

TEMPORAL VARIATION OF GENDER IN *ARALIA HISPIDA* VENT. (ARALIACEAE)

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In many flowering plants inbreeding may be reduced by dichogamy, a difference in the timing of dehiscence of anthers and receptivity of stigmas in individual flowers. However, considerable geitonogamy (inter-flower pollination on an individual) can occur if flowers on the same plant are in different developmental conditions. Restriction of geitonogamy can be achieved if all flowers on an individual at a given time are in the same sexual phase. This condition is particularly well documented in the Umbelliferae where plants alternate between male and female functions several times, as synchronized cohorts of umbels bloom sequentially (Müller, 1883; Ponomarev, 1960; Cruden and Hermann-Parker, 1977).

Temporal differences in the functioning of male and female organs of flowering plants are a common feature of monoecious and andromonoecious taxa (Mae-Kawa, 1924; Lloyd, 1972; Gilbert, 1975; De Jong, 1976; Bawa, 1977; Frankel and Galun, 1977; Webb, 1979; Primack and Lloyd, 1980). Nevertheless, the description and functional analysis of these complex sexual systems have lacked a firm theoretical basis (Charlesworth and Charlesworth, 1979). The recent formulation of techniques for the measurement of gender expression in plant populations (Lloyd, 1979, 1980) has aided the development of quantitative approaches to plant mating systems. Such quantification is likely to assume new importance in light of the recent proposals by Willson (1979),

Bawa (1980), and Givnish (1980) that differences in sexual function among the members of a population of hermaphrodites may be involved in the evolution of dioecy via sexual selection (but see Thomson and Barrett, 1981).

Lloyd (1980) contrasts the 'phenotypic gender' of a plant, which depends on the ratio of male to female functioning flowers, to the 'functional gender,' which depends on the ratio of offspring produced through ovules and pollen. Both measures can range from 0 (extreme maleness) to 1 (extreme femaleness). Functional gender is determined by the interaction of the phenotypic gender of an individual with the sexual composition of the interbreeding population. The number of offspring produced by the pollen of an individual will depend on the number of other pollen-bearing flowers which are competing to fertilize available ovules (see Janzen, 1977; Willson, 1979).

Values for functional gender estimated by Lloyd (1980) are based on the total production of male and female flowers during the flowering season. However, if the sex ratio in a population is not constant through time, there may be variation in the functional gender of individuals not accounted for by Lloyd's formulation. More accurate estimates of gender can be obtained by using daily counts of flower production. We observed the flowering behavior of *Aralia hispida* Vent. (Araliaceae), an andromonoecious, clone-forming perennial herb which exhibits synchronized protandry, in sufficient detail to calculate estimates of gender which reflect the temporal heterogeneity of sex expression.

In this paper we describe the proportion

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of hermaphrodite flowers in three populations of *A. hispida* and summarize the reproductive behavior (timing and success) of individual flowers and ramets. We then show that at the clonal and population levels these behaviors result in complex spatial and temporal patterns of gender expression. An estimate of gender which accounts for temporal variability is then developed and the adaptive significance of male and female flowering patterns is discussed.

General Description of Aralia hispida

Aralia hispida occurs principally in disturbed sandy sites such as clearings, roadsides and burnt areas in mixed coniferous and hardwood forests of northeastern North America (Gleason and Cronquist, 1963). Populations of *A. hispida* are composed of small colonies comprised of vegetative and reproductive ramets.

Flowering ramets of *A. hispida* are variable in size (0.1–2 m) and in the numbers of umbels (1–27) and flowers (72–1,068). During about a six-day period the flowers of the single, terminal, primary umbel open centripetally and function as males (i.e., anthers dehisce and nectar is secreted); they then shed both anthers and petals and the nectar dries. After all flowers in the umbel have completed the male phase, those which opened last become female. The onset of female function in hermaphrodite flowers is indicated by the lengthening and divergence of the five styles (see below), which remain appressed in male-only flowers. Most flowers again secrete nectar when functioning as females. Male-only flowers are found at the edges of umbels and hermaphrodite flowers are located centrally.

The female phase of the primary umbel then lasts for 2–3 days, after which time the secondary umbels synchronously enter a male phase, then a female phase as above. In all but small ramets, synchronized tertiary umbels then pass through male and female phases (extremely large plants may have some umbels in a quaternary order). Thus each ramet passes through alternating male and female states. Unless damaged by herbivores,

male-only flowers are retained through fruit development. It is thus possible to sample post-flowering plants before fruits are lost and classify flowers as (1) male-only, (2) hermaphrodite which set fruit, or (3) hermaphrodite which failed to set fruit. In a small proportion of flowers the status cannot be ascertained due to herbivory or incomplete development of reproductive organs. In our studies these categories were eliminated from the analyses.

The small green flowers of *A. hispida* are attractive to a variety of insect visitors, of which bumble bees (especially *Bombus vagans* F. Smith and *B. terricola* Kirby) are probably the most important pollinators. Fruits almost always contain five seeds and are purplish-black sarcochores eaten by vertebrate dispersers. As the fruits ripen and darken, the retained male-only flowers turn red, which may make the infructescence more conspicuous to birds.

MATERIALS AND METHODS

The three study sites at which experimental work was undertaken are in the vicinity of Doaktown, Northumberland Co., New Brunswick, Canada, and are referred to as Logging Road, Clearing, and Highway. At each of the three sites 50 flowering ramets were harvested at random to estimate variation in the proportion of male and hermaphrodite flowers among ramets and among umbel orders. All remaining experimental work was undertaken at the Logging Road site.

