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Size, gender, and sex change in dwarf ginseng, *Panax trifolium* (Araliaceae)

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Summary. Flowering individuals of dwarf ginseng may be either male or hermaphroditic. I recorded the sex expression and size of individuals in three populations for three or four years in order to 1) determine whether this bimodal distribution of sex expression was due to sex changing or genetic dimorphism, and 2) test predictions about a) the relationship between size and gender, and b) the association of size change and sex change. Twenty five to 37% of the flowering individuals in each population changed gender from one year to the next. Of the plants I followed for four years, 83% changed sex and 57% changed more than once. In each of these populations as well as two others, hermaphrodites were significantly larger than males. Gender dynamics of the three populations differed, but hermaphrodites tended to become smaller and were more likely to change gender than remain hermaphroditic the following year, whereas males tended to grow larger and were more likely to remain male than to change gender. Dwarf ginseng is clearly a diphasic (sex changing) species in which sex expression is determined primarily by size. A difference between genders in the immediate resource costs of reproduction appears to be an important determinant of sex change and gender phase ratios in populations.

Key words: Araliaceae – Ginseng – *Panax* – Sex allocation – Sex change

Sex changing, i.e., switching between two distinct phases of sex expression, represents an extreme response to conditions affecting reproductive success through female and male function. Thus, sex changers are ideal for studies of the ecological contrasts between maternity and paternity. Although it is rare, sex changing occurs in a variety of organisms including sponges, cnidarians, polychaetes, molluscs, crustaceans, echinoderms, fish, and flowering plants (see reviews by Charnov 1982; Policansky 1982; Lloyd and Bawa 1984; Schlessman 1988). Lloyd and Bawa (1984) introduced the term diphasy for sex change in plants, in part to emphasize the conceptually useful distinction between environmentally determined gender phases and genetically determined sexual morphs. Nevertheless, sex change is well entrenched in the literature, so I use it synonymously with diphasy and gender change.

The sex expression of plants may vary both spatially and temporally and have both genetic and environmental components. Even in populations that are dioecious, individuals may occasionally bear some flowers of the opposite sex ("leaky" dioecy or "inconstancies"; Freeman et al. 1980; Bawa and Beach 1981; Lloyd and Bawa 1984). Furthermore, there is some evidence that in certain species both genetic dimorphism and environmental cues have significant effects on the observed sex ratio (Freeman and McArthur 1984; "dimorphism with phase choices" of Lloyd and Bawa 1984). Thus it is important to know not only that sex-changing occurs but also what proportion of individuals are capable of changing. Clearly distinguishing between diphasy and genetic dimorphism requires observation of the sex expression of individuals in natural populations over two or more consecutive reproductive periods (Schlessman 1986). Few such studies have been published, so the number of well-documented cases of diphasy is exceedingly small.

Theory for the evolution of sex changing has been based on the "size advantage" hypothesis, which states that natural selection will favor sex-changing when "an individual succeeds most efficiently as a member of one sex when small or young, and as a member of the other sex when it gets older or larger" (Ghiselin 1969). Leigh, Charnov and Warner (1976) noted that the size-advantage hypothesis predicts that individuals should first express the sex for which the cost (immediate resource expenditure, loss of future reproductive potential, or both) of reproducing when small is less. Changing sex is often viewed as something that an individual will do only once (c.f. cover of Trends In Ecology and Evolution, June 1988). However, most, if not all, diphasic plants may change several times (Schlessman 1988). The size advantage hypothesis predicts that these multiple changes are due to increases and decreases in plant size.

Dwarf ginseng (*Panax trifolium* L., Araliaceae) is a perennial, spring-ephemeral herb of the North American eastern deciduous forest. C.T. Philbrick and I indepen-

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dently observed that in a given year some individuals have only staminate flowers while others have only hermaphroditic ones (there are also some vegetative individuals with no flowers). Philbrick (1983) suggested that dwarf ginseng might be androdioecious, i.e. that the males and hermaphrodites might be genetically determined morphs. However, theorists had asserted that androdioecy was evolutionarily unstable, and no entirely convincing case of androdioecy had been found (Lloyd 1975; Charlesworth and Charlesworth 1978; Charlesworth 1984). C. Webb (personal communication) examined herbarium collections and noted that the roots of males were smaller than those of hermaphrodites. Thus Webb (cited in Lloyd and Bawa 1984) proposed that dwarf ginseng was diphasic, i.e. that males and hermaphrodites were gender phases of a cosex. Meanwhile, I initiated a long-term study of natural populations with the intent of discerning whether dwarf ginseng was androdioecious or diphasic. Elsewhere, I have reported that 1) dwarf ginseng can change from male to hermaphrodite and from hermaphrodite to male, 2) the reproductive effort of hermaphrodites is eight times that of males, and 3) the mean dry root weight of hermaphrodites is significantly greater than that of males, which is significantly greater than that of vegetative plants. I concluded that dwarf ginseng is in fact diphasic, and that sex expression is determined primarily by size (Schlessman 1987, 1988, 1990).

