

FLORAL SEX RATIOS AND LIFE HISTORY IN *ARALIA NUDICAULIS* (ARALIACEAE)

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Darwin (1877) suggested that the resources allocated to reproduction differ between the sexes in certain species of dioecious flowering plants. Recent workers have postulated that differential expenditure on reproduction between sexes may account for the unequal sex ratios found in many dioecious species (Harris, 1958; Putwain and Harper, 1972; Lloyd, 1973; Lloyd and Webb, 1977; Melampy and Howe, 1977; Grant and Mitton, 1979; Hancock and Bringhurst, 1980). However, there is a lack of quantitative data concerning differences in reproductive effort of males and females under field conditions. It may seem intuitively obvious that females allocate greater amounts of resources to reproduction due to the requirements of fruit and seed development, but the extent and pattern of differences throughout the reproductive period have not been documented in natural populations.

Although sex ratios of unity have been reported, deviations from this are frequently observed (Lloyd, 1973, 1974; Opler and Bawa, 1978; Hancock and Bringhurst, 1980; Webb and Lloyd, 1980). Lloyd (1973) has related biased sex ratios to life history, arguing that male-biased ratios tend to occur in iteroparous perennials of great longevity. Under the assumption that reproductive effort is greater in females, and that some limitation to energy expenditure exists, repeated flowering would restrict clonal propagation in females compared with males. This would result in an increase in the number of male relative to female inflorescences. Male-biased ratios, then, are explained as a consequence of repeated reproduction rather than as a result of direct selection.

Aralia nudicaulis (wild sarsaparilla) is

a rhizomatous perennial that occurs throughout the boreal forest zone of North America with extensions south into shaded woodlands of the U.S.A. *Aralia nudicaulis* is dioecious, possessing flowers of one sex only on a given individual. Rare flowering shoots contain perfect flowers (Scoggan, 1979) or separate male and female flowers. These floral types were found in less than 1% of the flowering shoots sampled for this study and are not considered further.

In common with many of the herbaceous understory species of the boreal forest (e.g., *Pteridium aquilinum*, *Clintonia borealis*, *Cornus canadensis*), *A. nudicaulis* forms extensive clones which are probably of considerable age. Clonal growth in *A. nudicaulis* results from an extensive, subterranean rhizome system. Typically, clones (genets) are composed of scattered aerial shoots (ramets) which are either vegetative or reproductive. All ramets have a single, ternately compound leaf borne on a long petiole. In flowering ramets, this is subtended by a short naked scape terminated by a single umbellate inflorescence. The leaf and inflorescence are born on a short vertical shoot which arises from the underground rhizome. Fragmentation of underground parts as well as the complexity and extent of the rhizome system make identification of individual genets virtually impossible. Hence, in this study, all references to sex ratio refer to the sex ratio of flowering ramets.

Field observation during 1978 indicated that a greater number of male than female flowering ramets occurred in forest sites of central New Brunswick, Canada. To extend these observations, surveys of ramet sex ratio in different habitats were made during 1979 and 1980. In order to compare

the growth of male and female ramets and to test the hypothesis that reproductive expenditure in females is greater than in males, the patterns of dry weight allocation were measured throughout the growing season. This paper presents the results of these studies and also describes differences in the phenology of flowering between the sexes of *A. nudicaulis*.

MATERIALS AND METHODS

Field studies were undertaken in the vicinity of Doaktown, central New Brunswick, where *Aralia nudicaulis* is abundant in the understory of spruce-fir forests. Although *A. nudicaulis* is widespread, its distribution in forest sites is patchy and the density of flowering ramets is often low. Large flowering populations occur commonly along roadsides in these areas.

The sex ratios of flowering ramets of *A. nudicaulis* in forest sites and along roadsides were surveyed at peak flowering at 14 locations in a 50 × 10 km area around Doaktown during 1979 and 1980. Ten surveys used 2-m wide strip transects ranging from 1–4 km in length; the remaining samples were undertaken at sites chosen subjectively for a high flowering density. At each location all reproductive ramets were scored for sex type. To obtain information on the sex ratio during the flowering period, five censuses of a roadside population were conducted during a 12-day period.

