Spatial pattern, floral sex ratios, and fecundity in dioecious *Aralia nudicaulis* (Araliaceae)

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Aralia nudicaulis L. (Araliaceae) is a perennial understory herb of the boreal forest which forms large clones by means of an extensive subterranean rhizome system. Populations are dioecious and pollinated primarily by bumble bees. To examine the relationships between the spatial pattern of sexual morphs and female fecundity, all flowering ramets were mapped in a 1-ha block of spruce–fir forest in central New Brunswick and the fecundity of females determined. Within the block, *A. nudicaulis* exhibited a 2.5:1 sex ratio of male/female flowering ramets. Ramets of the sexual morphs were negatively associated owing to cloning and a reduced likelihood of flowering in female ramets under dense canopy compared with males. Pattern analysis of the sex ratio of flowering ramets revealed a monotonic decline in variance with block size indicating that samples of sex ratio using small quadrats are likely to give misleading estimates for this species. The fecundity of females exhibited no systematic positional variation within the forest block. In most cases fecundity was not correlated with male and female flowering density, ramet sex ratio, and several subjectively estimated habitat variables. It is proposed that the long flight distances of pollinators, pollen carry-over, and the predominance of male flowers at the site interact to dampen out spatial effects on fecundity.

Introduction

In outbreeding plants the mating success of individuals may be strongly influenced by the proximity and density of compatible neighbours (Levin and Kerster 1969*a*, 1969*b*, 1974; Wyatt 1977; Wyatt and Hellwig 1979; Silander 1978; Antonovics and Levin 1980). Such spatial effects are likely to vary with the breeding system of the species, and with the number of mating groups in a population. Species with homomorphic incompatibility systems are less likely to experience inbreeding and reduced fecundity because a large number of incompatibility groups are often present in populations (Emerson 1939; Wright 1939; Bateman 1947, 1952; Fisher 1963; Nettancourt 1977; Lawrence and O'Donnell 1981). In contrast, dioecious and heterostylous species with two (dioecy and distyly) or three (tristyly) mating groups may be particularly sensitive to the spatial pattern and density of compatible neighbours (Mulcahy 1967; Levin 1975; Ornduff and Weller 1975; Barrett 1977*a*; Wyatt and Hellwig 1979).

The significance of spatial relationships to the breeding structure of populations has become evident from studies of gene flow in entomophilous plants. Levin and Kerster (1969*a*, 1969*b*) have demonstrated that the foraging behaviour of insect pollinators renders the pollen component of gene flow both nonrandom and density dependent. Nonrandom pollination, which is primarily a result of restricted near-neighbour foraging patterns, can lead to genetical subdivision and the local differentiation of plant populations (Wright 1946; Levin and Kerster 1969*a*, 1974; Schaal 1974, 1975; Levin 1978, 1979).

As a consequence of the difficulty in distinguishing genotypes, analysis of mating patterns in clonal plants can be complex. This is particularly the case in species in which clones occupy large areas and clonal fragmentation occurs. An abundance of inflorescences may restrict pollinator movement away from a clone and thus limit the level of cross-pollination (Antonovics and Levin 1980). In self-compatible species this can lead to considerable inbreeding as a result of geitonogamy (Barrett 1977*b*). In self-incompatible species, restricted foraging on extensive clones may result in pollen loads composed primarily of incompatible pollen. In such instances, fecundity may be reduced as a result of competition for germination sites on the stigmatic surface and (or) biochemical interactions among pollen grains. In dioecious species all pollination is cross-pollination and capable of effecting seed set. Thus the important factors influencing mating success are likely to involve the frequency of sexual morphs in populations, their spatial pattern, and the abundance and behaviour of pollinators.

To assess the importance of some of these factors we undertook a detailed analysis of fecundity patterns in a natural population of *Aralia nudicaulis* L. (Araliaceae) in central New Brunswick. The study addressed the

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following specific questions: (*i*) What is the spatial pattern of flowering in the sexual morphs of *A. nudicaulis*? (*ii*) At what spatial scale is variation in the sex ratio of flowering ramets of *A. nudicaulis* at a maximum? (*iii*) What factors (e.g., local sex ratio, proximity to nearest males) influence the level of fruit set of females and at what spatial scales can they be discerned? This paper presents the results of the study and discusses the implications for studies of the breeding structure of clonal plants.

