Effects of deer herbivory on population dynamics of American ginseng (*Panax quinquefolius* L.)

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Introduction

We examined the impact of herbivory by white-tailed deer (*Odocoileus virginianus*) on the population growth rate of American ginseng (Panax quinquefolius) using data from a long-term monitoring study on public land in Missouri. Ginseng is not generally considered a preferred browse species, as evidenced by the fact that mature individual plants within a browsed colony often remain untouched, and individual leaves of browsed plants may be left intact. Nonetheless, ginseng suffers substantial browsing damage, possibly because it resides in the cool, moist habitats favored by deer during hot and dry summer months, and because it grows in close proximity to favored browse species.

While numerous studies have examined the effect of deer browse on plants (reviewed in Russell et al. 2001), few have used matrix population analysis to evaluate the effects of deer browse on herbivory on plant population growth rates (but see Rooney and Gross 2003 and Knight 2004). Rather than studying the impact of herbivory on individual fitness components, this method judges the effects of herbivory over multiple seasons on the lifetime fitness of plants.





Figure 2. Study site is located in Franklin County (highlighted) in Missouri. More precise location information is not given for conservation reasons, but is available from the authors if needed.

Study System

American ginseng (*Panax quinquefolius*) is a long-lived perennial herb of North American deciduous forests (Figure 1), found in moist but well-drained soils. Considered a rare plant by many, it is probably best characterized as widespread but scarce everywhere that it is found (McGraw et al. 2003). This limited form of distribution can be explained by considering its history as a highly valuable and heavily harvested forest crop. Ginseng roots have been harvested in Canada and the United States for export to Asia since 1720 (Carlson 1986).

American ginseng is non-clonal, each genet producing an aerial stem, bearing a whorl of 1 to 4 (or rarely more) palmately compound leaves. Determinate growth prevents any further production of leaves after the initial unfurling of the stem in spring. Multiple drupes containing 1 to 3 seeds form during summer, ripening in late summer or fall. Seeds require 20 months dormancy, germinating the second spring after they mature. Longer dormancy in the form of a seed does not appear to occur (Anderson et al. 1993, Charron and Gagnon 1991). Size of plants provides a good measure of vigor: seeds are produced only by 2, 3 and 4 leaf plants, and plants with more leaves generally produce more seeds (Charron and Gagnon 1991). Plants may live as long as 60 years (Charron and Gagnon 1991).

Methods

The population of ginseng monitored in this study is comprised of 591 plants located in a 10.7 km2 area on public land in east central Missouri (Figure 2). Individual plants are identified with engraved aluminum nails and have been monitored three times a year (late April, early June, and late July) since 1998. Data recorded include height, number of leaves, leaflets, pedicels, drupes and seeds. Percentage damage to leaves and reproductive parts and cause of damage are also recorded.

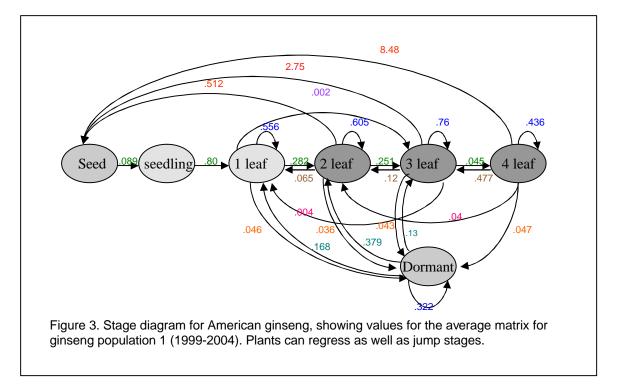
Plants that do not present above-ground stems are examined to determine if a viable root and bud still exist below ground, or if the root has died or been disturbed by mammal burrowing. Plants that appear to have viable roots are declared dormant for that season, and are examined in future years to determine if they re-emerge. If they do not reemerge after three years, they are re-classified as dead from the time they were originally listed as dormant. Dormancy of 1 to2 years (3 years for one individual) has been documented in the population.

Demographic matrix model construction

A projection matrix model shows the transition probabilities of movement between stage classes from one period to the next. The model is

 $n_{t+1} = An_t$

where the vector nt is the number of individuals in each stage class at time t and the vector nt+1 is the number of individuals in each stage class at time t+1. The matrix A is composed of rates of survival, growth and/or fecundity for each stage class from one period to the next (Caswell 2001). For this study, our demographic matrix consisted of seven stages: seeds, seedlings, 1 leaf plants, 2 leaf plants, 3 leaf plants, 4 leaf plants and dormant plants (Figure 3).



Fecundity

Fecundity is determined by averaging the numbers of seeds produced by each stage class. Germination rates are calculated as the percentage of seedlings that result from seeds produced two years earlier (seeds require 20 months dormancy). This assumes that the survival of the seed during the year between dispersal and germination is 100%, a simplification that overestimates seed survival and underestimates germination rates, but which should nonetheless give an accurate measure of the number of seeds that survive to germinate.

