Growth and reproduction of American ginseng (*Panax quinquefolius*) in Wisconsin, U.S.A.

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The phenology and development of southern Wisconsin populations of wild ginseng (*Panax quinquefolius* L.) are described. In natural forests, ginseng plants grow slowly, and most plants do not reach reproductive maturity until they are at least 8 years old. Ginseng flowers are perfect, but maturity of male and female reproductive parts is separated temporally in each flower. Ginseng individuals are not obligate outcrossers, and the flowers are visited by generalist pollinators. Exclusion of pollinators did not reduce fruit or seed set. Aging techniques usually underestimate age. Number of leaves (plant stage) is a more appropriate indicator of development than is the number of "annual" stem scars on the rhizome. The number of seeds produced by a plant may be predicted from the number of leaves and the leaf area of the largest leaflet. Accurate estimates of the number of ginseng plants in an area can be made by sampling early in the summer. However, projections of survival and reproductive success in a ginseng population must account for mortality and for plants that senesce early in the summer months before producing seeds. We recommend that ginseng harvesting in Wisconsin be allowed only after September 1 to insure that fruits on mature plants are ripe.

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Les auteurs décrivent la phénologie et le développement du ginseng sauvage (*Panax quinquefolius* L.) dans le sud du Wisconsin. Dans les forêts naturelles, les individus de ginseng croissent lentement et la plupart des plantes n'atteignent pas la maturité reproductrice avant l'âge de 8 ans. Les fleurs sont parfaites, mais les organes reproducteurs mâles et femelles d'une même fleur ne sont pas matures en même temps. Les individus de ginseng ne sont pas obligatoirement allogames et leurs fleurs sont visitées par des pollinisateurs généralistes. L'exclusion des pollinisateurs ne diminue pas le nombre de fruits et de graines. Les techniques d'estimation de l'âge sous-estiment habituellement l'âge réel. Le nombre de feuilles est un meilleur indicateur du développement que le nombre de cicatrices "annuelles" de tiges sur le rhizome. Le nombre de graines produites par une plante peut être prédit par le nombre de feuilles et la surface du foliole le plus grand. Un estimé précis du nombre de plantes de ginseng dans une région peut être obtenu en échantillonnant tôt au cours de l'été. Cependant, le projection de la survie et du succès de la reproduction dans une population de ginseng doit tenir compte de la mortalité et de la sénescence hâtive (avant la production des graines) de certains individus au cours des mois d'été. Les auteurs recommandent que la récolte du ginseng au Wisconsin ne soit permise qu'après le 1er septembre, afin d'assurer que les fruits des plantes matures soient mûrs.

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Introduction

American ginseng (*Panax quinquefolius* L.) has been important economically since the early 18th century, when it was discovered growing in Canada by a Jesuit missionary (Schorger 1969). Because of potential overexploitation, ginseng was listed as a threatened species (1973) in the CITES (Convention on International Trade in Endangered Species) treaty. In response to that listing and other Federal (United States) action (Carpenter 1980), scientists in several American states and Canadian provinces within the natural range of the plant have begun to study the status of ginseng in the wild. The purpose of these studies (e.g., in Wisconsin, Kentucky, and Missouri, U.S.A., and Ontario, Canada) has been to determine population characteristics, and to develop management plans to ensure survival of the naturally occurring plants under continuing harvesting pressures.

The objectives of our paper are (*i*) to describe the phenology and development of wild ginseng, and (*ii*) to present the results of experimental studies on reproductive biology and survival.

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Materials and methods

Phenological observations (i.e., seasonal timing of plant development, flowering, and fruit set) were made during two growing seasons (1978, 1979) at 20 sites in seven southern Wisconsin counties.

From the 20 sites, 3 wooded sites in southern Wisconsin were selected for life history studies. These three study sites were on private land and were believed to be protected from ginseng harvesting. No evidence of harvesting was seen in these sites until late July 1979, when many plants in one experiment in one site were harvested before final data on fruit

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aturation could be collected. The sites were each approximately 2 ha in size. Each contained a large population of productive individuals, in contrast to known harvested sites here vegetative individuals predominated. Nondestructive perimental methods were used in this study, to protect isting populations of ginseng. Plant age was estimated by cavating (but not removing) rhizomes and counting annual em scars. The plants were then recovered with soil. Aging as done in late summer to prevent damage during the owering and fruiting season. Some of the problems associated with age determination are discussed in detail by arpenter (1980). In many cases, the age of ginseng plants is nderestimated by the number of stem scars on the rhizome.

