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PHENOTYPIC GENDER IN SEX CHANGING DWARF GINSENG, PANAX TRIFOLIUM (ARALIACEAE)[1]

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Dwarf ginseng (*Panax trifolium* L., Araliaceae) is a diphasic ("sex changing") species in which one phase has staminate flowers and the other has hermaphroditic flowers. In order to determine the relative allocations of the hermaphroditic gender phase to male and female functions, variation in population gender phase ratios, pollen production and viability, and ovule and seed production were documented. Gender phase ratios are highly male-biased. Dwarf ginseng is self-compatible, and both gender phases have viable pollen capable of effecting fertilization. Males produce more flowers and more viable pollen per anther than hermaphrodites. The phenotypic gender of hermaphrodites is extremely female-biased; it is likely that hermaphrodites function essentially as females. Sexual selection may have a role in the evolution and maintenance of differences between the gender phases in allocation to male function.

Diphasy ("sex choice") is a rare sexual system in which individual plants may alternate between two distinct, environmentally determined phases of sex expression (Charnov, 1982; Policansky, 1982; Lloyd and Bawa, 1984; Schlessman, 1988). In most diphasic species, one phase produces only pollen, while the other produces both pollen and ovules (Lloyd and Bawa, 1984; Schlessman, 1988). Individuals expressing the hermaphroditic phase may vary in allocations to female and male reproductive functions and in success as maternal and paternal parents, i.e., they may vary in phenotypic and functional gender (Lloyd, 1979, 1980; Lovett Doust and Lovett Doust, 1983; Lloyd and Bawa, 1984). The potential for gender variation among individuals expressing the hermaphroditic phase raises several questions: How much gender variation occurs among plants in the hermaphroditic phase? How different are the gender distributions of the two phases? Are the phases differentiated in terms of allocation to paternal as well as maternal function? Do the phases differ in male reproductive success?

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Dwarf ginseng (*Panax trifolium* L., Araliaceae) is a diphasic species in which the smallest individuals are vegetative, producing leaves but not flowers; larger plants are males with staminate flowers, and the largest plants are hermaphrodites with hermaphroditic flowers (Philbrick, 1983; Schlessman, 1987, 1988). From year to year, one-fourth to one-third of the reproductive individuals change phase from male to hermaphrodite or hermaphrodite to male (Schlessman, 1987, 1988, unpublished data). To the best of my knowledge, dwarf ginseng is the only species for which the above questions have been addressed. For example, although *Arisaema dracontium* (Araceae) is thought to be diphasic, with the male phase producing staminate flowers and the hermaphroditic phase producing both staminate and pistillate flowers, it is not known whether pollen from plants in hermaphroditic phase is functional (Lovett Doust and Cavers, 1982). In this paper I describe variation in the standardized phenotypic gender (as defined by Lloyd and Bawa, 1984) of the hermaphroditic phase of dwarf ginseng.

Standardized phenotypic gender is a quantitative description of a plant's allocations to female and male functions, relative to the allocations of other individuals in the population. For dwarf ginseng, calculations of standardized phenotypic gender require data on the frequencies of expression of each gender phase, pollen production by plants in each phase, and seed set by the hermaphroditic phase. Here these data are presented as well as other information relevant to describing variation in gender. Phenotypic gender of the hermaphroditic phase is shown to be extremely female-

biased, and whether phenotypic gender is likely to be a good estimate of functional gender is considered. The implications of my results for understanding differences between the gender phases in their allocations to male function are also discussed.

MATERIALS AND METHODS

The plant—Dwarf ginseng is a spring ephemeral herb of the eastern North American deciduous forest. It perennates from a short rhizome attached to a globose, tuber-like root. A shoot bud formed the previous spring develops into a single stem that bears a whorl of three leaves and terminates in a simple umbel of flowers; the smallest plants have leaves but no flowers. Plants in the male phase have staminate flowers with five stamens and a reduced, nonfunctional gynoecium, while those in the hermaphroditic phase have hermaphroditic flowers with five stamens and either three or four uniovulate carpels. Elsewhere, I have called plants with hermaphroditic flowers females (Schlessman, 1987, 1988). The carpels are partially fused, producing a compound ovary (pistil) with separate styles. For illustrations see Philbrick (1983) and Schlessman (1987). Hermaphroditic flowers are strongly protandrous, and anthesis within hermaphroditic inflorescences is highly synchronous. In the field, there is very little, if any, overlap between pollen presentation and stigmatic receptivity within hermaphroditic inflorescences (Philbrick, 1983; Schlessman, personal observations).

