AN ECOLOGICAL STUDY OF AMERICAN GINSENG (*Panax quinquefolius* L.) IN THE MISSOURI OZARK HIGHLANDS:

EFFECTS OF HERBIVORY AND HARVEST, ECOLOGICAL CHARACTERIZATION AND WILD SIMULATED CULTIVATION

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In Partial Fulfillment of the Requirements for the Degree

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thesis entitled:

AN ECOLOGICAL STUDY OF AMERICAN GINSENG (Panax quinquefolius L.) IN THE MISSOURI OZARK HIGHLANDS:

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Presented by Susan J. Farrington

A candidate for the degree of Master of Science

And hereby certify that in their opinion it is worthy of acceptance.

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DEDICATION

To my dad: I hope to be the forester you wanted to be. Thanks for instilling in me your love of nature.

And to my mom: you showed me that going back to school later in life isn't such a bad

thing after all.

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ABSTRACT

American ginseng (*Panax quinquefolius* L.) is a long-lived, increasingly rare, and highly valued understory herb. Despite its long history of harvest, there are still large gaps in our knowledge of ginseng's ecology. Understanding its ecological requirements, its life history, and its population stressors, such as deer herbivory and harvest, allows natural resource managers to protect it and its ecological role in natural communities. The first study presented here uses eight years of demographic data collected from six populations in east-central Missouri to examine life history characteristics and the effects of herbivory by white-tailed deer (*Odocoileus virginianus* Zimm.) and harvest on its population dynamics. The majority of seedlings observed as long as 7 years after emergence were still non-reproductive, and projections indicate it may take 15 years for a seedling to produce enough seeds to replace itself. Deer browse disproportionately affected reproductive stage classes. In the year following browse, plants were more likely to regress in stage class and produced fewer pedicels. While the projected population growth rate was found to be growing during all of the years of the study, deer browse

resulted in a significant decrease in the projected population growth rate ($\lambda = 1.064$ in the "no herbivory" matrix and $\lambda = 1.035$ in the ambient matrix). Annual harvest was found to be sustainable only if no more than 8% of the 3- and 4-leaf plants are removed. If seed from harvested plants is sown at an appropriate depth (2 cm) to improve germination success, up to 52% of the 3-leaf and 62% of the 4-leaf plants can be harvested annually. The second study addressed the ecological requirements of ginseng in the Missouri Ozark Highlands. The 19 ginseng sites characterized exhibited few signs of recent disturbance (grazing, timber harvest, or land conversion) and low occurrence of exotic species, but root harvest was likely in many of the sites, as indicated by the scarcity of plants even in sites known to formerly sustain larger colonies. While all stage classes were observed across the populations, there was a noticeable absence of 4-leaf plants in many of the sites. In the third study, seed germination trials were conducted to determine the most appropriate depth at which to sow ginseng. Seeds sown on the soil surface germinated at the lowest rates and those sown between 1 and 3 cm germinated at the highest rates. Depth of sowing was not found to affect the survival of seedlings after one year. The cultivation of "wild simulated ginseng" may ease harvest pressure on wild populations. Recommendations for choosing appropriate habitats for growing "wild simulated" ginseng and methods for sowing are presented based on the findings of these studies.

CHAPTER 1: INTRODUCTION

Ginseng background

American ginseng (*Panax quinquefolius* L.) is a long-lived perennial herb of deciduous hardwood forests, found in cool microclimates characterized by rich but welldrained soils. Wen and Nowicke (1999) describe twelve species in the genus *Panax*, three of which are used medicinally: Korean ginseng or ginseng (*P. ginseng* C.A. Meyer), sanchii (*P. notoginseng* (Burkill) F.H. Chen) and American ginseng. The term "ginseng" hereafter refers to American ginseng (*Panax quinquefolius* L). Ten of the twelve species of *Panax* are Asian; one other species in the genus (dwarf ginseng, *P. trifolius* L.) is native to North America, but is not used medicinally or commercially.

The native range of American ginseng extends from the eastern to southern and central United States, and as far north as southern Quebec and Ontario (USDA-NRCS 2005a). Peak abundance is in the southern Appalachians (Foster 1996, NatureServe 2005). In Missouri, at the western edge of its range, it is mostly found in the Mississippi and Missouri river hills and the river hill sections of the Ozarks, with some scattered rare populations in southwestern and northwestern counties (Steyermark 1963, USDA-NRCS 2005a). Ranked locally as vulnerable or imperiled in at least half of its range, its global ranking is now listed as vulnerable (NatureServe 2005). 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. It is eagerly sought by root diggers and frequently poached from protected lands, contributing to its increasing scarcity.

The history of ginseng harvesting in North America

Ginseng roots have been harvested in North America for export to Asia since 1720 (Carlson 1986). The primary consuming nation is China, where Asian ginseng (Panax ginseng) has long been valued as a tonic that replenishes vital energy, increases virility, strength and blood volume, promotes appetite and wisdom and quiets the spirit (Foster 1996). A French Jesuit priest in China during the early 1700's published a letter in 1713 suggesting that ginseng might possibly be found growing in other countries, and suggested that the forests of eastern Canada were similar to the forests in which it was found in China (Shorger 1969). A fellow priest in Canada read this letter and began searching, and discovered American ginseng near Montreal in 1716. Within a few decades, it had also been discovered in New England and a frenzy of harvesting took place in both Canada and the U.S. (Shorger 1969). Daniel Boone employed several diggers to help him harvest ginseng in Kentucky in the fall and winter of 1787-88 and also bought ginseng from other diggers, amassing 12 to 15 metric tons altogether. He also harvested ginseng through the winter of 1788-89 (Hammon 1999). To be able to dig all winter, the plants were most likely more numerous and larger than they are today, since only the largest of plants today have stems that are persistent enough to be noticeable into the winter months.

As the frontier expanded, booms of American ginseng harvesting followed the westward expansion (Lass 1969). From 1821 to 1899, an average of 171,450 dried kg of wild ginseng was exported per year, peaking in 1822 when over 337,500 dried kg were exported (Carlson 1986). By the late 1800's, the largest and most accessible populations

of ginseng had been harvested heavily, and many states enacted legislation to set harvest seasons to allow plants to reproduce before being harvested (Lass 1969).

Cultivation of ginseng was mastered during the 1880's, and this was looked to as a replacement for wild ginseng. At first, cultivated ginseng commanded higher prices than wild ginseng, but the Chinese market ultimately preferred the wild root. Purported to hold their potency longer than cultivated roots, wild roots have a very different appearance. The cultivated root grows to maturity in approximately four years, is smoother, fatter, shaped like a carrot with few irregularities and is cream colored. The wild root that grows in untilled soil under natural conditions and competition requires a minimum of seven to ten years to grow to maturity, its slow growth resulting in a gnarly, often-forked dark tan root with many concentric growth rings (Hankins 2000). The darker the root, the older it is assumed to be, and the more valuable it is in the market (Guo et al. 1995). The wild root continues to be highly prized by the Asian market, and commands a much higher market price than the cultivated root (\$56 -\$225/dried kg for wild roots versus \$3 to \$6/dried kg for cultivated roots (Anderson et al. 2002)). The entire root is removed when American ginseng is harvested, since whole roots are worth more than pieces of roots.

The ginseng market today

In recent years, the market for cultivated American ginseng has become saturated, due to the development of large ginseng farming operations producing American ginseng in China. The market for wild American ginseng, however, is still strong, and an average of over 43,200 kg (dry wt) of roots has been harvested yearly since 1989 (USFWS 2005).

One hundred to three hundred roots, depending on size, comprise 2.2 dried kg (one dried lb) of ginseng today. In Missouri in 2003, 2.2 kg of dried roots contained an average of 206 roots (Tim Smith, Missouri Department of Conservation, 2004, personal communication). Missouri's harvest of ginseng ranked 10th and 11th of 19 states in 2003 and 2004 (USFWS figures 2005). Harvest of wild ginseng roots from Missouri was 1124 kg of dried root in 2002, 1063 kg in 2003 and 725 kg in 2004 (T. Smith, 2005, personal communication). A typical dried root today weighs less than 3 grams, one quarter to one third of its original green weight. Missouri's harvest of 1124 kg in 2002 translates to approximately 500,000 plants, and at \$158 per kg (the rate paid in Missouri in 2003 by one large dealer, A. Lockard, 2004, personal communication), represents a value of approximately \$178,000.

It is unknown, however, how much of this harvest comes from "wild simulated" ginseng, ginseng which is sown in forested habitats and allowed to grow "naturally" with no further effort to cultivate it. Wild simulated ginseng is indistinguishable from truly wild ginseng, and is therefore an increasingly valuable forest crop. As there are few locations left in Asia where wild ginseng can grow "naturally," this presents an opportunity for North American farmers to grow "wild simulated" ginseng on their forested land. Seeds sown in the appropriate habitat will germinate and grow "naturally" with no additional effort required of the farmer. Ginseng grown in this manner cannot be distinguished from truly wild ginseng, and commands an equally high market price.

In contrast to wild ginseng or wild simulated ginseng, "woods-grown" ginseng and "cultivated" ginseng are typically planted in dense plantings, usually in tilled raised beds. "Woods-grown" ginseng utilizes natural tree shade, and "cultivated" ginseng

utilizes artificial shade structures. The high density of such plantings typically necessitates the use of fungicides and pesticides to combat disease and pest problems. Depending on its quality, "woods-grown" ginseng is sometimes marketed as wild.

Research objectives

Despite its high value and long history of harvest, there are still large gaps in our knowledge of the ecology of wild American ginseng. The understanding of its ecological requirements, its life history, and its population stressors, such as deer herbivory and harvest, allows natural resource managers to protect it and its ecological role in natural communities. Only recently have harvest age limits been imposed, a standard method of regulating animal harvests. If future generations are to enjoy the long tradition of hunting for ginseng roots, and the thrill of finding "old-growth" ginseng, much more needs to be understood. This study arises from this need.

Chapter 2 analyzes the results of a long-term demographic study of ginseng in east-central Missouri to determine the length of time required for ginseng to reach reproductive status and to contribute to a self-sustaining population. It also examines the effects of herbivory by white-tailed deer (*Odocoileus virginianus* Zimm.) and harvest by humans on ginseng's population dynamics.

Chapter 3 presents the results of a study to characterize the ecological site conditions and requirements of ginseng in the Missouri Ozark Highlands.

Chapter 4 describes a study to determine the appropriate depth at which to sow ginseng in the Missouri Ozark Highlands.

Chapter 5 provides guidelines to landowners in Missouri for selecting appropriate locations in which to sow wild simulated ginseng, and sowing instructions, based on the findings from Chapters 3 and 4.

CHAPTER 2: EFFECTS OF HERBIVORY BY WHITE-TAILED DEER (Odocoileus virginianus Zimm.) AND HARVEST ON THE DEMOGRAPHY OF AMERICAN GINSENG (Panax quinquefolius L.)

Introduction

The use of matrix population analysis to study long-lived plants

The study of the demography of a long-lived iteroparous perennial like American ginseng presents significant challenges. Traditional life-tables are difficult to apply to a long-lived organism because of the large number of years required to follow a cohort from establishment to death. The amount of seed produced each year is meaningless without an understanding of the probability that a seed will become a seedling and the probability that a seedling will become a reproducing adult. American ginseng also provides unusual obstacles for any traditional growth model: growth from one stage to another is not linear: plants can progress to a larger size or they can regress to a smaller size (Zenger 1983, Charron and Gagnon 1991, Anderson 2002). They can also remain dormant for one or more seasons (Carpenter and Cottam 1982, McGraw and Furedi 2005).

A matrix population modeling approach provides an opportunity to gauge the health of a population and to judge the effects of forces such as herbivory or harvesting on the population. A projection matrix shows the transition probabilities of movement from one class to another in a period of time. Matrix population modeling as first outlined by Leslie (1945) was based on age classification, and was difficult to apply to long-lived plants for the same reason that traditional life tables are difficult to utilize. Lefkovitch (1965) provided a method by which organisms could be classified according to size or stage, a system that is biologically more appropriate for plants (Caswell 2001). Only in

recent years, however, have computer programs made the complex computations necessary to exploit matrix models accessible to the non-mathematician (Caswell 2001).

The population growth rate (λ) is the dominant eigenvalue of the matrix and represents the projected growth rate of a population once it has reached its stable stage distribution. If $\lambda > 1$, the population is projected to be growing; if $\lambda < 1$, the population is projected to be declining.

Assumptions of the matrix population model

The population growth rate is only assumed to be accurate if the population's vital rates as represented in the projection matrix remain constant. Nature is not static, and these vital rates may be expected to vary (Pfister 1998). A matrix population model cannot provide a forecast of what *will* happen to a population; it can only project what *would* happen if vital rates remained the same (Bierzychudek 1999, Caswell 2001). Beissinger and Westphal (1998) argue that demographic models should not be used to make predictions far into the future, perpetuating errors with each time step. Rather, they should be used for short-term predictions, and should be validated with actual data. Demographic matrix models are therefore a useful tool to compare treatments or management options.

The population growth rate (λ) is the rate expected when the population reaches its stable stage distribution. A given population may or may not be close to its stable stage distribution, and may behave very differently in the short term if it is not close (Bierzychudek 1999).

Matrix population models typically assume that population change is density independent, though individual matrices can be created for differing treatments of density (Rausher and Feeney 1980, Doak 1992). Caswell (2001) also discusses matrix models that incorporate density dependence. Herbivores may be more strongly attracted to denser populations: for example, large patches of blooming *Trillium grandiflorum* may serve as "flags" to attract the attention of passing deer, while isolated plants may go unnoticed (Knight, personal communication).

One drawback of shorter term studies is that it is very difficult to adequately portray adult mortality in a long lived species from just two or three years of data, particularly if the sample sizes are not large (Elderd et al. 2003). Other rare transitions, such as dormancy, also present challenges. Short term studies tend to inflate mortality estimates by assuming that dormant plants are dead (Menges 2000).

Matrix population models become more accurate and realistic when more years and populations are studied (Moloney 1988, Bierzychudek 1999, Menges 2000). The best studies combine multiple years and multiple populations. Data from two cycles (typically years) are required to create one transition matrix: the more transitions that are represented, the more accurately the model can reflect variability between years. A model based on multiple populations can more accurately portray variability among populations.

Demographic studies of American ginseng

Considering the long history of the harvest of American ginseng and the voluminous writings concerning it, it is surprising that until recently there was little published about the biology, phenology and population dynamics of wild American

ginseng. Most of the early writing about ginseng focused on the cultivated plant, and assumptions were made incorrectly that wild plants grew in a similar manner to those in cultivation (Nash 1898). The impetus to understand better the demography of wild ginseng populations came about in 1975 when ginseng was listed in Appendix II of CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora). This listing mandates that before American ginseng can be exported, the managing authority (the US Fish and Wildlife Service) must certify that the roots have been legally obtained and that harvest of the roots is not detrimental to the species' survival. The USFWS requires that each state that wishes to export ginseng submit annual information regarding the amount of ginseng harvested, biology of ginseng in the state, and harvest regulations. To show that harvest is "non-detrimental," an understanding of the ecology and demography of the species is essential.

Several demographic studies of wild American ginseng have emerged since the CITES listing (Table 2.1). One of the first studies to address these concerns was conducted by Carpenter (1980), investigating the history of ginseng harvest in Wisconsin, and surveying both dealers and harvesters in the state. She marked plants at one site and collected data from these plants for 2 years (1978-79), though she does not state how many plants were marked. Many plants in the second year did not "match" the plants in the first year, and only 16 plants were present in both years, none of which changed stage in that time.

Citation	Study location	Length of study	Number of populations	# plants at start	# plants at end	Number of plants aged
Carpenter 1980	Wisconsin	2 yrs	1	n/a	-	80
Zenger 1983	Missouri	5 yrs	1	102	237	237
Charron and Gagnon 1991	Quebec	3 yrs	4	345	386	n/a
Van der Voort 2005	West Virginia	3 yrs	6	673	613	-
McGraw and Furedi 2005	West Virginia	5 yrs	7	625	884	-
This study	Missouri	8 yrs	6	245	644	-

Table 2.1. Demographic studies of American ginseng (*Panax quinquefolius* L.)

Carpenter aged 80 plants by counting the concentric growth rings on the rhizome, and conducted pollination experiments on 38 plants. She also visited nine ginseng locations, describing the ginseng population structure, compiling information on associated species and monitoring 95 plants during the summer of 1979. She created a stage-based matrix model to run harvest models, using her own field data as well as data from previous studies of cultivated ginseng. Her model had five stages: seeds, one-leaf plants, two-leaf plants, three-leaf plants and four-leaf plants. With only two years of data and a limited number of plants observed, her matrix model is extremely simplified, and its findings are of limited utility. Nonetheless, the breadth of this study is impressive, and it contributed many important observations concerning the biology of wild ginseng.

Zenger (1983) marked 102 plants at one location in east central Missouri near Eolia¹ and followed them for five growing seasons (1978-1982). He observed high seedling survival rates, ranging from 93.7% to 100% for all the transitions except the one beginning in 1980, an exceptionally hot and dry year: seedling survival in the spring of

¹ Zenger also marked plants in two other locations in Missouri, one near Branson and the other near Marthasville. Both sites were devastated by root poachers after the first season of observation and were therefore not included in his study.

1981 was 66.7%. As would be expected in a long-lived perennial, he observed very high adult survival rates. He aged his plants and used this data to create an age-based matrix population model for ginseng. His model is biologically problematic in that it assumes that ginseng only lives to 20 years of age (though the only 20-year-old plant he observed did not die), and some age classes had no data. Although he acknowledged that ginseng seeds take 18 months to germinate, he assumed 12 months in his model. The transition rate for seed to seedling was also estimated, based on the ages he observed in his plants and the cohorts they must have belonged to. This ignores the death of cohort members that were no longer present when he aged his plants. A stage-based model would have been more appropriate for American ginseng, and he did attempt to create one, but incorporated only four stages: 1-leaf, 2-leaf, 3-leaf and 4-leaf (no stage for seeds or seedlings). Zenger's overall observations of a wild ginseng population are valuable contributions to the understanding of ginseng biology, phenology and pollination, but his demographic models are limited in their applicability.

Charron and Gagnon (1991) undertook a more ambitious demographic study near Montreal, Quebec, marking and following 142 plants in 2 populations for 3 years and 203 plants in 2 other populations for 2 years. They created a stage-based model containing six stages: seeds, seedlings, 1-leaf plants, 2-leaf plants, 3-leaf plants and 4-leaf plants, and found very low seedling survival (from 8% to 31%), but high survival for large adults (>90%). An accurate seed to seedling transition rate could not be determined in so few years of observation, given ginseng's 20 month dormancy requirement, so they estimated this rate by counting each year's seedlings and the seeds produced that year. Their estimates for annual recruitment ranged from 1% to 15%. Population growth rates (λ)

varied considerably between populations and even between years: Population 1: λ =.99 and 1.05, Population 2 λ =1.18 and 1.19, Population 3: λ =.88 and Population 4: λ =1.05. The small size of each population may be responsible for the high degree of variability observed in this study.

Van der Voort (2005) compared the population growth rate of ginseng in the center of its range (West Virginia) to that found by Charron and Gagnon at the northern margin of its range. She marked individual plants in six populations and censused them at least twice a season for three years (1998-2000). The three smallest populations were grouped together to make one population of 102 plants; the other three populations ranged in size from 97 to 387. Van der Voort applied the same class divisions as Charron and Gagnon, except that she grouped 3- and 4-leaf plants together due to low numbers of 4-leaf plants. Seed to seedling transition rates were determined using the same method as for Charron and Gagnon. Two transition matrices were created for each population. Population growth rate estimates were considerably lower than those for the Quebec populations: for seven of the eight matrices λ was less than 1.0, and for six matrices λ was less than or equal to 0.95.

McGraw and Furedi (2005) studied seven populations of ginseng in West Virginia (the same six as Van der Voort plus one more) over 5 seasons (2000-2004). Plants were censused for demographic data in mid to late May and early to mid August, and were monitored every three weeks from June to October for evidence of deer herbivory. Seed survival and germination rates were calculated based on a germination experiment using cultivated ginseng seeds, and included the presence of a seed bank in the calculations. The matrices consisted of five classes: seeds, 1-leaf plants (including both seedlings and

1-leaf juveniles), 2-leaf plants (also considered juveniles), small adults (3-leaf plants with smaller leaf area), and large adults (3-leaf plants with larger leaf area and 4-leaf plants). Dormant plants were assigned to their class of the previous year during the year they were absent instead of being assigned to a dormant stage class. This leads to a lower reproductive rate expected from the size class in which they were entered, as dormant plants cannot reproduce. They found the mean population growth rate for the four years to be λ =.973, indicating the population was declining by 2.7%. They also conducted population viability analysis and found the minimum viable population to be approximately 800 plants.

Evaluating consequences of herbivory and the use of matrix population analysis

Numerous studies have examined the effects of herbivory on plants, assessing its impacts on fitness components including root and shoot growth, plant form, physiology, increased susceptibility to disease, reduction of competitive ability, and the loss of female reproductive fitness by reduced seed set or delay of seed ripening (reviewed in Crawley 1989, Huntly 1991, Crawley 1997). The effect of herbivory on male reproductive fitness in the form of lowered pollen production was studied by Strauss et al. (2001). These studies, however, do not reveal how herbivory regulates plant populations (Crawley 1989), nor does quantifying effects on one component of fitness provide a good estimate of lifetime reproductive output (McGraw and Caswell 1996).

While attempting to monitor the lifetime reproductive output of a long lived iteroparous perennial may be impractical, a matrix population modeling approach can be applied to judge the effects of herbivory from one or more seasons on the lifetime fitness

of a plant. The use of matrix modeling allows us to examine the overall effect of herbivory on a plant population's growth rate, and also allows us to evaluate the relative importance of herbivory on different stages of a plant's life cycle. Since herbivores occur in varying densities from site to site and from year to year, stochastic matrix models can be used to approximate these varying conditions.

Effects of herbivory on population dynamics

The population growth rate is a more accurate representation of the relative health of populations than individual measurements of fitness. For example, a study may find a significant reduction of seed production as a result of herbivory, but if plant recruitment is not seed limited, this may not significantly affect the biology of the species (Crawley 1989, McPeek and Pekarsky 1998).

The population growth rate also provides a standard measurement to compare across populations or species under differing conditions and management (McPeek and Pekarsky 1998). An experiment that excludes herbivores from one or more sites can yield separate matrices for protected and unprotected populations (Rausher and Feeny 1980, Louda and Potvin 1995, McEvoy and Coombs 1999, Kelly and Dyer 2002). Matrices developed from sites that are subject to differing severity, intensity or timing of herbivory can be compared (Doak 1992, Bastrenta et al. 1995, Ehrlén 1995b, Lesica 1995, Shea and Kelly 1998, Hunt 2001, Garcia and Ehrlén 2002, Tolvanen et al. 2002, Rooney and Gross 2003, Fröberg and Eriksson 2003, Ehrlén 2003). Individual plants that have been damaged can be separated from those of the same population that have not been

damaged, and separate matrices can be compared for the two groups (Knight 2004, McGraw and Furedi 2005).

The majority of studies reviewed found that effects of florivory and predispersal seed predation were slight compared to the effects of leaf herbivory. This was particularly true in most of the long lived perennials studied (Lesica 1995, Ehrlén 1995b, Ehrlén 1996, Fröborg and Erikkson 2003), though one study (Kelly and Dyer 2002) did find significant negative effects of inflorescence feeding on the long lived perennial *Liatris cylindracaea*. Elasticity analysis shows the proportional effect of small changes to each transition rate on the population growth rate. Elasticity analysis of long lived organisms generally reveals that the life stage most important to population growth is survivorship of adults, while reproduction is of relatively low importance (Lesica 1995, Crone 2001, Knight 2004). Herbivory that primarily affects reproduction and does not affect adult survivorship is considered unlikely to have a pronounced effect on the population growth rate of long-lived organisms unless there is a large reduction in reproductive potential.

The presence of herbivory in a population can cause shifts in elasticity values (Knight 2004). For herbivory to substantially affect the population dynamics of a species, it should affect one or more life stages that are relatively important to the population growth rate (Pfister 1998, Ehrlén 2003). Stages that tend to have the highest elasticity are those stages that tend to be the least variable (Ehrlén and van Groenendael 1998, Pfister 1998, de Kroon et al. 2000, Saether and Bakke 2000). Pfister (1998) and Ehrlén (2003) interpret this negative correlation as evidence that natural selection acts against high variability in life stages that are highly important to the population dynamics. For example, if seedling survival is highly variable, it is unlikely that the population growth

rate will be most dependent on seedling survival. Instead, survival of adults is more likely to be important.

Whereas elasticity analysis is prospective, evaluating how hypothetical changes in vital rates might alter λ , life table response experiment (LTRE) analysis is retrospective, decomposing the observed differences in λ for two matrices based on the actual contributions of each demographic vital rate (Caswell 1989, 2000).

Timing and intensity of herbivory

The variability in the effects of herbivory found in different studies may be explained by factors such as the timing of the herbivory within the life cycle of the plant and the intensity of the attack. Doak (1992) found that the population growth rate of dwarf fireweed, *Epilobium latifolium*, was little affected by frequent attacks of low intensity damage, but attacks involving high intensity damage suppressed growth even when such attacks occurred infrequently. He suggests that the frequency, severity and timing all play a role in the importance of herbivory to a plant's growth rate, and can only be understood through adequate modeling.

Ehrlén (1995a, 1995b) found that meristem damage inflicted by mollusks early in the season on *Lathyrus vernus* (spring vetchling) was more detrimental to λ than grazing and seed predation inflicted later in the season. In the temperate deciduous forest that *Lathyrus* inhabits, the delay in growth caused by the mollusk damage resulted in the plants missing the most favorable period of growth before canopy closure.

Garcia and Ehrlén (2002) performed artificial clipping experiments and found that defoliation imposed early in the growing season had a larger impact on the population

growth rate than defoliation during the middle of the growing season. Growth was least affected by late season defoliation.

The effects of herbivory may be increased or decreased by the cumulative effects of a series of good or bad years. Hunt (2001) monitored *Atriplex vesicaria* (bladder saltbush) for six and a half years in six month cycles. Three consecutive cycles (summer, winter, and summer) were extremely dry, and an increase in adult mortality was observed on heavily grazed plots (which was not observed during single cycles of poor rainfall).

Bastrenta et al. (1995) also found that effects of leaf herbivory on λ varied depending on the plant's abiotic environment: a sequence of poor years was projected to cause a shift in age structure toward older plants, and a subsequent good year resulted in high reproduction from these older plants. The increase in the population growth rate during this good year was disproportionately larger than would be expected due to the influence of the previous poor years. The simulations, however, were based on data collected in only two years, one poor and one favorable, and thus must be viewed with caution.

Knight (2003) found that early season deer browse was more detrimental than late season browse, and was more likely to cause reproductive *Trillium grandiflorum* plants to regress to a non-reproductive stage in the year following herbivory. Furedi (2004) found that early browse versus later browse had a significant negative effect on ginseng's leaf area in subsequent years. This effect was more pronounced when the plants were browsed for 2 consecutive years.

Deer herbivory

White-tailed deer (*Odocoileus virginianus* Zimmerman) are considered by some to be a keystone herbivore in the eastern deciduous forest (McShea and Rappole 1992, Waller and Alverson 1997, Rooney 2001). Deer meet the definition of keystone species as presented by Paine (1969): they are seen to affect the distribution or abundance of many other species, they affect community structure by modifying patterns of relative abundance of competing species and by affecting the abundance of species at multiple trophic levels. It is unclear, however, whether their impact is disproportionate to their population size, as has recently been stressed in discussion of keystone species (Power et al. 1996), or if their large impact is due simply to their large numbers.

Management of deer herds in the earlier part of the 20th century was directed toward increasing their numbers and improving wildlife habitat. The success of such managements and the increased interface between urban and suburban areas with fragmented forested habitat has resulted in a sharp increase in deer populations in many parts of this country (Alverson et al. 1988, Waller and Alverson 1997). The decline of large carnivores may also play a role in the increased number of deer (reviewed in Côté et al 2004).

There are numerous studies examining the ecological impacts of deer (reviewed in Côté et al. 2004), including an increasing number of studies that have focused on the effects of deer browse on herbaceous plants (reviewed by Russell et al. 2001). Deer have been shown to selectively browse larger plants over smaller plants (Anderson 1994, Knight 2003, McGraw and Furedi 2005). Plants of some species may not flower again for several seasons after defoliation (Whigham 1990), or may produce fewer flowers in the
year following browse (Furedi 2004). Browsed plants may regress in size (Anderson 1994, Rooney and Waller 2001, Knight 2003). Populations subject to heavy deer browse may shift in stage distribution from larger reproductive plants to smaller nonreproductive plants (Anderson 1994, Augustine and Frelich 1998, Knight 2003). Species of spring flora that are unable to persist when subjected to intense herbivory may not be able to reestablish even when herbivory is reduced to low levels (Webster et al. 2005).

While many studies have evaluated the effects of deer herbivory on individual fitness components of plants, only a few studies have used matrix population analysis to evaluate the effects of deer herbivory on plant population growth rates. Rooney and Gross (2003) studied nine populations in Wisconsin and Michigan of *Trillium grandiflorum*, a preferred browse species of white-tailed deer (Augustine and Frelich 1998). Rooney and Gross's two year study combined the 9 populations, totaling 2390 plants, into one matrix and found that even at relatively low browse rates, population growth rates were negatively affected.

