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# Floral Phenology of Sex-changing Dwarf Ginseng (Panax trifolium L., Araliaceae)

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ABSTRACT.—This report documents phenological differences between the gender phases of a diphasic plant, *Panax trifolium*. Pollen presentation by males peaks later than pollen presentation by hermaphrodites and closely coincides with presentation of receptive stigmas by hermaphrodites. Males also have longer periods of pollen presentation than do hermaphrodites. Our results suggest that male-male competition has affected the differentiation of gender phases with respect to male reproductive traits.

INTRODUCTION

Selection for successful pollen donation is hypothesized to be a major force in floral evolution. Competition among pollen donors (male-male competition) has been invoked to explain the evolution of a variety of floral traits, including the sizes of floral parts and inflorescences and the amounts and timing of pollen and nectar production (Stephenson and Bertin, 1983; Willson, 1983; Lloyd, 1984; Sutherland and Delph, 1984; Stanton *et al.,* 1986; Charlesworth *et al.,* 1987; Queller, 1987; Bertin, 1988; Harder and Thompson, 1989; Barrett and Eckert, 1990). Because most angiosperms produce hermaphroditic flowers, the effects of variation in floral traits on paternal function may be confounded with effects on maternal function. For example, larger inflorescences may receive as well as donate more pollen than smaller ones. In one recent study, paternity analysis showed that male reproductive success was less strongly correlated with inflorescence size than was female reproductive success (Broyles and Wyatt, 1990).

Evidence for male-male competition in flowering plants has been sought from dioecious species, in which paternal and maternal functions are segregated on different individuals (Stephenson and Bertin, 1983). In such studies, the larger inflorescences, longer flowering periods, and earlier initiation of flowering of males have been cited as evidence for male-male competition (Wilson, 1979, 1983; Bawa, 1980; Stephenson and Bertin, 1983; Charlesworth *et al.,* 1987; Queller, 1987; Barrett and Eckert, 1990; Bertin, 1988). While differences between the sexes in inflorescence size are reasonably well-documented, phenological data tend to be more anecdotal (Lloyd and Webb, 1977; Charlesworth *et al.,* 1987). Few studies have ascertained the statistical significance of phenological differences between sexes (but *see* Flanagan and Moser, 1985; Allen, 1986; and Carr, 1991), and none has examined how phenological variation among males affects their success as pollen donors. Furthermore, the interpretation of differences in floral phenology between the sexes of dioecious species is confounded because those phenological differences may have evolved as correlates of the separation of sexes, rather than as consequences of male-male competition. Specifically, phenological differences between the sexes of dioecious species may be proximate results of either differing reproductive costs or niche segregation. Here we report a study of variation in floral phenology between and within gender phases of the sex-changing (diphasic) species, dwarf ginseng (*Panax trifolium* L. Araliaceae). Because the gender phases of dwarf ginseng are environmentally determined, interpretation of phenological differences be-

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tween gender phases is more straightforward than that of differences between genetically determined sexes. To our knowledge, this is the first report of phenological variation within a population of sex-changing plants.

Dwarf ginseng is a cosexual, nonclonal, spring ephemeral herb of the eastern deciduous forest. It perennates from a short underground rhizome that is attached to a small, globose root. In a given year, an individual produces a single whorl of leaves and, if it is large enough, a single simple umbel of flowers (see Fig. 1 in Schlessman, 1987). Small reproductive plants express the male gender phase and bear only staminate flowers, while larger ones express the hermaphroditic phase and bear only perfect (i.e., hermaphroditic) flowers (the smallest plants are vegetative; Schlessman, 1987, 1991). The staminate flowers of male-phase plants are very similar to the perfect flowers of hermaphrodite-phase plants, except that the former lack developed and functional gynoecia (Philbrick, 1983; Schlessman, 1990). Over several seasons, an individual may change gender in either direction and switch gender several times (Schlessman, 1991). Hereafter we refer to plants in the male phase as males and those in the hermaphroditic phase as hermaphrodites. Dwarf ginseng is pollinated by small solitary bees and by flies (Philbrick, 1983). Although it is genetically self-compatible, strong intra- and interfloral protandry effectively prevent self-pollination (Schlessman, 1990). On average, males produce two to three times as many flowers per plant and about 1.2 times more viable pollen per flower as do hermaphrodites (Philbrick, 1983; Schlessman, 1987, 1990). Estimates of phenotypic gender strongly suggest that hermaphrodites are functionally female (Schlessman, 1990).

