

Consequences of harvesting for genetic diversity in American ginseng (*Panax quinquefolius* L.): a simulation study

JENNIFER M. CRUSE-SANDERS^{1,3,*}, J.L. HAMRICK¹
and JORGE A. AHUMADA²

¹Department of Plant Biology, 2502 Plant Sciences Building, University of Georgia, Athens, GA 30602, USA; ²USGS/National Wildlife Health Center, 6006 Schroeder Rd., Madison, WI 53711, USA; ³Current address: Rancho Santa Ana Botanical Garden, 1500 North College Avenue, Claremont, CA 91711-3157, USA; *Author for correspondence (e-mail: jennifer.cruse-sanders@cgu.edu)

Received 29 April 2003; accepted in revised form 7 November 2003

Key words: Allozymes, Araliaceae, Conservation, Genetic diversity, Ginseng, Harvest, Management, Medicinal plant, Non-timber forest products, *Panax*, Population genetic structure, Simulation, Sustainable use

Abstract. American ginseng, *Panax quinquefolius* L., is one of the most heavily traded medicinal plants in North America. The effect of harvest on genetic diversity in ginseng was measured with a single generation culling simulation program. Culling scenarios included random harvest at varying levels, legal limit random harvest and legal limit mature plant harvest. The legal limit was determined by the proportion of legally harvestable plants per population (% mature plants per population). Random harvest at varying levels resulted in significant loss of genetic diversity, especially allelic richness. Relative to initial levels, average within-population genetic diversity (H_c) was significantly lower when plants were culled randomly at the legal limit (Mann–Whitney $U = 430$, $p < 0.001$) or when only mature plants were culled (Mann–Whitney $U = 394$, $p < 0.01$). Within-population genetic diversity was significantly higher with legal limit mature plant harvest ($H_c = 0.068$) than when plants were culled randomly at the legal limit ($H_c = 0.064$; $U = 202$, $p < 0.01$). Based on these simulations of harvest over one generation, we recommend that harvesting fewer than the proportion of mature plants could reduce the negative genetic effects of harvest on ginseng populations.

Introduction

As plant populations become small, they are at increased risk of extinction as a result of population demographic shifts, increased inbreeding, and genetic isolation and drift (Shaffer 1981; Gilpen and Soulé 1986; Menges 1991; Primack 1993; Briggs and Walters 1997). Economically important plants extracted from the wild are at additional risk, because harvest further reduces effective population size and compounds loss of genetic diversity and the threat of extinction. The impact that harvesting has on plant populations depends on the part of the plant collected, the plant's biology, its range and distribution, and the economic value associated with harvested materials (Sheldon et al. 1997). Populations of harvested plants may go extinct more rapidly due to overcollection than they do from population fragmentation and habitat destruction alone (Vance 2002).

American ginseng, *Panax quinquefolius* L., is one of the most heavily traded medicinal plants in North America. It produces a branched tuberous root, which is collected for use in herbal medicines. This species is non-clonal, therefore an entire individual is removed from the population when a root is harvested. In 1996 alone, 64 metric tons of wild ginseng roots were harvested from eastern North American forests, resulting in the mortality of millions of plants from eastern North America (Robbins 1998, 2000). In states where ginseng is harvested, the United States Fish and Wildlife Service (USFWS) mandates that the oldest plants, those with three or more leaves, can only be collected after mid-August. This sampling scheme is designed to give plants a chance to reproduce, set seeds and replace themselves in the population. Additionally, ginseng harvesters are required to plant seeds from plants collected at the collection site (Robbins 1998). Experienced collectors locate and harvest all large plants from a population (Lewis 1988) and harvesters frequently move seeds (and roots) between populations and to new sites. As a result, wild ginseng populations may disappear within a few years (Lewis 1988; Nantel et al. 1996).