Knight (2004) studied 482 individuals of *Trillium grandiflorum* in one population in Pennsylvania for three years, creating an "ambient" matrix, consisting of the transition rates for all individuals over the two time periods, and a "no herbivory" matrix, consisting of the transition rates for individuals that were not browsed in the first year of each period. She found the population growth rate of the ambient population to be declining (λ =0.97), while the growth rate of the "no herbivory" matrix showed a growing population (λ =1.018).

McGraw and Furedi (2005), described above, examined the effect of deer herbivory on populations of American ginseng in West Virginia and found that deer

herbivory substantially decreases the population growth rate. Following Knight's method, they created a "no herbivory" matrix composed of plants that were not browsed and found the "no herbivory" population to be growing at an annual rate of 2.1% (λ =1.021), compared to the "current" deer browsed population which was found to be declining by 2.7% (λ =0.973).

Harvest of wild American ginseng

The sustainability of harvest of American ginseng roots is largely evaluated through examination of the quality and quantity of roots that are harvested each year: as long as quality and quantity remains somewhat constant, harvest of wild ginseng is presumed to be sustainable (Gagnon 1999). Since wild simulated ginseng cannot be distinguished from truly wild ginseng, it is possible that wild populations have been over harvested, while wild simulated ginseng has helped to keep the trade strong. Woodsgrown ginseng has also been exported as wild ginseng. New regulations issued in August of 2005 by the U.S. Fish and Wildlife Service may better illuminate how much ginseng is wild simulated or woods grown. The regulations prohibit export of roots less than ten years old (a previous regulation issued in 2003 prohibited export of wild roots less than five years old). The new regulations state that wild simulated and woods-grown ginseng need only be five years old to be exported, but a grower must prove it is forest cultivated by providing records of seed or root purchases.

There have been several studies concerning the effects of harvesting on ginseng populations. Charron and Gagnon (1991) applied a simplified harvest analysis to their demographic data to determine the amount of annual harvest that their populations could

withstand. Their method was based on that of Enright and Ogden (1979): the percentage of individuals that can be harvested equals $100(\lambda - 1/\lambda)$. This method distributes harvest evenly among all stages, which is not a realistic expectation, since the typical harvester is likely to take all of the larger sized plants (Carpenter 1980) and they may or may not take smaller plants. The seed to seedling transition rate was increased to show the effect of harvesters planting seeds of harvested plants. Their findings show a range of acceptable harvest from 0% during bad years to 16% during good years.

Nantel et al. (1996) used this same data to run more sophisticated harvest simulations, and found the maximum annual harvest rate that the populations could sustain to be little more than 5%. If harvests were conducted only every five years, even the removal of 30% of the 3 and 4-leaf plants caused the population growth rate to decline. They also calculated the minimum viable population to be approximately 170 plants based on the Charron and Gagnon data. Since only about a dozen populations in Canada were known to exceed that number, they concluded that most populations could not support any harvesting without threats to their long-term survival. (Canada does not currently allow any export of wild ginseng, though ginseng may be harvested within regulations for personal use).

McGraw (2001) studied 915 herbarium specimens of ginseng from 17 herbaria, aging and measuring them. He found that plants have declined in size since 1900 in the midwestern, Appalachian and southern states, though northern populations do not show this decline. He points to the possibility that harvesting could be selecting for smaller plants by removing the largest individuals from the population. Alternately, harvesters

could also be over collecting from optimal sites, leaving ginseng to grow in suboptimal locations where it does not achieve as large a stature.

Van der Voort et al. (2003) investigated the ability of ginseng to recover from harvest through regeneration from root or rhizome fragments and a seed bank. In one experiment, they collected 18 plants from 5 to 21 years of age for re-planting and assigned them to seven treatments: intact plants (roots, root hairs and rhizomes), intact rhizomes, distal rhizomes, proximal rhizomes, intact roots, distal roots and proximal roots. Not surprisingly, the intact plants regenerated the best (50% survived 4 years). None of the proximal rhizomes and 1 (of 6) of the distal rhizomes survived 4 years. Four of the 17 intact roots survived, as did 5 of the 14 proximal roots and 1 of 14 of the distal roots.

These figures show that ginseng has some limited capacity to regenerate from root fragments, but since harvesters are generally careful to extract as much of the complete root as possible, very little is likely to be left behind. Since age of harvested plants must now be verified, harvesters must remove the rhizome and keep it with the harvested root. If any part of the root is left behind, it is likely to be the distal root, which showed poor regeneration ability (and which in Van der Voort's study was comprised of the full lower half of the root, most likely more than a harvester would leave behind). On the other hand, root fragments in Van der Voort's experiment were removed from their original location and transplanted to a new forest setting: pieces left by a harvester would not experience transplant shock and should maintain at least some intact root hairs.

Van der Voort and her colleagues also simulated a "complete" harvest of all ginseng plants in a 1 m x 2.5 m plot containing four 1-leaf plants, one 2-leaf plant, and

eighteen 3-leaf plants. During the following year they observed a 2-leaf plant that presumably was either dormant in the growing season when they harvested or had abscised early that season. They continued to observe the population for five years after the "harvest" and found that in two years the numbers of plants exceeded the original population, but the majority of plants were 1-leaf plants, and only one plant was reproductive. Even after five years, only 5 plants were reproductive. They attribute the survival of the "harvested" colony to a residual seed bank.

Van der Voort (2005) also used her demographic analysis to examine the effect of harvest by "non-compliant", "compliant" and "steward" harvesters. The first type of harvester takes smaller plants and harvests out of season, the second obeys all regulations and scatters seeds (which may not be ripe at start of harvest), and the last obeys all regulations and waits until berries are ripe before harvesting, planting all berries at 2 cm deep. To simulate harvest, Van der Voort constructed an ambient "no harvest" matrix and compared it to harvest matrices for each type of harvester. The growth rate for the ambient matrix was projected to be 1.039, non-compliant harvest was 0.852, compliant harvest was 0.933, and steward harvest actually resulted in a higher growth rate of 1.041 (due to increased recruitment from planted seeds).

Cruse-Sanders et al. (2005) examined the effect of harvest on the genetic diversity of ginseng populations using a single generation culling simulation program. They found that random harvest at varying levels resulted in a significant loss of genetic diversity and that a non-random removal of the mature plants of the populations resulted in higher within-population genetic diversity than was the case for random harvests. Their harvest simulation assumed no new recruitment. Though harvesters should in theory re-plant

seeds from harvested plants and thus maintain the within-population genotypic variation, this cannot be assured, as not all harvesters are equally concerned about preserving the species or adhering to regulations. Cruse-Sanders and her co-authors recommend that mature plants should be harvested at lesser numbers than their proportions in any given population to reduce the negative effects of harvest.

Research objectives

This study analyzes data collected during eight years of intensive monitoring of individually marked ginseng plants in six populations in east-central Missouri. No other published study has followed individual American ginseng plants for so long a time period. Using this data, this study asks the following research questions:

How many years does an average ginseng seedling require to mature and begin reproduction?

Once reproduction has begun, how many years does an average ginseng plant require to produce enough seeds to replace itself? What effect does deer browsing have on ginseng's population dynamics? Are there sustainable levels of ginseng harvest?

Methods

Study system

American ginseng (*Panax quinquefolius* L.) is a geophytic herbaceous perennial, capable of living to at least sixty years of age (Charron and Gagnon 1991). Roots from the Catskill Mountains in New York have been aged at 100 years (S. Harris, personal communication). Ginseng emerges in mid spring (mid to late April in Missouri) during the leafing-out of the forest canopy. It is non-clonal, each genet producing a determinate aerial stem (rarely twin stems), bearing a whorl of 1 to 4 (or rarely more) palmately compound leaves (each leaf is typically referred to as a "prong" by ginseng growers and harvesters) (Anderson et al. 2002). Mature leaves are typically composed of five leaflets, though leaves with three or four leaflets are also common. Determinate growth prevents any further production of leaves after the initial unfurling of the stem in spring.

The stem terminates in a single, simple umbel of greenish-white flowers. The peduncle is present when the stem and leaves unfurl in spring. Flowers are perfect, though the staminate and pistillate parts may be separated in time (Carpenter and Cottam 1982). Ginseng is self-compatible (Carpenter and Cottam 1982, Lewis and Zenger 1982, Schlessman 1985) but it cannot produce seeds asexually (Schlessman 1985). Pollination between flowers is effected by generalist pollinators such as halictid bees (family Halicitidae) and flies (families Syrphidae, Anthomyiidae, Calliphoridae) (Duke 1980, Carpenter and Cottam 1982, Lewis and Zenger 1983, Schlessman 1985, Catling and Spicer 1995). Flowers on a given plant open over a period of several weeks during the summer (Carpenter and Cottam 1982, Schlessman 1985). A cluster of berries forms by mid to late summer, each berry 0.5 to 1cm long (Anderson et al. 2002) and containing 1

to 3 seeds. Berries ripen from green to red in late summer or fall; ripening times vary by populations (McGraw et al. 2005). Leaves turn yellow and senesce in fall, and may senesce early if stressed. The leaves of smaller and younger plants senesce earlier in the season than do those of larger and more mature plants (Carpenter and Cottam 1982, Lewis and Zenger 1982).

Seedlings have one leaf, generally composed of three leaflets, and the leaf is attached at the root collar. Two buds form at its base: one will become next year's stem and one is dormant unless there is damage to the first (Anderson et al. 1993). One-year-old plants generally have only one leaf, joined to the stem instead of the root collar as for seedlings. The leaf is typically composed of three leaflets, though it can have four or five leaflets. As plants age, they gradually add more leaflets and leaves. Size of plants provides a good measure of vigor: only 2-, 3- and 4-leaf plants produce seeds, and plants with more leaves generally produce more seeds (Charron and Gagnon 1991). Anderson (1996) found that leaflet number was more highly correlated with measures of vigor than was leaf number (since a two-leaf plant can have 10 leaflets and a three-leaf plant might only have 9 leaflets).

Growth is not linear: a three-leaf plant one year can regress to a 2-leaf or even a 1-leaf plant in the following year. Growth can also omit a stage: a 1-leaf plant can become a 3-leaf plant in the next growing season (evidence from this study). Plants can also remain completely dormant for one or more seasons (McGraw and Furedi 2005, evidence from this study).

Ginseng's root system consists of a primary fleshy storage root joined apically to a rhizome. Along the rhizome, adventitious roots form along several nodes and often one

or more of these will develop into a secondary fleshy storage root (Anderson et al. 1993). The more branched the root, and the more it resembles the figure of a person (the socalled "man-root"), the higher its value in the Asian market (Guo et al. 1995).

The rhizome is composed of internodes added annually, forming a circle with two bud scars. The age of the plant can be determined by counting these pairs of bud scars (assuming that the rhizome has not been broken during the plant's lifetime and that it has not remained dormant during some growing seasons). The rhizome is gradually pulled by contractile activity of the adventitious roots to an almost horizontal position (Anderson et al. 1993).

Reproduction has been considered to be possible only by means of seed production, but Van der Voort et al. (2003) show at least the possibility of propagation from root fragments. Dispersal of ginseng seeds appears to be primarily gravitational, as the berries fall from the parent plants. Since ginseng is often found growing on slopes, the berry has the opportunity to roll down the slope for at least a short distance. Sometimes when a plant bends over, seeds are dispersed uphill or laterally on a slope. Ginseng seed may be dispersed by birds or more likely by small mammals (Van der Voort 2005); deer have been ruled out as dispersers (Furedi and McGraw 2004).

Ginseng seeds exhibit deep simple morphophysiological dormancy (Baskin and Baskin 1998), requiring warm followed by cold stratification before germination can occur. The embryo develops within the seed until germination occurs, generally 18-20 months after the berry developed. Anecdotal reports state that some ginseng seeds will germinate in just eight to nine months and that seeds that ripen first are the most likely to

exhibit this characteristic (Carpenter 1980), but this has not been proven and should be studied further.

The ability of seeds to remain viable in the soil longer than 18-20 months in the form of a seed bank was inferred by Lewis (1988) and Van der Voort et al. (2003), and was proven by Van der Voort (2005) in a germination experiment conducted in 1996. Transects were sown with 16,000 ginseng berries (uncleaned, from a wild simulated ginseng grower), and germination was assessed in 1998, 1999 and 2000. While germination on southern exposures was very poor (less than 2%), germination on northern exposures was 10.0% after 20 months (the expected time for germination), 12.5% after 32 months, and 2.4% after 44 months. This proves that at least some seeds may remain viable up to four years after seeds are dispersed.

Ginseng's seed bank is likely to be relatively short lived. At approximately 5 x 4 x 2 mm (Carpenter 1980), the seeds of ginseng are relatively large, and are disc-shaped, not spherical. Bekkar et al. (1998) found that smaller seeds and seeds shaped most spherically were most likely to be long-lived. It is also less common for shade-tolerant ground flora to be held long-term in seed banks (Brown and Oosterhuis 1981, Thompson 1992). In a study of a population decimated by poachers, Lewis (1988) found that the seed bank appeared to play itself out in 5 years.

Study site

The six populations of ginseng monitored in this study are located in a 28 km² area on public land in the Ozark Highlands of east central Missouri. More specific

location information is withheld to protect the population: researchers may contact the author for further information if needed.

The site features steep slopes in the Eminence dolomite formation. Elevation of the ginseng sites averages 180 meters, and local relief ranges between 45 to 75 meters. Soils are deep, cherty silt loams. The landscape is second-growth oak forest, and the overstory is composed of white oak (*Quercus alba*), red oak (*Q. rubra*), Shagbark hickory (*Carya ovata*) and sugar maple (*Acer saccharum*). Common understory components of the ginseng locations include spicebush (*Lindera benzoin*), pawpaw (*Asimina triloba*) and bladdernut (*Staphylea trifolia*).

Monitoring methods

Ginseng populations were originally located between 1995 and 2000 by Missouri Department of Natural Resources staff members searching areas they considered to be likely ginseng habitat within a 28 km² region. In 1995 plants were censused in two areas or "zones", but were not individually identified. Population zones were added during the next three years: six population zones were identified by 1998 (Table 2.2), ranging from 11 to 118 plants, and averaging 41 plants each. Each population zone ranged from 0.25 ha to 1.0 ha in size, and each zone was located 0.5 km to 3.6 km from one another (average distance between population zones was approximately 1.7 km).

Within each population zone groupings of plants (colonies) were located 5 to 20 meters from one another. Colonies averaged 6.4 plants each and ranged from 1 to 72 plants. Population zones were expanded periodically (especially in 2000) to include

newly located near-by colonies, and new seedlings were incorporated as they appeared.

By 2005, the population zones ranged from 26 to 217 plants, and averaged 107 plants.

	Zone A	Zone A Zone B Zone C		Zone D	Zone E	Zone F	Total
1998	118	11	27	38	22	29	245
1999	122	15	46	46	30	35	294
2000	119	15	68	136*	33	87*	458
2001	118	17	90	138	32	92	487
2002	117	20	88	155	32	104	516
2003	119	27	95	188	34	104	567
2004	125	21	94	195	41	120	596
2005	126	26	101	217	42	132	644

Table 2.2. Number of American ginseng plants in each population zone in east central Missouri study site.

* Increases in these populations reflect an expansion of the study to include further colonies in this zone. Only plants present in each of the years of a transition are included in matrix model construction.

Individual labeling of plants began in 1998. Within each population zone, colonies were identified with a buried steel spike nail, and the distance and azimuth to a recognizable landmark was recorded. Photographs were taken of each new colony and its associated landmarks. Individual plants were identified with engraved aluminum roofing nails (7 cm long) pressed into the ground beside the rhizome, and the distance and azimuth was recorded from either the colony spike nail or from the engraved aluminum nail of another plant in the colony. Both the larger spike nails and the smaller aluminum nails were pushed into the ground so that their heads were slightly below ground level, and soil and leaves were placed on top of the nails to obscure them. This precaution was necessary to prevent notice of the plants by poachers, and also to ensure that the nails were not easily displaced. The nails were re-located using photographs, measurement from landmarks and metal detectors. Two types of metal detectors were utilized: the

larger (White's Classic IISL) was used to locate the steel spike nails for each colony as well as to locate general areas where plants were marked by smaller individual nails. The smaller metal detector (White's Electronic Bullseye 120mm Waterproof Sensing Probe) had greater resolution, and was used to pinpoint the precise location of the nail that marked each plant. This pinpoint probe enabled the re-location of nails that were shoved down into the ground after being trodden upon by deer.

In the fall of 1998, twenty-seven plants were removed by poachers. To protect plants from further poaching, a special dye was applied to the roots of 3 and 4-leaf plants beginning in the spring of 2001. This dye was created by Jim Corbin of the Consumer Services Plant Protection section of the North Carolina Department of Agriculture. The coded dye combines a fluorescent orange powdered dye with molecules of silica that contain a second dye color assigned by Corbin to a specific area where ginseng is protected. These dyes are combined with powdered nutrients that ginseng absorbs deeply into its root when the mix is sprinkled onto the junction of the rhizome and the root. Although it is non-toxic to both the plants and people, the orange color of these roots identifies them as poached roots. A dealer acquiring such roots risks having their entire inventory confiscated. If these roots are confiscated, the dyed silica molecules identify the location from which the roots were taken, aiding in prosecution of the poacher and return of any viable roots to their natural habitat.

Monitoring of the plants was conducted by staff members of the Missouri Department of Natural Resources and the Missouri Department of Conservation and this author. Plants were monitored three times each year: the first monitoring occurred in late April, when most of the plants and seedlings have emerged, and before most deer browse

or any other damage had occurred. Data recorded included stage, height, number of leaves and leaflets, number of pedicels, damage to leaflets, the severity of damage per leaflet (slight (<10%), moderate (10-49%), extreme (50-99%) or total (100%)), and the cause of damage. Damage from invertebrates was noted separately from damage caused by deer browse.

Deer browse damage could be distinguished from that of other mammals by examining the cut stems: deer generally leave ragged and torn stems, while rodents or rabbits generally leave clean and angled cuts. Damage from vertebrate herbivores other than deer is rare in ginseng habitats. Plants can also be damaged by hail, fallen branches, animals or humans trodding on them; this was recorded as mechanical damage.

The second monitoring occurred in early June. By this time all seedlings and plants had emerged for the season, stems had elongated to their final height, pedicels were fully formed, and some berries had formed. Data recorded included all of the above, plus number of berries. Any loss of reproductive structure and cause of loss (when determinable) was noted.

The final monitoring occurred in late July, when berries were fully formed. Data collected included all of the above, except stage and height, since full height is attained by early June. Berries were examined to determine how many seeds each held. Some of the berries were ripe (red) at this time. Most red berries were still on the plant, or had only just fallen and could be found below the plant. If fruit had fallen and could not be located, red pedicels were counted to obtain the number of ripened fruit that had already abscised. If berry number was estimated in this manner, the average number of seeds per

berry was applied to the missing berries. In 1999, a fourth monitoring event was conducted in late August, collecting the same data as for July.

The area surrounding each colony was examined closely for seedlings. Seedlings were distinguished from older 1-leaf plants by feeling and looking for the small crook in the stem that indicates the attachment of the petiole to the stem in older plants. (As mentioned above, seedling leaves are attached at the root collar, so there is no crook found in the stem). Ginseng seedlings can be distinguished from similar looking seedlings of other species by the presence of lines of small unbranched hairs about 1 mm long, visible to the naked eye, on the upper side of the leaflets along the major veins (Anderson et al. 2002).

Plants that did not present aboveground stems were examined to determine if a viable root and bud existed below ground, or if the root had died or been disturbed by mammal burrowing. Plants that appeared to have viable roots were declared dormant for that season, and were examined in future years to determine if they re-emerged. If they did not reemerge after two consecutive years of dormancy, they were re-classified as dead from the time they were originally listed as dormant. Dormant plants by this definition cannot die: a dormant plant must re-emerge in a later season.

Some stems that had been observed in April were found to be missing in the June and July inventories, leaving no evidence as to what caused their disappearance. In this instance, the plant was labeled as UMS (unexplained missing stem) for that monitoring period.

Plants that appeared to be dead were recorded as RD (root dead: if the root was found but appeared desiccated or rotted), RG (root gone: if no root could be found) or RS

(root stolen: if the root appeared to have been removed by poachers). All plants with these codes were re-examined the following year to confirm this status before they were removed from the inventory.

Helicopter deer count

Staff from the Department of Natural Resources censused deer in the 28 km² study area by flying very low in a helicopter when a minimum of 10 cm of snow was on the ground. Based on trial flights over known herds in fenced areas of east central Missouri, it was determined that such counts miss 22% of a deer herd (Beringer et al. 1998). This proportion was therefore added to the counts obtained.

Precipitation

Monthly precipitation totals and average precipitation totals (based on data from 1971-2000) for the nearest weather station (approximately 10 km from the study site) were taken from climatological data recorded by the National Oceanic and Atmospheric Administration (NOAA 1999-2005).

Statistical analysis

Linear regression was used to determine if (1) height predicted stage class and (2) total monthly precipitation for each growing season predicted population growth rate. Chi-square analysis was used to determine if browsed plants were more likely than unbrowsed plants to (1) regress in size, (2) die, or (3) remain dormant in the year following total browse. This analysis was also performed to compare the effects of early season browse versus late season browse. All statistical analyses were conducted using SAS (SAS Institute 2002-03).

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 n_t is the number of individuals in each stage class at time t and the vector n_{t+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, the demographic matrix consisted of seven stages: seeds, seedlings, 1-leaf plants, 2-leaf plants, 3-leaf plants, 4-leaf plants and dormant plants (Figure 2.1).

Fecundity was determined by averaging the numbers of seeds produced by the number of individuals in each stage class. Seed to seedling transition rates were calculated as the percentage of seedlings that result from seeds produced two years earlier (based on the assumption that seeds require 18-20 months dormancy). This assumes that the survival of the seed during the year between dispersal and germination is 100%, a simplification that may overestimate seed survival and underestimate germination rate, but which should nonetheless give an accurate measure of the proportion of seeds that survive to become seedlings. This also assumes that seeds either germinate in 18-20 months or die. In reality, some seeds may germinate earlier, and some may remain dormant and germinate later. However, given the number of years that the population was



Figure 2.1. Life cycle drawing of American ginseng showing possible transitions between stages (growth, stasis, regression and dormancy) and the resulting transition matrix.

followed, the seed to seedling transition rates over the years should represent the demography of this population.

The alternative to the method employed here is to perform a germination test in which seeds are sown and dug up during the year before germination to test for viability. Given the scarcity of available wild ginseng seed, such a test would have to use cultivated seeds, which might provide different results than the seeds of the wild plants observed. Also, seeds sown artificially do not truly replicate the natural process of seed burial and may overestimate seed survival and longevity in the soil (Thompson et al. 1997).

It is likely that a few seedlings were missed by the monitoring crew despite careful searching of each colony and the area surrounding it. Some of these missed seedlings were picked up during the following year as new 1-year-old plants. When it was determined that a new 1-leaf plant was not a seedling and appeared by its root to be no more than 1-year-old, it was added to the seed to seedling transition rate for the previous year.

The six populations were combined together to create one transition matrix for each transition period: 1999-00 (n=294), 2000-01 (n=458), 2001-02 (n=487), 2002-03 (n=516), 2003-04 (n=567) and 2004-05 (n=596) (Appendix 1). Pooling of the populations was necessary to obtain sufficient sample size to provide well-parameterized matrices.

Although monitoring of individually marked plants began in 1998, the first transition matrix begins 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 2000-01 reflects an expansion of the study to incorporate more colonies within two of the zones. Throughout the study, new colonies and/or new plants were

occasionally discovered and were added to the inventory (Appendix 2). To create accurate transition rates, only plants observed in both years of a given transition period were used in calculating rates. For example, if new colonies included seedlings, they were not included in the calculation of that year's seed to seedling transition rate, since there was no information on the number of seeds that produced these seedlings.

Plants listed as dormant in the last monitoring period (2005) have not yet been verified as truly dormant: some will likely be found to be dead in future years. To account for this, dormancy rates for 2005 were estimated using an average of the dormancy rates from the previous 5 transition matrices. Plants listed as dormant in both 2004 and 2005 were assumed to be dead, as dormancy for two consecutive seasons was found to be rare during the previous seven years of observation.

The plants removed from the population by root poachers in 1998 were not included in the analysis, since they were removed prior to the first year of the first transition matrix. After this event, only one other plant appeared to be removed by poachers until the fall of 2004, when 18 roots were removed from the same area that sustained the poaching in 1998. Analysis of the 2004-05 transition was run two ways: the main analysis excluded these harvested roots, since the primary objective was to examine the effects of deer herbivory on the population. The roots were then included in the secondary analysis to determine the effect of a poaching event on the population growth rate.

Ambient and "no herbivory" matrices

Data from all of the years were combined to create an "ambient" matrix, representing a population experiencing varying intensities of deer herbivory. To quantify how removal of herbivory would alter population dynamics, data from plants that were completely unbrowsed during the first year of each transition were grouped together to create a "no herbivory" matrix 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. Two sets of average "ambient" and "no herbivory" matrices were created: one that included the poached roots from 2004 (all of which were unbrowsed), and one that excluded these roots (Appendix 3).

Individual transition matrices for each year were not separated into "no herbivory" matrices due to low sample size of unbrowsed plants for each individual transition. Only by combining all years of unbrowsed plants was sufficient sample size obtained to accurately sample for confidence limits.

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. Each data set included the stage of each plant in the first year, its stage in the second year and the number of seeds it produced in the first year. To sample

the seed to seedling transition, the appropriate number of seeds that were produced in the year prior to the first year of the transition was included in the data set. The number of germinating seeds observed in the second year of the transition dictated how many of these seeds were listed as transitioning to seedling status, and the remainder transitioned to dead status. The population growth rate was calculated from each of the 1000 bootstrap matrices using adaptations of a program written in MATLAB (2002) by Tiffany Knight. The 95% confidence interval is obtained by discarding the lowest 2.5% estimates and the highest 2.5% estimates.

Lower sample size of plants in the first transition (1999-00) made it impossible to use the bootstrap method to repeatedly sample the two rarest stages: dormant plants and 4-leaf plants. For this matrix only, the transition rates for these two stages were calculated from the original data set for 1999-00 and were entered directly into the program, bypassing the bootstrap sampling. All other transitions in this matrix were bootstrap sampled as above.

To obtain confidence intervals for the ambient matrix, all of the data sets were combined together and sampled to create the bootstrap data sets. To obtain confidence intervals for the "no herbivory" matrix, the data for all plants not browsed in the first year of the transition were combined together and sampled to create the bootstrap data sets. Since dormant plants by definition cannot be browsed and cannot therefore be separated from the ambient population, transition rates for dormant plants re-emerging to become 1-, 2- or 3-leaf plants and dormant plants remaining as dormant plants are the same for both the ambient and "no herbivory" matrices. Seed to seedling transition rates are also the same for both matrices.

LTRE (Life Table Response Experiment) analysis

Life table response experiment (LTRE) analysis was conducted to assess the relative contributions of each vital rate to the change in λ from the "ambient" matrix to the "no herbivory" matrix. The differences between each vital rate in the "ambient" and "no herbivory" matrices were multiplied by the sensitivity (s_{ij}) of each vital rate. Sensitivities were derived from an average matrix, which had vital rates halfway between the values for the "ambient" and "no herbivory" matrices of the "conductory" matrix (Caswell 2001). Contributions of vital rates to λ were summed according to five categories: fertility, growth, stasis, regression and dormancy.

Harvest matrix model construction

To simulate the effects of harvest, a stochastic simulation program written in Matlab (2002) by Tiffany Knight and following the method of Caswell (2001) was adapted by the author to include variable levels of harvest at variable intervals. The six transition matrices provide six "environments" from which to draw at random. This method assumes that each environment is independent (there are no carry-over effects from one year to the next), and that each environment is identically distributed (each has an equal probability of occurring). The population vector is begun at the stable stage distribution of the mean matrix, and is multiplied by a randomly chosen matrix for 50,000 simulations to produce the stochastic population growth rate. To add the effects of harvest to the population, the randomly chosen transition matrix is multiplied by a diagonal harvest matrix (Lefkovitch 1967) at specified intervals. The diagonal harvest matrix (Table 2.3) shows the proportion of individuals left in each stage following harvest.

Table 2.3. An example of a diagonal harvest matrix, showing the surviving percentages of each stage class after harvest. In this example, 5% of seedlings, 1-leaf and 2-leaf plants have been removed, leaving 95% behind. 54% of 3-leaf plants have been removed, leaving 46% behind, and 70% of 4-leaf plants have been removed, leaving 30% behind.

	Seed	Seedling	1-leaf	2-leaf	3-leaf	4-leaf	Dorm
Seed	1	0	0	0	0	0	0
Seedling	0	0.95	0	0	0	0	0
1-leaf	0	0	0.95	0	0	0	0
2-leaf	0	0	0	0.95	0	0	0
3-leaf	0	0	0	0	0.46	0	0
4-leaf	0	0		0	0	0.3	0
Dorm	0	0	0	0	0	0	1

To estimate the effects of harvest, several different scenarios were modeled. The first, Harvest Model 1, is the simplest, examining the number of 3- and 4-leaf plants that can be removed from the population before the population growth rate (λ) is projected to decline. The ambient matrices for each year were used in each stochastic model.