Study populations—Populations were studied at four sites in southeastern New York State, each within 48 km of Poughkeepsie: Harvard Black Rock Forest (BR); Institute of Ecosystem Studies, Cary Arboretum of the New York Botanical Garden (C); Stony Kill Environmental Education Center (SK); and Taconic State Park (T). There was one population at each site except BR, which had two populations separated by 0.4 km. The study populations were in mixed deciduous forest, near to but somewhat drier than the swampy flood plains of streams. At these sites, flowering began in early May while the canopy was still open, and fruits matured in late May and early June as the canopy trees leafed out and the understory became shaded.

Calculation of phenotypic gender—The formula for standardized phenotypic femaleness (G_p) given by Lloyd and Bawa (1984) was used, which is $G_p = d_i/d_i + l_iE$, where d_i is the maternal allocation of individual i, l_i is the paternal allocation, and $E = \Sigma\ d_i/\Sigma\ l_i$ for a representative sample of a population. In an earlier paper, Lloyd (1980) presented this equation as an estimate of "functional gender." This equation is strictly applicable only if subsets of the population do not differ in the frequency of self-fertilization (Lloyd, 1980). Maternal allocation (d) was measured by counting ovules to give ovule-based phenotypic femaleness (G_{po}), and also by counting seeds to give seed-based phenotypic femaleness (G_{ps}; Lloyd, 1980). Paternal allocation was measured by counting stamens (flowers × five) and adjusting for differences between gender phases in production of stainable, presumably viable pollen. The gender phase ratios (male : hermaphrodite) of the samples used to obtain d_i's and l_i's were approximately 1:1 and were quite different from the male-biased phase ratios of the populations from which they came (see Table 1). To correct for this in the calculation of E, $\Sigma\ l_i$ was first multiplied by the inverse of the phase ratio of the sample to obtain $\Sigma\ l_i$ for a phase ratio of exactly 1:1, and then that product was multiplied by the estimated phase ratio of the population. Values of G_p may range from zero to one. For convenience, phenotypic femaleness is reported as $G_p \times 100$.

Gender phase ratios and production of pollen, ovules, and seeds—For each population, phase ratios were determined by marking off a grid that included at least 95% of the flowering individuals and recording the gender phases of all reproductive individuals in the grid. The significances of differences from a 1:1 ratio were determined by G-tests and the sequential Bonferroni technique (Rice, 1989). Numbers of flowers, anthers, ovules, and seeds were recorded for smaller samples of randomly chosen plants that had been marked to study phase change and for other purposes (Schlessman, 1987, 1988, unpublished data). The significances of differences in flower numbers between males and hermaphrodites were determined with *t*-tests and the sequential Bonferroni technique. Determinations of per anther pollen production and pollen stainability were made with flowers from C 82. One mature, undehisced anther from each of 39 staminate and 34 hermaphroditic flowers, each from a different plant, was macerated in aniline blue/lactophenol. The total number of pollen grains and the number of normally shaped, fully stained grains were recorded. Ovule number was determined by counting styles. To determine seed set, the percentage of ovules that became seeds, the number of carpels that swelled with developing seeds was counted.