To document the flowering schedule of ramets at this site, 50 ramets were selected before flowering commenced. The ramets represented a nearly complete sample along 100 m of road edge. Two ramets died during the flowering period (June 28–August 7, 1979). All newly opening flowers were marked daily by marking the flower pedicels with felt-tip marking pens. Umbels of each ramet were identified with various colors of thread and were harvested progressively as fruits ripened. Thus, the dates of anthesis and fate of each of the 15,552 flowers in the sample were recorded.

The height of each of the 48 ramets was

recorded and all ramets were classified into 14 'clonal groups' of close neighbors. All ramets in the same clonal group were within 0.5 m of each other; different clonal groups were separated from one another by at least 5 m. Thus groups or colonies are separated discretely enough in space that it is unlikely that ramets in different groups belong to the same clone. We are less certain that all members of a group belong to the same clone, but experience in excavating other clones suggests that they probably do.

Since clonal differences in gender have implications for the evolution of gender patterns, an analysis of covariance was performed on the relationship between the proportion of hermaphrodite flowers (arcsine-transformed), plant height, and genet membership. Height was entered as a covariate. Genet membership, determined by spatial pattern, was a main factor with 14 possible levels ('clones'). Parallel analyses for fecundity were also carried out.

To determine whether colonies of ramets ('clonal groups') were in sexual-phase synchrony, a 315 m transect was established during peak flowering. The 225 flowering ramets along the transect were sampled at two day intervals, between July 17–August 6, and the sexual phase and umbel order in flower recorded.

Observations of the average time course of events during anthesis of individual flowers were made at 2-hr intervals during daylight hours. To determine the period of receptivity of stigmas, pollen was applied at different times to stigmas previously bagged in paper Pollentector® bags (Carpenter Paper Co., Des Moines, Iowa). After hand-pollination the flowers were rebagged and fruit and seed set determined. Unpollinated bagged flowers were left as controls.

RESULTS

Flowering Behavior of Individual Flowers and Ramets

Timed observations of anthesis of individual flowers are summarized in Figure 1a. The sample includes male and hermaphrodite flowers since there were no

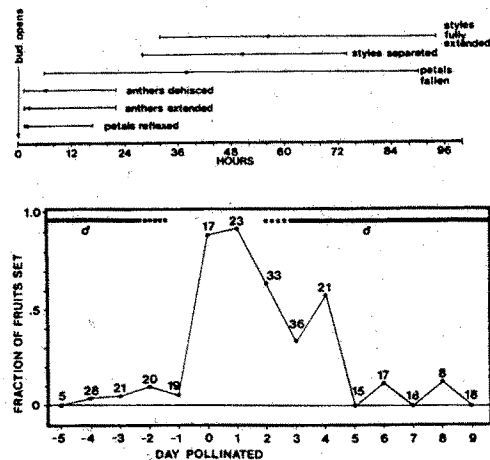


FIG. 1a. The time course of flowering in individual florets of *Aralia hispida*. Ranges are indicated by bars. Sample sizes vary with the character measured: for petal reflection $n = 66$ florets; for anther extension, $n = 59$; anther dehiscence, $n = 37$; petal drop, $n = 26$; stylar divergence, $n = 17$; stylar extension, $n = 16$. The great range in stylar divergence times results from the greater synchrony of female function than male function of hermaphrodite flowers (see text, also Fig. 2). 1b. Results of timed pollinations to confirm the coincidence of stylar divergence and stigmatic receptivity in *Aralia hispida*. Sample sizes (number of hand-pollinated flowers) are shown for each treatment. Day 0 is the day on which styles diverged. The heavy horizontal bars with the ♂ symbol indicate periods of pollen availability on a typical ramet.

apparent differences in the timing of the male phase in the two flower types. Bud break, anther and petal extension are usually completed during one day. The divergence of the styles occurs approximately three days after flower opening and dehiscence of the anthers, but this interval varies, being longer in earlier flowers (see below). The results of timed crosses in Figure 1b confirm that stylar divergence and stigmatic receptivity coincide, and that receptivity remains moderately high for about four days thereafter. Most stigmas cannot be pollinated geitonogamously when they first open because pollen is unavailable, but most are still potentially receptive when pollen from the next order of umbels becomes available (see Cruden and Hermann-Parker, 1977).

