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Source: *Bulletin of the Torrey Botanical Club*, Apr. - Jun., 1985, Vol. 112, No. 2 (Apr. - Jun., 1985), pp. 129-133

Published by: Torrey Botanical Society

Stable URL: <https://www.jstor.org/stable/2996409>

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Floral biology of American ginseng (*Panax quinquefolium*)¹

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SCHLESSMAN, M. A. (Dept. Biology, Vassar College, Poughkeepsie, NY 12601). Floral biology of American ginseng (*Panax quinquefolium*). Bull. Torrey Bot. Club 112:129–133. 1985.— In a population of *Panax quinquefolium* in southeastern New York, reproductive individuals produce bisexual flowers with either a two-styled ovary containing two ovules or a one-styled ovary containing a single ovule. The number of flowers produced, the ratio of two- to one-styled flowers, and the percentage of ovules maturing into seeds all increase with plant size. Flowers are capable of autogamy. Xenogamy is effected by syrphid flies and halictid bees. Fecundity appears to be regulated by the availability of resources.

Key words: *Panax*, ginseng, floral biology, phenology, mating system

Knowledge of the biology of *Panax quinquefolium* L. has economic as well as scientific value. For approximately 230 years, roots of American ginseng have been collected for export to the Orient (Fulder 1980). The Department of Agriculture estimated that 224.5 metric tons of naturally grown and cultivated American ginseng were exported from the United States from October 1981 through March 1982 (USDA 1982). The following year, a business news article reported that 80,000 to 100,000 pounds of “wild” roots are traded annually (Goolrick 1983). As a result of prolonged and often intense commercial pressures, *P. quinquefolium* is considered uncommon, threatened, rare, or endangered in well over three-fourths of its range (ICAC 1981).

When this study was initiated, the floral biology of *Panax quinquefolium* was very poorly known. Although Smith (1944) described the flowers as bisexual, Graham (1966) implied that some were unisexual. Floral visits by halictid bees and syrphid flies were observed by Duke (1980), but Lewis and Zenger (1982) cautiously referred to the flowers as “presumably entomophil-

ous and bisexual.” Subsequently, Carpenter and Cottam (1982) and Lewis and Zenger (1983) reported bisexual, self-compatible, often protandrous flowers. Although Hu et al. (1980) noted variation in the number of seeds per fruit, they did not determine the causes of that variation.

In this paper I present results of observations and experiments on the floral biology of a population of *Panax quinquefolium* in southeastern New York. My purpose is to elucidate the floral morphology, floral phenology and mating system of American ginseng. This study differs from previous investigations in that particular attention is devoted to variation in floral morphology and the possible effects of such variation on seed production.

Materials and Methods. THE PLANT. *Panax quinquefolium* perennates from a short rhizome surmounting a taproot. The single aerial shoot bears one to four (or rarely more) palmately compound leaves (known to ginseng growers as “prongs”) in a single whorl, and terminates in a single, simple umbel of flowers. Size and number of leaves increase with age, as estimated by the number of bud scars on the rhizome (Lewis & Zenger 1982; Carpenter & Cottam 1982; Lewis 1984). The fruits are bright red drupes.

PROCEDURES. Observations and mating system experiments were conducted in 1982 and 1983 in a population approximately 40 miles north of New York City in Westchester County, New York. The population consisted of about 220 individuals. In 1982, 48

¹This study was supported by a Cottrell College Science Grant from the Research Corporation, and by a Grant-in-Aid from the Beadle Fund of the Vassar College Sigma Xi Club.

²Tim L. McCabe identified floral visitors. Edith Bernosky, Jerry Calvin, Stephanie Hafford, and James Heitz provided technical assistance.

Received for publication June 10, 1984 and in revised form February 14, 1985.

of 113 individuals in the 3-leaved size class were included in this study. With that exception, natural fruit and seed production was assessed for all reproductive individuals in both years.

