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POPULATION DYNAMICS OF THE AMERICAN GINSENG *PANAX QUINQUEFOLIUM* (ARALIACEAE)¹

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ABSTRACT

A 3-yr study of an aged population of American ginseng revealed four morphological classes among plants 1–18 yrs old. The youngest and smallest plants had a single prong of 3–5 leaflets and the oldest had four prongs with up to 20 leaflets. Age was positively correlated with prong and leaflet number. Prong development was linear, but not annual, i.e., a two-pronged plant formed from the single prong stage on an average only after 4.5 years, a third prong arose after 7.6 years, and the fourth prong after 13.5 years. All one-pronged plants were juveniles and, depending on the year, 22–44% of two-pronged plants were also juveniles. After the formation of an inflorescence during the two-pronged stage, flowering was annual thereafter. Flower number per inflorescence was correlated with morphological class and age. Most plants that developed flowers formed fruit (80–89%), except during the summer of 1980 when only 47% of flowering plants successfully matured fruit in a season typified by low precipitation and humidity, and high temperature. Younger adults in particular were more susceptible to failure in producing propagules and to earlier annual abscission under these stressful conditions than older members of the population. In fact, 53% of all flowering plants failed to develop fruit in 1980 compared to only 14% and 21% the previous 2 yrs. Seed survival was low and variable, the long after-ripening period undoubtedly contributing to this vulnerable stage in the life cycle. Once germinated and established, however, seedling survival and development to adulthood, as well as adult survivorship, were high (97%). Even though a long-lived, woodland geophyte, year-by-year fluctuations in reproductive capacity, seed germination, and time of aerial stem abscission were marked. Annual growing-season dormancy, previously reported as a general phenomenon for American ginseng, was not found.

PANAX QUINQUEFOLIUM L. (AMERICAN GINSENG), once frequent in eastern North America, is a threatened or endangered species in many areas because of overzealous collecting of roots for commercial purposes. The export value of wild and cultivated roots reached \$39 million in 1980, an increase of 76% above 1979 (Patty, 1981). Nonetheless, little is known of the biology of American ginseng and as demand rises, with a concomitant disruption of indigenous populations, it may become even more difficult to study the species under natural conditions.

Our intention is to document part of the life

history of the species by examining the development of a population over time. The data may be usefully applied to programs for re-establishing the species where extirpated and to commercial endeavors where woods-grown crops are planned (Lewis, 1980a).

THE SPECIES—This long-lived (50+ yrs) herbaceous perennial, a geophyte, is found infrequently in the understory of the climax deciduous forests, appearing after the leaf canopy has partially or fully developed. It consists of a thick taproot, often branched, that abruptly narrows apically to a gnarled rhizome that grows horizontally to erect (Fig. 1). The rhizome is characterized by large scars that form as a result of the annual abscission or accidental loss of the single subterminal aerial stem. These annual scars are well-marked and, because the rhizome does not decay, the plant can be aged. A single new bud forms apically to the current growth and gives rise to the solitary stem of next year's growth aboveground. Rarely two or more buds develop, resulting in multiple stems the next year.

The aerial stem is deciduous, often following a heavy frost. At the summit of the stem,

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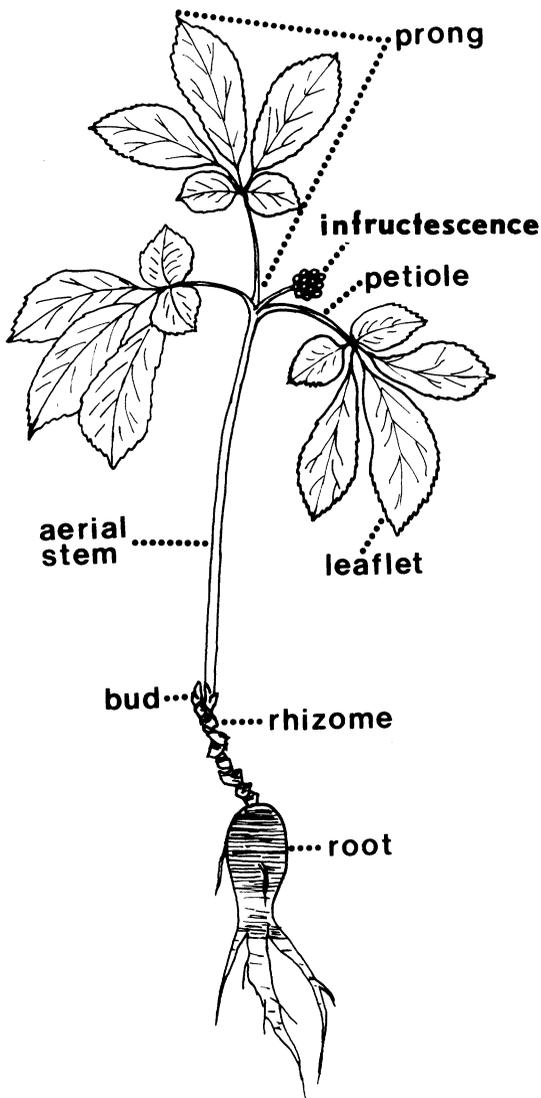