TABLE 1. *Gender phase ratios for ginseng. For each sample, the H) is significant (table-wide sequential Bonferroni test). P lowed by different letters are sig one another at an experimen of 5% (G-tests). Samples are and year (see MATERIALS*

Sample	Males	Hermaphrodites
BR2 84	127	8
C 82	3,664	511
C 83	3,498	590
C 84	5,317	1,257
SK 84	727	208
T 84	227	60
T 85	768	167

Controlled pollinations—self-pollination in the abse field was assessed by enclos in fine mesh bags suppor Inflorescences were bagge were in bud, then left und developed. All other con were made with plants hou cage in the Vassar College E Some hermaphrodites were and not pollinated, other and hand-crossed with poll or hermaphrodites, and t hand-selfed. Crosses were recently dehisced anthers t Stigmas were considered t the styles were fully elonga surface was enlarged and t linations (both autogamou and geitonogamous, or be attempted in the same wa dry often prevented transf obviously receptive stigm

TABLE 2. *Inflorescence sizes for coefficients of variation (V*) difference between males and test on $\log_{10}$ transformed da*

Sample	$\bar{x}$
BR1 83	14
BR2 84	14
C 82	22
C 83	16
C 84	20
C 85	23
SK 83	19
SK 84	21
SK 85	14
T 83	18
T 84	21
T 85	17

TABLE 1. *Gender phase ratios for four populations of dwarf ginseng. For each sample, the difference from 1:1 (M/H) is significant (table-wide $P < 0.05$, G-tests and sequential Bonferroni test). Proportions of males followed by different letters are significantly different from one another at an experiment-wide significance level of 5% (G-tests). Samples are identified by population and year (see MATERIALS AND METHODS)*

Sample	Males	Hermaphrodites	% Male	Ratio (M/H)
BR2 84	127	8	94.1[a]	15.9:1
C 82	3,664	511	87.8[b]	7.2:1
C 83	3,498	590	85.6[c]	5.9:1
C 84	5,317	1,257	80.9[d]	4.2:1
SK 84	727	208	77.8[e]	3.5:1
T 84	227	60	79.1[e]	3.8:1
T 85	768	167	82.1[f]	4.6:1

Controlled pollinations—The potential for self-pollination in the absence of insects in the field was assessed by enclosing hermaphrodites in fine mesh bags supported by wire stakes. Inflorescences were bagged while the flowers were in bud, then left undisturbed until fruits developed. All other controlled pollinations were made with plants housed in an insect-free cage in the Vassar College Biology Greenhouse. Some hermaphrodites were emasculated in bud and not pollinated, others were emasculated and hand-crossed with pollen from either males or hermaphrodites, and the remainder were hand-selfed. Crosses were made by touching recently dehisced anthers to receptive stigmas. Stigmas were considered to be receptive when the styles were fully elongated and the stigmatic surface was enlarged and translucent. Self-pollinations (both autogamous, or within flowers, and geitonogamous, or between flowers) were attempted in the same way, but floral protandry often prevented transfers of fresh pollen to obviously receptive stigmas. Thus, some self-pollinations may have involved pollen with reduced viability or stigmas that were not receptive.

RESULTS

Phase ratios and production of pollen, ovules, and seeds—Phase ratios ranged from 3.5:1 to 15.9:1 (male : hermaphrodite; Table 1) and were always significantly male-biased. There was no clear pattern of phase ratio variation within or among populations. Males produced two to three times as many flowers per plant as hermaphrodites (Table 2), and in each sample the difference was significant. In ten of 12 samples the inflorescence sizes of males were more variable than those of hermaphrodites. Since flowers of males and hermaphrodites had the same number of stamens (five), the cumulative anther production of the male phase was at least seven times (2×3.5) greater than that of the hermaphroditic phase. Similar results were reported by Philbrick (1983).

Pollen production per anther was 476 ± 91 grains for males and 419 ± 122 grains for hermaphrodites (mean $\pm$ standard deviation), and a two-tailed t-test on square root transformed data showed that the difference was significant ($t = 2.12$, df = 71, $P = 0.04$). Pollen stainabilities were strongly skewed towards high values and were not amenable to parametric analysis. Medians and ranges were 96% and 74–99% for males, and 93% and 69–97% for hermaphrodites. A Mann-Whitney U-test showed that the difference was very highly significant ($U_s = 240$, $t_s = 14.94$, $P < 0.001$). Thus, males produced about 1.16 times as much stainable pollen per anther as hermaphrodites. This was incorporated into the gender estimates by multiplying the paternal allocations