A harvester may seek to harvest all plants that are of harvest size (Carpenter 1980), but some may be obscured by being dormant during a given growing season, or by senescing prematurely due to deer herbivory. In Harvest Model 2 it was assumed that dormant plants and plants totally browsed by deer during the summer were obscured from harvesters in the fall, and that all non-dormant and all non-browsed 4-leaf and 3-leaf plants are harvested. The ambient matrices for each year were used in each stochastic model.

In Harvest Model 3, it was assumed that all non-dormant and non-browsed 4-leaf plants are harvested, but the number of 3-leaf plants harvested was based upon the observed average percentage of 3-leaf plants harvested in two poaching events at this study site. The ambient matrices for each year were used in each stochastic model.

If there is little or no deer herbivory in a given population, it can be assumed that fewer plants will be hidden from harvesters. In Harvest Model 4, the effect of deer browse was removed, and it was assumed that only dormant plants were obscured from harvesters. The "no herbivory" matrices were used in the stochastic model.

While only 3- and 4-leaf plants are harvested in these models, reflecting some states' regulations that only plants of at least 3 leaves be harvested and federal regulations that only 10-year-old roots can be exported, irresponsible harvesters may remove younger plants to replant on their own property and/or careless harvesters are likely to disturb and possibly kill smaller ginseng plants growing beneath the larger adults. Even the most careful harvester is likely to disturb at least some of the younger plants that are often found clustered beneath the larger reproductive plants. The second, third and fourth models are therefore run to reflect both "responsible" harvesting practices (minimal collateral damage to smaller plants).

The interval between harvests is varied from 1 year to 5 years and 10 years in each of the models. Finally, the models consider the possible effect of harvesting on the seed to seedling transition and fecundity: harvesters in most states are required to replant seeds from harvested plants. If a "responsible" harvester plants the seeds from the plants he harvests, there will likely be an increase in the seed to seedling ratio for these seeds. Seeds that drop naturally are vulnerable to predation and desiccation, and seeds planted at the recommended depth of 2 cm experience higher germination than those left on the surface (McGraw 2000, and results from this study, see Chapter 4). However, it is likely that some seeds will have dropped from the plants before the legal harvest season opens,

and therefore even the most responsible harvester will probably not plant all of the seeds from a harvested population. The seed to seedling transition is calculated based on the average seed to seedling transition for the berries that are likely to have dropped before harvest begins, and an increased seed to seedling transition (based on the above germination experiments) for the likely number of berries remaining on the plants when "responsible" harvest is conducted.

An "irresponsible" harvester may pocket the seeds from harvested plants, either to sell or to re-plant elsewhere. The fecundity for "irresponsible" harvesting is therefore reduced by the proportion of berries that are likely to remain on the plant when harvest season begins. It is also possible that an "irresponsible" harvester would harvest out of season, before berries are ripe, thereby reducing the fecundity to zero. This simulation was also presented in each model.

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Results

Plant height

Plants attained most of their seasonal height early in the season: height measurements taken in late April accounted for an average of 87.0% of the final height attained by each plant (Table 2.4). There was a positive relationship between height and stage class (linear regression, y = .3544x + 2.9743, $r^2 = .347$, p < .001).

stage class observed 1998-2005, number of leaflets and height. Standard deviations are shown in parentheses. Stage n # leaflets Height (cm)

Table 2.4. Stage class description: number of plants (n) in each

oluge		11 100	aneto	ricigi	
Seedling	366	3.0	(± .02)	8.6	(± 2.6)
1-leaf	926	3.5	(± 0.8)	10.2	(± 3.0)
2-leaf	1184	8.7	(± 1.4)	10.7	(± 3.3)
3-leaf	1132	14.0	(± 1.3)	17.5	(± 5.7)
4-leaf	80	18.1	(± 1.5)	25.1	(± 7.4)

Reproductive biology and phenology

Berries were produced by 2-, 3- and 4-leaf plants. Two 1-leaf plants were observed at this study site to produce a few flowers, but no seeds were produced. Berries contained 1 to 3 seeds, averaging 1.12 (\pm 0.61) seeds per berry on 2-leaf plants, 1.24 seeds per berry on 3-leaf plants (\pm 0.40) and 1.38 seeds per berry on 4-leaf plants (\pm 0.23). Under the ambient deer browse conditions in this study, 2-leaf plants produced an average of 3.9 flowers, 0.38 berries and 0.45 seeds (Table 2.5). Three-leaf plants produced an average of 17.1 flowers, 2.1 berries and 2.7 seeds. Four-leaf plants produced an average of 39.7 flowers, 6.0 berries and 8.6 seeds. The number of seeds produced was highly variable, as is indicated by the large standard deviations. Plants in the "no herbivory" dataset produced more seed per individual in each size class: 2-leaf plants produced 0.54 seeds, 3-leaf plants produced 3.6 seeds and 4-leaf plants produced 13.2 seeds. This difference is significant for 3-leaf plant seed production (one-tailed t-test, t = 1.65, p <.001, df = 1848) and marginally significant for 4-leaf seed production (one-tailed t-test, t = 1.66, p = .053, df = 120).

Table 2.5. Reproductive output of each stage class. Number of pedicels per plant, percent of pedicels producing fruit, mean number of seeds per reproductive plant, mean number of seeds per plant in class in ambient population and in "no herbivory" matrix. Standard deviations are shown in parentheses.

Stage	n	Mean # plan	pedicels per t in class	% pedicels forming drupes	Mean per repi pl	# seeds roductive ant	Mear per pla (ar	n # seeds ant in class nbient)	Mean # seeds per plant in class (no herbivory)		
2 leaf	1184	3.9	(± 5.8)	10.0%	2.7	(± 2.0)	0.4 5	(± 1.2)	0.54	(± 1.3)	
3 leaf	1132	17.1	(± 12.9)	12.4%	5.9	(± 5.3)	2.7	(± 4.5)	3.6	(± 4.9)	
4 leaf	80	39.7	(± 16.3)	17.4%	15.8	(± 9.0)	8	(± 10.3)	12.9	(± 11.1)	

The timing of berry ripening varied widely among the six populations studied

(Table 2.6). Monitoring in late July often revealed red berries, but it was not uncommon to find red and/or fallen berries in one population zone and all green berries in another

population zone on the same day.

Table 2.6. Numbers of berries produced in each population zone and percentage of red berries observed in late July. In 2003, color of berries was only recorded for Population A.

	200)3	20	04	200	2005		
Zone	Berries	Red	Berries	Red	Berries	Red		
Α	158	31.6%	214	90.7%	148	26.4%		
В	18	n/a	6	0.0%	2	0.0%		
С	66	n/a	80	3.8%	18	22.2%		
D	186	n/a	224	36.2%	167	35.3%		
Е	73	n/a	41	41.5%	34	0.0%		
F	87	n/a	64	10.9%	34	0.0%		
Yearly average 31.6%			48.0%		25.3%			
Average	based on a	II three years				38.2%		

Recruitment and mortality

Annual recruitment for the ginseng populations monitored ranged from 3.97% to 16.7% and averaged 8.5%. Mortality (Table 2.7) was highest for seedlings (16.8%) and 1-leaf plants (11.9%). Two-leaf and three-leaf plants exhibited low mortality (4.3% and 3.2%). No four-leaf plants died during the course of this study. One 4-leaf plant, however, regressed to a 3-leaf plant and died the following year, and three 4-leaf plants regressed to 3-leaf plants and were among the 18 plants removed by poachers in 2004.

	Seedling		1 leaf		2 leaf		3 leaf		4	eaf
	%	n	%	n	%	n	%	n	%	n
1998-99	16.0	25	8.0	76	3.7	81	0.0	55	0	4
1999-00	23.5	34	29.6	81	6.5	93	2.7	75	0	6
2000-01	17.1	41	7.8	103	7.1	154	3.7	136	0	7
2001-02	12.8	39	13.9	122	3.1	162	2.1	145	0	8
2002-03	16.0	50	6.8	103	1.8	69	4.3	161	0	18
2003-04	15.6	63	11.1	135	2.8	181	3.5	170	0	9
2004-05	18.8	34	8.2	165	7.1	172	4.6	193	0	15
Average	16.8		11.9		4.3		3.4		0	
Total (n)		286		785		912		935		67

Table 2.7. Mortality rates and total population size (n) for each stage class 1998 to 2005.

The year of highest seedling and 1-leaf plant mortality was 2000, following a drought from July of 1999 through April of 2000, when precipitation for eight of the ten months was below normal. A prescribed fire was held in part of one population zone in October of 1999, and another prescribed fire was held in March of 2000 in two other population zones. Both of these fires burned more intensely than normal, and a portion of the mortality of the smallest ginseng plants can be attributed to fire loss. Lanscape-scale prescribed burns were conducted to restore glade/woodland natural communities and some of the ginseng forest community was included. At least 15 of the 24 1-leaf plants

and 3 of the 8 seedlings that died were not subjected to fire: a few died due to rodent burrowing damage, and 11 that were grouped together were rooted very loosely in a mixture of loose rock talus: these most likely succumbed to drought. Mortality of larger size classes was not affected by the fires or drought. A low intensity prescribed burn conducted in two population zones in January of 2003 did not appear to affect mortality of plants in any size class.

Seedling survival and progression to reproductive maturity

This study followed the progression of seven cohorts of seedlings (totaling 286 seedlings) for 1 to 7 years after seedling status (Table 2.8). Mortality was highest for seedlings and 1-year-old plants, and was lower for 2-, 3- and 4-year-old plants. Five- and 6-year old plants exhibited somewhat higher mortality (12.5% and 10.0%), but the sample sizes for these two classes were small and each death was therefore more important in the average rate.

Nearly all one-year-old plants (97.5%) were 1-leaf plants (Table 2.9). Two-yearold plants were still largely 1-leaf plants (79.2%), although some had moved to the 2-leaf stage (16.9%). By three years of age, more than half (55.6%) of the plants were still 1leaf, while more than a third (41.1%) of the plants had moved to the 2-leaf stage. At four years, a small percentage (3.4%) of the plants attained the 3-leaf stage for the first time. At six and seven years, most plants (70.3%) are still either 1- or 2-leaf plants.

Flowering and reproduction began as early as 2 years of age for a few individuals (1.6% of the population flowered and 1.1% produced seed), but most plants even at 6 and 7 years of age (83.8%) were still non-reproductive. Two-leaf plants in the six year age

class produced an average of 0.08 seed. Three-leaf plants in the six year age class produced an average of 1.8 seeds, and 3-leaf plants in the 7 year age class produced an average of 2.33 seeds. This illustrates that these age classes have not yet reached average adult potential, as the average 2-leaf plant in the population produced 0.45 seed per individual, and the average 3-leaf plant produced 2.7 seeds.

	Seedlings in cohort	Survival to 1 year	Survival to 2 years	Survival to 3 years	Survival to 4 years	Survival to 5 years	Survival to 6 years	Survival to 7 years
1998 seedlings	25	21	14	14	12	12	10	9
% survivorship		84.0%	56.0%	56.0%	48.0%	48.0%	40.0%	36.0%
seeds					(1)	(4)	(3)	(3)
1999 seedlings	34	26	23	21	20	20	18	
% survivorship		76.5%	67.6%	61.8%	58.8%	58.8%	52.9%	
seeds					(1)	(4)	(7)	
2000 seedlings	41	34	30	30	28	28		
% survivorship		82.9%	73.2%	73.2%	68.3%	68.3%		
seeds					(7)	(2)		
2001 seedlings	39	34	30	26	25			
% survivorship		87.2%	76.9%	66.7%	64.1%			
seeds				(6)	(2)			
2002 seedlings	50	42	35	33				
% survivorship		84.0%	70.0%	66.0%				
seeds				(0)				
2003 seedlings	63	53	51					
% survivorship		84.1%	81.0%					
2004 seedlings	34	27						
% survivorship		79.4%						
Average survival		82.9%	72.6%	65.6%	61.2%	60.0%	47.5%	36.0%
Average yearly mortality		17.1%	12.9%	6.1%	6.6%	0.0%	12.5%	10.0%

Table 2.8. Number of seedlings in each cohort for each year of the study and percent survivorship. Number of seeds produced by individuals in each age class are in parentheses.

Table 2.9. Number (n) and percent (%) of ginseng plants occupying each stage one to seven years after seedling status. Number and percent of plants producing flowers in each age class, number and percent of plants producing seeds, number and percent of plants that lost their reproduction due to deer browse, average seeds produced per reproductive plant and average seeds produced by 2-leaf and 3-leaf plants.

	1 year		2 years		3	3 years 4 yea		years	5 years		6 years		7 years	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%
1 leaf	232	97.5%	145	79.2%	69	55.6%	39	45.9%	18	30.0%	10	35.7%	2	22.2%
2 leaf	2	0.8%	31	16.9%	51	41.1%	39	45.9%	32	53.3%	12	42.9%	2	22.2%
3 leaf	0	0.0%	0	0.0%	0	0.0%	3	3.5%	9	15.0%	5	17.9%	3	33.3%
Dormant	4	1.7%	7	3.8%	4	3.2%	4	4.7%	1	1.7%	1	3.6%	2	22.2%
Total	238		183		124		85		60		28		9	
# plants producing flowers	0	0.0%	3	1.6%	7	5.6%	16	18.8%	28	46.7%	11	39.3%	5	55.6%
#plants producing seed	0	0.0%	2	1.1%	2	1.6%	6	7.1%	6	10.0%	4	14.3%	2	22.2%
# plants lost peduncle to browse	-	-	1	33.3%	3	42.9%	2	12.5%	2	7.1%	2	18.2%	1	20.0%
Average seeds per reproducing plant		-	1.0			3.0 1.		1.8	1.7		2.5		3.5	
Average seeds per plant in age class		-	(0.01	0.05		0.13 0.17		0.17	0.36		0.78		
Avg seeds produced by 2-lf plants			(0.06	0.12		0.15		0.28		0.08		0.00	
Avg seeds produced by 3-lf plants				-		-		1.67		0.11		1.80		2.33

Deer browse prevented at least some of the plants in each age class from reaching their reproductive potential. Overall, 15.7% of the plants followed since they were seedlings that formed peduncles lost their reproductive parts to deer browse.

Given an average recruitment rate of 8.5%, and average survival to 7 years of 36%, the likelihood that a seed will give rise to a seven-year-old plant is 3.06%. To

ensure one surviving seven-year-old, 33 seeds must be produced. At an average rate of 2.7 seeds per year, a 3-leaf plant would require approximately 10 years to produce this amount of seed.

Dormancy

During the course of this study, 68 plants were dormant for one or more growing seasons, accounting for an average of 2.7% of the population (ranging from 1.2% to 5.4% each year). Four-leaf plants were most likely to go dormant (Table 2.10), followed by 3-leaf plants and 2-leaf plants. Seedlings and 1-leaf plants were observed to go dormant the least. Dormant plants re-emerged most frequently as 2-leaf plants (44.8%) and 1-leaf plants (28.4%). They less frequently re-emerged as 3-leaf plants (16.4%) or remained dormant for another year (10.4%). No dormant plants were observed to re-emerge as 4-leaf plants. The majority of plants that emerged from dormancy (64.3%) remained in the same stage they occupied prior to entering dormancy, while 25% regressed in size and 10.7% increased in size (most of the increases were seedlings moving to the 1-leaf stage, but two 1-leaf plants progressed to 2-leaf plants after dormancy).

	Seedling		1-leaf 2-leaf		eaf	3-l€	eaf	4-leaf		Dormant		
	n	%	n	%	n	%	n	%	n	%	n	%
1998-99	25	0	76	0.0	81	2.5	55	3.6	4	0	4	25.0
1999-00	34	0	81	1.2	93	8.6	75	8.0	6	0	5	20.0
2000-01	41	0	103	1.9	154	3.2	136	0	7	0	16	18.8
2001-02	39	5.1	122	3.3	162	1.9	145	2.8	8	12.5	10	0
2002-03	50	2.0	103	0.0	169	1.8	161	1.2	18	0	10	0
2003-04	64	1.6	135	2.2	181	1.7	170	4.7	9	11.1	6	16.7
Average		1.6		1.6		2.9		3.0		3.8		11.8

Table 2.10. Number of plants in each stage class each year and percent that was dormant the following year. The final column shows the number of dormant plants each year and the percent that remained dormant the following year.

Dormancy for more than one growing season was a rare occurrence: one threeleaf plant (plant # 1) was observed to remain dormant for three years after a rodent burrow intersected its rhizome. It finally re-emerged as a 2-leaf plant, re-attained 3-leaf status the following year, went dormant again the following year, re-emerged as a 2-leaf and went dormant again.² Four plants were observed to be dormant for two consecutive growing seasons. Plant #148 was a 3-leaf plant prior to going dormant for two years, reemerging as a 3-leaf plant and remaining 3 leaves for seven consecutive growing seasons³. Plant # 111 was a 2-leaf plant for two years prior to going dormant for two years, re-emerging as a 1-leaf plant and remaining a 1-leaf for three growing seasons before regaining 2-leaf status in the fourth season after dormancy. Plant # 306 started as a 4-leaf plant, regressed to 3 leaves, went dormant for 2 years, re-emerged as a 3-leaf plant that grew to 3 leaves the next year, went dormant for two years, re-emerged as a 1-leaf plant, remained a 1-leaf plant one more year and then died.

Distribution of stage classes

The distribution of plants by stage class is seen to shift during the course of the study (Figure 2.2). Seeds accounted for the largest percentage of the population in all years, averaging 51.4% of the total population. From 1998 to 2002 2-leaf plants represented the next largest stage class, but in 2004 and 2005, 3-leaf plants outnumbered

² This plant was of the first plants monitored in 1995 and therefore has been observed for 11 years. It was the only plant in its colony, so could not be mistaken for other plants prior to individual marking of plants.

³ This plant was also one of the earliest plants monitored and was followed for 10 years. As an outlier in its colony, it could not be mistaken for other plants. The observation of its dormant bud for two years (and no apparent damage to the root) led to the decision to individually mark plants in this study.



Figure 2.2. Stage distribution of ginseng population 1998-2005.

2-leaf plants. Four-leaf plants and dormant plants were the rarest stages in the population, averaging 1% and 1.5% of the population.

Population growth rate

The population was projected to be maintaining or growing during the six transition periods. The population growth rate (λ) ranged from a low of λ =1.004 for 2001-02 to a high of λ =1.058 for 2003-04 (Figure 2.3).



Figure 2.3. Projected ginseng population growth rate (λ) 1999-2005. Error bars indicate the 95% confidence intervals. When $\lambda > 1$, the population is growing; when $\lambda < 1$, the population is declining.
Deer herbivory patterns

Deer remove one or more leaves when browsing ginseng: browsed plants in this study suffered an average loss of 83.4% of leaf surface (Table 2-11). It was not uncommon to find plants that were partially browsed, and intact plants could often be found standing alongside completely browsed plants. The majority (73%) of browsed plants, however, were completely browsed (all leaves removed), and a shriveled stem was often all that remained of the plant. The annual proportion of the ginseng population that suffered the loss of all leaves to deer herbivory ranged from 11.4% to 31.3%.

Table 2-11. Number of non-dormant ginseng plants each year, percentage of plants browsed, percent leaf loss per browsed plant, and percentage of plants totally browsed. Averages for all years combined are presented in the last column.

	1998	1999	2000	2001	2002	2003	2004	2005	1999-05	
Non-dormant plants (N)	241	289	441	476	501	559	579	602	461	
% plants browsed	12.0	23.5	24.0	35.9	31.5	19.1	17.3	21.9	23.6	
% leaf loss per plant	7.0	17.1	19.0	32.9	27.2	14.7	13.6	19.2	19.5	
% leaf loss per browsed plant	57.8	72.6	79.1	91.6	86.4	76.6	78.8	87.4	82.6	
% plants totally browsed	3.7	13.8	15.9	31.3	24.0	11.4	11.6	16.8	16.8	

Reproductive parts of the plant were sometimes browsed along with the leaves. If reproductive parts were left intact, they were almost always observed to abort if all leaves were removed before fruit had finished developing. If even a few leaflets were left intact, the fruit continued to develop and the stem did not shrivel. Reproductive parts of the plant were also sometimes browsed when no leaves were damaged. This occurred to 4.8% of the 4-leaf plants in this study, and 1.5% of the 3-leaf plants. Deer were more likely to browse plants in larger stage classes (4-, 3- and 2-leaf) than smaller stage classes (1-leaf and seedling) ($\chi^2 = 275.366$, df = 4, p < .001). Plants in the larger stage classes also suffered a larger proportion of leaf loss (F=62.25, p<.001, df = 4) (Figure 2.4). Deer browsing therefore disproportionately affected the reproductive stage classes.



Figure 2.4. Proportion of leaf loss to deer browse per individual in each stage class. Larger plants are subject to more damage by browse than smaller plants (p<.001, df=4).

Timing of browse appears to be critical; plants damaged earlier in the season were more negatively affected than those browsed later in the season. The pattern of total browse in early June versus late July is shown in Figure 2.5. Forty percent of all plants that were totally browsed had suffered this fate by early June. Plants that were totally browsed by early June 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 < .001). Plants that



Figure 2.5. Proportion of ginseng population totally browsed by early June and proportion totally browsed by late July.

were totally browsed later in the season (by the end of July) were no more likely than unbrowsed plants to revert to a smaller stage class ($\chi^2 = 0.008$, df = 1, p = 0.927).

Smaller plants (1-leaf and seedlings) that were totally browsed by early June were more likely to die than were unbrowsed smaller plants ($\chi^2 = 24.175$, df = 1, p < .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). Thus while smaller plants were less likely to sustain browsing damage, if they sustained total browse early in the season, they were disproportionately negatively affected. Plants that were totally browsed by early June were no more likely to go dormant in the following season than were plants that had not been browsed ($\chi^{2} = 0.140$, df = 1, p = 0.709). Nor were plants that were browsed later in the season more likely to go dormant in the following season: on the contrary, they were less likely to go dormant if they were browsed later in the season than were unbrowsed plants ($\chi^{2} = 4.558$, df = 1, p = .033).

Three-leaf plants that were totally browsed by early June produced 47.1% fewer pedicels in the year following browse, while 3-leaf plants that were not browsed produced 1.3% more pedicels in the following year. Three-leaf plants unbrowsed in early June but totally browsed in late July produced 29.4% fewer pedicels in the year following browse. Thus while early browsing appeared to be most detrimental to the ginseng population, late browsing had at least some negative consequences.

Browsing continued throughout the growing season. In 1999, a fourth monitoring was conducted in late August, and additional plants were observed to be totally browsed by deer (the proportion of the population totally browsed was 4.2% in early June, 13.8% in late July, and 19.4% in late August). Of the 19 additional plants consumed in August, 42.1% were 1-leaf plants, 26.3% were non-reproductive 2-leaf plants, and 31.6% were reproductive 3-leaf plants. It is not known if the seeds on these browsed plants dropped off the plants before they were browsed. The potential loss of seeds to late browse was 31 seeds, or 7.2% of the total seeds produced in 1999.

Invertebrate herbivory patterns

Herbivory by invertebrates was common in the population (an average of 41.2% of the plants were affected), but it resulted in very little overall damage. The average

proportion of leaf loss to invertebrate browse was 0.3% in June and 0.8% in July. While total browse by invertebrates such as snails or slugs early in the growing season is likely to be detrimental to small plants, very few plants suffered total invertebrate browsing by early June (0.2%). It is likely that snails or slugs removed some seedlings that were never observed by the monitoring crew, but the number of missed seedlings should be small. In a germination study (see Chapter 4), invertebrates consumed 9 of 347 seedlings (2.5%) in the first year and 9 of 756 seedlings (1.2%) in the second year. Most of the seedlings consumed emerged in late April and were consumed in early to mid May. None of the seedlings that were consumed in the first year of the germination test returned in the second year.

Unexplained missing stems

The number of unexplained missing stems was relatively consistent during each year, accounting for an average of 1.5% of the total non-dormant population in June, and an additional 3.6% in July. Just over half (51.2%) of the missing plants were seedlings or 1-leaf plants. The remaining plants (48.8%) were 2-, 3- or 4-leaf plants. The missing 2-, 3- and 4-leaf plants represented 2.8% of the total plants in these three size classes.

When a fourth monitoring event was conducted in late August of 1999, an additional 7.3% plants had unexplained missing stems, including another 4.0% of the plants in the 2-, 3- and 4-leaf size classes. It is likely that most of the unexplained stems were the result of total deer browse, but conclusive evidence that deer were responsible was lacking.

Helicopter deer counts and removal of deer by managed hunts

A helicopter survey conducted in January of 1999 estimated 7.5 deer per km² in the 28 km² study area. A second helicopter count held in January of 2001 estimated 14.0 deer per km². The preliminary results from the ginseng monitoring study led to the decision to hold managed deer hunts to reduce the deer herd. In December of 2001, 75 deer were harvested, and in December of 2002, 64 deer were harvested. Most of the deer removed were does. A helicopter count conducted in January of 2003 estimated 5.8 deer per km². The helicopter deer counts closely parallel the proportion of plants in the ginseng population that were completely browsed by early June of each year Figure 2.6).



Figure 2.6. Proportion of ginseng population totally browsed in early June contrasted with deer density counted by helicopter over snow.

Precipitation

Monthly precipitation totals for 1999-2005 are shown contrasted with average monthly precipitation (Figure 2.7). Growing season precipitation is shown in Table 2.12. No relationship was found between total growing season precipitation and the population growth rate (linear regression, y = .000095x + 1.03, $r^2 = 0.3$, p = .921).

Vear	Precipitation (cm)	Deviation from	λ
i cai	(611)	atorago procip	Λ
1999	42.1	-7.9	1.047
2000	48.6	-1.5	1.006
2001	44.2	-5.9	1.004
2002	59.7	9.6	1.026
2003	41.2	-8.9	1.062
2004	74.9	24.9	1.045

Table 2.12. Total precipitation for the growing season (March through July) recorded by NOAA at a weather station approximately 10 km from the study site. The ginseng population growth rate (λ) is presented for the transition beginning in the year shown.

Effects of herbivory on population dynamics

The ginseng population was projected to be growing in each of the years it was studied, though its projected growth rate was very close to 1.00 during two of the transitions. These transitions correspond with the years of highest deer density (14 deer per km², Figure 2.8) and highest proportion of total herbivory experienced by the ginseng population early in the growing season (Figure 2.9). After a managed hunt was held in December of 2001, the proportion of ginseng plants totally browsed by June decreased from 12.1% to 10.4%, and the population growth rate projection increased to 1.0267 After another managed hunt was held in December of 2002, the deer density was censused at 5.8 deer per km², the proportion of plants browsed early dropped to 4.3%, and the population growth rate projection rose to 1.058.







Figure 2.8. Population growth rate (λ) of ginseng populations for 1999-2005 contrasted with deer density counted from helicopter over snow.



Figure 2.9. Proportion of ginseng population totally browsed by deer by early June of the year shown contrasted with the ginseng population growth rate (λ) for 1999-2005.

When the "ambient" and "no herbivory" pooled matrices (Figure 2.10) are examined, increases in fecundity and stasis are seen in the "no herbivory" population. The projected population growth rate of unbrowsed plants in the "no herbivory" matrix (λ =1.064) is significantly higher than that of the ambient population (λ =1.035) (Figure 2.11).

Reproductive values are highest for 3- and 4-leaf plants, the largest adults in the ginseng population, and the most likely to be browsed. The high reproductive values for 3- and 4-leaf plants reflects the low probability that seeds and seedlings will survive to reproductive size. In the "no herbivory" matrix, there is a significant increase in the reproductive value of 3- and 4-leaf plants (Figure 2.12).

Stable stage distribution for the "no herbivory" matrix shows a significant increase in the proportion of seeds in the population, a decrease in the proportion of 2-leaf plants, and a decrease in the proportion of 3-leaf plants (Figure 2.13).

Elasticity analysis revealed that as expected for a long-lived perennial, the most influential stage is the larger adult stage, in this case the 3-leaf stage: small changes in the proportion of 3-leaf plants that remain 3-leaf plants have the largest effect on ginseng's population growth rate. Elasticity values in the "no herbivory" matrix are not significantly different than those for the ambient matrix (Figure 2.14).



Figure 2.10. Life cycle diagram of American ginseng showing transition probabilities for the ambient population (A) versus the "no herbivory" population (B).



Figure 2.11. Population growth rate (λ) of the "ambient" matrix and the "no herbivory" matrix for 1999-05. Error bars indicate the 95% confidence intervals.



Figure 2.12. Reproductive values of the "ambient" matrix compared to the "no herbivory" matrix 1999-05. Error bars indicate the 95% confidence intervals.



Figure 2.13. Stable stage distribution of the "ambient" matrix compared to the "no herbivory" matrix 1999-05. Error bars indicate the 95% confidence intervals.



Figure 2.14. Elasticity values of the "ambient" matrix compared to the "no herbivory" matrix. Error bars indicate the 95% confidence intervals.

LTRE Analysis of the effects of herbivory

The life table response experiment (LTRE) analysis shows the largest contribution to the difference in λ from the "ambient" and "no herbivory" matrices was from four transitions: 3-leaf plants remaining 3-leaf plants, 4-leaf plants remaining 4-leaf plants, 3leaf plants producing seed and 4-leaf plants producing seed (Table 2.13).