We predicted that if male-male competition had influenced the reproductive traits of dwarf ginseng, males would have (in addition to larger inflorescences) longer periods of pollen presentation than hermaphrodites, and that the phenology of pollen presentation by males would coincide more closely with that of stigma receptivity than would pollen presentation by hermaphrodites. We also predicted that if male-male competition was maintaining such differences between the gender phases, statistical correlations among inflorescence size, length of pollen presentation, and the number of receptive stigmas that an individual could potentially pollinate would be stronger for males than for hermaphrodites.

## MATERIALS AND METHODS

Our study site at the Institute of Ecosystem Studies, Cary Arboretum of the New York Botanical Garden, was in mixed deciduous forest, near to but slightly higher and drier than the swampy floodplain of a small stream. In 1983, we recorded inflorescence sizes and floral phenologies for 136 flowering individuals, 41 hermaphrodites and 95 males. These plants had been marked previously for long-term studies of gender change, and were chosen without regard to their size, location or any other factor known or suspected to affect the traits examined in this study. Except for 2 days of continuous rain (4 and 6 May) we recorded floral phenologies from the beginning of anthesis (1 May) until no individual was presenting pollen (19 May). For each plant, we counted the numbers of flowers presenting either pollen (pollen visible in dehisced anthers) or receptive stigmas (styles fully elongated, stigmas enlarged and translucent).

Because little is known about the behavior of the pollinators of dwarf ginseng we used three contrasting assumptions about the nature of competition among plants presenting pollen on the same day to estimate the numbers of receptive stigmas that each potential pollen donor might have pollinated. First, we assumed that there was no "same day competition," and calculated the number of receptive stigmas available to a donor by merely summing the numbers of flowers with receptive stigmas over all days on which that donor presented pollen. This method incorporated only variation among donors in the timing

TABLE 1.—Variation between and within gender phases of dwarf ginseng in inflorescence size and floral phenology. All data are per individual, Herms. = hermaphrodites. In A, n = sample size, C.L.'s = 95% confidence limits, and P's are for one-tailed tests, and results are back-transformed from log-transformed data. In B, N.S. = P > 0.05

| | A. Differences between gender phases | | | | | |
| | Herms. (n = 41) | | Males (n = 95) | | Males > Herms.? | |
| | | | | | Unpaired | |
| Trait | Mean | C.L.'s | Mean | C.L.'s | $t$ | P |
|---|---|---|---|---|---|---|
| Inflorescence size (number of flowers) | 6.7 | 6.2–7.3 | 18.6 | 17.4–20.0 | 13.3 | 0.0001 |
| Days presenting pollen | 2.8 | 2.4–3.2 | 11.7 | 11.2–12.3 | 24.4 | 0.0001 |
| Male stage flowers per day presenting pollen | 5.2 | 4.5–5.9 | 5.8 | 5.5–6.2 | 1.8 | 0.039 |
| Days presenting stigmas | 5.3 | 4.6–6.2 | — | — | — | — |

| | B. Variation within gender phases: regressions on inflorescence size | | | |
| | Herms. | | Males | |
| | $r^2$ | P | $r^2$ | P |
|---|---|---|---|---|
| Days presenting pollen | 0.02 | N.S. | 0.01 | N.S. |
| Male-stage flowers per day presenting pollen | 0.21 | 0.0039 | 0.58 | 0.0001 |