Floral visitors were observed during several 30-minute periods spanning the daylight hours. Floral visitors were collected for identification and for confirmation that they carried ginseng pollen. Specimens for studies of floral anatomy were fixed in absolute ethanol and acetic acid (3:1, v:v), cleared in 7M NaOH, and stained with dilute aniline blue to assess the degree of ovule development.

To determine the timing of stigmatic receptivity, flowers that had been hand pollinated at various phenological stages were collected two to four hours after pollination, then fixed and cleared as above. Cleared flowers were stained according to Martin (1959) and examined under ultraviolet (UV) illumination with a microscope equipped for epi-fluorescence. The presence of pollen tubes indicated that stigmas were receptive at the time of pollination.

Mating system experiments were conducted in the field with individuals bearing either three or four leaves. To test for agamospermy, all the flowers of three individuals were emasculated in bud, and insects were excluded with fine mesh bags. Self-compatibility was assessed by bagging inflorescences of several individuals while in bud, then making hand pollinations among flowers of each inflorescence. To compare the efficacy of self- and cross-pollination, flowers of bagged inflorescences were emasculated in bud and cross-pollinated by hand.

Two experiments were designed to assess the capability for selfing without the aid of pollinators. In the first experiment, inflorescences were bagged and left undisturbed until fruit developed. In this test, seeds may have resulted from either autogamous or geitonogamous selfing. In the second experiment, most of the floral buds were removed in such a way that the four or five remaining ones were too far apart to shed pollen on one another when the flowers opened. In this second experiment sexual reproduction could result only from autogamy.

Xenogamous pollination was assessed by emasculating all buds of several individ-

uals and determining their seed set. Indirect estimates of the mating system were made by calculating the outcrossing indices (OCI's) and the pollen to ovule ratios (P/O's) of individual flowers (Cruden 1977).

Results. FLORAL MORPHOLOGY AND SEED SET. All flowers were morphologically bisexual with five (or rarely four) calyx teeth, five greenish-white petals, five stamens, and an inferior ovary with one or two (or rarely three) styles. One-styled flowers developed only one ovule. Abortion of an ovule in one-styled flowers produced ovaries that were asymmetrical and slightly smaller than those of two-styled flowers. The two floral forms could be distinguished by ovary size and shape as well as by style number. Small (two-leaved) individuals produced fewer flowers and a larger proportion of one-styled flowers than larger (three- and four-leaved) individuals (Table 1). Kruskal-Wallis one-way analyses of variance for flower number and per cent one-styled flowers by leaf number were conducted for each year. In both 1982 and 1983, differences among the means were significant ($P < .05$).

Because the withered styles persisted, it was possible to determine whether fruits had developed from one- or two-styled flowers. Therefore, seed set could be evaluated as the percentage of ovules that matured into seeds. Seed set tended to increase with plant size (Table 1), however the differences among means for plants of various sizes were significant only in 1983 (Kruskal-Wallis one-way ANOVA: 1982 $P = .561$; 1983 $P = .001$).

Table 1. Reproductive features of *Panax quinquefolium*. For each year, data are grouped by morphological class, i.e., the number of leaves on the plant. Means (\bar{X}) and standard deviations (\pm S.D.) are given when n , the number of plants in each morphological (size) class, is ≥ 7 .

Year	No. of Leaves	n	No. of Flowers	Per cent one-styled (flowers)	Per cent seed set
1982	2	13	6 \pm 4	93 \pm 15	20 \pm 21
	3	48	14 \pm 8	60 \pm 40	29 \pm 24
	4	1	27	11	27.5
	Total	62	13 \pm 8	66 \pm 39	27 \pm 23
1983	2	2	8	100	12
	3	17	9 \pm 8	71 \pm 41	14 \pm 12
	4	7	20 \pm 8	20 \pm 25	45 \pm 17
	Total	26	12 \pm 8	59 \pm 44	22 \pm 20

FLORAL PHENOLOGY, POLLINATORS, AND MATING SYSTEM. In both 1982 and 1983, flowering began during the second week of June and continued through the third week of July. The largest (four- and some three-leaved) individuals tended to flower earlier in the season than smaller ones. Within inflorescences, flowers matured centripetally over a period of one to three weeks. As buds opened, the petals reflexed to become perpendicular to the floral axis. Soon after the petals reflexed, filaments of the stamens ceased elongation and the anthers dehisced. At about the same time, the styles reached maximum length and their apparently receptive stigmatic tips bent away from each other. After the styles matured, the stamens and later the petals abscised. The entire sequence was completed in two or three days.

