

ANNALS OF THE NEW YORK ACADEMY OF SCIENCES

Issue: *The Year in Ecology and Conservation Biology*

Ecology and conservation of ginseng (*Panax quinquefolius*) in a changing world

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American ginseng (*Panax quinquefolius* L.) is an uncommon to rare understory plant of the eastern deciduous forest. Harvesting to supply the Asian traditional medicine market made ginseng North America's most harvested wild plant for two centuries, eventually prompting a listing on CITES Appendix II. The prominence of this representative understory plant has led to its use as a phytometer to better understand how environmental changes are affecting many lesser-known species that constitute the diverse temperate flora of eastern North America. We review recent scientific findings concerning this remarkable phytometer species, identifying factors through its history of direct and indirect interactions with humans that have led to the current condition of the species. Harvest, deer browse, and climate change effects have been studied in detail, and all represent unique interacting threats to ginseng's long-term persistence. Finally, we synthesize our current understanding by portraying ginseng's existence in thousands of small populations, precariously poised to either escape or be drawn further toward extinction by the actions of our own species.

Keywords: ginseng; *Panax quinquefolius*; deer browsing; climate change; harvest; extinction vortex

Introduction

The understory herb layer constitutes, on average, more than 80% of the total plant species in forest communities.¹ These accessible ground-layer plants serve as resources for animal mutualists, herbivores, predators, fungal mutualists, diseases, and a diverse microbial community. As such, the long-term fate of herbaceous plants largely determines the overall biodiversity trend in forests. Extinction of forest herb populations, locally or globally, must be balanced by immigration of new species, or overall forest community diversity will decline.

In order to gauge the threats to forest herbaceous plant populations, a bottom-up approach would involve extensive instrumentation of forest understory environments to measure the changes in those environments over time and space. Although it would be inaccurate to describe Project NEON (National

Environmental Observation Network)² as solely an instrumentation exercise, such efforts represent a large percentage of the project's focus. The ecological interpretation of data gathered in this way presupposes detailed knowledge of how organisms will respond to changes in the observed environment.

Long ago, Clements and Goldsmith³ suggested a top-down alternative—the *phytometer* approach—asserting that the best way to study the environment is to measure the response of the plant itself. At the time, well-characterized crop plants were used to measure environmental effects. However, in the past few decades, a strong case has been made for using native plants to measure environmental effects, particularly in natural settings.^{4,5} In the past three decades a small community of ecologists has focused their attention on one particularly well-known understory herb—the medicinal plant, *Panax quinquefolius* L.—hereafter referred to as American

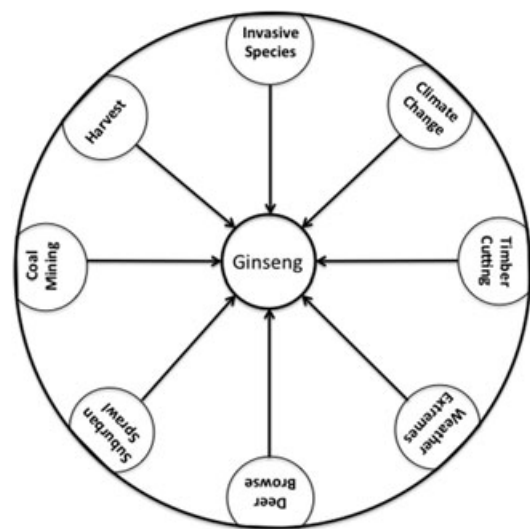


Figure 1. Ginseng as a phytometer to measure direct and indirect effects of human activities and policies in the forest environment (simplified and modified from Ref. 6).

ginseng, or just ginseng (Supporting Fig. S1). Members of our laboratory have referred to these studies, collectively, as Project GEON (Ginseng Environmental Observation Network) (Fig. 1).

On the face of it, selecting a medicinal plant harvested from the wild as the representative understory plant species for ecological study would seem to be a serious mistake. However, the harvesting of ginseng motivated the listing on CITES Appendix II in 1975, which, in turn, prompted early studies of its population growth and ecology.^{7–11} These studies demonstrated that ginseng was a long-lived, widespread perennial plant, and that it exhibited the slow life history typified by forest understory plants generally, rendering it suitable for demographic studies and for the use of both individuals and populations as phytometers. The most atypical characteristic of ginseng was the appetite and accompanying reverence of Asian cultures for the curative powers of the twisted, gnarly storage root.¹² The economic demand driven by this appetite results in the wild ginseng harvest. The harvesting of ginseng adds direct human interaction to the set of factors influencing the plant, which, in turn, means that scientific research on the species has a salience for the public that might be lacking for a less well-known species.

One purpose of this review is to take stock of the expanding scientific literature on American gin-

seng ecology and conservation biology in order to identify factors likely to influence the long-term fate of the species, and by proxy, other herbaceous understory plants. We emphasize the scientific literature because of the large circulating body of unsubstantiated information concerning this plant, which ranges from folklore to presumption to repeated but unquantified observations by nonscientists. By focusing on scientific findings, we identify aspects of this tradition that are supported by evidence. While we occasionally refer to the literature on cultivated, woods-grown or wild-simulated ginseng growing approaches, our emphasis here is on the ecology and conservation of natural populations. This leads to the second purpose of this review; to identify critical gaps in our understanding that could ultimately lead to better management of forest understory species and extinction prevention.

Brief history of the ginseng–human relationship

In North America, ginseng was considered a botanical resource of minor importance for the Native American apothecary,¹³ although this varied widely among tribes.¹⁴ In the early 1700s, with assistance from Native Americans, members of the Jesuit order confirmed the taxonomic relationship of *P. quinquefolius* to *P. ginseng*, a relative on the Asian continent that had been revered for its medicinal properties for millennia. *P. ginseng* had become extremely rare in Asia, most likely due to overharvest and deforestation.¹² American ginseng, though considered by the Chinese to possess different “powers” than Asian ginseng, was nevertheless valued for its medicinal properties. Thus when *P. quinquefolius* was discovered by Jesuits in North America, the market was sufficiently profitable to stimulate intense wild harvest, eventually reaching an industrial scale.¹³ Reports of dried root exports in huge quantities suggest much larger natural population densities than are observed today. For example, in one typical year (1841), more than 290,000 kg of dry ginseng roots were shipped from North America to the Asian continent. Although average root size was larger in the 1800s than it is today,¹⁵ even a conservative estimate would suggest that this represents at least 64 million roots. The total annual harvest during the 1800s was therefore approximately an order of magnitude greater than the wild harvest in the most recent

decade (2001–10; USFWS 2011, CITES nondetriment finding).

The relative scarcity of wild ginseng by the end of the 1800s led to intense efforts to cultivate the plant to satisfy continuing market demand.¹³ These efforts frequently met with failure, though the reasons for this were not always clear. Grown at high densities, both root and leaf fungal diseases wiped out many crops, often after multiple seasons of cultivation and expense. Theft was also a problem given the high value of the root. Inadequate soil or climatic conditions affected other experiments in cultivation. Volatile market prices confounded entrepreneurial farmers who invested hundreds of dollars, hoping to cash in on the bonanza. Finally, roots produced under cultivation were typically not the twisted gnarly phenotype prized by Asian buyers, and fetched a lower price. Despite these problems, a small cadre of growers, particularly in Wisconsin, Ontario, and much later in the dry valleys of British Columbia, succeeded in commercializing ginseng farming. The price differential with the crop's wild ancestor drove two separate harvest systems that continue to the present.

American ginseng was listed on Appendix II of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) in 1975. All species listed on Appendix II are considered to be susceptible to extinction in the absence of trade controls. Trade of any species listed on Appendix II requires a permit and all species are subject to an annual "no detriment" finding in order to maintain permitted trading status. Ginseng was listed due to concern over existing high levels of harvest.¹⁶ The CITES ginseng program is managed at the federal level by the U.S. Fish and Wildlife Service.¹⁶ USFWS required states to implement a ginseng regulatory structure, including harvest seasons, recordkeeping regarding sales, and a set of rules for harvesters. In the early years of CITES regulation, harvest seasons varied widely among states; however, range-wide studies showed no biological basis for this variation.¹⁷ Most states are converging toward a uniform start date of September 1, which increases the possibility of planting ripe seeds that will allow recovery of the population. Record-keeping requirements are modest, primarily involving the recording of sales events to facilitate monitoring of total harvest as well as per root biomass (see Ref. 16). Harvest and permitting requirements vary on state and U.S. For-

est Service Land. Harvest on private land does not generally require a permit; however, diggers must secure permission from the landowner. Federal law requires that all wild-harvested ginseng plants are at least five years of age.¹⁸ Most states also strongly suggest or require that all seeds of harvested plants be sown *in situ* at the harvest site.

Geographic distribution

American ginseng historically was found in rich, cool hardwood forests extending from southern Québec and Ontario, south to northern Georgia, and west as far as Minnesota, eastern Oklahoma, and northern Louisiana.¹⁹ Throughout this wide range, however, natural populations vary from frequent to uncommon to rare across the landscape, but they are almost always small, generally being made up of fewer than 200 individuals.^{20,21}

Contrary to conventional wisdom, the species does not appear to have very specialized habitat requirements. While populations may be more frequently encountered in mixed mesophytic forests with canopy species such as maple, tulip poplar, basswood, and black cherry, they can also be found in drier oak-hickory dominated forests, or moister sites with a walnut or sycamore canopy, though they are rarely encountered in floodplain forests or the most xeric, south-facing, and ridgetop sites. Populations also occupy sites ranging from flat to steep hillsides, and at least in the middle of its range, on all aspects. While populations in the south tend to be found in the mountains, in the north they are at lower elevations, and in the middle of the range, elevations vary from 200 to > 1000 meters.^{10,20–23} Soils supporting ginseng populations are also variable, ranging from moderately acid to near neutral and having textures ranging from loamy sand to silty clay.^{10,20,22} In Arkansas and Indiana, A-horizon levels of phosphorus and calcium were similar to those of sites hospitable to other forest species, although potassium levels were low.^{20,22} Variation in soil pH, slope, aspect, and elevation among 30 representative natural populations across seven states is shown in Figure 2. Given these facts, ginseng can be considered to have a most uncommon sort of rarity;²⁴ small populations, large geographic range, and a broad niche.