Here, I evaluate those conclusions with previously unpublished data from my four-year study of size and sex expression in several populations of dwarf ginseng by asking: 1) What proportion of individuals exhibit gender change, and how often do those individuals change? 2) What is the relationship between size and gender? and 3) What is the relationship between size change and gender change?

Materials and methods

Plant and study sites

Dwarf ginseng perennates from a short rhizome attached to a globose, tuberous root. Each spring, a single new shoot arises from a bud that was formed near the end of the previous growing season (personal observation). Thus, size (root weight) at the end of one growing season should be a predictor of the amount of resources available for production of leaves, flowers and fruits in the following season. The shoot consists of a single stem that bears a whorl of three leaves and terminates in a simple umbel of flowers (the smallest plants are vegetative, with shoots but no flowers). Each of the three leaves has three (occasionally five) leaflets, and the middle leaflet of each leaf is always the largest. Male plants have staminate flowers with five stamens and a reduced, non-functional gynoecium; while hermaphroditic plants have perfect flowers with five stamens and either three or four partially fused, uniovulate carpels. Hermaphrodites typically produce six to eight flowers, while males have 15 to 20 or more (Philbrick 1983; Schlessman 1987, 1990). The phenotypic gender (allocations to male and female functions, relative to other individuals in the population; Lloyd and Bawa 1984) of hermaphrodites is highly female-biased, and they probably function almost exclusively as females (Schlessman 1987, 1988, 1990). For illustrations see Philbrick (1983) and Schlessman (1987).

I used 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). The study populations were in mixed deciduous forest, near to but somewhat drier than the swampy flood plains of streams.

Statistics

Unless otherwise noted, I followed the procedures of Sokal and Rohlf (1981). For analyses comprised of several component tests or of several different tests of the same null hypothesis, I determined the table-wide significance of each test statistic by the sequential Bonferonni method (Rice 1989) with a significance level of 0.05. The sequential Bonferonni method adjusts for the number of simultaneous tests to prevent the overly liberal determinations of significance that occur when each test is judged individually (Rice 1989).

Gender dynamics

I marked the locations of individuals with plastic stakes and recorded their sex expression for four years (1982–85) at C, and for three years (1983–85) at SK and T. By examining the size and number of floral buds, I was able to unambiguously "sex" plants as soon as their shoots emerged in the spring. I chose males and hermaphrodites haphazardly, i.e. without regard to size or any other aspect of the plant or its location within the population that might affect its future size. I increased the sample size at C in both 1983 and 1984, and in each population I marked new individuals to replace those that died or, rarely, could not be relocated. Thus, some individuals were observed for only two years (one possible sex change) while others were followed for three or four years (two or three possible sex changes). Each year after a plant had been marked, I recorded its status as hermaphroditic, male, vegetative, or dead (marker present but no shoot emerged). For each gender phase, I estimated the overall frequency of gender change (changes in status between male and hermaphroditic) from yr x to yr x + 1. This required correcting for differences between the male:hermaphrodite ratios of my marked samples, which were usually near 1:1, and those of entire populations, which were highly male-biased (methods are given in Schlessman 1990). I used log-linear models (Fienberg 1980; Sokal and Rohlf 1981; Freeman 1987) to evaluate the influences of gender in yr x, site, and year on status (vegetative, male, hermaphrodite, or dead) in yr x + 1. I used G-tests with Williams' correction to determine whether mortality and the propensity to become vegetative were independent of gender, and Zar's method for testing differences among proportions (1974, one-tailed with continuity correction) to evaluate differences between gender phases in their propensity to change gender.