Table 2 summarizes the results of hand cross pollinations to determine the timing of stigmatic receptivity. Pollinations were most successful when performed after anthers had fallen. However, pollen tubes were present in one half of the styles pollinated during anther dehiscence, and in approximately one quarter of those pollinated before anther dehiscence. The success of pollinations made before anther dehiscence indicates that many flowers were not protandrous. Instead, there was an hermaphroditic phase when pollen was released, followed by a female phase when the anthers had dehisced but the stigmas remained receptive.

The only regular floral visitors were halictids (*Dialictus* sp.) and syrphids (*Mesograptus boscii* Macq., *Melanostoma mellinum* L.). Individuals collected after visiting two or three ginseng inflorescences were carrying ginseng pollen. Both syrphids and

halictids occasionally visited two or more flowers on the same inflorescence. Pollinators were infrequent. During a 30-minute period, I seldom saw more than three different visitors on any one plant.

For flowers from this population, the outcrossing index (OCI) (Cruden 1977) was: 2 (corolla 4 mm wide) + 0 (flowers homogamous + 0 (stigmas and anthers on the same level, i.e., not spatially separated) = 2. Cruden found that species with an OCI of 2 tended to have mixed mating systems in which autogamy predominated over xenogamy. Because anthers from one- and two-styled flowers did not differ in size, I used single anthers from five flowers of each type to determine pollen production. The mean number of pollen grains per anther was 1313 (S.D. \pm 164, $n = 10$). Therefore, the pollen to ovule (P/O) ratios are 3282:1 for two-styled flowers and 6565:1 for one-styled flowers. The former ratio suggests predominant xenogamy, while the latter is characteristic of flowers that are clearly adapted for outcrossing (see Cruden 1977, Table 1). Individuals with both types of flowers will have inflorescence P/O's between these two extremes.

Mating system experiments are summarized in Table 3. Flowers that were emasculated and bagged to test for agamospermy (AGA) produced no seeds. These results, along with those of the other mating system experiments, rule out asexual seed production. The two experiments on selfing in the absence of insects produced rather dissimilar results. Seed set of inflorescences in which most of the buds had been removed in order to assess autogamy was significantly

Table 2. Stigmatic receptivity of *Panax quinquefolium* flowers pollinated at three phenological stages.

Stage	No. of flowers	No. of styles	Per cent styles with pollen tubes
Before anther dehiscence	26	44	27
During anther dehiscence	48	90	50
After anthers fallen	13	23	61
Totals	87	157	45

Table 3. Mating system experiments for *Panax quinquefolium*. AGA = tests for agamospermy; SC = self-compatibility (hand self-pollination); A/G = tests for autogamous or geitonogamous selfing (bagged, undisturbed); A = tests for autogamous selfing only; X = tests for xenogamy; HX = hand cross-pollination.

Treatment	No. of flowers	Per cent seed set
AGA	19	0
SC	57	43
A/G	142	37
A	24	48
X	60	38
HX	20	31

higher than that of inflorescences that were bagged and left undisturbed (A vs A/G; $X^2 = 4.28$, $P < 0.05$). In contrast, hand selfing of all flowers did not increase seed set over that of bagged inflorescences (SC vs A/G; $X^2 = 0.67$, $P > 0.05$). Flowers that were emasculated to enforce xenogamy (X) produced almost the same proportion of seeds as self-pollinated ones (A/G). Hand crossing (HX) did not increase seed set over that of the other experiments.