TABLE 2. *Inflorescence sizes for the male and hermaphroditic gender phases of dwarf ginseng. Means ($\bar{x}$), ranges, and coefficients of variation (V*) corrected for sample size (n) are given for untransformed data. For each sample, the difference between males and females is significant (Table-wide $P < 0.05$, two-tailed t-tests and sequential Bonferroni test on $\log_{10}$ transformed data)*

	Males				Hermaphrodites			
Sample	$\bar{x}$	Range	V*(%)	n	$\bar{x}$	Range	V*(%)	n
BR1 83	14	5–25	34	34	6	2–9	27	27
BR2 84	14	6–26	33	50	5	2–8	36	50
C 82	22	10–35	27	50	8	4–12	26	51
C 83	16	7–30	34	52	7	4–11	27	33
C 84	20	1–45	38	101	7	4–12	28	83
C 85	23	9–35	36	86	8	4–14	30	46
SK 83	19	8–35	38	50	7	4–13	32	49
SK 84	21	3–39	43	50	8	3–13	36	51
SK 85	14	5–30	41	50	8	4–13	32	29
T 83	18	7–36	44	57	9	4–11	26	53
T 84	21	8–38	32	72	9	4–13	32	48
T 85	17	6–29	41	24	8	5–10	23	33

TABLE 3. *Seed set (% ovules that matured to seeds, per plant) for four populations of dwarf ginseng. Samples are identified by population and year (see MATERIALS AND METHODS)*

Sample	% Seed set*		
	$\bar{x}$	S.E.	n
BR 83	83.73	3.64	30
BR 84	78.31	4.20	42
C 83	77.97	3.21	33
C 84	75.60	2.99	60
C 85	71.85	2.35	47
SK 84	80.41	3.98	27
SK 85	74.79	4.11	29
T 83	85.11	2.93	53
T 84	85.16	2.53	38
T 85	87.15	2.59	33

* $\bar{x}$ = mean, S.E. = standard error, n = sample size.

(numbers of stamens) of hermaphrodites by 1/1.16 = 0.86. Philbrick (1983) obtained very similar results for stainability but a much greater difference between gender phases in pollen grains per anther (1.3:1, male : hermaphrodite).

All flowers of hermaphrodites had either three or four ovules. Four-ovuled flowers were rare—more than one per plant was never found. Mean seed set per plant varied from 71.85% at C in 1985 to 87.15% at T in 1985 (Table 3).

Controlled pollinations (Table 4)—When pollinators were excluded, emasculated hermaphroditic flowers produced no seeds, indicating that pollination and fertilization are necessary for seed set. The mean seed set of bagged, undisturbed hermaphrodites in the field was 1.3%. Philbrick (1983) conducted a similar experiment and obtained zero seed set. In my greenhouse experiment, repeated hand self-pollinations resulted in a mean seed set of 56.8%. Taken together, these results showed that while dwarf ginseng is self-compatible, in the absence of floral visitors, synchronous protandry is highly effective in limiting selfing. The greenhouse selfing experiment was designed to maximize opportunities for self-fertilization and detection of self-compatibility. The results of that experiment are not a good estimate of the frequency of self-pollination in nature because pollen was not removed by floral visitors, and senescence of stamens was delayed relative to that observed in the field (personal observations). Thus, the overlap between pollen presentation and stigmatic receptivity was greater in the greenhouse experiment than it was in the field, and that probably increased the likelihood of self-fertilization. Because the field experiments and my observations of floral phenology in the field indicated that the frequency of self-pollinations in nature was quite low, no selfing was assumed in these calculations of phenotypic gender.

There was no significant difference between the mean seed sets from crosses using pollen from males and hermaphrodites (two-tailed t-test on angular transformed data, $t = 0.34$, $df = 15$, $P = 0.74$). This established that viable (stainable) pollen from both gender phases is capable of effecting fertilization. Seed set from crosses was higher than that from hand-selfs, but the difference was not significant (two-tailed t-test on angular transformed data, all crosses vs. hand-selfs, $t = 1.49$, $df = 20$, $P = 0.15$).