Ambient matrix

Five transitions (1999-00 (n=295), 2000-01 (n=470), 2001-02 (n=500), 2002-03 (n=540), 2003-04 (n=591) were combined to create an average matrix for the ambient population (Table 1).

The jump in numbers of plants monitored in 2000-01 reflects an expansion of the study to incorporate more colonies. This expansion was considered when determining each transition rate: only plants observed in both years of a given transition period were used in calculating rates. For example, if seedlings were recorded in new colonies not previously observed, these seedlings were not included in the calculation of that year's germination rate.

No herbivory matrix

To quantify how removal of herbivory would alter population dynamics, unbrowsed plants from the first year of each transition were grouped together to create a 'no herbivory' matrix (Table 2) following the method of Knight (2004). This simulates the removal of the direct effects of herbivory (i.e. browsing), but does not take into account indirect effects of browsing (e.g. deer trampling) or carry over effects of browsing that

last longer than one season. This method does, however, take into account deer preference to browse certain stages (see Browse patterns section).

Confidence intervals

Following the method of McPeek and Kalisz (1993) and Caswell (2001), a bootstrap data set was created to sample individuals with replacement from the original demographic data set for each matrix model. This process was repeated 1000 times to create 1000 bootstrap data sets. The population growth rate was calculated from each of the 1000 bootstrap matrices using MATLAB (2002). The 95% confidence interval is obtained by discarding the lowest 2.5% estimates and the highest 2.5% estimates.

Table 1. Average matrix for the ambient population1999-2004.								Table 2. 'No herbivory' matrix for the unbrowsed population 1999-2004.							
	seed	sdling	1 leaf	2 leaf	3 leaf	4 leaf	dorm		seed	d sdling	1 leaf	2 leaf	3 leaf	4 leaf	dorm
seed	0	0	0	0.51	2.75	8.48	0	seed		0 0	0	0.56	3.73	9.63	0
sdling	0.09	0	0	0	0	0	0	sdling	0.0	9 0	0	0	0	0	0
1 leaf	0	0.8	0.56	0.06	0	0	0.17	1 leaf		0 0.81	0.57	0.06	0	0	0.17
2 leaf	0	0	0.28	0.6	0.12	0.04	0.41	2 leaf		0 0	0.29	0.6	0.1	0	0.41
3 leaf	0	0	0	0.25	0.76	0.48	0.13	3 leaf		0 0	0	0.25	0.79	0.45	0.13
4 leaf	0	0	0	0	0.04	0.44	0	4 leaf		0 0	0	0	0.05	0.47	0
dorm	0	0.01	0.05	0.04	0.04	0.05	0.29	dorm		0.01	0.03	0.04	0.04	0.08	0.29

Browse patterns

Deer typically remove one or more prongs (leaves) when browsing ginseng. A shriveled stem is often all that remains of the plant. Reproductive parts of the plant may or may not be removed during browse, but will usually abort if all leaves are removed before fruit have developed.

Deer are more likely to browse larger (2, 3 and 4 leaf) plants, and thus disproportionately affect the reproductive stage classes (Figure 4).

Browsed plants are more likely to revert to a smaller size class than unbrowsed plants (Figure 5).

Demography

Seed production and germination rates varied considerably year to year, but recruitment was always low. Mortality of seeds (no germination) averaged 91%. Of the plants that germinated, seedling mortality was highest (12%), followed by 1 leaf plants (10%), 2 leaf plants (4%) and 3 leaf plants (1%). No four leaf plants were observed to die during the six years of this study.

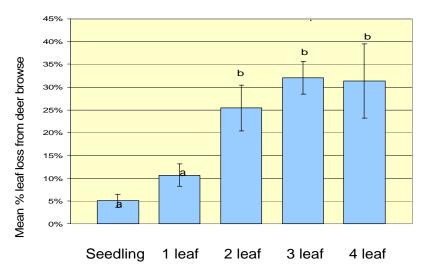
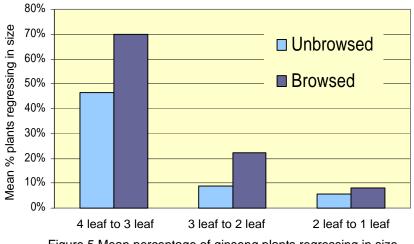
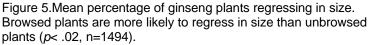


Figure 4. Mean percentage of leaf loss from deer browse to different stage classes of ginseng. Larger size classes (2,3 and 4) are subject to significantly more damage than smaller classes (seedlings and 1 leaf) (p<.0013, n=25).

