

Evidence for decline in stature of American ginseng plants from herbarium specimens

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Abstract

American ginseng (*Panax quinquefolius* L.) has been harvested from the wild to supply the Asian herbal market for more than 200 years. As a CITES Appendix II listed species, ginseng trade has been monitored since 1975 and evidence for no detrimental effects of harvest is required annually by the US government. One kind of evidence gathered to gauge harvest effects has been mean root size and age, however the short-term nature of the data set limits possible inferences. In this study, 915 herbarium specimens from 17 herbaria were aged and measured to extend the time-transect to 186 years. Nine of 11 size-related traits showed statistically significant declines, most of this change occurring since ca. 1900. Multivariate analyses confirmed the overall decline in plant size. Age of herbarium specimens did not significantly decline during the same interval. Plants collected from northern populations did not decline in size, while plants from midwestern, Appalachian and southern states showed sharp declines in stature. Assuming herbarium specimens are representative of a consistent portion of natural populations, either direct or indirect effects of environmental change or human harvest could explain the rapid change in ginseng stature. Understanding the implications of such plant stature changes will require examining the effects of size on harvest probability and reproduction in the context of population viability analyses. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Ginseng; *Panax quinquefolius*; Phenotypic change; Herbarium specimens; Harvest

1. Introduction

A major goal of conservation ecology is the detection of decline in uncommon species before they become threatened or endangered (Hellawell, 1991; Primack, 1995). The basis of this emphasis on early detection is the general premise of conservation biology that probability of extinction is inversely related to population size (Shaffer, 1981). Too often, however, preventing extinction becomes a rear-guard set of actions based on insufficient ecological data when it is already too late to ensure survival. Despite the recognized importance of early detection of species-wide population declines, the urgency associated with preventing extinction of large numbers of rare species threatened by human actions has generally precluded a significant research focus on early prevention.

One circumstance in which attention has been paid to uncommon species prior to their becoming globally rare is that of species which are harvested from the wild and traded in international markets because in this instance a known downward pressure is acting on natural populations. Harvested species that appear to meet some criterion of ‘potentially declining’ may require regulation. Such species are listed in the CITES treaty (Convention on International Trade in Endangered Species), which is revisited periodically to update the list of species of concern. American ginseng (*Panax quinquefolius* L.) was placed on Appendix II of CITES in 1975, and in the US, the Office of Scientific Authority is charged with making a no-detriment finding for harvest prior to permitting continued trade. The primary data used to make this finding are total harvest figures by state and sporadically collected data on weight per root.

Direct evidence for population decline in ginseng from long-term monitoring efforts is lacking from the published literature. However, several kinds of indirect information suggest that ginseng may be declining in abundance. In the mid-1800s, ca. 170,000 kg of dried

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ginseng roots was exported annually from the US (Carlson, 1986), while in the period from 1989 to 1996, only 58,000 kg was exported per annum (Robbins, 1998). Harvest does not necessarily reflect natural abundance, nevertheless reduced harvest is a likely consequence of reduced natural population sizes. Anecdotal evidence suggests that inaccessible microsites have more ginseng than accessible microsites. For example, ginseng has been observed growing in dense patches of stinging nettles (*Urtica dioica* L.), under low canopies of spicebush [*Lindera benzoin* L. (Blume)], and even on tops of flat-topped perched rocks isolated on all sides from the forest floor by a cliff (pers. obs., 1998, 1999). In addition, experimental plots with either planted or natural populations have been harvested with regularity, even on sites where harvesting is illegal (Anderson et al., 1984; D. Gagnon, pers. commun., 1997; pers. obs., 1998, 1999). Finally, when environments are sampled randomly, ginseng is frequently found in what is considered by many to be ‘suboptimal’ habitats (Van der Voort, 1998), e.g. on south-facing slopes.

Another kind of indirect evidence for harvest impact on ginseng would be shifts in size and age distribution. Since size is roughly correlated with age (Anderson et al., 1984), and harvest focuses on the large end of the size distribution, a long-term impact of harvest should be the reduction in mean size and age of plants in the field. Indeed, this is the rationale for using mean root mass as an indicator of population effects when making a ‘no detriment’ finding. Harvest of large individuals results in a disproportionate reduction in recruitment since fruit production is highly size-dependent. Simulations of harvest by Charron and Gagnon (1991) and Nantel et al. (1996) showed that removal of these largest plants can rather quickly reduce population growth rates below the critical threshold of 1.