Phenotypic gender—Sample means for ovule-based phenotypic femaleness ($G_{po} \times 100$) were uniformly high, ranging from 90.9 at SK in 1984 to 98.5 at BR in 1984 (Table 5). This extreme female bias in phenotypic gender occurred because males were much more numerous and produced considerably more pollen per plant than hermaphrodites. As there was no variability in the number of stamens per flower and almost no variability in the number of ovules per flower, within-sample variation in G_{po} was quite low. Variation among samples was primarily due to differences among populations in gender phase ratios and flower production by males, which together largely determined the size of the equivalence factor (E) in the formula for phenotypic gender.

Sample means for seed-based phenotypic femaleness ($G_{ps} \times 100$) ranged from 92.3 for C 84 to 94.8 for T 85 (Table 5). I expected seed set of less than 100% to lower mean lower G_{ps}'s relative to G_{po}'s, because maternal allocation (d_i) decreased while male allocation (l_i) remained the same. However, this occurred in only three of the six samples. The greatest difference between means for ovule- and seed-based phenotypic femaleness was 4.7 for BR2. Less than full seed set had a minimal effect on phenotypic gender because it did not appreciably change the equivalence factor (E), and l_iE remained very small relative to d_i.

DISCUSSION

Phenotypic gender as an estimate of functional gender—Standardized phenotypic gender, as defined by Lloyd and Bawa (1984), quantifies a plant's sex allocations relative to those of other individuals in the population. Ovule-based phenotypic gender (G_{po}) describes prepollination sex allocations, or what Delesalle (1989) has called prospective gender (see also Lloyd, 1980). If differences among individuals in G_{po} are adaptive, they should

TABLE 4. *Seed set from controlled p which were carried out in a green*

Treatment
Emasculated
Bagged, undisturbed in field
Hand-selfed
Crossed, male-phase pollen
Crossed, hermaphrodite-phase
All crosses

* $\bar{x}$ = mean, S.E. = standard error,

reflect variation in the indivi for reproductive success via f function. The G_{po}'s for dwarf g compared to other individual tion, the prepollination sex al maphrodites are highly fem G_{po}'s suggest that individuals roditic phase function essenti

The actual proportions of obtained via maternity and mine its functional gender (I 1984). Although seed-based a measure of maternal fitnes cannot be used to test predi relationship between pheno tional gender because they lac measure of paternal fitness. ternal fitness is proportiona vestment, G_{ps}'s can be taken timates of functional gender. why this should be true for c presented below. The G_{ps}'s f suggest that in years when hermaphroditic phase, indivi or more of their fitness via n

How far off could these e factors that determine func dwarf ginseng are gender ph lationships between ovule pro ternal success and pollen pro ternal success via cross-poll frequency of self-fertilization. of phenotypic gender in this s documented variation in all except the relationship betw ment and paternity via crossi rate. I assumed that paternal portional to paternal investm was no self-pollination.

The lack of a relationshi production and outcrossing s dividuals siring the same num seeds) would lower function cause the proportion of out thered by hermaphrodites proportion of pollen from h

TABLE 4. *Seed set from controlled pollinations of dwarf ginseng. Floral visitors were excluded from all treatments, which were carried out in a greenhouse unless otherwise stated*

Treatment	Seed set per plant (%)[a]			
	$\bar{x}$	S.E.	Range	n
Emasculated	0	—	0	8
Bagged, undisturbed in field	1.3	0.9	0–6	9
Hand-selfed	56.8	11.5	20–80	5
Crossed, male-phase pollen	75.4	11.7	20–100	8
Crossed, hermaphrodite-phase pollen	76.0	9.2	8–100	9
All crosses	75.7	7.1	8–100	17

[a] $\bar{x}$ = mean, S.E. = standard error, n = sample size.

reflect variation in the individuals' prospects for reproductive success via female and male function. The G_{po}'s for dwarf ginseng show that compared to other individuals in the population, the prepollination sex allocations of hermaphrodites are highly female-biased. The G_{po}'s suggest that individuals in the hermaphroditic phase function essentially as females.