Within populations, the dispersion pattern is highly clumped,^{25,26} with cluster size ranging greatly from isolated individuals with no plants in a 3 m

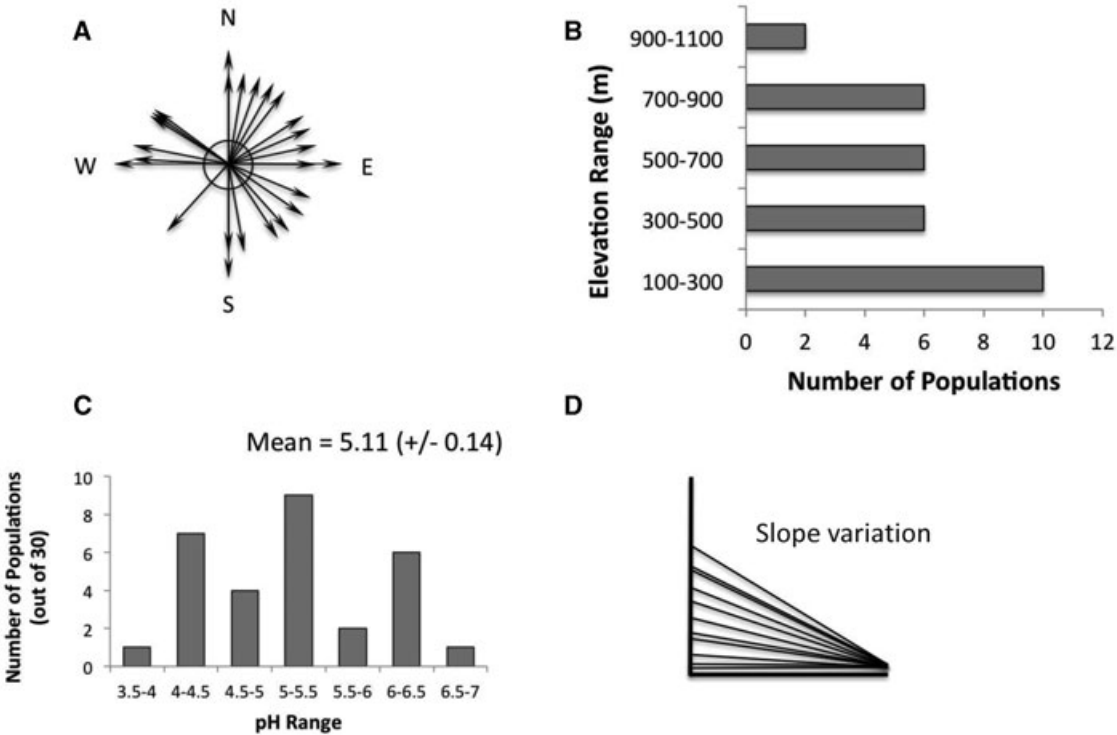


Figure 2. Range of (A) aspects, (B) elevations, (C) soil pH, and (D) slopes occupied by 30 representative natural populations of American ginseng.

radius to >100 plants within a 1 m^2 area.²⁷ For one typical large population (total $N = 369$) censused in 2011, there were 50 clusters with a mean cluster size of 7.38 plants/cluster (range; 1–28 plants). Genetic analyses have suggested such clusters to be, at least in part, family groupings resulting from limited seed dispersal.²⁵

Life history

Patterns of growth

The basic morphology, phenology, and overall life history of ginseng have been well documented.^{7,8,10,20} The perennating organ consists of a fleshy taproot supporting a short underground rhizome. Additional root structures develop either from the side of an existing root or from the rhizome, leading to the typical multibranched storage organ prized by harvesters. An aboveground stalk (sometimes referred to as a sympodium) is attached to the apical end of the rhizome, and consists of fused leaf petioles and peduncle. In plants with more than one leaf, the petiole of each leaf branches laterally from a point at the stalk apex, while the peduncle

grows vertically from the center. Stalks can support up to four (rarely five or six¹⁰) palmately compound leaf blades and potentially one umbellate inflorescence. Each leaf is referred to as a prong, a colloquial ginseng-specific term. Aboveground growth is determinate; leaves and flowers lost cannot be replaced within a growing season.

Because each senesced annual stalk leaves one scar on the rhizome, plants can be aged by counting the scars on the rhizome.²⁸ Age is positively, and nonlinearly, related to leaf area and stalk height; the relationship, however, varies among individuals, among microsites within populations, as well as among populations.²⁹ Figure 3 illustrates the variability in the age–size relationship for three large natural populations. Young plants are small and exhibit low variance in size, but as they age, plant size variation increases dramatically, probably reflecting many kinds of factors, both environmental and genetic, that cause variable growth rates. As is true for most plants, size is a better predictor of flower and fruit numbers than age.^{8,20,29} Although estimates of maximum lifespan vary from 25 to 30 years²⁰ to

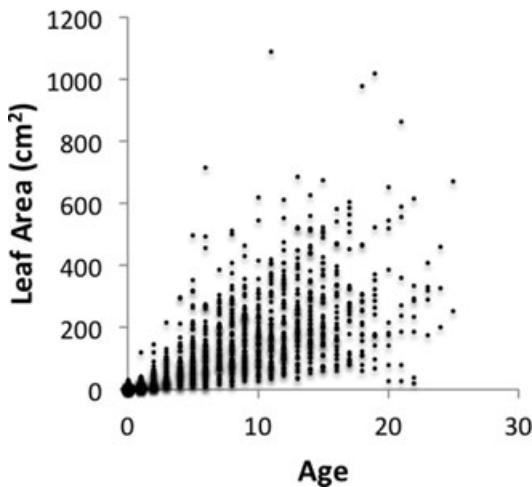


Figure 3. Relationship of age and size (measured as leaf area) in three natural populations of American ginseng.

more than 50 years,^{8,10} in most natural populations few individuals live more than 25 years.²⁹ Harvesting in a given population removes the larger and often older individuals, obscuring accurate determination of potential lifespan. Unharvested older individuals likely die from a variety of causes, most of which are poorly documented. Indeed, the cause of mortality as plants age is one of the greatest unknowns regarding ginseng life history.

The morphology of ginseng allows delineation of a series of discrete life stages:^{7,8,10,20} seeds, first-year seedlings, older one-leaf seedlings, two-leaved juveniles, and three- to five-leaved adults. Seedlings typically possess one leaf with three leaflets, although four or five leaflets may occur in the second or later years. In natural populations (vs. cultivation) plants may remain in the one-leaf seedling stage for two to five years or occasionally longer. For juveniles and adults, transition to a larger leaf number-class does not occur on a yearly basis, and stasis or retrogression to a lower leaf number is not unusual. Within a given leaf number class, undisturbed plants often grow from year to year as measured by number (3–5) and size of leaflets on each leaf. Once plants reach the two-leaved stage, flowering is possible.

The annual phenology of *P. quinquefolius* conforms to that of a summer green geophyte³⁰ whose leaves mature synchronously along with the overstory canopy, and whose senescence is variable. In Wisconsin and Illinois, juvenile and adult plants emerge in April–May, with inflorescences starting to

develop slightly later than the leaves.^{7,20} Leaves fully expand about one month after plant emergence. Flowers mature centripetally beginning in mid-June to mid-July.³¹ Fruit ripening within an inflorescence is also asynchronous;¹⁷ mature, reddened fruits are observable in certain sites and years by late July,^{7,20} although across the range fruit ripening more typically occurs in late August to early September.¹⁷ Fruit dispersal continues to mid-October and is followed directly by plant senescence. Seedling and juvenile plants tend to senesce earlier than adults.⁷ By senescence the rhizome has developed buds containing leaf and floral primordia for the following year.^{20,32} For a more detailed anatomical description of the phenological stages of germination and plant development see Ref. 33. Specific dates of these phenological stages vary geographically with elevation, aspect, latitude and year.^{17,20} At least some of this variation reflects the temperature and precipitation regime experienced by the population.

Seed dispersal in time and space

Ginseng seeds require at least 21 months (two winters) after dispersal in the fall for after-ripening due to their deep simple morphophysiological dormancy,³⁴ a syndrome common among forest herbaceous perennials.³⁵ Experiments using commercially obtained seed show that embryo growth is minimal for the first 9–10 months after dispersal (September–mid-May), but over the next 4–5 months cotyledons grow rapidly and the endocarp softens and splits.³⁶ Stratification temperatures of 20° C are best at promoting such development.³⁷ Once the morphological component of dormancy is broken, a physiological dormancy mechanism prevents the seeds from germinating until after their second winter.³⁵ Seeds occasionally have been observed to germinate only nine months after dispersal, that is, during their first spring, but this is rare.^{37,38} Seeds from red, ripe fruits are much more likely to germinate than seeds from green fruits.¹⁷

While some seeds are capable of germinating 21 months after dispersal, others may persist in the soil for three, four, or even five winters after dispersal, depending on site characteristics.³⁹ This has led to an understanding of the age-structured seed bank that builds in a time-delay for germination ranging from 21 to 45 months. Although modeling experiments have demonstrated that population growth rates are relatively insensitive to this

time-delay, the seed bank could nevertheless play an important role in recovery from harvest and persisting through poor environmental conditions.⁴⁰

Most fruits drop close to the parent plant⁸ similar to many forest herbs,⁴¹ with the potential to be later cached by small mammals such as mice or chipmunks.⁴² The red, fleshy drupes have the hallmarks of fruits that are dispersed by birds, and if seeds remain viable within the bird digestive system, this could provide an opportunity for long-distance dispersal. Consumption rates by animals and the accompanying dispersal distances are not known for natural populations, but could play an important role in metapopulation dynamics as well as migration in response to environmental change since dispersal by gravity is typically limited.

Seedling ecology

Consistent with findings of broad distribution, seedling emergence, seedling survival, and the consequent net recruitment rate were not significantly affected by aspect.²³ Leaf litter depth, however, had a large effect: shallow (ambient) litter increased all three measures of seedling success relative to bare soil.²³ Following establishment, light regime may play an important role in growth. Fournier *et al.*⁴³ related growth of seedlings to diurnal and seasonal variation in the light environment of a deciduous forest canopy in Québec. Mean daily sunfleck durations of up to two hours positively affected biomass, explaining up to 56% of the variation in root and shoot dry mass. For plants experiencing sunfleck durations of more than two hours per day, diffuse and direct photon flux density had a positive impact, and explained 69% of the variation in shoot mass and 52% in root mass, leading to the conclusion that light is an important limiting factor for much of the summer growth period.⁴³ Summer green geophytes have been shown to respond more rapidly to sunflecks than spring green herbs.⁴⁴ They also acclimate to the lower irradiance environment after canopy closure through reductions in light compensation point,⁴⁵ although few measures of photosynthetic properties of ginseng have been made.⁴⁶

Reproductive biology

Ginseng flowers have five sepals, petals, and stamens, and a single inferior ovary with one to three ovules.^{32,47} Ovule number can be determined by style number, although styles do not separate until anther dehiscence.^{31,32} Most flowers begin with

two ovules, but some of them abort an ovule very early and the two styles remain fused.^{47,48} Individual ovules may not get fertilized, or they may abort after fertilization. The number of seeds produced by a single fruit can be readily determined by counting lobes. Structurally, the fruits are berry-like drupes,⁸ and are often referred to as berries.

Commonly reported visitors to the flowers are small bees (Halictidae: *Lasioglossum*) and flies (Syrphidae).^{7,49} Species in both of these groups have been found to carry pollen,^{8,31,50} with larger pollen loads collected from the bees.⁵⁰ Visitation rates tend to be low (e.g. three or fewer visitors in 30 minutes of observation³¹). Other types of insects observed to carry pollen in low amounts include bugs (*Lygus lineolaris*), ants (*Lasius* sp.) and flies (*Delia* sp.).⁵⁰

Although ginseng does not reproduce asexually,²⁰ production of two stalks from one rhizome occurs occasionally.⁸ Experimentally planted pieces of root and rhizome can regenerate plants by activating adventitious vegetative buds.⁵¹ Several studies have documented the mixed-mating system of the species.^{7,28,31,38} The absence of viable seed production from bagged, emasculated plants suggests that the species is not capable of apomixis.³¹ However, with anthers left in place, seed production occurs, demonstrating that self-pollination is a component of the breeding system.^{7,31} On the other hand, at least some of the genetic diversity of populations is due to outcrossing.^{52,53}

Selfing had been thought to be solely *via* geitonogamy because the flowers were reported to be protandrous;⁷ however, the degree of protandry varies among individuals and populations, with at least some flowers having simultaneous stigma maturation and anther dehiscence.²⁸ The presence of pollen tubes before the anthers dehisced and the styles separated in 27% of hand-pollinated flowers led Schlessman³¹ to conclude that autogamy is possible, though pollen tubes were most prevalent in flowers pollinated after the anthers dropped off. Schluter and Punja⁴⁷ concur that autogamy is likely, but for the reason that anther dehiscence is staggered within a flower, and anthers are still present when stigmas separate. They did find, however, that pollen germination and pollen tube growth occurred only in flowers whose styles had started to separate; they suggested that because stigma separation was not always obvious at the time of flower collection, Schlessman³¹ may not have been able to tell that

it had already begun when he observed the pollen tubes. Geitonogamy remains probable as well, due to the proximity of flowers in the inflorescence. The level of geitonogamy will be restricted by the fact that the flowers of an inflorescence open centripetally over a one- to four-week period^{7,31,47} and no more than eight flowers²⁸ or 10% of flowers⁴⁷ in an inflorescence were open at any one time.