Table 2.13. Life table response experiment for American ginseng showing the relative contribution of the change in each vital rate from the "ambient" (A) matrix to the "no herbivory" (NH) matrix. Sensitivities (s_{ij}) are derived from the average matrix of the "ambient" and "no herbivory" matrices.

Transition	a _{ii} ^{NH} - a _{ii} ^A	S _{ij}	Contribution to $\Delta\lambda$
2-If to seed	0.0876	0.0120	0.0011
3-If to seed	0.9123	0.0141	0.0129
4-If to seed	4.5211	0.0010	0.0046
seed to sdlg	0.0000	0.6016	0.0000
sdlg to 1-lf	0.0030	0.0654	0.0002
sdlg to 2-lf	-0.0035	0.1021	-0.0004
sdlg to dorm	-0.0024	0.0941	-0.0002
1-If to 1-If	0.0060	0.1447	0.0009
1-If to 2-If	0.0064	0.2259	0.0015
1-If to 3-If	0.0002	0.3032	0.0001
1-If to dorm	0.0008	0.2083	0.0002
2-If to 1-If	-0.0020	0.1695	-0.0003
2-If to 2-If	-0.0042	0.2648	-0.0011
2-If to 3-If	0.0023	0.3552	0.0008
2-If to dorm	0.0032	0.2440	0.0008
3-If to 1-If	-0.0016	0.1988	-0.0003
3-If to 2-If	-0.0285	0.3106	-0.0089
3-If to 3-If	0.0416	0.4167	0.0174
3-If to 4-If	-0.0011	0.5936	-0.0007
3-If to dorm	-0.0033	0.2862	-0.0009
4-If to 2-If	-0.0317	0.0223	-0.0007
4-If to 3-If	-0.0704	0.0299	-0.0021
4-If to 4-If	0.1027	0.0426	0.0044
4-If to dorm	-0.0005	0.0205	0.0000

Summing these results, the combined vital rates for stasis contributed the most to the difference in λ (0.0215), followed closely by fertility (0.0185) (Figure 2.15). The third

largest sum was the contribution of regression in size, which was negative (-0.0123), indicating that fewer plants regressed in the "no herbivory" matrix than in the ambient matrix. Growth (0.0015) and dormancy (-0.0002) contributed very little to the difference between the two matrices.



Figure 2.15. Sum of the relative contributions of vital rates for fertility, growth, stasis, regression in size and dormancy to the difference in population growth rates (λ) between the ambient matrix and the "no herbivory" matrix

Patterns of harvest by poachers

Twenty-seven plants were lost to poaching in one colony during the fall of 1998. At the time of the harvest, there was no size restriction imposed on roots to be exported. Eight 3-leaf plants were removed, as well as five 2-leaf plants, thirteen 1-leaf plants and 1 seedling. It is possible that the smallest plants were killed accidentally when the larger plants were removed, or they could have been harvested for re-planting elsewhere. These plants represented 50.9% of the total plants in this colony, and 22.9% of the total plants in the population zone. Harvested 3-leaf plants represented 53.3% of the total 3-leaf plants in this colony, harvested 2-leaf plants represented 38.5% of the 2-leaf plants, and harvested 1-leaf plants represented 61.9% of the 1-leaf plants. There was only one 4-leaf plant in this colony at that time, and it had been totally browsed in late July, effectively hiding it from the poacher. Only one of the 3-leaf plants that were not harvested had been browsed by late July; six other plants were not browsed in late July and were not harvested. Given that browsing continues throughout the season, it is possible that the harvestable plants left behind were browsed after the July census, making them less apparent to the poacher.

This same colony and two adjacent colonies were poached six years later in the fall of 2004. By this time, U.S. Fish and Wildlife Service regulations required that any ginseng roots to be exported must be five years of age or older. Sixteen 3-leaf plants and two 2-leaf plants were removed in this event: no smaller plants were missing.

In both poaching events, the identifying nails for these plants were not found, despite the use of both types of metal detectors. No mammal burrows were noted near the location of any of the missing plants. Several rocks were noted to be upturned with the mossy side facing down. More than six months of fall, winter and early spring rains (along with winter frost heaving) erased most evidence of soil disturbance by the poacher.

All of the plants removed during this second poaching event and most of the harvestable plants left behind by the poachers were listed as unbrowsed in late July of

2004. This author visited one of the poached colonies in the last week of August of 2004 to collect leaflets for a genetic study being conducted by Rebecca Anderson in Illinois. The colony had not yet been poached, as one leaflet each was collected from two of the plants that were later removed by the poachers. No fruit remained on the plants in this colony, making it harder for harvesters to locate plants, and protecting the seeds from the poachers. Several plants in the colony were observed to be senescing early, either naturally or due to disease. These may have been some of those that the poacher did not remove.

The poached plants from 2004 represent 38.3% of the total number of plants in the three colonies and 14.4% of the population zone. They represent 51.6% of the 3-leaf plants in the three colonies and 20% of the 2-leaf plants. Of the combined population zones monitored in this study, they represent 8.3% of the 3-leaf plants, 1.2% of the 2-leaf plants, and 3.0% of the total population.

Effect of poaching event on the population growth rate

When the fate of these 18 plants is included in the 2004-2005 transition matrix, the death of these plants lowers the projected population growth rate by 3.2% (from λ = 1.044 to λ =1.012). The inclusion of this one harvest event in the overall dataset for 1999 to 2005 lowers the average projected population rate by 0.8% (from λ = 1.035 to λ =1.027). If harvest events took place annually, the effect could be much larger.

Harvest model simulations

Harvest Model 1 examines the simulated harvest of 3-leaf and 4-leaf plants from the population. If more than 8% of the 3- and 4-leaf plants are harvested annually, the population growth rate projected to decline (at 9% harvest, $\lambda = 0.9990$ (confidence limits = 0.9968, 1.0013)). If harvest is conducted every five years, harvesting rates greater than 38% of the 3-leaf and 4-leaf plants projects a declining population growth rate (at 39% harvest, $\lambda = 0.9993$ (confidence limits = 0.9970, 1.0017). If harvest is conducted every ten years, up to 69% of the 3- and 4-leaf plants can be removed before the growth rate is projected to decline (at 70% harvest, $\lambda = 0.9998$, confidence limits = 0.9973, 1.0024).

Harvest model 2 (Table 2.14) shows the results of a simulated harvest of all nondormant and non-browsed 4-leaf (62%) and 3-leaf plants (70%). When no further adjustments are made to the model, the harvest model projects a decline in growth if harvest is conducted every year or every five years. If harvest is conducted every ten years, the population is projected to sustain itself, but confidence limits show the possibility of decline.

When harvesters properly plant the berries they find in early September, the seed to seedling transition rate is adjusted to .498 for "responsible" harvesting.⁴ The population is then projected to grow if harvest is conducted every five years or ten years. Annual harvest is projected to cause a decline in the population despite responsible seed planting and no collateral mortality.

⁴ This rate reflects the average germination (8.5%) for the berries that were observed to be red by the end of July (38%), and which are expected to have dropped before the start of harvest season, and 75% germination (McGraw 2000) for the remaining seeds that the harvester encounters and sows at 2 cm.

narvesting practices, f seed from harvested is for λ are in				Harvest scenario	62% of 4 leaf harvested	70% of 3 leaf harvested Fecundity reduced to 0		02% of 4 lear narvested	70% of 3 leaf harvested Fecundity reduced by 62%	62% of 4 leaf harvested	70% of 3 leaf harvested 33% of smaller plants killed	62% of 4 leaf harvested 70% of 3 leaf harvested 33% of smaller plants killed	Fecundity reduced by 62%
Irresponsible" f ble" planting of onfidence limit			t interval	10 years	0.9916	(.9878 .9953)		7088.0	(.9925 .9979)	0.9783	(.9756 .9809)	0.9723 (.9695 .9752)	
onsible" and "I d on "responsil naller plants. C ted scenario.			nsible" harvest	5 years	0.9454	(.9408 .9499)		0708.0	(.9450 .9555)	0.9217	(.9190 .9243)	0.9098 (.9067 .9128)	
shown for "Resp d fecundity (based ral damage to sm under the indical	ם growth rate	("Irrespoi	1 year	0.7684	(.7681 .7687)		0.8024	(.8016 .8032)	0.6258	(.6245 .6271)	0.5857 (.5850 .5865)	
n growth rate (A) is g transition rate and plants), and collate to maintain or grow	Ginseng populatio		interval	10 years	1.0000	(.9974 1.003)		1.0294	(1.027 1.0319)	0.9970	(.9944 .9996)	1.0270 (1.0246 1.0294)	
nseng populatio seed to seedlin from harvested ion is projected			onsible" harvest	5 years	0.9636	(.9610 .9662)		1.0138	(1.0114 1.0162)	0.9575	(.9549 .9601)	1.0087 (1.0063 1.0111)	
arvested. The gi en harvest, the emoval of seed idicates populat			"Resp	1 year	0.8397	(.8381 .8413)	71000	0.9071	(.9661 .9681)	0.8065	(.8050 .8081)	0.9338 (.9328 .9347)	
3 leaf plants (70%) are há varying the interval betwe plants or "irresponsible" ri parentheses. Bold print in				Harvest scenario	62% of 4 leaf harvested	70% of 3 leaf harvested		02% or 4 lear narvested	70% of 3 leaf harvested Seed-sdlg increased to .498	62% of 4 leaf harvested	70% of 3 leaf harvested 5% smaller plants killed	62% of 4 leaf harvested 70% of 3 leaf harvested 5% of smaller plants killed	Seed-sdlg increased to .498

Table 2.14. Harvest Model 2. Harvest under ambient deer browse pressure. All apparent (non-dormant and non-browsed) 4 leaf plants (62%) and

When a small amount of collateral mortality is incorporated into the model (5% of 1-leaf and 2-leaf plants are accidentally killed), this harvest rate is no longer sustainable for any of the three harvest intervals.

When the proper planting of berries (increased seed to seedling transition rate) is coupled with the collateral mortality to smaller plants, the population is projected to decline if harvested annually. The population is projected to sustain itself if harvested every five years, and to grow if harvested every ten years.

Examining "irresponsible" harvesting practices for Model 2, when the fecundity is reduced to zero (reflecting out of season harvest prior to berry ripening), the population is projected to decline for all harvest intervals. If the fecundity is reduced by 62% (reflecting the removal of berries encountered on the plants when harvest season commences), the population is still projected to decline for all harvest intervals. When fecundity is not altered, but 33% of the smaller plants are either carelessly killed or purposefully removed, the population is projected to decline for all harvest intervals. The death of these smaller plants is seen to have a larger negative effect on the population growth rate than the alteration of fecundity.

Harvest model 3 (Table 2.15) applies the same rate of harvest of 4-leaf plants as above (62%), but a lower rate of 52% for 3-leaf plants (averaging observations from this study that harvesters removed 53.3% of 3-leaf plants from the poached colony in 1998 and 51.6% in 2004). At this harvest rate, the population is projected to decline if harvest is conducted annually or every five years, but is projected to grow if harvest is conducted every ten years.

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nant and non-browsed) 4 leaf plants (62%) and 52% of 3 leaf plant Jlation growth rate (A) is shown for "Responsible" and "Irresponsibl Jling transition rate and fecundity (based on "responsible" planting ested plants), and collateral damage to smaller plants. Confidence ected to maintain or grow under the indicated scenario.	Ginseng pol	"Responsible" harvest interval	rest scenario 1 year 5 years 10 year	of 4 leaf harvested 0.8714 0.9844 1.0110 of 3 leaf harvested (.8698.8731) (.9820.9869) (1.0086 1.0	of 4 leaf harvested 1.0093 1.0317 1.0379 of 3 leaf harvested (1.0083 1.0104) (1.0294 1.0340) (1.0356 1.0 -sdlg increased to .498	of 4 leaf harvested 0.8402 0.9791 1.0082 of 3 leaf harvested (.8386.8419) (.9767.9816) (1.0057 1.0 maller plants killed	of 4 leaf harvested 0.9772 1.0273 1.0361 of 3 leaf harvested (.9762.9782) (1.0251 1.0296) (1.0337 1.0 f smaller plants killed -sdlg increased to .498

Table 2.15. Harvest Model 3. Harvest under ambient deer browse pressure, and based on observation of harvest events. All apparent (non-

When berries are properly planted (increasing the seed to seedling transition rate), the population is projected to grow at all harvest intervals. Slight collateral damage without increased recruitment is projected to be sustainable only at the ten year harvest interval. And when collateral damage and increased recruitment are combined, the harvest model shows a declining population if harvest is conducted annually, but a growing population if it is conducted every five or ten years.

When "irresponsible" harvesting practices are incorporated into the model, the population is projected to decline for every scenario except when there is no collateral damage to plants and harvest is conducted no more frequently than every ten years. At this interval, the population is projected to just barely grow if fecundity is either reduced or eliminated when harvest is conducted.

Harvest model 4 (Table 2.16) removes the effect of deer browse, utilizing the "no herbivory" matrices in the stochastic model. All apparent (non-dormant) 4-leaf (97%) and 3-leaf (97%) plants are harvested. When no further adjustments are made to the model, the population is projected to decline if harvest is conducted annually or every five years. If harvest is conducted every ten years, the population is projected to sustain itself, but confidence limits show the possibility of decline.

When recruitment is increased due to "responsible" planting of seed from harvested plants, the population is projected to decline if harvested every year, to sustain itself if harvested every five years, and to grow if harvested every ten years. If 5% collateral loss is sustained by the smaller plant classes, the population is projected to decline at each harvest interval. The increase in recruitment, however, offsets the

Table 2.16. Harvest Model 4. Harvest in the absence of deer herbivory utilizing the "no herbivory" matrices. All non-dormant 4 leaf plants (97%) and non-dormant 3 leaf plants (97%) are harvested. The ginseng population growth rate (λ) is shown for "Responsible" and "Irresponsible" harvesting practices, varying the interval between harvest, the seed to seedling transition rate and fecundity (based on "responsible" planting of seed from harvested plants), and collateral damage to smaller plants. Confidence limits for λ are in parentheses. Bold print indicates population is projected to maintain or grow under the indicated scenario.

sible" harvest interval	5 years 10 years Harvest scenario	0.9141 0.9914 97% of 4 leaf harvested (.9093 .919) (.9873 .9954) 97% of 3 leaf harvested Fecundity reduced to 0	0.9263 0.9960 97% of 4 leaf harvested (.9232 .9294) (.9932 .9989) 97% of 3 leaf harvested Fecundity reduced by 62%	0.8941 0.9773 97% of 4 leaf harvested (.8904.8978) (.9739.9807) 97% of 3 leaf harvested 33% of smaller plants killed	0.87550.968097% of 4 leaf harvested(.8722.8788)(.9648.9711)97% of 3 leaf harvested33% of smaller plants killed33% of smaller plants killed
(A) "Irrespons	1 year	0.7570 (.7567 .7574)	0.7821 (.7815 .7827)	0.5863 (.5853 .5873)	0.5542 (.5537 .5547)
interval	10 years	1.0030 (.9999 1.0061)	1.0435 (1.0407 1.0463)	0.9995 (.9963 1.0027)	1.0410 (1.0382 1.0438)
onsible" harvest	5 years	0.9427 (.9392 .9462)	1.0071 (1.0039 1.0102)	0.9358 (.9323 .9394)	1.0014 (.9983 1.0045)
"Resp	1 year	0.8127 (.8114 .8140)	0.9292 (.9285 .9300)	0.7786 (.7774 .7798)	0.8941 (.8934 .8948)
					-

Ginseng population growth rate

collateral mortality enough to project the population to sustain itself if harvested every five years, and the population is projected to grow if harvested every ten years.

Overall, "irresponsible" harvesting practices result in a declining population in all cases except in Harvest Model 3 when only 52% of the 3-leaf plants are removed. If no smaller plants are damaged and harvest is conducted only every ten years, the population is projected to sustain itself despite losing 62% or all of its fecundity.

To summarize, when seeds from harvested plants are not sown at 2 cm, annual harvest is only sustainable if no more than 8% of the 3- and 4-leaf plants are removed. If seeds from harvested plants are planted at 2 cm, annual harvest is only sustainable if no more than 52% of the 3-leaf and 62% of the 4-leaf plants are removed. If 5% of the smaller plants are accidentally killed during harvest, then only 42% of the 3- and 4-leaf plants can be harvested annually. If all apparent 3- and 4-leaf plants are harvested, harvest is only sustainable if seeds from harvested plants are sown at 2 cm and harvest is only conducted every five years or more. If seeds from harvested plants are not sown at 2 cm, harvest of all apparent 3- and 4-leaf plants is not sustainable even if harvest is only conducted every 10 years.

Discussion

Time required for a ginseng seedling to become a mature reproductive individual

Wild American ginseng is slow to grow and reproduce, and eight years of intensive monitoring was not sufficient to determine the average length of time required for a ginseng seedling to become a mature reproductive individual. While a few 3- and 4year-old plants produced a few seeds for the first time, most plants in this study were not yet reproducing at 2 and 4 years of age. Even at 6 and 7 years, plants were still not reproducing seeds at the 2.7 seed per year rate that average 3-leaf plants produced.

The number of seeds produced per individual in each age class in this study was considerably lower than those presented by Anderson et al. (1984). They found that 4year-old plants produced an average of 0.3 seeds, 5-year-olds produced 2.0 seeds, 6-yearolds produced 3.8 seeds, and 7-year-olds produced 5.6. Their study, however, aged the roots of only 38 plants, and then applied a regression equation to estimate the age of other plants. Deer herbivory at the Missouri study site may play a role in the differing results. The Illinois authors do not provide levels of browse or deer herd size for their study sites, but given that the study took place over 20 years ago, it is possible that deer were not so numerous at that time. Regional differences in soil fertility and climate may also play a role as their study was conducted in northern, central and southern Illinois. Deeper and more fertile soils found in northern and central Illinois may have hastened the time required for juvenile plants to mature.

Carpenter and Cottam (1982) studied ginseng in Wisconsin, and found that most plants that successfully produced seed were 8-years-old or older. Lewis and Zenger (1982) reported that flowering begins at 3 and 4 years of age, but did not provide ages at

which fruiting begins. Additional studies carried out for longer periods of time and in different regions of ginseng's natural range are needed to more clearly define the average age at which a plant becomes a mature reproductive individual.

Time required for a ginseng seedling to replace itself

The data provided by this long term study were not sufficient to determine the number of years it requires a wild ginseng seedling to produce enough seeds to replace itself. It is clear, however, that at this study site, it will take longer than 10 years for a ginseng seedling to produce enough seeds to be likely to replace itself. Even if it is assumed that an 8-year-old plant reaches average reproductive capacity, the average 3-leaf plant would require more than 10 years to create the 33 seeds required to replace itself. Zenger (1983) found that 4-leaf plants were on average 14.8 years old; if an 8-year-old 3-leaf plant produces 2.7 seeds a year until it becomes a 4-leaf plant at 14 years of age, and then produces an average of 8.6 seeds per year, it would produce 33 seeds by the age of 15.

In this study area, the prediction that it could take 15 years for a seedling to reach sufficient seed production to replace itself may be optimistic because it assumes average 3-leaf seed production by year eight and no harvest. It also assumes no dormancy, no regression, and no mortality beyond the seventh year. This assessment is based on a population that is experiencing deer herbivory at levels from 5 to 14 deer/km². The reproductive capacity of the "no herbivory" population is higher (3.6 seeds per 3-leaf plant and 13.2 seeds per 4-leaf plant), suggesting that a population subject to little or no

deer browse will produce individuals capable of replacing themselves more quickly than one that is subject to heavier deer browse.

Reproductive limitation may be a problem in small populations, and a form of Allee effect was demonstrated for ginseng by Hackney and McGraw (2001). Although ginseng exhibits a high natural rate of self pollination (Schlessman 1985), Hackney and McGraw speculated that the reduced per-individual fertility they observed was most likely due to pollinator and/or pollen limitations, and may have been due to reduced pollinator effectiveness. Allee effects in small ginseng populations may therefore lengthen the time required for a plant to produce enough seeds to replace itself.

Recruitment and mortality

The recruitment rates observed in this study (3.97% to 16.7%, averaging 8.5%) are very similar to those observed by Zenger (1983), ranging from 1.1% to 18.1%, and averaging 8.9%. Charron and Gagnon (1991) estimated recruitment rates in Quebec to be 0% to 15.0%, with the average of the mean matrix calculated at 14.3%. Van der Voort (2005) estimated the average recruitment rate of six West Virginia populations to be 9.1% from 1998 to 2000, and Furedi (2004) estimated the recruitment rate of the same six populations plus one more to be 25.9% from 2000 to 2004. Different methods were used by Van der Voort (2005) and Furedi (2005) to estimate recruitment rates: Van der Voort based her estimate on observation of the number of seeds and seedlings produced in the same year, while Furedi incorporated the assumption of a seed bank and calculated recruitment rates based on seed germination trials and testing of viable seeds.

Seedling mortality rates observed in this study (12.8% to 23.5%, averaging 16.8%) are somewhat higher than those observed by Zenger (1983), ranging from 0% to 6.3% for most years and 33.3% for the seedlings of 1980. Both of these Missouri studies, however, observed much lower seedling mortality rates than those observed in West Virginia by Van der Voort (45.2%) and in Quebec by Charron and Gagnon (1991) (69% to 100). Charron and Gagnon cite the much colder climate of the Quebec population (the northernmost edge of ginseng's natural range) as possibly responsible for their markedly high seedling mortality rate.

This study's findings of high adult survival rates (>95% once the 2-leaf stage is attained) concurs with the findings of Zenger (1983) and Charron and Gagnon (1991), and is typical of a long-lived forest herb (Bierzychudek 1982). The adult mortality rates observed by Van der Voort (2005) and Furedi (2004) were slightly higher (6.7% and 12.8% respectively), which may be due either to the higher density of deer at their location or to harvest activity.

Berry ripening phenology

The berries observed in this study ripened over a period of a month or more, and there was considerable variability from one population to another and from one year to the next. A small number of plants from populations A and D in this study were monitored in August and September, 2003 for a study concerning the timing of berry ripening (McGraw et al. 2005). The plants in these two Missouri populations ripened earlier than any of the other 31 populations observed in 9 states; the Missouri berries were ripe on August 15, and many had already abscised. McGraw proposed that the Missouri data might be aberrant for the state, based on the finding by Lewis and Zenger (1982) observing another population in east-central Missouri that found all berries still green during the third week of August, 1978. However, red berries were observed July 1, 2004 on a few plants in a large population in Shannon County, located in southern Missouri (Farrington, personal observation), while a large population in Ozark County near the border of Missouri and Arkansas had no ripe berries at all on August 18, 2004 (Farrington, personal observation). There appears to be considerable variation in the timing of berry ripening among populations in Missouri.

Effect of precipitation on the population growth rate

Although precipitation fluctuation would seem likely to affect the population growth rate of a plant, there is no apparent relationship in this study between growing season precipitation totals and the population growth rate of the ginseng population studied. Given that ginseng is a long-lived geophytic perennial, it is likely that none of the precipitation fluctuations observed during the period of this study were large enough to have a significant effect on ginseng's growth rate. Zenger (1983) monitored a ginseng population in east-central Missouri from 1978-1983. During 1980, a record year of extreme heat, drought and low humidity in Missouri, he noted a marked decrease in the percentage of plants forming fruit (47% versus 80% and 89% in the two previous years). Plants that did manage to form fruit, however, formed as much fruit per reproductive plant as did reproductive plants in other years. Zenger also observed lower recruitment in 1980 (1.1%) and lower seedling survival (66.7%) from 1980 to 1981. While there were spikes of abnormally dry and abnormally wet months during the course of this study, there was only one period of time in which abnormal weather persisted for more than two months. The driest period of the study was from late summer and fall of 1999 through the winter and spring of 2000 when rainfall was below normal for eight of the ten months. The drought was relieved by above normal rainfall in May of 2000, and normal to above normal precipitation persisted through the rest of the growing season. The rate of plants found to be totally browsed in early June of 2000 was considerably higher than the previous year, although the overall rate of plants totally browsed by late July was only slightly higher than the previous year. It is possible that during the dry spring, deer were grazing in the comparatively moister microclimates that ginseng inhabits, and as rains returned to the area and the vegetation became lusher, deer roamed more widely and switched to alternate foods.

This pattern was also noted in reverse during 2005, when April rainfall was well above normal, and the percentage of plants totally browsed in early June was found to be relatively low, whereas rainfall in May, June and July was below normal, and the percentage of plants totally browsed in late July was found to be relatively high. Since the deer herd has not been counted at the study site since January of 2003, this pattern of browse cannot be compared to actual deer counts. But given that no hunting has been conducted since December of 2002, it is likely that the deer population was rising during 2005.

Dormancy

Lewis and Zenger (1982) reported that they found no evidence of growing season dormancy. They did, however, note a ginseng stem that was not present during one of the growing seasons they observed, and hypothesized that the stem may have been damaged prior to observation, discounting the possibility that the plant was dormant for a season. Carpenter and Cottam (1982) suggested that harvesters' observations that ginseng sometimes "sits out" a growing season were most likely attributable to early die-back of the stems. Carpenter and Cottam did, however, acknowledge that true growing season dormancy occurred rarely, and attributed it to damage to the root, such as that caused by transplantation or by animal/insect activity.

McGraw and Furedi (2005) documented dormancy in the West Virginia ginseng populations they observed, but stated that dormancy of 1-leaf plants was found to be very rare compared to that of larger plants. This Missouri study by contrast found that on average, seedlings and 1-leaf plants experienced dormancy at a rate about half that for larger plants. Overall, during any given year dormancy accounted for an average of 2.7% of the population.

While damage to the rhizome appeared to account for the subsequent growing season dormancy of some of the plants in this study, many plants that were documented as dormant for one or more seasons appeared to have intact roots and dormant buds. Shefferson et al. (2001) related growing season dormancy of *Cypripedium calceolus* ssp. *parviflorum* (small yellow lady's slipper orchid) to the number of freezing days in spring, precipitation and average spring temperature. No apparent relationships between weather phenomena and the percentage of dormant ginseng plants could be seen in this study, and

no relationship could be found between growing season dormancy and total herbivory by deer during the prior season. The causes of growing season dormancy in wild plants have seldom been discussed in the literature and warrant further study.

Deer herbivory patterns

Herbivory patterns observed in this study suggest that ginseng is not a preferred browse species for white-tailed deer. Though frequently consumed by deer, two-thirds of the plants were not browsed at all even during the highest years of deer browsing, and just over a quarter of the most productive 3-leaf plants were totally browsed. Over a quarter of the plants that were browsed were not completely browsed, and completely intact plants were often found adjacent to browsed plants. Browsing of ginseng plants continued through the growing season: more plants were browsed in mid to late summer than during late spring and early summer. If ginseng is considered a preferred species, it might be expected that the largest percentage of the browsed plants would be browsed earlier in the season as deer would selectively choose their favorite food first. These patterns suggest that while deer find ginseng to be quite palatable, it is not a highly preferred browse species.

While ginseng is not a preferred browse species, it nonetheless suffers substantial negative effects, especially among the largest plants, since deer disproportionately browsed the reproductive classes. On average, 4-leaf plants produce 15.8 seeds per reproductive plant, and 3-leaf plants produce an average of 5.9 seeds per reproductive plant. Since 27.6% of the 4-leaf plants and 26.6% of the 3-leaf plants were totally browsed by deer, much of their potential seed production is thwarted by deer browse.

The level of deer browse in the ginseng population is likely to be somewhat higher than is indicated in this study. At least some of the unexplained missing stems are likely to be attributable to deer browse, though this could not be proved with certainty. The number of unexplained missing stems was minimal in June, but increased in July and increased again in August during the one year August monitoring was conducted.

While monitoring was typically conducted until the end of July, a fourth monitoring event was held in late August of 1999 to verify that browsing by deer continued later into the season. However, since most berries had ripened and abscised by late August, it was predicted that August browse was likely to have minimal negative effects, and August monitoring was discontinued. Late season browsing appears to be less detrimental than early season browsing, as indicated by the lack of significant differences in regression or mortality for plants browsed in late July. Late browse may, however, have some negative effect on the vitality of the plants as indicated by the lowered numbers of pedicels created by 3-leaf plants following total browse in July. Deer browsing late in the season may also consume berries or cause their arrest in development. Ginseng berries do not survive the passage through the digestive system of a deer (Furedi and McGraw 2004).

Although deer browse that occurred later than July was not normally monitored in this study, its demographic effects are nonetheless captured in the transition matrix model. Consumption of berries late in the season results in the lowering of the seed to seedling transition rate, and a reduction in pedicels in the following year lowers the fecundity rates. Both of these effects would appear in the transition for the year following the browse event, indicating a delayed effect of deer browse on the population.

Effects of deer herbivory on ginseng's population dynamics

This study illustrates that even a non-preferred browse species can be negatively affected by moderately high densities of deer. At 14 deer/ km², ginseng's population growth rate was projected to be less than half a percent a year ($\lambda = 1.004$). Given that the deer density at this particular study site is nearly half that of other public land in east central Missouri (e.g. over 27 deer/ km² at Cuivre River State Park in 1999) (K. McCarty, 2004, personal communication), browsing pressure at higher densities of deer might be expected to cause the ginseng population growth rate to decline. Deer density for the seven ginseng populations in the West Virginia study (McGraw and Furedi 2005) was estimated in 2002 based on pellet counts at 15 deer/ km² to 49 deer/ km² (Furedi 2004).