and length of pollen presentation. Second, we assumed that all donors presenting pollen on a given day were equally successful, *i.e.,* we assigned each donor an equal share of the stigmas that were receptive on that day. This "per inflorescence competition" measure was based on work by Thomson *et al.* (1982) and Thomson (1988), who found that the frequencies of visits by solitary bees and flies to *Aralia hispida* was not related to inflorescence size, and on similar results for dwarf ginseng (Schlessman, 1987, 1991). Third, we assumed that the success of potentially competing donors was proportional to the numbers of pollen presenting flowers they had on a given day. For this "per flower competition," we assigned each donor a share of the receptive stigmas that was proportional to the donor's share of the pollen presenting flowers.

Because the gender phase ratio (males per hermaphrodite) of our sample (95:41 = 1.6:1) was significantly smaller than the actual ratio of our study population (4.2:1), we had to adjust our sample size of hermaphrodites for our second and third methods for assessing phenological access. Else, we would have overestimated the numbers of receptive stigmas available to each male and the numbers of hermaphrodites potentially competing with males for access to receptive stigmas. We randomly selected 23 of the 41 original hermaphrodites, which gave a new ratio of 95:23 = 4.1:1. The mean inflorescence size for our subsample of 23 hermaphrodites (6.6 flowers) was not significantly different from that of all 41 (t = 0.171, d.f. = 62, P = 0.865; *see* also Table 1).

We used a nonparametric test (Estabrook *et al.,* 1982) to determine the significance of differences among phenological curves. This test compares the maximum difference (D) between cumulative fractions of two samples that have reached a particular phenological stage (*e.g.,* anther dehiscence, stigmatic receptivity) to critical values based on the two sample sizes. For *t*-tests and regressions we followed Sokal and Rohlf (1981).

## RESULTS

Male inflorescences were significantly larger than hermaphroditic ones. Within male inflorescences, flowers matured asynchronously, so that less than one-third of them (an av-
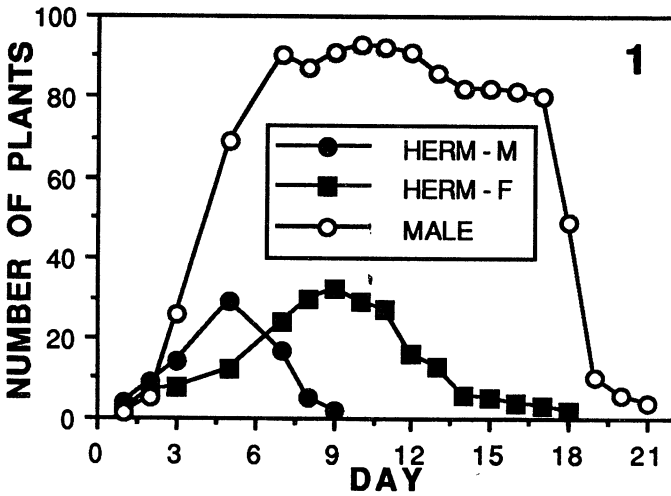
FIG. 1.—Floral phenology of dwarf ginseng. Numbers of plants presenting pollen (male, herm-m) or receptive stigmas (herm-f) per day

erage of 5.8 out of 18.6) were presenting pollen on each day that an inflorescence had pollen-presenting flowers. In contrast, hermaphroditic flowers were highly synchronous, with almost all flowers of an inflorescence (an average of 5.2 out of 6.7) presenting pollen at the same time. Thus, males had both longer periods of pollen presentation and more pollen-presenting flowers per day than did hermaphrodites (Table 1A).