At a fundamental level, reproductive success can be attributed in a multiplicative manner to its components: probability of producing an inflorescence, the number of flowers per inflorescence, the proportion of flowers producing fruit, and the number of seeds per fruit. The first two components tend to increase with plant size.^{7,8,31,47} In six Kentucky populations, the probability of producing an inflorescence in 2-leaf plants was 40–90%, whereas three- and four-leaf adults did so 90–100% of the time. Reproductive two-leaf plants had a mean of 5–10 flowers per inflorescence, while reproductive adults had mean flower numbers of 8–43 flowers per plant, with the mean varying considerably among populations. Also, in the six Kentucky populations, the proportion of flowers that matured into fruit did not vary among size classes and likewise seeds per fruit did not vary among size classes.

In very small populations or isolated clusters, indirect evidence for pollinator limitation was found in experimental populations, resulting in an Allee effect.⁵⁴ However, even when pollination is facilitated, seed set may be well below its potential.^{38,45,47} Schluter and Punja⁴⁷ observed pollen tube growth in the persistent styles of fruits that had been aborted. Seed set rose from 38% in flowers from intact inflorescences to 48% when most of the flower buds had been removed.³¹ At least some of the reduction in seed set below potential is likely due to internal and external resource limitation. Internal resource limitation is reflected in the positive relationship between age or size and the proportion of flowering plants that produce fruit, as well as the total numbers of fruits and seeds produced.^{7,8,20,29}

Demography

Several life history properties of ginseng lend themselves to demographic studies. Distinct stages with contrasting survival, growth, and reproductive properties allow the population to be logically divided into classes. The static aboveground size of plants within a year means that precise census tim-

ing is not required to assign individuals to classes (vis-à-vis plants that grow continuously through the season). The nonclonal nature of individuals makes counting genets straightforward. Precise counts of predispersal seed numbers make fertility calculations easy. Large, visible seeds that have limited dormancy make incorporation of the seed bank into demographic models relatively easy with supplementary seed cage studies. Finally, relatively small population sizes mean that censuses can be readily performed for entire populations.

The first formal attempt to model population dynamics of ginseng was carried out by Charron and Gagnon¹⁰ for four populations near the northern edge of the range in Québec. This study ignored age structure in the seed bank, and the five remaining stage classes were determined by leaf number, with one-leaf new seedlings being distinguished from older one-leaf seedlings. Charron and Gagnon¹⁰ compared plant size and age as predictors of plant survival, growth and reproduction, concluding that size was the more important arbiter of performance. Therefore, a 6×6 stage-based population projection matrix was assembled for each population; two populations for three transition years and two for one transition year. Despite limited sample sizes ($60 \leq N \leq 132$), the transition probabilities in these matrices established that ginseng had the characteristic slow life history common to many understory herbaceous plants. Survival, growth, and reproduction varied sharply among classes with the seed and seedling stages being the most vulnerable. A long prereproductive period was evident as many one-leaf and two-leaf plants remained in the same class from one year to the next. Adult stage fertilities were low (40 seeds per four-leaf adult being the highest observed), but later comparisons with other studies suggest these are actually relatively high fertilities compared to central or southern populations.

The dominant eigenvalue of the transition matrix yields the finite rate of increase, λ . Charron and Gagnon concluded that λ was near 1, indicating stable population sizes when at the stable stage distribution, again similar to what has been observed for other understory herbaceous plants. Several other studies of ginseng population dynamics have employed matrix population models to estimate λ as a synthetic measure of population performance in the context of studies of harvest,^{26,56} deer browse,^{57,58} both harvest and deer browse,⁵⁹

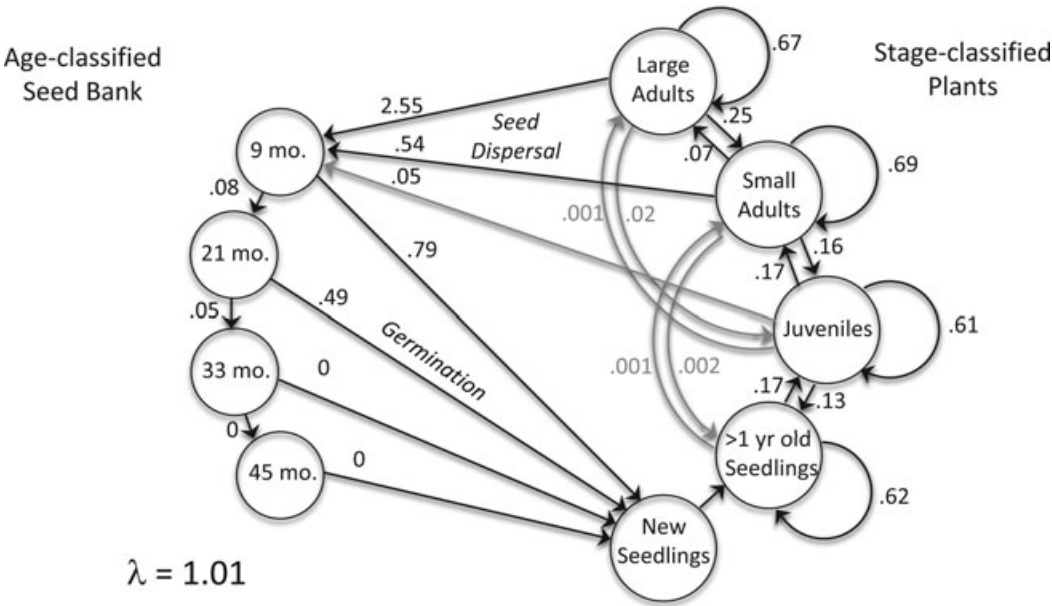


Figure 4. Life cycle diagram showing an age-classified seed bank and a stage-classified population of plants. Arrows show possible transitions among ages and stages between spring of one year and spring of the following year. Arrows in gray are occasionally observed, but with lower frequency than other transitions. The numbers on each arrow represent average transition probabilities for one population of ginseng in northern West Virginia measured over 11 transition years. For this population new seedlings were pooled with more than one-year-old seedlings.

and climate change.³⁹ These studies have used slight variations of the life cycle diagram (Fig. 4) to formulate matrix models, often including age structure in the seed bank, and dividing small and large adult classes based on leaf area instead of number. The results of these studies will be described elsewhere in this review.

Nantel *et al.*¹¹ performed the first population viability analysis (PVA) on ginseng. They used data from Ref. 10 in stochastic matrix model projections to determine the minimum viable population size (MVP⁶⁰) and to investigate the effects of harvesting. MVP was estimated at 172 plants for the Québec populations, a value considerably lower than an estimate (MVP = 800 plants) made for seven West Virginia populations subjected to high but ambient rates of deer browse near the center of the range.⁵⁸ Souther⁶¹ later estimated a lower MVP for twelve more widespread populations (MVP = 55). The latter two studies are discussed elsewhere in this review; however, the variation in MVP estimates suggests that more research is needed to narrow the confidence limits on this quantity. At the upper end of the scale, there are very few known natural populations that would exceed MVP, but at the lower end,

most populations would be considered safe from extinction over the next several decades.

Sensitivity and elasticity analyses identify transition probabilities most influencing λ in absolute and relative terms, respectively.⁵⁵ In ginseng, λ is most sensitive in absolute terms to rapid growth to larger size classes, particularly for seedling and juvenile classes (Table 1). In addition, a premium is placed on earlier reproduction. Elasticity patterns show that proportional increases in λ are greatest for the stasis transitions (Table 1).

A particularly useful strategy for understanding variation in λ among populations is the Life Table Response Experiment (LTRE). LTREs explain differences in λ as effects of differences in the transition probabilities (a_{ij}) and the sensitivity of λ to changes in a_{ij} .⁵⁵

$$\Delta\lambda = \sum_{ij} (a_{ij, pop1} - a_{ij, pop2}) * S_{ij}.$$

Each term in the summation is associated with a particular transition probability, and thus it is possible to evaluate the contribution of each transition and its associated sensitivity to the contrasting λ between two populations. LTREs have been performed

Table 1. Transition probabilities, sensitivities, and elasticities for the average matrix from 11 transition years for one population of ginseng in north-central West Virginia

Transition probabilities	9 mo. seeds	21 mo. seeds	33 mo. seeds	45 mo. seeds	Seedlings	Juveniles	Small adults	Large adults
9 mo. seeds	0	0	0	0	0	0.0477	0.5443	2.5538
21 mo. seeds	0.0834	0	0	0	0	0	0	0
33 mo. seeds	0	0.0500	0	0	0	0	0	0
45 mo. seeds	0	0	0	0	0	0	0	0
Seedlings	0.7934	0.4948	0	0	0.6150	0.1334	0.0016	0
Juveniles	0	0	0	0	0.1671	0.6144	0.1609	0.0181
Small adults	0	0	0	0	0.0013	0.1673	0.6885	0.2490
Large adults	0	0	0	0	0	0.0014	0.0688	0.6713

Sensitivities	9 mo. seeds	21 mo. seeds	33 mo. seeds	45 mo. seeds	Seedlings	Juveniles	Small adults	Large adults
9 mo. seeds	.	.	.	.	.	0.0938	0.0578	0.0119
21 mo. seeds	0.0388	.	.	.	.	.	.	.
33 mo. seeds	.	0	.	.	.	.	.	.
45 mo. seeds	.	.	.	.	.	.	.	.
Seedlings	0.0797	0.0065	.	.	0.2044	0.1141	0.0703	.
Juveniles	.	.	.	.	0.4822	0.2692	0.166	0.0343
Small adults	.	.	.	.	0.9279	0.5181	0.3194	0.066
Large adults	.	.	.	.	.	1.0858	0.6693	0.1383

Elasticities	9 mo. seeds	21 mo. seeds	33 mo. seeds	45 mo. seeds	Seedlings	Juveniles	Small adults	Large adults
9 mo. seeds	0	0	0	0	0	0.0044	0.031	0.0301
21 mo. seeds	0.0032	0	0	0	0	0	0	0
33 mo. seeds	0	0	0	0	0	0	0	0
45 mo. seeds	0	0	0	0	0	0	0	0
Seedlings	0.0623	0.0032	0	0	0.1238	0.015	0.0001	0
Juveniles	0	0	0	0	0.0794	0.163	0.0263	0.0006
Small adults	0	0	0	0	0.0012	0.0854	0.2166	0.0162
Large adults	0	0	0	0	0	0.0015	0.0454	0.0915

for ginseng to dissect the demographic effects of deer browse,⁵⁷ harvester types,⁵⁶ deer browse and harvest,⁵⁹ and are discussed below.

Harvest effects: demographic

Harvest rates. Estimating a rate of harvest is complicated for an economically valuable species that is rare and widely spaced across a broad geographic area.²¹ Add to that the secretive culture that surrounds harvest of ginseng and estimating rates of harvest becomes even more difficult. Nonetheless, several different harvest rate estimates have been made using a variety of approaches.

McGraw *et al.*²¹ estimated a harvest rate of 4.9% for natural populations across the state of West Virginia by calculating two independently estimated statistics: (1) the number of roots harvested (based on annual total root mass reported to USFWS divided by the mean root mass per plant), divided by (2) total number of plants in the entire state (based on plant densities determined by quasi-randomly sampling of the landscape multiplied by the land area of the state comprising suitable habitat). Large error estimates in both numbers are possible. Harvested root numbers could be incorrect since total root mass sold could include an unknown amount

of wild simulated or woods cultivated root and mean root mass was estimated only crudely *via* haphazard sampling. The total plant number in the state could incorporate even larger error since the quadrat sampling could have been biased, and the total suitable habitat was also a crude estimate.