Fig. 1. Sketch of a 9-yr-old *Panax quinquefolium* ($\times\frac{1}{2}$).

whorled "leaves" develop, called prongs, each consisting of a petiole and from 3 to 5 palmately compound leaflets (Fig. 1). These prongs are not strictly equivalent to leaves, for they lack axillary buds at their junctures with aerial stems. Seedlings initially have three leaflets. In subsequent years the young plants develop 4 or 5 leaflets and eventually two and more prongs.

When reproductive, individuals develop a peduncle at the juncture of the prongs. Reproduction is sexual, or very rarely asexual by rhizomatous fragmentation. Anthesis occurs predominantly from June to August. The inflorescence is a solitary umbel (rarely a second umbel forms along the peduncle axis) with few

(young plants) to many (older plants) pedicelled flowers. The flowers are small and greenish-white, five-merous, and presumably entomophilous and bisexual.

The fruit is typically a two-seeded (pyrenes) drupe that is globose and about 1 cm in diameter. A bright red exocarp and stony endocarp develop at maturity in late summer or early autumn. The seed is about 3 mm in length, subglobose, and requires an after-ripening that averages 20 months.

MATERIALS AND METHODS—Observations were made in east-central Missouri near Eolia during October 1977 and June to October 1978–1980. A second site in southwestern Missouri was studied for 1 yr before it was completely eradicated by root diggers. The Eolia site is a sloping (30–42°) deciduous woods dominated by *Acer saccharum* and *Tilia americana* and to a lesser extent *Ulmus rubra*. The trees reach 15 m with their scattered saplings being the principal understory. Spring ephemerals such as *Claytonia virginica*, *Dicentra cucullaria*, *Sanguinaria canadensis*, and *Uvularia grandiflora*, the fern *Botrychium virginianum*, and the weedy *Parthenocissus quinquefolia* typify the herbaceous plants though none forms a dense population. Within the 23 × 27-m study area, that encompasses the whole population, American ginseng is the dominant estival ombrophyte (shade-loving plant) at a density in 1980 of 0.2 plants per m². The next nearest population is about 0.4 km distant and no other is known nearby. The soil is shallow and rocky, and overlies limestone. The surface is thinly covered by leaf litter, or sometimes the litter is washed down the slope to the creek below or is trapped by fallen logs, stumps, and trees.

Each plant was labeled, numbered, and located on a map drawn of the population and other major species. Three (1979, 1980) or four (1978) times a year data were gathered on prong and leaflet number, condition of the leaflets, presence or absence of inflorescences, number of fruits, time of abscission, and gain and loss of plants. In 1980 rhizomes were carefully exposed to count their scars in order to determine age and then recovered.

Means in the text and Table 1 are given with ± 1 standard deviation. Various relationships were tested using a least-squares linear regression analysis. Correlation coefficients (r) and significance levels (P) are given in the text.

RESULTS—*Age structure and morphology*—Ages in 1980 ranged from 1 to 18 yrs for a population of 113 individuals (Fig. 2). The average age of the population was 6.8 ± 3.5 yrs