Demographic research on ginseng has determined that the minimum viable population size for ginseng is 172 plants (Nantel et al. 1996), which includes the seedling through adult stage, yet most population censuses fall below that level (Gagnon 1999; Rock et al. 1999). Based on estimates of population growth rates, the maximum sustainable rate of annual harvest for ginseng is approximately 5% of plants at or above the three-leaf stage (Nantel et al. 1996). For a population of 172 plants with natural age class distribution (average proportion of mature plants in protected populations is 0.385), a 5% harvest rate would yield approximately 3 plants per year. This vastly underestimates actual harvest levels from wild populations, which are left with few to no plants in the oldest, most reproductive age classes.

Previous research found that protected populations maintain higher levels of genetic diversity and that the largest (oldest) stage class maintains significantly more genetic diversity than smaller (younger) plants (Cruse-Sanders and Hamrick 2004). In this study, we simulated culling of *P. quinquefolius* plants at different intensity levels to determine the effect of harvest on genetic diversity. We are interested in answering two specific questions: What is the effect of harvesting at various intensities on genetic diversity? And, does mature plant harvest at legal limits maintain genetic diversity within populations?

Methods

Study organism

Panax quinquefolius L. is a member of the Araliaceae, a family with approximately 700 species (Heywood 1993). The genus *Panax* consists of 12 species, 2 found in eastern North America and 10 in Asia (Wen and Zimmer 1996). The market for American ginseng has fluctuated throughout the 20th century but has steadily

increased since the mid-1900s. Most exports have been to Hong Kong but the USA also exports ginseng to Australia, Malay, Chile, and Canada. In 1977, the US Fish and Wildlife Service implemented the regulation of the Convention on International Trade in Endangered Species (CITES). *P. quinquefolius* is listed in Appendix II of the CITES agreement, indicating that its trade is regulated to protect its continued natural existence. Currently the major source of wild ginseng is Kentucky, West Virginia, and Tennessee and over 90% of the plants harvested are exported (Robbins 1998).

P. quinquefolius extends from Quebec and Manitoba south to North Florida, and west to Louisiana, Arkansas, and Oklahoma. It is a long-lived forest herb, and wild populations are scarce and difficult to locate. Aerial shoots develop in late spring and vegetation is persistent until late autumn. Green fruits first appear in late June and July, but redden and ripen on the plant starting in August. Ginseng reproduces exclusively by seed after a pre-reproductive period of at least 3 years (Anderson et al. 1993; Nantel et al. 1996).

Demographic research on *P. quinquefolius* has used number of leaves as the size class variable and found that the number of leaves is a good indicator of the biomass of underground structures (Lewis and Zenger 1982; Charron and Gagnon 1991; Anderson et al. 1993). In undisturbed populations the three-leaved size class is the most abundant followed by the seedling size class, and there is a large annual variation in seedling recruitment (Gagnon 1999). The size class structure of harvested populations is different, notably with a lack of four-leaved plants and fewer or no three-leaved plants (Gagnon 1999). The three- and four-leaved size classes represent the bulk of reproductive individuals within a population and loss of individuals from these size classes affects the ability of populations to recover from a harvesting event (Anderson et al. 1993; Gagnon 1999). For comparisons between size classes, we grouped plants into juvenile (one- and two-leaf plants) and mature (three- and four-leaf plants) categories.

Population genetic studies

To determine the level of genetic diversity within wild populations of *P. quinquefolius*, we sampled leaflets from individuals within 16 focal populations for use in allozyme electrophoresis. During 1999 and 2000, leaf samples were collected from six protected populations that occurred in national parks and ten unprotected populations at sites where permits are issued for limited ginseng harvest (Table 1). Freshly clipped leaves were kept in a cooler until they were brought to the University of Georgia where they were crushed in a mortar with a pinch of sea sand and 'camellia' buffer (Wendle and Parks 1982) within 48 h of sampling. Enzyme extracts were then absorbed onto chromatography paper wicks and stored at -70°C until analysis. Allozyme analysis followed procedures outlined in Cruse-Sanders and Hamrick (2004).