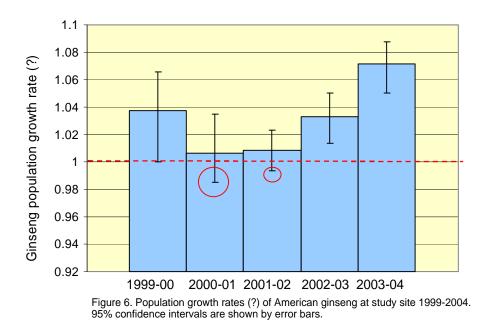




Effects of deer density on population growth rate

The ginseng population was found to be growing in each of the years it was studied, though its growth rate was very close to 1 during two of the years, and confidence intervals allow that in two of the four transition periods, the population rate could actually be declining (Figure 6). These two years correspond with the years of highest deer density (14 deer per km2, Figure 8). After two managed deer hunts were held, the deer density was counted at 5.8 deer per square kilometer, and the population growth rate rose to 1.033 and 1.072 in the next two transitions.

When unbrowsed plants are separated from the ambient population, growth rates increase even further (Figure 7).



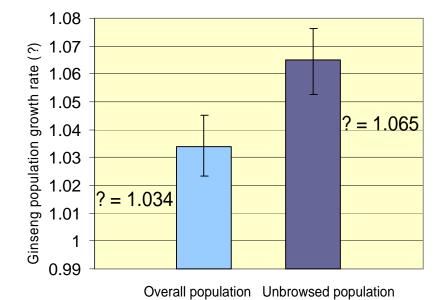


Figure 7. Population growth rate (?) of the average ambient matrix and the average no herbivory matrix for 1999-04. Error bars indicate the 95% confidence intervals. ? is the dominant eigenvalue of the transition matrix, and is the population's asymptotic growth rate (?= e^r) (Caswell 2001).

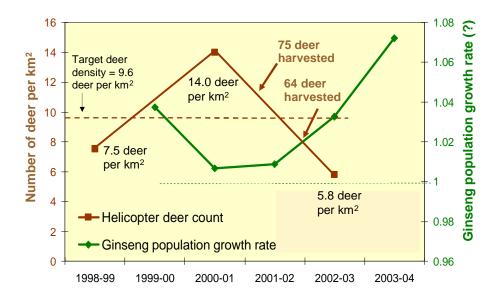


Figure 8. Population growth rate (?) of ginseng populations 1999-2004 contrasted with deer density. Helicopter counts over snow include addition of 22% (Beringer et. al. 1998).

Effects on elasticity

Elasticity values show the proportional effect of small changes to each transition rate on the population growth rate, and as such, they are often used to pinpoint transition rates to focus conservation efforts. The presence of herbivory in a population can cause shifts in elasticity values (Knight 2004).

As expected in a long-lived perennial plant, larger 3-leaf plants are the most important, and they are also the most often browsed (as seen in Figure 4). In the absence of browse, a trend toward higher elasticity of these larger plants can be seen.

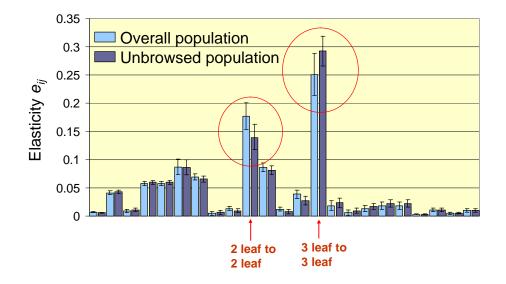
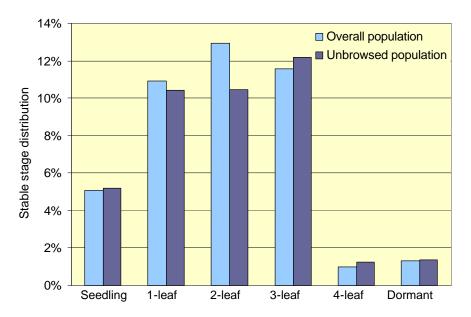
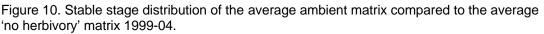


Figure 9. Elasticity values of the average ambient matrix compared to the average 'no herbivory' matrix. A trend toward larger plants can be seen in the unbrowsed plants, though this difference is not statistically significant.

Effects on stable stage distribution

After sufficient multiplications of the population vector, the population reaches a stable stage distribution (the right eigenvector of the matrix). (Caswell 2001). Comparing the distribution of the ambient matrix to the 'no herbivory' matrix, we see a trend toward smaller plants (1-leaf and 2-leaf) in the ambient population and toward larger adults in the unbrowsed population.





Conclusions

This study illustrates that even a non-preferred browse species can be negatively affected by high densities of deer. The deer density at this particular study site is nearly half that of other public land in Missouri (e.g. over 27 deer per square kilometer at Babler State Park and Cuivre River State Park in 1998 and 1999 respectively) (McCarty 2004). Given that browse at 14 deer per km2 lowered ginseng's growth rate almost to the level of no growth, browse at higher densities of deer might be expected to cause the ginseng population growth rate to decline. Based on studying a preferred browse species (Trillium grandiflorum), Anderson (1994) recommends 4 to 6 deer per km2 as a management target.

Ginseng is also exposed to human harvesting pressure. Even where it is protected from harvest, poaching remains a serious problem (Robbins 1998). Our study suggests deer herd reduction to moderate levels can assist in maintaining increasingly rare populations of American ginseng.

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