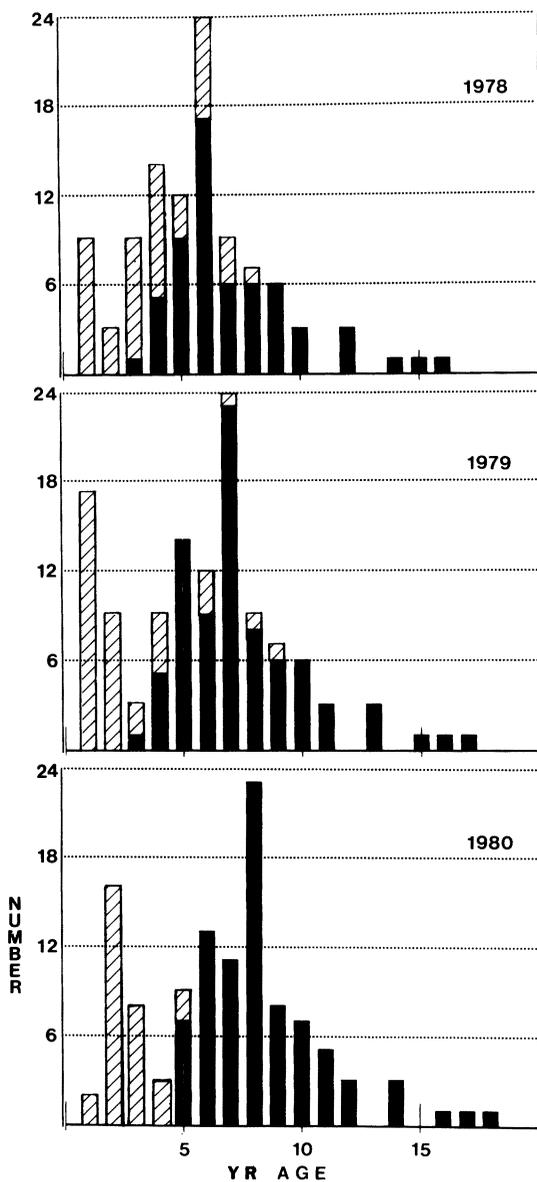


Fig. 2. Frequencies of flowering (solid bars) and non-flowering (hatched bars) plants of *Panax quinquefolium* by age class from 1978–80.

with the 1973 age class being predominant. Annual recruitment varied markedly, but a period of major expansion occurred 5 to 10 yrs ago when over three-fifths of the population was recruited.

Aboveground *Panax quinquefolium* can be divided into four morphological classes based on prong number (Table 1). One-pronged plants had 3–5 leaflets, predominantly 3, two-pronged plants had 6–10 leaflets, three-pronged plants had 13–15 leaflets, with 15 particularly common, and a new four-pronged class developed in 1980 with 19–20 leaflets. The one-pronged

plants varied in age from 1 to 6 yrs. Those having two prongs ranged widely from 3 to 16 yrs, plants with three prongs also were divergent in age, 4 to 17 yrs, but clustered between 6 and 10 yrs and predominantly 8 yrs, while plants having four prongs were generally much older, 11–18 yrs (Table 1). In 1980 there was a correlation between age and morphological class as measured by both prong number ($r = 0.796$, $P < 0.001$) and leaflet number ($r = 0.807$, $P < 0.001$).

Age is thus correlated with morphological class of aboveground portions of *Panax quinquefolium* (comparable data for root size and weight do not exist). Unlike many plants (Harper, 1977), size as reflected by leaflet and prong numbers is an important predictor of age, for the more numerous the leaflets and prongs, the older the plants. Maximum aerial growth known to us is reached when a plant produces five prongs, although four is more commonly the maximum. Once a plant achieves a morphological level, stable periods of varying intervals are typical: short for two-pronged plants before the next level is obtained, longer for three-pronged plants before a greater number is reached, and so forth. Our data show that on an average a one-pronged plant will be 4.5 ± 1.6 yrs old before it develops a second prong, that a two-pronged plant will be 7.6 ± 2.4 yrs of age before developing a third prong, and that a three-pronged individual will average 13.5 ± 3.3 yrs of age before adding a fourth prong. Expression of this orderly, vegetative growth may be restrained or accelerated by environmental factors, for under cultivation, when husbandry provides more optimal conditions, roots from three- and four-pronged plants are dug after only 3 or 4 yrs of planting (Hartman, 1979).

Total prong (and leaflet) number among the 102 plants alive in 1978 increased 17.1% (21.3%) by 1979 and 4.1% (5.8%) from 1979 to 1980. A majority of the increase was due to the development of additional prongs at the stem apex, although the formation of new leaflets within a prong class also contributed to the overall increase in the biomass and photosynthetic capabilities of the population.