Detailed observations of the flowering phenology of individually marked male and female ramets were undertaken at two roadside and two forest sites. All reproductive ramets in 2-m strip transects from 1–2 km in length were censused at 1 or 2 day intervals throughout the flowering period in June, 1980. At each census the number of ramets in flower in the sample and the proportion of flowers in anthesis within inflorescences were determined. The criteria used for determining the anthesis period of flowers were anther dehiscence for males and stylar divergence for females. Cross-pollinations of female flowers of various ages were performed to

determine the receptivity period of stigmas. A pair of male and female inflorescences, which were starting anthesis, were selected on 13 consecutive days and censused for flower number at daily intervals in order to determine the synchrony of flowering within individual inflorescences.

A one hectare block of spruce-fir forest, known to contain a high density of flowering ramets, was subdivided into 100 10 × 10 m plots to determine the density and distribution of female and male inflorescences. The locations of the 1,743 flowering ramets in the block were mapped during 1979. Densities of male and female flowering ramets were then calculated for plots containing inflorescences of one sex only and for plots containing both sexes.

A study of the patterns of dry weight allocation in female and male flowering ramets was undertaken in a 100 × 500 m area of spruce-fir forest. Harvests were performed at weekly intervals for a 9-wk period beginning on June 4, 1979, at the commencement of flowering. Two additional harvests were conducted in the post-reproductive period during August and September. Thirty ramets of each sex were sampled in the first five harvests and 15 of each in the last six harvests. All harvests involved stratified random samples. Ramets were subdivided into four components: petiole, leaf blade, scape, and reproductive structures (pedicels, flowers and fruits). All plant parts were oven-dried to constant weight before weighing. In this study, we define reproductive effort as dry weight allocated to reproductive structures and scape as a proportion of above ground biomass of flowering ramets.

RESULTS

Floral biology.—*Aralia nudicaulis* has numerous small, white flowers that are superficially similar between the sexes. Both males and females have five stamens and a pistil with five styles, although only one type of sexual structure is usually functional in an inflorescence. In female flowers, the filaments of stamens are

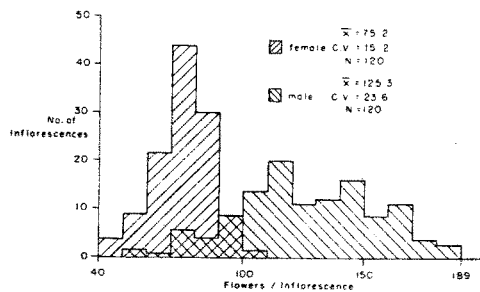


FIG. 1. Distributions of the number of female and male flowers in inflorescences of flowering ramets of *Aralia nudicaulis*.

short, anthers contain no pollen, and petals and stamens fall off within the first two days of stigma receptivity. The styles generally lengthen and diverge after the flower opens. In male flowers, filaments are long, styles are short, but remain appressed and petals and stamens are persistent for at least one week. Thus, sexes are easily identified during the flowering period in June. In some males, the styles lengthen and diverge after the filaments and anthers have been shed, and occasionally ovaries will begin to swell. The developing fruit are aborted in all but 1% of these cases, however, so the flowers remain functionally male.

Inflorescences differ in secondary characters as well as in primary sex expression. Female inflorescences have a mean of 75.2 flowers (Fig. 1) compared with 125.3 in males ($t = 17.30$, $P < .001$). The range of flower number is narrower in females, with the coefficients of variation significantly different at $P < .01$ (no overlap between 99% confidence limits). The sexes also differ in several aspects of their flowering phenology. In three of the four populations sampled during 1980, the cumulative flowering curve for female ramets is significantly different from that of males using a non-parametric Kolmogorov-Smirnov two-sample test (Fig. 2). Female inflorescences on average begin flowering earlier than males. This difference is based on functional rather than morphological criteria since anther dehiscence and stylar divergence were used to determine the period of anthesis. Timed crosses of

TABLE 1. Fruit set in artificially pollinated flowers of different ages in *Aralia nudicaulis*. Age (in days) measured from time of stylar divergence.

Age	N	% Fruit set
0	5	100
1	83	92
2	50	92
3	50	88
4	31	97
5	8	100
6	16	100
8	21	5
10	7	0

female flowers, protected from insect visitors by bagging, indicated that flowers pollinated at stylar divergence set maximum numbers of fruits and that stigmatic receptivity lasts for up to six days (Table 1).