Natural history of *Aralia nudicaulis*

Aralia nudicaulis (Wild Sarsparilla) is a rhizomatous perennial which occurs in the understory of much of the boreal forest of North America. In common with many boreal forest herbs, *A. nudicaulis* forms large clones. Clonal growth is by means of an extensive, subterranean rhizome system. Typically, clones (genets) are composed of aerial shoots (ramets) which are either vegetative or reproductive. Ramets have a single compound leaf and, if reproductive, the leaf is subtended by a single umbellate inflorescence. Ramets of a clone are interconnected by the rhizome system and occasional fragmentation, as well as the complexity and size of the system, make identification of individual genets an almost impossible task. In this study all references to sex ratio refer to the sex ratio of flowering ramets.

Aralia nudicaulis is dioecious, possessing flowers of one sex on a given individual. In central New Brunswick, where all studies were undertaken, the flowering period encompasses the first 3 weeks of June. During this period the major insect visitors to inflorescences are bumble bees, principally *Bombus vagans* F. Smith but also *B. ternarius* Say. Other minor visitors observed included andrenids, halictids, and syrphids. Further details of the floral biology, flowering phenology, and growth patterns of the sexual morphs of *A. nudicaulis* can be found in Barrett and Helenurm (1981) and Bawa *et al.* (1982).

Surveys of flowering ramets of *A. nudicaulis* from different habitats in central New Brunswick revealed a male predominance in forested sites (Barrett and Helenurm 1981). In contrast, sex ratios of unity were characteristic of disturbed sites such as roadside edges. These authors suggest that the lower density of female flowering ramets in forest sites is due to a reduced flowering capacity in females under low-light regimes in comparison with males. This difference may be a result of the greater resource expenditure on reproduction in female ramets because of the costs of fruit and seed production. Information on the spatial patterns of flowering of the sexual morphs collected in the present study provides further evidence to support this hypothesis.

Methods

The sample block

A square 1-ha sampling block was established in spruce-fir forest 5 km SE of Doaktown, N.B. The site was chosen subjectively; previous investigations (Barrett and Helenurm 1981) revealed substantial numbers of flowering ramets of both sexes at this locality. However, the density and sexual composition of the stand were in no way exceptional for a forested site.

During June 1979 the block was subdivided by means of graduated chains into one hundred 10 × 10 m plots. Within each plot the positions of all flowering ramets were mapped to the nearest 25 cm and their sex recorded. After they had finished flowering, all reproductive female ramets were marked with tags and covered by drawstring bags of nylon bridal-veil mesh to prevent loss of developing fruits. One of the leaflets on each female shoot bearing an inflorescence was sprayed with fluorescent paint to aid in relocating females during the harvest period. All 100-m^2 subdivisions of the 1-ha block contained flowering ramets of *A. nudicaulis*.

On July 25, 1979, when fruits were near full maturity, the female infructescences were harvested individually. The numbers of pedicels and fruits per ramet were recorded. Seeds per fruit were not counted after an initial sampling showed that virtually all fruits contained a full complement of five seeds. Some female ramets had failed to produce fruit. These were recorded but not harvested.

During early July three habitat variables were assessed subjectively, using a five-point scale, in each of the 100 subdivisions of the forest block. Two persons were involved in independent assessments of each plot and close agreement was obtained in the vast majority of plots. The variables assessed were degree of tree-canopy closure, development of bracken and shrub layer, and density of *Clintonia borealis* (Ait.) Raf. (Liliaceae). This species blooms synchronously with *A. nudicaulis* in early June and both species are primarily pollinated by bumble bees.

Block size analysis of spatial pattern

Pattern analysis was performed on the spatial-distribution data of male and female flowering ramets within the 1-ha block. The block was progressively subdivided into smaller nested component square quadrats (4, 16, 64, 256, and 1024 quadrats) and the densities of male and female ramets within each quadrat were calculated for each of the five block sizes. The variances of density for males and females were also obtained. The analysis identifies the spatial scale of aggregation (patch size) as that block size showing the greatest variance in density (see Grieg-Smith 1957 and Kershaw 1973 for discussion of the technique).

Variable radius analysis of fecundity correlates

The coordinate positions of the 499 female and 1244 male flowering ramets allowed calculation of the sets of neighbours "experienced" by each flowering female ramet at a range of spatial scales. All flowering ramets within a given radius of each female were identified and fecundity correlations were then computed for all females. The fecundity measure used was the number of fruits produced per ramet divided by the number of flowers per ramet. This value, after arc-sine transformation, was then related to six other variables. Three of these concerned the local composition of the *A. nudicaulis* stands: the density of male flowering ramets within the chosen radius, the flowering female density, and the ratio of these numbers (males/female). The remaining variables were the subjective estimates of habitat within the radius. Each of these estimates was calculated as the simple mean of the habitat measure for all flowering ramets within the radius. Each set of six correlations was computed for 20 radii ranging from 2 to 40 m in 2-m increments. As the radius increased, the sample size was reduced because fewer females had their surrounding circles entirely contained within the mapped hectare.

