North America. Houghton-Mifflin Co., Boston. 606 p.
PUTWAIN, P. D. AND J. L. HARPER. 1972. Studies in the dynamics of plant populations. V. Mechanisms governing the sex ratio in *Rumex acetosa* and *R. acetosella*. *J. Ecol.*, **60**:113-129.
SMALL, J. K. 1933. Flora of the Southeastern United States. Published by author, New York. 1554 p.
WALLACE, C. S. AND P. W. RUNDEL. 1979. Sexual dimorphism and resource allocation in male and female shrubs of *Simmondsia chinensis*. *Oecologia*, **44**:34-39.
WILLSON, M. 1983. Plant reproductive ecology. John Wiley and Sons, New York. 282 p.

SUBMITTED 4 FEBRUARY 1985 ACCEPTED 29 JULY 1985