Synchrony within hermaphroditic inflorescences and among hermaphroditic plants produced distinctly different phenological curves for presentation of pollen and stigmas (Figs. 1, 2). The maximum difference occurred on day 5 (Fig. 2, D = 59%, P < 0.01). The period
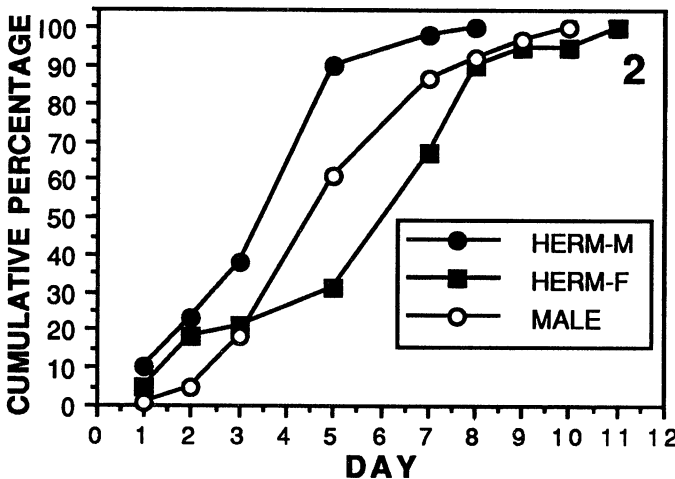


FIG. 2.—Floral phenology of dwarf ginseng. Cumulative percentages of plants having presented pollen or receptive stigmas per day

TABLE 2.—Variation between and within gender phases of dwarf ginseng in numbers of receptive stigmas available to be pollinated. All data are per individual, Herms. = hermaphrodites. In A, n = sample size, C.L.'s = 95% confidence limits, and P's are for one-tailed tests, and results are back-transformed from log-transformed data

| Type of competition among pollen donors presenting pollen on the same day | A. Differences between gender phases | | | | | |
| | Herms. (n = 23) | | Males (n = 95) | | Males > Herms.? | |
| | | | | | Unpaired | |
| | Mean | C.L.'s | Mean | C.L.'s | t | P |
| No same-day competition | 133 | 108–165 | 544 | 517–571 | 19.9 | 0.0001 |
| Per inflorescence competition | 2.5 | 1.2–2.0 | 6.5 | 6.1–6.9 | 12.4 | 0.0001 |
| Per flower competition | 2.6 | 1.9–3.5 | 5.7 | 5.1–6.4 | 5.7 | 0.0001 |

| | B. Variation within gender phases: regressions on inflorescence size | | | |
| | Herms. | | Males | |
| | $r^2$ | P | $r^2$ | P |
| No same day competition | 0.04 | N.S. | 0.03 | N.S. |
| Per inflorescence competition | 0.06 | N.S. | 0.04 | 0.0457 |
| Per flower competition | 0.02 | N.S. | 0.03 | N.S. |

of stigma presentation by hermaphrodites was longer than their period of pollen presentation (Table 1A, paired t = 13.822, P = 0.0001). Maximum differences among the phenologies of pollen presentation by males and pollen and stigma presentation by hermaphrodites also occurred on day 5 (Fig. 2). The phenology of males was significantly different from that of pollen presentation by hermaphrodites (D = 29%, P < 0.05), but not significantly different from that of stigma presentation (D = 20%, P > 0.05).

Within gender phases, length of pollen presentation was not correlated with inflorescence size (Table 1B). In contrast, variation in inflorescence size explained 58% of the variation in numbers of flowers presenting pollen per day for males, and 21% of such variation for hermaphrodites (Table 1B).

The mean amount of overlap between pollen presentation by individual donors and presentation of receptive stigmas was larger for males than hermaphrodites (Table 2A, "no same-day competition"). This, plus the fact that males presented more pollen per day than hermaphrodites, resulted in higher potential for pollen donation by males, regardless of our assumptions about competition among simultaneously presenting donors (Table 2A). Regressions of our estimates of numbers of receptive stigmas available for pollination on inflorescence size revealed only one marginally significant relationship, and in all cases the amount of variation in phenological access that could be explained by variation in inflorescence size was negligible (Table 2B).