Size and gender

For a non-destructive measure of size, I used the sum of the lengths of the three fully expanded middle leaflets (measured to the nearest mm) of each individual. Although there may have been some variation due to conditions of the current year, leaf size should have been correlated with the amount of resources available at the end of the previous year (see *The plant and study sites*). For a haphazardly collected sample of 25 vegetative, 34 male, and 30 hermaphroditic individuals from BR in 1983, the sum of middle leaflet lengths was strongly and very highly significantly correlated with both the total of all leaflet lengths ($r = 0.85$, $P < 0.001$) and with root dry weight ($r = 0.85$, $P < 0.001$). In a similar sample from C in 1985 (four vegetative, 30 male, 20 hermaphroditic), the sum of middle leaflet lengths was strongly and very highly significantly correlated with leaf area as determined with a Li-Cor leaf area meter ($r = 0.88$,

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Table 1. Estimated percentages of individuals in the entire population that changed gender, by population and years of transition (yrs x and $x+1$). C = Cary, SK = Stony Kill, T = Taconic. Population male:hermaphrodite ratios necessary for these estimates were available only for the transitions shown (see Materials and methods)

Transition	Gender phase ratio (M:H; yr x)	% that changed gender		
		Hermaphrodites	Males	Hermaphrodites + males
C 82–83	7.2:1	83	31	37
C 83–84	5.9:1	59	28	32
C 84–85	4.2:1	60	28	34
SK 84–85	3.5:1	50	16	25
T 83–84	3.8:1	57	17	25

Table 2. Percentages of individuals followed for three or more years that changed gender various numbers of times. Only transitions between male and hermaphroditic (e.g. H–H–M, M–H–M) were scored as gender change, individuals that became vegetative (e.g. M–V–M) were scored as remaining the same gender; n = sample size, M = remained male, H = remained hermaphroditic

Population	Observed 3 yrs						Observed 4 yrs					
		No. of changes					No. of changes					
		0		1	2		0		1	2	3	
	n	M	H			n	M	H				
Cary (C)	72	33	6	33	28	35	17	0	26	34	23	
Stony Kill[a] (SK)	39	33	15	33	18	–	–	–	–	–	–	
Taconic (T)	59	27	8	34	31	–	–	–	–	–	–	

[a] Percentages total 99 due to rounding

$P < 0.001$). In addition to these samples, I measured leaflet lengths of individuals from a different population at BR in 1984, and of individuals at C, SK, and T that had been marked to detect gender change and for other purposes. In 1984 and 1985, a few vegetative plants that had been either male or hermaphroditic in previous years were measured. I used one-tailed t-tests to test the predictions that males would be larger than hermaphrodites and hermaphrodites would be larger than males.

Size change and gender change

I used G-tests with Williams' correction to determine the significance of differences between the proportions of individuals of each gender that became larger or smaller; and Zar's method (see above) to test the predictions that 1) males that became larger would be more likely to change gender than those that remained the same size or became smaller, and 2) hermaphrodites that became smaller would be more likely to change than those that remained the same size or became larger.

Results

Gender dynamics

Gender changes occurred in both directions, from male to hermaphrodite and from hermaphrodite to male (raw data in Appendix). Between 25% and 37% of all flowering individuals changed from one year to the next (Table 1). Multiple changes were common (Table 2). Eighteen to 31% of individuals followed for three years changed twice, as did 34% of those followed for four years. Twenty three percent of the individuals followed for four years changed three times. Thirty five to 48% of the plants followed for three years did not change, and 76% of the non-changers remained male. Only 17% of plants followed for four years did not change, and all of those remained male.

Table 3. Goodness-of-fit tests for log-linear models of gender dynamics (data in the Appendix). Y = yrs of transition, P = population, G = gender yr x, S = state yr $x+1$, * = significant table-wide. Models 1–7 included the three-way interaction [YPG]. Models 8–10 included the two-way interaction [YG]

Model	Tested significance of	x^2	P
A. Cary, Stony Kill and Taconic; 82–83 and 84–85			
1. [YPS][YGS][YGS]	[YPGS]	9.24	0.161
2. [YPS][PGS]	[YGS]	15.46	0.075
3. [YPS][YGS]	[PGS]	15.94	0.194
4. [YGS][PGS]	[YPS]	19.73	0.072
5. [PS][GS]	[YS]	41.23	0.016
6. [YS][PS]	[GS]	46.90	0.003*
7. [YS][GS]	[PS]	78.43	$\ll$0.001*
B. Cary only; 82–83, 83–84, and 84–85			
8. [GS][YS]	[YGS]	10.82	0.094
9. [GS]	[YS]	19.14	0.085
10. [YS]	[GS]	24.34	0.004*