The time sequence of flowering in a sin-

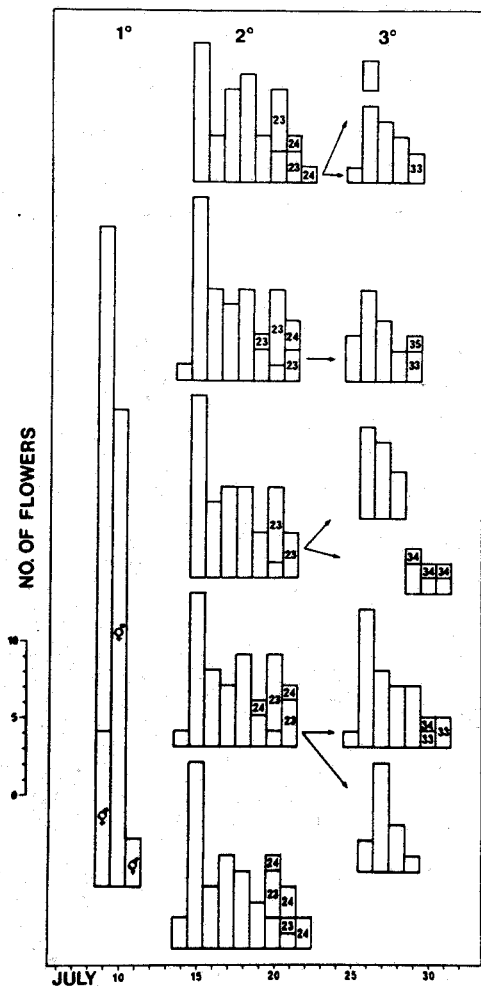


FIG. 2. The flowering pattern of a representative ramet of *Aralia hispida*. The single primary, five secondary, and seven tertiary umbels are each shown separately. All flowers have a date of male opening (anther dehiscence), and hermaphrodite flowers have a date of female opening (stylar divergence) as well. The bars of the histogram refer to male openings only. Empty sections of the bars represent male-only flowers, while sections containing ♂ symbols or numbers represent hermaphrodite flowers. Where a number is given, it gives the date of female function for the flowers whose male function date is shown by the bar section. Where only the ♂ symbol is given, the date of female function was not recorded.

gle ramet is illustrated in Figure 2. Especially noteworthy is the degree of internal synchrony among umbels and the lack of overlap between the male and female

phases. Flowers open as males during 20 days, whereas females open during seven days. Only the later opening flowers in an umbel are hermaphroditic and the proportion of hermaphrodite flowers declines with umbel order (and see below).

Hermaphrodite flowers have two "openings," one male and one female. The 45 hermaphrodite flowers in the secondary umbels of this ramet opened as males during a four-day period (June 19–22) whereas the female openings lasted for only two days (June 23–24). Variance of the male opening time is significantly greater than that of female opening of the same flowers ($F_{44,44} = 2.551$, $P < .005$). The female bloom is more compressed. Hermaphrodites which open early as males are 'held' for as long as five days before opening as females, while later flowers begin female function only two days after male opening. Similar patterns are evident among the other orders of umbels.

Population Variation in Hermaphroditism and Fecundity

The overall partitioning of the numbers of flowers and flower types (male and hermaphrodite) among umbels is similar in the three populations sampled (Table 1). Approximately half the flowers in the three populations of *A. hispida* are produced on the secondary umbels. Flower production declines in subsequent umbel orders. As noted above, the proportion of hermaphrodite flowers decreases with umbel order, i.e., as the season progresses. Among the three populations the proportion of hermaphrodite flowers is quite similar (Highway 26.6%, Clearing 29.9%, Logging Road 35.3%).

Fecundity, defined as the proportion of hermaphrodite flowers which set fruit, generally declines with umbel order although at the Logging Road site fecundity is highest in flowers of the secondary umbels (Table 1). In all populations the fecundity of tertiary umbels is lower than in primary and secondary umbels. Ramets with quaternary hermaphrodite flowers occurred in the Highway sample only;

TABLE 1. *The proportion of hermaphrodite flowers and male flowers and fecundity in three populations of Aralia hispida in New Brunswick.*

Population	Umbel level	Total fls. in sample	Freq. fls. at level	♂		♀		Fecundity*
				No. of fls.	Freq.	No. of fls.	Freq.	
A. Clearing site (N = 51)	1	1,481	.200	1,066	.719	415	.281	.970
	2	4,062	.548	1,070	.263	2,992	.737	.949
	3	1,843	.249	76	.041	1,767	.959	.921
	4	21	.003	0	0	21	1.000	—
	Total	7,407	1.000	2,212	.299	5,195	.701	.958
B. Highway site (N = 49)	1	1,849	.155	1,468	.794	381	.206	.932
	2	5,590	.470	1,460	.261	4,130	.739	.926
	3	3,924	.330	226	.058	3,698	.942	.841
	4	530	.045	11	.021	519	.979	.818
	Total	11,893	1.000	3,165	.226	8,728	.734	.922
C. Logging Rd. site (N = 50)	1	1,552	.174	1,044	.673	508	.327	.970
	2	4,479	.502	1,737	.388	2,742	.612	.991
	3	2,813	.315	373	.133	2,440	.867	.887
	4	82	.009	0	0	82	1.000	—
	Total	8,926	1.000	3,154	.353	5,772	.647	.972

* Fecundity = # fruiting flowers/# hermaphrodite flowers.

these exhibited the lowest values for fecundity recorded in the study.

The means, standard deviations and ranges of flowering characters measured on the 48 ramets intensively studied at the Logging Road site are given in Table 2. There is considerable variation in the expression of most characters in the sample. A greater than ten-fold range exists in number of flowers produced, and the phenotypic gender of the ramets, expressed as the fraction of hermaphrodites, ranges from 0.136–0.487.

Control of Hermaphroditism and Fecundity

Field observations suggested that larger ramets produced a higher proportion of hermaphrodite flowers. If femaleness were more costly than maleness it would be reasonable to predict a greater proportion of hermaphrodite flowers in larger ramets. However, the degree of hermaphroditism also seemed to vary, independently of size, among the aggregations of ramets that probably corresponded to clones. This occurred in the absence of any obvious differences in microhabitat among 'clonal groups,' although small scale edaphic differences or past blooming history obviously cannot be ruled out.