If flowering is depicted as the percentage of the total number of flowers functioning on a given day, a similar pattern emerges (Fig. 3). In three of the four populations female flowers tend to open earlier than male flowers, although the peak flowering times of the two sexes are similar. In a third roadside population surveyed at weekly intervals during 1979, 40% of all female flowers ($n = 305$ ramets) opened during the first week of flowering, compared with 11% of the male flowers ($n = 318$ ramets). During the second week 60% and 74% of female and male flowers opened, respectively, and during the third week the last 1% of female flowers opened compared to the remaining 15% of male flowers. At this site females reached peak flowering earlier than males and anthesis in male inflorescences extended past the completion of female flowering.

Female inflorescences take fewer days to reach full bloom than males (Table 2). The difference is statistically significant ($\bar{x} = 4.9$ days in ♀, $\bar{x} = 7.4$ days in ♂; $t = 4.3$, $P < .001$). This pattern does not reflect a difference in the rate of flower opening ($\bar{x} = 13.8$ flowers/day in ♀, $\bar{x} = 17.3$ flowers/day in ♂; $t = 1.36$, NS) but simply results from female inflorescences containing fewer flowers than males.

Sex ratios.—Because of the phenologi-

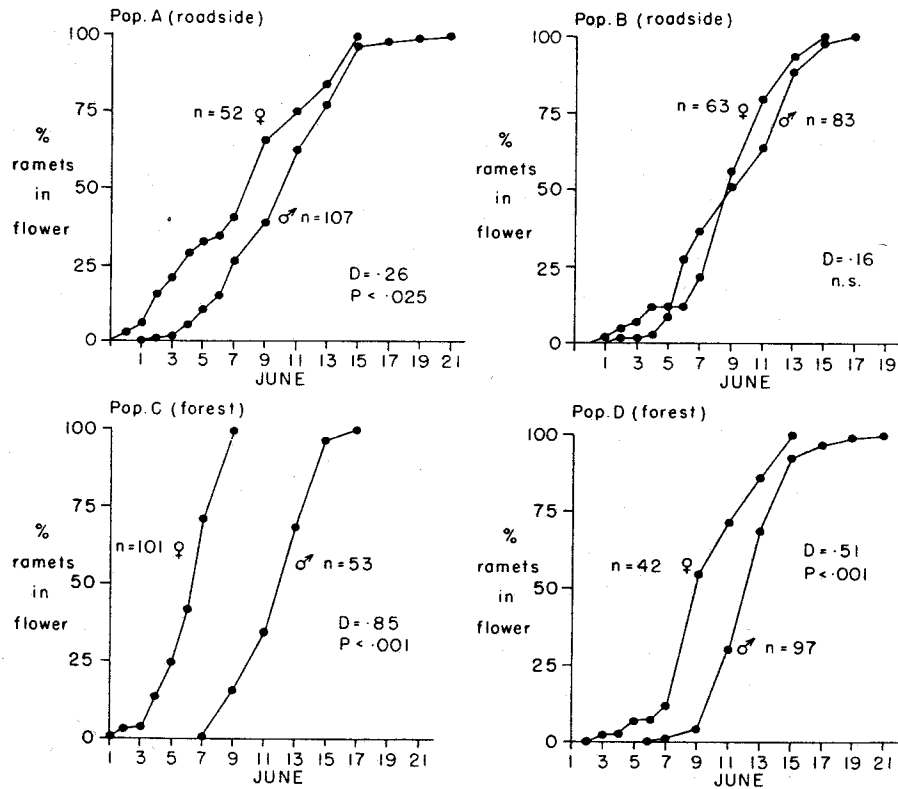


FIG. 2. Cumulative flowering curves of female and male ramets in four New Brunswick populations of *Aralia nudicaulis* during 1980.

cal differences between males and females, the sex ratio of flowering ramets is not constant throughout the flowering period. In repeated surveys of a roadside population, the ratio of male to female inflorescences steadily increased from 0.76 on June 2 to 1.10 on June 14 (Table 3). The former value departs significantly from unity ($\chi^2 = 4.55$, $P < .05$). The total number of inflorescences scored during each survey rose from 254 on June 2 to 600 by June 8, but dropped thereafter due to the termination of flowering in many ramets. These data indicate the importance of obtaining sex ratios at or just after peak flowering, when the sex of all ramets can be identified.