For log-linear modeling, I analyzed the data in two subsets: all populations for 1983–85, and C alone for 1982–85. I made the first analysis on a four-way contingency table with data classed by years of transition, population, gender in year x, and status in year x + 1 (Table 3A). The three-way interaction among transition, population and gender was fixed by design and therefore included in all models. None of the tested three- or four-way interactions were significant. Only population and gender had significant effects on status, and the effect of population was stronger than that of gender. The analysis for C alone was a three-way table with data classed by years of transition, gender in year x, and status in year x + 1 (Table 3B). The fixed two-way interaction between transition and gender was included in all models. The three-way interaction among transition, gender and status was not significant, and only gender had a significant effect on status.

Because the log-linear models showed that gender dynamics depended upon population and gender, but not years of transition, I combined transitions within populations and made all further analyses on each population separately (data summarized in Fig. 1). In each popula-

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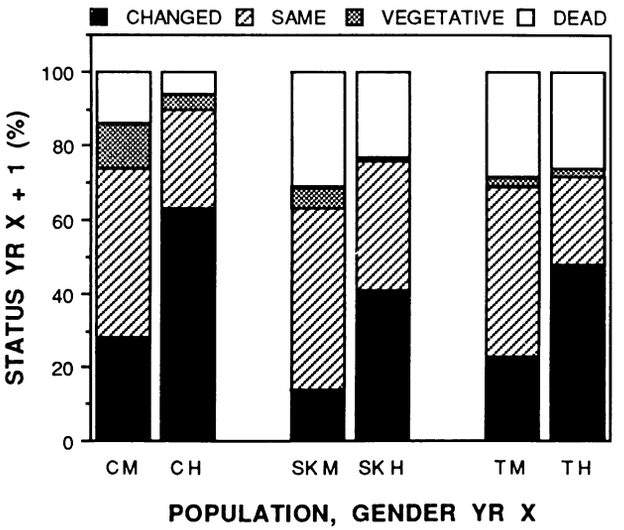


Fig. 1. Gender dynamics of dwarf ginseng. Data are grouped by population and gender in yr x (raw data in Appendix). Shading represents proportions of individuals that changed gender, remained the same gender, became vegetative, or died by yr $x+1$

Table 4. Tests of significance of differences between gender phases in mortality and the proportions of surviving individuals that became vegetative and changed gender (Fig. 1, raw data in Appendix). * = significant table-wide

A. Tests of the null hypothesis that mortality by yr $x+1$ was independent of gender in yr x

Population	G_{adj}	P
Cary	3.35	>0.05
Stony Kill	1.38	>0.05
Taconic	0	>0.05

B. Tests of the null hypothesis that surviving and becoming vegetative in yr $x+1$ was independent of gender in yrs x

Cary	7.45	<0.01*
Stony Kill	2.70	>0.05
Taconic	0.18	>0.05

C. Tests of the null hypothesis that individuals that were hermaphroditic in yr x equally or less likely than those that were male in yr x to survive and change gender in yr $x+1$

Population	Z	P
Cary	5.38	<0.0005*
Stony Kill	4.48	<0.0005*
Taconic	3.49	<0.0005*

tion, mortality was independent of gender (Fig. 1, Table 4A). Males were significantly more likely than hermaphrodites to become vegetative at C, but not at SK or T (Fig. 1, Table 4B). In all three populations, hermaphrodites changed gender significantly more often than males (Fig. 1, Table 4C). This difference between phases in the likelihood of gender change is clearly not due to differential mortality or differential probabilities of becoming vegetative. At C, the difference in the probabilities of becoming vegetative is too small to account for the difference in gender change.

Table 5. Sample sizes for data summarized in Fig. 2, and tests of the null hypothesis that the mean sizes of hermaphrodites were equal to or less than those of males. For each of the tests, P was ≤ 0.0005 and the result was significant table-wide. Degrees of freedom (1, df) are approximate when variances are unequal

Sample	Sample size (n)			$X_H \leq X_M$?	
	V	M	H	t	1, df
BR1 83	25	34	30	7.34	47
BR2 84	0	50	50	7.66	85
C82	0	50	50	9.06	99
C83	0	52	31	10.26	81
C84	6	99	83	10.44	180
C85	12	89	49	8.43	136
SK83	0	49	45	5.55	79
SK84	4	49	50	7.29	97
SK85	4	48	34	5.14	80
T83	0	58	60	6.55	116
T84	0	70	48	5.07	116
T85	4	49	33	4.01	80