To provide base-line information on genetic diversity within populations before simulated harvest, gene and genotype frequencies were estimated for each

Table 1. Population ID, protection status, either protected (P) or unprotected (U), and initial estimates of within-population genetic diversity included in culling simulations. For random harvest simulations, varying proportions of individuals from initial populations were randomly culled (see text). For legal limit random harvest, the proportion of plants harvested in the simulation was based on the proportion of adult plants per population. Genetic diversity parameters estimated were % polymorphic loci (P), average numbers of alleles (allelic richness), and expected heterozygosity (genetic diversity, H_e).

ID	Status	N	% mature plants	P	Allelic richness	H_e
NC6	P	43	50	25.0	21	0.106
NC7	P	52	10	18.8	19	0.047
NC14	P	87	10	43.8	24	0.079
NC15	P	106	10	18.8	20	0.057
NC17	P	96	30	31.3	21	0.071
NC22	P	48	30	6.3	17	0.007
GA1	U	61	20	31.3	22	0.106
GA2	U	48	10	31.3	23	0.090
GA3	U	66	50	43.8	24	0.151
GA4	U	104	50	18.8	21	0.043
NC10	U	27	40	18.8	20	0.059
NC12	U	34	40	31.3	22	0.150
NC13	U	39	30	31.3	22	0.047
NC18	U	64	20	31.3	21	0.071
WV19	U	100	20	37.5	22	0.027
MD21	U	94	20	31.3	21	0.026
Average		67		28.2	21	0.071

population as described in Cruse-Sanders and Hamrick (2004; Table 1). These statistics include percent polymorphic loci (P), allelic richness and expected heterozygosity (H_e). Significant differences in P and allelic richness with culling were determined with non-parametric Kruskal–Wallis H tests (SAS Institute 2000). Similarly, a non-parametric Kruskal–Wallis H test for significant differences in expected heterozygosity (H_e) between the different harvest types was performed on jackknifed values (Weir and Cockerham 1984; SAS Institute 2000). A two-sample Mann–Whitney U test was used to determine if there was a difference between two contrasts; initial versus harvested and initial versus mature (SAS Institute 2000).

Simulation program

Single generation harvest simulations were performed with a program written in C. This represented a one-time harvest event (with no other new individuals added to the populations), during which a given number of plants were culled and the resulting change in genetic diversity calculated. Initially, a unique plant identification and multilocus genotype for each individual in the populations were entered.

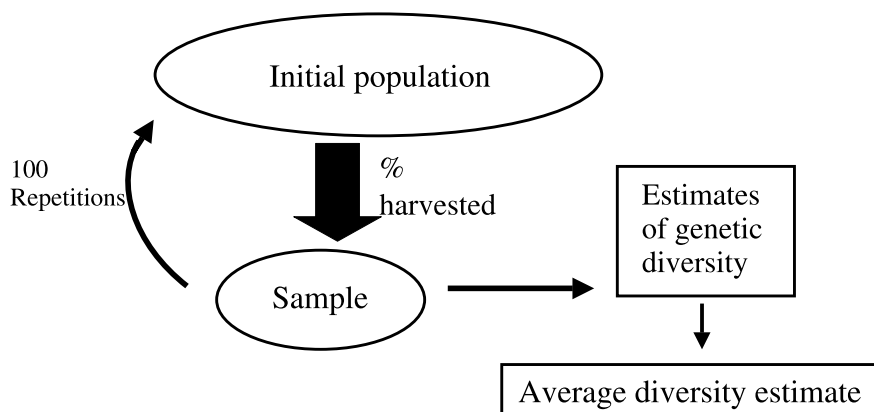


Figure 1. Model of simulated culling program. Random culling of genotypes occurred over a single generation, % harvested varied between 10 and 80%. Average diversity estimates were calculated after 100 repetitions.

The program first enumerated every individual and determined the total number of individuals. It then randomly selected a proportion of plants at each harvest level (10–70% of the population) to remain in the population (Figure 1). At each harvest level, the program calculated the population genetic parameters: P , AP , A_e , H_o , H_e , and allelic richness. At each harvest level, the program repeated the culling 100 times starting with the same initial populations and randomly selecting individuals to cull at each replication. Average population genetic estimates and standard deviations were calculated over the 100 replications.