## DISCUSSION

*Phenological differences between gender phases.*—Our study is the first to document the floral phenology of a diphasic species. Our findings that (1) pollen presentation by males closely coincides with that of stigma presentation by hermaphrodites, but is significantly different from that of pollen presentation by hermaphrodites, and (2) males present pollen longer than do hermaphrodites, strongly suggest that male-male competition has been a force in the evolution of the floral phenology of dwarf ginseng. To date, similar data and

conclusions are available only for dioecious species. Below we compare our findings to those for dioecious taxa and consider alternative explanations for our results.

Most phenological studies of dioecious species report that males begin flowering before females (Allen, 1986; Bawa, 1983; Lloyd and Webb, 1977; Stephenson and Bertin, 1983; Webb, 1976), but occasionally the sexes start flowering at the same time (*e.g.*, Carr, 1991) or females begin before males (*e.g.*, Barrett and Helenurnm, 1981; Flanagan and Moser, 1985). Several explanations for these disparate observations have been proposed, including male-male competition and differential resource utilization for males flowering first (Darwin, 1871; Lloyd and Webb, 1977; Webb, 1976), as well female-female competition for pollinators and niche differentiation for females flowering first (Barrett, 1984; Barrett and Helenurnm, 1981). The phenological difference in pollen presentation between hermaphroditic and male dwarf ginsengs could be explained in two ways. First, one might assume that the entire floral phenology of hermaphrodites has remained essentially unchanged and that pollen presentation by males has been shifted later in time to more closely coincide with the receptivity of stigmas on hermaphrodites. This is the male-male competition view that we favor. The alternative possibility that pollen presentation by hermaphrodites has been shifted earlier seems far less likely, because the primary selective force on the phenology of hermaphrodites is probably completion of fruit maturation before canopy closure (Schlessman, 1987). Furthermore, avoidance of inbreeding is not a plausible explanation for the phenological differences between hermaphrodites and males, since the strong intra- and interfloral protandry of hermaphrodites both limits selfing and promotes xenogamy. Because protandry is widespread, and very likely ancestral in Araliaceae (Schlessman *et al.*, 1990), the most parsimonious scenario is that the nondiphasic ancestors of dwarf ginseng had essentially the same floral phenology as hermaphrodites do now.

That male dwarf ginsengs present pollen longer than hermaphrodites do is an immediate consequence of two traits, larger inflorescence size and less synchronous maturation of flowers within inflorescences. While male-male competition is the best explanation for these differences between males and hermaphrodites, there are at least three alternatives.

First, the larger inflorescences of males might be a proximate physiological consequence of their lower reproductive effort (*see* below). An analogous explanation has been offered for more frequent flowering and consequently higher lifetime flower production by the males of some dioecious species (Armstrong and Irvine, 1989; Lloyd and Webb, 1977). In those species, higher lifetime flower production could be a proximate result of the loss of maternal function and its resource costs, rather than an evolutionary consequence of male-male competition. However, because gender change is common and frequent in dwarf ginseng, individuals that are presently in the male phase may incur the costs of maternal function in the future and may have already incurred them in the past. Three lines of evidence indicate that in dwarf ginseng, the resource costs of maternal function are indeed higher than those of paternal function: (1) males are smaller than hermaphrodites; (2) reproductive effort is much larger for hermaphrodites (biomass of inflorescences for males or infructescences for hermaphrodites as a percentage of root biomass, Schlessman, 1987); (3) in the year following fruit production, a plant is much more likely to have become smaller and change gender to male than to have grown larger and remain hermaphroditic (Schlessman, 1991).

Second, if both paternal and maternal reproductive success were pollen limited, selection might favor larger, more attractive inflorescences and prolonged flowering by hermaphrodites as well as males (Carr, 1991; Lloyd and Webb, 1977; Willson, 1979, 1983). Three lines of evidence indicate that the maternal reproductive success of dwarf ginseng is resource- rather than pollen-limited: (1) a preliminary experiment by Schlessman (1991) indicated

that hand-pollination in the field does not increase seed set; (2) as noted above, plants usually become smaller and change gender after they have produced seeds, and (3) size-dependent diphasy with small males and larger hermaphrodites is difficult to explain if maternal success is not resource-limited.