Since size data have been collected only within the short time since the CITES listing, we have a limited view of size distribution changes in natural populations. To extend this record, the present study exploited the record of individuals kept by herbaria throughout the eastern US. Although this method has not been used to examine size changes within species previously, other studies have used the temporal record in herbarium specimens to examine distributional, morphological and physiological changes in a way not possible with short-term field studies (Penuelas and Azconbieto, 1992; Beerling and Woodward, 1993; Baddeley et al., 1994; Burgman et al., 1995; Pitcairn et al., 1995; Miller, 1996; Herpin et al., 1997; Penuelas and Estiarte, 1997; Berenbaum and Zangerl, 1998; McElwain, 1998).

Concerning ginseng, we asked three specific questions based on the analysis of 915 specimens from 17 herbaria: (1) Have ginseng herbarium specimens changed in size over the past two centuries?; (2) Has the mean age of herbarium specimens declined with time, as might be

expected with continued harvest pressure?; and (3) Is there geographic variation in age- or size-related changes over time, or are these changes range-wide?

2. Methods

Herbarium specimens of *P. quinquefolius* were requested from 17 herbaria from across the range of the species to ensure widespread sampling. Few details of the project were provided to herbarium curators so specimens selected for the study would not be biased.

A total of 915 specimens were received. For each specimen, several attributes were recorded, including (1) collection date, (2) state of specimen origin, (3) root length (only where intact roots were present), (4) rhizome length, (5) sympodium width at the base, (6) sympodium height, (7) number of prongs (leaves), (8) peduncle length, (9) inflorescence width, (10) leaf petiole length (beyond the sympodium), (11) leaflet petiole length (for longest leaflet), (12) width of the longest leaf, and (13) length of the longest leaf. Some of these characters change through the growing season, but in order to maximize sample size, no specimens were culled by date of collection. Other measures such as biomass, were unavailable as sampling would require destroying the collection sheet.

Where intact rhizomes were present, age was determined by counting annual bud scars along the length of the rhizome. While in theory this procedure gives a precise age estimate, some error in this determination was possible because scars were on the underside of the stem and incompletely visible from above. Age determinations were likely to be correct within ca. 3 years, however, and this error would not have been biased by specimen collection date since bud scars were equally visible on old specimens and new specimens.

Linear regression analyses were used to examine the relationship between ginseng size variables [variables (3)–(13) above] and collection date (question 1). The possibility of a decline in age with collection date (question 2) was also examined with linear regression of age on date. Correlation among size variables suggested that multivariate analysis of the effect of collection date was warranted as well. A principal components analysis was performed [on variables (5)–(13), above], and the first principal component axis score was regressed on collection date. A second analysis, canonical correlation (MANOVA platform; SAS JMP v. 3.2, SAS, 1994), was performed with size variables [(5)–(13), again] as multiple Ys related to collection date: Wilks’ Lambda was used as the test statistic to determine significance.

Herbarium specimens did not always include county information. Therefore the state in which a specimen was collected was used to classify specimens into geographic regions. For convenience, the four regions

recognized were: (1) Midwest (OH, IN, IL, IA, MO), (2) South (AR, LA, MS, AL, GA, SC), (3) Appalachian (TN, KY, VA, NC, WV, PA, MD), and (4) Northern (WI, MI, NY, VT, MA, CT, NY, and Canada). An analysis of covariance model was used to test whether ginseng from different regions changed in size or age differently over the past 186 years (heterogeneity of slopes; Sokal and Rohlf, 1995). The model included region and collection date as main effects, and the interaction of region and collection date was the term of interest in the model. Removed from the geographic analyses were any specimens from outside the natural range of ginseng and any specimens from Delaware and New Jersey which did not fit neatly into the Northern or Appalachian groups. For all statistical analyses, I used SAS JMP v. 3.2 (SAS, 1994).