Fifty-nine mature, unopened flower buds on 20 plants at one site were dissected and examined. At a second site, muslin ugs (10 × 5 × 5 cm) were used to exclude pollinators from florescences on 20 plants, while another 20 plants were left nbagged. Plants were assigned to treatment groups randomly. the second and third sites, leaves, leaflets, flowers, and uits were counted, and plant height (for all plants) was easured as the length of stem from the ground to the base of e petioles. The leaf area of the largest leaflet of each plant as traced on paper in the field. The tracings were cut out and eighed, and area was estimated by comparison with a paper out of known area. Multiple linear regression by the method backward elimination (Draper and Smith 1966) was used to cidate vegetative characters that best predicted flower, it, and seed production.

The presence or absence of plant hoppers on plants was corded at one site.

During two growing seasons marked and mapped populations in two sites were visited to determine plant survival ring the summer.

Results

Phenology

Plants emerged in April–May and grew to full height nd leaf size by late May. Flower buds (if present) were small, and clustered tightly on a short peduncle while the eaves expanded. During May and early June, the eduncle elongated and the flower buds enlarged. By te May or early June, the outermost flowers of the mbel had opened. Ginseng has perfect flowers (Table) and is protandrous. The stigmatic lobes extend orizontally, with stigmatic surfaces exposed, after the thers are lost. The flowering period (for one population of more than 50 plants in one site observed in 1979) sted for 6 weeks, and each plant flowered for 1 to 3 eeks. Small plants (those with two or three leaves) enerally flowered later than large plants (those with our leaves), although there was much variation in this attern. Once flowering had occurred, fruits were set apidly. Fruit set occurred between late June and late uly. The new terminal bud on the rhizome was formed uring July and enlarged during the rest of the summer. Fruits remained green until middle to late August or arly September. As the fruits turned red, they were easily dislodged from the inflorescences. Seeds were dispersed when fruits dropped to the ground in late August and September. At southern Wisconsin sites, fruits ripened (i.e., turned red) in late August in 1978 and during middle to late August in 1979. In 1979, 42% of all seeds on 20 plants were borne in fruits that had ripened by August 15. Aboveground plant parts died back during the period June–October, leaving the rhizome to perennate.

TABLE 1. The frequency of flowers of *P. quinquefolius* (on naturally occurring plants of three stages) bearing the indicated numbers of sexual floral parts

No. of leaves	No. with five stamens and two stigmas	No. with five stamens and three stigmas	No. with four stamens and two stigmas
2	1	1	0
3	29	6	1
4	17	3	1

Life history observations and experiments

Plants of four stages (as defined by leaf number) were present in natural wild populations (Table 2). Leaf number was significantly correlated with age, as determined by the number of stem scars on the rhizome ($p < 0.05$; Fig. 1).

Of 25 plants aged in one protected woods, 16 produced no flower buds (Fig. 2). Only one of the plants with eight or fewer scars produced any flowers. This plant had four stem scars, produced four flowers, and did not produce mature fruits. Plants with 8 to 22 stem scars produced from 0 to 46 flowers. The number of flowers produced was correlated with age (Fig. 2; $r = 0.5606$, df = 23, $p < 0.05$). All correlations between number of leaves, number of leaflets, number of flower buds, height, and leaf area of the largest leaflet were significant ($p < 0.01$; Table 3). The highest correlations were found between (*i*) the number of leaves × number of leaflets, (*ii*) number of flower buds × height, (*iii*) number of flower buds × leaf area of the largest leaflet,

TABLE 2. Description of stages (as defined by leaf number) in naturally occurring plants of *P. quinquefolius*

No. of leaves (stage)	No. of leaflets* (range)	Average height (cm)	Bears flowers	N
1	*3*–5	5	No	>100
2	8–*10*	No data	Rarely	>100
3	11–*15*	21.5	Yes	26
4	16–*20*	30.7	Yes	12

*Modal values are italic.