Size and gender

In each of four populations, the mean size of hermaphrodites was significantly greater than that of males (Fig. 2, Table 5). For the sample from BR in 1983, males were significantly larger than vegetative plants (one-tailed test, $t=6.47$, d.f. $=1, 44$, $P \ll 0.001$). In all other samples, vegetative plants comprised very small, nonrandom groups of previously reproductive individuals; thus statistical tests of size differences were inappropriate. Nevertheless, it is noteworthy that in each case the mean size of previously reproductive vegetative plants was less than that of males.

Size change and gender change

Males in all populations were significantly more likely to grow larger than to become smaller, whereas in two of three populations hermaphrodites were more likely to become smaller than to grow larger (Table 6A). Males that grew larger were more likely to change gender than those that became smaller, but the difference was significant only for C (Table 6B). Hermaphrodites that became smaller were more likely to change than those that grew larger, but again the difference was significant only for C (Table 6C).

Discussion

Here I have estimated that 25% to 37% of flowering individuals change gender from year to year. The only comparable published data on the overall frequency of changes in populations of other diphasic species are for jack-in-the-pulpit (*Arisaema triphyllum,* Araceae), in which the gender phases are male and female. From Bierzychudek (1982, 1984) I calculated the frequency of sex changing as 17.6% for the Fall Creek site and 10.0%

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Table 6. Tests of predictions about size change and gender change. * = significant table-wide

A. Tests of the prediction that males would be more likely to increase in size than to decrease, while hermaphrodites would be more likely to decrease in size than to increase

Gender yr x	Population	Size yr $x+1$		G_{adj}	P
		Larger	Smaller or same		
Male	Cary	115	37	41.90	<0.0005*
	Stony Kill	35	12	11.50	<0.0005*
	Taconic	57	30	8.50	<0.0025*
Hermaphrodite	Cany	58	74	1.95	>0.25
	Stony Kill	19	36	5.29	<0.0125*
	Taconic	24	42	4.94	<0.0125*

B. Tests of the prediction that males which grew larger would change gender to hermaphrodite more often than those which became smaller or remained the same size

Population	Size yr $x+1$	Gender yr $x+1$		Z	P
		Male	Hermaphrodite		
Cary	larger	67	48		
	smaller	34	3	3.76	<0.0005*
Stony Kill	larger	21	14		
	smaller	7	5	0.10	>0.90
Taconic	larger	34	23		
	smaller	23	7	1.56	>0.05

C. Tests of the prediction that hermaphrodites which became smaller would change gender to male more often than those which became larger or remained the same size

Cary	larger	23	35		
	smaller	51	23	3.50	<0.0005*
Stony Kill	larger	8	11		
	smaller	19	17	0.78	>0.5
Taconic	larger	12	12		
	smaller	31	11	1.94	>0.05

for the Brooktondale site, and from Lovett-Doust and Cavers (1982) I calculated 0.6% and 28% for the Dingman and Campus sites. Gender changes appear to be more common in dwarf ginseng than in jack-in-the-pulpit. Nevertheless, the fact that changes are common does not completely rule out the existence of genetically determined sexual morphs. One could suppose that some individuals are genetically capable of changing while others are not; or perhaps that there are two genetic morphs, each with different propensities for changing (dimorphism with phase choice, Lloyd and Bawa 1984). However, my data on the sex expression of individuals over three or four years show that the existence of two genetic morphs is highly unlikely. Although about 40% of the individuals followed for three years did not change, 78% of the non-changers stayed male. This is very weak evidence for a male genetic morph because the low probability of a diphasic plant becoming hermaphroditic is consistent with observations that the vast majority of flowering individuals are small and male. The plants that remained hermaphroditic for three years are slightly more problematic, but they constituted only 22% of the non-changers (9% of the total). This is not a large proportion considering that it includes individuals that spent one or two seasons in the vegetative state. Of the plants observed for four years, only 17% did not change, and all of those remained male. Thus the evidence for genetic morphs is extremely weak, and it appears likely that longer term observations will show conclusively that they do not exist. Furthermore, the observation that hermaphrodites were significantly larger than males is predicted by the size advantage hypothesis for diphasy, but is inconsistent with genetic dimorphism. The high male:hermaphrodite ratios of dwarf ginseng are also inconsistent with genetic dimorphism but easily explained by diphasy (Charnov and Bull 1989). The best interpretation is that males and hermaphrodites are environmentally determined gender phases, not genetic morphs. Dwarf ginseng is diphasic, not androdioecious.