At all umbel levels, the presumed clonal identity of ramets explains a significant component of the variance in the proportion of hermaphrodite flowers, after adjustment for height (Table 3). Height itself is an insignificant influence at the primary level, but is highly significant at higher umbel levels and weakly significant over all umbels. As expected, the correlation between ramet height and degree of hermaphroditism is positive. If genetic factors are determining phenotypic gender, in addition to ecological factors, the influence is most strongly expressed in the primary umbels. At lower umbel levels, ramet size emerges as an equally strong correlate.

In contrast, fecundity patterns are relatively uninfluenced by clonal identity but ramet height has highly significant effects at the secondary and tertiary levels (Table 3).

Temporal Patterns of Gender

The sexual condition of a population of protandrous plants will be male at the onset of flowering and female at the end of bloom. In *A. hispida*, where ramets exhibit several cycles of gender alternation, it is of importance to establish whether such cycles are evident at the population

TABLE 2. Mean, standard deviation and range for flowering characters of ramets in a population of *Aralia hispida* in New Brunswick. (n = 48 ramets.)

Character	\bar{x}	SD	Range
Total fls. per ramet	324.0	202.4	72.0-1,068.0
Total umbels per ramet	9.3	5.3	3.0-27.0
Number of days in flower	23.2	5.7	13.0-36.0
Height (cm)	60.6	14.9	28.5-93.0
Dry weight (g)	5.0	3.4	0.9-13.8
Fraction of fls. in 1° umbel	.211	.114	.057-.574
Fraction of fls. in 2° umbels	.570	.113	.340-.906
Fraction of fls. in 3° umbels	.218	.180	0.0-.531
Fraction of ♂ fls.	.301	.078	.136-.487
Fraction of ♂ fls. in 1° umbel	.636	.221	.226-1.000
Fraction of ♂ fls. in 2° umbels	.296	.128	.0270-.811
Fraction of ♂ fls. in 3° umbels (n = 37)	.104	.078	0.0-0.233

level. Presumably if different ramets commence flowering at varying times any waves of gender expression at the population level would be dampened. However, damping was not complete for the subpopulation of 48 ramets utilized for flower counts (Table 2). In these ramets the variation in date of initial blooming (SD = 3.03 days) is relatively small in comparison to the mean 'wave length' of ramets (average no. of days between primary and secondary flowering peaks = 8.92, SD = 1.22, N = 48; and between secondary and tertiary peaks = 10.12, SD = 1.09, N = 25). The population

flowering curve (Fig. 3a) and the ratio of female-functioning to male-functioning flowers through time (Fig. 3b) confirm that the wave-form expression of gender found in individual ramets was translated to this subpopulation of ramets as a whole.

The census-transect data of 225 ramets provide further evidence of this type of periodicity (Fig. 4a). Although the proportion of male ramets declined almost monotonically during the period sampled, two modes are present even in this large sample of ramets (Fig. 4b). Flowering curves based on the numbers of flowers

TABLE 3. Summary of analyses of covariance to determine the dependence of hermaphroditism and fecundity on ramet size and presumed clonal origin in *Aralia hispida*. The 14 'clones' are treated as a main factor with 14 possible levels and ramet height as a covariate. Proportional data (n = 48 ramets) are arcsine-transformed. Degrees of freedom vary because not all ramets produced tertiary umbels or hermaphrodite flowers at the tertiary level.

Variates	Sources of variation					
	Height			Clonal origin		
	F	d.f.	P	F	d.f.	P
1. Fraction of ♂						
a) in 1° umbel	1.264	1,33	ns	4.958	13,33	<.001
b) in 2° umbels	44.885	1,33	<.001	4.868	13,33	<.001
c) in 3° umbels	7.292	1,22	.013	3.535	10,22	.007
d) in all umbels	3.850	1,33	.055	3.942	13,33	<.001
2. Fraction of ♂ which set fruit						
a) in 1° umbel	.714	1,33	ns	.674	13,33	ns
b) in 2° umbels	25.194	1,33	<.001	1.642	13,33	ns
c) in 3° umbels	10.392	1,16	.005	2.752	9,16	.037
d) in all umbels	1.321	1,33	ns	.362	13,33	ns

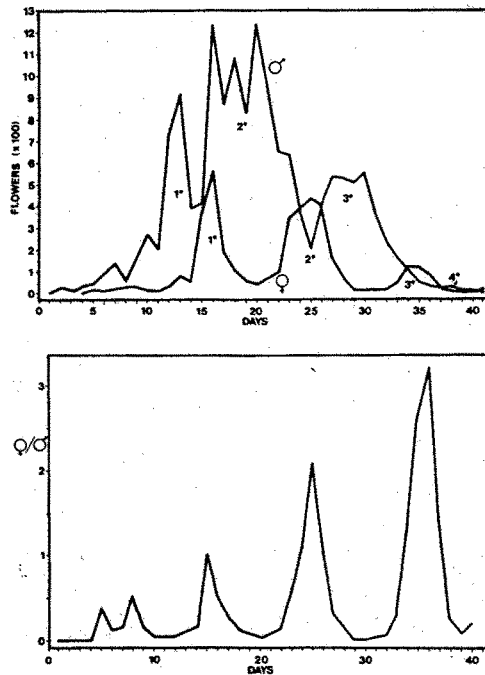


FIG. 3a. The flowering through time of the Logging Road subpopulation of *Aralia hispida*. The total numbers of florets opening as males and as females each day are given. 3b. The ratio of female to male flowers in the Logging Road subpopulation of *Aralia hispida* as a function of time. The troughs indicate periods of intense competition among males for mates.

rather than the sex of ramets would of course show sharper peaks than those illustrated.