Third, if the nondiphasic ancestors of dwarf ginseng were partial selfers and "over produced" flowers to allow selective abortion of inbred progeny, selection might have favored a reduction in the size of hermaphroditic inflorescenses during and after the evolution of diphasy (Charlesworth *et al.*, 1987). For dwarf ginseng, this situation is implausible. As we noted above, strong intra- and interfloral protandry very likely limited selfing in nondiphasic ancestors of dwarf ginseng. Also, everything about the natural history of dwarf ginseng indicates that selection favors maximization of seed production by hermaphrodites. Schlessman (1988) has proposed that hermaphrodites may actually overproduce ovules to increase the likelihood that they will mature the largest number of seeds possible.

*Inflorescence size and pollen presentation.*—Prolongation of pollen presentation by asynchronous maturation of anthers within and among flowers is hypothesized to be an important mechanism for enhancing the paternal reproductive sucess of animal-pollinated plants (Harder and Thomson, 1989; Harder and Wilson, 1994). Thus, our finding that none of the variation in length of pollen presentation within gender phases could be explained by variation in inflorescence size was unexpected. Perhaps an already weak relationship was further obscured by effects of the physical environment on the timing of floral maturation, anther dehiscence, and pollen removal. Alternatively, if pollen viability declined rapidly after anthers dehisced (Harder and Wilson, 1994), our method of scoring pollen-presenting flowers may have overestimated the duration of effective pollen presentation. The most parsimonious explanation for the absence of a significant correlation between inflorescence size and length of pollen presentation for hermaphrodites is phylogenetic constraint, as the synchronized, strong intra- and interfloral protandry that accounts for the lack of an increase in duration of pollen presentation with inflorescence size in hermaphrodites is probably a highly canalized ancestral trait. An alternative, though not mutually exclusive, explanation for strongly synchronous protandry among the flowers of an individual hermaphroditic inflorescence would be that it maximizes the attractiveness of the inflorescence when stigmas are receptive, thus promoting reception of adequate amounts of pollen (Augspurger, 1980; Carr, 1991).

Given that within-gender variation in inflorescence size did not account for any of the variation in length of pollen presentation, it is not surprising that within-gender correlations between inflorescence size and numbers of stigmas available for pollination were weak and insignificant. Nevertheless, males did show the strongest (marginally significant) correlation, and this is consistent with our prediction that male-male competition should exert a stronger effect on males than on hermaphrodites.

*The functional gender of dwarf ginseng hermaphrodites.*—Two of our results provide further support for the view that the hermaphroditic phase is functionally female (Schlessman, 1987, 1988, 1990). First, the period of pollen presentation by hermaphrodites is shorter than that of receptive stigma presentation. Second, the relatively strong synchrony of flowering among hermaphrodites produces only a small amount of overlap among the pollen-presenting and stigma-presenting stages of different hermaphrodite plants. In effect, a large proportion of the hermaphrodites' pollen appears to be prevented from reaching receptive stigmas simply because it is presented too soon. If hermaphrodites were realizing a significant proportion of their reproductive success through pollen donation, one would expect to find more variation among the phenologies of individual hermaphrodites. But if hermaphrodites are in fact functional females, the occurrence of stigma receptivity with the

peak of pollen presentation by males might maximize their attractiveness to pollinators at the optimal time for receiving pollen.

Our results provide sound evidence that male-male competition has affected the evolution of differences between the gender phases of dwarf ginseng in the timing and amount of pollen presentation. However, to answer the question of whether male-male competition is currently acting to maintain these differences we must measure actual male reproductive success. Barrett and Eckert (1990) noted that results from observational studies of dioecious species have prompted experimental tests of sexual selection theory using plants. Diphasic plants offer a rare but highly appropriate system for such experiments.

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