The size and gender dynamics of dwarf ginseng indicated that the genders differed in the net amount of resources (e.g., photosynthates) that they were likely to accumulate during the growing season. Males were two to three times more likely to grow larger than to become smaller, indicating that they are usually able to increase their stored resources. In contrast, hermaphrodites in

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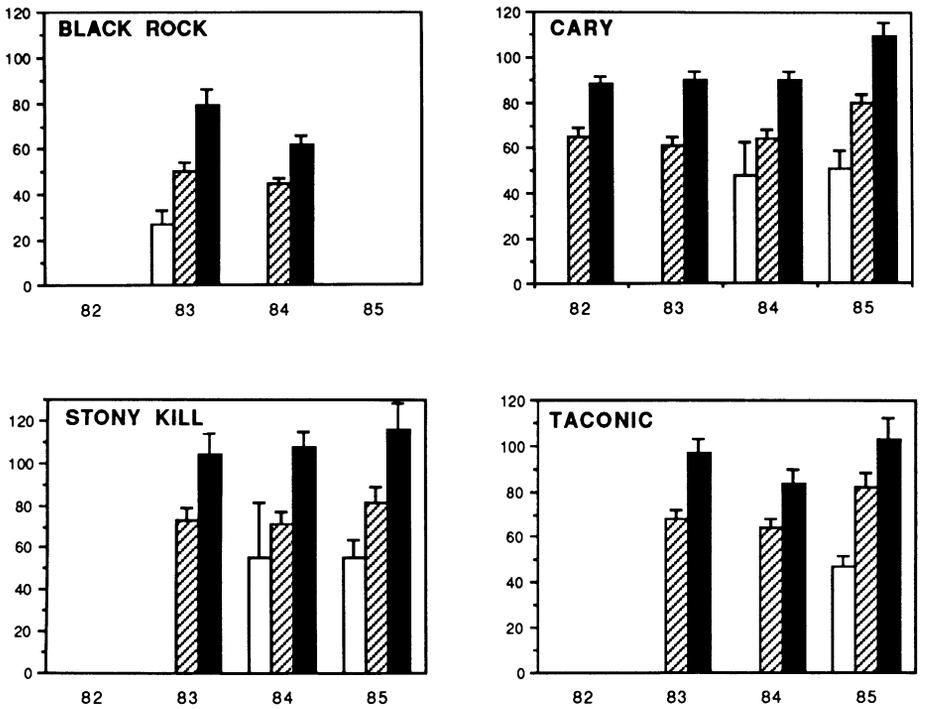


Fig. 2. Means plus 95% confidence intervals for samples of vegetative (white bars), male (hatched bars) and hermaphroditic (black bars) individuals from five populations of dwarf ginseng. The 1983 and 1984 samples from Slack Rock Forest were taken from different populations (see Materials and methods)

two of three populations were significantly more likely to become smaller than to grow larger, indicating that maturation of fruits usually required more resources than an individual could accumulate. Assuming each individual had a size threshold that determined whether it was male or hermaphroditic, this difference in the direction of size change helps to explain why hermaphrodites were two to three times more likely to change than males. Hermaphrodites that became smaller tended to change more often than those that grew larger, and males that grew larger tended to change more often than those that became smaller. Although these differences were statistically significant in only one of three populations, it does appear that hermaphrodites were much more likely to decrease in size and pass under the threshold for gender change than males were to increase in size and pass over the threshold. Thus, individuals are likely to spend most of their lives at sizes too small to be hermaphrodites, and the lifetime fitness gained from flowering as a male when small may be greater than the costs (Schlessman 1987). Results for jack-in-the pulpit were similar to mine (Bierzychudek 1984, Figs. 2, 3). Female jack-in-the-pulpits that became smaller were more likely to change than those that grew larger ($Z = 3.55$, $P < 0.0005$), and males that grew larger changed more often than those that became smaller ($Z = 1.92$, $P < 0.05$).