Roadside and forest populations of *A. nudicaulis* differ in the sex ratios of flowering ramets (Table 4). Four of the five roadside surveys yielded virtually equal

numbers of male and female inflorescences, while the fifth was slightly female-biased. In the forest, however, seven surveys revealed a marked preponderance of males and two had sex ratios not differing significantly from unity. In general the forest sites have male-biased sex ratios while roadsides exhibit approximately equal numbers of male and female flowering shoots.

In the one hectare forest block the density of flowering ramets in 10×10 m plots containing ramets of one sex differed significantly between males and females (Table 5), with males having a greater density ($P < .01$). This difference between males and females was maintained in plots containing ramets of both sexes ($P < .01$, paired *t* test) although the density of each sex was reduced ($P < .01$ and $P < .05$ for σ and φ , respectively). The percent

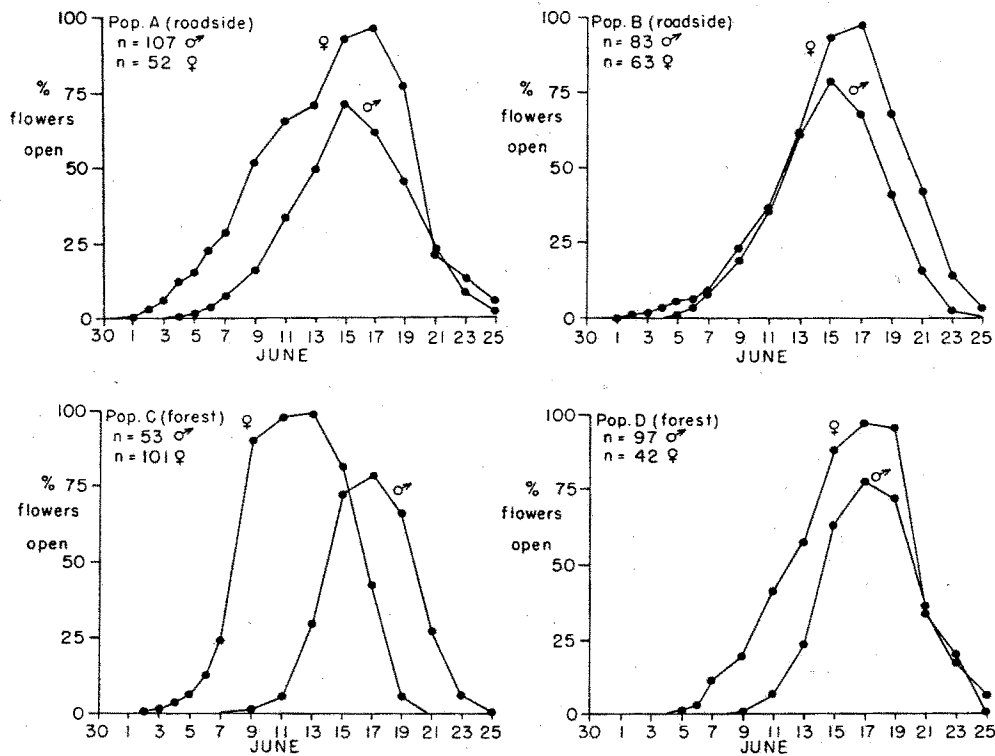


FIG. 3. Phenology of female and male flowers of *Aralia nudicaulis* in four New Brunswick populations during 1980.

reduction in density, 47% for males and 35% for females, was not significantly different between the sexes ($t = 0.78$ following arcsin transformation; Sokal and

Rohlf, 1969). The overall density, regardless of sex, is very similar for plots containing both or only one type of inflorescence (Table 5).

TABLE 2. Flowering phenologies of male and female inflorescences of *Aralia nudicaulis*. Pairs were chosen daily for 13 consecutive days.

Days	♂ No. of fls./infl.	No. of days for all fls. to open	Av. rate of flower opening/day	♀ No. of fls./infl.	No. of days for all fls. to open	Av. rate of flower opening/day
1	116	7	16.6	62	4	15.5
2	132	7	18.8	18	6	3.0
3	96	11	8.7	70	4	17.5
4	153	9	17.0	65	6	10.8
5	99	8	12.4	76	5	15.2
6	111	9	12.4	51	5	10.2
7	151	8	18.9	79	7	11.3
8	154	6	25.6	69	4	17.2
9	69	5	13.8	82	6	13.6
10	192	5	38.4	65	4	16.2
11	126	7	18.0	79	5	15.8
12	79	7	11.3	45	2	22.5
13	88	7	12.6	68	6	11.3
\bar{x}	120.5	7.4	17.3	63.8	4.9	13.8

TABLE 3. Changes in sex ratio of male and female ramets during the flowering period of a roadside population of *Aralia nudicaulis* in New Brunswick.