Observed rates of harvest of natural monitored populations may provide more meaningful numbers. One estimate showed harvest rates that varied from 0.45% to 3.04% annually for a set of seven populations over four growing seasons.⁵⁸ This analysis was later expanded to include 30 populations in seven states censused bi-annually for several years (5–11 years, depending on the population). On an annual basis a mean of 15% of populations showed evidence of harvest, and a total of 1.3% of individual plants were confirmed harvested.²⁷ Over the entire study period, 13 of 30 populations (43%) were harvested at some point, with six of those 13 being harvested multiple times. The 30 populations, while spanning a large geographic range (New York south to Virginia, and west to Indiana and western Kentucky) and being considered representative, were also not truly random; for example, populations on private lands were underrepresented, and those in nature preserves were overrepresented. In addition, in these populations every plant was labeled cryptically by a numbered nail that would have been exposed once a harvester started digging; this could have either stimulated further exploration and harvest or inhibited further harvest. In addition to this possible source of bias, harvest rates were likely underestimated because some harvest events were no doubt undetected by the passing of months between census intervals or by efforts of harvesters to disguise their presence.

Once a population is discovered by a harvester, what is the harvest intensity? A variety of harvester types can be identified based on the number and sizes of plants removed. Occasionally, harvest appears to be for personal consumption because a very small number of roots are dug despite many plants being found nearby. More typically, harvesters dig a larger proportion of what they find; however, some clearly leave behind a few large plants, as strongly recommended by stewardship-oriented harvesters,¹⁴ while others remove virtually any plant they can find, including plants that are under the size limits set by regulations;²⁷ (see the section below on compliance with regulations).

One study equipped harvesters (trusted individuals with knowledge of ginseng identification and habitat preferences) with GPS units and directed them to flag as many plants as possible within a two-hour period.²⁶ A mean of 35 legal size plants were found per harvester out of a total of 135 harvestable plants in the population (26%). This represented 9% of all the plants in the population.

The total harvest rate is given by the probability of a population being discovered (estimated above at 15% annually) multiplied by the proportion of plants taken once a population has been encountered (9%, estimated above). The product, (1.35%) provides yet another estimate of the annual harvest rate, but one that should not be taken too literally based on the assumptions that go into that calculation. Nevertheless, taken with the other estimates, it seems likely that the true rate of harvest of plants from the wild is in the range of 1–5% annually, and that it varies among harvesters, land use classes, and years.

Compliance with harvest regulations. Hardin⁶² made famous the tragedy of the commons paradigm 45 years ago when writing about overexploitation of natural resources. Individuals will often severely deplete a resource even when they know their actions will negatively affect the long-term availability of that resource. In the case of ginseng, self-interested harvesters could be driven by competition, rationalized by the idea that if they do not harvest a plant they have discovered, someone else will. Competition for a limited resource could encourage resource preemption by early harvest, including harvest in advance of the onset of the season. Bailey⁶³ conducted extensive interviews with ginseng diggers and dealers in West Virginia. His research suggested that some of the traditions associated with the culture of ginseng harvest in the state were diminishing. For example, the practice of digging was traditionally passed down through generations (typically through males) and included respect for the resource. This respect translated into active seed planting and restricted harvest on a voluntary basis. Entire populations were not removed at one time. Some plants were explicitly left behind to provide time for maturation, additional seed production and a guarantee of resource presence at a later date. However, the network of diggers and dealers was also an aging one, with many diggers

reporting that younger family members were less inclined to spend time outdoors in pursuit of ginseng. Bailey⁶³ also found a relationship between the rate of unemployment and harvest volume; more ginseng was dug in periods of economic stress, suggesting the wild harvest was acting as an economic fallback in difficult times.

Freese⁶⁴ discussed the ocean environment as the ultimate “open access” habitat or commons, available to all, and exceedingly difficult to monitor. American ginseng occurs in an extensive sea of forest over a wide geographic range, making it impossible to monitor the vast majority of harvest activity. Freese⁶⁴ maintained that where commercially important species occur in such habitats, they will continue to be harvested as long as there is immediate profit to be made, that is, consumer demand will drive continued harvest. Successful sustainability in open access habitats likely depends on the ultimate management of the resource belonging to those who actively harvest it. Further, these managers of the resource must receive a major share of the economic benefits derived from its use in order for sustainability to be achieved.⁶⁴

Research conducted on 30 natural populations of ginseng in seven states for 5–11 years looked specifically at rates of compliance with regulations set by state and federal governments.²⁷ The authors documented violations in regard to season, location and plant size (20%, 65%, and 82% of events, respectively). Of all observed harvests during the study period, only 6% were entirely legal and only 1.4% of harvested plants were legally harvested in relation to all three aspects of the study. Well-guarded populations (e.g., military bases) were not harvested. However, open-access lands where harvesting was prohibited by law (e.g., state parks and nature reserves) were especially vulnerable: 65% of observed harvest events occurred on such lands. The cultural and historical complexity of wild harvest of ginseng dramatically complicates harvest monitoring and management. If the majority of ginseng harvest occurs illegally, engaging diggers as the primary managers of the resource will be challenging.

Demographic simulations of harvest. The early demographic studies of ginseng in Québec focused on harvest effects^{10,11} in order to inform management of the species. Population growth rate varied, but the majority of the estimates showed λ 's

greater than 1.0 (i.e., the populations were increasing), with an average rate of increase of about 3% per year. When harvest was included in the demographic model under varying environmental conditions, λ declined with increasing rates of harvest. Elasticity analyses revealed that changes affecting larger adult plants had the greatest effect on the populations.¹⁰ In a later analysis of the same demographic data,¹¹ the authors estimated a minimum viable population (MVP) size of 172 plants needed to prevent population extinction from stochastic environmental variation (probability of population survival > 95% over 100 years). There are only one dozen known ginseng populations in Canada that exceed this minimum number.¹¹ Both studies concluded that low rates of harvest (1–8%) in southern Québec may be sustainable if performed optimally.

Van der Voort and McGraw⁵⁶ explored the consequences of alternative harvester behaviors on the population dynamics of American ginseng. Drawing on known behaviors, they developed three harvester types and ran demographic simulations on wild ginseng populations, partitioning the sources of differences in population growth rates using a life table response experiment (LTRE). The simulations showed that ignoring size class limits and harvest season onset dates dramatically affected population growth rates. They also concluded that harvesting in a manner merely compliant with regulations was not sufficient to maintain stable population growth rates. Rather, populations must be stewarded. Two-leaved juveniles also had a large influence on population growth rates; avoiding harvest of those small plants was critical, as shown by LTRE comparisons of compliant versus noncompliant harvesters. Harvesters who employ a stewardship strategy gain the most benefit by harvesting at a time of year when seeds are ripe, then planting seeds, which later ensures high germination rates and recovery from the harvest event. Van der Voort and McGraw⁵⁶ concluded that existing laws in many states at the time were inadequate to protect wild ginseng populations. Since that publication, three high-harvest states (West Virginia, Kentucky, and Tennessee) have moved the start of their harvest seasons from August 15 to September 1, ensuring greater potential for harvest to be done in a nondetrimental fashion. Demographic simulations show that a stewardship-oriented harvester, who complies with these later season onset dates, self-limits harvest intensity, and

optimally plants ginseng seeds 2 cm deep at the time of harvest, can sustain population growth rates equal to that of unharvested populations.

Farrington *et al.*⁵⁹ conducted demographic simulations that took into consideration the interacting effects of ginseng harvest and white-tailed deer (*Odocoileus virginianus*) browse. Harvest and browse had negative effects on the population dynamics of ginseng; however, the effects were nonadditive. The presence of browse reduced λ , but only marginally; λ was still > 1.0 . LTREs demonstrated that deer browse had a positive effect on ginseng survival because browse actually protected large plants by making them invisible to harvesters. Farrington *et al.*⁵⁹ also found that “responsible” seed planting (i.e., seeds planted at a depth of 2 cm) at the time of harvest resulted in higher growth rates than plants harvested “irresponsibly” (no seed planting).

Observed effects of harvest on populations. Recovery of two well-characterized small populations of ginseng from severe harvest has been documented. Lewis⁹ monitored a population in Missouri that was decimated by harvest the year after plants were thoroughly censused. In fall of 1996, all visible ginseng plants were removed in a complete experimental harvest in West Virginia.⁵¹ Both studies showed rapid recovery of the total aboveground population size (Fig. 5A for West Virginia); however, stage structure was much slower to recover. Lewis⁹ deduced that the seed bank must have been responsible for the early regrowth of the Missouri population, and in West Virginia, the same pattern was seen.⁵¹ In Missouri, after five years, only 25% of plants in the population were reproductive versus 66% before harvest. In West Virginia, the adult portion of the population also recovered slowly but steadily for the first decade after harvest (Fig. 5B).

This resulted in seed production and a pulse of recruitment in 2008. An unknown event resulted in additional adult mortality, such that the adult population remains far below preharvest levels. The built-in resistance to harvest through the presence of a seed bank left by older, more fecund individuals may not be present in populations with reduced fertilities.

Harvest effects: genetic. Wild harvest can affect the genetic diversity and evolution of targeted species, as shown by numerous examples from fisheries, forestry, and game management.^{65–68} The results of this interaction between humans and wild species are frequently reduced genetic diversity, unintentional selection against desirable traits, and ultimately reduced population viability. The introduction of individuals to reverse population declines also has genetic consequences, namely outbreeding depression—reduced fitness resulting from introduction of maladapted alleles or the breakup of coadapted gene complexes.⁶⁹ As with other wild-harvested species, these genetic issues are cause for concern for ginseng conservation.

Harvest of plants from the wild can clearly affect patterns of genetic diversity.^{65,70} Because harvest acts as an independent bottleneck event, each population would have a unique set of their alleles lost or fixed, resulting in a high level of interpopulation differentiation combined with low levels of intrapopulation diversity for a targeted species. This impact of harvest is consistently observed in patterns of genetic variation in ginseng, although these have been assessed with a variety of sampling regimes, marker systems, and statistics.^{25,52,53,71–75} Genetic variation within and among contemporary populations of ginseng is likely influenced by harvest history, but this may also be exacerbated by

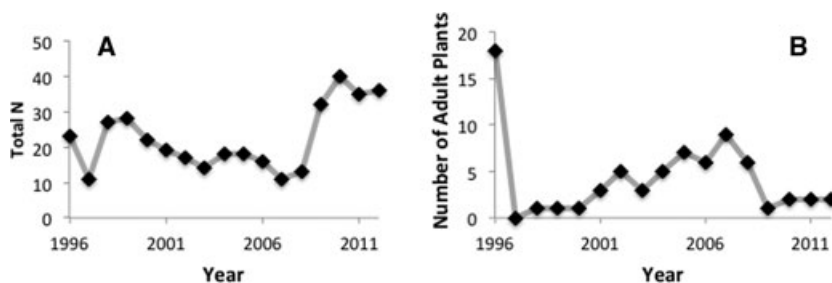


Figure 5. Recovery of (A) the total population, and (B) the adult (three-leaved) component of the population after experimental harvest in 1996 for a small population in northern West Virginia.

life-history characteristics that reduce gene flow. Within populations, plants within 2 m of one another tend to be genetically related;⁵³ this level of genetic structure is the result of limited pollen movement and/or seed dispersal.⁷⁶ While less is known about seed dispersal, the largely autogamous breeding system of ginseng would limit pollen movement. Interpopulation genetic differentiation estimates (G_{ST}) for ginseng range between those typical of plants with mixed mating systems and those typical of inbreeding dicots.⁷⁷ Limited pollen or seed movement would reduce gene flow among populations and thereby increase divergence.⁷⁷

The consequences of harvest for genetic diversity in ginseng populations have been determined by both modeling and field studies. A simulation study conducted by Cruse-Sanders *et al.*⁷⁸ found that harvesting as few as 10% of mature (>2 leaves) plants in populations significantly reduced genetic diversity. The results from the simulation study were supported by comparisons of protected populations to those legally open to harvest.⁵³ Levels of expected heterozygosity (H_e) were significantly lower in unprotected populations ($H_e = 0.070$) than in protected populations ($H_e = 0.076$). Unprotected populations showed evidence of recent bottleneck events, while no such events were detectable in any protected populations. In contrast, Obae and West⁷⁹ did not find reduced genetic variability in populations in high harvest versus low harvest regions, but this was likely due to a small sample size ($n = 4$) in the high harvest region.