To compare a harvest of the oldest individuals (legally permitted) with random harvest of the same intensity, we first determined the percentage of mature plants per population and then simulated a random harvest of an equivalent percentage of plants (Table 1). In the results we called this simulation the ‘legal level random harvest.’ The legal level random harvest was compared to a mature plant harvest, which provided a baseline estimate of the effect of legal harvest. The mature plant harvest was not a simulation; instead it consisted of culling out all mature plants from the population and recalculating genetic diversity estimates.

Results

Random harvest across varying levels

There was no difference among protected and unprotected populations in response to simulated random harvest over a single generation. In all populations genetic diversity and allelic richness decreased to some degree with increasing harvest level. Average genetic diversity estimates over 100 repetitions were plotted with their standard deviations. Each point on the graph (Figure 2a and b) represents the

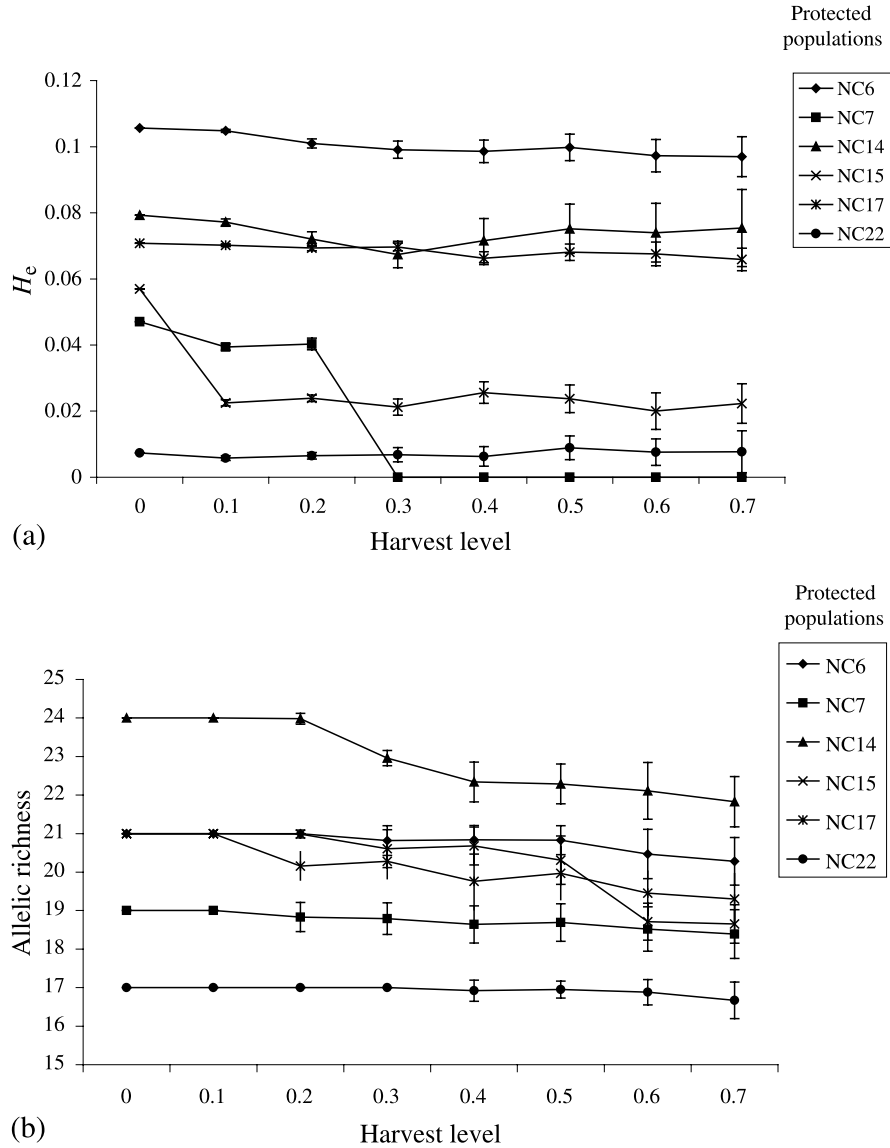


Figure 2. Change in genetic diversity with random culling at various harvest levels over a single generation for six protected populations from the southern Appalachian Mountains. Change in average expected heterozygosity (H_e) (a) and allelic richness (b). Error bars represent standard deviations over 100 repetitions.