Asymmetries between genders in the probabilities of size and gender change are important for understanding diphasy and male-biased gender phase ratios in dwarf ginseng, but they may not be characteristic of all diphasic plants. Again, the only comparable published data are for jack-in-the-pulpit. At Bierzychudek's Fall Creek site, the proportions of individuals that grew larger from 1978 to 1979 were 52% for males and 57% for females (from Bierzychudek 1984, Figs. 2, 3). The result for male jack-in-the-pulpits was in the direction I predicted for dwarf ginseng, but the null hypothesis that males were more likely to become smaller than larger could not be rejected ($G = 0.08$, $P > 0.25$). The result for females was not what I predicted for dwarf ginseng, and it is also not significant ($G = 0.96$, $P > 0.05$). The differences between dwarf ginseng and jack-in-the pulpit in proportions of hermaphrodites or females that became smaller may have been due to differences in seed set. For dwarf ginseng, mean seed set per hermaphrodite ranged from 72% to 87% (Schlessman 1990), while for female jack-in-the-pulpits, half or more set no seeds at all (Policansky 1981, Bierzychudek 1982). A hand pollination experiment led Bierzychudek (1982) to conclude that seed set by jack-in-the-pulpit was pollen-limited, while a similar experiment indicated that this was not the case for dwarf ginseng (Schlessman, unpublished). Thus, many female jack-in-the-pulpits may have remained female because they did not incur the cost of maturing fruit. Pollen limitation of female reproductive function may have contributed to the female-biased gender phase ratios occasionally observed in jack-in-the-pulpit and some diphasic orchids (Schaffner 1922; Gregg 1975; Lovett-Doust and Cavers 1982).

The data presented here strongly support my earlier conclusion that sex expression in dwarf ginseng is determined primarily by the size of the root at the end of the previous growing season (Schlessman 1987). Lovett-Doust and Cavers (1982) and Bierzychudek (1984) reached similar conclusions for jack-in-the-pulpit, and this may be a general result for sex changers that differentiate new shoot buds near the end of the growing season. However, other historical factors (e.g., past levels of hormones) and current conditions may also influence sex expression (Bierzychudek 1984). Either historical factors

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APPENDIX. Gender dynamics for three populations of dwarf ginseng, n = sample size

Population	Transition	Gender yr x, n	Status yr $x+1$			
			Hermaphrodite	Male	Vegetative	Dead
C	82–83	Male, 26	8	10	2	6
		Hermaphrodite, 24	2	20	0	2
	83–84	Male, 50	14	30	3	3
		Hermaphrodite, 46	14	27	3	2
	84–85	Male, 105	29	44	16	16
		Hermaphrodite, 77	23	46	3	5
SK	83–84	Male, 40	5	18	4	13
		Hermaphrodite, 44	20	15	0	9
	84–85	Male, 45	7	24	1	13
		Hermaphrodite, 34	7	17	1	9
T	83–84	Male, 66	10	37	2	17
		Hermaphrodite, 61	13	35	0	13
	84–85	Male, 66	21	23	2	20
		Hermaphrodite, 44	13	15	2	14

(past reproductive effort) or current conditions (allowing for greater leaf expansion) might explain why, in my study, a relatively large proportion of hermaphrodites that grew larger also changed gender. For species with less distinctly seasonal reproductive patterns, or with lengthy periods of inflorescence development, immediate environmental conditions may be as important or more important than size at the end of the last reproductive episode. Light is clearly important for sex-changing orchids in the genera *Catasetum* and *Cycnoches* (Gregg 1975, 1978, 1982; Zimmerman 1989). Condon and Gilbert (1990) have suggested that size-related gender change in the cucurbitacous vines *Gurania* and *Psiguria* (Condon and Gilbert 1988) is not mediated by size per se, but rather by the fact that only large vines have been able to reach the top of the forest canopy where there is more light.

In this study there were significant differences in gender dynamics among populations. Such variation has also been found for jack-in-the-pulpit, and Bierzychudek (1984) suggested that it was due to genetic differences among populations. But the alternative hypothesis that it represented responses of similar genotypes to different environments was supported by transplant experiments (Lovett-Doust and Cavers 1982). Nevertheless, there is no theoretical reason to exclude the possibility of continuous genetic variation within populations of sex changers for response to conditions affecting sex expression. Studies designed to detect such variation would be worthwhile.