3. Results

Nine of 11 size-related morphometric traits of ginseng herbarium specimens showed statistically significant ($P < 0.01$) declines in size over the 186 year time span represented by the sample (Table 1). Plots of the regressions suggested that most of the decline occurred between 1900 and the present. Therefore, the data set was divided into pre-1900 and post-1900 specimens. Prior to 1900, only two of the 11 variables exhibited significant declines; sympodium width and pedicel

length. After 1900, all but two of the characters were showing significant reductions in size ($P < 0.01$ in eight characters, $P < 0.05$ in one). The magnitude of the size changes ranged from a 9.8% decline for leaf number to a 42.7% decline for peduncle length. The two characters related to plant height (sympodium height and peduncle length) showed the most dramatic decline (Fig. 1). Fig. 2 illustrates graphically the change in dimensions with a scale drawing of two ginseng plants, one based on mean dimensions predicted by regression for 1900 and the other predicted for the year 2000.

As expected for such traits, morphometric characters were correlated (Table 2). Therefore the significant declines in size may not reflect independent changes, but a correlated response to some pressure on overall size. Multivariate analysis affirmed the general decline in stature of ginseng plants in the 20th century, with a significant negative slope for the regression of principal component score 1 (which was positively correlated with all size variables) on collection date ($P < 0.0001$). The canonical correlation (MANOVA platform; SAS JMP v. 3.2) also showed a significant negative overall relationship in the whole-model test (Wilks' Lambda 0.914, $P = 0.0002$).

Since harvesters will tend to remove larger, older individuals from natural populations, one possible explanation for a reduction in size of collected specimens is reduced mean age of adults in the field. However, the regression of age on collection date revealed that herbarium

Table 1

Slopes (and associated r^2 and probabilities for the test of the null hypothesis that slope = 0) for all specimens (the undivided data set), for specimens collected prior to 1900, and for specimens collected after 1900^a

Dependent variable	Undivided data set Slope (r^2 , P)	Pre-1900 data Slope (r^2 , P)	Post-1900 data Slope (r^2 , P)	Percent decline since 1900
Root length	-0.0058 (0.001, 0.5942)	-0.0470 (0.016, 0.3679)	-0.0284 (0.015, 0.0993)	29.2
Rhizome length	-0.0036 (0.011, 0.0598)	+0.0034 (0.004, 0.5315)	-0.0083 (0.010, 0.0101)	11.2
Sympodium width	-0.0043 (0.032, < 0.0001)	-0.0140 (0.036, 0.0208)	-0.0052 (0.026, 0.0007)	21.7
Sympodium height	-0.0315 (0.022, < 0.0001)	0.0270 (0.002, 0.5350)	-0.0634 (0.048, < 0.0001)	25.8
Leaf number	-0.0017 (0.011, 0.0017)	-0.0006 (0.000, 0.8394)	-0.0031 (0.020, 0.0002)	9.8
Peduncle length	-0.0245 (0.045, < 0.0001)	-0.0510 (0.039, 0.0059)	-0.0297 (0.036, < 0.0001)	42.7
Inflorescence width	-0.0023 (0.018, 0.0003)	-0.00241 (0.003, 0.4455)	-0.0027 (0.011, 0.0115)	18.0
Leaf petiole length	-0.0068 (0.019, < 0.0001)	-0.0347 (0.007, 0.5694)	-0.0266 (0.003, 0.1820)	12.5
Leaflet petiole length	-0.0031 (0.0182, < 0.0001)	-0.0061 (0.012, 0.1197)	-0.0042 (0.017, 0.0006)	22.5
Width of longest leaf	-0.0080 (0.0504, < 0.0001)	-0.0086 (0.010, 0.1454)	-0.0099 (0.040, < 0.0001)	18.3
Length of longest leaf	-0.0144 (0.0489, < 0.0001)	-0.0156 (0.011, 0.1341)	-0.0186 (0.041, < 0.0001)	17.7

^a The percent decline is estimated based on the regression equations. Slopes $\neq 0$ ($P < 0.05$) are shown in bold.