Results

Distribution of flowering ramets in the block

Figure 1 illustrates the distribution of the 1244 male and 499 female flowering ramets within the 1-ha block. Of the one hundred 100-m^2 plots, 56 contained males and females, 26 males only, and 18 females only. Males occurred in 82 of the plots whereas females occurred in 74 plots. Thus, the 2.5:1 preponderance of males was only partially due to their more widespread occurrence throughout the block. It was the tendency of male flowering ramets to bloom more densely that accounted for most of their numerical dominance. The average density of males in male-only plots was significantly higher than the flowering density of females in female-only plots (♂ = 22.3, ♀ = 9.2; $t = 3.15$, $p < 0.01$). A similar pattern was evident in plots containing both males and females (♂ = 11.9, ♀ = 6.0; $t = 3.23$, $p < 0.01$). Note that these values pertain to flowering ramets only. The distribution and density of vegetative ramets of both sexes in the block is unknown.

The flowering ramets of the sexes of *A. nudicaulis* were negatively associated in the 100-m^2 plots; the product-moment correlation of their densities is significant ($r = -0.337$, df = 98, $p < 0.01$). The pattern of negative association was in part due to cloning but also arose from an apparent difference in male and female response to light levels. Flowering ramets occurred more frequently in plots with higher light levels under a more open canopy (Table 1). However, this tendency was significantly more pronounced in females compared to males (Fig. 2). The reduced likelihood of female flowering under dense canopies contributed to the negative association between the sexes. It should be noted, however, that within canopy-cover types, males and females were also negatively associated (product-moment correlation (r) of ♂ and ♀ densities in 100-m^2 plots within canopy-closure types 0 = −0.234, 1 = −0.453, 2 = −0.392, 3 = −0.188, 4 = −0.329). Thus, the negative association had a cloning component and a light-response component. The probable causes of these patterns are discussed more fully elsewhere (Barrett and Helenurm 1981).

Pattern analysis of flowering ramet sex ratio

A monotonic decline of the variance (mean square) of density with block size occurs for flowering ramets of both sexes (Fig. 3). To eliminate the difference between the sexes in flowering density, the coefficient of variation can be plotted instead of variance. When this procedure is undertaken the curves for males and females virtually coincide (Fig. 4). There appears to be no intermediate patch size for either sex. Presumably if an area of many hectares was mapped, variance in density would eventually rise at some large block size including habitats in which *A. nudicaulis* occurred rarely or was absent.

As might be expected, variation in the sex ratio (ratio of ♂/♀) also declines monotonically (Fig. 5). The absence of flattening in this curve implies that any spatial pattern in sex ratio is expressed at a very large scale. Extensive sampling would therefore be necessary to provide an overall measure of the sex ratio of a population. This is clearly evident when the 1-ha block is divided into square quarters of 2500 m^2 in size. The sexual composition and sex ratio of the four quarters are (1) 147♂/227♀ = 0.65, (2) 515♂/49♀ = 10.51, (3) 420♂/105♀ = 4.00, (4) 162♂/118♀ = 1.37. The large-scale negative association between the sexes causes more than an order of magnitude separation in the sex ratios of the adjacent first and second quarters.

Fecundity patterns

Summary statistics of various size parameters for female inflorescences and fecundity are given in Table 2. The frequency distribution of fecundity is illustrated in Fig. 6. The distribution is strongly bimodal, with substantial percentages of nonfruiting inflorescences and of inflorescences with a large number of fruits. The mean fecundity is 68% but the modal fecundity class is 90–100%. Because inflorescences without fruits were noted but not harvested, the estimates of flower number, umbel number, and inflorescence height do not include these ramets.

Among ramets which set fruit (arc sine transformed), fecundity is positively correlated both with flowers per inflorescence ($r = 0.417$, $n = 221$, $p < 0.001$) and inflorescence height ($r = 0.267$, $n = 218$, $p < 0.001$). As flower number and inflorescence height are themselves correlated, partial correlations were used to determine whether fecundity remained correlated with each of the two size variables, while the other was held constant. Both remain positively correlated, although flower number ($r = 0.231$, $n = 215$, $p < 0.001$) appears more important than height ($r = 0.169$, $n = 215$, $p < 0.01$) in influencing fecundity.