Indirect genetic effects result from small population sizes and low levels of genetic diversity following harvest. Chief among these effects is increased inbreeding. Studies from other species suggest that reduced density of conspecifics would increase the proportion of seeds produced by self-pollination, and when outcrossing takes place, reduced genetic diversity would mean a greater likelihood that nonself-pollen would be genetically similar.⁸⁰ In fact, results from allozyme analyses of ginseng suggest that offspring in wild populations are largely the products of inbreeding.²⁵ Such mating between close relatives may result in reduced fitness in offspring, that is, inbreeding depression. Alternatively, the deleterious recessive alleles primarily responsible for inbreeding depression may be purged from populations with histories of inbreeding. Successive generations of inbreeding will ex-

pose alleles to elimination by natural selection, and therefore, inbreeding may not lead to inbreeding depression in these species. However, a meta-analysis by Byers and Waller⁸¹ suggests that purging is inconsistent among plant species, and substantial decreases in offspring fitness are possible even for predominantly self-pollinating species.⁸² This is especially likely where inbreeding has increased only recently in the history of a population, as is likely in ginseng since evidence suggests populations were much larger only 300 years ago. One study directly examined the consequences of inbreeding for ginseng in three natural populations.³⁸ Relative to those produced by cross-pollination, offspring of self-pollination had reduced stem height and leaf area, the latter of which is a trait positively correlated with longer term survival.³⁸ Thus, a shift in breeding system toward more mating among relatives and greater selfing due to smaller population sizes will reduce fitness.

Anecdotal accounts have reported the planting of seeds from cultivated populations into wild populations by managers and harvesters.^{53,74,75} Assuming these seeds germinate and grow into adult plants, subsequent outcrossing with wild plants could produce offspring with traits more similar to cultivated plants.³⁸ The degree to which populations in the wild derive from cultivated seed is an ongoing debate in the management of ginseng.¹⁸ At least six separate studies have applied genetic markers to this question.^{52,71,72,74,75} Three of these studies purported to show evidence of genetic introgression of cultivated genotypes into wild populations.^{52,74,75} These studies used different molecular markers and sampling protocols, some of which were more robust than others. Boehm *et al.*⁵² found that one of the 14 wild populations they sampled was genetically similar to a cultivated source. However, this population was actually a small number of transplants ($N = 15$) to a woodland garden in Pennsylvania. Also using RAPD variation, Schlag and McIntosh⁷⁴ found evidence that one of seven wild populations in Maryland contained plants genetically similar to a cultivated population derived from out-of-state seed sources. Harvesters provided the genetic source material for the assessment by Schlag and McIntosh; thus the conclusion that the original populations were wild is circumstantial. Relative to a truly random sample of wild populations, the approaches of these two studies would increase the

likelihood of sampling a population supplemented with cultivated seeds by harvesters.

Young and coauthors⁷⁵ analyzed a much larger sample of plants from wild and cultivated sources ($N = 489$) using microsatellite markers. They found that some of the wild-collected samples were genetically similar to a Wisconsin/cultivated group. They interpreted this result as suggestive of widespread planting of cultivated seed in natural settings. However, it is not clear how they sampled or identified wild populations in any state, or how many wild-collected samples fell into this group. Grubbs and Case⁷² published the most comprehensive and transparent study that addresses genetic differences between wild ($N = 31$) and cultivated ($N = 12$) populations throughout the range of ginseng. Unlike other assessments, the majority of wild populations were located and sampled by state and independent botanists, rather than harvesters. They found that one unique allele (*Idh2*) was found exclusively in wild populations and there was no evidence of introgression of cultivated genotypes into wild populations. However, showing that introgression of genes from cultivated plants into wild populations has occurred is complicated by several factors. Many cultivated populations have been recently derived from wild populations and they are often the products of independent accessions of wild-derived roots and seeds.^{52,83,84} The studies to date have either lacked the rigorous sampling^{71,74,75} or the fine-scale genotyping methods⁸⁵ to conclusively detect introgression. In summary, it is likely that harvesters are introducing cultivated seed into some wild populations, but the majority of ginseng populations in the wild are not products of this practice. The issue is important as CITES is specifically concerned with protection of wild populations.

Harvest can alter the evolution of ginseng by directly changing the relationship between phenotypic traits and fitness, that is, the pattern of phenotypic selection. In a simulation study, human harvesters selectively removed larger adult plants, which were likely more apparent in the dense forest understory.²⁶ The outcome of this process is that larger plants lose their fitness advantage, and this effect is exacerbated when harvesters remove seeds. In *Saussurea laniceps* (Himalayan snow lotus), such size-selective harvest has led to the dwarfing of plants in the wild.⁸⁶ Two studies suggest that similar dwarfing may be happening in ginseng.^{15,29}

The overall size of herbarium specimens has declined over the last century, and this effect was most pronounced among specimens collected from geographical areas with high levels of harvest.¹⁵ In the wild, plants from populations with a high harvest index—defined as the proportion of seedlings and juvenile plants—had smaller leaf areas and stem heights than plants of the same age in populations with a low harvest index.²⁹ Environmental variation could also be a factor in these results, although these changes are consistent with human-induced evolution in many other species.⁶⁷

Deer browse effects

In addition to human harvest, browsing by white-tailed deer (*O. virginianus* Zimm.) is a pressure likely contributing to the decline of American ginseng populations. As a result of strict hunting regulations, land-use changes, and loss of top predators, white-tailed deer are now the most abundant wild ungulates in North America. According to archeological evidence of deer consumption rates by Native Americans and early European settlers,⁸⁷ deer densities are currently two to four times higher than presettlement densities in much of the United States.^{88,89} As keystone herbivores in the eastern deciduous forest, large deer herds can alter biotic communities within forest ecosystems.^{90–94} The building body of evidence suggests that deer are negatively affecting many aspects of the forest community by depressing the growth of valuable tree^{93,95,96} and herbaceous species^{97–102} and altering species richness and abundance.^{89,95,96,98,103,104} Several studies have documented the effects of deer browsing on American ginseng.^{57–59,105} White-tailed deer may be exacerbating the rarity of ginseng, as herbivory, within some populations, occurs at high rates and deer are seed predators of ginseng.¹⁰⁵

Though human harvesters and deer both remove plant tissue, harvesters remove the root, which results in death of the plant, and they may (or may not) plant seeds to encourage reproduction. Deer effects are likewise variable, but generally affect only aboveground plant parts: deer may remove a portion or all of the leaves, reproductive structures and stalk (Fig. 6), but typically leave the root intact. The loss of aboveground biomass may temporarily remove the plant from a population in the season in which browsing occurs but, as a perennial herb, the potential for regrowth in the following season

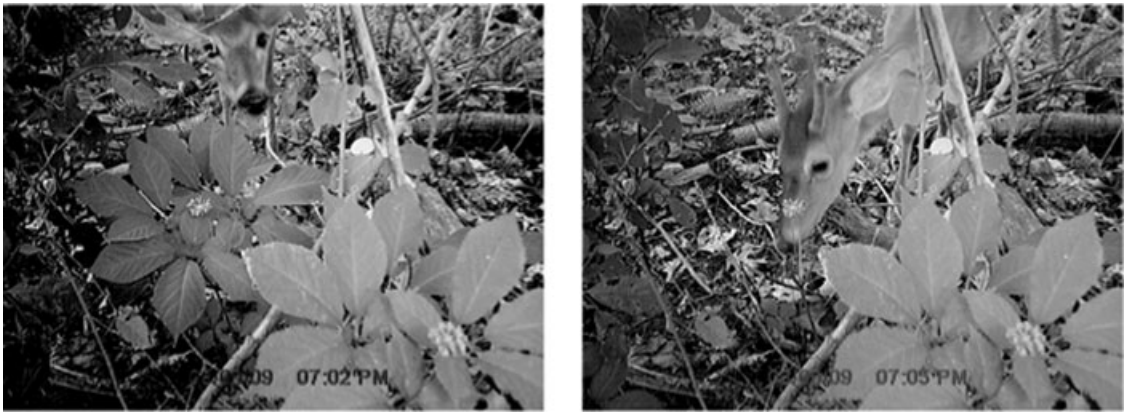


Figure 6. Game camera image sequence showing browsing of ginseng by a young white-tailed deer. In this instance, the leaves were consumed but the infructescence was left intact.

remains since the ginseng root is not damaged. Deer may also hinder new recruitment in a population by consuming fruits, since seeds are destroyed during the digestive process.¹⁰⁵

Deer browsing affects the size distribution and fertility of plants in a population. In studying browse rates and patterns of browse in natural and experimental ginseng populations, Furedi⁵⁷ found that plant characteristics and microsite conditions related to apparency influence browse susceptibility. Larger plants (i.e., plants with a greater leaf number, leaf area, and stalk height) were more likely to be browsed than their smaller, shorter counterparts. Similar results were reported by Farrington *et al.*⁵⁹ Reproductive plants were more susceptible to browse than nonreproductive ones. Plants in open, unprotected areas were more likely to be browsed than those hidden by fallen logs, rocks, and shrubs and located farther from deer trails. Other studies have reported that food choices made by deer result in morphological changes in plant populations.^{91,93,95,96}

By following the fate of individual plants in natural ginseng populations over multiple consecutive growing seasons, Furedi⁵⁷ found that negative effects of browse were carried over into the following year. Generally, relative growth rate of leaf area and stalk height were reduced, an effect that was further compounded with consecutive years of browse. Reproduction in the year following browse was also reduced either by the production of fewer buds per inflorescence (an effect further exacerbated by two years of browse) or the absence of a reproductive

structure altogether. Although mortality from deer browsing is difficult to differentiate from dormancy, browsing was associated with nonemergence in the year(s) following browse. Given that true whole plant dormancy is thought to be rare or nonexistent, most of the absences were probably mortality. These patterns are consistent with effects of ungulate herbivory reported in other plant species.^{59,97,99,106,107}

The collective negative effects of deer browsing were integrated by determining effects on λ and partitioned with an LTRE. Furedi⁵⁷ and McGraw and Furedi⁵⁸ showed that the overall population growth rate for seven populations in northern West Virginia was 0.973 (i.e., declining by 2.7%) in the presence of deer browsing but that the same populations would have increased by 2.1% annually ($\lambda = 1.021$) with the removal of the direct effect of browse. The LTRE showed that lowered values for growth transitions of juveniles and small adults were together responsible for about one half of the reduction in λ caused by deer browsing.⁵⁷ Reduction in the proportion of large adults staying large adults contributed to one fourth of the reduction in λ . Finally, reduced fertility of large adults explained the remaining one fourth of the λ difference between browsed and unbrowsed populations.

Using population viability analyses (PVA), McGraw and Furedi⁵⁸ expanded on the demographic work to examine the effects of current browse levels on stochastic population projections over the next 100 years. Given the current browse rates, the minimum viable population size was calculated at approximately 800 individuals, much higher than

all seven populations used in the study. In fact, out of 30 long-term demography study populations,²⁷ none would be considered viable under current deer browse rates. A 50% reduction in deer browsing would be required to achieve viability of any of the 30 natural populations.

Given that both deer browsing,^{57,58} and harvest⁵⁶ separately have negative effects on λ , Farrington *et al.*⁵⁹ used demographic matrix models and LTREs to examine whether these two effects were additive in Missouri populations of ginseng. They found that both pressures negatively affected λ , but that the effects were nonadditive. Browsing resulted in a 2.9% decrease in λ ($\lambda = 1.038$) with an additional 4.3% decline ($\lambda = 0.995$) with the addition of responsible harvest; an effect similar to responsible harvest alone ($\lambda = 0.995$). Deer browsing reduced λ by decreasing fertility, stasis, and growth and increasing the regression rates of larger, reproductive plants, but contributed positively to survival in the presence of harvest pressure because browsing conceals a plant from harvesters. Deer tend to browse the larger size classes of plants; the same ones being targeted by harvesters. In the harvest scenario, these plants are outright killed by harvest. On the other hand, harvest reduced λ by reducing stasis, growth, and regression rates of the larger, reproductive plants, but the effects of browse were moderated by the positive effect of seeds being replanted by harvesters (under the responsible harvester scenario).

