

Interactive Effects of Harvest and Deer Herbivory on the Population Dynamics of American Ginseng

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Abstract: *Few demographic models for any species consider the role of multiple, interacting ecological threats. Many forest herbs are heavily browsed by white-tailed deer (*Odocoileus virginianus*) and a number of these are also harvested for the medicinal, floral, or horticultural trades. Previous studies of the viability of American ginseng (*Panax quinquefolius*) have separately examined the effects of harvesting and deer herbivory. We followed individually marked ginseng plants in 6 populations for 8 years and documented deer browse levels, conducted helicopter surveys to estimate the deer herd size, and documented 2 ginseng harvests. We used this long-term data set to develop a stochastic demographic model that quantified the separate and interactive role of these threats to ginseng viability. Although harvesting and deer herbivory negatively affected ginseng population growth, their effects were not additive. Deer herbivory negatively affected population growth in the absence but not in the presence of harvesting. Life table response experiments revealed that in the presence of harvesting, deer herbivory had some positive effects on vital rates because browsed plants were less apparent to harvesters. Ginseng populations that were harvested responsibly (i.e., planting seeds from harvested individuals) had higher growth rates than those that were harvested irresponsibly. We concluded that both deer populations and harvesting must be managed to ensure sustainable populations of American ginseng. Our findings underscore the importance of long-term monitoring to assess threats to viability and the need for a broad ecological understanding of the complexity of ecosystem management.*

Keywords: American ginseng, ginseng harvest, herbivory, life table response experiment, matrix model, *Odocoileus virginianus*, *Panax quinquefolius*, white-tailed deer

Efectos Interactivos de la Cosecha y la Herbivoría de Venados sobre la Dinámica Poblacional del Ginseng Americano

Resumen: *Pocos modelos demográficos para cualquier especie consideran el papel de múltiples amenazas ecológicas interactuantes. Muchas hierbas de bosque son forrajeadas intensamente por venados cola blanca (*Odocoileus virginianus*) y algunas también son cosechadas para el mercado medicinal, floral u hortícola. Estudios previos de la viabilidad del ginseng americano (*Panax quinquefolius*) han examinado separadamente los efectos de la cosecha y de la herbivoría de venados. Monitoreamos plantas de ginseng marcadas en seis poblaciones durante ocho años y documentamos el nivel de forrajeo, realizamos muestreos en helicóptero para estimar el tamaño de la manada de venados y documentamos dos cosechas de ginseng. Utilizamos estos datos de largo plazo para desarrollar un modelo demográfico estocástico que cuantificó el papel separado e interactivo de estas amenazas a la viabilidad del ginseng. Aunque la cosecha y la herbivoría de venados afectaron negativamente al crecimiento de la población de ginseng, sus efectos no fueron aditivos. La herbivoría afectó negativamente al crecimiento poblacional en ausencia pero no en presencia de cosecha. Los experimentos de respuesta de tabla de vida revelaron que, en presencia de cosecha, la herbivoría de venados*

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tenta algunos efectos positivos sobre tasas vitales porque las plantas forrajeadas fueron menos aparentes para los cosecheros. Las poblaciones de ginseng que fueron cosechadas responsablemente (i. e., sembrando semillas de individuos cosechados) tuvieron tasas de crecimiento más altas que las que fueron cosechadas irresponsablemente. Concluimos que se debe manejar tanto a las poblaciones de venados como la cosecha para asegurar poblaciones sustentables de ginseng americano. Nuestros resultados acentúan la importancia del monitoreo a largo plazo para evaluar las amenazas a la viabilidad y de la necesidad de un mayor entendimiento ecológico de la complejidad del manejo de ecosistemas.

Palabras Clave: cosecha de ginseng, experimento de respuesta de tabla de vida, ginseng americano, herbivoría, modelo matricial, *Odocoileus virginianus*, *Panax quinquefolius*, venado cola blanca

Introduction

Multiple factors affect the persistence of plant populations, and these factors may have interactive effects on population dynamics. Although habitat destruction and invasion of alien species are primary threats to imperiled plant species (Wilcove et al. 1998), many forest herbaceous species experience heavy browsing by white-tailed deer (*Odocoileus virginianus*) and harvest for the medicinal, floral, or horticultural trade (e.g., trillium [*Trillium* spp.], goldenseal [*Hydrastis canadensis*], ramps [*Allium tricoccum*], galax [*Galax urceolata*], and several orchid species [reviewed in Whigham 2004]). The effect of such factors on population viability can be examined by collecting demographic data, explicitly considering how the factor affects demographic vital rates, and incorporating both into a population-projection model. Few forest herbs have been studied in detail, however, and few demographic models consider the role of multiple interacting ecological threats (but see Knight 2004).

The effects of deer browse and harvesting by humans have been examined separately for American ginseng (*Panax quinquefolius*), and each poses a significant threat to persistence (e.g., Nantel et al. 1996; McGraw & Furedi 2005; Van der Voort & McGraw 2006). We examined the combined effect of browse and harvest. Because deer browse does not typically kill a ginseng plant, but often makes it less apparent to harvesters, we hypothesized that when harvesting pressure is high, low levels of deer herbivory may actually benefit ginseng populations.