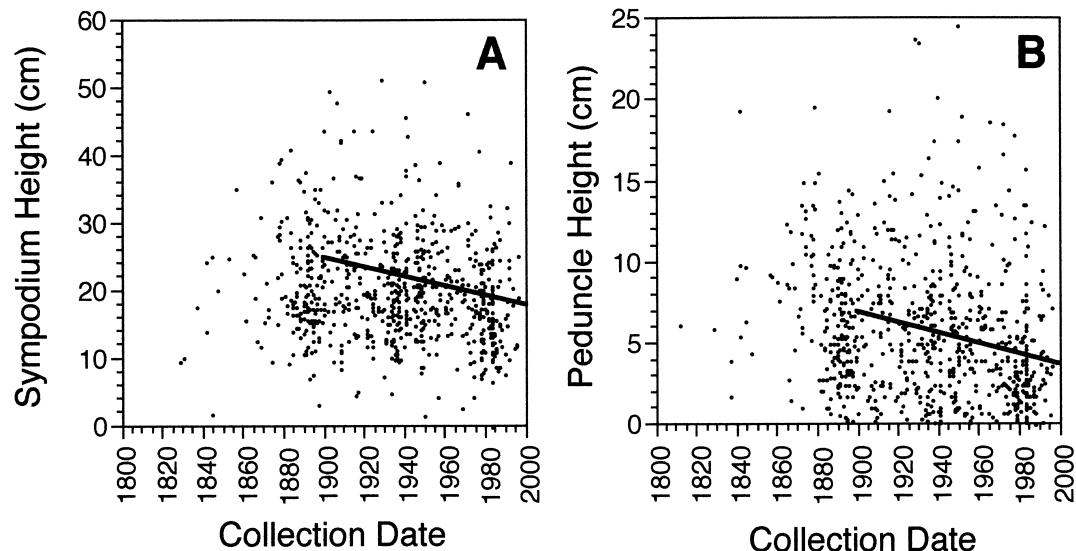


Fig. 1. Decline in (A) sympodium height, and (B) peduncle height of ginseng herbarium specimens collected over the past 186 years. Regression line for the period from 1900 to present is shown.

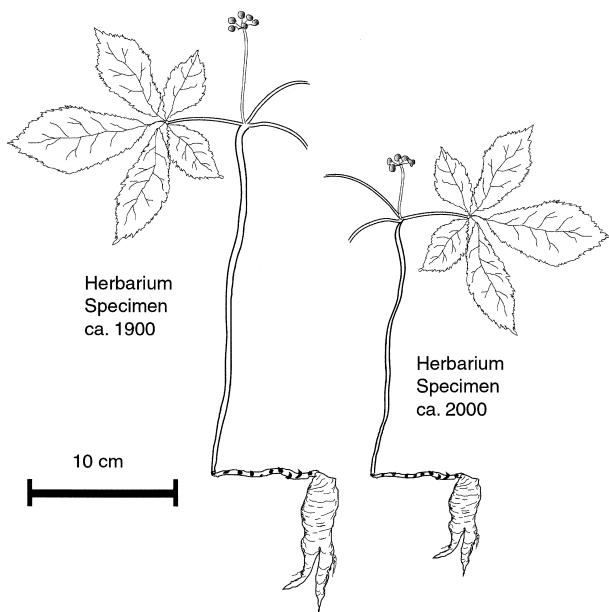


Fig. 2. Scale drawing of roots, rhizomes and shoots of herbarium specimens predicted by regression for 1900 and 2000.

specimens have not become younger with time (Fig. 3). Indeed, while plants certainly grow in size over their first few years, for herbarium specimens, which largely consist of reproductive adults, there was no correlation of age with size variables other than rhizome length ($r=0.66$, $P<0.0001$), sympodium width ($r=0.17$, $P=0.0158$), and root length ($r=0.18$, $P=0.0173$). Rhizome length is correlated with age because the rhizome incrementally grows without shrinking as each year's segment is added. The root also tends to expand indeterminately. Only the increase in sympodium width (which may reflect root resources) suggests that age is

related to size in ways that are not simply required by the architecture of the growth form.

For 10 of 11 morphometric measures related to size, geographic regions differed in their size changes (significant Region \times Collection Date interaction, ANCOVA; Table 3). As illustrated by separate regression lines by region for sympodium height, leaf length and peduncle height, northern populations showed no size change in the herbarium record, while midwestern, Appalachian and southern specimens declined the most (Fig. 4). In general, southern, Appalachian and midwestern specimens were larger than northern specimens in the early 1800s, but the reverse was true by the late 1900s. The patterns of change in phenotype varied somewhat from trait to trait. Southern specimens showed the greatest decline in leaflet size, while midwestern specimens declined in sympodium height more than the other regions. Southern populations showed a particularly remarkable decline in peduncle height; 70% in the last century alone. Multivariate analysis was not possible with this data set because a large fraction of herbarium specimens were missing one or more of the data points used in the analyses. This reduced sample size in specific regions to a level too small to be reliably used to test for regional differences in response to collection date.