Interactions with other species

Herbivores

Vertebrate consumers other than deer affect ginseng only infrequently. Vole damage to roots is frequently cited as a major problem in dense woods grown or cultivated patches of ginseng, but rarely observed in the wild, although rodent excavation near roots does occur, and large roots do disappear from censused populations for unknown reasons (McGraw, personal observation). Growers blame shrews for consuming berries and seeds, and occasional observations of partially consumed berries and piles of shredded seed coats under large reproductive plants are seen in the wild, but no definitive proof of the causative agent has been obtained to date. Turkey populations have been resurgent in the past 3 decades over much of ginseng's range and uprooted ginseng plants have been attributed to their extensive scratching.

In addition to their role as pollinators, a variety of invertebrates consume ginseng stems, leaves, flowers, and fruits. Because ginseng is cultivated, many of these interactions are well known.¹⁰⁸ Insect herbivores include aphids (especially on the peduncle), cutworms (stalk), four-lined plant bugs (leaves), leaf hoppers (leaves), leaf rollers (leaves), stink bugs (fruits and seeds), spittle bugs (inflorescence, seeds), grasshoppers (leaves), and thrips (leaves). Slugs leave feeding holes in the leaves. Most of these herbivores cause enough damage in cultivation to cause growers to resort to spraying their plantings with pesticides. In natural populations, no assessments have been done on either the frequency or effects of these interactions.

Plant competition

No studies have examined the extent of competition between ginseng and neighboring native herbaceous plants in natural populations. However, more than 4,000 ginseng plants in 30 natural populations were used as circular quadrat centers to gauge potential for competitive encounters with nonnative, invasive plants.¹⁰⁹ The *Panax*-centric sampling method assured that the quantification of invasion was relevant to ginseng. Within a radius of 2 m, all invasive herbaceous species were tallied, within 5 m, all non-native shrub species were noted, and within 10 m, all exotic trees. By these criteria 63–70% of ginseng populations and 29–37% of individual plants were exposed to invasive plants. The most abundant invasives overall were shrubs (*Rosa multiflora*, *Berberis thunbergii*, and *Lonicera* sp.). The most abundant tree species was *Ailanthus altissima*. The most abundant herbaceous invasive was garlic mustard (*Alliaria petiolata*). The latter two species have known allelopathic effects on native plants. The mere presence of invasives, however, does not demonstrate competitive effect. A follow-up experimental study compared the effects of planted *A. petiolata* with that of a planted native species, *Viola striata*, around target ginseng plants.¹¹⁰ *Alliaria* increased seedling mortality, and treatment of soil with activated carbon reduced this effect somewhat, suggesting it may have been due to allelopathy. Survivor growth rate, root length, root:shoot ratio and biomass were all not differentially affected by competition from *Alliaria*.

The presence of ginseng in the vicinity of tree-of-heaven (*A. altissima*), another purportedly

allelopathic plant, prompted a second experiment comparing growth of ginseng under canopies of *Acer saccharum* (sugar maple; native nonallelopathic), *Juglans nigra* (black walnut; native allelopathic), and *A. altissima* (nonnative allelopathic)¹¹¹ (Hanna *et al.*, in review). Contrary to their expectation, they found ginseng performed best under *Ailanthus*, and worst under *A. saccharum*. This prompted the authors to speculate whether *Ailanthus* may have chemically inhibited soil organisms with pathogenic effects on ginseng.

Diseases

The primary diseases of ginseng are fungal. In fact, disease outbreaks in dense cultivated or wild simulated plantings are, along with poaching, primary reasons why growing ginseng is viewed as a risky proposition.^{12,13} *Alternaria* blight causes leaf lesions, and may cause leaf abscission before normal senescence. *Cylindrocarpon* starts as brown spots on the root surface and spreads until the root dies. Several other fungal diseases have devastated plantings of ginseng. As with invertebrate pests, however, much less is known about the frequency and impact of fungal disease in natural populations. Studies are needed in order to understand possible mechanisms of density dependence, causes of mortality in older individuals, selective forces on dispersal characteristics, and indirect effects of climate variation.

Climate change

As of 2012, the atmospheric CO₂ concentration was 25% higher than in 1957, when David Keeling began monitoring atmospheric CO₂ at Mauna Loa, Hawaii;^{112,113} current levels exceed natural variation in CO₂ for the past 800,000 years.¹¹⁴ Future CO₂ concentrations will depend largely on fossil fuel-use and carbon sequestration.^{112,115} To account for uncertainty in these parameters, the Intergovernmental Panel on Climate Change (IPCC) developed a series of emission scenarios, which represent alternative futures based on differing demographic, economic, and technological trajectories.^{112,115} Using these emission scenarios, climate models project, on average, global temperature rises of 1.3–6.1 °C beyond preindustrial levels by 2100, as well as increases in temperature variation and extreme weather events.¹¹⁶ Regional projections indicate that the eastern United States will experience

temperature rises between 2.3 and 5.6 °C by the end of the century, with the greatest warming occurring in the winter months, due primarily to increases in winter temperature minima. Projections of precipitation are more uncertain than those of temperature, though there is high consensus among climate models that variation in precipitation will increase, making both drought and heavy rain events more frequent in the eastern United States.¹¹² Even if humans cease to combust fossil fuels to meet energy demands, some degree of climatic change will occur,¹¹⁷ meaning that species of native flora and fauna, like ginseng, face an inevitably warmer, more variable future.

The relationship between climate and ginseng demography has been assessed using long-term census data for populations within the central portion of ginseng's range.³⁹ Analyses of population growth rate response to temporal and spatial variation in climate demonstrated that precipitation influences ginseng population growth, such that there is a range-wide parabolic relationship between λ and total growing season precipitation (April 15th–September 30th).³⁹ This response pattern roughly corresponds with expectations of bioclimatic envelope approaches frequently used to model species' response to climate change. In the case of temperature, however, the response pattern differed from such expectations, and instead revealed that populations are responding uniquely to temperature in a manner suggesting that they are locally adapted. In years in which temperatures are similar to long-term mean conditions at a site, λ values peak, whereas in years in which temperatures deviate from mean conditions, in either direction, λ values decline (Fig. 7A and B; reprinted from Souther and McGraw³⁹). This pattern is repeated across geographic space and among sites that differ substantially in relation to the abiotic and biotic environment. The population-level climatic niche, defined as the span of temperatures where $\lambda \geq 1$, is only about 2 °C (mean maximum growing season temperature) and is uniform across populations. This population-level climatic niche is much narrower than would be predicted by the range of temperature, approximately 10 °C, that ginseng occupies spatially.³⁹

In order to test for local adaptation to climatic factors, many researchers perform reciprocal transplants across latitudinal or elevation gradients. This

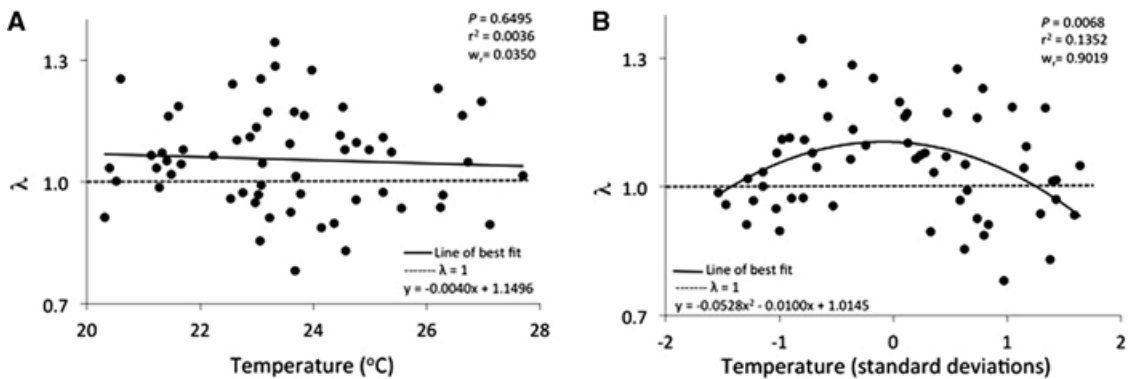


Figure 7. Response of the population growth rate (λ) to (A) mean maximum growing-season temperature and to (B) mean maximum growing-season temperature expressed in relation to deviation (SD) from site-specific means.

experimental design confounds the effects of temperature with other environmental factors that covary with temperature along such gradients. To explicitly examine genetic variation in physiological, phenological, growth, and reproductive response of ginseng to temperature, a controlled growth chamber experiment was performed.¹¹⁸ Two populations of ginseng from sites that differed in elevation were exposed to three temperature treatments. Two temperature treatments corresponded to mean conditions at each population's home site, while the third was incrementally warmer than the previous two treatments and represented temperature conditions by the end of the century corresponding to IPCC projections. Populations differed in response to temperature with regard to traits presumably related to fitness, including measures of reproduction and photosynthesis, suggesting genetically based differences in population response to temperature. However, the pattern of response was complex, and, in general, did not indicate local adaptation to temperature. Disparity between response patterns of ginseng in the field and in controlled conditions suggests that indirect temperature effects, mediated through biotic and abiotic covariates of temperature (e.g., pollinator abundance and behavior, pathogen effects, soil moisture, and light levels) may be more important determinants of ginseng demographic response than the direct effect of temperature alone.¹¹⁸ In general, elevated temperatures increased early senescence and respiration rates, and depressed growth, reproduction, and photosynthesis.

The sensitivity of ginseng to alterations in temperature regime prompted a formal analysis of ex-

tinguishing risk posed by climate warming.⁶¹ Up to 12 years of demographic data from 12 ginseng populations spanning a wide range of latitudes ($36^{\circ}54'\text{N}$ to $42^{\circ}38'\text{N}$) and longitudes ($-74^{\circ}05'\text{E}$ to $-84^{\circ}05'\text{E}$) were used to parameterize population projection matrices for a population viability analysis, which quantified extinction risk of ginseng populations under four climate scenarios. Warming of only 1°C over the next 70 years ($1.4^{\circ}\text{C}/100$ years), a rate derived from the A1B IPCC emissions scenario (now a low-end warming projection), significantly increased extinction risk relative to a no warming scenario. Because extinction risk varies as a function of population size, PVAs were conducted for 99 initial population sizes ranging from 20 to 1,000 individuals. The greatest disparity in extinction risk between the A1B and no warming scenario occurred in population sizes of 30–150 individuals, and peaked at a population size of 40 individuals. At this population size, extinction risk was nearly six times greater for the A1B scenario (70-year extinction risk = 81%) compared to a no warming scenario (70-year extinction risk = 13%) (Fig. 8).⁶¹ Notably, the majority of natural ginseng populations are small, typically consisting of less than 150 individuals, indicating that a significant proportion of ginseng populations are at risk of extirpation as a result of increasing temperatures.⁶¹

The fate of ginseng as climate change occurs will not be a simple function of demographic response, but will also depend on spatial and evolutionary responses.¹¹⁹ While long distance dispersal is possible for ginseng, dispersal distances are typically short. Ginseng pollen is estimated to travel less than 100 m from the adult plant, and a study that tracked

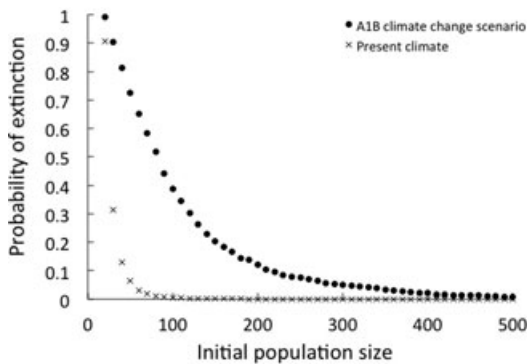


Figure 8. Probability of extinction as a function of the initial population size for two warming scenarios.

the secondary dispersal of 16,000 ginseng berries found that 90% of ginseng seeds remained within 2 m of the point of dispersal.^{42,120} Supporting experimental findings of pollen and seed dispersal, as discussed above, studies of neutral genetic variation have revealed high genetic differentiation among ginseng populations, with as much as 63% of total genetic diversity explained by among population allelic differences, indicating that gene flow among populations has historically been low.^{25,72} Additionally, fine-scale genetic structure exists over small spatial scales (< 2 m), signifying localized seed dispersal that results in juveniles clustering around parent plants.²⁵ Low dispersal potential in combination with habitat fragmentation and rapid warming rates suggests ginseng populations may be unable to spatially track the climatic conditions to which they are adapted.