Sampling date	N	Male	Female	Ratio	χ^2
June 2	254	110	144	0.76	4.55*
June 4	307	137	170	0.81	3.55
June 6	510	242	268	0.90	1.33
June 8	600	308	292	1.05	0.43
June 14	504	264	240	1.10	1.14

* $P < .05$ on hypothesis of 1:1 sex ratio.

Growth patterns.—The total dry weight of reproductive ramets increased until late July in both sexes, with females heavier at all but the first of the eleven harvests (Fig. 4a). A two-way ANOVA showed no significant interaction between sex and harvest time while both factors were significant at $P < .001$ (Table 6a). That the difference between the sexes is not due solely to fruit development in females can be seen in Figure 4b. With two exceptions, the vegetative component (petiole and leaf) of female reproductive shoots was heavier than the vegetative fraction of males. Again, sex and harvest were highly significant sources of variation ($P < .001$) with no interaction detected using a two-way ANOVA (Table 6b). Initial relative growth rates were calculated for the vegetative fraction of both sexes over the first

three harvests (replicated through random grouping). The value for females ($0.310 \pm 0.098 \text{ wk}^{-1}$) is significantly greater than that for males ($0.154 \pm 0.066 \text{ wk}^{-1}$) at $P < .01$ ($t = 3.22$, $n = 6$). The senescence rate, calculated as the negative of relative growth rate over the last two months of harvests, does not differ between sexes ($0.439 \pm 0.322 \text{ wk}^{-1}$ for females, $0.318 \pm 0.068 \text{ wk}^{-1}$ for males, $t = 0.82$, $n = 5$).

The patterns of dry weight allocation within female and male ramets from flowering through to senescence are illustrated in Figure 5. The proportions of dry weight found in petiole and leaf are similar in both sexes; it is primarily in reproductive structures and scapes that they differ. At peak flowering, the reproductive effort (including the scape) of male ramets is $17.1 \pm 4.4\%$ compared to $10.1 \pm 2.5\%$ in females ($t = 7.50$, $n = 30$, $P < .001$) but declines steadily thereafter as the scapes and inflorescences wither. In female ramets reproductive effort increases as fruit matures, reaching a maximum of $23.3 \pm 8.9\%$ on July 9. Although not all of the fleshy, purple-black sarcochores have matured by mid July, predation and removal by dispersal agents reduced the biomass of female reproductive structures sampled in the field. By late August no fruits are

TABLE 4. Sex ratios of male and female ramets of *Aralia nudicaulis* from roadside and forest sites in New Brunswick.

Habitat	Area sampled (m × km)	N	Male	Female	Ratio	χ^2
Roadside 1	50 × 0.1	623	318	305	1.04	0.19
Roadside 2	2 × 2.0	360	184	176	1.05	0.18
Roadside 3	2 × 2.0	240	125	115	1.09	0.42
Roadside 4	2 × 1.0	180	93	87	1.07	0.20
Roadside 5	2 × 5.0	356	149	207	0.72	9.45**
Forest 1	30 × 0.1	671	467	204	2.29	103.08*
Forest 2	30 × 0.1	550	437	113	3.87	190.87*
Forest 3	40 × 0.1	522	340	182	1.87	47.82*
Forest 4	2 × 1.0	98	91	7	13.00	72.00*
Forest 5	2 × 1.0	123	64	59	1.08	0.20
Forest 6	2 × 1.0	110	54	56	0.96	0.04
Forest 7	2 × 1.0	90	62	28	2.21	12.84*
Forest 8	2 × 1.0	118	78	40	1.95	12.24*
Forest 9	2 × 1.0	147	133	14	9.50	96.33*

* $P < .001$ on hypothesis of 1:1 sex ratio.
 ** $P < .005$ on hypothesis of 1:1 sex ratio.

TABLE 5. Density and distribution of 1,244 male and 499 female ramets of *Aralia nudicaulis* in a one hectare forest block in New Brunswick. The block was subdivided into 100 10 × 10 m plots.