4. Discussion

The null hypothesis that the dimensions of herbarium ginseng specimens have not changed over the past two centuries is firmly rejected by this study. Moreover the contrast between plants from northern populations, which have not changed in size, and plants in the remainder of the range, which have declined in size, is

Table 2

Correlation coefficients for 11 size variables measured on ginseng herbarium specimens^a

Variable	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
(1) Root length										
(2) Rhizome Length	0.15									
(3) Sympodium width	0.25	0.30								
(4) Sympodium height	0.18	0.16	0.50							
(5) Leaf number	0.18	0.18	0.30	0.33						
(6) Peduncle length	0.21	0.21	0.56	0.54	0.28					
(7) Inflorescence width	0.18	0.23	0.52	0.43	0.24	0.67				
(8) Leaf petiole length	-0.04	0.02	0.29	0.46	0.19	0.57	0.36			
(9) Leaflet petiole length	0.19	0.16	0.63	0.50	0.26	0.68	0.58	0.37		
(10) Width of longest leaf	0.24	0.15	0.56	0.53	0.20	0.68	0.59	0.47	0.70	
(11) Length of longest leaf	0.26	0.28	0.65	0.63	0.22	0.80	0.62	0.47	0.70	0.80

^a Coefficients in bold are significantly different from 0 ($P < 0.05$).

remarkable. Any explanation of the causes of size decline must account for this regional pattern. These observations may well provide some insight into the recent history of this species, but caution is in order in interpreting these results.

A first caution involves an important assumption that herbarium specimens are in some respect consistent representatives of plants in their natural environments. Herbarium specimens are deposited by a variety of individuals (amateur botanists, students, trained taxonomists, and other professionals) for a variety of reasons, including documenting the presence of a species at a locale, providing a sampling of the range of phenotypes, and providing material for taxonomic study (Jones and Luchsinger, 1986). Clearly herbarium specimens cannot be considered a truly random collection of individuals

from a population. Typically, herbarium specimens will be biased toward the collection of adult plants because of the importance of reproductive parts in taxonomic study. Therefore, historical inferences from herbarium data are limited to the portion of the total ginseng population vulnerable to collection by botanists.

Furthermore, in making inferences about natural populations of ginseng using this data set, we must assume that the propensity of botanists to collect plants

Table 3
Results of ANCOVAs showing the differential reduction in size traits of ginseng depending on geographic region^a

Dependent variable:	Geographic region	Collection date	Region * date
	<i>F</i> (prob > <i>F</i>)	<i>F</i> (prob > <i>F</i>)	<i>F</i> (prob > <i>F</i>)
Root length	0.61 (0.6104)	0.001 (0.9751)	0.63 (0.5942)
Rhizome length	3.02 (0.0030)	0.93 (0.3354)	3.03 (0.0295)
Sympodium width	5.07 (0.0018)	7.93 (0.0050)	5.15 (0.0016)
Sympodium height	3.19 (0.0231)	8.37 (0.0039)	3.18 (0.0237)
Leaf number	5.37 (0.0012)	23.15 (< 0.0001)	5.22 (0.0014)
Peduncle length	4.62 (0.0033)	30.51 (< 0.0001)	4.75 (0.0027)
Inflorescence width	5.46 (0.0010)	16.02 (< 0.0001)	5.47 (0.0010)
Leaf petiole length	6.03 (0.0005)	20.74 (0.0004)	6.08 (0.0004)
Leaflet petiole length	4.55 (0.0036)	12.29 (0.0005)	4.63 (0.0032)
Width of longest leaf	4.37 (0.0046)	29.17 (< 0.0001)	4.56 (< 0.0036)
Length of longest leaf	7.25 (< 0.0001)	33.44 (< 0.0001)	7.50 (< 0.0001)

^a Shown are *F*-values associated with each term in the statistical model, followed by significance levels. Statistically significant effects are shown in bold.