average over 100 samples within decreasing population sizes (harvest level). Therefore, the point at 0.10 harvest level represents the average of 100 samples of 90% of the plants within a population, whereas the point at the 0.70 harvest level is

Table 2. Average within population estimates of genetic diversity. Initial estimates are based upon the original survey of allozyme diversity within the 16 populations (Cruse-Sanders and Hamrick 2004). See text for description of random, mature plant, and legal limit random harvest. Diversity estimates include percent polymorphic loci (P), expected heterozygosity (H_e), as well as allelic richness. Average values with * indicate a significant difference from initial values at $p < 0.001$.

	N	P	H_e	Allelic richness
Initial	16	30	0.071	21.25
Random harvest	16	28	0.064*	20.87
Mature plant harvest	16	27	0.068*	20.93
Legal limit random harvest	16	29	0.066*	21.08

the average of a much smaller sample (100 repetitions of a 30% sample from the original population).

With simulated random harvest over varying harvest levels, we found a significant decrease in H_e with increasing harvest level over just one generation in almost all of the populations. In most cases, H_e dropped significantly below initial levels between the 10 and 30% levels of harvest. Among protected populations, H_e significantly dropped below initial levels in 5 out of 6 populations, with expected H_e falling to zero in NC7 before the end of the simulation (Figure 2a). A similar pattern was seen among unprotected populations (data not shown). Although significant in most instances, the drop in H_e was not large (Figure 2a). Allelic richness decreased more than H_e with simulated culling (Figure 2b). The standard deviation in H_e and allelic richness among repetitions increased as harvest level increased.

Legal harvest level: mature plants versus random harvest

The proportion of mature plants (three- and four-leaf plants) per population varied between 10 and 50% (Table 1). Therefore, the percentage of plants harvested randomly or by mature plant harvest had the same range in the simulation program (Table 2). The total number of populations included in the legal level mature plant versus legal level random harvest simulation was 16, with a 10% harvest in four populations, 20% harvest in four populations, 30% harvest in three populations, 40% harvest in two populations, and 50% harvest in three populations.

Average within-population genetic diversity (H_e) significantly decreased with culling treatment at legal levels relative to initial levels (Kruskal–Wallis = 27.8, $df = 2$, $p < 0.001$; Table 2). Relative to initial levels, average within-population genetic diversity (H_e) was significantly lower when plants were culled randomly (Mann–Whitney $U = 430$, $p < 0.001$) or when mature plants only were culled (Mann–Whitney $U = 394$, $p < 0.01$). Within-population genetic diversity was significantly higher with legal limit mature plant harvest ($H_e = 0.068$) than when plants were culled randomly at the legal limit ($H_e = 0.064$; $U = 202$, $p < 0.01$). Neither random nor mature plant culling resulted in significantly different average

allelic richness or P compared with initial levels (allelic richness: Kruskal–Wallis $H = 0.87$, $df = 2$, $p = 0.648$; P : Kruskal–Wallis $H = 2.62$, $df = 2$, $p = 0.269$).

To determine the effect of harvesting below a threshold level, we limited harvest to a proportion of harvestable plants which included: zero level harvest in populations in which the proportion of adults was below 20% ($N = 4$), and 10% harvest in all other populations ($N = 12$). There was a significant decrease in genetic diversity (H_e) with proportional harvest compared to average initial levels ($U = 171$, $p < 0.001$). However, there was no significant difference in allelic richness or P with proportional harvest compared with initial levels (allelic richness: $U = 250$, $p = 0.621$; P : $U = 239$, $p = 0.349$).