Sex distribution	No. of 100 m ² plots	Av. density per plot	Av. density per plot	Overall density per plot	t
♂	26	22.3 ± 16.5	—	16.9 ± 14.9	3.15**
♀	18	—	9.2 ± 7.3		
♂ + ♀	56	11.9 ± 12.6	6.0 ± 4.0	17.8 ± 12.6	3.23**
t		3.14**	2.37*	0.30 NS	

* $P < .05$, ** $P < .01$.

left on infructescences. Petiole, leaf and scape decrease in dry weight in both sexes from late July onward, but leaves are shed more readily and supporting structures remain. The scape is especially persistent in females, often remaining after all other parts have disintegrated or been removed by grazers.

Reproductive effort measured at peak flowering is negatively correlated with total biomass in both males ($r = 0.559$, $t = 3.57$, $P < .01$) and females ($r = 0.378$, $t = 2.16$, $P < .05$). Thus, in spite of a positive correlation between the weight of the vegetative and reproductive fractions in both sexes ($r = 0.434$, $t = 2.55$, $P < .02$ for females; $r = 0.379$, $t = 2.17$, $P < .05$ for males), there is a tendency for larger ramets to have a relatively small reproductive effort and vice versa. Although flower number is positively correlated with the weight of scape and reproductive structures in males ($r = 0.371$, $t = 2.11$, $P < .05$) this relationship does not hold in females ($r = 0.218$, $t = 1.18$, $P < .30$). Female ramets with a greater reproductive biomass will not necessarily have more flowers per inflorescence whereas in males, flower production increases with reproductive biomass.

DISCUSSION

Secondary sex characters in dioecious flowering plants are genetic differences between males and females in characters other than the androecia and gynoecia (Lloyd and Webb, 1977). Although secondary sex characters are a feature of both plants and animals, such dimorphisms between the sexes tend to be less pronounced

in plants, due to their sedentary habit and absence of behavioral adaptations. Some secondary sex characters in dioecious plants appear to have a direct adaptive value, whereas other features of sexual dimorphism are viewed simply as consequences of the different roles of male and female plants rather than as products of direct selection (Lloyd and Webb, 1977). In particular, different growth rates have been interpreted as the result of the differential expenditure on reproduction (Darwin, 1877; Lloyd, 1973; Hancock and Bringham, 1980). However, there are few studies of the patterns of resource allocation in natural populations of dioecious species, so that arguments concerning reproductive costs lack a quantitative basis.

It is generally assumed that the reproductive effort (Harper and Ogden, 1970) of females is greater than that of males. Our results demonstrate that in *Aralia nudicaulis* this relationship changes during the season. In fact, both the reproductive effort and the absolute biomass of reproductive structures of male ramets is significantly higher than of females in early June, due to the larger number of flowers on male inflorescences. However, the relationship is reversed within a 2-wk period, as a result of the rapid termination of female flowering and concomitant swelling of fruits. Reproductive expenditure in females increases during June and July as fruits mature and, for a 6-wk period, female flowering ramets incur a cost not experienced by males. Assuming dry weight to be an adequate measure of metabolic cost (Hickman and Pitelka, 1975) and that

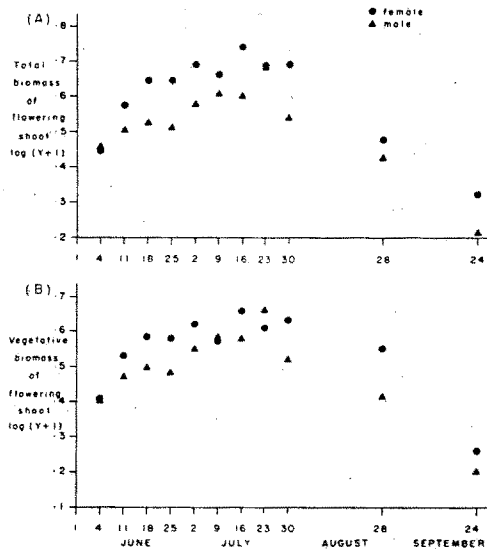


FIG. 4. Seasonal changes in the total biomass and vegetative biomass of female and male flowering ramets of *Aralia nudicaulis*.

there is some overall limitation on energy expenditure, it seems likely that males would have more resources available for maintenance, vegetative growth, or flowering in subsequent years than females. This argument assumes that the ramets of *A. nudicaulis* behave as semi-autonomous units. It is quite possible that at the genet level the total reproductive effort of males exceeds that of females because of the ap-

TABLE 6. Two-way ANOVA, $\log(Y + 1)$ transformation of the effect of sex and harvest time on the total biomass of flowering shoots and the vegetative biomass of flowering shoots in *Aralia nudicaulis*.