Although the ginseng population in this study was projected to be growing by 3.4% ($\lambda = 1.035$) even under ambient deer browse, it was projected to grow by 6.4% if deer herbivory was removed. The West Virginia ginseng populations studied by McGraw and Furedi (2005) were projected to be declining by 2.7% under ambient conditions, and were projected to grow by 2.1% if the effect of browsing was removed.

Reproductive values in this study are significantly higher for 3- and 4-leaf plants when the effects of deer herbivory are removed, and are also slightly higher for 2-leaf plants. This difference reflects the consumption of flowers and fruit by deer and the abortion of fruit when plants are browsed completely before fruits have developed sufficiently. It also reflects the lowered fertility in the year following deer browse: plants that experience total browse by June are more likely to regress in size, and smaller size classes produce fewer seeds. Even plants that are totally browsed later in the season and

which do not regress in size during the following year are likely to produce fewer pedicels than they did prior to browse.

Stable stage distribution is also seen to shift when the effects of deer herbivory are removed. Under ambient conditions, there are proportionately more 2-leaf plants than 1-leaf plants, and 3-leaf plants make up the largest proportion of the population. In the absence of herbivory, the proportions of 1-, 2- and 3-leaf plants decline slightly, and the proportion of seeds increases markedly. Seedlings also increase slightly, and 1-leaf plants slightly outnumber 2-leaf plants. This shift in proportions reflects an increase in reproduction and increased survival of younger plants when herbivory is removed from the population.

The population observed moved closer to its stable stage distribution after two managed hunts were conducted to reduce the deer population. In 2004, 3-leaf plants outnumbered 2-leaf plants for the first time, and the proportions of each class closely resemble that of the stable stage distribution for the "no herbivory" matrix. This also represents the year of the highest projected population growth rate ($\lambda = 1.058$).

Elasticity analysis shows that the population growth rate is most sensitive to small changes in the proportion of 3-leaf plants that remain 3-leaf plants, and the proportion of 2-leaf plants that remain 2-leaf plants. There is little difference in the elasticity values for the ambient and the "no herbivory" matrices, indicating that while the individual transition rates shift from one matrix to the other, the impact of each transition rate does not significantly change, at least under the browsing pressure observed in this study. It is possible that greater browsing pressure could cause significant shifts in elasticities, as was seen in Knight (2004).

Elasticity analysis can help conservation managers target life stages that are most vulnerable. Elasticity analysis is just one tool, however, and must be used cautiously along with a sound understanding of the biology of a species. Shortcomings of elasticity analysis are discussed by Mills et al. (1998), who suggested that variation in sensitivities and elasticities over space and time may result in changes in the qualitative rankings of elasticities. They also pointed out that while conservationists may focus on one stage alone as being the most important, even stages with low elasticity values should not be ignored. These stages tend to exhibit the widest variance, and large changes in low ranked vital rates may have as much an effect on λ as small changes in vital rates with higher elasticity ranking. This is borne out in the ginseng population studied here: the transition rate from seed to seedling varied considerably from year to year (ranging from .0397 to .1671). Applying the average seed to seedling transition rate (0.8503) to the year with the lowest rate raises the projected population growth rate by 2.7%. Although the elasticity value for this transition rate is relatively low, large fluctuations (most likely caused in part by the removal of seeds by deer browse) have a large impact on the population growth rate.

LTRE analysis reveals that the reduction in stasis, particularly that of 3-leaf plants, contributed the most to the change observed in λ between the "no herbivory" and "ambient" matrices. This was also shown by other studies of woodland herbs (Ehrlen 1995b, Knight 2004, Furedi 2004), and could be predicted based on the high elasticity values associated with stasis. Fertility, however, was also a major contributor, despite its relatively low sensitivity values. Because the increase in fertility associated with the
removal of herbivory was large, it has a large effect on the change in λ despite low elasticity values.

Effect of harvest on the population growth rate

The removal by poachers of just 18 roots in the fall of 2004 (3% of the total population) cut the ginseng population's projected growth rate by more than half (from a growth rate of 4.4% to a growth rate of 1.2%). The large effect of the removal of mostly 3-leaf plants can be predicted by the importance of 3-leaf plants to the population: 3-leaf plants contributed 72% of the total seeds produced each year, and had a 75% probability of remaining a 3-leaf plant from one year to the next.

When comparing this study to others it should be noted that other studies have not excluded harvested plants from their transition matrices, and thus the mortality due to harvesting may be attributed to other population stressors, such as deer herbivory. While deer herbivory and harvest are both detrimental to ginseng's projected population growth rate, it appears that harvest has a greater effect. A small amount of herbivory, particularly late season herbivory, might almost be viewed as beneficial if it protects plants from being detected by harvesters.

Harvest is particularly harmful to the population if it is conducted annually, and the harvest simulation model shows that annual harvest of more than 8% of the 3- and 4leaf plants is not sustainable. This finding is in close agreement with the finding by Nantel et al. (1996) that little more than 5% of 3- and 4-leaf plants could be harvested. Annual harvest becomes more sustainable if the harvester properly plants seeds from the harvested plants. Even so, no more than 52% of the 3-leaf plants and 62% of the 4-leaf plants can be removed annually, and no smaller plants can be accidentally killed. Even with all these assumptions, the population growth rate is projected to barely sustain itself or to grow very slightly. The effect of increased deer herbivory, severe drought, disease outbreak or any other negative impact would likely cause the population growth rate to decline below the sustainable level.

While annual harvest of a small percentage of plants from a population would be sustainable, it is unlikely that a harvester would be so conscientious. This is particularly true if the harvested location is a readily accessible public site. If a harvester expects other harvesters to visit the site, he or she will be less likely to leave any plants behind for others to harvest (Carpenter 1980). If the harvester knows of a remote location, unlikely to be discovered by anyone else, then he or she may harvest conservatively each season, allowing roots to grow to larger and more valuable sizes before removing them. Based on this author's search for wild ginseng populations to characterize (Chapter 3 of this study), extremely few ginseng sites in Missouri are likely to be considered remote. Accessibility becomes even easier when the abundance of all-terrain and off-road vehicles are considered.

Management recommendations

Wild American ginseng faces many 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 this study and that of McGraw and Furedi (2005) indicate, ginseng sustainability is also threatened by increasing herds of white-tailed deer. Loss of habitat to forest conversion and development is also a threat.

Management of deer herds

This study suggests that deer herd reduction to moderate levels can assist in maintaining increasingly rare populations of American ginseng. While the ginseng population in this study was found to be growing very slightly at the level of 14 deer/ km² (36.4 deer per mi²), higher densities of deer at this site could be expected to cause the ginseng population growth rate to decline. And if a non-preferred browse species just barely grows at the level of 14 deer/km², more preferred browse species might be expected to decline at this deer density. This study and that of McGraw and Furedi (2005) show that reducing the density of deer is likely to increase ginseng's growth rate. Given the pressure of both legal and illegal harvest to ginseng populations, maintaining ginseng's population growth rate at higher levels is desirable.

The number of deer that a given region can support will vary, 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 good estimate, but a minimum of 10 cm of total

snow cover is required. Scheduling staff and a helicopter to perform such a count on short notice is both 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. The use of "indicator" species to gauge intensity of deer browsing has been discussed in numerous papers (e.g. Anderson 1994, Balgooyen and Waller 1995, Webster and Parker 2000, Webster et al. 2001, Fletcher et al. 2001). To be an effective indicator, a species should be palatable to the deer and should suffer progressively greater amounts of damage as the deer herd increases. A preferred browse species such as *Trillium* spp. may not be the best choice to monitor: if deer herds have remained at elevated populations long enough, preferred browse species may already be extirpated.

This study began in part to monitor the size of the deer herd at the study site, reasoning that ginseng is an increasingly rare herb that appeared to be adversely affected by excessive deer browse. It also provided staff an opportunity to gauge poaching pressure on the ginseng population, and to take actions to protect it.

Intensive monitoring of each individual plant in this study provided invaluable information, but also required a great deal of effort and expense. The monitoring alone in this study required over 400 person hours each season; this does not include any of the time required to establish the study, create monitoring sheets, enter the data, and to analyze the data.

However, results from this intensive effort may provide guidance for less intensive forms of monitoring. This study showed that the rise and fall in the percent of plants totally browsed by deer closely paralleled the rise and fall in the size of the deer

herd, and that total browse occurring by early June was more detrimental than that which occurred later in the season. When less than 10% of the ginseng population suffered total browse in early June (as was seen in 1999 and 2003-05), the ginseng population grew at levels of 4% or greater. When total browse in early June was close to or exceeded 10%, the ginseng population was seen to grow more slowly. If the browse levels found in this study are used as a guide, total browsing of more than 10% of the ginseng population in early June signals the need to reduce the deer herd.

Unfortunately, ginseng is far from the perfect indicator species to monitor deer browse. It is not common throughout the forest, and even where present, it can be elusive and hard to identify. Another drawback is its vulnerability to poaching. Poachers could decimate ginseng populations being monitored as indicators of deer herbivory, thus severely complicating the analysis of herbivory effects. But if a land manager chooses to monitor ginseng for other reasons, monitoring the number of ginseng plants totally browsed in early June can indicate when management of deer herds should be implemented. It is extremely important that monitoring of ginseng is conducted very discreetly, and that all study sites and plants be only cryptically marked.

Harvest regulations

The findings of this study appear to justify the recent move by the U.S. Fish and Wildlife Service to restrict export of roots to those 10 years of age and older. This regulation presents harvesters with the dilemma, however, of determining the age of a plant before digging up its root. Counting the neck scars of a plant in situ is difficult under the best of circumstances, and takes considerable time and effort. While it is safe to

assume that 4-leaf plants are ten years old or older, there are very few 4-leaf plants to be found in most ginseng populations, and restricting export to 4-leaf plants would severely restrict the amount of ginseng that could be harvested. Not all 3-leaf plants are ten years old or older, and this study found that a few 6 and 7-year-old plants were 3-leaf plants producing 3 and 4 berries each. Alternatively, it is not uncommon for a considerably older plant to revert in stage class, even to a 2-leaf plant. The best advice that can be given to responsible harvesters is to restrict their harvest to larger 3-leaf plants, and to leave the smaller 3-leaf plants.

Twenty-three years after the implementation of the CITES listing, Robbins (2000) pointed to the deficiency in knowledge of the population and conservation status of ginseng in each of the states that is approved to export it. He pointed to the need for systematic and continuous monitoring of the plant throughout its range. This study is one step toward accomplishing this goal.

Much more needs to be accomplished to determine if continued exportation of wild American ginseng will be detrimental to the species survival, and to determine how to maintain the species throughout its range at a level consistent with its historic role in the ecosystem. Long term studies need to be carried out throughout ginseng's natural range, and more data is needed to determine at what age the average ginseng plant is likely to produce enough seeds to replace itself. Lack of funding and staffing are the largest impediments to such research. Given the value of American ginseng as an export crop, funding should be given a high priority.

Additional questions for further study

There are many opportunities for further study concerning wild American ginseng. For example, more study is needed to understand animal seed dispersal of ginseng, especially the role that birds might play or may have played in the past.

The longevity of seeds in the soil warrants further study: how long can ginseng seeds persist and still remain viable? How often does seed germinate after only 8 months instead of the usual 18-20 months, and what are the factors that would cause seeds to break dormancy early? Is there a link between early berry ripening and germination in only 8 months?

Will a berry continue to ripen after the plant has been completely browsed? This study has observed that berries will abort if they are not fully formed when total browse occurs, but will green, fully-formed berries continue to ripen and develop if the plant is totally browsed? Will the seeds from these berries germinate at a normal rate?

Recruitment varied considerably in this study, and the likelihood of a seed becoming a seedling depends partly on whether it is consumed by seed predators. Common rodents found in the ginseng habitats of this study site are white-footed mice (*Peromyscus leucopus* Rafinesque) and chipmunks (*Tamias striatus* L.). How do the rise and fall of these rodent populations affect the population dynamics of ginseng?

As mentioned earlier, growing season dormancy provides an interesting study topic, and a difficult one, given that plants must be individually marked and followed for multiple years to document dormancy. Given its relative rarity, a large number of plants would have to be followed. Even in this large long-term study, the small sample size of dormant plants made it difficult to analyze the relationships that might cause dormancy.

The effects of different types of timber harvest on ginseng populations warrants study. It seems likely that dormant season selective harvest would have no long term ill effect on ginseng, and might even increase its vigor and prevent disease by letting in a little more light and air circulation. What are the effects of a clear cut on a healthy ginseng population, given its physiological need for shade? Can stressed plants simply go dormant and wait until shade returns? What effect does competition from thickly resprouting woody species after a clear cut have on ginseng?

Finally, the effects of fire on ginseng populations is a topic that has not yet been studied. From the limited data available in this study, it appears that high intensity prescribed burns may cause mortality in the smallest stage classes, but that low intensity fire is not likely to damage plants of any size. More data are needed to verify these findings. A related question is how does the intensity of a prescribed burn affect seed germination?

These questions hint at the many research opportunities that should be addressed if we are to fully comprehend the demography and ecology of wild American ginseng, and the effects of its continued harvest and export.

CHAPTER 3: ECOLOGICAL CHARACTERIZATION OF AMERICAN GINSENG IN THE MISSOURI OZARK HIGHLANDS

Introduction

The habitat characteristics of wild American ginseng have been studied at the heart of its native range in the Appalachians (e.g. Rock et al. 1999, McGraw et al. 2003), in Wisconsin (Carpenter 1980, Anderson 1996), in Illinois (Anderson et al. 1993) and in Arkansas (Fountain 1982, Fountain 1986), but relatively little research has been conducted at its western range edge in Missouri. Lewis and Zenger (1982) and Lewis (1988) investigated the biology and demography of two Missouri populations, but only briefly described the study sites. No other studies have been conducted describing the site characteristics of ginseng in Missouri.

Fountain (1982, 1986) examined 12 ginseng populations in 4 physiographic provinces of Arkansas (3 populations on Crowley's Ridge in northeast Arkansas, 4 in the Boston Mountains of northwest Arkansas, 2 on the Springfield Plateau province in northcentral Arkansas and 3 in the Ouachita Mountains of western Arkansas). Topographic characteristics and soil analysis was conducted, and herbaceous and woody vegetation were described. Anderson et al. (1993) characterized 33 ginseng populations in Illinois, including 16 northern sites, 7 sites and 10 southern sites.

Studying site conditions furthers an understanding of the ecological role of ginseng both at the community level and at the eco-regional level. This increasingly rare and highly valued species cannot be preserved without the knowledge and understanding of the natural communities in which it resides. Natural resource managers can utilize the information provided by this study to target the communities where ginseng is found, and

landowners can utilize it to select appropriate locations in which to sow "wild simulated" ginseng.

Research objectives

To identify the natural communities and ecological requirements of ginseng in the Ozark Highlands Section of Missouri, the following research questions were asked regarding site characteristics of ginseng populations in this ecological section:

At what slope position, slope steepness and aspect does ginseng typically occur? What is the average canopy closure?

Can topographic variables be used to generalize or predict ginseng locations?

What woody species are associated with ginseng presence in the overstory,

midstory and understory? What is the average basal area?

What woody and herbaceous species might be used as "indicators" of a suitable ginseng location?

What soil characteristics and nutrient levels are found in ginseng locations?

Methods

Random selection of sites to characterize ginseng habitat was not possible because ginseng is a heavily harvested and increasingly rare forest herb, and most random points even in the best of habitat would not reveal any ginseng plants. Also, neither ginseng's presence nor its absence in the landscape can be assumed to be "natural." Harvest of ginseng has occurred in Missouri since the mid 19th century, and this has likely caused the extirpation of ginseng in some locations. In other locations, ginseng may be present or more abundant than is "natural" because harvesters have spread the seed to these new locations. Thus no ginseng location can truly be defined as a "natural" population, nor can the absence of ginseng be said to indicate a location where ginseng does not occur. Since the objective of this study was to aid Missouri landowners in choosing appropriate sites for growing ginseng, it was not deemed necessary that a site be verified as "naturally occurring." Sites were chosen that supported healthy and reproducing ginseng colonies in "natural" (non-cultivated) forested settings. Criteria for site selection were the presence of at least a dozen ginseng plants, including at least some reproductive plants and some evidence of recent reproduction (preferably the presence of seedlings). These criteria were waived in three locations with fewer than 12 plants because these sites were deemed as very suitable ginseng habitat based on all indicators, and illegal harvest of ginseng seemed likely to have caused the lowered numbers of plants at each site.

Sites were chosen based on available information provided by government officials, ginseng dealers and harvesters. In addition, this author investigated several places that looked likely to support ginseng, based on studying topographical maps. This

"cold" searching was not fruitful in several instances, but did provide one of the sites characterized in this study. An attempt was made to collect data from sites as widespread geographically in the Ozark Highlands Section as possible. In all, nineteen sites in six subsections and thirteen counties (Figure 3.1) were characterized. More specific location information is withheld to protect the ginseng populations. Eleven of the sites were located on public land. Although harvest of ginseng roots was not permitted at any of these sites, this does not ensure that illegal harvest had not occurred. The remaining 8 sites were privately owned. Missouri state regulations allow harvest of ginseng roots on private land with the landowner's permission.

A standard monitoring protocol was established based on the protocol of Anderson et al. (1993) and Fountain (1982). A circular plot measuring 0.05 ha (12.6 m radius) was established at each site with the largest proportion of ginseng plants located at plot center. All ginseng plants in the circular plot were counted, and recorded by stage class (seedling, 1-leaf, 2-leaf, 3-leaf and 4-leaf). No plants with more than 4 leaves were observed. One site featured such a large number of ginseng plants that counting each stem in the circular plot would have been very difficult. For this one site, the total number of plants was estimated based counting the plants in three randomly placed circular plots measuring .0005 ha (1.26 m radius). This site had been seeded by the former landowner between 50 and 60 years earlier. Though ginseng may or may not historically have been found on this site (this is unknown), it was clearly a thriving and large population, and was therefore included in the study.

Slope position and slope shape were noted, and slope percent was measured using a Suunto clinometer. Slope aspect was recorded standing at plot center. Topographic

exposure (the protection from wind and sun based on surrounding topography) was estimated as "exposed" (protected on one side or less), "moderate" (protected on two or three sides) or "protected" (protected on all sides). Any disturbance to the site (deer herbivory, timber harvesting, ginseng harvesting, erosion or wind damage) was noted. No evidence of livestock grazing was noted in any of the sites.



Fig 3.1. Missouri counties where ginseng site data were collected (dark grey shading).

Canopy closure was measured at plot center using digital hemispherical photographs taken with a Nikon Coolpix 5700 SLR digital camera (5.0 megapixels) and a Nikon FC-E8 fisheye converter lens. The camera was positioned and leveled on a tripod Im above the ground. Canopy closure measured at this height should approximate the conditions at the level of the ginseng plants. Photographs were analyzed utilizing Gap Light Analyzer software (Version 2.0, Frazer et al. 1999).

The diameters of all trees greater than 5 cm at breast height (1.3 m) were measured, and their species was recorded. Understory stems less than 5 cm dbh were identified to species and counted. Understory density, and basal area and density of combined midstory and overstory were calculated for each site. Dominant overstory species were identified at each site based on the highest proportion of basal area. Data from all sites were then pooled, and importance values (the sum of relative basal area, relative frequency and relative density) were calculated for overstory trees (dbh >9 cm) and midstory trees (dbh >5 cm and \leq 9 cm).

All herbaceous species located in the plots were recorded. Since each site was visited only once, and data were collected between late May and late August, some early ephemeral herbaceous species would not be apparent at the time that data were collected. Some species of sedges (*Carex* spp.) and grasses (Poaceae) were unidentifiable due to the lack of mature fruit. Species that could not be readily identified in the field were collected (as permitted) for later identification. Nomenclature follows Yatskievych (1999) and Yatskievych and Turner (1990).

To determine which herbaceous species might serve as ginseng indicators, species were ranked according to their Coefficients of Conservatism (Ladd 1993). This system of ranking plants relative to one another was developed to distinguish non-facultative plants that may be found in many habitats (assigned a ranking of 0) from plants that are most obligate to intact natural habitats (assigned a ranking of 10).

Soil samples were collected from the first 15 cm of the soil profile, using a JMC 1.88 cm diameter soil sampling tube. Samples were air dried and submitted to the University of Missouri Extension Soil and Plant Testing Laboratory for analysis.

Results

General site characteristics

Fourteen of the populations (74%) occurred on sites that featured moderate topographic protection, and four of the populations (21%) were protected on all sides (Table 3.1). One site (S01 in Shannon County) was protected on only one side. Elevation ranged from 102 m to 302 m and averaged 214 m.

Sixteen of the ginseng populations (84.2%) occurred on slopes. Slope incline was variable, ranging from 8% to 78% (Figure 3.2). The ginseng populations tended to be found on lower to mid slope positions. Only three populations extended to upper slope positions. Shape of slope was typically concave. Three populations (15.8%) were located on level ground. Thirteen of the populations (68.4%) were located on slopes that featured northern aspects: five aspects were northeast, and eight were northwest (Figure 3.3). Only 3 sites (15.8%) occurred on southern aspects. Canopy closure was relatively consistent among the sites, ranging from 85.7% to 93.1% and averaging 90.8%.

Size and structure of ginseng populations

The number of ginseng plants found within the plot at each site varied from a low of 6 to a high of 1563. When the one very large planted population is removed, the number of ginseng plants ranges from 6 to 97/0.05 ha plot (mean = 37.3, SD = 28.0). At twelve of the ginseng locations (68.4%), ginseng plants were also observed in the general area outside of the circular plot. The large planted location (S1) had a great many plants surrounding the 0.05 ha plot. Another population (O1) was also quite large: it was being monitored for other purposes, and a thorough search of the larger surrounding area

	Disturbance present?	Deer browse	Deer browse	Rock slides	Ginseng harvested past 2 yrs; logged 10 yrs ago	Ginseng harvest likely	Deer browse	No apparent disturbance	Deer browse	Ginseng harvest likely	Recent flash flooding	No apparent disturbance	No apparent disturbance	Logged 30 yrs ago; ginseng harvest approx. 5 yrs ago	Recent ginseng harvest	Ginseng harvest likely	Deer browse	Deer browse	Ginseng harvest in past and maybe recently	No apparent disturbance - old growth sugar maple		
Topographic	exposure	protected	moderate	moderate	moderate	moderate	moderate	protected	protected	moderate	moderate	moderate	moderate	moderate	exposed	moderate	moderate	protected	moderate	moderate		
Canopy closure	%	92.5	89.7	88.7	92.7	90.9	85.7	90.5	91.9	91.2	91.3	92.6	93.1	92.3	90.7	90.2	90.7	88.2	91.9	90.7	90.8	1.8
activities and a	Siope position	lower	mid to lower mid	lower to upper	lower mid	lower to upper	lower	lower	mid	lower mid	level	lower	level	mid upper	mid	lower	mid	level	lower mid	lower		
Slope	. %	78	42	74	25	42	31	47	29	60	0	36	0	ø	31	55	40	0	59	42	36.8	23.4
1000	pect	ШN	MN	MN	MN	SE	MN	NΝ	NΝ	MN	ī	SE	·	Ш И	SE	ШN	NE		ЫN	NN		
×	AS	32	354	334	320	95	340	280	338	322	0	92	0	38	120	20	60	0	36	308		
Elevation	(m)	229	210	222	156	280	180	185	168	249	270	229	282	102	228	174	180	160	302	276	214.8	53.4
more plants	nearby?	yes	yes	yes	yes	ou	yes	yes	ou	ou	yes	ou	yes	yes	yes	ou	yes	ou	yes	no		
# ginseng plants	in plot	19	70	50	97	œ	44	85	12	15	70	28	19	35	1563	9	27	6	53	25	118	351
, and the second s	county	Boone	Boone	Boone	Bollinger	Dent	Franklin	Franklin	Franklin	Howell	Ozark	Oregon	Reynolds	Ripley	Shannon	Shannon	St. Louis	St. Louis	Texas	Washington	Mean	Std. deviation
Date	visited	6/25/2004	5/21/2005	5/20/2005	7/9/2005	7/2/2005	5/31/2004	6/1/2004	6/19/2004	7/8/2005	8/17/2004	6/22/2005	8/16/2005	7/1/2005	7/1/2004	6/25/2005	6/14/2004	6/19/2004	7/8/2005	6/26/2005		
Site	₽	B1	B2	B3	BL1	5	Ŧ	F2	F3	Ħ	6	OR1	Ł Ł	RI1	S1	S2	SL1	SL2	Т1	W1		

Table 3.1. Ginseng sites characterized in the Ozarks Highlands Section of Missouri. Bold print indicates low, high and outlying observations.



Figure 3.2. Percent slope of 19 ginseng sites in the Ozark Highlands Section of Missouri.



Figure 3.3. Aspect of ginseng sites, showing percentage of 16 sites that occurred on slopes with azimuths between the indicated value. Number of sites is given in parentheses. Three sites not shown were level, featuring no slope or aspect.

by three people revealed 863 additional plants. The Bollinger County site (B1) was also surrounded by numerous scattered colonies of ginseng. The remaining sites had approximately a few dozen scattered plants outside of the circular plot.

At seven of the locations (31.6%), including all of the smallest populations, ginseng was much harder to find, and few if any ginseng plants were observed outside the plot. The size of these isolated populations ranged from 6 to 28 plants. All life stages were present across the populations, but there was a noticeable absence of 4-leaf plants in many populations (Figure 3.4).

Evidence of harvest activity

Botanist Alan Brant observed evidence of poaching at the Bollinger County site (BL1) during the previous two seasons. Two sites (H1 and T1) were recommended to the author by former harvesters, so it is known that these colonies have experienced harvest in the past, but it is unknown how recently harvest has occurred. The largest planted location (S1) was harvested by the landowner during the last several years. One location (S2) revealed just six widely scattered and relatively small plants despite careful searching over a large area. This Shannon County site was extremely rich in herbaceous species, and had been surveyed ten years earlier by Alan Brant, who found numerous ginseng plants inhabiting the location at that time (A. Brant, 2005, personal communication). Another site (D1) also seemed to have far fewer plants than the site could support, and the eight plants that were found were widely scattered from the lowermost to the uppermost portion of the slope. The remaining sites presented no direct evidence of harvest, but harvest activity could not be ruled out at any of the sites.



Evidence of disturbance

One of the level sites studied (O1) had sustained flooding earlier in the growing season, but it was verified by nearby residents that the flooding was of brief duration (flash flood). Six sites exhibited evidence of deer browsing, and some plants may not have been apparent in these sites due to total deer herbivory. All sites except one occurred in second growth forest habitat, and were most likely logged between 60 and 100 years ago. The exception (W1) was a stand of old growth sugar maple. One site (BL1) was selectively logged approximately ten years ago. Two sites (H1 and T1) were selectively logged within the past 20 years. Sites RI1 and F2 were logged between 30 and 40 years ago. Two sites (B1 and B3) were very steep and prone to rock slides. No evidence of recent cattle grazing or disturbance by wild hogs was found at any of the locations.

Soil analysis

Laboratory nutrient analysis revealed widely varying results (Table 3.2). Soil pH ranged from 4.5 to 7.2. Calcium ranged from 1124 kg/ha to 12470 kg/ha. Even when these two most extreme results are excluded, the range for calcium still extended from 1971 kg/ha to 10261 kg/ha.