American ginseng is a long-lived perennial herb of deciduous hardwood forests, and it is found in cool microclimates characterized by rich but well-drained soils. Ranked locally as vulnerable or imperiled in at least half of its range, its global ranking is vulnerable (NatureServe 2007). Considered a rare plant by many, it is probably best characterized as “widespread but scarce everywhere that it is found” (McGraw et al. 2003).

American ginseng is a highly valuable and heavily harvested forest crop. Roots have been harvested in North America for export to Asia since 1720 (Carlson 1986). The entire root is removed when American ginseng is

harvested because market preference is for intact roots. In the United States an average of over 43,200 kg (dry weight) of roots (45–135 roots/kg) is harvested each year (USFWS 2005). Although cultivation of ginseng was mastered during the 1880s, wild roots are purported to be more potent and are favored by Asian buyers (Hankins 2000).

Demographic matrix models of ginseng in Québec reveal that even low levels of harvesting (e.g., harvesting 30% of large-stage plants every 5 years) are not sustainable (Charron & Gagnon 1991; Nantel et al. 1996). Demographic data from West Virginia show that ginseng population dynamics are significantly influenced by the behavior of the harvester (Van der Voort & McGraw 2006). Negative effects on the population growth rate are reduced by harvesting later in the season, limiting the harvest, and planting seeds from harvested plants. In addition to affecting population growth rates, harvesting may decrease the genetic diversity of populations (Cruse-Sanders et al. 2005), promote smaller phenotypes (McGraw 2001), and negatively affect fitness (Mooney & McGraw 2007).

White-tailed deer densities have increased dramatically throughout the eastern and Midwestern United States over the past 60 years (Alverson et al. 1988; Waller & Alverson 1997; Côté et al. 2004). Numerous researchers have examined the negative ecological effects of high deer densities (reviewed in Côté et al. 2004), and an increasing number are focusing on herbaceous plants (reviewed by Russell et al. 2001). Demographic matrix models are used to link heavy deer browse with reduction in the population growth rate of perennial herbs (Rooney & Gross 2003; Knight 2004). Deer browse determines whether ginseng populations grow or decline toward extinction in West Virginia (McGraw & Furedi 2005).

We considered the simultaneous effects of human harvesting and deer browse on ginseng population dynamics. Previous ginseng studies have excluded seedlings and/or dormant plants from their models. We monitored ginseng populations for 8 years and were therefore able to obtain adequate sample sizes for rare stage classes, which allowed us to create a more complete and biologically realistic demographic model.

Methods

Study Species

American ginseng is a geophytic herbaceous perennial, capable of living at least 60 years (Charron & Gagnon 1991). Ginseng emerges in mid spring (mid to late April in Missouri) during canopy leaf out. It is not clonal; each genet produces a determinate aerial stem (rarely twin stems) with a whorl of 1–4 (rarely more) palmately compound leaves composed of 3–5 leaflets (Carpenter & Cottam 1982). Determinate growth prevents any further production of leaves after the initial unfurling in spring. The stem terminates in a simple umbel of greenish-white flowers. The peduncle is present when the stem and leaves unfurl. A cluster of berries forms by mid to late summer, and each berry contains 1–3 seeds.

Ginseng seeds exhibit deep simple morphophysiological dormancy (Baskin & Baskin 1998), typically germinating 18–20 months after the berry develops. Although seeds may remain viable in the soil longer than 18–20 months (Van der Voort 2005), germination is reduced to 2.4% by 44 months. In a study of a ginseng population decimated by poachers, Lewis (1988) suggests that the seed bank appears to play itself out within 5 years.

Seedlings have 1 leaf, usually composed of 3 leaflets. As plants age, they gradually add more leaflets and leaves. Plants generally do not produce seeds until they have at least 2 leaves. Size of plants provides a good measure of vigor: plants with more leaves generally produce more seeds (Charron & Gagnon 1991). Growth is not linear: a 3-leaf plant can regress to a 2-leaf or even a 1-leaf plant in the following year. Development can also skip a stage. Ginseng may exhibit prolonged dormancy, remaining dormant during the growing season for 1–3 years (Farrington 2006). Prolonged dormancy of longer than one growing season is rare.

Study Site

The 6 populations of ginseng we monitored are within a 28-km² area in the Ozark Highlands of east central Missouri. The area features steep slopes in the Eminence dolomite formation with soils of deep, cherty silt loams. Elevation of the sites ranged from 162 to 204 m, and local relief ranged between 45 and 75 m. Aspect was northeast to northwest for 2 populations, east for 2 populations, and southwest to west for 2 populations. The forest was second-growth oak forest of white oak (*Quercus alba*), red oak (*Q. rubra*), shagbark hickory (*Carya ovata*), and sugar maple (*Acer saccharum*).