Source of variation	SS	d.f.	MS	F
a) Total biomass of flowering shoot				
Sex	0.7424	1	0.7424	47.0836*
Harvest	4.2659	10	0.4266	27.0531*
Interaction	0.2347	10	0.0235	1.4889
Error	4.8567	308	0.1580	
b) Vegetative biomass of flowering shoot				
Sex	0.2876	1	0.2876	16.7724*
Harvest	4.0176	10	0.4018	23.4275*
Interaction	0.2473	10	0.0247	1.4421
Error	5.2819	308	0.0172	

* $P < .001$.

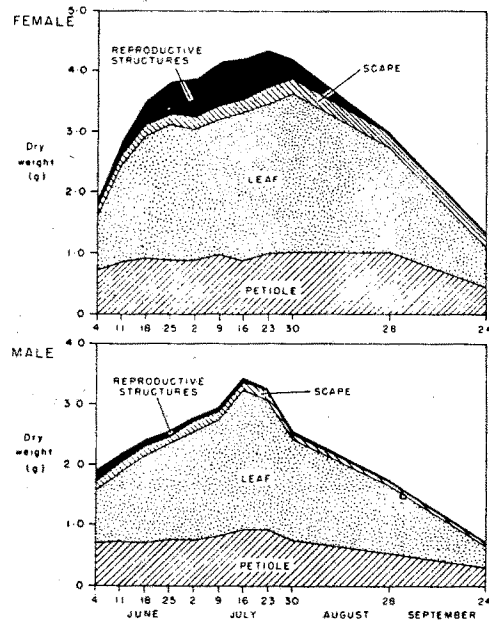


FIG. 5. Seasonal changes in the patterns of dry weight allocation in female and male flowering ramets of *Aralia nudicaulis*.

parently greater flowering propensity of male ramets (see below).

An interesting finding of this study is that male and female ramets differ in several growth characteristics. Female flowering ramets exceed males in both total and vegetative biomass. This feature is related to the greater growth rate of the vegetative parts of female ramets as well as to the production of fruits. Differences in relative growth rate between the sexes were only evident in the month of June. During this period the understory is open and incident light levels are greatest. During July and August, heavy shading develops due to the formation of an extensive canopy of bracken. For the remainder of the season little shoot growth occurs and senescence rates are similar in male and female ramets.

In the perennial *Rumex acetosella*, Putwain and Harper (1972) found a marked asynchrony in the vegetative growth patterns of the sexes. Male shoots are precocious in early growth and senesce earlier than females. The earlier senescence of

males is also a feature of several annual species such as *Cannabis sativa* (Cook, 1914), *Trinia glauca* (Correns, 1928) and *Spinacia oleracea* (Sneep, 1962; Onyekwelu and Harper, 1979). Correns (1928) has attributed earlier male senescence to the shorter reproductive period of males. The similarity between male and female senescence rates in *A. nudicaulis* is probably related to the longevity and iteroparous nature of clones. Continued production of photosynthate and translocation of these resources into the underground rhizome is probably required for the growth of shoots in subsequent years.

While there is no apparent asynchrony in the growth and development of vegetative structures between the sexes of *A. nudicaulis*, clear differences in flowering phenology were observed. Females start flowering earlier than males both at the level of ramets and flowers in a population. Webb (1976) has suggested that early female flowering is necessary in sexually dimorphic New Zealand alpine Umbelliferae in order that cold winter temperatures do not damage developing fruit. Since fruiting and dispersal in *A. nudicaulis* occur during the warmest months of the year, it is unlikely that the early flowering of females is associated with inclement weather. Other explanations of the factors responsible for asynchronous flowering patterns between the sexes are required.

Early female flowering may be associated with competition for pollinators among the floral morphs. Since male inflorescences produce nearly twice as many flowers, and each flower produces both nectar and pollen rewards, females may be at a competitive disadvantage if insect visitors are limiting. The early appearance of most female inflorescences may be required for the development of a search image in pollinators, especially in populations where females are at a numerical disadvantage. Observations of the foraging behavior and preferences of pollinators visiting male and female inflorescences would be valuable in testing this hypothesis. The asynchrony in flowering

does not seem to affect fecundity, as fruit-set is generally high (Barrett and Helenurm, unpubl. data). Early female flowering is to some extent compensated for by a period of stigmatic receptivity long enough to enable pollination and fertilization.