With the aid of a computer, a map of the patterns of fecundity throughout the 1-ha block was plotted. The map is available from the authors on request. No

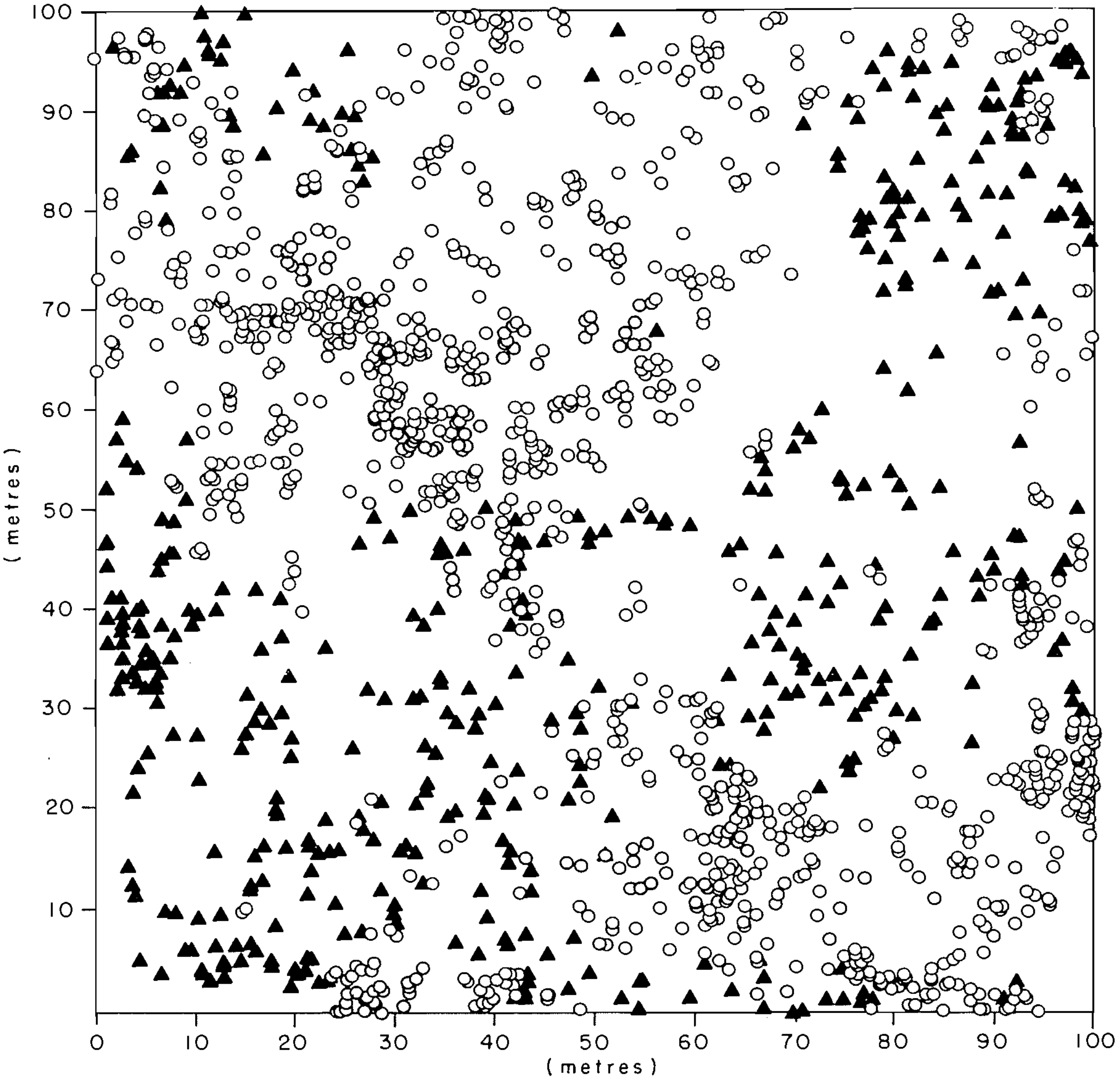

FIG. 1. Distribution of male (n = 1244) and female (n = 449) flowering raments of *Aralia nudicaulis* within a 1-ha block of spruce–fir forest in central New Brunswick in summer 1979. ○, male inflorescence; ▲, female inflorescence.

systematic positional variation in fecundity within the block was apparent by inspection. Results from the correlation analysis support this observation. Fecundity was not correlated with any of the six independent variables tested (Figs. 7 and 8). Only at the largest radii do significant simple correlations emerge. However, at these points the sample sizes are small and the biological significance of the correlations is unclear. Fecundity in females is positively correlated with female density, uncorrelated with male density, and negatively correlated with the ratio of males to females. Partial correlations of fecundity to male density, with the effect of female density held constant, are statistically insignificant for all radii from 2–38 m and significantly negative at the 40-m radius ($r = -0.651$, $p < 0.01$).