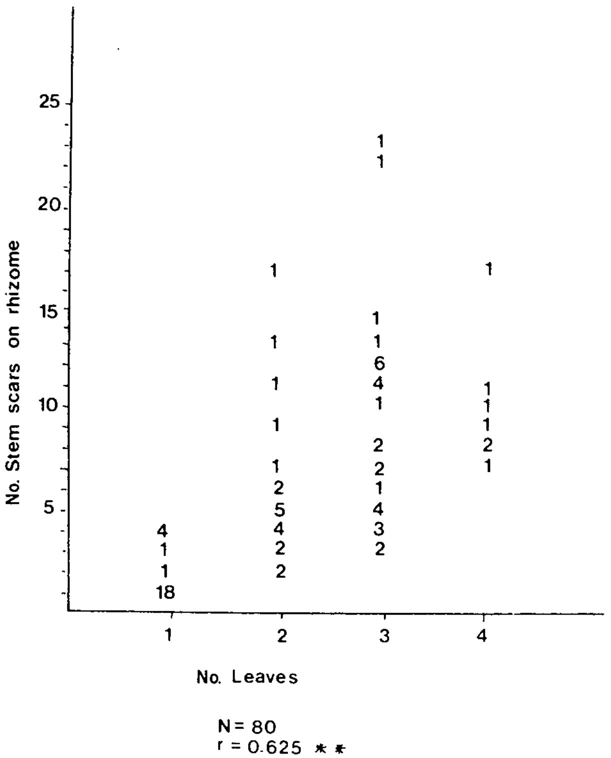

FIG. 1. The relationship between the number of stem scars on the rhizome and the number of leaves of *P. quinquefolius*. Frequency is shown on the graph. We reject the null hypothesis (that the means for the four stages are equal; $F_{(3,76)} = 21.07$, $p < 0.0001$).

and (*iv*) the number of leaflets × height. The number of flowers on a plant was significantly correlated with plant height and leaf area (Table 3).

Small bees (family Halictidae) were observed in great numbers during the ginseng flowering period. Plants with inflorescences bagged to exclude pollinators during the flowering season did not differ significantly from unbagged plants in either number of fruits set ($F_{(1,33)} = 0.87$; $p = 0.357$) or number of seeds set ($F_{(1,33)} = 0.69$; $p = 0.411$).

Three vegetative characters best predicted reproductive characteristics. In all regression analyses, the candidate predictors were number of leaves, number of leaflets, plant height, and leaf area of the largest leaflet. Plant height and leaf area of the largest leaflet explained 79.2% of the variance in number of flowers produced ($p < 0.01$). The number of leaves and leaf area explained 78.8% of the variance in number of fruits set ($p < 0.01$). The number of leaves and leaf area explained 81.4% of the variance in number of seeds set ($p < 0.01$).

Shoots of plants with one or two leaves are least likely to persist throughout the growing season (Fig. 3). Because we did not conduct any destructive sampling, it was not possible to determine whether plants that did not persist had died or gone dormant. By July 22, 22% of all plants (stages 1–4) were no longer present above ground. By August 11, 37% of all plants were no longer visible above ground.