Discussion

Both protected and unprotected populations responded with a similar decrease in genetic diversity to random harvest simulation over one generation. Average genetic diversity decreased with increasing harvest level, as would be expected since harvested populations represent a subset of the initial population. Similarly, the standard deviation increased with harvest level, because smaller samples are less representative of original diversity in the initial populations. This effect is expected because variation among samples increases as sample size decreases (Schoen and Brown 1991). As diversity among populations (or the samples that harvested populations represent) increases, the ability to predict H_e decreases (Schoen and Brown 1991). Based on the results from our simulations we would have difficulty predicting the level of genetic diversity that would remain in any one population under a high harvest regime.

Because harvested populations represent divergent samples of the genetic diversity originally present in populations, variation in genetic diversity among populations (F_{ST}) should increase with harvest. Genetic structure among unprotected populations in our geographic survey was significantly greater than among protected populations in the southeastern Appalachian Mountains (Cruse-Sanders and Hamrick 2004). Presumably, harvest pressure on unprotected populations has led to genetic bottlenecks and the fixation of different alleles in different populations leading to increased genetic structure throughout ginseng's geographical range (Cruse-Sanders and Hamrick 2004). Our simulation program supports this finding because variation among harvested populations increased along with harvest pressure. Theoretically, population bottlenecks, which can result from harvest, should result in greater decrease in allelic richness than H_e over the first few generations because rare alleles are lost first (Nei et al. 1975; Allendorf 1986; Luikart and Cornuet 1998). We found similar results based on our simulations of random harvest over one generation in which there was a greater decrease in allelic richness compared to H_e even at higher harvest levels (Figure 2a and b).

Genetic diversity decreased with increasing harvest level, which can be equated to the effect of different collection strategies depending on various habits of harvesters. Indeed, research on harvested populations of *Allium tricoccum* in Quebec

led Nantel et al. (1996) to identify two types of harvesters: 'choosy' harvesters who collect fewer larger plants and 'busy' harvesters who extract many smaller plants along with large plants. Considering results of varying levels of random culling in *P. quinquefolius* (Figure 2a and b), at lower harvest levels a choosy harvester should produce smaller drops in allelic richness and H_e as well as lower variation in diversity remaining in the population after harvest. Alternatively, a busy harvester should have the impact shown on the right sides of Figure 2a and b with larger decreases in genetic diversity within populations and more variation among collections of plants. Thus, we would expect a choosy harvester to have less impact on genetic diversity in ginseng populations than a busy one. Nantel et al. (1996) came to a similar conclusion regarding a lower impact of choosy harvesters on demography and growth rate in *A. tricoccum* populations.

Current strategies for achieving sustainable harvest in American ginseng involve setting aside areas where collection is not permitted and restricting harvest to plants with three or more leaves (mature plants). These approaches are foci for resource management, especially fisheries studies (Roberts 1997; Allison et al. 1998; Mangel 1998; Milner-Gulland et al. 2001). Generally, harvesting models have determined that never harvesting heavily, even in large populations, was the most sustainable approach, although not the most profitable (Milner-Gulland et al. 2001). Ultimately this is the problem for ginseng management. Because ginseng collectors can earn up to \$1105 per kg (\$500 per lb) (Robbins 1998, 2000), they have little incentive to leave legally harvestable roots in the ground. With current management recommendations, all plants with three or more leaves can be collected where harvest is permitted. Therefore, the threshold for legal harvest is any proportion of a ginseng population at the three-leaf size class or above. Theoretical studies based on demography and population growth rates have found that harvesting strategies that involve culling all individuals above a threshold perform poorly and are of limited use for management (Milner-Gulland et al. 2001). Alternatively, proportional threshold strategies, which allow harvesting a proportion of the difference between threshold population size and estimated population size are expected to provide more sustainable options. Although the estimated minimum viable population size for ginseng is 172 plants (Nantel et al. 1996; Gagnon 1999), most populations do not meet this criterion. For practical purposes, the proportional threshold for ginseng (as it is currently managed) would fall below the proportion of mature (three- and four-leaf) plants in the population.