Discussion

In plants with clonal growth, estimates of clone size can be obtained if the species under study displays a visible genetic polymorphism. Using this approach Cahn and Harper (1976) demonstrated fine-scale intermingling of clones and considerable genetic diversity in

TABLE 1. Distribution of male and female flowering ramets of *Aralia nudicaulis* in relation to canopy closure in a 1-ha block of spruce–fir forest in central New Brunswick in summer 1979. Closure index: 0 most open canopy to 4 most closed

	Closure index				
	0	1	2	3	4
No. of 100-m^2 plots	8	17	61	7	7
Observed ♂ ramets	122	205	775	73	69[a]
Expected ♂ ramets	100	211	759	87	87[a]
Observed ♀ ramets	67	111	285	19	17[b]
Expected ♀ ramets	40	85	304	35	35[b]
Ratio♂/♀	1.82	1.85	2.72	3.84	4.06

[a] $\chi^2 = 11.65$, df = 4, $p < 0.05$.
[b] $\chi^2 = 44.14$, df = 4, $p < 0.001$.

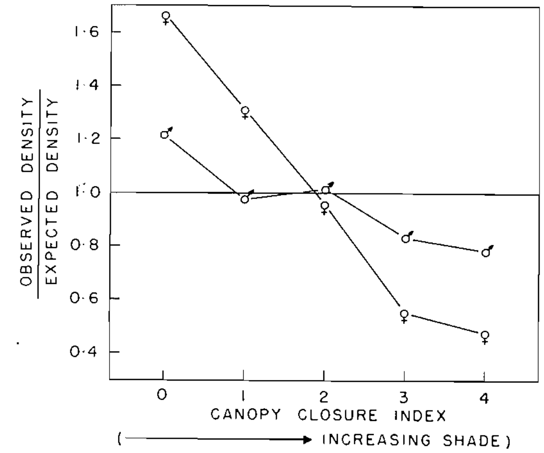

FIG. 2. Density responses of male and female flowering ramets of *Aralia nudicaulis* to canopy closure. The female response is significantly stronger than the male response, based on a 2 × 5 contingency table of the raw density data in Table 1 (G = 18.61, df = 4, $p < 0.001$).

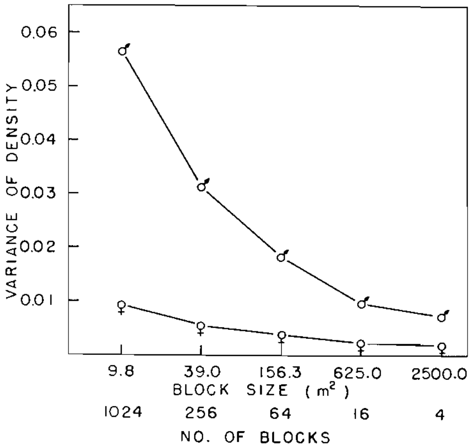

FIG 3. Relationship between the variance (mean square) of density and block size in male and female flowering ramets of *Aralia nudicaulis* within a 1-ha block of spruce–fir forest in central New Brunswick.

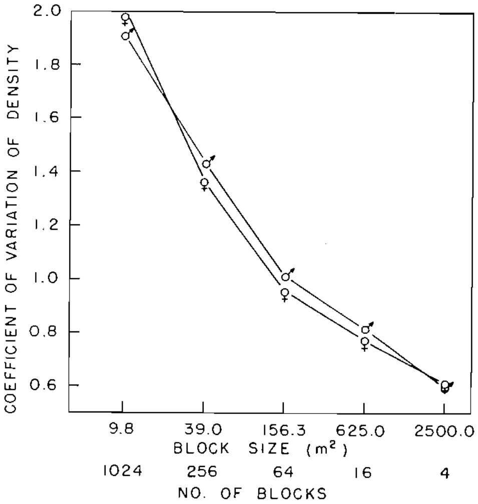

FIG. 4. Relationship between the coefficient of variation of density and block size in male and female flowering ramets of *Aralia nudicaulis* within a 1-ha block of spruce–fir forest in central New Brunswick.