The actual proportions of a plant's fitness obtained via maternity and paternity determine its functional gender (Lloyd and Bawa, 1984). Although seed-based G_p's incorporate a measure of maternal fitness (seed set), they cannot be used to test predictions about the relationship between phenotypic and functional gender because they lack an independent measure of paternal fitness. However, if paternal fitness is proportional to paternal investment, G_{ps}'s can be taken as reasonable estimates of functional gender. Several reasons why this should be true for dwarf ginseng are presented below. The G_{ps}'s for dwarf ginseng suggest that in years when they express the hermaphroditic phase, individuals obtain 90% or more of their fitness via maternity.

How far off could these estimates be? The factors that determine functional gender in dwarf ginseng are gender phase ratio, the relationships between ovule production and maternal success and pollen production and paternal success via cross-pollination, and the frequency of self-fertilization. The calculations of phenotypic gender in this study incorporate documented variation in all of these factors except the relationship between male investment and paternity via crossing, and the selfing rate. I assumed that paternal success was proportional to paternal investment and that there was no self-pollination.

The lack of a relationship between pollen production and outcrossing success (i.e., all individuals siring the same number of outcrossed seeds) would lower functional femaleness because the proportion of outcrossed seeds fathered by hermaphrodites would exceed the proportion of pollen from hermaphrodites in the pollen pool. However, several lines of evidence suggest that males, which produce at least twice as much pollen per individual as hermaphrodites, are indeed better pollen donors than hermaphrodites. First, the males have a greater than threefold advantage in numbers of individuals, and the nearest neighbors of hermaphrodites tend to be males (personal observations). Thus, pollinator moves from male to hermaphrodite are more likely than those between hermaphrodites. Second, males have larger inflorescences than hermaphrodites, and in several species of the Araliaceae and Apiaceae with inflorescences similar to those of dwarf ginseng, rates of pollinator visitation increase with inflorescence size (Thomson, Maddison, and Plowright, 1982; Thomson, 1988; Schlessman, unpublished data). Third, males and hermaphrodites differ in the timing of pollen presentation. Males present pollen over longer periods than hermaphrodites, and, at the population level, overlap of anther dehiscence with stigma presentation is greater for males (Schlessman, Underwood, and Graceffa, 1989; Schlessman, unpublished data). All of these factors will tend to make males more successful pollen donors than hermaphrodites. It is difficult to imagine how a postpollination mechanism that lowered the success of pollen

TABLE 5. *Ovule- (G_{po}) and seed-based (G_{ps}) standardized phenotypic femaleness of hermaphrodite-phase individuals of dwarf ginseng. Samples are identified by population and year (see MATERIALS AND METHODS)*

Sample	$G_p \times 100$[a]					
	Ovule-based			Seed-based		
	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n
BR 84	98.5	0.05	43	93.8	3.28	42
C 83	93.6	0.12	31	93.7	0.28	30
C 84	95.3	0.08	60	93.2	1.63	60
SK 84	90.9	0.45	41	92.3	0.41	41
T 83	93.4	0.05	27	93.6	0.27	27
T 84	94.8	0.12	38	94.6	0.23	38

[a] $\bar{x}$ = mean, S.E. = standard error, n = sample size.

from males relative to that of pollen from hermaphrodites could evolve, since it would both lower an individual's male-phase reproductive success and tend to exclude the vast majority of potential mates for its hermaphroditic phase.

In any case, because gender phase ratios are so strongly male-biased, the absence of a relationship between an individual's pollen production and its success as a cross-pollen donor has a negligible effect on functional gender. Consider a hypothetical population of nine individuals with a gender phase ratio of 3.5:1 (seven males, two hermaphrodites), six flowers per hermaphrodite, seed set per hermaphrodite of 72%, and no selfing. A hermaphrodite would mother 12.96 (six flowers × three ovules/flower × 0.72) seeds and father 1.62 (12.96 seeds of the other hermaphrodite ÷ eight potential fathers) seeds. Its functional femaleness would be 89 ([12.96 ÷ 12.96 + 1.62] × 100) which is very close to the estimates reported in this study.