Based on simulated culling of ginseng populations for one generation, we found that harvesting mature plants from a population significantly reduces genetic diversity within populations. In fact, we found that a harvest level of 10% in only those populations in which the proportion of mature plants was greater than 20% (below 'legal harvest' and threshold level) resulted in a significant loss of genetic diversity. Current legal rates of harvest in ginseng populations are high enough to significantly decrease population genetic diversity within one generation. Previously published harvest strategies based on demographic studies of ginseng recommend a level between 0 and 16% of the population depending on environmental conditions (Charron and Gagnon 1991; Nantel et al. 1996). The

effect of a 0–16% harvest rate on genetic diversity depends on initial population size and the evenness of allele frequencies in the population (Nei 1975; Allendorf 1986). This rate is below legally allowable rates for most populations, yet limiting culling to below 16% of population size could reduce the genetic impacts of harvest.

Our simulation program is a first step in determining the effects of harvest on genetic diversity and ultimately the evolutionary impacts it has for species of harvested plants. A more complex model would include multiple years along with recruitment and/or dispersal into the population to estimate the genetic effects of harvest over time. We are currently developing a more complex model, which will be useful for predicting the long-term evolutionary effects of harvest for this species. To develop a successful management strategy for ginseng, we must integrate population genetic information with a model of population growth in simulations over multiple generations. Results from fisheries management studies have determined that the simplest strategies are often more successful than complex ones, and are usually easier to implement (Ludwig and Walters 1985; Milner-Gulland et al. 2001). Based on our simulations of harvest over one generation, we recommend that harvesting less than the proportion of mature plants could diminish the negative genetic effects of harvest on ginseng populations. However, considering the natural forests where wild ginseng grows, actual enforcement of such limits would be nearly impossible without complete participation of the ginseng hunters responsible for collecting the roots.

Acknowledgements

The authors thank J. Ambrose, M. Crawford, G. Kauffman, R. Malcolm, S. McBride, J. McGraw, T. Patrick, J. Rock, T. Stallins, J. Sullivan, and C. Wentworth for their help in locating and sampling populations. We thank the U.S. Forest Service, Coweeta Long Term Ecological Research Site, Great Smoky Mountain National Park, and Georgia Department of Natural Resources Natural Heritage Program for granting permission to study ginseng populations; R. Pappert, C. Richards, and C. Deen for help in the lab; S.J. DeWalt for help with data analysis, J. Affolter and A. Otero with manuscript preparation. Financial support was received from the Plant Biology Department Palfrey Fund. J.M.C.-S. also thanks the National Council of State Garden Clubs for a scholarship received during her doctoral studies.

References

- Anderson R.C., Fralish J.S., Armstrong J.E. and Benjamin P.K. 1993. The ecology and biology of *Panax quinquefolium* L. (Araliaceae) in Illinois. *American Midland Naturalist* 129: 357–372.
- Allendorf F.W. 1986. Genetic drift and the loss of alleles versus heterozygosity. *Zoo Biology* 5: 181–190.
- Allison G.W., Lubchenco J. and Carr M.H. 1998. Marine Reserves are necessary but not sufficient for marine conservation. *Ecological Applications* 8(1): 579–592 (Suppl. S).