The transect data confirm the impression gathered in the field that 'clonal groups' (1) tend to be synchronized with respect to their sexual phase and (2) tend to switch from one developmental stage (umbel order) to the next during the same period. For statistical confirmation of this pattern the hypothesis that the sexual phase of a ramet is independent of its nearest neighbor is tested by a contingency table (Table 4). The hypothesis is rejected, the data indicating a significant tendency for neighboring ramets to be in similar sexual and developmental phases. The data tested in Table 4 are from the first sampling date (July 17); tests carried out on successive censuses give similar results.

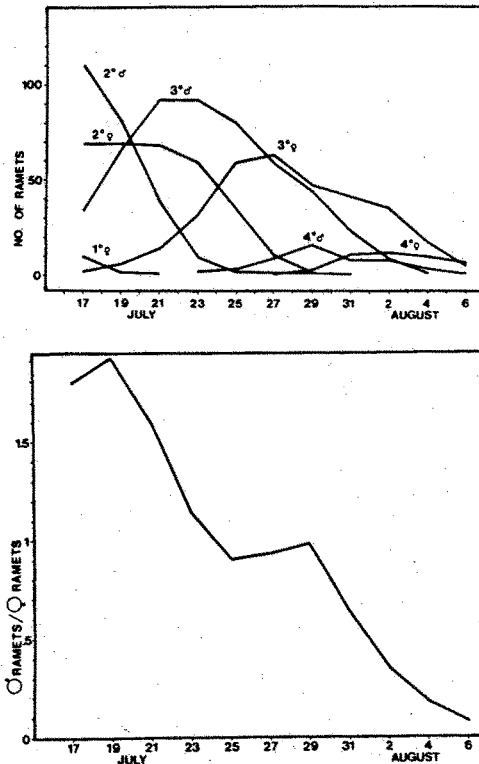


FIG. 4a. The numbers of ramets in each sexual phase through time for the Logging Road census transect of 225 ramets of *Aralia hispida*. Only the latter half of the flowering period was monitored. 4b. The ratio of male to female ramets for the Logging Road census transect of *Aralia hispida* ramets. Even in this large sample ($n = 225$), the sex ratio shows peaks in time.

The complete data set for the sexual and developmental stages of the 225 ramets from July 17–August 6 is available on request from the authors.

DISCUSSION

The flowering behavior of *Aralia hispida* results in complex patterns of gender expression at the population level. Temporal heterogeneity in population sex ratio affects the functional gender in ways not addressed by Lloyd's measure G (Lloyd, 1980): Specifically, plants which are in their male phase when most other plants are female might be expected to fertilize more ovules than those which bloom dur-

TABLE 4. Contingency table comparing the sexual phase of a ramet of *Aralia hispida* with the sexual phase of its nearest neighbor. (Ramet n is compared to ramet $n + 1$). The brackets indicate rows and columns which were pooled to raise expected values to at least five before calculating χ^2 . There is a highly significant tendency for neighboring ramets to be in the same sexual phase ($\chi^2 = 91.84$, d.f. 4, $P < .001$).

		Phase of ramet $n + 1$						
		1°♂	1°♀	2°♂	2°♀	3°♂	3°♀	
Phase of ramet n	1°♂	0	0	1	0	0	0	1
	1°♀	0	0	6	4	1	0	11
	2°♂	1	6	66	27	6	0	106
	2°♀	0	3	30	30	7	0	70
	3°♂	0	1	5	9	19	1	35
	3°♀	0	0	1	0	0	0	1
		1	10	109	70	33	1	224

ing periods of more intense male competition. A modified gender index G^* can be derived which takes this temporal heterogeneity into account by estimating the male and female success of each ramet on each day of its bloom and summing over time; details are given in the Appendix.

Although G and G^* are ostensibly measures of the same quality, the two values for the 48 flowering ramets of *A. hispida* seldom coincide. A significant positive relationship exists between the measures, but there is considerable scatter ($r^2 = .465$). The ramets with the most extreme disparities between G and G^* had G/G^* ratios as high as 1.9 and as low as 0.7. G^* varies more than G , although smooth curves are evident for both in plots of gender-rank as a function of gender (Fig. 5). A smooth curve indicates a monomorphic population, with continuous variation in gender, rather than a sexually dimorphic population (Lloyd, 1980).

Deviations of G^* from G illustrated in Figure 5 show an interesting pattern. G^* is reduced relative to G , i.e., a ramet's reproduction is more male-biased, when the ramet is out of sex-phase synchrony with the population. Synchrony is measured by the product-moment correlation r between the male flowers produced each day by the ramet and the male flowers produced by the population. This occurs because ramets which are out of phase are by definition bearing male-functioning flowers at a time when most of the pop-

ulation is bearing female-functioning flowers. As a result such male flowers encounter an abundance of potential mates and little competition from other males.

A ramet's success in reproduction through pollen, as measured by the estimated number of fruits produced paternally per male flower, is negatively correlated with the degree of synchrony between the ramet and the population (Fig. 6). Some of the scatter in this relationship is attributable to 'clone group' differences; ramets which are located closely in space tend to occupy similar regions of the figure.