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References

Bawa KS, Beach JH (1981) Evolution of sexual systems in flowering plants. Ann M Bot Gard 68:254–274

Bierzychudek P (1982) The demography of jack-in-the-pulpit, a forest perennial that changes sex. Ecol Monogr 52:335–351

Bierzychudek P (1984) Determinants of gender in jack-in-the-pulpit: the influence of plant size and reproductive history. Oecologia 65:14–18

Charlesworth B, Charlesworth D (1978) A model for the evolution of dioecy and gynodioecy. Am Natur 112:975–997

Charlesworth D (1984) Androdioecy and the evolution of dioecy. Biol J Linn Soci 23:333–348

Charnov EL (1982) The Theory of Sex Allocation. Princeton University Press, Princeton

Charnov EL, Bull JJ (1989) Non-fisherian sex ratios with sex change and environmental sex determination. Nature 338:148–150

Condon MA, Gilbert LE (1988) Sex expression of *Gurania* and *Psiguria* (Cucurbitaceae): neotropical vines that change sex. Am J Botany 75:875–884

Condon MA, Gilbert LE (1990) Reproductive biology and natural history of neotropical vines *Gurania* and *Psiguria* (= *Anguria*). In: Bates D, (ed) Biology and Chemistry of Cucurbitaceae. Cornell University Press, Ithaca

Fienberg SE (1980) The Analysis of Cross-classified Categorical Data. 2nd ed. The MIT Press, Cambridge

Freeman DC, Harper KT, Charnov EL (1980) Sex change in plants: old observations and new hypotheses. Oecologia 47:222–223

Freeman DC, McArthur ED (1984) The relative influences of mortality, nonflowering and sex change on the sex ratios of six *Atriplex* species. Bot Gaz 145:385–394

Freeman DH, Jr. (1987) Applied Categorical Data Analysis. Marcel Dekker, Inc., New York

Ghiselin MT (1969) The evolution of hermaphroditism among animals. Quart Rev Biol 44:189–208

Gregg KB (1975) The effect of light intensity on sex expression in species of *Cycnoches* and *Catasetum* (Orchidaceae). Selbyana 1:101–113

Gregg KB (1978) The interaction of light intensity, plant size, and nutrition on sex expression in *Cycnoches* (Orchidaceae). Selbyana 2:212–223

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Gregg KB (1982) Sunlight-enhanced ethylene evolution by developing inflorescences of *Catasetum* and *Cycnoches* and its relation to female flower production. Bot Gaz 143:466–475
Leigh EG, Charnov EL, Warner RR (1976) Sex ratio, sex change, and natural selection. Proceedings of the National Academy of Sciences 73:3656–3660
Lloyd DG (1975) The maintenance of gynodioecy and androdioecy in angiosperms. Genetica 45:325–339
Lloyd DG, Bawa KS (1984) Modification of the gender of seed plants in varying conditions. Evol Biol 17:255–338
Lovett-Doust J, Cavers PB (1982) Sex and gender dynamics in jack-in-the-pulpit, *Arisaema triphyllum* (Araceae). Ecology 63:797–808
Philbrick CT (1983) Contributions to the reproductive biology of *Panax trifolium* L. (Araliaceae). Rhodora 84:97–114
Policansky D (1982) Sex change in plants and animals. Ann Rev Ecol Syst 13:471–495
Rice WR (1989) Analyzing tables of statistical tests. Evolution 43:223–225

Note added in proof. As this paper went to press, J.K. Zimmerman reported the gender dynamics of 186 individuals of *Catasetum viridiflavum* over a 2 yr period (Ecology 72:597–608)

Schaffner JH (1922) Control of the sexual state in *Arisaema triphyllum* and *Arisaema dracontium*. Am J Bot 9:72–78
Schlessman MA (1986) Interpretation of evidence for gender choice in plants. Am Natur 128:416–420
Schlessman MA (1987) Gender modification in North American ginsengs. BioScience 37:469–475
Schlessman MA (1988) Gender diphasy ("sex choice"). In: Lovett-Doust J, Lovett-Doust, L (eds) Plant Reproductive Ecology: Patterns and Strategies. Oxford University Press, New York, pp 139–153
Schlessman MA (1990) Phenotypic gender in sex-changing dwarf ginseng, *Panax trifolium* (Araliaceae). Am J Bot 77:1125–1131
Sokal RR, Rohlf FJ (1981) Biometry. 2nd ed. W. H. Freeman and Co., New York
Zar JH (1974) Biostatistical analysis. Prentice-Hall, Inc. Englewood Cliffs
Zimmerman JK (1989) Evolutionary ecology of *Catasetum viridiflavum*, an orchid that changes sex. Ph.D. dissertation, University of Utah, Salt Lake City

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