Soil texture analysis was conducted for 18 of the 19 soil samples: one sample did not contain enough soil for this analysis due to accidental partial loss of soil during the drying process. The largest component in soil texture at the majority of sites was either silt (9 sites) or sand (7 sites). Clay was the largest component in soil texture at only 2 sites. The majority of soils were classified as either silt loam or sandy loam.

sity of Missouri Extension Soil and Plant Testing Laboratory. One ation analysis. Lowest and highest observations are shown in bold.		CEC NO3-N NH4-N Sand Silt Clay	meq/100 g ppm ppm % % Texture	29.8 42.3 8.4 32.5 40.0 27.5 clay loam	9.7 0.8 10.6 10.0 75.0 15.0 silt loam	25.0 0.0 8.6 22.5 47.5 30.0 clay loam	10.9 1.0 7.1 37.5 52.5 10.0 silt loam	22.7 3.6 8.4 47.5 32.5 20.0 loam	12.1 23.8 6.2 20.0 70.0 10.0 silt loam	18.2 35.5 7.4 52.5 30.0 17.5 sandy loam	11.3 28.0 4.9 10.0 80.0 10.0 silt loam	12.7 2.4 11.6 32.5 50.0 17.5 silt loam	16.5 13.3 8.9 52.5 37.5 10.0 sandy loam	22.8 4.5 8.4 42.5 40.0 17.5 loam	9.3 0.3 4.9 72.5 20.0 7.5 sandy loam	11.7 0.9 5.5 17.5 70.0 12.5 silt loam	25.3 24.2 8.8 55.0 25.0 sandy clay loam	30.3 35.9 11.2 n/a n/a n/a	10.7 26.7 6.2 10.0 75.0 15.0 silt loam	12.3 28.6 7.1 12.5 75.0 12.5 silt loam	19.0 1.6 10.5 70.0 22.5 7.5 sandy loam	17.8 1.4 6.1 35.0 52.5 12.5 silt loam	17.3 14.5 7.9 35.1 49.7 15.1	9.3 0.0 4.9 10.0 20.0 7.5	30.3 42.3 11.6 72.5 80.0 30.0	60 150 21 202 202 63
e Unive aracteriz		¥	ı kg/h	546	218	574	263	356	243	351	294	257	262	523	95	241	546	637	214	190	318	440	l 345.	t 94.5	8 636.	7 153
ed by th duct chi		Mg	kg/ha	395	286	357	311	1688	329	1298	370	839	867	1362	174	351	1735	2419	258	352	732	1042	798.1	174.4	2418.	6357
conducte soil to con		Са	kg/ha	12470	1971	10361	2697	7208	2755	5848	3624	3725	5417	7715	1124	2295	8190	9271	2471	3036	6472	5362	5369.0	1123.9	12469.5	3174.9
amples, ount of s	Bray	- L	kg/ha	6.8	0.0	10.1	18.0	12.4	74.3	14.6	50.6	12.4	12.4	34.9	10.1	7.9	7.9	12.4	78.8	16.9	20.3	15.8	22.4	6.8	78.8	21.8
of soil s ent amo		O.M.	%	8.1	3.2	9.3	5.5	10.6	5.1	7.6	3.3	6.4	6.7	7.8	3.4	4.3	11.7	10.8	2.7	4.2	18.8	8.1	7.2	2.7	18.8	3.9
Ilysis c sufficie	N.A.	meq/	100g	0.0	4.0	0.0	3.5	0.0	4.5	0.0	1.5	1.0	1.0	0.0	6.0	5.0	0.0	0.0	4.0	4.0	1.5	1.5	2.0	0.0	6.0	2.1
iry and tain a t			Ηd	7.2	5.1	7.0	5.7	7.1	5.5	7.0	6.1	6.5	6.4	6.9	4.5	5.2	7.0	7.1	5.2	5.3	6.4	6.2	6.2	4.5	7.2	0.8
Laborato d not cont		# ginseng plants		19	70	50	97	8	44	85	12	15	70	28	19	35	1563	9	27	6	53	25				_
Table 3.2. sample di			Site ID	B1	B2	B3	BL1	D	Н Н	F2	F3	Ħ	0	OR1	R1	RI1	S1	S2	SL1	SL2	Т1	W1	Mean	Minimum	Maximum	Std deviatior

Basal area and density

Total Basal

Total basal area of each site (overstory and midstory combined) averaged 15.8 m^2 /ha (68 ft²/acre), ranging from 5.5 m² to 30.5 m²/ ha (23.7 ft²/acre to 131 ft²/acre) (Table 3.3). Mean overstory and midstory density was 536.8 stems/ha, ranging from 320 stems to 840 stems. Mean understory density was 1591.6 stems/ha, ranging from 860 stems to 2360 stems.

Site code	area (m² per ha)	Density (# of stems per ha)	Dominant overstory species	Understory density (# stems/ha)
F2	30.5	380	Acer saccharum, Quercus rubra	1140
F1	24.8	660	Quercus alba	1320
R1	24.5	840	Quercus macrocarpa	1740
01	21.5	600	Juglans nigra, Quercus rubra	2260
W1	21.2	400	Acer saccharum	1680
BL1	18.6	580	Acer saccharum	1020
F3	18.1	320	Fraxinus americana	1380
B1	17.0	320	Quercus muhlenbergii, Tilia americana	1260
T1	16.8	760	Tilia americana	1260
D1	14.6	600	Platanus americanus, Fraxinus americana	1800
H1	13.9	620	Acer saccharum	2100
B2	13.4	660	Acer saccharum	860
B3	12.5	380	Acer saccharum	2080
OR1	11.2	540	Quercus muhlenbergii, Carya tomentosa	2360
SL1	10.9	500	Acer saccharum	1140
RI1	10.2	640	Quercus alba	1940
S2	9.5	420	Nyssa sylvatica	2000
SL2	5.9	520	Fraxinus pennsylvanica	2100
S1	5.5	460	Juniperus virginiana	800
Mean	15.8	536.8		1591.6
Std dev	6.6	145.8		493.8
Median	14.6	540.0		1680.0

Table 3.3. Basal area at nineteen ginseng sites, and dominant overstory species.

Woody species composition

Sugar maple (*Acer saccharum* Marshall) exhibited the highest importance value in the overstory (Table 3.4) and was the leading dominant at 7 study sites. If basal area alone is considered, the next dominant species was white oak (*Quercus alba* L.), but importance values are higher for basswood (*Tilia americana* L.) and bitternut hickory (*Carya cordiformis* (Wangenh.) K.Koch) primarily because of the higher density (stems per ha) and higher frequency (occurring in more sites). Other species with importance values greater than 10.0 include American elm (*Ulmus americana* L.), slippery elm (*Ulmus rubra* Muhlenb.), white ash (*Fraxinus americana* L.), chinkapin oak (*Quercus muhlenbergii* Englem.) and musclewood (*Carpinus caroliniana* Walter).

Sugar maple also had the highest importance value in the midstory at the nineteen ginseng sites, but was closely followed by musclewood and pawpaw (*Asimina triloba* L.(Dunal)) (Table 3.5). Other important midstory species included flowering dogwood (*Cornus florida* L.), American elm, slippery elm, ironwood (*Ostrya virginiana* (Miller) K. Koch), basswood and white oak.

The understory of the nineteen sites was dominated by pawpaw, spicebush and sugar maple, both in frequency of occurrence and in density (Table 3.6). Other important understory species include flowering dogwood, ironwood, musclewood and bladdernut (*Staphylea trifoliata* L.).

Woody species	Common name	Basal Area (m ^{²/} ha)	Relative basal area	Density (stems per ha)	Relative density	Freq. (% sites found in)	Relative freq.	I.V.		
Acer saccharum	Sugar maple	3 87	25 47	91.6	26.2	78 9	11 2	62.9		
Tilia americana	Basswood	1 23	8 12	33.7	9.6	52 6	7.5	25.2		
Carva cordiformis	Bitternut hickory	0.86	5.65	23.2	6.6	42.1	6.0	18.3		
Quercus alba	White oak	1.51	9.95	15.8	4.5	26.3	37	18.2		
Ulmus americana	American elm	0.59	3.86	17.9	5.1	47.4	6.7	15.2		
Ulmus rubra	Slipperv elm	0.93	6.09	12.6	3.6	26.3	37	13.4		
Fraxinus americana	White ash	0.87	5.76	10.5	3.0	31.6	4.5	13.3		
Quercus muehlenbergii	Chinkapin oak	0.76	5.00	12.6	3.6	31.6	4.5	13.1		
Carpinus caroliniana	Musclewood	0.18	1.18	22.1	6.3	36.8	5.2	12.7		
Juglans nigra	Black walnut	0.60	3.98	7.4	2.1	26.3	3.7	9.8		
Cornus florida	Flwr dogwood	0.13	0.85	11.6	3.3	31.6	4.5	8.6		
Sassafras albidum	Sassafras	0.18	1.16	7.4	2.1	31.6	4.5	7.7		
Quercus macrocarpa	Bur oak	0.80	5.30	3.2	0.9	5.3	0.7	6.9		
Quercus rubra	Northern red oak	0.33	2.17	4.2	1.2	21.1	3.0	6.4		
Nyssa sylvatica	Black gum	0.27	1.80	5.3	1.5	21.1	3.0	6.3		
Platanus occidentalis	Sycamore	0.34	2.27	5.3	1.5	15.8	2.2	6.0		
Fraxinus pennsylvanica	Green ash	0.36	2.38	4.2	1.2	15.8	2.2	5.8		
Carya ovata	Shagbark	0.26	1.69	5.3	1.5	15.8	2.2	5.4		
Morus rubra	Red mulberry	0.11	0.75	5.3	1.5	21.1	3.0	5.2		
Juniperus virginiana	East. redcedar	0.15	0.99	9.5	2.7	5.3	0.7	4.4		
Ostrya virginiana	Ironwood	0.05	0.34	5.3	1.5	15.8	2.2	4.1		
Carya lacinosa	Shellbark hickory	0.18	1.17	4.2	1.2	10.5	1.5	3.9		
Carya tomentosa	Mockernut	0.15	0.96	3.2	0.9	10.5	1.5	3.4		
Planera aquatica	Water elm	0.07	0.43	5.3	1.5	5.3	0.7	2.7		
Prunus serotina	Black cherry	0.03	0.21	3.2	0.9	10.5	1.5	2.6		
Cercis canadensis	Redbud	0.05	0.32	2.1	0.6	10.5	1.5	2.4		
Celtis occidentalis	Hackberry	0.03	0.19	2.1	0.6	10.5	1.5	2.3		
Acer rubrum	Red maple	0.02	0.15	2.1	0.6	10.5	1.5	2.2		
Asimina triloba	Pawpaw	0.02	0.16	4.2	1.2	5.3	0.7	2.1		
Aesculus glabra	Ohio buckeye	0.03	0.21	3.2	0.9	5.3	0.7	1.9		
Juglans cinerea	Butternut	0.08	0.56	1.1	0.3	5.0	0.8	1.6		
Acer negundo	Boxelder	0.04	0.23	2.1	0.6	5.3	0.7	1.6		
Liquidambar styraciflua	Sweet gum	0.04	0.24	1.1	0.3	5.3	0.7	1.3		
Total basal area m ² per ha 15.12										
Standard deviation		0.72								

Table 3.4. Overstory (dbh >9cm) species found growing with ginseng, ranked by importance value (I.V. = relative basal area + relative density + relative frequency).

Table 3	3.5. Midstory (dbh >5 and ≤9cm) species found growing with ginseng	, ranked by importance
value	(I.V. = relative basal area + relative density + relative frequency).	
		From

Woody species	Common name	Basal Area (m ^{²/} ha)	Relative basal area	Density (stems per ha)	Relative density	freq. (% sites found in)	Relative freq.	I.V.
Acer saccharum	Sugar maple	0.135	17.12	36.8	17.4	57.9	13.3	47.8
Carpinus	ougai mapic	0 110	13.96	33.7	15.0	36.8	8.4	38.3
caroliniana	Musclewood	0.110	10.00	00.7	10.0	00.0	0.4 T 0	00.0
Asimina triloba	Pawpaw	0.101	12.77	30.5	14.4	31.6	7.2	34.4
Cornus florida	Flwr dogwood	0.063	8.00	16.8	8.0	31.6	7.2	23.2
Ulmus americana	American elm	0.043	5.44	10.5	5.0	36.8	8.4	18.9
Ulmus rubra	Slippery elm	0.054	6.80	11.6	5.5	26.3	6.0	18.3
Ostrya virginiana	Ironwood	0.044	5.52	11.6	5.5	31.6	7.2	18.2
Tilia americana	Basswood	0.039	4.97	10.5	5.0	26.3	6.0	16.0
Quercus alba	White oak	0.032	4.05	7.4	3.5	15.8	3.6	11.1
Planera aquatica	Water elm	0.037	4.64	8.4	4.0	5.3	1.2	9.8
Quercus muehlenbergii	Chinkapin oak	0.019	2.47	5.3	2.5	21.1	4.8	9.8
Prunus serotina	Black cherry	0.013	1.64	3.2	1.5	15.8	3.6	6.7
Celtis occidentalis	Hackberry	0.018	2.28	4.2	2.0	10.5	2.4	6.7
Morus rubra	Red mulberry	0.017	2.14	4.2	2.0	10.5	2.4	6.5
Aesculus glabra	Ohio buckeye	0.009	1.19	2.1	1.0	10.5	2.4	4.6
Sassafras albidum	Sassafras	0.008	0.96	2.1	1.0	10.5	2.4	4.4
Cercis canadensis	Redbud	0.007	0.93	2.1	1.0	10.5	2.4	4.3
Liriodenaron tulipifera	Tulip tree	0.008	1.00	2.1	1.0	5.3	1.2	3.2
Carya cordiformis	Bitternut hickory	0.006	0.81	1.1	0.5	5.3	1.2	2.5
Nyssa sylvatica	Black gum	0.006	0.78	1.1	0.5	5.3	1.2	2.5
Carya ovata	Shagbark hickory	0.005	0.67	1.1	0.5	5.3	1.2	2.4
Carya tomentosa	Mockernut	0.004	0.51	1.1	0.5	5.3	1.2	2.2
Diospyros virginiana	Persimmon	0.004	0.51	1.1	0.5	5.3	1.2	2.2
Fraxinus quadrangulata	Blue ash	0.003	0.33	1.1	0.5	5.3	1.2	2.0
Juniperus virginiana	Eastern redcedar	0.002	0.26	1.1	0.5	5.3	1.2	2.0
Viburnum rufidulum	Rusty blackhaw	0.002	0.26	1.1	0.5	5.3	1.2	2.0
Total basal area m ² p	0.788							
Standard deviation	0.036							

Species	Common name	Frequency (% sites)	# stems per ha		
Asimina triloba	Paw paw	78.9	474.7		
Lindera benzoin	Spicebush	63.2	287.4		
Acer saccharum	Sugar maple	63.2	134.7		
Cornus florida	Flowering dogwood	57.9	28.4		
Ostrva virginiana	Ironwood	52.6	27.4		
Carpinus caroliniana	Musclewood	42.1	136.8		
, Staphylea trifolia	Bladdernut	36.8	136.8		
Ulmus rubra	Slippery elm	36.8	29.5		
Fraxinus americana	White ash	36.8	18.9		
Quercus muehlenbergii	Chinkapin oak	36.8	10.5		
Hydrangea arborescens	Wild hydrangea	26.3	54.7		
Tilia americana	Basswood	26.3	21.1		
Celtis occidentalis	Hackberry	26.3	15.8		
Viburnum rufidulum	Rusty blackhaw	26.3	14.7		
Aesculus glabra	Ohio buckeye	26.3	10.5		
Carya cordiformis	Bitternut hickory	26.3	9.5		
Ulmus americana	American elm	26.3	6.3		
Rosa multiflora*	Multiflora rose	21.1	11.6		
Cercis canadensis	Redbud	21.1	9.5		
Fraxinus pennsylvanica	Green ash	21.1	5.3		
Nyssa sylvatica	Black gum	15.8	4.2		
Corylus americana	Hazelnut	10.5	8.4		
Ribes missouriensis	Gooseberry	10.5	6.3		
Morus rubra	Red mulberry	10.5	3.2		
Sambucus canadensis	Elderberry	10.5	3.2		
Sassafras albidum	Sassafras	10.5	3.2		
Rhus aromatica	Aromatic sumac	10.5	2.1		
Planera aquatica	Water elm	5.3	18.9		
Ulmus alata	Winged elm	5.3	10.5		
Hamamalis vernalis	Witch hazel	5.3	8.4		
Juniperus virginiana	Eastern red cedar	5.3	4.2		
Carya laciniata	Shellbark hickory	5.3	2.1		
Platanus occidentalis	Sycamore	5.3	2.1		
Acer rubrum	Red maple	5.3	1.1		
Bumelia languinosa	Gum bumelia	5.3	1.1		
Carya tomentosa	Mockernut hickory	5.3	1.1		
Cornus drummondii	Rough dogwood	5.3	1.1		
Euonymus atropurpeus	Wahoo	5.3	1.1		
Fraxinus quadrangulata	Blue ash	5.3	1.1		
llex decidua	Possum haw	5.3	1.1		
Quercus rubra	Red oak	5.3	1.1		
Quercus velutina	Black oak	5.3	1.1		
Symphiocarpus orbiculatus	Coral berry	5.3	1.1		

Table 3.6. Understory woody species found growing with ginseng in nineteen ginseng populations in the Ozark Highlands Section of Missouri.

* exotic species

Herbaceous species and vines

A total of 110 herbs, 12 ferns, 15 grasses, 15 sedges and 14 vines were identified in the nineteen ginseng study sites (Appendix 4). Fifty-three species ranked 5 or higher in the Coefficients of Conservatism scale (Table 3.7).

Of the 166 species identified, only Virginia creeper (*Parthenocissus quinquefolia* (L.) Planchon) was found in all sites, but this common vine of Missouri forests ranks only 3 in the Coefficients of Conservatism scale, and is therefore unlikely to serve as an indicator of ginseng habitat. Three relatively conservative species (Coefficients of Conservatism ranking of 6) were found in approximately three quarters of the locations: Jack-in-the-pulpit (*Arisaema triphyllum* L.(Schott)), wild yam (*Dioscorea quaternata* (Walter) J. Gmelin) and bellwort (*Uvularia grandiflora* Sm.). Other important species of the same ranking but lower frequency include wild ginger (*Asarum canadense* L.), long-awned wood grass (*Brachyelytrum erectum* (Roth) P. Beauv.), northern maidenhair fern (*Adiantum pedatum* L.), and goldenseal (*Hydrastis canadensis* L.).

Species ranked higher on the Coefficient of Conservatism scale did not tend to occur in more than one fifth to one third of the ginseng sites, but given the conservative nature of these species, their presence might be considered potential indicators of ginseng habitat. These species include white bear sedge (*Carex albursina* Sheld.), white lettuce (*Prenanthes alba* L.), carrion flower (*Smilax lasioneuron* Hook.), American spikenard (*Aralia racemosa* L.), bulblet fern (*Cystopteris bulbifera* (L.) Bernh.), white baneberry (*Actaea pachypoda* Elliott), Virginia snakeroot (*Aristolochia serpentaria* L.), black cohosh (*Cimicifuga racemosa* (L.) Nutt.) and walking fern (*Asplenium rhizophyllum* L.).

Table 3.7. Conservative herbaceous species found growing with ginseng, ranked by Coefficients of Conservatism (C.C.) and frequency (% sites occupied).

Scientific name	Common name	C.C.	Frequency (%)
Carex albursina	White bear sedge	10	21.1
Prenanthes alba	White lettuce	9	21.1
Smilax herbacea	Carrion flower	8	26.3
Aralia racemosa	Spikenard	8	15.8
Cystopteris bulbifera	Bulblet fern	8	15.8
Actaea pachypoda	White baneberry	7	36.8
Aristolochia serpentaria	Virginia snakeroot	7	36.8
Cimicifuga racemosa	Black cohosh	7	26.3
Asplenium rhizophyllum	Walking fern	7	21.1
Aster cordifolius	Heart-leaved aster	7	15.8
Hybanthus concolor	Green violet	7	15.8
Polygonatum biflorum	Solomon's seal	7	15.8
Arisaema triphyllum	Jack-in-the-pulpit	6	78.9
Dioscorea quaternata	Four-leaf yam	6	78.9
Uvularia grandiflora	Bellwort	6	73.7
Asarum canadense	Wild ginger	6	57.9
Brachyelytrum erectum	Long-awned wood grass	6	57.9
Adiantum pedatum	Northern maidenhair fern	6	52.6
Hydrastis canadensis	Goldenseal	6	42.1
Hepatica nobilis var obtuse	Round-lobed hepatica	6	15.8
Geranium maculatum	Wild geranium	5	52.6
Polystichum acrostichoides	Christmas fern	5	52.6
Sanguinaria canadensis	Bloodroot	5	52.6
Cystopteris protrusa	Lowland brittle fern	5	42.1
Hydrophyllum appendiculatum	Woolen breeches	5	31.6
Vitis aestivalis	Summer grape	5	31.6
Arabis laevigata	Smooth bank cress	5	26.3
Prenanthes altissima	Tall white lettuce	5	26.3
Verbesina virginica	White crownbeard	5	26.3
Viola pubescens	Yellow violet	5	26.3
Anemonella thalictroides	Rue anemone	5	21.1
Viola triloba	Three-leaved violet	5	21.1
Bromus pubescens	Woodland brome	5	15.8
Vitis vulpine	Frost grape	5	15.8

Discussion

This study confirms eastern studies showing that ginseng inhabits a wider niche than previously supposed (Rock et al. 1999, McGraw et al. 2003). Rock et al. (1999) created a model utilizing assumptions of where ginseng would most likely be found at Great Smoky Mountains National Park in the southern Appalachians and found ginseng most often in predicted rich cove forests, but also found that the abundance of ginseng was greater in small pockets of habitat deemed only "moderately suitable". McGraw et al. (2003) placed random transects in forests of the central Appalachians (mostly West Virginia) and found ginseng more often on east slopes (at mid and high elevations) and west slopes (at low elevations) than on expected low rich north slopes. While both of these studies found ginseng in greater abundance at less predicted locations, the authors attribute this as a potential artifact of many years of ginseng harvesting. Harvesters may have concentrated their efforts in the most likely ginseng locations, leaving sub-optimal locations to serve as refugia for ginseng populations.

The nineteen ginseng sites characterized in this study were not randomly chosen, and therefore may not be a representative sampling of the occurrence of ginseng in Missouri's Ozark Highlands. Personal bias did not affect which sites should be included in the study, since all sites that were located were included. Personal bias, however, may have influenced how some of the sites were located, since searches by the author and her sources were based on assumptions of where ginseng was likely to be found. It is quite possible, therefore, that ginseng may be found on an even wider range of sites than is indicated by this study.

General site characteristics

Although most of the ginseng sites studied occurred on slopes, three (15.8%) were located on level ground on stream terraces. While none of the sites studied by Fountain (1982) were located on level ground, 12.1% of the study sites in Anderson et al. (1993) were level. Although ginseng appears to be found on slopes more often in this broader Midwest region, these findings indicate that level areas can also be suitable growing areas for ginseng, provided they are well drained and not prone to sustained periods of flooding.

Ginseng was generally found on steeper slopes in this study than was found by either Fountain (1982) or Anderson et al. (1993). The average slope in Fountain's study was 28.8% and ranged from 2 to 50%. Anderson and his co-authors found that 48% of the sites were located on slopes of less than 20%, and 46% were located on slopes between 20% and 60%. By contrast, this study found only 21% of the sites on slopes of less than 20%, and 68% on slopes between 20% and 60%. Two sites (11%) were located on very steep slopes of greater than 70%. Large individual ginseng plants have also been noted to grow in crevices of rock ledges (Farrington, personal observation).

Aspect of the ginseng sites located on slopes was found to be predominantly northerly, as were most of the sites in the Arkansas and Illinois sites. Despite finding the majority of sites on northerly aspects, all three studies found some sites occurring at southerly aspects. If all three studies are combined, ginseng was found at sites representing each cardinal bearing, indicating that given proper conditions, it's possible for ginseng to grow on a slope facing any direction.

Mean canopy closure (90.8%) was found to be higher than the average of 80% reported by Fountain (1986). The difference may perhaps be due to differences in methodology, but Fountain does not describe his method. Anderson et al. (1993) does not report canopy closure.

While the degree of canopy of closure was found to be consistent, basal area values ranged widely among sites. Two of the sites with low basal areas (S2 and SL2) both featured higher than average understory stem densities. Thus shading at the herbaceous plant level may result from a well developed understory or midstory. The site with the lowest basal area (S1) was unexpectedly the site with the most ginseng plants (the Shannon County site that had been planted). Overstory and midstory stem density was slightly below average at this site, and understory stem density was the lowest of any site. Despite this, the canopy closure measured was equal to the mean (90.7%). High canopy closure despite low basal area and stem density can be explained at this site by the predominance of eastern redcedar. The branches of eastern redcedar are particularly dense and full, and account for a large proportion of the shading provided at this location.

Ginseng population size and structure and evidence of harvest

Considerable variation was seen in the number of ginseng plants found in each 0.05 ha plot. The smallest seven populations were isolated, with few or no ginseng plants found in the area surrounding the study plot. Such small and isolated populations may be limited in their ability to reproduce (Hackney and McGraw 2001). No seedlings were observed in three of the seven small and isolated populations.

Only one other population (O1) lacked any seedlings at all. This was a very large population, and the lack of seedlings observed in the plot could be an aberration. Given that smaller plants senesce earlier in the season than larger plants (Carpenter and Cottam 1982, Lewis and Zenger 1982), it is possible that seedlings had already senesced when this site was monitored in late August of 2004. It is also possible that seedlings washed away during a growing season flooding event at the site.

The population structure of the Missouri ginseng populations varied widely, possibly reflecting temporally variable structure which is common in many woodland herbs (reviewed in Whigham 2004). Varying levels of seedling recruitment appear to influence in part the differences observed in these nineteen ginseng populations. Two populations exhibit a higher proportion of seedlings than any other stage class, indicating a very successful year for recruitment. One of the sites that exhibited a high proportion of seedlings (SL1) has been observed for several years, and did not exhibit such a high proportion of seedlings in any other year. Three populations exhibit higher proportions of 1-leaf plants, possibly indicating a successful recruitment year in the recent past. Higher proportions of 2-leaf plants, as seen in nine populations, may either indicate a successful cohort moving up in stage, or more likely, a history of harvesting that has removed a proportion of the larger plants.

The effects of two previous years of harvest are quite evident in the stage structure exhibited by the Bollinger County site (BL1). This plot was dominated by 2-leaf plants; no 4-leaf plants and very few 3-leaf plants were observed. The loss of so many larger plants greatly diminished the reproductive potential of this population, and the proportions of seedlings and 1-leaf plants are low. Two populations that are known to

have experienced previous harvest (H1 and T1) both exhibit larger numbers of 2-leaf plants than 3-leaf plants, though the difference is not large, possibly indicating harvest has not taken place recently.

If the presence of more 2-leaf plants than 3-leaf plants indicates harvesting activity, then at least half of these sites exhibit signs of previous harvesting. The absence of 4-leaf plants at 13 of the 19 locations may also point to former or present harvest activity. Alternatively, these patterns may point to the presence of a high density deer population, which could be resulting in more regression in size class, as was demonstrated in Chapter 2. Eight of the 19 populations in this study (those in Boone, Franklin, and St. Louis counties) occur in areas that are likely to experience higher deer populations due to prohibitions on hunting and surrounding suburban habitat.

Soil analysis

The analysis of soil samples from the ginseng sites studied shows a high degree of variability which was also observed in the studies from Illinois (Anderson et al. 1993) and Arkansas (Fountain 1982) (Table 3.8). Average levels of calcium, magnesium and potassium were higher at Missouri's ginseng sites than at those of Illinois and Arkansas. Levels of phosphorous were lower in Missouri than those found in Illinois, and similar to those found in Arkansas. Soil texture in Missouri sites was similar to that found in Illinois sites. Arkansas sites exhibited higher proportions of clay content.

Calcium is the dominant cation in most forest soil solutions (Fisher and Binkley 2000). Persons and Davis (2005) cite two unpublished studies by Bob Beyfuss in New York and Jim Corbin in North Carolina that link high levels of calcium to healthy stands

of wild ginseng. Beyfuss coordinated with local ginseng harvesters, and asked them to provide him with a properly collected soil sample from their most productive harvesting location. He obtained 65 soil samples, and found that calcium averaged 4,515 (\pm 1,889) kg/ha, and pH averaged 5.0 (\pm 0.7).

		Р	Ca	Mg	К	Sand	Silt	Clay
Region	pН	kg/ha	kg/ha	kg/ha	kg/ha	%	%	%
Missouri Ozark Highlands (n=19)	4.5-7.2	22	5369	798	346	35.1	49.7	15.1
Illinois (Anderson et al. 1993)								
Southern Illinois (n=10)	4.4-6.0	45	1764	435	218	15.6	67.4	17.0
Central Illinois (n=7)	5.3-5.9	53	2992	573	156	34.3	45.7	20.0
Northern Illinois (n=16)	4.9-7.3	63	4011	697	204	41.5	38.0	20.5
Arkansas (Fountain 1982)								
Crowley's Ridge (n=3)	4.9-5.5	47	425	45	120	21.4	9.5	69.1
Boston Mtns (n=4)	4.6-5.4	12	1125	135	143	39.0	14.4	46.6
Springfield Plateau (n=2)	6.7-6.8	14	1375	70	60	34.3	19.2	46.5
Central Ouchita Mtns (n=3)	5.8-6.5	20	1600	82	85	32.2	11.4	56.4

Table 3.8. Comparison of analysis of soil samples collected from ginseng locations in Missouri, Illinois and Arkansas. All samples were collected from the first 0 to 15 cm of the soil profile.

Corbin collected soil samples from approximately 130 ginseng sites in the Great Smoky Mountains National Park. He rated each ginseng site as "good", "moderate" or "poor" based on plant size, age diversity of the stand and plant health (lack of disease or chlorosis of leaves). Corbin found average calcium levels to be 5624 kg/ha at "good" ginseng sites, 2993 kg/ha at "moderate sites" and 1479 kg/ha at "poor" sites. Corbin also states that a 5:1 calcium to magnesium ratio was found at "good" ginseng sites (J. Corbin, 2005, personal communication).

There was no apparent correlation in this study between ginseng quality or quantity and the levels of nutrients found in soil analysis. Few of the plants observed looked diseased or chlorotic. Two of the smallest populations (S2 and D1) had nutrient levels well above average, yet only a handful of plants were found. Both of these sites, however, were rich sites that appeared capable of supporting much larger populations of ginseng, and site S2 was known to have supported a larger population in the past. It is therefore very difficult to judge the quality of a site by the number or size distribution of the plants present, since a location at which only a few smaller plants are found may be one that previously supported a large colony and has been heavily harvested.

Nonetheless, this study appears to corroborate that high levels of calcium are found in ginseng locations: calcium was found to exceed 2000 kg/ha at 17 of the 19 sites. The site exhibiting the lowest calcium soil levels (1123 kg/ha at site R1) was located on level ground at the base of a spring. It is possible that the plants at this site were obtaining the calcium they required from the spring water flowing through the rhizosphere.