Given the low colonization potential of ginseng, future persistence may depend on ginseng's ability to adapt *in situ* to changing climatic conditions. Ginseng individuals are long-lived, characterized by long generation times, low rates of reproduction, and low within-population genetic variation.^{7,10,29} As in the case of a spatial shift in response to climate change, such characteristics suggest that the potential for an adaptive response to projected rates of warming will be limited.¹²¹ No studies have assessed within-population genetic variation in response to climate warming, a necessary condition for microevolutionary change.

Several important sources of uncertainty remain in projections of the response of ginseng to warming. Environmental factors, like CO₂ levels and precipitation regime, will change concomitantly with

warming. Increasing carbon dioxide levels may partially ameliorate negative effects of warming on population growth.¹²² However, effects of long-term exposure to enhanced CO₂ levels indicate that there are trade-offs, e.g. reduced longevity, associated with enhanced growth due to CO₂ fertilization,¹²³ and that CO₂ enrichment may have unanticipated effects, such as increasing herbivore densities for particular species.¹²⁴ Such effects may partially explain variable, species-specific demographic response to increased CO₂, despite a generally consistent increase in biomass accumulation across species.^{125,126}

At this juncture, not enough is known regarding the long-term response of ginseng to CO₂ variation to incorporate CO₂ effects into projection models. As measured by precipitation, a previous demographic study demonstrated a range-wide parabolic relationship between ginseng population growth rate and total growing season rainfall. While mean changes in precipitation will most likely influence ginseng demography, uncertainty in climate model projections of mean precipitation change precludes satisfactory incorporation of this variable in models of ginseng demographic response to climate change.

In addition to mean change in temperature and precipitation, extreme weather events, such as heat waves, droughts, and storms are projected to occur with greater frequency in the future.¹¹² The effects of droughts and storm events on ginseng demography have yet to be quantified; however, with respect to heat waves, greenhouse and growth chamber experiments have shown that exposure to temperatures that exceed home-site conditions by 3–6 °C significantly decrease seed production and photosynthetic rates, and increase early senescence.^{46,118} Counter to intuition, climate change may increase the frequency of spring frosts. Disproportionate winter warming increases the length of the transition period between winter and spring, when temperatures may both stimulate emergence and cause frost damage, thus rendering populations susceptible to freezes for a greater part of the year. Also, greater climatic variability increases the probability that freezing temperatures will follow a growth-stimulating warm period.¹²⁷ In 2007, early winter warming stimulated precocious emergence from winter dormancy in natural ginseng populations, and this was followed by frost. Individuals damaged by frost displayed decreased seed production and a reduction in foliar growth rates—effects that

persisted in the year following the frost event.¹²⁷ Stochastic events, though infrequent, can have lasting and dramatic consequences for demography.¹²⁷ Changes in the frequency of such events may be as important a determinant of ginseng persistence as mean changes in temperature, precipitation, and CO₂ concentration.

Biotic factors, such as incidence of disease, herbivory rate, and competition regime, will be altered as the climate changes.¹²⁸ Some of these factors, disease in particular, likely covary with temperature, and thus are implicitly included in the projection of ginseng response to warming mentioned above. Despite this, biotic interactions influence abundance and distribution of species and will no doubt shape response to climate change.^{128,129} As global temperatures exceed historical climatic variation, biotic interactions—complex and thus difficult to predict—will affect the fate of species, like ginseng, in unanticipated ways. While such ecological surprises add uncertainty to projections of ginseng response, observational and experimental findings strongly suggest that increasing global temperatures will have a pervasive, negative impact on ginseng populations.^{39,46,118,127}

Landscape-level change

The deciduous forests of the eastern United States have been subjected to substantial changes in forest composition, forest cover, and land-use since European colonization began.^{130,131} As a species almost exclusively found in the understory of the eastern deciduous forest, *P. quinquefolius* L. has undoubtedly been influenced by these alterations. In the following sections, we briefly describe the nature of these changes and their potential impacts on understory plants, such as ginseng.

Presettlement landscape

Presettlement forests in the eastern United States spanned over 300 million hectares.¹³⁰ Community characteristics of mixed-mesophytic old growth forests included decomposing large logs, canopy gaps, multiple vegetation layers, a diverse herbaceous understory, and soil rich in organic matter.^{132–136} Although notable for the large size and great ages of the oldest trees, particularly in protected coves, many of these forests were not undisturbed. Native Americans managed some of the forest, often starting fires to clear land for agriculture

or to improve game habitat.¹³⁰ Hurricanes resulted in massive blowdowns, particularly along mountain ridges.¹³³

Agriculture

European settlement sharply altered the landscape of the eastern forest in new ways. As settlers moved from the Atlantic coast toward the Mississippi River between the years of 1620 and 1872, approximately half of the eastern deciduous forest was cleared.¹³⁷ Effects of forest clearing on the abiotic and biotic factors of a forest were long lasting,^{138–140} and recovery rate was variable.^{139–141}

Much of the eastern deciduous forest was converted to agricultural use,^{138,140} a trend that peaked in the mid 1800s.¹⁴² On steep terrain throughout Appalachia, marginal farmlands were abandoned more frequently than they were cleared in the 1900s, a pattern that continues today. From 1973 to 2000, in the eastern United States, there was a net gain in forest cover.¹⁴³

Despite the positive trend of forest cover increase in the past several decades, postagricultural recovery of native forest diversity has been slow.¹⁴⁴ As an obligate understory species with a short-lived seed bank, ginseng was vulnerable to extermination in areas where forest was converted to agricultural land. There are conflicting conclusions regarding the effects of prior agriculture land-use on current forests; most evidence, however, suggests that postagricultural secondary forests exhibit lower herbaceous understory biodiversity¹³⁹ and altered species composition.¹⁴⁵ Lower levels of diversity are the result of many factors, including colonization limitations^{144,145} and residual environmental effects.^{146–148} Given ginseng's large seeds, dominant mode of dispersal by gravity, and low seed numbers, propagule limitation could play an important role in limiting the rate of repopulation of postagricultural forests by ginseng.¹⁴⁹

Timbering

In the mid-1800s, large-scale logging operations developed east of the Mississippi River in order to meet demand for wood fuel and wood products.¹³⁰ From the mid-1800s to the early 1900s, there was an eight-fold increase in the rate of lumber production nationwide.¹³⁰ In addition to the disturbances caused by the removal of large amounts of timber, the slash left behind by timbering operations was often ignited by sparks emitted by steam-powered railcars

that carried timber to and from the sawmills.¹⁵⁰ By the 1920s, much of the merchantable timber in the eastern deciduous forest was gone and the number of active timbering operations began to decline.¹³¹

Second growth timber in the same forests that were exploited in the early 1900s have since reached merchantable size.¹⁵¹ Timber market models predict that timber harvests nationwide will increase by one-third between 1995 and 2040.¹⁵² The cyclical disturbance typical of timber rotations will likely alter, and possibly degrade, a wide range of ginseng habitats. As understory environments change, the future of ginseng in these forests is uncertain.

The extent of habitat change caused by timber harvest is not fixed; the changes that occur depend upon the type and the intensity of timber harvest.¹⁵³ Following timbering, changes in understory microclimates occur. Light levels, mean temperature, and temperature fluctuations near the herbaceous layer increase, while humidity and soil moisture decline.^{153–155} A decrease in total canopy cover resulting from timber harvest alters the interaction between the understory and higher strata and alters competition within the herbaceous layer.¹⁵³ Moreover, the susceptibility of the forest area to invasion by nonnative species increases following a timbering event.^{156,157}

A consensus regarding the response of the herbaceous understory to a wide range of timber harvest disturbance gradients has not been reached.^{1,158,159} In addition, the response of ginseng populations to the environmental changes caused by timbering has not been investigated, but will likely depend on the disturbance intensity of each separate timbering event. Anecdotal information suggests that ginseng may be preadapted to sporadic, intermediate intensity canopy-opening events that are common in mature forests. For example, enhanced growth of ginseng plants has been observed one and two years following a single tree-fall event. Conversely, in areas where large amounts of the canopy were damaged in an ice storm, ginseng plants became yellow and dried before the end of the growing season. Interestingly, ginseng harvesters have reported the emergence of large ginseng plants in the early years following clear cutting; however, no populations have been followed through and beyond a timbering event to determine the net long-term effect.¹²

Wild ginseng populations are not confined to the small percentage of undisturbed old growth forest remaining in the United States; therefore, populations must have persisted following the extensive timbering that took place in the late 1800s and early 1900s. As an ongoing source of cyclical disturbance to the understory, the extent to which different timber harvest practices affect the population dynamics of ginseng must be quantified in order to place this widespread source of disturbance into broad perspective.

Surface mining

The natural range of ginseng overlaps that of the rich coal deposits found in the Anthracite, Appalachian, Eastern Interior, and Western Interior coal regions of the United States.^{19,160} Coal mining became a boom industry at the beginning of the twentieth century.¹⁶¹ As a result of improved technology, ease of extraction, and increased demand for coal, surface mining gained in popularity and scale in the 1950s.¹⁶² The controversial method of surface mining known as mountain top removal (MTR) mining has been used since the 1970s,¹⁶³ and expanded in the 1990s¹⁶⁴ due to the demand for low-sulfur bituminous coal in eastern Kentucky and southern West Virginia.^{164,165}

Before 1977, surface-mined areas were left unreclaimed about 40% of the time.¹⁶⁶ In 1977, the U.S. Government adopted the Surface Mining Control and Reclamation Act (SMCRA) in an effort to ameliorate the environmental damage imposed by mining. SMCRA requires that mined lands be reclaimed to the approximate original contour; the process and type of reclamation, however, is determined by the mine operator.¹⁶⁷ Often the postmining landscape is planted with grasses¹⁶⁸ because this type of reclamation is typically cheaper and faster.¹⁶⁹

Most coal extraction in the eastern United States now occurs *via* surface mining rather than underground mining.¹⁷⁰ In six of the northern and central Appalachian states, about 1.1 million hectares of forest have been directly affected by surface mining.¹⁷¹ According to estimates by the E.P.A., 330,225 hectares of forest in southern Appalachia were destroyed by MTR mining between 1992 and 2012.¹⁷² There are also indirect effects from surface mining, such as changes in soil chemistry,¹⁷¹ soil fertility,¹⁷³ water quality,¹⁷⁴ nutrient cycling,¹⁷⁵ and increased flooding.^{176,177} Surface mining increases

habitat fragmentation¹⁷⁸ and reduces the amount of interior forest in adjacent communities.¹⁷² While succession on previously un-reclaimed surface mines shows tree recruitment,¹⁷⁹ the native herbaceous understory is often absent or sparse.¹³⁹ Current trends in reclamation include restoring the surface-mined land using the Forestry Reclamation Approach (FRA). The FRA's primary goal is to increase timber production on previously surfaced-mined lands, with the belief that natural succession will generate a suitable habitat for herbaceous species over time.¹⁶⁸ FRA is a recent development, and it is early to judge whether overall forest diversity restoration is accelerated by this approach.