Census and Monitoring

Six populations of ginseng were monitored from 1998 through 2005. Within each population, we marked colonies of plants with a buried steel spike nail and

recorded the distance and azimuth to a recognizable landmark. Photographs were taken of each colony and its associated landmarks. We identified individual plants with engraved 7-cm aluminum roofing nails pressed into the ground beside the rhizome and recorded the distance and azimuth from either the colony spike nail or from the engraved aluminum nail of another plant in the colony. We pushed the larger spike nails and the smaller aluminum nails into the ground so that the heads were slightly below ground level and placed soil and leaves on top of the nails to obscure them. This precaution was necessary to prevent notice of the plants by poachers and to ensure that the nails were not easily displaced. To relocate nails, we used photographs, measurement from landmarks, and coarse-resolution and pinpoint metal detectors. These methods allowed us to relocate virtually all nails, even those pushed deeply into the ground by deer hooves.

We monitored plants at least 3 times each year: late April, early June, and late July. In the first census, most plants had emerged, and very little deer herbivory had occurred. The few plants that were completely browsed prior to the April census (<1%) were assigned their stage from the previous year. Stems had fully elongated by the second census, and berries were fully formed by the third census. Data recorded included stage, height, number of leaves and leaflets, number of pedicels, damage to leaflets, severity of damage per leaflet (slight, <10%; moderate, 10–49%; extreme, 50–99%; total, 100%), and the cause of damage. We visually examined all berries during the last census to determine the number of seeds. When berries had already fallen from a plant prior to the late July census, the number of red pedicels was counted and an average number of seeds per berry was assigned to each fallen berry.

Each population was examined closely for seedlings. Seedlings are distinguished from older 1-leaf plants by the presence or absence of a small crook in the stem found in plants that are not seedlings. The crook indicates the attachment of the petiole (seedling leaves are attached at the root collar).

Plants that did not present aboveground stems were carefully examined to determine if a viable root and bud existed. The root is usually at or just below the surface of the soil, allowing examination with minimal disturbance. Plants that appeared to have viable roots were declared dormant for that growing season and were examined in subsequent years. If plants did not reemerge, we reclassified them as dead from the time they were originally listed as dormant.

Deer Count

We censused deer in the 28-km² study area in January of 1999, 2001, and 2003. We flew low in a helicopter when a minimum of 10 cm of snow was on the ground

(to provide good visibility of the deer). Such flights over known herds in fenced areas of east-central Missouri miss 22% of a deer herd (Beringer et al. 1998). Therefore, we divided the number of deer we counted by 0.78 to obtain a more accurate estimate of the deer herd.

Demographic Matrix Model Construction

Our demographic matrix model considered annual transition probabilities and fecundity of plants in 7 stage classes: seeds, seedlings, 1-leaf plants, 2-leaf plants, 3-leaf plants, 4-leaf plants, and dormant plants. We determined stage-specific fecundity for each year by averaging the numbers of seeds produced by the individuals in each stage class. Seed to seedling transition rates were calculated as the percentage of seedlings that resulted from seeds produced 2 years earlier (assuming seeds require 18–20 months dormancy). In this calculation we assumed the survival of the seed during the year between dispersal and germination was 100%, a simplification that may overestimate seed survival and underestimate germination rate, but which should nonetheless provide an accurate measure of the proportion of seeds that transition to seedlings. Our model does not take into consideration the role of a seed bank. Nevertheless, we expected our model projections would be similar to those projected from a model that incorporated a seed-bank stage class because the seed bank for this species is short-lived, and our long-term study ensured that all seedlings were included in the model even if they were assigned to a younger cohort.

We combined the 6 populations to create one matrix for each transition period: 1999–2000 ($n = 294$), 2000–2001 ($n = 458$), 2001–2002 ($n = 487$), 2002–2003 ($n = 516$), 2003–2004 ($n = 567$), and 2004–2005 ($n = 596$). Pooling of the populations was necessary to obtain sufficient sample size for development of well-parameterized matrices.

Although individual marking of plants began in 1998, the first transition matrix began in 1999 to allow accurate derivation of the seed-to-seedling ratio (seeds from 1998 produced the seedlings of 2000). The increase in numbers of plants monitored in 2000–2001 reflected an expansion of the study to incorporate adjacent colonies within the populations. Throughout the study, we discovered new plants occasionally and added them to the inventory. If new mature plants were discovered, seedlings encountered nearby were not included in the seed-to-seedling transition rates because the number of seeds that created the seedlings could not be determined. During the final year of monitoring, we used an average of the prolonged dormancy rates from the previous 5 transition matrices to estimate dormancy rates. Plants listed as dormant during both of the final 2 growing seasons were assumed dead because prolonged dormancy for 2 consecutive seasons was rare during the previous 7 years of observation.

Ambient, No-Browse and Harvest Matrices

The 6 matrices represented the ambient population experiencing natural levels of deer herbivory. To quantify how removal of herbivory would alter population dynamics, data from plants that were not browsed during the first year of each transition were grouped together to create 6 no-browse matrices (see also Knight 2004). This simulates the removal of the direct effects of browsing, but does not take into account indirect effects such as deer trampling. We used each set of matrices to calculate separate estimates of the stochastic population growth rate (see later). We used the average (across all years) “ambient” and no-browse matrices to conduct life table response experiments (see later).