- Briggs D. and Walters S.M. 1997. *Plant Variation and Evolution*. 3rd edn. Cambridge University Press, New York.
- Charron D. and Gagnon D. 1991. The demography of northern populations of *Panax quinquefolium* (American ginseng). *Journal of Ecology* 79: 431–445.
- Cruse-Sanders J.M. and Hamrick J.L. 2004. Genetic diversity in harvested and protected populations of wild American ginseng, *Panax quinquefolius* L. (Araliaceae). *American Journal of Botany* 91: 540–548.
- Gagnon D. 1999. An analysis of the sustainability of American ginseng harvesting from the wild: the problem and possible solutions. Report to the Office of Scientific Authority of the US Fish and Wildlife Service.
- Gilpen M.E. and Soulé M.E. 1986. Minimum viable populations: processes of species extinction. In: Soulé M.E. (ed.) *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer, Sunderland, Massachusetts, pp. 19–34.
- Heywood V.H. 1993. *Flowering Plants of the World*. Oxford University Press, New York.
- Lewis W.H. 1988. Regrowth of a decimated population of *Panax quinquefolium* in a Missouri climax forest. *Rhodora* 90: 1–5.
- Lewis W.H. and Zenger V.E. 1982. Population dynamics of the American ginseng *Panax quinquefolium* (Araliaceae). *American Journal of Botany* 69: 1483–1490.
- Ludwig D. and Walters C.J. 1985. Are age structured models appropriate for catch-effort data? *Canadian Journal of Fishery and Aquatic Science* 42: 1066–1072.
- Luikart G. and Cornuet J.M. 1998. Empirical evaluation of a test for identifying recently bottlenecked populations from allele frequency data. *Conservation Biology* 12: 228–237.
- Mangel M. 1998. Evolutionary games and population dynamics. *Nature* 395: 32.
- Milner-Gulland E.J., Shea K., Possingham H., Coulson T. and Wilcox C. 2001. Competing harvesting strategies in a simulated population under uncertainty. *Animal Conservation* 4: 157–167.
- Menges E.S. 1991. The application of minimum viable population theory to plants. In: Faulk D.A. and Holsinger K.E. (eds) *Genetics and Conservation of Rare Plants*. Oxford University Press, New York, pp. 45–61.
- Nei M., Maruyama T. and Chakraborty R. 1975. The bottleneck effect and genetic variability in populations. *Evolution* 29: 1–10.
- Nantel P., Gagnon D. and Nault A. 1996. Population viability analysis of American ginseng and wild leek harvested in stochastic environments. *Conservation Biology* 10: 608–621.
- Primack R.B. 1993. *Essentials of Conservation Biology*. Sinauer, Sunderland, Massachusetts.
- Robbins C.S. 1998. American Ginseng: The Root of North America's Medicinal Herb Trade. TRAFFIC North America Report #B347.
- Robbins C.S. 2000. Comparative analysis of management regimes and medicinal plant trade monitoring mechanisms for American ginseng and goldenseal. *Conservation Biology* 14: 1422–1434.
- Roberts C.M. 1997. Ecological advice for the global fisheries crisis. *Trends in Ecology and Evolution* 12: 35–38.
- Rock J., Hornbeck H., Teitjen J. and Choberka E. 1999. Habitat modeling and protection of American ginseng (*Panax quinquefolius* L.) in Great Smoky Mountains National Park. Report for the U.S. National Park Service, Gatlinburg, Tennessee.
- SAS Institute, Inc. 2000. *SAS/STAT User's Guide, Version 8*. Vol. 1–3. SAS, Cary, North Carolina.
- Schoen D.J. and Brown A.H.D. 1991. Intraspecific variation in population gene diversity and effective population size correlates with the mating system in plants. *Proceedings of the National Academy of Science USA* 88: 4494–4497.
- Shaffer M.L. 1981. Minimum population sizes for species conservation. *Bioscience* 31: 131–134.
- Sheldon J.W., Balick M.J. and Laird S. 1997. *Medicinal Plants: Can Utilization and Conservation Coexist?* New York Botanical Garden, Bronx, New York.
- Vance N.C. 2002. Ecological considerations in sustainable use of wild plants. In: Jones E.T., McLain R.J. and Weigand J. (eds) *Nontimber Forest Products in the United States*. University Press of Kansas, Lawrence, Kansas, pp. 151–162.
- Weir B.S. and Cockerham C.C. 1984. Estimating F-statistics for the analysis of population structure. *Evolution* 38: 1358–1370.

- Wen J. and Zimmer E.A. 1996. Phylogeny and biogeography of *Panax* L. (the ginseng genus, Araliaceae): inferences from ITS sequences of nuclear ribosomal DNA. *Molecular Phylogenetics and Evolution* 6: 167–177.
- Wendel J.F. and Parks C.R. 1982. Genetic control of isozyme variation in *Camellia japonica* L. *Journal of Heredity* 73: 197–204.