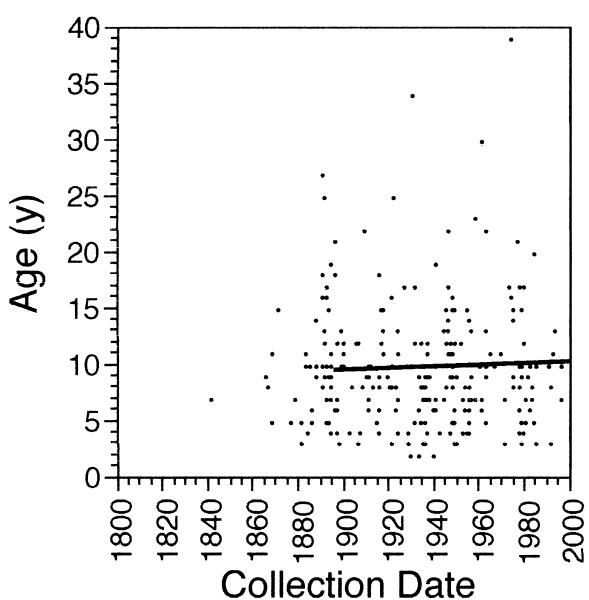


Fig. 3. Age of herbarium specimens as a function of collection date. Regression line for 1900 to present is shown.

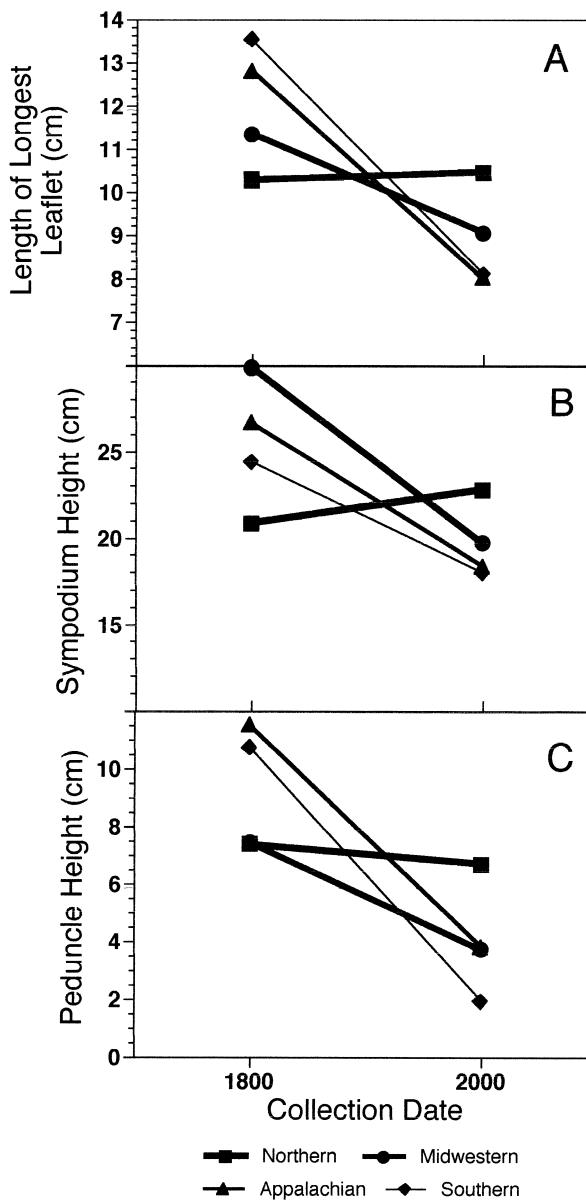


Fig. 4. Differential response of morphometric traits by region as a function of collection date. Lines show separate regressions for the period of 1800–2000 by geographic region, defined by clustering of states as described in the text.