We simulated the effects of annual harvest of ginseng roots based on 2 harvesting behaviors (responsible and irresponsible) and under 2 herbivory regimes (ambient and no browse) (Tables 1 & 2). We assumed responsible harvesters sowed seed from harvested plants at a depth of 2 cm (in accordance with the regulations of many states) and that irresponsible harvesters removed the seeds from harvested plants (either to sell the seeds or to sow the seeds elsewhere). Our harvest models therefore incorporated 8 stages, adding a category for planted seeds (Tables 1 & 2). We assumed both responsible and irresponsible harvesters removed the same number of plants, removed only 3- and 4-leaf plants (most state regulations restrict harvest of smaller plants), and began harvesting at the start of the Missouri harvest season (1 September). Ginseng berries ripen earlier in the Missouri Ozarks than other parts of the country (McGraw et al. 2005), so we assumed berries were ripe or had already fallen when harvest began.

Although harvest was prohibited at our study site, we observed harvest activity in 2 adjacent colonies in 1998 and 2004. Harvested plants were excluded from the ambient and no-browse matrices so that mortality due to harvest would not confound the effects of deer herbivory. When the harvests took place, many of the 3- and 4-leaf plants were obscured from the harvesters because they had already been completely browsed in that season. All of the unbrowsed plants in these stage classes were found and harvested by the illegal harvesters. Thus, our model assumes that 100% of the unbrowsed 3- and 4-leaf plants were harvested each year. The surviving plants in these stage classes have no fecundity because complete browsing prevents any fruit production. The stage transition of these browsed and unharvested 3- and 4-leaf plants are based on data pooled for browsed plants in these stage classes across all years (pooling data was necessary to achieve an appropriate sample size).

We calculated the natural seed to seedling transition on the basis of ambient seed-to-seedling rate estimated for each year (average across years = 0.091) for the berries that are likely to have dropped before harvest

Table 1. Matrix calculations for the harvested populations of ginseng in the presence of ambient levels of deer browse (values are averages across years).

Time t+1	Time t							
	seed (natural) ^a	seed (planted) ^b	seedling	1 leaf	2 leaves	3 leaves ^c	4 leaves ^c	dormant
Seed (natural)	0	0	0	0	0.5033	$(1-b_3) * f_3 * n$	$(1-b_4) * f_4 * n$	0
Seed (planted)	0	0	0	0	0	$(1-b_3) * f_3 * s$	$(1-b_4) * f_4 * s$	0
Seedling	0.091	0.745	0	0	0	0	0	0
1 leaf	0	0	0.8031	0.5708	0.0580	$b_3 * p_i$	0	0.2458
2 leaves	0	0	0.0049	0.2813	0.6081	$b_3 * p_r$	0	0.4667
3 leaves	0	0	0	0.0014	0.2520	$b_3 * p_s$	$b_4 * t_r$	0.1632
4 leaves	0	0	0	0	0	$b_3 * p_a$	$b_4 * t_s$	0
Dormant	0	0	0.0175	0.0175	0.0376	$b_3 * p_d$	$b_4 * t_d$	0.1243

^aSeeds fallen on the ground prior to harvest.

^bSeeds planted by harvester.

^cStage transitions are for plants that are browsed. Unbrowsed plants are harvested (killed). Plants in these stage classes produce seed prior to harvest. Key: b_3 , proportion of 3-leaf plants browsed = 0.241 (thus, $1-b_3$ is the proportion unbrowsed); f_3 , fecundity of unbrowsed 3-leaf plants = 3.7474 (browsed plants have no fecundity); n , proportion of seeds on harvested 3- or 4-leaf plants that fall to the ground prior to harvest = 0.38; s , proportion of seeds on harvested 3- or 4-leaf plants planted by harvester = 0.62 or 0 (responsible or not); p_i , proportion of browsed 3-leaf plants that regress to the 1-leaf stage class = 0.002; p_r , proportion of browsed 3-leaf plants that regress to the 2-leaf stage class = 0.198; p_s , proportion of browsed 3-leaf plants that stay in the 3-leaf stage class = 0.684; p_a , proportion of browsed 3-leaf plants that advance to the 4-leaf stage class = 0.038; p_d , proportion of browsed 3-leaf plants that enter the dormant stage class = 0.028; b_4 , proportion of 4-leaf plants browsed = 0.317 (thus, $1-b_4$ is the proportion not browsed); f_4 , fecundity of unbrowsed 4-leaf plants = 12.175 (browsed plants have no fecundity); t_r , proportion of browsed 4-leaf plants that regress to the 3-leaf stage class = 0.529; t_s , proportion of browsed 4-leaf plants that stay in the 4-leaf stage class = 0.471; t_d , proportion of browsed 4-leaf plants that enter the dormant stage class = 0.033.

begins (38%). Planted seeds had an increased seed-to-seedling rate (0.745) for the berries remaining on the plants (62%) when the responsible harvester artificially sowed the berries at a depth of 2 cm. We based the increased seed-to-seedling rate on a field study conducted by McGraw (unpublished data) that showed that the seed-to-seedling rate for fresh berries sown at 2 cm is 74.5%, whereas the rate for berries sown at 0 cm (mimicking the natural process) is 10.0%. In a similar field experiment, Farrington (2006) found a seed-to-seedling rate of 82.0% for stratified seed sown at 2 cm (seeds sown at 4 locations at 7 depths in a randomized Latin square formation

to equalize the effect of microenvironmental gradients). Irresponsible harvesters removed the seeds remaining on the plants (62%), reducing the fecundity for planted seeds to zero.