In all ramets, the estimated number of fruits fathered per male flower is highly variable from day to day. Male reproduction is usually concentrated in one or a few days even though male flower production is relatively constant through time. In contrast, female reproduction and female flower function match almost exactly because fecundity in the population is so high. Figure 7a compares female and estimated male reproduction through time for a selected ramet which was well synchronized with the population (the product-moment correlation r between male flowers produced by the ramet and by the population = .868). Over a third of the fruits produced by pollen from this ramet are fertilized by the 84 male flowers produced on July 16. These constitute only 16% of the total male flowers produced by the shoot. However, these male flowers

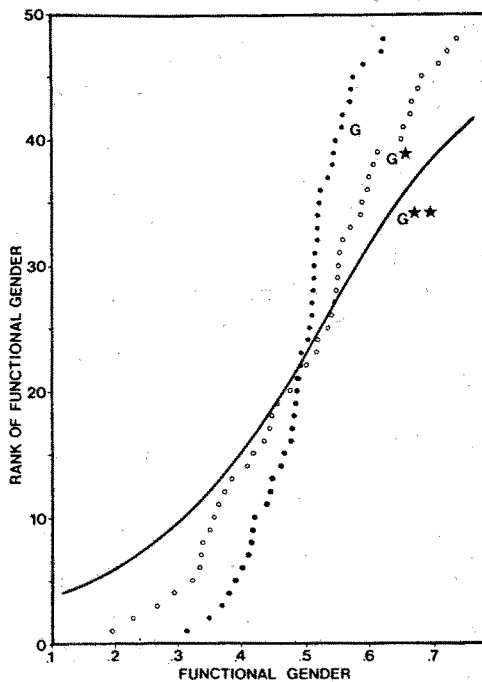


FIG. 5. Plots of the two functional gender estimates G and G^* and the ranks of those estimates (symbols) for the Logging Road subpopulation of *Aralia hispida*. This presentation, after Lloyd (1980), demonstrates a continuous range of gender within the sample, as opposed to discontinuous variation between essentially male- and female-functioning ramets. When temporal variation is taken into account, the variance in gender is more extreme (G^* compared to G), and if spatial variation were also included, the variance would be augmented further (G^{**}).

are not the most successful at reproduction, as Figure 7b illustrates. Male flowers produced on June 26 have the highest estimated offspring/fruit production ratio, slightly greater than unity. This is extremely high for a male flower and greater than is possible for female flowers.

Natural selection might be expected to increase the production of male flowers at "optimal times" if such times were predictable. However, these times are determined by the flowering behavior of the other members of the population, and it is unlikely that a plant can assess this behavior and respond to it in any but the most generalized way. The one predict-

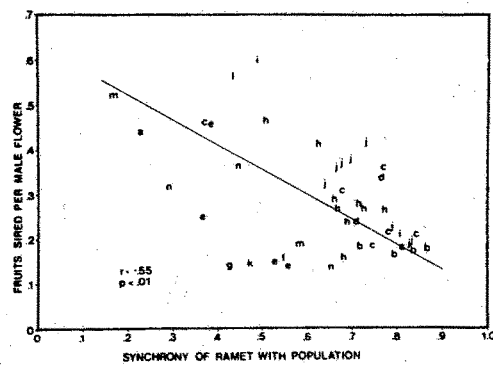


FIG. 6. The relative success of a ramet's male flowers as a function of synchrony with the population in *Aralia hispida*. Synchrony is measured by the product-moment correlation of daily male flower production by the ramet with production by the population. The letters identify apparently different clones; there is some tendency for ramets of a clone to cluster in this graph.

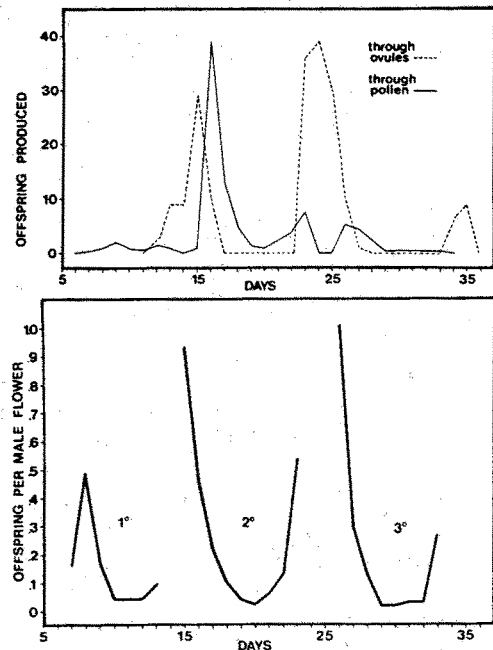


FIG. 7a. The estimated numbers of offspring (as fruits) produced through time by the pollen and ovules of a representative ramet of *Aralia hispida* which was well synchronized with the population. 7b. The reproductive efficiency of the male flowers produced by a representative ramet of *Aralia hispida* (see Fig. 7a) as a function of time, measured as the estimated number of fruits sired per male flower. The breaks between the curves represent days when the ramet functioned as a female only. The male flowers which are most successful are the earliest and latest produced within each umbel order.

able aspect of the relationship between individual and population bloom schedules is that most individuals will be synchronized with the population. This will mean that most umbels will have male success curves with the U- or J-shape evident in Figure 7b. The earliest, or latest, or both sets of flowers will usually be more successful than the middle. To the extent that flowering schedules are influenced by natural selection for efficient use of resources, this pattern of success should favor extended male flowering periods rather than tight synchrony within an umbel. Because female success is essentially uniform through time, there would be no selective advantage to spreading female flowering over many days, as in male flowering.