Flowering—From 1978 to 1980, all one-pronged plants were juveniles (nonflowering), some two-pronged plants were also juveniles (22.2–44.2%), but only two three-pronged plants were without an inflorescence (3.7% in 1979). Juvenile plants ranged in age from 1 to 8 yrs in 1978, from 1 to 9 yrs in 1979, and from 1 to 5 yrs in 1980 with an average age 2.5 to 3.7 yrs during this time (Fig. 2).

TABLE 1. *Morphological and reproductive features of Panax quinquefolium, 1978–1980*

Prong no.	Avg. age (yrs)	Plants		Leaflets		Flowering no.	Fruiting	
		No.	% ^a	No.	% ^a		no.	fr/plant
1978								
1	2.6 ± 3.2	22		78		0	0	
2	5.9 ± 2.4	52		475		29	23	2.0 ± 1.0
3	7.9 ± 2.7	28		399		28	26	5.6 ± 3.8
Total	5.7 ± 3.0	102		952		57	49	3.9 ± 3.4
1979								
1	1.4 ± 0.6	27	+22.7	85	+16.6	0	0	
2	5.8 ± 2.2	37	+28.8	335	-29.4	30	16	2.0 ± 0.9
3	8.2 ± 2.6	54	+92.8	789	+97.7	51	49	5.3 ± 3.3
Total	5.9 ± 3.4	118	+15.6	1,209	+26.9	81	65	4.4 ± 3.2
1980								
1	2.2 ± 0.7	24	-11.1	79	-7.0	0	0	
2	5.6 ± 1.7	21	-43.2	191	-43.3	15	1	2.0
3	8.6 ± 2.4	64	+18.3	929	+17.7	64	35	4.6 ± 3.9
4	13.5 ± 3.3	4		77		4	3	12.0 ± 2.7
Total	6.8 ± 3.5	113	-4.2	1,276	+5.5	83	39	5.2 ± 4.3

^a Percent annual increase.

Flowering plants increased from 55.9% of the population in 1978 to 73.5% in 1980: 71.4% of two-pronged plants flowered in 1980 as did all of the three- and four-pronged plants. Flowering plants ranged in age from 3 to 16 yrs (1978), 3 to 17 yrs (1979), and 5 to 18 yrs (1980), the average annual flowering age being 7.1 ± 2.7 (1978), 7.5 ± 2.7 (1979), and 8.4 ± 2.7 yrs. All plants over 9 yrs flowered (Fig. 2).

The number of flowers was significantly correlated with morphological class ($r = 0.618$, $P < 0.001$). In 1980, the youngest (two-pronged) plants averaged only 7.0 ± 1.8 flowers per inflorescence, whereas three-pronged plants averaged 20.1 ± 10.7 flowers in each inflorescence and the oldest (four-pronged) plants had an average flower number of 47.3 ± 6.1 . The average flower number of all potentially reproductive plants was 20.2 ± 12.8 .

Fruit formation—Of those plants that developed flowers in 1978 and 1979, the majority, 89.1% and 80.2%, respectively, formed fruit (Table 1). However, in the drought year of 1980 the number of flowering plants forming fruit decreased markedly to only 47% of the population. From June to August 1980, precipitation was far below average, average daily temperature maxima were the highest recorded on data available since 1941, and average relative humidity was among the lowest on record (Table 2). There appeared to be a direct relationship between poor fruit formation and climate, although the adverse weather could also have curtailed the activities or numbers of pollinators.

Apart from annual variation related to environmental factors, fruit production was correlated with prong number ($r = 0.380$, $P < 0.001$) and age ($r = 0.363$, $P < 0.001$). In 1978

TABLE 2. *Meteorological data at St. Louis International Airport, Missouri, June–August, 1978–80, compared to an annual averaged 30-yr period, 1941–70^a*

Year	Precipitation (cm) June–Aug	Temperature (F)						Relative humidity (%)		
		Averages			Daily maximum			Averages, 3 PM		
		Jun	Jul	Aug	Jun	Jul	Aug	Jun	Jul	Aug
1978	23.3	74.4	78.5	76.4	84.8	87.6	87.5	49	56	50
1979	19.3	76.5	79.2	78.4	86.9	88.3	87.6	42	47	49
1980	21.5	75.5	85.0	83.5	86.3	95.4	93.6	44	46	43
1941–70	27.9	74.9	78.6	77.2	84.9	88.4	87.2	56	56	59

^a Data are from the U.S. National Oceanic and Atmospheric Administration, National Climatic Center, Asheville, NC 28801, the site being about 74 km southeast of the study population.

and 1979, two-pronged plants accounted for only 24% of the fruit matured even though they represented nearly one-half of the plants that developed fruit; the remainder and majority of fruit were produced by three-pronged plants. In 1980, however, all but two fruits originated from older three- and four-pronged plants. Based on earlier frequencies, about ten of the two-pronged plants should have developed fruit in 1980. The drought conditions of that year apparently had a disproportionate affect on younger, smaller reproductive individuals.