Stochastic Population Growth Rate

We calculated the stochastic population growth rate (λ_s) by simulation. We assumed that the 7 years of our study represented the range of typical conditions, each of which was equally likely to occur in the future. (Annual precipitation at our study site during the 7 years

Table 2. Matrix calculations for the harvested populations of ginseng in the absence of deer browse (values are averages across years).

Time t+1	Time t							
	seed (natural) ^a	seed (planted) ^b	seedling	1 leaf	2 leaves	3 leaves ^c	4 leaves ^c	dormant
Seed (natural)	0	0	0	0	0.5652	$f_3 * n$	$f_4 * n$	0
Seed (planted)	0	0	0	0	0	$f_3 * s$	$f_4 * s$	0
seedling	0.091	0.745	0	0	0	0	0	0
1 leaf	0	0	0.8026	0.5723	0.0586	0	0	0.2458
2 leaves	0	0	0.0056	0.2897	0.6014	0	0	0.4667
3 leaves	0	0	0	0.0017	0.2546	0	0	0.1632
4 leaves	0	0	0	0	0	0	0	0
Dormant	0	0	0.0152	0.0186	0.0400	0	0	0.1243

^aSeeds fallen on the ground prior to harvest.

^bSeeds planted by harvester.

^cStage transitions for 3- and 4-leaf plants are for plants that are browsed. Unbrowsed plants are harvested (killed). Plants in these stage classes produce seed prior to harvest. Key: f_3 , fecundity of unbrowsed 3-leaf plants = 3.7474 (browsed plants have no fecundity); n , proportion of seeds on harvested 3- or 4-leaf plants that fall to the ground prior to harvest = 0.38; s , proportion of seeds on harvested 3- or 4-leaf plants planted by harvester = 0.62 or 0 (responsible or not); f_4 , fecundity of unbrowsed 4-leaf plants = 12.175 (browsed plants have no fecundity).

ranged from 82 to 133 cm, with an average of 105.9 cm. The 61-year average was 103.3 cm.) To calculate mean λ_s and 95% confidence intervals, we simulated population growth over 50,000 years. This method assumes that each environment is independent (there are no carry-over effects from 1 year to the next) and that each environment is identically distributed (each has an equal probability of occurring). The population vector was begun at the stable stage distribution of the mean matrix. For each year, 1 of the 6 matrices was chosen randomly. We calculated the mean λ_s and 95% confidence intervals from these 50,000 estimates of population growth. Calculations were conducted in a MATLAB (2002) program modified from Morris and Doak (2002). Six separate estimates of λ_s were calculated for each combination of our harvest conditions (no harvest, responsible harvest, irresponsible harvest) and browse conditions (ambient, no browse).

Life Table Response Experiment

Observed differences in λ_s between these matrices (e.g., ambient vs. no browse) were due to changes in multiple vital rates, but these vital rates did not contribute equally to the observed difference. We summed contribution of vital rates into 6 categories: prolonged dormancy, fecundity (average number of seeds produced per plant), germination, growth (change to a larger stage in the next year), regression (change to a smaller stage in the next year), and stasis (remaining the same stage from 1 year to the next). Changes in vital rates contribute greatly to the change in a population's growth rate if vital rates change dramatically between 2 matrices or if λ is sensitive to changes in that vital rate. We used life table response experiments (LTREs) (Caswell 1989, 2000) to decompose the contribution of each vital rate to the observed difference in λ . For each of our 6 harvesting and browse conditions, we calculated a mean matrix on the basis of 6 matrices from our 7 years of study and calculated the λ for each matrix. We focused on 3 of 15 possible LTRE comparisons: ambient versus no browse for populations that are not harvested; ambient versus no browse for populations that are responsibly harvested; and no harvesting versus harvesting responsibly for a population with an ambient level of deer browse.

Results

Deer Herbivory Patterns

Deer removed one or more leaves when browsing ginseng. Whereas the majority (73%) of plants that were browsed had all their leaves removed, some plants were only partially browsed. The annual proportion of the ginseng population that suffered loss of all foliage by late July ranged from 11.4 to 31.3% (mean = 16.8%). Reproductive parts of the plant were sometimes browsed along

with the leaves. Reproductive parts left intact almost always aborted if all leaves were removed before fruit had finished developing.

The size of a plant affected its likelihood of being browsed. Deer were more likely to browse plants in larger stage classes (4, 3, and 2 leaves) than smaller stage classes (1 leaf and seedling) ($\chi^2 = 275.366$, $df = 4$, $p < 0.001$).

Timing of browsing had a large impact on demographic consequences. Of the plants that were completely browsed, 40% had suffered this fate before early June. These plants were more likely than unbrowsed plants to revert to a smaller stage class in the year following browsing ($\chi^2 = 58.855$, $df = 1$, $p < 0.001$). Plants that were completely browsed later in the season (between early June and the end of July) had transition probabilities similar to unbrowsed plants ($\chi^2 = 0.008$, $df = 1$, $p = 0.927$).