Other aspects of the pollination of *Aralia hispida* which may be predictable in an evolutionary sense concern pollinator behavior. In pairwise choice experiments, both the major (bumble bee) and minor (solitary bees, wasps, flies) pollinators show significant preferences for umbels with more open flowers. They also prefer male-phase umbels to female-phase umbels with the same number of open flowers. In addition bumble bees establish individual foraging areas, within which they visit particular ramets in repeatable sequences ("traplines") (Thomson, unpubl. data).

Pollinator discrimination against female or few-flowered umbels may exert a selective force favoring compression of female flowering in time. That is, the disadvantage of femaleness may be compensated by the advantage of an effectively larger umbel. Although we have not yet done so, it should be possible by more choice experiments to determine the female/male umbel size ratio which equalizes the attractiveness of the sexes. Similar pollinator behavior may account for the shorter duration of flowering in female ramets compared with male ramets in the dioecious *Aralia nudicaulis* (Barrett and Helenurm, 1981).

Thus, male flowering suggests a "bet-hedging" strategy, usually considered a

response to environmental unpredictability (Stearns, 1976). The reproductive environment of *A. hispida* has both unpredictable and predictable elements; it is predictable that male mating success will be exceptionally high on certain days, but unpredictable when those days will be. In contrast, the general availability of pollen makes it unlikely that female success varies greatly over time within an umbel; thus selection may act mostly to ensure visitation.

The reduced fecundity of tertiary hermaphrodites may be due, in part, to reduced pollinator attraction caused by the small number of female-functioning flowers in most tertiary umbels. An additional explanation for reduced tertiary fecundity is that maternal resource depletion may increase the abortion rate of pollinated flowers (see Willson and Rathcke, 1974; Willson and Price, 1977; Stephenson, 1979). A third reason is that there is extremely little pollen available from quaternary umbels for fertilizing the latest females. All three factors may act in concert and we have few data at present with which to separate their effects, although we have observed individually marked bees that repeatedly visited male phase ramets on a foraging trapline but then dropped the ramets from the trapline when they turned female.

Spatial Patterns

The census data demonstrate that temporal patterns of flowering within and among clones of *A. hispida* greatly alter the expression of gender. This implies differential success in reproduction of flowers produced at various times during the season. Although we lack comparable data on spatial pattern, it is probable that the arrangement of ramets and genets in space may be at least as important as the timing of anthesis.

Synchronized protandry in a clone-forming species, such as *A. hispida*, will be less effective as an outbreeding mechanism if the ramets of a clone are not maintained in synchrony. Since outcross-

ing is at least the most obvious advantage for the separation of male and female functions in time, we presume that mechanisms which favor intracolon synchrony have been selected in *A. hispida*. Further studies are required to reveal the environmental and developmental bases of intracolon flowering synchrony in the species.

The sex-phase synchrony of ramets within genets and the cloning habit of *A. hispida* result in non-panmictic populations with spatial structure. As a consequence the effective population female/male ratio (EF) should probably be defined separately for each ramet over its neighborhood, rather than the entire population. In this case EF differs for each clone and results in increased locational variance of EF . This increases the overall variance in functional gender relative to the variance in phenotypic gender. If a new gender measure G^{**} could be estimated, which accounted for both temporal and spatial heterogeneity, the G^{**} -rank vs. G^{**} curve should depart from the G curve to a greater extent than the G^* curve does (Fig. 5). That is, spatial variation in mate competition would make some plants more male, others more female. Quantification of this effect would depend, as Willson (1979) has pointed out, on monitoring pollen flow and the success of male flowers.

Evolutionary Implications

Although the ecological consequences of temporal and spatial heterogeneity in population sex ratio are fairly apparent, treatment of the evolutionary implications must be speculative. Certainly there would be strong local competition for mates which could bear on the evolution of sexual expression (Hamilton, 1967; Maynard Smith, 1978). If genotypically similar plants tend to bloom synchronously, mate competition would be strongest among close relatives. Conversely, rare genotypes would have a great advantage in a population if genetic differences usually result in synchrony differences.

A rare genotype advantage due to asynchrony could increase the reproduction (through pollen) of new colonists establishing in an area dominated by large existing clones. This would have the effect of increasing effective gene flow relative to mean distances of seed and pollen dispersal. Presumably, it could also help drive the evolution of traits conferring greater dispersability. Finally, we would expect that the inherent unpredictability of such a heterogeneous system would retard the evolution of sexual specialization through sexual selection mechanisms (Willson, 1979) because features which produce, say, disproportionate male success in one place may not have much effect in another place, in the next generation. Although phenotypic gender may be heritable, functional gender is likely to show lower heritability, especially when the plant-to-plant variability is exaggerated by temporal heterogeneity (G^* vs. G).

In the related Umbelliferae where both true dioecy and "temporal dioecy" of the sort shown by *A. hispida* occur, Cruden and Hermann-Parker (1977) and Webb (1979) have suggested that dioecy is the derived condition. Since "temporal dioecy" promotes outcrossing it is of interest to consider the selective forces responsible for shifts to dioecy since outcrossing arguments are more difficult to apply. Cruden and Hermann-Parker (1977) suggest a hypothesis of greater efficiency of resource use by the separate sexes (and see Putwain and Harper, 1972; Freeman et al., 1976; Lloyd and Webb, 1977; Onyekwelu and Harper, 1979). Mechanisms of sexual selection might also be invoked (see Willson, 1979; Bawa, 1980; Givnish, 1980). However, in a clone-forming species, outcrossing may become disrupted as clone size increases because intracolon synchrony would tend to break down, fostering geitonogamy. The dioecious condition in *Aralia nudicaulis*, which forms very extensive clones in New Brunswick forests (Barrett and Helenurm, 1981), may have been derived from an *A. hispida*-like ancestor in connection with

ecological or evolutionary shifts promoting a larger clone size.