1-m^2 quadrats containing *Trifolium repens* L. (Leguminosae). In contrast, clone-forming species such as the grasses *Festuca ovina* L. and *Holcus mollis* L. (Harberd 1962, 1967), bracken fern, *Pteridium aquilinum (L.)* Kuhn (Oinonen 1967), and water hyacinth *Eichhornia crassipes* (Mart.) Solms. (Barrett 1977*b*, 1980) form extensive clones giving rise to large areas of genetic uniformity.

Our studies suggest that clone size in *Aralia nudicaulis* can be quite extensive with individual genets perhaps occupying areas in excess of 100 m^2. Isolated stands (probably clones) of a single sex observed outside the 1-ha forest block suggest that this value may considerably underestimate the size of larger clones. It should be emphasized, however, that several sources of error complicate attempts to estimate clone size in *A. nudicaulis*. Intermingling of several clones of the same sex cannot be detected and hence this results in

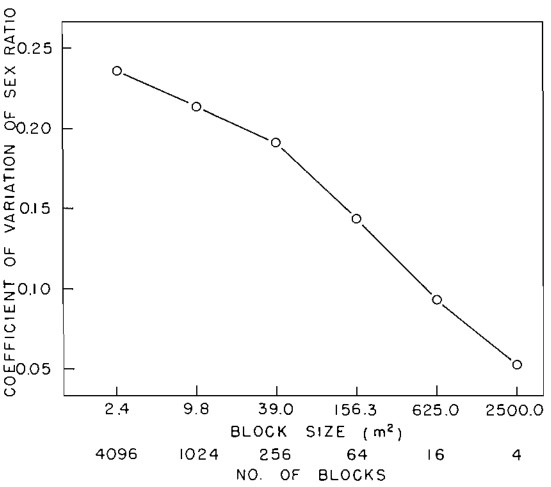

FIG. 5. Relationship between the coefficient of variation of flowering ramet sex ratio and block size in *Aralia nudicaulis* within a 1-ha block of spruce–fir forest in central New Brunswick.

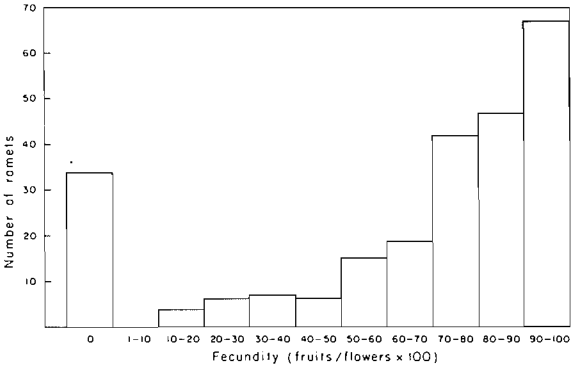

FIG. 6. Frequency histogram of fecundity in female ramets of *Aralia nudicaulis* during summer 1979 in a 1-ha block of spruce–fir forest in central New Brunswick.

TABLE 2. Summary statistics of flower number, umbel number, height, and fecundity of female ramets of *Aralia nudicaulis* in central New Brunswick in summer 1979

Reproductive parameter	$\bar{x}$	SD	*n*
Number of flowers/inflorescence	55.30	14.00	221
Number of umbels/inflorescence	2.82	0.45	216
Height of inflorescence, cm	16.80	3.25	218
Fecundity (fruits/flowers)	0.68	0.31	245

overestimates of clone size. On the other hand the subterranean rhizome system of an individual clone is likely to be more extensive than the distribution of flowering ramets would indicate. This is particularly important where heavy shade restricts flowering and only vegetative ramets occur. Unfortunately, vegetative ramets of the sexes cannot be distinguished. Despite these problems, several interesting differences between the sexes in the spatial distribution of flowering ramets were revealed by this study.