Smaller plants (one leaf and seedlings) that were completely browsed by early June were more likely to die than unbrowsed smaller plants ($\chi^2 = 24.175$, $df = 1$, $p < 0.001$). Smaller plants browsed later in the season were no more likely to die than unbrowsed plants ($\chi^2 = 0.568$, $df = 1$, $p = 0.451$), and plants in the larger size classes were no more likely to die than unbrowsed plants, even if browsed completely by early June ($\chi^2 = 1.282$, $df = 1$, $p = 0.258$).

No difference in prolonged dormancy rates was observed between plants that were completely browsed by early June and plants that were unbrowsed ($\chi^2 = 0.140$, $df = 1$, $p = 0.709$). Contrary to expectations, plants browsed later in the season were less likely to experience prolonged dormancy during the following growing season than were plants that were unbrowsed ($\chi^2 = 4.558$, $df = 1$, $p = 0.033$).

Deer Counts

On the basis of the helicopter surveys, we estimated 7.5 deer/km² in the 28-km² study area in January 1999 and 14.0 deer/km² in January 2001. The preliminary results from the ginseng-monitoring study led to the decision to hold managed antlerless deer hunts to reduce the deer herd. Seventy-five deer were harvested in December 2001, and 64 were harvested in December 2002. From a follow-up helicopter count conducted in January 2003, we estimated 5.8 deer/km².

Effects of Herbivory and Harvest on Population Dynamics

Deer herbivory and harvest affected multiple ginseng vital rates. The removal of deer browse increased stasis, growth and fecundity rates, and decreased regression rates of larger reproductive plants (3- and 4-leaf plants) (Fig. 1). Harvest reduced stasis and growth and regression rates of 3- and 4-leaf plants (Tables 1 & 2). The responsible practice of sowing berries from harvested

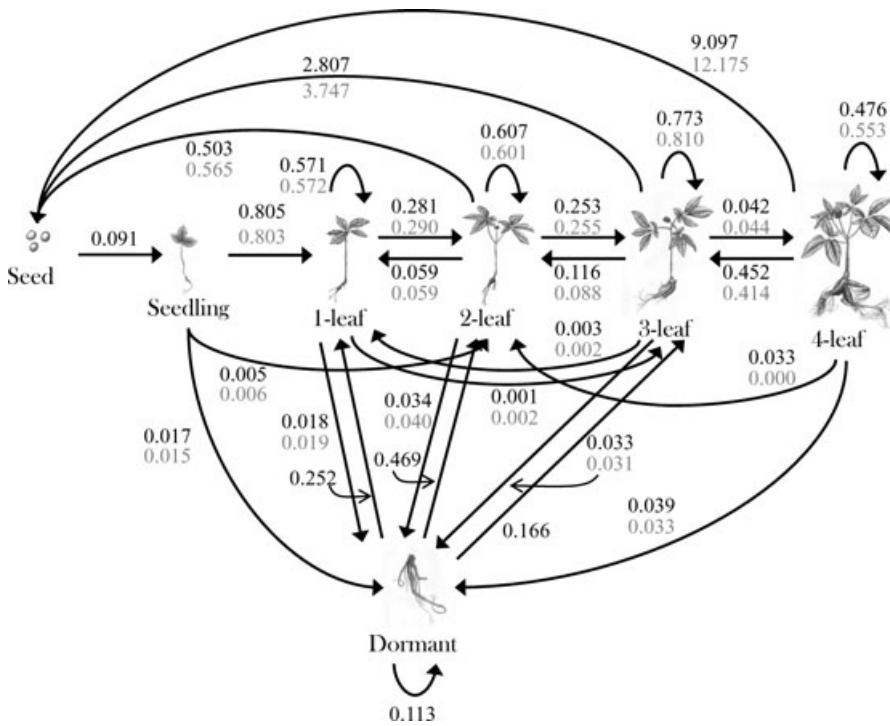


Figure 1. Annual life-cycle diagrams of American ginseng showing vital rates for the ambient population (black values) and the no-browse population (gray values). Drawings of plants show each stage class and arrows show transition probabilities from one year to the next. Drawings by P. J. Hanly.

plants increased the seed to seedling transition rate. The irresponsible practice of removing seeds decreased fecundity rates.

Stochastic Population Growth Rate

Ginseng’s stochastic population growth rate differed significantly among our harvesting and browsing conditions (Fig. 2). The stochastic population growth was highest ($\lambda_s = 1.067$) when the model excluded harvesting and

browsing. Incorporation of ambient deer browse into the model decreased λ_s by 2.9% ($\lambda_s = 1.038$). The addition of responsible harvest to the ambient browse model decreased λ_s by an additional 4.3% to 0.995, a rate that projected the population to decline very slightly. Virtually the same growth rate ($\lambda_s = 0.997$) was projected when the model excluded deer browse but included responsible harvest. Irresponsible harvest was equally unsustainable for the ambient population and the unbrowsed population ($\lambda_s = 0.837$).