SUMMARY

Aralia hispida Vent. (Araliaceae), a herbaceous, clone-forming, entomophilous perennial of disturbed forest sites in eastern North America, is andromonoecious. Synchronized cycles of protandry occur as each umbel order flowers and the periods of anthesis of flowers of successive orders do not overlap. Hence individual ramets exhibit alternating phases of gender expression during the flowering season and the separation in time of male and female function promotes outbreeding.

In three New Brunswick populations the proportion of hermaphrodite flowers decreased in successive umbels and ranged from 27–35% of the total number of flowers in the populations. The fecundity of hermaphrodite flowers also declined with umbel order although the values obtained (92–97%) were high for an outbreeding species. The presumed clonal identity of ramets explained a significant component of the variance in production of hermaphrodite flowers following analysis of covariance. Size of ramets had a weakly significant influence and the size and degree of hermaphroditism were positively correlated.

Surveys of the gender and developmental stage of flowering of *A. hispida* ramets indicated that 'clonal groups' tended to be synchronized with respect to gender and umbel stage. This flowering behavior leads to complex temporal and spatial patterns of gender expression. A ramet's success in reproduction through pollen is negatively correlated with the degree of synchrony between the ramet and the population. A dynamic measure of functional gender (G^*) is formulated which accounts for temporal variation in the expression of gender. An adaptive explanation for differences in the phenology of male and female function in *A. hispida* is presented.

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APPENDIX

Mathematical Formulations of Gender

Lloyd (1980) uses 'phenotypic gender' and 'functional gender' in two ways depending on whether 'gamete estimates' based on flower numbers or 'seed estimates' based on successful reproduction are measured. In this discussion we consider the latter only; definitions and symbols used are presented in Table 5, and in most cases follow Lloyd.

Lloyd's functional gender G_i is a static measure which estimates the ratio of the number of offspring produced by plant i through ovules to the number produced by pollen. The maternal contribution is the number of seeds produced, although we will use the number of fruits instead since the proportionality constant of 5.0 seeds per fruit cancels out in the calculation of gender. The paternal contribution is estimated by assuming that the fraction of all fruits in the population fertilized by pollen from plant i equals the proportion of all male flowers in the population produced by plant i . This estimation requires

an assumption of panmixis in both space and time (see Lloyd, 1980), violations of which are considered above.

A plant of a given phenotypic gender will have a greater (more female) functional gender G when it occurs in a population with many other male flowers since its own male flowers will face strong competition. Lloyd expresses this relationship by an equivalence factor (here denoted by EF) equal to the ratio of females to males. When $EF = 1.0$, $PF_i = G_i$. In general the static functional gender is:

$$G_i = f_i / (f_i + l_i EF),$$

and its relationship to the static phenotypic gender is:

$$G_i / P_i = (f_i + l_i) / (f_i + l_i EF).$$

In *A. hispida* there is great temporal variation in f_i , l_i , and EF . An expression equivalent to Lloyd's G_i

which takes this into account is derived as follows. The numerator (production through ovules) is simply the number of fruits produced by plant *i*, as above: $f_i = \sum_t f_{it}$; the denominator (production through pollen) is the sum over all days of the number of fruits fathered by plant *i* = (total fruits in population) ×

((male flowers of plant *i*)/(all males flowers)) = $(\sum_t f_{it}) / (\sum_t l_{it})$. Thus the dynamic functional gender is:

$$G^*_i = \frac{\sum_t f_{it}}{\sum_t \left[\left(\sum_t f_{it} \right) \cdot \frac{l_{it}}{\sum_t l_{it}} \right]}$$

TABLE 5. Algebraic terms used in the formulation of static and dynamic gender estimates. The equations for static gender G_i and most of the symbols follow Lloyd (1980).

	Symbol	Definition
Static formulation	<i>i</i>	subscript index for plants or ramets
	<i>t</i>	subscript index for time (days)
	<i>d</i>	number of female-functioning flowers
	<i>l</i>	number of male-functioning flowers
	<i>f</i>	number of flowers which set fruit
	<i>P</i>	phenotypic gender based on flowers (Lloyd's "gamete estimates") $P_i = d_i/l_i$
	<i>PF</i>	phenotypic gender based on fruits (Lloyd's "seed estimates") $PF_i = f_i/l_i$
	<i>E</i>	population female/male flower ratio (Lloyd's 'equivalence factor' for gamete estimates) $E = \sum_i d_i / \sum_i l_i$
	<i>EF</i>	equivalence factor for seed estimates $EF = \sum_i f_i / \sum_i l_i$
	<i>G</i>	functional gender, i.e., no. of gametes passed on through ovules/no. passed on through pollen, based on seed estimates. (An equivalent term may be defined from gamete estimates by substituting <i>d_i</i> for <i>f_i</i> and <i>E</i> for <i>EF</i> .) $G_i = f_i / (f_i + l_i EF)$
Dynamic formulation	G^*	G adjusted for temporal variation in ramet and population sex expression $G^*_i = \frac{\sum_t f_{it}}{\sum_t \left[\left(\sum_t f_{it} \right) \cdot \frac{l_{it}}{\sum_t l_{it}} \right]}$