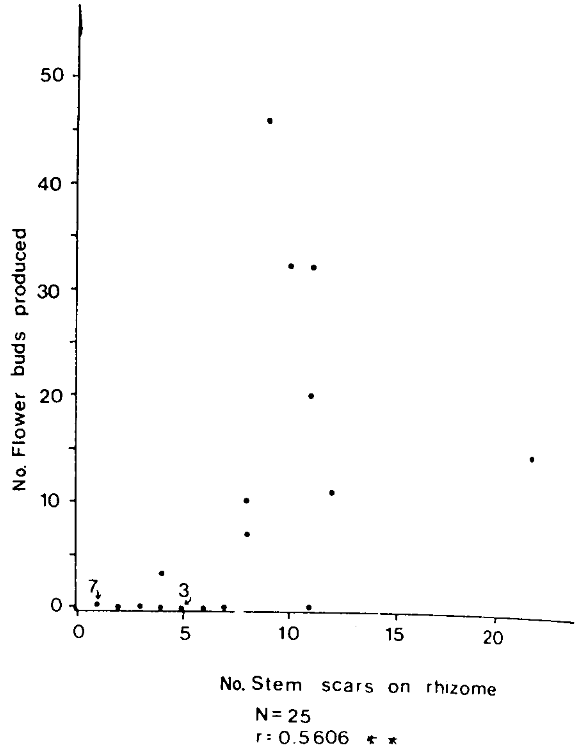

FIG. 2. The relationship between the number of flower buds produced per plant of *P. quinquefolius* and the number of stem scars on the rhizome.

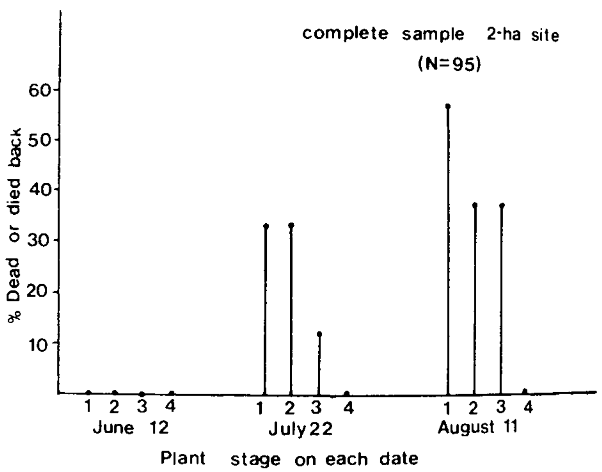

FIG. 3. The proportion of plants dying or senescing in each of four stages (as defined by leaf number) of ginseng growth, in one population (N = 95).

Plant hopper (family: Flatidae) immatures were common on peduncles of developing inflorescences and during flowering. Two-way analysis of variance, using leaf number and presence–absence of plant hoppers as treatments and number of seeds produced as the response variable, was used to assess the relationship between plant hoppers and seed yield. Plants with four leaves produced significantly more seeds than plants with three leaves ($p < 0.005$). Plants with plant hoppers also produced significantly more seeds than plants without plant hoppers ($p < 0.005$). The interaction (plant hoppers × leaf number) was not significant ($0.5 < p < 0.75$).

TABLE 3. Correlation coefficients (r) for five characteristics of reproductive (three- and four-leaved) plants of *P. quinquefolius* (N = 35)

	No. of leaves	No. of leaflets	No. of flower buds	Height
No. of leaflets	0.912			
No. of flower buds	0.671	0.767		
Height	0.709	0.808	0.848	
Leaf area (largest leaflet)	0.492	0.592	0.804	0.742

Discussion

References in the literature to ginseng plants being polygamodioecious (Fernald 1950) are probably accounted for by the dichogamous flowering sequence. There is some variation in the number of male and female sexual parts, but all flowers seen in this study were perfect.

Ginseng has perfect flowers, and each flower has mature anthers or pistils but not both. Furthermore, each inflorescence contains both functionally male and female flowers simultaneously and the flowers are closely packed on the inflorescence. Pollination is believed to occur between flowers within an inflorescence, or between plants if pollinators are present. Since bagged plants did not differ from unbagged ones in fruit or seed production, the flowers within an inflorescence may be compatible with each other, or each flower is self-compatible, or the flowers are apomictic. Two limited experiments produced no evidence to support within-flower pollination or apomixis in ginseng (Carpenter 1980). Failure of within-flower pollination is likely due to the temporal separation in male and female function, rather than to physiological incompatibility.