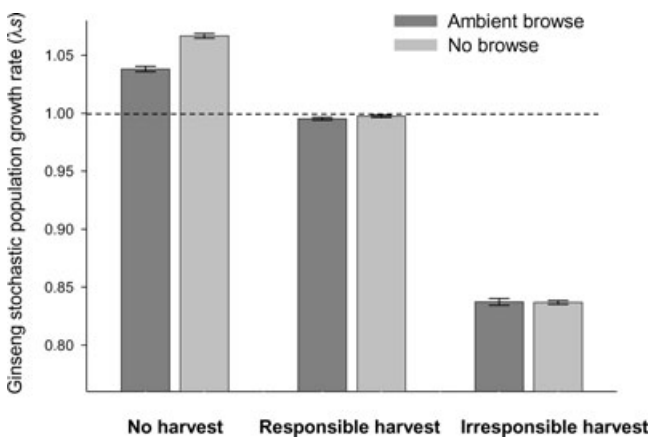


Figure 2. Stochastic population growth rate (and 95% CIs from 50,000 estimates) of 6 pooled populations of American ginseng under 6 conditions in which harvest and herbivory varied. When $\lambda_s > 1$, the populations are projected to grow.

LTRE Analysis

The LTRE analysis revealed that in an unharvested population, the removal of deer browse in our model increased the population growth rate primarily due to increases in fecundity and stasis (Fig. 3a). By contrast, in a responsibly harvested population, the removal of deer browse had almost no effect on the population growth rate primarily because removing browse increased fecundity but decreased stasis (Fig. 3b). In a responsibly harvested population, browsed plants produced no seeds, whereas unbrowsed plants produced seeds that remained in the population. Nevertheless, browsed 3- and 4-leaf plants are hidden from harvesters and thus have higher probability of stasis than unbrowsed plants, which are all killed. In a population experiencing ambient deer herbivory, the population growth rate was higher when plants were not harvested compared with when plants were responsibly harvested, but the negative effect of harvest on growth and stasis was moderated by the positive effect of

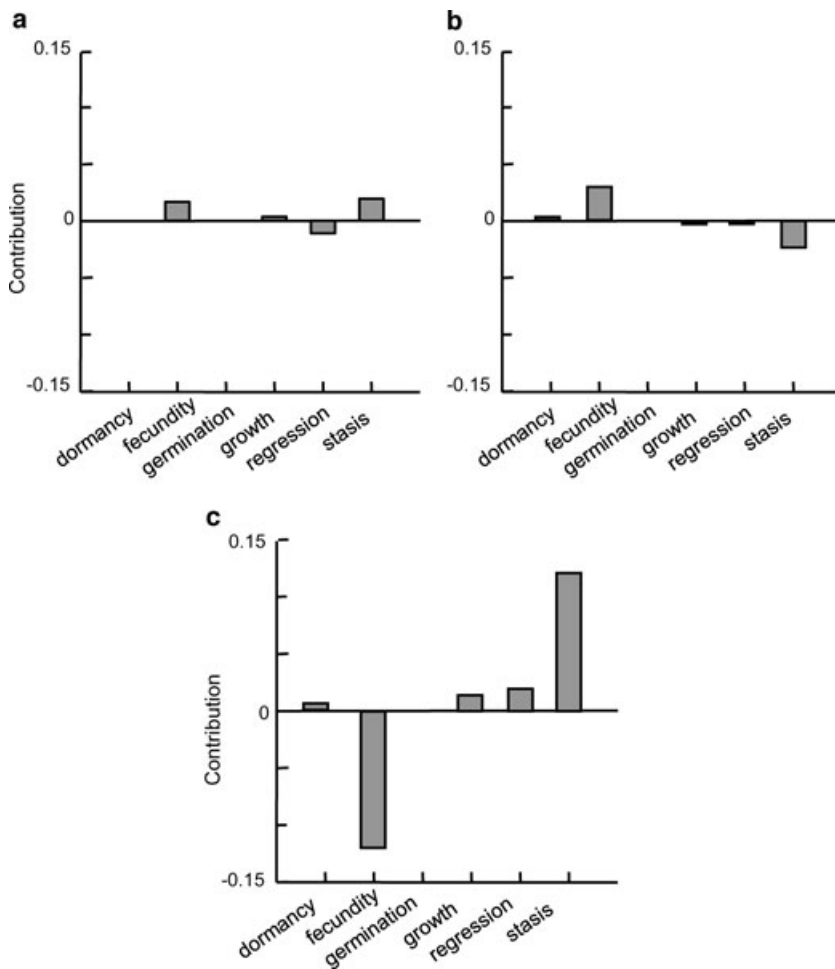


Figure 3. Results of life table response experiment for American ginseng that decomposed the difference in population growth between types of vital rates (dormancy, fecundity, germination, growth, regression, and stasis). Contribution is the magnitude of the negative or positive influence of each vital rate on λ between 2 conditions. Shown are 3 separate contrasts between types of harvesting and herbivory conditions: (a) no browse versus ambient browse (no harvest); (b) no browse versus ambient browse (responsible harvest); and (c) no harvest versus responsible harvest (ambient herbivory).

increased germination of seeds sown by the responsible harvester (Fig. 3c).