Fruit maturation was gradual during August to October, 1978. By the third week of August all exocarps were green, with many varying in size and maturity. On 11 September, 40% were still green, but the remainder had turned greenish-red (2.6%), red (44.3%), or brown (4.27%), the latter presumably abortive. Some mature fruit had abscised (9.4%), but the majority had not. By 6 October all fruits were red. Two-thirds (67.7%) were persistent while the others had abscised (27.1%) or were brown and abortive (5.2%).

Reproductive plants not forming fruit—The absence of fruit production among flowering plants involved at least three phenomena: 1) abortion following fertilization; 2) partial fruit development due to environmental or other factors; and 3) sterility because of poor or no pollination. As 14%, 21%, and 53% of all flowering plants between 1978 and 1980 failed to produce fruit, these phenomena were responsible to a large extent in reducing the reproductive potential of the population, particularly in 1980. Furthermore, as flowering plants averaged 20.2 flowers per inflorescence and the average number of fruit during the 3 yrs was only 4.4 ± 3.5 per plant, the majority of plants setting fruit had additional potential for increasing yields. Some of these additional flowers appeared green and nonabortive, but unfortunately floral diversity and frequency and fruit development have not been examined in *Panax quinquefolium*.

Seed production and development—Based on a total sample of 10,499 seeds, Stoltz and Garland (1980) found that seeds averaged 1.9 ± 0.48 per fruit. Fruit was one-seeded (16.3%), commonly two-seeded (77.0%), and infrequently three-seeded (6.5%) or four-seeded (0.2%). Extrapolating from their data, our population yielded 365 seeds in 1978, 540 seeds in 1979, and 376 seeds in 1980.

Fruit abscission occurred primarily in September and October, the fruit being passively disseminated near the parent or rolling down

the slope until coming to rest. Additionally, the bright red color of the exocarp suggests a considerable investment to make the fruit attractive to animals which might serve in seed dispersal (Janzen, 1969; Wilbur, Tinkle and Collins, 1974). The mealy mesocarp is probably also palatable to some animals. Exocarp-mesocarp ingestion may be the only goal with the seeds being dropped thereafter, a factor that would ultimately favor the thick stony-walled pyrenes being successfully disseminated.

After-ripening of 18–22 months is required for the majority of *Panax* seeds before germination. Some may germinate as early as 8 months following dissemination (Baranov, 1966) and others may germinate only after prolonged periods in the soil. Considering 20 months an average time for germination, only two seedlings developed in 1980 from the 1978 seed cohort of 365. (Some seeds may have germinated in 1979 and still others may not germinate until 1981 or later, so this is only an average time until experimental evidence is available.) This was a recruitment success of only 0.55%. Although this value is only approximate, it suggests a high seed mortality without germination during the prolonged after-ripening period and therefore a highly vulnerable stage in the life cycle of the species.

Seedling development, morphology, and survival—In 1978, eight new seedlings represented 9.3% of the total population, in 1979 17 seedlings were added (16.2%), but in 1980 only two seedlings were established (1.7%). All developed by June and possessed a single prong with three leaflets. The eight seedlings formed in 1978 were extant in 1979 and 1980, and of the 16 established during 1979 all but one survived through 1980. Seedlings thus survived at a high level and contributed little to population mortality.

By the second year of growth, most plants still had the three leaflet morphology, although one plant had developed four leaflets and another five leaflets. After an additional year, however, only one plant from the 1978 cohort remained with the basic three leaflets, whereas one had four leaflets, three had five leaflets, and three had formed two prongs totalling 6, 7, and 9 leaflets each. Such developmental variation of juveniles from the same cohort may reflect genetic and microenvironmental differences. Formation of additional leaflets and/or prongs was not an annual event and may be prolonged considerably among wild plants in contrast to those grown optimally under cultivation.