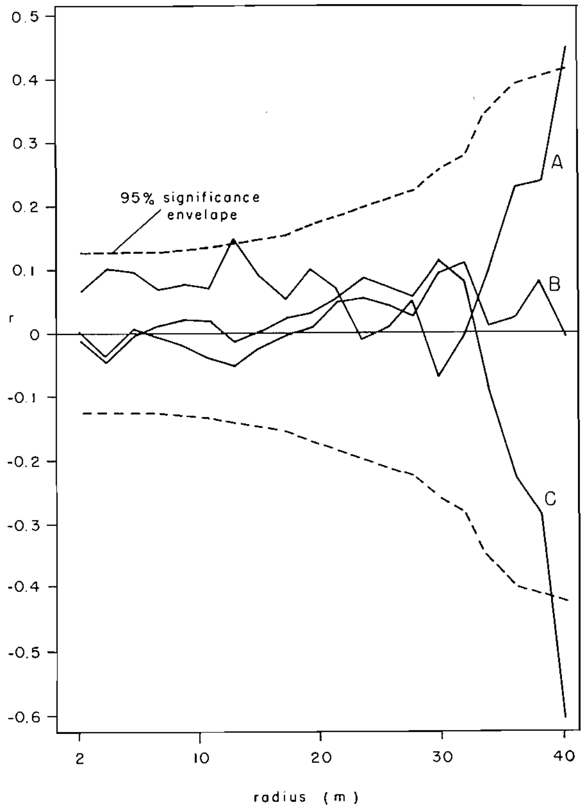

FIG. 7. Product-moment correlations of female fecundity in *Aralia nudicaulis* with sexual composition at various spatial scales in a 1-ha block of spruce–fir forest in central New Brunswick. A, the number of female ramets; B, the number of male ramets; C, the sex ratio (male ramets/female ramets).

At the site the flowering ramets of males and females were spatially segregated (Bawa and Opler 1977; Melampy and Howe 1977) and negatively associated. The spatial segregation (contagious distribution) of flowering ramets is primarily the result of the extensive cloning habit of the species which results in a strong tendency for near-neighbour inflorescences to be of the same sex. However, the negative association of ramets in the one hundred 100-m^2 plots may also result from differences between the sexual morphs in flowering behaviour. Under the low-light regime of dense canopy there appears to be a reduced likelihood of flowering in females compared with males. These observations support the hypothesis advanced by Barrett and Helenurm (1981) that the causes of the male-biased sex ratio of flowering ramets in forest sites of New Brunswick are ecological in nature and involve differences between the sexual morphs in reproductive behaviour. It is important to note that this explanation does not concern genetic sex

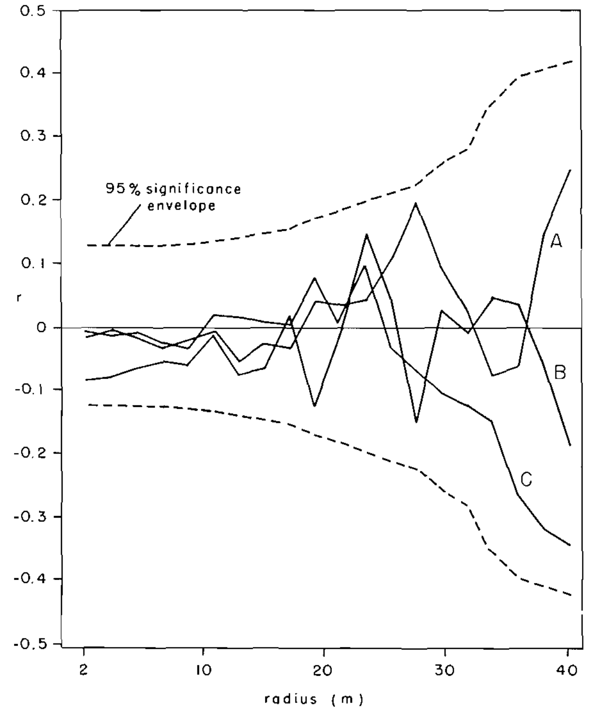

FIG. 8. Product-moment correlations of female fecundity in *Aralia nudicaulis* with three habitat variables at different spatial scales in a 1-ha block of spruce–fir forest in central New Brunswick. A, the cover of the shrub/bracken layer; B, the cover of tree canopy; C, the density of *Clintonia borealis*.

ratios of *A. nudicaulis*. These cannot be determined accurately because of clonal growth and rhizome fragmentation.

In a recent study, Meagher (1980, 1981) documented the spatial patterns of males and females in the dioecious lily, *Chamaelirium luteum* (L.) Gray (Liliaceae). His study contrasts with ours because *C. luteum* exhibits no clonal propagation. Hence the sex ratios Meagher estimated are based on the numbers of genotypes that flowered (approximately one third) while ours bear no relationship to genotype numbers. Meagher's main concern was to examine subtle negative associations of males and females which he demonstrated at several spatial scales. He further showed that sex ratio varies with vegetation type as determined by ordination and cluster analysis. Rather than using an ordination to subsume numerous habitat variables, we have shown a direct response of sex ratio to a canopy-cover (light) gradient. Although this probably shows a light-mediated sexual difference in flowering propensity (see Barrett and Helenurm 1981) rather than the distributional difference found by Meagher, the resulting negative sexual association has similar implications for pollination and fecundity.