Discussion. FLORAL MORPHOLOGY AND SEED SET. This study corroborates the low natural fecundity of *Panax quinquefolium* (Carpenter & Cottam 1982; Lewis & Zenger 1982). Lewis and Zenger suggested that low seed set is due to inadequate pollination and abortion of fertilized ovules. My study shows that pre-fertilization abortion of ovules in one-styled flowers also affects seed production.

There are no previous reports of one-styled, single-ovuled flowers in *Panax quinquefolium*. However, I have found one-styled flowers in three natural populations and on several herbarium specimens. According to Hara (1970), Asiatic species of *Panax* may have "male" flowers with short styles united in a single column. In *P. quinquefolium* the styler column of one-styled flowers also appears to consist of two fused parts. The "male" flowers of Asiatic ginsengs may be functionally hermaphroditic. A non-functional styler column is present in staminate flowers of *Panax trifolium*, the sole New World congener of American ginseng (Philbrick 1983; Schlessman, personal observations). Perhaps the one-styled flowers of *P. quinquefolium* represent an intermediate step in the evolution of functional maleness. Complete elucidation of the significance of one-styled flowers in American ginseng awaits further study of populations throughout the range of the species.

FLORAL PHENOLOGY AND MATING SYSTEM. Previous studies of *Panax quinquefolium* have assessed floral dichogamy by visual observations and comparisons of fruit production by bagged and unbagged inflorescences. For two of three populations, it was concluded that protandry was well developed. Yet in one of those, 77.8 per cent of bagged flowers produced fruit (Lewis & Zenger 1983). Lewis and Zenger implied

that these fruits were the results of geitonogamous pollinations. Citing unpublished data, Carpenter & Cottam (1982) concluded that fruits set by bagged inflorescences were due to geitonogamy rather than apomixis or autogamy. Kinsler (1982) also reported that bagged inflorescences produced fruit.

My results show that for *Panax quinquefolium*, visual observation alone is inadequate for determining stigmatic receptivity. Over one-fourth of the visually immature stigmas I pollinated were receptive (Table 2, before anther dehiscence). I suggest then that the protandry reported in previous studies was not as strong as it appeared, and that autogamy, as well as geitonogamy, contributed to fruit production by bagged inflorescences.

The outcrossing index (OCI) of 2 indicates that flowers of *Panax quinquefolium* are morphologically adapted for a mixed mating system of autogamy and xenogamy. In my mating system experiments, selfed inflorescences produced the same proportion of seeds as outcrossed ones (Table 3, A/G vs X). Compared to these results, the pollen to ovule (P/O) ratio of 3282:1, which is characteristic of xenogamous flowers, seems anomalously high. Perhaps the high P/O ratio promotes adequate pollination even though pollinator visits are infrequent. The P/O ratio could also be a retained ancestral trait.

REGULATION OF SEED PRODUCTION. This study reconfirms observations that the fecundity of *Panax quinquefolium* is positively correlated with age and size (Carpenter & Cottam 1982; Lewis & Zenger 1982; Lewis 1984). My hand pollinations failed to significantly increase seed set over that of bagged or naturally pollinated plants (Table 3, SC vs A/G, HX vs X). However, when I removed all but a few floral buds, per cent seed set from autogamous selfing was significantly greater than that of bagged flowers (A vs A/G). These results suggest that female reproductive success is regulated by the amount of resources allocated to reproduction (i.e., reproductive status, Lloyd & Bawa 1984), rather than by the abundance or efficiency of pollinators.

Plants may regulate investment in reproduction by varying the number of flowers produced, the relative amounts of pollen

and ovules produced by individual flowers, and the number of fertilized ovules that mature into seeds (Lloyd 1980). In this study, the number of flowers per plant, the ratio of two- to one-styles flowers, and the proportion of ovules that matured to seeds all increased with size (Table 1). Thus, it appears that all three kinds of regulation may occur in *Panax quinquefolium*. Relationships among the age, size and gender of American ginseng will be examined in a subsequent paper.

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