The direct and indirect loss of the eastern deciduous forest habitat caused by surface mining has no doubt extirpated thousands of ginseng populations. Based on extensive quadrat censusing, an estimate was made by McGraw *et al.*²¹ that there is a ginseng density of 18.26 plants per hectare in deciduous forests of the region, including areas near surface mining. Assuming this density is a realistic estimate, in the past 20 years about six million ginseng plants have been lost due to MTR mining alone. The ability of ginseng to grow on old unreclaimed sites and mined lands that have been reclaimed to a forest is not known. As with postagricultural lands, restoration of ginseng to these sites would likely require assisted relocation, or it would require decades if not centuries to occur naturally.

Acid deposition

The effects of acid deposition on terrestrial and aquatic ecosystems have become global concerns over the past several decades.^{180–182} Sulfur dioxide and nitrogen oxides are commonly released into the atmosphere as a result of automobile exhaust and industrial plants, among other sources, falling as acid precipitation on vast areas of forests downwind.^{180,183,184} Acid precipitation alters soil properties, and particularly affects the cation balance in the soil, resulting in depletion of calcium and other important cations.^{180,184} Reduced available calcium and lowered pH in forest soils inhibits growth in many plant species.^{184–187} Research suggests that ginseng populations located in soils rich in calcium typically grow larger and are less susceptible to disease than ginseng grown in less calcium-rich soils.^{188,189} In fact, in southern Appalachia,

ginseng grown on calcium-poor sites actually displayed stunted growth.^{188,189}

No studies have directly tested the effect of acid precipitation on natural populations of ginseng; however, much work has focused on effects on tree species. The high-elevation mountains of the eastern United States are of particular interest in the study of acid precipitation, as the thin soils are subjected to high amounts of acid precipitation in the form of fog as well as rain and snow. A decline in the growth of tree species such as *Picea rubens* and *A. saccharum* has been detected in many high elevation study sites in the northeast United States.^{184–187} Far less research has been performed to address the response of the herbaceous understory to acid precipitation. However, Lodhi¹⁹⁰ found that experimental acid rain applications caused a significant reduction in the biomass of multiple herbaceous species found in Missouri.

Suburban sprawl

The rate of suburbanization has increased substantially in the eastern United States since 1973. Over a 27-year period, 1.9 million hectares have been converted from forest to suburban landscapes.¹⁴³ Theobald¹⁹¹ predicted that by 2020, urban and suburban development will increase across the United States by 2.2% and 14.3% respectively. As urban and suburban areas spread, forest land area is both lost and fragmented.¹⁹² Habitat fragmentation results in decreased species richness and abundance.¹⁹³ Furthermore, fragmentation reduces pollinator abundance and diversity, which may lead to reduced seed set among the plants in the fragmented populations.¹⁹⁴ The division of populations into smaller subunits also increases the susceptibility of ginseng to population-level extinction caused by demographic and environmental stochasticity.¹⁹⁵ Increase in the frequency of edge environments with fragmentation can, in turn, affect the viability of forest interior species¹⁹⁶ such as ginseng.

Synthesis

Figure 1 of this review represented a simple starting point for studying factors affecting herbaceous plants in the eastern deciduous forest, using ginseng as a phytometer. By emphasizing individual plant responses to environmental factors, then linking them to demographic effects, the body of research

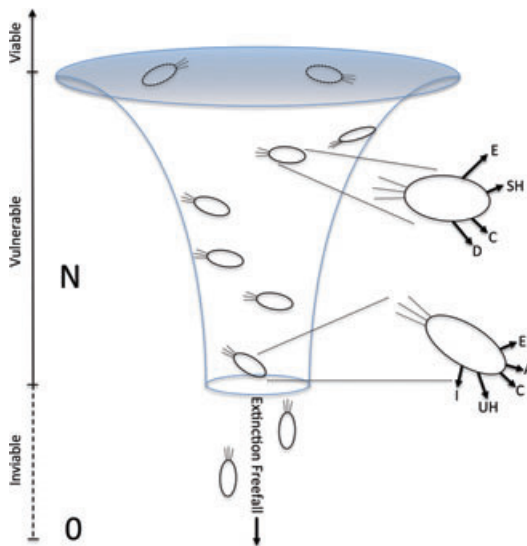


Figure 9. Representation of the extinction vortex¹⁹⁸ containing ginseng populations subject to negative and positive forces acting differentially in each population. Vectors of change: E = exponential growth, SH = stewardship harvest, C = climate warming, D = deer browse, A = acidification, UH = unsustainable harvest, I = inbreeding. N is the population size.

to date suggests a more nuanced understanding of the present status of ginseng populations (Fig. 9).

Thousands of small natural populations of ginseng exist in habitats experiencing a unique set of negative and positive forces, resulting in population decline (down the vortex), stability, or increase (up the vortex). Different forces will act with changing probabilities as a function of position within the vortex. The reviewed studies show three dominant forces acting at all population sizes; harvest, deer browse, and climate change. All three appear to be exerting downward pressure regardless of population size. Toward the bottom of the vortex, at the lowest N 's, additional factors such as the Allee effect and inbreeding depression are expected to be more significant, accelerating decline. The proportions of populations experiencing each trajectory are unknown. The precise boundaries between inviable and vulnerable populations and between vulnerable and viable populations are not known. The categories represent a theoretical construct, and vulnerability to extinction is a continuous probability function of population size, but we do not yet have a thorough understanding of this function.

What stands out as we survey vectors affecting ginseng population fates is the pervasiveness of

direct and indirect human actions. Massive landscape level changes (agriculture, timbering) since European settlement had direct negative effects on forest herb communities. Layered on top of this in the case of ginseng, the long history of harvest was responsible for reducing population sizes to the point where most are now small, and likely fall into the “vulnerable” or “inviable” class. Species with life histories such as ginseng may recover from such effects, albeit slowly. More subtle but widespread environmental changes such as acid precipitation or ozone pollution effects are also, obviously, caused by humans, though their effects on ginseng are unknown. More recent human effects, such as surface mining and suburban sprawl, eliminate habitat, shrinking the funnel and reducing the total number of populations substantially. These latter changes are directional, ongoing, and likely permanent.

Two of the indirect effects of human actions appear overwhelmingly important to the future of species such as ginseng. Deer overpopulation and consequent overbrowsing is an indirect effect of mismanagement of the ecosystem, in turn caused by very effective management of the deer herd for the hunting constituency.⁹⁴ Climate change is an indirect effect of human reliance on fossil fuel burning and, thus far, a lack of political will to solve the problem.¹⁹⁹ Large uncertainties exist for both factors. Overbrowsing by deer will invariably have negative effects on ginseng populations as long as deer populations are high; however, the future of high deer populations is not guaranteed: ecological surprises, such as uncontrolled disease outbreaks could reduce the herd. Alternatively, society may reach a tipping point in public opinion, and the desire for deer herd control could outweigh the political sway currently held by hunters, prompting changes in the way deer are managed.

While there is uncertainty about whether the political will can be summoned to address climate change, the scientific consensus is that, even if this occurs, major climate shifts are already happening and will continue. More uncertainty surrounds the complex biotic response to climate change, and the consequences of those responses for whether a particular native species will persist or go extinct in a changing world.¹²⁸ For ginseng, the response of fungal diseases or insect herbivores to a warmer, possibly wetter, climate may be more important than direct effects on growth. While invasive plant species

are not presently having large, pervasive effects on ginseng, this could change rapidly as native plants decline in forest interiors and niche space is opened for effective colonizers. These ecological surprises may trigger future changes in prevalent vectors acting on each population in ways we cannot at present predict.

If species such as ginseng are to persist, powerful natural forces may play roles. Every species has the potential to grow exponentially, even those with slow life histories such as ginseng. The fact that ginseng exists at historically low population sizes suggests that it may be far below its carrying capacity, and therefore released to a degree from density-dependent population regulation. In addition, we have very little understanding of ginseng metapopulation dynamics: in particular, how frequently can long-distance dispersal occur and how often are new populations successfully founded? We know natural selection may bring about fundamental changes in the ability of populations to resist negative factors such as deer browse and climate change, and to take advantage of opportunities such as invading post-agricultural forests. Research is urgently needed to understand whether sufficient additive genetic variation exists within populations to allow adaptation to play a significant role in persistence through environmental change.

Owing to the pace and intensity of environmental change brought about by direct and indirect effects of human actions, natural processes may be inadequate to prevent a rapid flushing of populations down the extinction vortex. In this case, for the species to survive, human intervention may be required. Such intervention can take many forms, and successful intervention will require more fundamental scientific understanding. For example, explicit efforts can be made to reintroduce or restore ginseng populations to formerly occupied habitats. The best strategies for accomplishing this, however, have not been determined and will rely on improved predictive understanding of soil requirements as well as the importance of the genetic background of seed sources.

As climate change continues, managed relocation of populations may be necessary to match ecotypes with their climatic requirements. This will be challenging without a better understanding of the indirect effects of climatic adaptation, and the ways in which populations are adapted to local sites inde-

pendent of climate. Questions concerning the scale of relocations necessary for success, and the consequences of the introduction of new genotypes for extant populations, need to be addressed.

While perhaps unique to wild harvested species, the opportunity for altering population fates by improving management strategies exists, given our current understanding. Current ginseng harvest practices range from unsustainable, which can cause rapid population decline, to stewardship, which may grow populations. Unethical behavior by harvesters is partly to blame for the former; clearly law enforcement is presently inadequate to stem such behavior. An obvious solution is to house ginseng management programs within state agencies, such as Wildlife Departments, that have natural resource law enforcement as part of their mission.⁶³ In addition, harvest regulations have been slow to change in response to better ecological understanding: while harvest seasons have evolved, minimum age requirements are still national policy even though size is clearly a far better predictor of reproductive success than age. Given that harvesters can be stewards if they plant adequate numbers of mature seeds, encouraging this behavior with size-minimums and optimized harvest seasons can change harvest from a downward vector to a neutral or upward vector for population change. Replacing the age requirement would also allow planting of detached rhizomes as a means of clonally propagating the harvested individual and further mitigating harvest effects (presently, intact rhizomes are required to prove that the age-requirement is met).

If both natural and human-initiated processes do not reverse the loss of populations from the extinction vortex, increased rarity will have one further consequence as long as the wild ginseng market persists: prices for roots would rise rapidly. This would trigger further unethical harvest, followed by harvest ban, and the inevitable black market for wild ginseng roots. At that point, conservation of the species would become increasingly difficult, with challenges similar to those being carried out on behalf of the tiger, rhinoceros or elephant. The difference in the case of tigers, rhinoceroses, or elephants is that they are large, charismatic mammals that have developed a constituency all their own. For a modest herbaceous plant such as American ginseng, a more likely fate would be that experienced by its

sister species, *P. ginseng*, on the Asian continent, long ago. The species would persist in cultivation, but it would continue its evolution in that environment into a different organism, eventually losing traits that would allow persistence in the wild. The species, *P. quinquefolius*, as we know it, would be extinct.

Although the scenarios depicted by our current understanding of ginseng ecology and the effects of environmental change are discouraging, the scientific research accomplished so far has been valuable in clarifying areas of real concern (unsustainable harvest practices, overbrowsing by deer, and climate change) and pointing to possible solutions (improved management policies, rebalancing the community structure, and managed relocation). As a plant species with medicinal value in Asian culture, economic and cultural value in Appalachia, value as part of a functional, diverse forest understory, and potential value for western medicine, ginseng's worth as a target for conservation is evident. To the extent that ginseng is a phytometer for general effects on herbaceous plants, population studies of ginseng illustrate the magnitude of the diverse challenges faced by plants in a changing world.

Conflicts of interest

The authors declare no conflicts of interest.

Supporting Information

Additional Supporting Information may be found in the online version of this paper.

Fig. S1. Artist's rendering of a small cluster of American ginseng plants in autumn in a natural understory setting. Watercolor by Susan Bull Riley.

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