Selfing would have a stronger effect on functional gender because it would increase the paternal success of hermaphrodites while decreasing the number of ovules available to males. As has been argued above, bagging experiments show that for dwarf ginseng there is essentially no selfing in the absence of floral visitors, and phenological observations indicate that opportunities for pollinator-mediated selfing are rare. The actual rate of self-pollination in nature is probably quite low. To illustrate the effects of a low selfing rate, consider the hypothetical conditions above but with 15% selfing, which I believe is an overestimate. A hermaphrodite would father 1.94 (12.96 × 0.15) seeds via selfing and 1.38 (11.02 ÷ 8) seeds via crossing. Its functional femaleness would be 80 ([12.96 ÷ 12.96 + 1.94 + 1.38] × 100). This is somewhat lower than my estimates but still consistent with my prediction that hermaphrodites function primarily as females. Selfing rates would have to be exceedingly high to make this prediction incorrect. Continuing with the hypothetical example, a very high selfing rate of 60% gives a functional femaleness of 61, which is still clearly female-biased. As long as there are some males in a population, the functional gender of hermaphrodites will be female-biased unless the selfing rate is 100%.

Differentiation of the gender phases with respect to male allocation—Dwarf ginseng differs from other species in which diphasy is known or suspected in that the ovule-bearing gender phase has only hermaphroditic flowers, rather than a combination of staminate and pistillate flowers or only pistillate ones (see Lloyd and Bawa, 1984; Schlessman, 1988). The explanation for this is probably phylogenetic, as all other species of *Panax* have hermaphroditic flowers. Although some Asiatic species are reported to produce some "male" flowers with a single stylar column (Ohwi, 1965; Hara, 1970), such flowers could be functionally hermaphroditic like the single-styled flowers of *Panax quinquefolium* (Schlessman, 1985). The simplest interpretation of the reduced gynoecia of male phase inflorescences in dwarf ginseng is that they are vestigial. Diphasy probably evolved via intercalation of the male gender phase in populations of individuals that previously had only hermaphroditic flowers (Schlessman, 1987). A form of sexual selection (male-male competition) may have acted to increase pollen production (per anther) and inflorescence size in the male phase.

The highly male-biased gender phase ratios reported here and by Philbrick (1983) appear to be products of the dynamics of phase change. Smaller, younger plants are vegetative or male, and changes from male to hermaphrodite are much less common than those from hermaphrodite to male (Schlessman, 1987, 1988, unpublished data). In the evolution of diphasy, increasingly male-biased phase ratios would have established a new mating environment in which the phenotypic and functional genders of the hermaphroditic phase became female-biased without any changes in the numbers of ovules or pollen grains produced by hermaphroditic flowers. Once the functional gender of the hermaphroditic phase became female-biased, selection against deleterious mutations affecting pollen may have become less intense, resulting in decreased pollen viability compared to the male phase. However, a more proximal and perhaps more likely explanation is that the physiologies of sex expression in the two phases have different effects on pollen (Pharis and King, 1985; Chailakhyan and Khrianin, 1987).

In conclusion, both ovule-and seed-based calculations of the phenotypic gender of the hermaphroditic phase of dwarf ginseng are extremely female-biased. The phenotypic gender of hermaphrodites is determined primarily by their mating environment, i.e., the high proportions of males in the population, and not by their own sex allocations. Thus, assumptions about the existence and exact form of a relationship between an individual's allocation to male function and its success as a paternal parent do not affect my prediction that hermaphrodites function essentially as females. Selfing rates that would be high enough to make

my prediction incorrect are very u
ferences between the gender pha
rescence size and per flower poller
may be results of sexual selection
male phase. Further studies of the
among inflorescence size, pollen d
postpollination success will be nec
termine whether these differenc
maintained by selection, and to
the functional gender of hermaph
male-biased.

LITERATURE CITE

CHAILAKHYAN, M. KH., AND V. N. KHRIA
uality in plants and its hormonal regu
Verlag, New York.