Annual mortality of the population—Only two plants died during 1978 and 1979. An additional plant, absent aboveground in June 1979 (Lewis, 1980b), had not died and by the spring of 1980 a normal aerial stem had developed. This may occasionally occur in the population, for a year later we observed a broken defoliated two-pronged stem by a fallen branch. However, mortality increased to 7.1% (eight plants) from the previous 2-yr average of only 1% due in part to the accidental loss of three plants when a 9-m² section of the embankment collapsed and buried or washed them away in the small stream below. The remaining five individuals (4.4%) died of unknown causes. Annual mortality during the 3-yr study period was, therefore, very low.

Annual abscission—Each autumn aerial parts of *Panax quinquefolium* physiologically abscise where the stem attaches the rhizome. Leaflets turn yellow and often rust-colored before falling; fruit also abscises during this time. Abscission, and broken or otherwise damaged and destroyed aerial stems, varied annually in the population: for example, by early October 1979, a particularly moist growing season at the population site according to the resident owner, only 4.2% of the aerial stems had abscised, whereas a year earlier abscission had occurred among 13.7% of the plants, and a year later among 20.4%. As discussed above, the last summer was low in precipitation and relative humidity, and high in temperature, so that in contrast to 1979 marked environmental stress during 1980 on limited resources may account for the earlier abscission of more plants than usual.

Age of the plants is also related to the loss of aboveground stems. By 6 October 1980, ten one-pronged plants $\bar{x} = 2.5 \pm 0.9$ yrs of age accounted for 43.5% of the total plants abscised, while 13 two- to four-pronged plants, averaging 9.9 ± 4.0 yrs, represented the remainder. However, the younger single-pronged individuals comprised only 21.4% of the population, so that their abscission rate by early October was twice that of the older multiple-pronged plants.

What effects had early defoliation on future leaflet development and fruit production of individuals? By early September 1978, for example, eight plants had lost one or more prongs or all of their aerial parts. Their total number of preloss leaflets was 84; by 1979 the same plants possessed a total of 103 leaflets, and by 1980 a total of 107, increases of 22.6% and 3.9%, respectively, in years following defoliation. Rather than showing decreased or static

leaflet growth rates, these plants compared favorably with values of 21.3% and 5.8% for total population leaflet increases in 1979 and 1980 (Table 1). Fruit production also increased among these plants from 25 in 1978 ($\bar{x} = 3.1$) to 32 in 1980 ($\bar{x} = 4.0$), a 28% rise over 2 yrs. This rate is equivalent to the average increase of 1.2 fruit per plant among those forming fruit. Therefore, defoliation during one growing season did not reduce the vegetative or reproductive potential of this geophyte in years following the damage, perhaps because of compensating photosynthetic efficiency or of substantial energetic reserves of stored food in the large taproot.

Annual dormancy—Johnson (1960) stated that rhizomes do not always produce aerial parts annually. "It seems they skip years occasionally for rest and recuperation." In fact there is wide acceptance among ginseng diggers that as much as one-third of the population remains dormant during a growing season, but there is no evidence of this from our study. Perhaps their mistaken impression relates to the variable abscission and breakage of aerial stems. Up to one-fifth of the population may be devoid of aboveground parts by early October and two-fifths by the middle of October when much ginseng root digging occurs. Nevertheless, under stressful conditions typical of marginal populations (e.g., *Delphinium*; Epling and Lewis, 1952) or generated by major flooding (cultivated *Panax quinquefolium*; Settles, 1980) some plants may not appear annually, but lacking these extremes and quantification of the phenomenon for American ginseng, it must be considered a rare event negatively related to the energetics of resource accumulation by the individual with no adaptive role.

DISCUSSION—Because of limited annual seedling and adult mortality in the study population, the observed frequency of age classes may be similar to actual establishment of plants following emergence year by year. Based on this assumption, the population was founded about 18 yrs ago in 1963 by one or a few seedlings with the first in situ cohort possible 12 to 14 yrs ago from 1967 to 1969. Up to that time only modest reproductive levels would be consistent with the lower levels of fecundity among the younger two-pronged plants that would have dominated the population. By 1970 or 1971 sufficient numbers of three-pronged reproductive plants were established to produce large numbers of fruit and set the stage for the major expansion of the population through 1976 dur-

ing which time 60% of the whole was formed. More recently, annual recruitment has varied strikingly among adjacent age classes and, like that of *Liatris aspera* (Kerster, 1968), is probably due to variations in seed germination and seedling survival success. However, successful recruitments in 1978 and particularly in 1979 show that the population has not entered senescence, but continues to gain modestly in total numbers.