Corbin's finding that the ratio of calcium to magnesium is generally 5:1 is also corroborated by this study. The ratio is equal to or exceeds a 5:1 ratio in twelve of the ginseng sites, and is close to this ratio in five more sites. The two sites with the highest calcium levels (B1 and B3) have much lower calcium to magnesium ratios (20:1).

Woody indicator species

Sugar maple represented the most important overstory species overall, and might therefore serve as an indicator species of good ginseng growing sites. Examination of individual sites, however, reveals a diversity of dominant species including oaks (white, chinkapin and bur), basswood, black walnut, white ash, black gum, and even eastern redcedar.
Anderson et al. (1993) also found sugar maple to be highest in importance value, primarily due to its dominance in the northern and southern Illinois. White oak was found to be dominant in the central Illinois sites. Fountain (1986) found white oak to be most important overall, but each province in Arkansas was dominated by a different species: tulip-poplar (*Liriodendron tulipifera* L.) at the Crowley's Ridge sites, white oak at the Boston Mountains sites, white ash at the Springfield Plateau sites, and mockernut hickory at the Ouachita Mountains sites. It is apparent from these diverse findings that sugar maple may indicate a good ginseng growing site, but it is by no means a required component of a good growing site.

Sugar maple was also the most important component of the midstory, closely followed by musclewood and pawpaw. This concurs with the findings of Anderson et al. (1993) in Illinois, where sugar maple was also the leading component, followed by ironwood, slippery elm, sassafras and basswood. Fountain (1986) did not separate the midstory from the understory. He found flowering dogwood to be most important in the understory, followed by ironwood, mockernut hickory, white oak and black gum, and pawpaw. The understory in this study was dominated by pawpaw, spicebush and sugar maple.

Herbaceous indicator species

While no single herbaceous species emerged as an indicator species for ginseng locations, a suite of species emerged that may be useful in assessing suitable habitat, including Jack-in-the-pulpit, wild yam, bellwort, white bear sedge, white lettuce, carrion flower, American spikenard, bulblet fern, white baneberry, Virginia snakeroot, black

cohosh, wild ginger, goldenseal, wild geranium and bloodroot. One grass, long-awned wood grass (*Brachyelytrum erectum* (Schreb.) P. Beauv.), was found in 58% of the ginseng locations and is relatively easy to identify. A former ginseng harvester referred to this grass as "sang grass" because his father used it as an indicator of likely ginseng abundance (P. McKenzie, 2005, personal communication). Two sedges were frequently found in ginseng locations: wood sedge (*Carex blanda* (Dewey)) and white bear sedge (*Carex albursina* (Sheld.)). The latter is a very conservative species and is readily identifiable by its very wide leaves. Good fern indicators include walking fern (*Asplenium rhizophyllum* L.), Christmas fern (*Polystichum acrostichoides* (Mihx.) Schott), northern maidenhair fern (*Adiantum pedatum* L. var. pedatum), rattlesnake fern (*Botrychium virginianum* (L.) Sw. var. virginianum) and lowland brittle fern (*Cystopteris* protrusa (Weath.) Blasdell).

The plants found by Anderson et al (1993) are listed in detail in Anderson et al. (1984). They reported 48 herbs (including 1 grass and 1 sedge), 6 ferns and 12 vines that occurred in at least 25% of the sites in one or more of the 3 sectors of Illinois. Species occurring in at least 25% of all of the Missouri sites in this study included 40 herbs (including 1 grass, 2 sedges), 4 ferns and 6 vines. In comparing the species list between the two studies, 70% of the species found in a quarter or more of the Missouri sites were also found in a quarter or more of at least one sector of Illinois (Table3.9).

The most common herbs in Illinois ginseng sites were false Solomon's seal (*Maianthemum racemosum* (L.) Link *ssp. racemosum*), Jack-in-the-pulpit, enchanter's nightshade (*Circaea lutetiana* L.), bloodroot (*Sanguinaria canadensis* L.), wild licorice (*Galium circaezaens* Michaux), wild geranium (*Geranium maculatum* L) and sweet

Table 3.9. Herbaceous species found in 25% or more of all ginseng sites in Missouri and ginseng sites in at least one sector in Illinois (Anderson et al. 1984). Missouri Coefficients of Conservatism ranking (C.C.) and frequency in Missouri ginseng sites are presented.

Common name Actaea pachypoda White baneberry		C.C.	Frequency	
		7	36.8%	
Arisaema triphyllum	Jack-in-the-pulpit	6	78.9%	
Asarum canadense	Wild ginger	6	57.9%	
Circaea lutetiana	Enchanter's nightshade	1	63.2%	
Desmodium glutinosum	Pointed tick trefoil	3	57.9%	
Desmodium nudiflorum	Bare-stemmed tick trefoil	4	26.3%	
Dioscorea quaternata	Four-leaf yam	6	78.9%	
Galium circaezans	Wild licorice	4	57.9%	
Galium concinnum	Shining bedstraw	4	42.1%	
Geranium maculatum	Wild geranium	5	52.6%	
Geum candense	White avens	2	42.1%	
Hydrastis canadensis	Goldenseal	6	42.1%	
Hydrophyllum appendiculatum	Woolen breeches	5	31.6%	
Impatiens sp.	Jewelweed	3	47.4%	
Maianthemum racemosum	False solomon's seal	4	78.9%	
Osmorhiza claytoni	Hairy sweet cicely	3	36.8%	
Phlox divaricata	Blue phlox	4	68.4%	
Phryma leptostachya	Lopseed	2	36.8%	
Pilea pumila	Clearweed	4	26.3%	
Podophyllum peltatum	May apple	4	42.1%	
Polygonum virginianum	Virginia knotweed	1	31.6%	
Sanguinaria canadensis	Bloodroot	5	52.6%	
Uvularia grandiflora	Bellwort	6	73.7%	
Viola pubescens	Yellow violet	5	26.3%	
Viola sororia	Blue violet	2	84.2%	
Ferns				
Adiantum pedatum	Northern maidenhair fern	6	52.6%	
Botrychium virginianum	Rattlesnake fern	4	52.6%	
Cystopteris protrusa	Lowland brittle fern	5	42.1%	
Polystichum acrostichoides	Christmas fern	5	52.6%	
Vines				
Menispermum canadense	Moonseed	4	47.4%	
Parthenocissus guinguefolia	Virginia creeper	3	100.0%	
Smilax hispida	Bristly greenbriar	3	26.3%	
Smilax lasioneuron	Carrion flower	8	26.3%	
Toxidendron radicans	Poison ivv	1	68.4%	
Vitis aestivalis	Summer grape	5	31.6%	
	9.4P0			

cicely (*Osmorhiza claytonia* (Michaux) C.B. Clarke). Common ferns included rattlesnake fern, lowland brittle fern and Christmas fern.

Fountain (1986) reported a total of 28 species of herbaceous plants (including grasses and ferns) occurring in the 12 Arkansas sites, and identified as most common Christmas fern, tick trefoil (*Desmodium* spp.), false Solomon's seal, wild yam, rattlesnake fern, bedstraw (*Galium* spp.), northern maidenhair fern, and broad beech fern (*Thelypteris heaxonoptera* (Michx.) Fée). He did not list the other species observed. All of the most common species found by Anderson and Fountain were also found commonly in the ginseng sites in this study, with the exception of broad beech fern, which was found in just one Missouri location.

Natural community description

The species found in this Missouri study correspond well to those listed by Nelson (2005) as characteristic of two terrestrial natural communities in Missouri: mesic loess/glacial till forest and mesic limestone/dolomite forest. The mesic loess/glacial till forest type is characterized as occurring on lower backslopes in ravines found in breaks and hills of landscapes highly dissected by streams. Soils are predominantly silt loams and silty clay loams, and are well drained and very deep. Dominant canopy species are varied, but include the species noted in this study: northern red oak, white oak, sugar maple, basswood, white ash, bitternut hickory and black walnut. Understory species include pawpaw, musclewood and shade tolerant shrubs such as spice bush. Canopy closure is nearly complete. The number of herbaceous species is high, and nearly all characteristic species listed by Nelson (including ginseng) were found in one or more of the ginseng sites in this study. This forest type is found in northern Missouri and along the northern and eastern edges of the Ozark Highland Section. Sites in this study that fit this community description include one site in Boone County (B2), one in Franklin County (F3), the Bollinger County site (BL1) and one St. Louis County sites (SL1).

Most of the remaining sites are best described by a closely associated natural community, the mesic limestone/dolomite forest type. This forest community is found in similar landscapes as the mesic loess/glacial till community, and is characterized by the same species with the addition of calciphiles such as chinkapin oak and bladdernut. Soils are moderately deep silt loams overlaying clay residuum of limestone or dolomite formations, and are slightly more alkaline. This forest type is scattered throughout much of the state, including most of the Ozark Highlands Section.

The three sites located on level ground (O1, R1 and SL2) are best described by the dry-mesic bottomland forest type, found on elevated bottomland in narrow valleys, and subject to occasional flash flooding (but not to sustained periods of saturation). This forest type is restricted in Missouri to the Ozark Highlands Section.

Nelson (2005) cites potential threats to these forest types as logging, sugar maple invasion due to complete absence of fire, grazing, excessive browsing by white-tailed deer, exotic species invasion, trail erosion, root digging and conversion to other uses. The ginseng sites visited in this study exhibited a few of these threats including root digging, damage from deer browsing, conversion to sugar maple, and some trail erosion. It is unclear whether sugar maple conversion would negatively affect ginseng, as it is very shade tolerant and is frequently associated with sugar maple. Nonetheless, the loss of

diversity in the natural community brought about by sugar maple invasion may have indirect negative consequences for ginseng.

Exotic species were virtually absent in the ginseng sites visited. Multiflora rose (*Rosa multiflora*) was observed in four sites, but was present only as isolated stems, and given its high light requirements, it would not be expected to thrive under the closed canopy. Dandelion (*Taraxacum officinale*) was observed in the one unusual planted site in Shannon County, but was not abundant. Nelson cites the exotic species most likely to threaten these natural communities as garlic mustard (*Alliaria petiolata* (M. Bieb.) Cavara & Grande), which was not observed in any of the ginseng sites. Land managers seeking to protect ginseng and its natural communities should be aware of this serious threat and act quickly to prevent its spread if it is observed.

CHAPTER 4: EFFECTS OF SOWING DEPTHS ON GERMINATION SUCCESS OF "WILD SIMULATED" AMERICAN GINSENG

Introduction

Information concerning the best methods of sowing wild American ginseng is limited. One seed germination trial was conducted in West Virginia (McGraw 2000) to address current federal guidelines that require ginseng root diggers to plant seed from the ginseng they harvest at the collection site. Without direction, harvesters have sown seed at depths ranging from 0 to 10 centimeters (McGraw 2000). McGraw's single germination trial was conducted in one location, with six treatment depths in 2 cm increments from 0 to 10 cm. McGraw found germination to be highest for seeds sown 2 centimeters deep, and his findings led the US Fish and Wildlife Service to recommend that root diggers plant seeds from collected ginseng plants at this depth.

Van der Voort (2005) conducted a large seed germination experiment in West Virginia, but the purpose of the study was to test the presence of a seed bank in American ginseng. No differences in seed depth were included in this study; all 16,000 berries were broadcast along transects.

Given how the economic importance of ginseng as a forest crop, there is a need to look at the effect of depth on germination of ginseng seeds in a forested setting. Numerous brochures and instruction manuals recommend how and where to sow ginseng, but none point to scientific studies to support their recommendations. Providing sound recommendations to growers may influence the likelihood of growing success or failure. With the proper information, landowners of forested land have an opportunity to grow a valuable crop with minimal effort. Encouraging wild simulated cultivation may alleviate some of the poaching pressure on native wild ginseng populations, and provides landowners with an incentive to maintain high integrity forested habitat.

Ginseng seeds exhibit deep simple morphophysiological dormancy (Baskin and Baskin 1998), requiring warm followed by cold stratification before germination can occur. Ginseng seeds sown in McGraw's study were fresh seeds, still encased in their berries (as would be the seeds sown by a root harvester). Ginseng growers, however, typically purchase stratified ginseng seed. These seeds have been stored for one year in moist sand, and are therefore clean (no berries remaining). They are shipped in mid fall to be sown immediately, and are expected to germinate the following spring, allowing the seed purchaser to bypass one year of the eighteen months required for ginseng seed to germinate.

Conducting germination trials in different locations and climatic conditions may aid policy makers in refining their recommendations to root diggers for sowing seed from plants collected. Recommending to these harvesters the most effective depth at which to sow seeds may increase reproduction success from their efforts, and may help to perpetuate the species. This also has implications for ecological restoration efforts.

This study asks the following questions:

Does sowing depth affect germination of American ginseng sown in the Missouri

Ozark Highlands? If so, which treatments differ? Does location within the Ozark Highlands affect germination? Does sowing depth affect future survivorship of seedlings?

Methods

Study sites

Seed germination trials were conducted using stratified seeds sown in November of 2003 and again in November of 2004. The seeds were sown in four Missouri ecological subsections (Meramec River Hills, Osage River Hills, Outer Ozark Border, and Gasconade River Hills). Locations were chosen to approximate natural ginseng habitat as described by Anderson et al (1993) and Rock et al. (1999). Sites were located on moderate slopes, at mid to lower slope positions, and were generally concave linear in shape. The canopy at each site consisted of mature trees providing greater than 80% shading. All sites featured northeast aspects, with moderate topographic protection, providing shelter from winds.

The Meramec River Hills location was on public land in Franklin County near the Meramec River. The study site was on the lower part of a 21% slope, facing northeast (68°). The canopy was dominated by white oak (*Quercus alba*) and the understory by pawpaw (*Asimina triloba*) and spicebush (*Lindera benzoin*). The soil has been characterized as a well-drained Bardley cherty silt loam overlaying Eminence dolomite (USDA-NRCS 2003a, Nigh and Schroeder 2002).

The Osage River Hills location was on private land in Osage County adjacent to the Osage River. The study site was located toward the bottom of a 19% slope, facing northeast (16°). The canopy dominants were white oak in the overstory, and hackberry (*Celtis occidentalis*), Ohio buckeye (*Aesculus glabra*), and musclewood (*Carpinus caroliniana*) in the understory. The soil has been characterized as a moderately well-

drained Gatewood silt loam overlaying Gasconade dolomite (USDA-NRCS 2003b, Nigh and Schroeder 2002).

The Outer Ozark Border location was on public land in Boone County near Cedar Creek north of the Missouri River. The study site was located midslope on a 47% slope, facing northeast (60°). The canopy was dominated by white oak and shumard oak (*Quercus shumardii*), with bitternut hickory (*Carya cordiformis*) in a co-dominant position. The understory was composed of ironwood (*Ostrya virginiana*), spicebush, sugar maple and musclewood. The soil has been characterized as a well drained Clinkenbeard flaggy clay loam overlaying Mississippian limestone (USDA-NRCS 2003c, Nigh and Schroeder 2002).

The Gasconade River Hills location was on public land in Maries County along Cedar Creek east of the Gasconade River. The study site was located on the lower part of a 16% slope, facing northeast (24°). The canopy dominants were white oak and northern red oak (*Quercus rubra*), with sugar maple dominating the mid canopy and the understory. The soil has been characterized as a well drained Moko gravelly clay loam overlaying Gasconade dolomite (USDA-NRCS 2005b, Nigh and Schroeder 2002).

Sowing method

Stratified seeds were purchased from a local ginseng grower (Barney Frye's Ginseng Patch) in 2003 and a different local grower (Ozark Mountain Ginseng) in 2004. The seeds were received in September (2003) and October (2004) and were cleaned with a 10% bleach solution to minimize fungal colonization. The seeds were float tested and any seeds that floated were removed. Smaller seeds and any badly discolored seeds were

removed so that the remaining seeds were relatively uniform. The seeds from the first supplier (2003) contained many discolored seeds; the seeds from the second supplier (2004) required very little sorting. The seeds were kept moist in a refrigerator until they were sown in late November.

In November of 2003, 245 stratified seeds were sown at each of the four locations at 7 treatment depths, from 0 cm to 6 cm in one centimeter increments. (Total for all locations = 980 seeds sown, 140 per treatment). Five 0.25 m^2 plots were placed haphazardly. Each plot was located no closer than 1 m to one another and no farther than 10 m of one another, avoiding large rocks or other obstacles. Steel rebar was placed at each corner. Each 0.25m^2 plot consisted of 7 rows by 7 columns of individually sown seeds, for a total of 49 seeds in each plot. Each seed was spaced 8.3 cm apart horizontally and vertically. This spacing would be close for mature plants, but was deemed sufficient to prevent competition between emerging seedlings.

Assignment to treatment depth was in accordance with a randomized Latin square design (Figure 4.1), which ensured that each treatment was found in each column and each row of the square. This method equalizes the effect of micro-environmental gradients such as soil moisture, nutrients and slope. The same randomized Latin square was used for all plots so that a wooden planting template could be made with the locations and depths of each seed marked. This eased the difficulty of planting each seed at a different depth. A wooden dowel with graduated centimeter markings was used to make the hole for each seed, which was dropped down the hole then covered with soil. Seeds planted at the 0 cm treatment were placed on the ground at the appropriate location and were depressed very slightly to minimize the possibility of being washed down slope.

2	1	5	3	4	0	6
6	5	2	0	1	4	3
0	6	3	1	2	5	4
5	4	1	6	0	3	2
4	3	0	5	6	2	1
1	0	4	2	3	6	5
3	2	6	4	5	1	0

Figure 4.1. Randomized Latin square showing treatment depths (0 to 6 cm). Each treatment depth appears in each row and each column, and is interspersed throughout the square. Seeds were sown according to this pattern in each plot.

Sowing took place in late November, after leaf fall. Prior to sowing, the leaf cover was gently pulled away from each plot, and after sowing, the leaf cover was placed back on top of the plots to preserve soil moisture. This mimics the natural process: ginseng berries abscise between August and September, and the falling leaves serve as their mulch.

This process was repeated in late November of 2004. Five new quarter-meter plots were haphazardly placed beside the 2003 plots, and seeds were sown as before.

Monitoring method

Seed plots were monitored weekly from mid-April until late May (monitoring ceased after no new germination was recorded), and soil moisture at the depth of 2 cm

was noted each week. The wooden planting template was placed over each quarter-meter plot so that the exact location of each seed could be ascertained and a monitoring sheet with grids for each seed was used to record germination success. The week that each germinant emerged was also recorded.

Each seedling was examined carefully to ensure it was a ginseng seedling. Ginseng seedlings superficially resemble black snakeroot (*Sanicula canadensis*) seedlings and Virginia creeper (*Parthenocissus quinquifolia*) seedlings. If there was any doubt as to identity, a hand lens was used to examine the upper surface of the leaflets: ginseng has a line of erect hairs along the midrib of the leaflet (Anderson et al. 2002). If a seedling was not fully unfurled and its identity could not be determined with certainly, the grid on the monitoring sheet was marked with a question mark and the plant was reexamined during the following week. Sometimes only a stem was found where a seedling had germinated, the apparent victim of snail or slug herbivory. In these cases, the stem would be examined very closely to determine its species. If identified as ginseng, these stems were counted as successful germinating seedlings, though their future survival was in doubt.

In April-May of 2004, the germination success was recorded for seeds sown in November of 2003. In April-May of 2005, the germination success was recorded for seeds sown in November of 2004, and the plots from 2003 were monitored for new germination and survivorship of previous seedlings. New seedlings in 2003 plots were distinguished from returning plants both by their location (monitoring sheets from 2004 identified the location where each returning plant should be found), and by careful examination: older plants have a slight crook or bump where the petiole joins the stem. In

a seedling, there is no separation between stem and petiole (the stem is the petiole), and therefore no crook. Seedlings sown on or near the surface could also often be identified by the presence of the seed at the base of the cotyledon. These examinations allowed confirmation of new germination as opposed to possible missed germination in 2004.

The area surrounding each location was searched for any evidence of natural ginseng populations that could interfere with the results of this germination experiment. No other ginseng plants were found at three of the locations. Two small non-reproductive non-seedling ginseng plants were found at the Boone County site in the spring of 2004, located approximately 8 m upslope from the germination plots. A thorough search was then conducted for any mature ginseng in the area and for any seedlings that did not appear to be emerging in the exact locations where the seeds had been sown. No evidence of either was found. The area was searched again in 2005, and only one of the two plants found in 2004 was present.

Statistical analysis

The data were analyzed for an effect of treatment (depth), site, interaction between treatment and site, and row and column of the Latin square on the proportion of germination. Proportions were derived from the forty-nine individual positions within each of the five Latin squares at each location. Four locations resulted in a total of 28 proportions per treatment. All proportions were arcsine square root-transformed prior to statistical analysis. Analysis of variance (ANOVA) was used to test for an effect of treatment using SAS PROC GLM (SAS Institute 2002-03), and treatment means were tested using Fishers LSD. The magnitude and significance of the trend in the germination

response as treatment depth increased was tested using linear, quadratic and cubic orthogonal polynomial contrasts. The data were also analyzed separately by location for an effect of treatment.

Finally the data were analyzed for an effect of treatment on the proportion of surviving seedlings that germinated in the first year, using SAS PROC GENMOD. The survivorship data were not analyzed separately by location due to small sample size.

Results

2003 cohort germination

During the first spring of the germination trial (2004), seeds were first observed to germinate during the week of April 12 and the last germination was observed May 20. The majority of the seeds that germinated (79.7%) emerged by the last week of April. A total of 347 seeds sown in 2003 germinated (35.4%). An effect of treatment depth was detected (F=3.54, p=.0029) (Figure 4.2). No effect of site was detected (F=.49, p=.6899), there was no significant interaction between site and treatment (F=1.30, p=.2014), nor any effect of row (F=.78 p=.7556) or column (F=.94, p=.5463) of the Latin square. Seeds sown on the soil surface (0 cm treatment) germinated at the lowest rate (22.1%). As shown by LSD analysis, this was significantly lower than germination of seeds sown at all other treatments with the exception of those sown at 5 cm deep. Seeds sown at 3 cm deep germinated at the highest rate (45%). The cubic polynomial contrast (F=5.41, p=.0217) indicates significant curvature in the germination trend. Germination showed an upward trend beyond the 0 cm treatment, as demonstrated by a marginally significant linear contrast (F=3.87, p=.0516). Germination leveled off as treatment depth increased, as indicated by the significant quadratic poloynomial contrast (F=8.21, p=.0049).

During the second year of observation (spring 2005), substantial additional germination was observed in the 2003 cohort plots: 318 new seedlings emerged from the 633 seeds that had not germinated the previous year. Three-quarters of the new seedlings (75.5%) emerged by the last week in April. The number of new seedlings at each treatment depth did not differ significantly from the number at each treatment depth that



Figure 4.2. Observed germination in 2004 of ginseng seeds sown in four locations (counties) in 2003. Seeds sown at 0 cm germinated at a significantly lower rate than those sown at all other depths except 5 cm (F=3.54, p=.0029). No effect of location was detected (F=.49, p=.6899). A total of 980 seeds were sown (245 seeds at each site), and 347 (35.4%) germinated in 2004.

emerged in 2004 (X^2 =5.395, p=.494). When added to the 347 seeds germinated in 2004, the total germination of 2003 seeds was 67.9% (665 of 980 seeds). Analysis found an effect of treatment (F= 5.61, p=.0012), an effect of site (F=8.33, p<.001), and a significant interaction between site and treatment (F=2.15, p=.0077). As before, there was no effect of row (F=.85, p=.6624) or column (F=.93, p=.5562). Due to the effect of site, and the interaction between site and treatment, the sites were analyzed separately (Figure 4.3).



Figure 4.3. Cumulative germination by site (county) in 2004 and 2005 of ginseng seeds sown in 2003, showing significant differences. At each site, 245 seeds were sown, 35 per treatment. In Franklin county (a), there was no significant effect of treatment (F=1.65, p=.1693). In Osage County (b), seeds sown at 1 cm germinated at a marginally higher rate than all other treatments except 2 cm (F=2.33, p=.0580). In Boone County (c), seeds sown at 0 cm germinated at a significantly lower rate than all other treatments (F=11.49, p<.001). In Maries County (d), seeds sown at 0 cm germinated at a significantly lower rate than all other treatments except 6 cm (F=3.70, p=.0063).

At the Franklin County site, no significant effect of treatment was detected (F=1.65, p=.1693). At the Osage County site, the treatment effect was marginally significant (F=2.33, p=.0580). Seeds sown at 5 cm germinated at the lowest rate (57.1%), and seeds sown at 1 cm germinated at the highest rate (91.1%). The significant quadratic

polynomial contrast (F=4.73, p=.0377) indicates that germination leveled off as treatment depth increased.

At the Boone County site, the treatment effect was highly significant (F=11.49, p<.001). Seeds sown at 0 cm germinated at the lowest rate (14.3%) and this was significantly lower than the germination rate of seeds sown at all other treatments. Seeds sown at 2 cm germinated at the highest rate (77.1%). Germination increased significantly beyond the 0 cm treatment, as indicated by the significant linear polynomial contrast (F=14.87, p=.0006), then leveled off and decreased as indicated by the significant quadratic (F= 44.31, p<.001) and cubic (F= 8.67, p=.0062) polynomial contrasts.

At the Maries County site, the effect of treatment was significant (F=3.70, p=.0063). Seeds sown at 0 cm germinated at the lowest rate (48.6%), a significantly lower rate than those sown at all other levels except those sown at 6 cm. Seeds sown at 2 cm germinated at the highest rate (85.7%). Germination leveled off beyond the 0 cm treatment, as indicated by the significant quadratic polynomial contrast (F=16.65, p=.0003).

2004 cohort germination

Germination for the 2004 cohort was first observed April 10, 2005 and continued until May 20, 2005. Nearly all (95.1%) of the germinating seedlings emerged by the last week in April. Average germination for seeds sown in 2004 was 77.1% (756 of 980 seeds germinated). Analysis found an effect of treatment (F=7.10, p=.0002), an effect of site (F=12.48, p<.0001), and a significant interaction between site and treatment (F=1.57, p=.0776). There was no effect of row (F=1.35, p=.1446) or column (F=1.15, p=.3031) of the Latin square. Due to the effect of site, and the interaction between site and treatment, the sites were analyzed separately (Figure 4.4).



Figure 4.4. Germination by site (county) in 2005 of ginseng seeds sown in 2004, showing significant differences. At each site, 245 seeds were sown, 35 per treatment. In Franklin county (a), there was no significant effect of treatment (F=1.20, p=.3326). In Osage County (b), seeds sown at 0 cm germinated at a significantly lower rate than all other treatments (F=8.04, p<.0001). In Boone County (c), seeds sown at 0 cm germinated at a significantly lower rate than seeds sown at 1,2,3 and 4 cm (F= 6.0, p=.0003). In Maries County (d), seeds sown at 0 cm germinated at a significantly lower rate than seeds sown at 1,2,3 and 5 cm (F=2.95, p=.0221).

At the Franklin County site, as before, there was no significant effect of treatment (F=1.20, p=.3326). At the Osage County site, the effect of treatment was significant

(F=8.04, p<.0001). Seeds sown at 0 cm germinated at the lowest rate (45.7%), a significantly lower rate than those sown at all other treatments. Seeds sown at 2 cm germinated at the highest rate (97.1%). Germination increased significantly and then leveled off after the 0 treatment, as indicated by the significant quadratic (F=31.58, p<.0001) and cubic (F=11.87, p=.0017) polynomial contrasts.

At the Boone County site, the effect of treatment was significant (F= 6.0, p=.0003). Seeds sown at 0 cm germinated at the lowest rate (40.0%), a significantly lower rate than seeds sown at depths between 1 and 4 cm. Seeds sown at 1 cm germinated at the highest rate (97.1%). Germination increased significantly after the 0 cm treatment, and then decreased at each successive depth after 1 cm, as indicated by the significant quadratic (F= 18.20, p=.0002), cubic (F= 6.72, p=.0146) and marginally significant linear (F= 3.87, p=.0584) polynomial contrasts.

At the Maries County site, the effect of treatment was significant (F=2.95, p=.0221). Seeds sown at 0 cm germinated at the lowest rate (68.6%), and this rate was significantly than that for those sown at 1, 2, 3 and 5 cm. Seeds sown at 1 cm germinated at the highest rate (97.1%). Germination increased significantly and then leveled off after the 0 treatment, as indicated by the significant quadratic (F=5.97, p=.0207) and cubic (F= 7.13, p=.0121) polynomial contrasts.

Survivorship of seedlings

Of the 347 seedlings observed in 2004, 288 (83.0%) returned in the spring of 2005 (Figure 4.5). There were no significant differences in survivorship among the sowing depth treatments (χ^2 =5.53, p=.4778).



Figure 4.5. One year survivorship of ginseng seedlings sown at different depths. Proportion is survivorship in 2005 of 347 seedlings observed in 2004. No significant effect of treatment depth was detected (X^2 =5.53, p=.4778).

Discussion

Most effective and least effective seed depths

This study found differences in germination among the four sites, though all were chosen to best approximate natural ginseng habitat and were similar in many regards. Nonetheless, there are consistencies in the findings of the eight trials (four sites x 2 years). Seeds sown on the surface of the soil performed worst in all but two of the trials. Seeds sown between 1 and 3 cm performed best in the trials. These findings agree with the findings in West Virginia by McGraw (2000), and confirm that a sowing depth of 2 cm is a good recommendation for planting of seed by root harvesters.