Female inflorescences have a narrower range of flower number (40–110) in comparison with males (50–189). Moreover, in females there is no correlation between reproductive biomass and flower production, whereas these variables are positively correlated in males. A similar situation occurs in *Triplaris americana*, where inflorescence production and size are positively correlated only in males (Melampy and Howe, 1977). These relationships suggest a more rigid control of flower production in females, which may result from the greater resource expenditure on reproduction by females. If flower production were to be increased in females, the average fitness of offspring might be reduced due to a limitation of resources.

Male-biased sex ratios have been interpreted as consequences of the unequal cost of reproduction in dioecious plants. However, differential growth and survival of the sexes will only occur if resources are limiting (Freeman et al., 1976). The roadside and spruce-fir forest habitats may differ in this respect, resulting in the different ramet sex ratios observed in this study. The critical difference between the habitats is probably light. In the forest, plants are heavily shaded, but there may be enough light on the cleared roadside edges that female clones have similar growth rates and produce as many flowering shoots as males. In the forest, any resource limitation may have greater adverse effects on the growth and flowering capacity of female than male ramets.

The difference in flowering ramet sex ratios of *A. nudicaulis* in roadside and forest sites may also be related to the age of populations. Disturbed sites in the boreal forest favor seedling establishment and represent younger seral stages than the older forest sites where no seedlings were observed. Older populations would

be predicted to have a greater proportion of male ramets than those more recently established because repeated episodes of reproduction would amplify the bias due to cumulated periods of differential growth and survival. Similar ecological explanations to account for male-biased sex ratios have been proposed in several other dioecious species (Harris, 1968; Franken, 1970; Lloyd, 1973; Opler and Bawa, 1978).

A greater expenditure on reproduction in females could result in both reduced vegetative growth of clones and early mortality compared with males. Either of these processes would lead to a male-biased sex ratio. The smaller size and relative growth rate of male ramets of *A. nudicaulis* cannot be used as evidence to refute the differential vegetative growth hypothesis since ramet growth patterns do not necessarily reflect genet growth. In *Asparagus officinalis*, Robbins and Jones (1926) found that male plants are larger than females and produce more shoots. However, the weight of individual female shoots exceeds that of males. In *Populus tremuloides* clones in Colorado, Grant and Mitton (1979) described greater growth rates of female ramets compared to those of males, but it is not known if this particular growth parameter indicates an overall difference between the sexes in ramet production and clone size.

Data from the one hectare forest block are useful in evaluating the causes of the male-biased ramet sex ratio. The density of flowering ramets of males was significantly higher than that of females when plots containing only one of the sexes were compared. This pattern was also maintained in mixed plots. These data suggest a difference in flowering propensity (whether due to differential ramet production or a difference in the proportion of flowering ramets) rather than differential mortality between the sexes. Given the extensive nature of clones one would not expect the density of flowering shoots within clones to differ between sexes if only differential mortality was involved. It seems likely that differences in the flow-

ering propensity between male and female clones is the major factor responsible for the male-biased sex ratios of flowering ramets of *A. nudicaulis* in forest sites of central New Brunswick. Long-term censusing of marked clones would enable verification of this hypothesis.

SUMMARY

Aralia nudicaulis (Araliaceae) is a rhizomatous perennial which forms extensive clones and possesses a dioecious breeding system. In central New Brunswick, surveys of flowering ramets along roadsides revealed a 1:1 sex ratio. In forest sites however, a male-biased sex ratio occurs. Flowering female ramets of *A. nudicaulis* differ from males in a range of secondary sex characters. These include: significantly fewer flowers per inflorescence, earlier average flowering, greater total biomass, greater vegetative biomass, and higher relative growth rate during flowering. Reproductive effort in male ramets is significantly higher than in females at peak flowering. Subsequently, male inflorescences wither while female reproductive effort increases to a maximum during fruit maturation. Thus, for a 6-wk period, female ramets incur a cost not experienced by males. The timing and rate of senescence of male and female ramets are similar. A lower density of flowering female ramets in forest sites suggests that the flowering capacity of females is reduced under low light regimes in comparison with males. This is probably due to the greater resource expenditure associated with fruit production in females.

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