Flowering develops only after the formation of the two-pronged (6+ leaflets) state and is essentially continuous thereafter. However, some plants may remain two-pronged for several years and not flower. The earliest flowering plants were 3 yrs of age; they had few flowers and only rarely formed fruit, but after 9 yrs of age, all plants developed flowers and most had fruit.

This developmental pattern, exemplified by greater age, vegetative growth, and sexual productivity, was altered during 1980 when adverse environmental factors (low precipitation, low relative humidity, high temperature) affected potential fecundity by a 47% decrease in fruit production. Reproductive patterns may be affected significantly in other organisms by environmental uncertainties (Wilbur, 1976) as a result of reduced resources available for fruit production (e.g., *Catalpa speciosa*; Stephenson, 1980). The environment may also modify vegetative growth, for bud initials giving rise to aerial stems are formed on rhizomes during the previous growing season and their formation at that time under adverse conditions and limited resources could affect development during subsequent years. Environmental stress may also affect pollination vectors adversely, for even though the flowering of *Panax quinquefolium* is prolonged and may extend for several months during parts of June, July, and August that time may be a high-risk period in terms of insect-mediated sexual reproduction.

Although fruit abortion and predation prior to abscission were observed, they were minor compared to the number of fruit that never fully developed and the number of flowers in an inflorescence that remained green and undeveloped for long periods. Perhaps for some flowers sexual reproduction was pollinator limited (Schemske et al., 1978) while others were staminate, for both bisexual and unisexual flowers have been reported for *Panax* (Graham, 1966) though not specifically for *P. quinquefolium*. The nature of the immature fruit is unknown.

Early abscission and damage of aerial stems accounted for considerable loss of the photosynthetic potential of leaflets, yet neither was

sufficiently severe to reduce growth or reproductive capability of individuals in subsequent years. Morphological development and fruit production of affected plants were at pace with the population as a whole. Moreover, there was no delay in flowering as described for *Senecio jacobaea* (van der Meijden and van der Waals-Kooi, 1979) or reduced fecundity following fruit formation found for another Missouri understory herb, *Asclepias quadrifolia* (Chaplin and Walker, in press).

Only one life cycle could be followed during the time span of this study. In 1978 the population of 102 plants consisted of one- to three-pronged individuals of which 55.9% flowered. Of these, 89.1% formed 192 fruits from which two seedlings were established in 1980 following an average 20-month after-ripening period. This represented the smallest annual cohort of new plants during the past 13 yrs.

Seed mortality during this time was high and proved the most precarious portion of the life cycle. The probability that a seed will give rise to an adult in this population was estimated at only 0.55%. Once established, however, the probability of a seedling surviving and developing to adulthood was high (97%), as Watkinson and Harper (1978) found for *Vulpia fasciculata*. The modest 3-yr mortality rate appeared density-independent (Jeffries, Dary and Rudnik, 1981), for the greatest toll was clearly related to an embankment collapse and the remainder could easily be explained by limited rodent predation and/or plant diseases. The high-risk period was therefore undoubtedly during the prolonged after-ripening period before seed germination, at which time selection forces could be manifested.

Of the 25 seedlings established during 1978 and 1979, all but one were alive 1 and 2 yrs later. Vegetative diversity two years following establishment included plants with 3 to 9 leaflets and 1 to 2 prongs, a surprisingly great morphological variation among 2-yr olds from the same cohort.

As Solbrig, Newell, and Kincaid (1980) described for *Viola sororia*, the larger the plant, the greater the seed set and potential contribution to the next generation. In addition, size for *Panax quinquefolium* was also age-dependent, for unlike *V. sororia* there was an orderly increase in size with age from 1 to 4 prongs. Environmental stresses may markedly alter such regulation, however, and result in reduced reproductive capability and variation in abscission time.

For those interested in reestablishing American ginseng where extirpated or in developing woods-grown crops, this study shows that seed

germination tends to be low, that plant development is slower than observed under cultivated conditions, and that many flowering plants fail to produce fruit or do so later and in fewer numbers than expected from observations of cultivated plants. These features suggest that projects involving restoration of populations in the eastern North American forests or development of commercially viable woods-grown crops require long-ranged planning and management for their success. However, once seedlings and more mature plants are established, our data show that mortality is generally low so that given ample time populations will thrive.