While this study found similar germination results to those found by McGraw at the 2 cm sowing depth (an average of 82.9% for this study versus 75.4% for McGraw's study), it found higher germination at other depths than did McGraw. McGraw's germination success of seeds sown on the surface was only 10.0%, while seeds sown on the soil surface in this experiment averaged a germination rate of 51.8% for the eight trials. Perhaps the difference may be attributed to the fact that McGraw planted fresh berries while this study used clean stratified seed. The bright red berries lain on the surface of the soil in McGraw's study would be far more likely to gain the attention of seed predators such as mice and chipmunks (Carpenter 1980, Van der Voort 2005) than the dull brown cleaned seeds of this study. Also, McGraw's seeds had to survive two seasons to germinate while the seeds in this study only had to survive one season (though many DID survive two seasons for germinating, including many planted on the soil surface). McGraw's germination rate of 10.0% corresponds well with the germination rate observed in the study population of natural ginseng reported on in Chapter 2: the

seed to seedling transition rate for six Missouri populations averaged 8.5% from 1999-2005. It may be that ginseng growers experience higher germination from broadcasted cleaned seeds than would be expected from natural dispersal of ginseng berries.

There were also differences between the two studies at the 4 cm depth (74.6% for this study versus 47.3% for McGraw) and at the 6 cm depth (63.6% versus 25.8%). It is unknown what accounts for these differences. Since the germination of seeds sown at 2 cm deep is similar in both studies, it is not likely that underground seed predation is significantly greater for McGraw's seeds than for the seeds in this study, nor is the presence of the berry likely to account for the difference. It is possible that varying soil textures affecting moisture or temperature levels at deeper levels are responsible for the differences. Since McGraw's study was conducted only once, perhaps the weather conditions during the trial affected germination success.

Effect of site

Site appears to have an influence on the success of germination, especially for seeds sown on the surface of the soil. One site (Boone County) in this study experienced considerably lower germination at the 0 treatment (14.29% for 2003 seeds and 40.0% for 2004 seeds) than the other sites. This site featured the steepest slope of the four sites (47% versus 16-21%). Its aspect of 60° was more easterly than two of the sites, and the drier conditions created by the combination of a more exposed site and a steeper slope may explain the poorer germination of surface sown seeds here. One of the sites in this study, Franklin County, exhibited no significant effect for treatment in either of the years this study was conducted. Even though this site featured the most easterly aspect of the

four sites (68°), it was heavily shaded by low-growing pawpaw and spicebush and appeared to be the most mesic of the four sites.

While site appears to have strongly influenced the success rate of seeds sown on the surface of the soil, it does not appear to influence greatly the success rate of seeds sown at other depths.

Delayed germination

An unexpected result was the low germination (35.4%) in the first year of this trial and subsequent large number of seedlings germinating from this cohort in the second year after sowing (32.4% of the total seeds, or 50.2% of the remaining seeds). While Van der Voort (2005) demonstrated the presence of a seed bank, it seems surprising that so few seeds would germinate in the first year, particularly since 77.1% of the 2004 cohort of seeds germinated in their first year after stratification. The supplier of the 2003 cohort was contacted to ensure that all seeds had been stratified for one year before purchase in 2003 and this was confirmed. It is possible, however, that these seeds did not receive adequate warm stratification: they were shipped earlier in fall than were the seeds in 2004. Seeds with deep simple morphophysiological dormancy require that the period of warm germination be composed of first a period with warmer temperatures (summer), followed by a period of slightly less warm temperatures (autumn) (Baskin and Baskin 1998). The seeds may have been removed from their stratification beds too early in fall, and storage in the refrigerator until planting may have prevented many of them from receiving the remainder of their warm stratification requirement. These seeds might

therefore not have been able to break dormancy until they had experienced the appropriate length and fluctuation of warm stratification during the following year.

Survivorship of seedlings

It was expected that one year survivorship of seedlings would vary significantly among treatments, especially for the zero treatment. This was not the case, at least in the one year that this could be measured, and given the relatively small sample size of approximately 50 plants per treatment. Possibly the results would be different if tested over several years with larger sample sizes. It is also possible that no difference was detected because once a seedling emerges and becomes established, it may be able to develop a deep enough root system in the first season to offset any disadvantage of starting life from epigeous germination.

CHAPTER 5: RECOMMENDATIONS FOR GROWING "WILD SIMULATED" AMERICAN GINSENG IN THE MISSOURI OZARK HIGHLANDS

Site selection for growing American ginseng

Based on the findings of this study, it is likely that ginseng may be grown in more sites than might previously have been supposed. It will not, however, grow everywhere. Presented here are some guidelines for choosing an appropriate location.

Choose a location that is well shaded, either by mature trees or by a well developed understory. Canopy closure should be at least 85%, preferably more. A northern exposure (northeast to northwest) is preferable, but a southern exposure is adequate if it is sufficiently shaded, especially if it is surrounded by opposing slopes that provide added protection.

Ginseng prefers a moist, but well-drained location. Planting on a slope helps to ensure there is adequate drainage. While ginseng can grow on very steep slopes, a gentle slope provides more moisture and is easier to work on during planting and harvesting.

Look for companion species commonly found with ginseng. Good overstory trees include sugar maple, basswood, white oak, and bitternut hickory, black walnut, chinkapin oak and white ash. In southeastern Missouri locations, tulip poplar is a good companion tree. If pawpaw, spicebush, musclewood or bladdernut are found in the understory and the site is adequately drained, it is very likely to be a good place to plant ginseng.

Herbaceous species to look for include jack-in-the-pulpit, wild yam, bellwort, wild ginger, long-awned wood grass, maidenhair fern, Christmas fern, wild geranium lowland brittle fern, goldenseal and bloodroot. If two or three of these species are growing, it's likely to be a good location to sow ginseng. Rarer species to look for

include white bear sedge, white lettuce, carrion flower, spikenard, bulbet fern, white baneberry, Virginia snakeroot, black cohosh, or walking fern. If one or more of these species is present, it's probably a very good place to grow ginseng. If none of the above species are present, obtain a soil sample. If calcium is found to be high (more than 2000 lbs/acre (2250 kg/ha)), then consider planting ginseng if all other conditions are met. If a site is judged suitable but calcium is found to be less than 1000 lbs/acre (1125 kg/ha), Person and Davis (2005) recommend adding gypsum (100 lbs/1,000 ft² (5 kg/m5 kg/m²)) immediately after fall seeding and before covering with leaves.

Practical considerations in choosing a location include choosing a spot that is as protected from poachers as possible. This may make choosing a less than optimal location a good choice, as a poacher is more likely to investigate a rich northern slope than a marginal southeastern slope.

Sowing wild simulated America ginseng

Based on the findings of this study, ginseng seeds should be sown at a depth of approximately 1 in (1 to 3 cm). While this method is ideal, it is not always practical, depending on how many seeds a ginseng grower is sowing. An efficient way to sow numerous seeds at this depth is to dig a long furrow (running up and down the slope to provide good airflow), drop the seeds into the furrow and cover. Digging of furrows, however, isn't always practical in a natural forest setting, and can lead to high density of plants if the grower is not careful. To prevent disease problems that may arise from unusually high densities, Persons and Davis (2005) recommend no more than 2 mature plants/ft² (22 plants/m²). A grower may prefer to simply broadcast the seeds, accepting

that a higher percentage of seeds will be lost in this method. If the site chosen is mesic, the aspect is mostly northerly, and the slope is gentle, this may be the most efficient course of action, and Persons and Davis (2005) recommend a sowing rate of 4 to 5 seeds/ft² (44 to $55/m^2$). If the site is less ideal, and if the slope is steeper, the time and effort should be taken to bury the seed. This study and that of Van der Voort (2005) found substantially lower germination of broadcasted seeds on eastern and southern aspects.

Seeds will have the best chance to survive if they are covered with a 1 to 2 in (2.5 to 5 cm) layer of leaves as natural mulch. This can be accomplished most easily by sowing the seeds before the leaves fall for the season, allowing the falling leaves to cover them naturally. The disadvantage of this method is that forests of Missouri often experience dry and hot weather during the fall, and the ginseng seeds are sensitive to drying out. To avoid this problem, the seeds in this study were sown in November, when all the leaves had fallen and leaves were placed immediately atop the newly sown seeds.

If seeds are broadcasted, best results will be achieved if leaf fall has already occurred. The leaves should be raked clear, and the seeds are scattered directly on the soil surface. Leaves are then raked back on top of the seeds, the raking action helping to work the seeds down into the soil. To save effort, rake a 1.5 m (5 ft) wide swath across a slope at a time, pulling the leaves down slope. After broadcasting the seed, move up the hill and clear the next swath, pulling the leaves down on top of the area just sown. For the last swath, pull leaves from above down onto the sown seeds, leaving a bare patch above. This method is recommended by Persons and Davis (2005).

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Appendix 1. Yearly transition matrices for six combined populations of American ginseng in east-central Missouri. Matrix for 2004-05 is shown excluding and including harvested roots.

1999-2000									
	Seed	Sdlg	1-lf	2-lf	3-lf	4-lf	Dorm		
Seed	0	0	0	1.151	3.67	9	0		
Sdlg	0.113	0	0	0	0	0	0		
1-lf	0	0.765	0.444	0.022	0	0	0		
2-lf	0	0	0.247	0.581	0.04	0	0.6		
3-lf	0	0	0	0.247	0.84	0.667	0.2		
4-lf	0	0	0	0	0.01	0.333	0		
Dorm	0	0	0.012	0.086	0.08	0	0.2		
			2000-01						
	Seed	Sdlg	1-lf	2-lf	3-lf	4-lf	Dorm		
Seed	0	0	0	0.474	3.53	18.14	0		
Sdlg	0.046	0	0	0	0	0	0		
1-lf	0	0.829	0.641	0.084	0.01	0	0.13		
2-lf	0	0	0.262	0.643	0.13	0.143	0.56		
3-lf	0	0	0	0.169	0.79	0.429	0.13		
4-lf	0	0	0	0	0.04	0.429	0		
Dorm	0	0	0.019	0.032	0	0	0.19		
			2001-02						
	Seed	Sdlg	1-lf	2-lf	3-lf	4-lf	Dorm		
Seed	0	0	0	0.21	2.3	1.25	0		
Sdlg	0.04	0	0	0	0	0	0		
1-lf	0	0.821	0.443	0.068	0.01	0	0.4		
2-lf	0	0	0.377	0.574	0.13	0	0.5		
3-lf	0	0	0.008	0.309	0.73	0.125	0.1		
4-lf	0	0	0	0	0.08	0.75	0		
Dorm	0	0.051	0.033	0.019	0.03	0.125	0		

	2003-04							
	Seed	Sdlg	1-lf	2-lf	3-lf	4-lf	Dorm	
Seed	0	0	0	0.591	3.45	10	0	
Sdlg	0.08	0	0	0	0	0	0	
1-lf	0	0.813	0.637	0.055	0	0	0.17	
2-lf	0	0.016	0.23	0.586	0.11	0	0.5	
3-lf	0	0	0	0.315	0.76	0.444	0.17	
4-lf	0	0	0	0	0.06	0.444	0	
Dorm	0	0.016	0.022	0.017	0.05	0.111	0.17	

_		Seed	Sdlg	1-lf	2-lf	3-lf	4-lf	Dorm
	Seed	0	0	0	0.464	2.72	9.467	0
	Sdlg	0.101	0	0	0	0	0	0
	1-lf	0	0.765	0.6	0.036	0	0	0.25
	2-lf	0	0.029	0.3	0.602	0.08	0	0.44
	3-lf	0	0	0	0.259	0.75	0.467	0.19
	4-lf	0	0	0	0	0.03	0.533	0
	Dorm	0	0.018	0.018	0.032	0.03	0	0.13

2004-05 (including harvested roots)

	Seed	Sdlg	1-lf	2-lf	3-lf	4-lf	Dorm
Seed	0	0	0	0.464	2.62	9.467	0
Sdlg	0.101	0	0	0	0	0	0
1-lf	0	0.765	0.6	0.036	0	0	0.25
2-lf	0	0.029	0.3	0.602	0.09	0	0.44
3-lf	0	0	0	0.259	0.81	0.467	0.19
4-lf	0	0	0	0	0.03	0.533	0
Dorm	0	0.018	0.018	0.032	0.03	0	0.13

duced, dead and	
s, seeds pro	
stage class	
1998-2005,	
mber of ginseng plants monitored in 6 Missouri populations from 16	
Appendix 2. Nu	unlocated plant

	196	38	196	96	200	00	20(01	200	12	20(33	200	4	200	5
	# of plants	# of seeds	# of plants	# of seeds												
Dormant	4	I	5	ı	16	ı	10	ı	14	I	9		16		42 ¹	
Seedlings	25	ı	34	ı	41	ı	39	ı	50	ı	64	ı	34	ı	79	ı
1-leaf plants	76	ı	81	ı	103	ı	122	ı	103	ı	135	ı	165	ı	141	ı
2-leaf plants	81	40	93	107	154	73	162	34	169	22	181	107	172	86	172	19
3-leaf plants	55	150	75	275	136	480	145	333	161	206	170	585	193	527	197	331
4-leaf plants	4	31	9	54	7	127	8	10	18	121	6	90	15	142	13	118
Total live plants	245		294		457		486		515		565		595		644	
Total seeds produced		221		436		680		377		349		782		755		468
# of colonies monitored ²	30		60		74		81		82		88		91		92	
# of new plants (not seedlings) included in live plant total			50		162		22		ი		5		34		16	
Roots stolen (harvested)	0		27		0		0		0		0		-		18	
Roots dead or gone			7		40		32		30		25		37		1 4	
Unlocated ³	0		-		0		0		0		0		0		14	
Total dead/unlocated	-		35		40		32		30		25		38		46	

¹ As dormancy of these plants must be verified in future years, average rates of dormancy were applied to plants in the 2004-05 matrix.

² New colonies were added to the study as they were located. The majority of these colonies were added between 1999 and 2000. Only plants and observed in both years of a given transition were used in creating transition rates for each matrix.

³ Unlocated stems were searched for in future years and were typically found to be dead. As status of unlocated stems in last year is uncertain, these plants were not included in 2004-05 matrix.

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ots	Dorm	0	0	0.284	0.448	0.164	0	0.104	ots	Dorm	0	0	0.284	0.448	0.164	0	0.104
stolen ro	4-lf	13.16	0	0	0	0.438	0.531	0.031	stolen ro	4-lf	13.16	0	0	0	0.438	0.531	0.031
ccluding	3-lf	3.624	0	0.002	0.094	0.808	0.043	0.028	cluding	3-lf	3.631	0	0.002	0.091	0.785	0.042	0.027
natrix ex	2-lf	0.542	0	0.06	0.604	0.257	0	0.035	matrix in	2-lf	0.54	0	0.059	0.603	0.257	0	0.034
bivory" r	1-If	0	0	0.583	0.291	0.002	0	0.019	rbivory"	1-If	0	0	0.583	0.291	0.002	0	0.019
"No her	Sdlg	0	0	0.808	0.004	0	0	0.017	No he	Sdlg	0	0	0.808	0.004	0	0	0.017
99-2005	Seed	0	0.085	0	0	0	0	0	99-2005	Seed	0	0.085	0	0	0	0	0
19		Seed	Sdlg	1-If	2-If	3-If	4-lf	Dorm	19		Seed	Sdlg	1-lf	2-If	3-If	4-lf	Dorm
	Ë	0	0	84	48	64	0	04		Ē	0	0	84	48	64	0	04
roots	Doi			0.2	0.4	0.1		0.1	oots	Doi			0.2	4.0	0.1		0.1
	ч —	S	\sim	0	2	\sim	~		~		10						
stolen	4-1	8.63	0		0.03	0.508	0.429	0.032	stolen	4-lf	8.635	0	0	0.032	0.508	0.429	0.032
xcluding stolen	3-lf 4-l	2.712 8.63	0	0.004	0.123 0.03	0.767 0.508	0.044 0.425	0.032 0.032	ncluding stolen	3-lf 4-lf	2.733 8.635	0	0.003 0	0.12 0.032	0.753 0.508	0.044 0.429	0.031 0.032
matrix excluding stolen	2-lf 3-lf 4-l	0.454 2.712 8.63	0 0	0.062 0.004	0.609 0.123 0.03	0.255 0.767 0.508	0 0.044 0.429	0.031 0.032 0.032	matrix including stolen	2-lf 3-lf 4-lf	0.453 2.733 8.635	0 0 0	0.061 0.003 0	0.607 0.12 0.032	0.255 0.753 0.508	0 0.044 0.429	0.031 0.031 0.032
mbient matrix excluding stolen	1-lf 2-lf 3-lf 4-l	0 0.454 2.712 8.63	0 0 0	0.577 0.062 0.004	0.284 0.609 0.123 0.03	0.001 0.255 0.767 0.508	0 0.044 0.426	0.018 0.031 0.032 0.032	Ambient matrix including stolen	1-lf 2-lf 3-lf 4-lf	0 0.453 2.733 8.635	0 0 0	0.577 0.061 0.003 0	0.284 0.607 0.12 0.032	0.001 0.255 0.753 0.508	0 0.044 0.429	0.018 0.031 0.031 0.032
3-2005 Ambient matrix excluding stolen	Sdlg 1-lf 2-lf 3-lf 4-l	0 0.454 2.712 8.63	0 0 0 0	0.805 0.577 0.062 0.004	0.008 0.284 0.609 0.123 0.03	0 0.001 0.255 0.767 0.508	0 0 0 0.044 0.426	0.019 0.018 0.031 0.032 0.032	9-2005 Ambient matrix including stolen	Sdlg 1-lf 2-lf 3-lf 4-lf	0 0 0.453 2.733 8.635	0 0 0 0	0.805 0.577 0.061 0.003 0	0.008 0.284 0.607 0.12 0.032	0 0.001 0.255 0.753 0.508	0 0 0 0.044 0.429	0.019 0.018 0.031 0.031 0.032
1999-2005 Ambient matrix excluding stolen	Seed Sdig 1-lf 2-lf 3-lf 4-h	0 0 0 0.454 2.712 8.63	0.085 0 0 0 0 0	0 0.805 0.577 0.062 0.004	0 0.008 0.284 0.609 0.123 0.03	0 0 0.001 0.255 0.767 0.508	0 0 0 0 0 0.044 0.426	0 0.019 0.018 0.031 0.032 0.032	1999-2005 Ambient matrix including stolen	Seed Sdlg 1-lf 2-lf 3-lf 4-lf	0 0 0 0.453 2.733 8.635	0.085 0 0 0 0 0	0 0.805 0.577 0.061 0.003 0	0 0.008 0.284 0.607 0.12 0.032	0 0 0.001 0.255 0.753 0.508	0 0 0 0 0044 0.429	0 0.019 0.018 0.031 0.031 0.032

Appendix 4. Herbaceous species, ferns, grasses, sedges and vines found growing in nineteen ginseng sites in the Ozark Highlands Section of Missouri.

Species	Common name	CofC	Frequency
Actaea pachypoda	White baneberry	7	36.8%
Agastache nepetoides	Yellow giant hyssop	4	5.3%
Agrimonia pubescens	Soft agrimony	3	36.8%
Agrimonia rostellata	Beaked agrimony	3	31.6%
Amphicarpa bracteata	Hog peanut	4	68.4%
Anemone virginana	Tall anemone	4	5.3%
Anemonella thalictroides	Rue anemone	5	21.1%
Aplectrum hyemale	Adam and Eve orchid	8	5.3%
Aquilegia canadensis	Columbine	6	5.3%
Arabis laevigata	Smooth bank cress	5	26.3%
Arabis missouriensis	Missouri rock cress	6	5.3%
Aralia racemosa	Spikenard	8	15.8%
Arisaema triphyllum	Jack-in-the-pulpit	6	78.9%
Aristolochia serpentaria	Virginia snakeroot	7	36.8%
Asarum canadense	Wild ginger	6	57.9%
Aster cordifolius	Heart-leaved aster	7	15.8%
Aster lateriflorus	Side-flowering aster	3	5.3%
Aster linariifolius	Flax-leaved aster	10	5.3%
Aster sagittifolius	Arrow-leaved aster	4	5.3%
Blephila ciliata	Ohio horse mint	5	5.3%
Blephila hirsuta	Wood mint	7	5.3%
Cacalia muhlengergii	Great indian plantain	6	5.3%
Caulophyllum thalictoides	Blue cohosh	8	5.3%
Cimicifuga racemosa	Black cohosh	7	26.3%
Circaea lutetiana	Enchanter's nightshade	1	63.2%
Clematis sp.	-		5.3%
Collinsonia canadensis	Richweed	9	5.3%
Cypripedium reginae	Showy lady's slipper	10	5.3%
Desmodium dillenii	Tall tick clover	3	5.3%
Desmodium glutinosum	Pointed tick trefoil	3	57.9%
Desmodium marilandicum	Small-leaved tick trefoil	5	5.3%
Desmodium nudiflorum	Bare-stemmed tick trefoil	4	26.3%
Desmodium rotundifolium	Round-leaved tick trefoil	6	10.5%
Dioscorea quaternata	Four-leaf yam	6	78.9%
Dioscorea villosa	Wild yam	5	5.3%
Elephantopus carolinianus	Elephant's foot	3	10.5%
Eupatorium purpureum	Purple joe pye weed	4	5.3%
Eupatorium rugosum	White snakeroot	2	52.6%
Euphorbia commutata	Tinted spurge	5	5.3%
Galium aperine	Annual bedstraw	0	10.5%
Galium circaezans	Wild licorice	4	57.9%
Galium concinnum	Shining bedstraw	4	42.1%
Galium pilosum	Hairy bedstraw	6	10.5%
Galium triflorum	Sweet-scented bedstraw	4	21.1%
Geranium maculatum	Wild geranium	5	52.6%
Geum candense	White avens	2	42.1%

Geum vernum	Spring avens	4	10.5%
Heliopsis helianthoides	False sunflower	5	5.3%
Hepatica nobilis var actua	Sharp-loped hepatica	7	5.3%
Hepatica nobilis var obtusa	Round-lobed hepatica	6	15.8%
Hybanthus concolor	Green violet	7	15.8%
Hydrastis canadensis	Goldenseal	6	42.1%
Hydrophyllum appendiculatum	Woolen breeches	5	31.6%
Hydrophyllum canadense	Canada waterleaf	7	5.3%
Impatiens sp.	Jewelweed	3	47.4%
Isopyrum biternatum	False rue anemone	5	10.5%
Krigia biflora	False dandelion	5	5.3%
Lactuca floridana	Blue lettuce	3	5.3%
Laportea canadensis	Wood nettle (Stinging nettle)	4	26.3%
Lespedeza violacea	Violet bush clover	4	10.5%
Maianthemum racemosum	False solomon's seal	4	78.9%
Monarda bradburiana	Horsemint	5	5.3%
Orchid sp.			5.3%
Osmorhiza claytoni	Hairy sweet cicely	3	36.8%
Osmorhiza longistylis var longistylis	Smooth sweet cicely	3	21.1%
Oxalis stricta	Yellow wood sorrel	0	26.3%
Passiflora lutea	Yellow passion flower	4	5.3%
Phacelia bipinnatifida	Forest phacelia	5	10.5%
Phlox divaricata	Blue phlox	4	68.4%
Phryma leptostachya	Lopseed	2	36.8%
Physostegia virginiana	False dragonhead	5	5.3%
Pilea pumila	Clearweed	4	26.3%
Podophyllum peltatum	May apple	4	42.1%
Polemonium repens	Jacob's ladder	4	5.3%
Polygonatum biflorum	Solomon's seal	7	15.8%
Polygonum virginianum	Virginia knotweed	1	31.6%
Prenanthes alba	White lettuce	9	21.1%
Prenanthes altissima	Tall white lettuce	5	26.3%
Prunella vulgaris var lanceolata	Self-heal	1	5.3%
Pycnanthemum tenuifolium	Slender mountain mint	4	5.3%
Ranunculus hipidus	Hispid buttercup	6	5.3%
Ruellia strepens	Smooth ruellia	3	5.3%
Sanguinaria canadensis	Bloodroot	5	52.6%
Sanicula canadensis	Black snakeroot	3	63.2%
Sanicula gregaria	Clustered black snakeroot	2	21.1%
Scutellaria incana	Downy scullcap	5	5.3%
Scutellaria ovata	Heart-leaved scullcap	5	5.3%
Senecio aureus	Golden ragwort	5	5.3%
Silene stellata	Starry campion	5	10.5%
Solidago caesia	Blue-stemmed goldenrod	7	10.5%
Solidago flexicaulis	Broad-leaved goldenrod	6	10.5%
Solidago petiolaris	Downy goldenrod	6	10.5%
Solidago ulmifolia	Elm-leaved goldenrod	4	5.3%
Stylophorum diphyllum	Celandine poppy	7	5.3%
Taraxacum officinale*	Common dandelion	0	5.3%
Teucrium canadense	Germander	2	5.3%

Thalictrum dasycarpum	Purple meadow rue	4	5.3%
Tradescantia ohiensis	Common spiderwort	4	5.3%
Trillium recurvatum	Red trillium	6	5.3%
Trillium sessile	Wake Robin	5	5.3%
Uvularia grandiflora	Bellwort	6	73.7%
Veratrum woodii	False hellebore	8	10.5%
Verbesina alternifolia	Yellow ironweed	4	15.8%
Verbesina helianthoides	Wing-stem	4	5.3%
Verbesina virginica	White crownbeard	5	26.3%
Viola pubescens	Yellow violet	5	26.3%
Viola sororia	Blue violet	2	84.2%
Viola sp.	Violet		5.3%
Viola striata	Cream violet	3	10.5%
Viola triloba	Three-leaved violet	5	21.1%

Ferns

Adiantum pedatum	Northern maidenhair fern	6	52.6%
Asplenium platyneuron	Ebony spleenwort	4	21.1%
Asplenium rhizophyllum	Walking fern	7	21.1%
Botrychium dissectum	Cut-leaved grape fern	8	10.5%
Botrychium virginianum	Rattlesnake fern	4	52.6%
Cystopteris bulbifera	Bulblet fern	8	15.8%
Cystopteris protrusa	Lowland brittle fern	5	42.1%
Cystopteris tennesseensis	Tennessee bladder fern	6	10.5%
Deparia acrostichoides	Silvery spleenwort	10	5.3%
Diplazium pycnocarpon	Narrow-leaved spleenwort	10	5.3%
Polystichum acrostichoides	Christmas fern	5	52.6%
Thelypteris hexagonptera	Broad beech fern	8	5.3%

Grasses

Brachyelytrum erectum	Long-awned wood grass	6	57.9%
Bromus pubescens	Woodland brome	5	15.8%
Danthonia spicata	Poverty grass	3	5.3%
Elymus hystrix	Bottlebrush grass	4	15.8%
Elymus villosus	Silky wild rye	4	5.3%
Elymus virginicus	Virginia wild rye	4	10.5%
Festuca subverticillata	Nodding fescue	4	21.1%
Glyceria striata	Fowl manna grass	4	5.3%
Muehlenbergii sobolifera	Rock satin grass	4	10.5%
Panicum boscii	Bosc's panic grass	5	10.5%
Panicum clandestinum	Deer tongue grass	4	5.3%
Panicum dichotomiflorum	Knee grass	0	5.3%
Panicum latifolium	Broad-leaved panic grass	6	5.3%
Panicum laxiflorum	Lax-flowered panic grass	6	5.3%
Poa sylvestris	Woodland blue grass	5	10.5%

Sedges

Carex aggregata	Glomerate sedge	7	5.3%
Carex albursina	White bear sedge	10	21.1%
Carex blanda	Wood sedge	3	36.8%
Carex cephalophora	Woodbank sedge	5	5.3%
Carex digitalis	Slender wood sedge	8	10.5%
Carex grisea	Narrow-leaved sedge	3	5.3%
Carex hirsutella	Hirsute sedge	4	5.3%
Carex hirtifolia	Hairy sedge	7	10.5%
Carex hitchcockiana	Hitchcock's sedge	9	5.3%
Carex jamesii	Grass sedge	5	5.3%
Carex oligocarpa	Few-fruited sedge	6	10.5%
Carex planispicata			5.3%
Carex rosea	Stellate sedge	4	10.5%
Carex sp.	Sedge		52.6%
Scleria triglomerata	Tall nut rush	7	10.5%
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Vines

Campsis radicans	Trumpet creeper	3	5.3%
Celastrus scandens	Bittersweet	3	5.3%
Menispermum canadense	Moonseed	4	47.4%
Parthenocissus quinquefolia	Virginia creeper	3	100.0%
Rubus sp.			21.1%
Smilax bona-nox	Saw greenbriar	3	10.5%
Smilax hispida	Bristly greenbriar	3	26.3%
Smilax lasioneuron	Carrion flower	8	26.3%
Smilax rotundifolia	Horsebriar	6	5.3%
Toxidendron radicans	Poison ivy	1	68.4%
Vitis aestivalis	Summer grape	5	31.6%
Vitis cinerea	Winter grape	4	5.3%
Vitis riparia	Riverbank grape	4	5.3%
Vitis vulpina	Frost grape	5	15.8%