of a particular size has not changed over the history of collection. A change could occur due to a change in the reasons for collecting or to ethical and economic considerations of the collectors. For example, in more recent times, botanists may have considered it ecologically unwise to collect the largest plants in a population, while this was not a consideration over a century ago. Alternatively, as the price of ginseng has risen, perhaps there was more motivation by amateur botanists to sell the largest roots, and deposit only smaller plants in the herbarium. We do know that the propensity to contribute herbarium specimens *sans* roots increased over time from ca. 60% in the early 1800s to more than 75%

by the end of the 20th century (logistic regression, $P=0.005$). However, this does not imply that botanists were less likely to deposit such specimens in herbaria. Indeed, it could be argued that the opposite tendency is more likely, since botanists might view it as positive to have their name associated with increasingly uncommon large specimens as such plants became rarer (a ‘trophy’ effect). Such possibilities must simply be admitted as an assumption of further interpretations. One argument against a change in collector propensities is that geographic variation does exist. Plants from northern populations were from several herbaria with contributions by dozens of collectors, yet there was generally no consistent size trend in these populations, while plants in the rest of the range were declining sharply. It seems unlikely that a change in propensity to collect would be region-specific.

Two broad classes of explanations can be offered for the broad-area declines in ginseng stature. First, an obvious hypothesis is that the decline in the dimensions of ginseng plants may have been driven by systemic wide-ranging environmental change (*sensu lato*). Causal factors could include increased acid precipitation, deer browsing, climatic warming, competition from invasive species, ozone pollution, or other airborne pollutants that have increased in the past century. A lengthy debate with little supporting data could be generated to implicate any one of these factors, and nothing would preclude more than one of them being relevant at different places across the range of the species. However, if environmental stressors are the explanation, they must be having an effect in southern, midwestern and Appalachian populations, but not in the north. Moreover, one might expect these effects to be present in some other herbaceous, nonharvested plant species with similar niches, however no such range-wide studies have been done.

A second class of hypotheses to explain ginseng’s decline involves direct and indirect interactions with human harvesters. A direct effect of harvesters on plant size might be manifested over two centuries of harvest pressure by removal of the largest and oldest plants from the populations, shifting toward a younger age structure on average. Such shifts have been seen in other heavily harvested species such as striped bass (Upton, 1997). While this shift may have occurred in natural populations of ginseng, this is clearly not the explanation for size decline in herbarium specimen stature. We were able to test this hypothesis directly by aging plants, and there was no decline in mean age through time. Recently, the minimum harvest age was set at 5 years. A further examination of the data did not show a decrease in the propensity of botanists to collect specimens older than this cutoff (logistic regression).

A particularly intriguing variation on the second class of hypotheses is that human harvest has driven natural selection, and hence microevolution, of ginseng toward

small stature. It is axiomatic that harvesters select against large plants because: (1) the economic return is greater for large roots than for small roots; if found, small plants will often be left in the population by harvesters to grow for harvest in a future year, (2) in some states, regulations stipulate size limits, guaranteeing greater harvest of large plants (this is a relatively recent phenomenon, and would not explain historical declines, however), and most importantly (3) the probability that a plant will be harvested depends on appärenz, and larger-leaved, taller plants, with large clusters of elevated red berries are more apparent than small plants. The herbarium specimens showed remarkable declines in height-related traits, which would be consistent with the ‘selection against appärenz’ hypothesis. Human harvesters kill the plant outright upon harvest, so the effect of harvest is not to stunt plants as a browser (such as deer) would do. Instead, a selective effect, to be lasting, would need to be transmitted via genes to the next generation. Thus, phenotypic selection against large size, combined with the existence of genetic variation in size (at a given age), would result in microevolution of a more dwarf phenotype over time.

One other possible indirect effect of human harvest could be the overcollection of ‘optimal’ sites (or micro-sites) for ginseng growth *vis-à-vis* suboptimal environments, resulting in a shift in abundance across the landscape. Over time, if ginseng plants were increasingly found in relatively poor sites for ginseng growth, the mean size of herbarium specimens might decrease because botanists would be increasingly likely to sample those sites.

Whatever the cause of ginseng plant size decline, it is one among several indicators suggesting vulnerability of this species. Presently, 19 states have been approved for export of ginseng based on scant real population data. Decline in mean size is difficult to interpret as an entirely negative indicator. On the one hand, smaller plants may propagate themselves sexually less effectively by annually producing fewer fruits and seeds. At the same time, smaller plants may be more difficult to find for harvesters due to reduced appärenz, and thus dwarfism may prove an adaptive response. Understanding the implications of such changes will require population viability analyses in which the consequences of shrinking plant sizes over the century time scale are appropriately incorporated.

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