LITERATURE CITED

- BARANOV, A. 1966. Recent advances in our knowledge of the morphology, cultivation and uses of ginseng (*Panax ginseng* C. A. Meyer). *Econ. Bot.* 20: 403–406.
- CHAPLIN, S. J., AND J. L. WALKER. In press. Floral display of a forest milkweed: energetic constraints and the adaptive value of the floral arrangement. *Ecology*.
- EPLING, C., AND H. LEWIS. 1952. Increase in the adaptive range of the genus *Delphinium*. *Evolution* 6: 253–267.
- GRAHAM, S. A. 1966. The genera of Araliaceae in the southeastern United States. *J. Arnold Arbor. Harv. Univ.* 47: 126–136.
- HARPER, J. L. 1977. *Population biology of plants*. Academic Press, New York.
- HARTMAN, G. F. 1979. Ginseng culture in Wisconsin. *In Proc. First Nat. Ginseng Conf.*, p. 66–68. Governor's Council on Agriculture, Frankfort, Ky.
- JANZEN, D. H. 1969. Seed-eaters versus seed size, number, toxicity and dispersal. *Evolution* 23: 1–27.
- JEFFRIES, R. L., A. J. DARY, AND T. RUDNIK. 1981. Population biology of the salt marsh annual *Salicornia europaea* agg. *J. Ecol.* 69: 17–31.
- JOHNSON, M. C. 1960. Our most valuable native plant, *Panax quinquefolium*. *Castanea* 25: 132–134.
- KERSTER, H. W. 1968. Population age structure in the prairie forb, *Liatris aspera*. *BioScience* 18: 430–432.
- LEWIS, W. H. 1980a. American ginseng: a forest crop. Missouri Department of Conservation, Jefferson City.
- . 1980b. Preliminary demographic study of a Missouri population of American ginseng (*Panax quinquefolium*). *In Proc. Second Nat. Ginseng Conf.*, p. 38–42. Jefferson City, Mo.
- VAN DER MEIJDEN, E., AND R. E. VAN DER WAALS-KOOI. 1979. The population ecology of *Senecio jacobaea* in a sand dune system. I. Reproductive strategy and the biennial habit. *J. Ecol.* 67: 131–153.
- PATTY, G. E. 1981. Ginseng. U.S.D.A. Foreign Agric. Circ. FTEA 2-81.
- SCHEMSKE, D. W., M. F. WILSON, M. N. MELAMPY, L. J. MILLER, L. VERNER, K. M. SCHEMSKE, AND L. B. BEST. 1978. Flowering ecology of some spring woodland herbs. *Ecology* 59: 351–366.
- SETTLES, D. B. 1980. Experimental cultivation techniques for American ginseng. *In Proc. Second Nat. Ginseng Conf.*, p. 27–33. Jefferson City, Mo.
- SOLBRIG, O. T., S. J. NEWELL, AND D. T. KINCAID. 1980. The population biology of the genus *Viola*. I. The demography of *Viola sororia*. *J. Ecol.* 68: 521–546.
- STEPHENSON, A. G. 1980. Fruit set, herbivory, fruit reduction, and the fruiting strategy of *Catalpa speciosa* (Bignoniaceae). *Ecology* 61: 57–64.
- STOLTZ, L. P., AND P. GARLAND. 1980. Embryo development of ginseng seed at various stratification temperatures. *In Proc. Second Nat. Ginseng Conf.*, p. 43–51. Jefferson City, Mo.
- WATKINSON, A. R., AND J. L. HARPER. 1978. The demography of a sand dune annual: *Vulpia fasciculata*. I. The natural regulation of populations. *J. Ecol.* 66: 15–33.
- WILBUR, H. M. 1976. Life history evolution in some milkweeds of the genus *Asclepias*. *J. Ecol.* 64: 223–240.
- , D. W. TINKLE, AND J. P. COLLINS. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. *Amer. Nat.* 108: 805–817.

APPENDIX

Panax, all-curing, is an adjectival form that may take any gender. In classical and medieval times such substantives were commonly used as neuters. As Linnaeus deliberately chose neuter adjectives, he thus intended *Panax* as a neuter substantive, a perfectly reasonable choice and one that *must* be followed according to Article 73 on the International Code of Botanical Nomenclature. Thus, the neuter ending “m” for adjectives like *quinquefolium*, *japonicum*, and *trifolium* is correct and should be adhered to. (The prefix *-panax*, recommended as masculine in Article 75A of the Code when used for modern compound genera, is a totally unrelated nomenclatural issue.)