CHARNOV, E. L. 1982. The theory o
Princeton University Press, Princet

DELESALLE, V. A. 1989. Year-to-year
notypic gender in a monoecious cu
thera undulata. *American Journal o*
39.

HARA, H. 1970. On the Asiatic spec
Panax. *Journal of Japanese Botany*

LLOYD, D. G. 1979. Parental strategie
New Zealand Journal of Botany 17:

———. 1980. Sexual strategies in plar
tative method for describing the gen
Zealand Journal of Botany 18: 103

———, AND K. S. BAWA. 1984. Modifi
der of seed plants in varying conditi
Biology 17: 255–338.

LOVETT DOUST, J., AND P. B. CAVERS.
allocation and gender in the green

my prediction incorrect are very unlikely. Differences between the gender phases in inflorescence size and per flower pollen production may be results of sexual selection acting on the male phase. Further studies of the relationships among inflorescence size, pollen dispersal, and postpollination success will be necessary to determine whether these differences are being maintained by selection, and to confirm that the functional gender of hermaphrodites is female-biased.

LITERATURE CITED

CHAILAKHYAN, M. KH., AND V. N. KHRIANIN. 1987. Sexuality in plants and its hormonal regulation. Springer-Verlag, New York.

CHARNOV, E. L. 1982. The theory of sex allocation. Princeton University Press, Princeton, NJ.

DELESALLE, V. A. 1989. Year-to-year changes in phenotypic gender in a monoecious cucurbit, *Apodanthera undulata*. *American Journal of Botany* 76: 30–39.

HARA, H. 1970. On the Asiatic species of the genus *Panax*. *Journal of Japanese Botany* 45: 197–212.

LLOYD, D. G. 1979. Parental strategies of angiosperms. *New Zealand Journal of Botany* 17: 595–606.

———. 1980. Sexual strategies in plants III. A quantitative method for describing the gender of plants. *New Zealand Journal of Botany* 18: 103–108.

———, AND K. S. BAWA. 1984. Modification of the gender of seed plants in varying conditions. *Evolutionary Biology* 17: 255–338.

LOVETT DOUST, J., AND P. B. CAVERS. 1982. Resource allocation and gender in the green dragon, *Arisaema dracontium* (Araceae). *American Midland Naturalist* 108: 144–148.

———, AND L. LOVETT DOUST. 1983. Parental strategy: gender and maternity in higher plants. *BioScience* 33: 180–186.

OHWI, J. 1965. Flora of Japan (in English). Smithsonian Institution, Washington, DC.

PHARIS, R. P., AND R. W. KING. 1985. Gibberellins and reproductive development in seed plants. *Annual Review of Plant Physiology* 36: 517–568.

PHILBRICK, C. T. 1983. Contributions to the reproductive biology of *Panax trifolium* L. (Araliaceae). *Rhodora* 84: 97–114.

POLICANSKY, D. 1982. Sex change in plants and animals. *Annual Review of Ecological Systems* 13: 471–496.

RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223–225.

SCHLESSMAN, M. A. 1985. Floral biology of American ginseng (*Panax quinquefolium*). *Bulletin of the Torrey Botanical Club* 112: 129–133.

———. 1987. Gender modification in North American ginsengs: dichotomous choice versus adjustment. *BioScience* 37: 469–475.

———. 1988. Gender diphasy ("sex choice"). *In* J. Lovett Doust and L. Lovett Doust [eds.], Plant reproductive ecology: patterns and strategies, 139–153. Oxford University Press, New York.

———, N. C. UNDERWOOD, AND L. M. GRACEFFA. 1989. Inflorescence size, phenology, and male reproductive success in sex-changing dwarf ginseng, *Panax trifolium*. *American Journal of Botany* 76: 122 (Abstract).

THOMSON, J. D. 1988. Effects of variation in inflorescence size and floral rewards on the visitation rates of traplining pollinators of *Aralia hispida*. *Evolutionary Ecology* 2: 65–76.

———, W. P. MADDISON, AND R. C. PLOWRIGHT. 1982. Behavior of bumble bee pollinators of *Aralia hispida* Vent. (Araliaceae). *Oecologia* 54: 326–336.