Discussion

Effects of Herbivory and Harvest

Our results showed that although deer herbivory and human harvest each negatively affected the population dynamics of American ginseng, the effects were not additive. Although deer herbivory decreased the population growth rate of American ginseng by decreasing fecundity, growth, and stasis, it also had a positive effect on survival because it hid plants from human harvesters. The interactive effects of deer browse and harvesting were especially strong in this species because deer preferred to browse the same larger plants sought by harvesters. Early browsing affected the population more negatively than late season browsing. These results correspond with findings for other plant species (Ehrlén 1995a, 1995b; Knight 2003). Nevertheless, even early browse in our study seldom caused direct mortality.

Although deer browse in our study negatively affected American ginseng's projected population growth rate, the ginseng populations were still projected to grow. By contrast, the West Virginia ginseng populations studied by McGraw and Furedi (2005) are projected to decline by 2.7% under ambient browsing conditions, and are projected to grow by 2.1% if the effect of browsing is removed. Deer density for the 7 ginseng populations in the West Virginia study was estimated at 15–49 deer/km² (Furedi 2004), whereas we estimated deer density at 5.8–14 deer/km². Although carrying capacity for deer varies according to site, the magnitude of the difference in the size of the deer herd in these 2 studies suggests that American ginseng may tolerate deer browse when herds are of moderate size but may not tolerate browsing at higher levels.

Although harvest results in plant death, our model showed that its influence on the population as a whole is not as severe when responsible harvest methods are used. Harvesting plants when seeds are ripe and sowing the ripe seeds from harvested plants at a depth of 2 cm increases reproductive success compared with ambient conditions (McGraw, unpublished data; Farrington

2006). The positive effect of increased germination partially counteracted the negative impact of harvest on growth and stasis of the population, buffering the negative effects of harvesting on population growth rate.

By contrast, the effect of irresponsible harvesting practices was solely negative and unsustainable. Our model of the irresponsible harvester addressed only one aspect of irresponsible harvesting: the removal of seeds found on the harvested plants at the start of the legal harvest season. In reality, irresponsible harvesters may harvest prior to the start of the legal season, preventing any possibility of reproduction (Bailey 1999). They may also remove plants smaller than legally allowed and may damage or kill smaller plants by careless digging. Thus, the impact of irresponsible harvesting practices on ginseng populations is likely to be more severe than our model demonstrates.

Harvesting severely affects the stage distribution of the population. In the absence of harvest (and ambient deer browse), 35% of the aboveground plants (i.e., seeds and dormant plants excluded) are in the 3- and 4-leaf stage classes. In the presence of responsible harvesting (and ambient deer browse), only 9% of the aboveground plants are in these largest 2-stage classes. Thus, in the presence of harvesting, most of the reproducing individuals in the population will be 2-leaf plants.

Ginseng does not appear to be a preferred browse species (we frequently observed unbrowsed plants standing adjacent to browsed plants), but it comingles with more preferred browse species in preferred deer habitat. We assume our no-browse model represents a ginseng population that is excluded from deer herbivory, but actual deer exclusion would also remove trampling and soil compaction and might increase competition and facilitation from other species. Some microhabitats might be more heavily targeted by deer or humans, further complicating the effects within our browse and harvest models.

Implications for Management

Like many forest herbs, wild American ginseng faces multiple threats to its continued existence and its ability to thrive. Even where it is protected from harvest, poaching remains a serious problem (Robbins 1998). As our results and those of McGraw and Furedi (2005) indicate, ginseng sustainability may also be threatened by high densities of white-tailed deer.

Our results show that on-site planting of ripe seed from harvested plants is crucial to ensure sustainable harvest of wild American ginseng. Although most state regulations currently require planting of seeds from harvested plants, it is difficult to verify compliance. Every effort must be made to educate harvesters about the importance of this practice.

It is equally important to the future viability of ginseng populations that deer herds be monitored and managed. The number of deer that a given site can support varies,

depending on many variables, including the available winter food supply, winter cover, and soil fertility. Determining the size of a deer population provides significant challenges. Counting deer over snow from a helicopter provides a reasonable estimate, but a minimum of 10 cm of total snow cover is required to provide good visibility. Scheduling staff and a helicopter to perform such a count on short notice is logistically challenging and expensive.

An alternative to counting the deer themselves is to monitor the damage they cause to the woody and herbaceous species in their habitats. Certain "indicator" species may be used to gauge the intensity of deer browsing (e.g., Anderson 1994; Webster et al. 2001; Fletcher et al. 2001). To be an effective indicator, a species should be palatable to the deer and its population should suffer progressively negative impacts as the deer herd increases. Although ginseng could serve an indicator species, it is not an appropriate choice for such monitoring because it is subject to legal and illegal harvesting. Mortality due to harvest can confound results of a deer browse study. A possible alternative is to monitor a preferred browse species such as *Trillium* spp., as proposed by Knight (2004).

Long-term studies are needed throughout ginseng's natural range to determine whether continued exportation of wild American ginseng will be detrimental to ginseng's survival and to determine how to maintain the species throughout its range at a level consistent with its historic role in the ecosystem. Our findings emphasize the importance of having a broad ecological understanding of the complexity of ecosystem management.

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