The pollinators observed on *Panax quinquefolius* are generalists in that they were also seen on two species of *Sanicula*, which flowered at the same time as *P. quinquefolius*. Other plants found in the same woods, and that have small white or inconspicuous flowers are *Actaea rubra*, *Actaea pachypoda*, *Aralia racemosa*, *Aralia nudicaulis*, *Circaea quadrisulcata*, *Cryptotaenia canadensis*, *Osmorhiza claytoni*, *Smilacina* spp. (2), and *Viburnum* spp. (2) (names according to Fernald 1950). Flowering in this group of species begins in May and continues through July (S. G. Carpenter, personal observation). Generalist bees may make use of all of these flowers throughout the season. The consequence for common abundant species is that outcrossing may be common. The consequence of generalist pollinators for widely spaced, rarer species, such as ginseng, is that pollen transfer between distant individuals is unlikely. *Panax quinquefolius* is not an obligate outcrosser.

The relationship between plant leaf number and number of "annual" stem scars is not a simple one. Knowledge of the number of stem scars on a plant (after year 1) does not always allow prediction of its size. Since aging techniques are also time consuming and underestimate actual age (Carpenter 1980), the results of this study suggest that leaf number is more useful as an indicator of development than is the number of "annual" stem scars. This inference is similar to that of Caswell and Werner (1978). Number of leaves and leaf area of the largest leaflet were the vegetative characters most useful in predicting number of seeds set. These data can be collected as early in the season as late May or June. This would make rapid surveys of a large number of populations possible in a single growing season, and would allow some prediction of potential reproduction in those populations.

Wild ginseng develops very slowly. In cultivation, ginseng produces one additional leaf each year, and the plants produce fruit in their 3rd year. In contrast, wild plants do not reproduce until they are at least 8 years old, much later in the life-span than is commonly reported by ginseng harvesters. Hu et al. (1980) reported a high death rate and low reproductive rate in the wild ginseng population they studied over 7 years.

Plants that have senesced during the summer, after the new terminal bud has formed, appear "dormant" at the time of fall harvesting. "Dormancy" has been cited by ginseng harvesters as a mechanism by which the plant "escapes" harvest. Our results indicate that the largest (i.e., most harvestable) plants are least likely to senesce early in the season. Furthermore, large plants that senesce early do not produce any seeds in that year. Reproductive potential determined early in the season (e.g., predicted from flower number or plant size) is never realized fully, even in an unharvested population, because some plants die back before fruits ripen. True dormancy (failure to produce a vegetative stem) has been observed in wild ginseng by ginseng harvesters. True dormancy may be recognized by an irregular pattern of stem scars on the rhizome. True dormancy is far less common than early senescence, and has been observed as the result of documented damage to the plant. The plant may also appear dormant if the bud is destroyed by animals before it emerges. It is likely that large roots can survive such damage better than seedlings. Fusion of two roots (S. G. Carpenter, personal observation) or mycorrhizal associations (MacDougall and Liebtag 1928) may enhance survival during recovery from damage (Carpenter 1980).

The results of this study provide information that is useful in the management of ginseng populations. The most accurate estimate of the number of ginseng plants in an area would result from sampling early in the summer. However, accurate estimates of total reproduction in a population would result from sampling later in the year. Senescence early in the summer will decrease total seed production more seriously in populations that have only plants of the earliest stages (e.g., harvested populations) than in unharvested populations.

The presence of plant hopper immatures did not decrease fruit production below that of plants where plant hoppers were absent. The insects may select and feed on plants that have high levels of translocating sugars. These plants later produce a large number of seeds, even if plant hopper immatures were found feeding during floral development. Many insects that were found on ginseng are "generalist" feeders and were also found on other herbs (Carpenter 1980). However, destructive insects (including sawfly larvae and their parasites, and several unidentified species) can defoliate ginseng and cause it to senesce early. Stink bug nymphs (family: Pentatomidae) and other unidentified species eat ripening seeds. Both forms of damage decreased total seed production in affected plants.

There appeared to be much year-to-year variability in the ripening of ginseng fruits and seeds. If green fruits are removed from the plant, the seeds are immature and will not germinate (Nash 1898). To ensure that the seeds planted by ginseng harvesters are mature and viable, the harvesting season should begin well after the average date that fruits are ripe. This date would be September 1 or later in southern Wisconsin. Experienced ginseng harvesters surveyed agree with this observation (Carpenter 1980). The State of Wisconsin presently allows harvesting to begin in mid-August.

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