The spatial distribution of flowering ramets of *A. nudicaulis* may be expected to influence the patterns of pollen flow within populations and hence fecundity. An intermingling of the sexual morphs would probably increase the level of pollination whereas pollen may become limiting for females in highly segregated populations. Female ramets in close proximity to a high density of male ramets might be expected to benefit in terms of mating success in comparison with isolated females. Effects of this type were demonstrated by Wyatt and Hellwig (1979) in a study of spatial pattern and fecundity in distylous populations of *Houstonia caerulea* L. (Rubiaceae). Positive correlations between fecundity and plant density have also been reported in the legumes *Astragalus canadensis* L. (Platt *et al.* 1974) and *Cassia biflora* L. (Silander 1978).

The results of the present study are in striking contrast to these earlier findings. Despite the spatial segregation of clones of *A. nudicaulis* and considerable heterogeneity in cover and plant associates, there was no apparent systematic positional variation in mating success within the 1-ha forest block. Fecundity was largely uncorrelated with any of the six independent variables tested. The absence of a correlation between female mating success and the local sexual composition of *A. nudicaulis* stands is particularly surprising. Presumably at some spatial scale the distribution and density of sexual morphs influence fecundity. Pollen must become limiting for females occurring large distances from the nearest males. Nevertheless, the levels of spatial isolation experienced by females in the forest block were not sufficient to create a substantially different pollination regime compared with females in close proximity to males. Several explanations are proposed to account for these findings.

The absence of spatial factors influencing fecundity in *A. nudicaulis* may be associated with pollinator foraging behaviour and the schedule of pollen deposition and receipt. The major insect visitors to flowers at the site are bumble bees. Field observations suggest that individual bees cover considerable distances on a single foraging run. This behaviour, coupled with significant levels of pollen carry-over, could result in sufficient pollen being deposited on most female stigmas, irrespective of their location in the population.

Early considerations of the phenomenon of pollen carry-over emphasized that most pollen was deposited on stigmas of the first few flowers following receipt (Levin and Kerster 1969*a*; Frankie *et al.* 1976). Recent experimental studies (Hartling 1979; Thomson and Plowright 1980) confirm this view but also demonstrate that complete pollen removal from insect bodies can be a slow process with some grains being deposited after 54 consecutive flower visits following initial receipt of pollen (Thomson and Plowright 1980). Long pollinator flights and significant pollen carry-over would reduce the likelihood of female ramets within large female clones receiving low pollen loads.

A substantial fraction (14%) of female ramets produced no fruits. It is possible that the failed inflorescences received no pollinating visits and the two modes of fecundity (Fig. 6) simply reflect visited and unvisited inflorescences. However, it seems more likely that the failure of some inflorescences to fruit is not associated with lack of pollination but rather postzygotic effects such as withdrawal of maternal support (Lloyd 1980) or damage (disease, herbivory, etc.). The observation that many of the failed inflorescences were stunted also raises the possibility that some were sterile.

In his theoretical studies of the breeding structure of populations, Wright (1943, 1946, 1951) developed the concept of genetic neighbourhoods. A neighbourhood is the area of a colony of organisms within which mating is assumed to be random. In Wright's models, the reference colony for panmixia is dioecious with a sex ratio of unity, random mating, and a Poisson distribution of number of offspring per parent. Using Wright's models, several workers (Kerster and Levin 1968; Levin and Kerster 1968, 1969*a*; Richards and Halijah 1978; Beattie and Culver 1979) have estimated neighbourhood size in different plant species using pollen- and seed-dispersal data. These studies suggest that neighbourhood sizes are considerably smaller than earlier workers appreciated owing to restricted gene flow (and see Levin and Kerster 1971).

Our results suggest that the area of neighbourhoods in *A. nudicaulis* may be considerable, particularly in comparison to short-lived, sexual, herbaceous species. Although the areas involved may be large, it is likely that the number of genotypes within a panmictic unit is small. We may surmise that many of the matings in the forest block involve the same pairs of maternal and paternal parents, particularly in highly segregated segments of the forest.

Finally, the analysis of spatial variation in flowering ramets of males and females indicates that samples which involve a limited number of small areas are likely to provide misleading estimates of sex ratio. To sample global sex ratios in clonal plants accurately requires a major sampling effort and this should ideally involve long transects rather than quadrats. In any event the local sex ratio, which is relatively simple to measure, may be of more relevance to many aspects of the reproductive biology of clonal plants.

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