Effects of harvester behavior on population growth rate affects sustainability of ginseng trade

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ABSTRACT

When long-term, intense levels of harvest nearly extirpated Chinese ginseng (*Panax ginseng* C. Meyer) in the early 18th century, commercial harvest of American ginseng (*P. quinquefolius* L.) began and large quantities of the roots were exported to East Asia. Annual export figures have fallen over the past 200 years, but demand for wild American ginseng has not abated. Persistent harvest of long-lived, slow-maturing species can have negative impacts on population growth rates, yet those closest to wild resources are often in a position to be the best stewards of that resource. This study explored the consequences of different harvester behaviors on the population dynamics of American ginseng. Drawing on known behaviors, we developed three harvester 'types' and ran demographic simulations on wild ginseng populations, partitioning the sources of differences in population growth rates using a life table response experiment (LTRE). The simulations showed that ignoring size class limits and harvest season onset dates dramatically affected population growth rates. Existing laws in many states are not adequate to protect wild ginseng populations. A stewardship-oriented harvester, who delays harvest onset by two weeks, self-limits harvest intensity and plants ginseng seeds at the time of harvest can reverse declining population growth rates.

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1. Introduction

Ginseng has been used in traditional medicine for several thousand years (Robbins, 1998). Long-term, intense levels of harvest nearly extirpated Chinese ginseng (*Panax ginseng* C. Meyer), also described as Asiatic, Oriental or Korean ginseng in the early part of the 18th century (Millspaugh, 1974). A Jesuit missionary hypothesized that if ginseng were to be found in North America, it was likely to be in Canada where environmental conditions resembled those for Chinese ginseng (Kimmens, 1975). His premise proved to be correct and American ginseng (*Panax quinquefolius* L.) was found growing in Canadian hardwoods (Kimmens, 1975). Word of the American species spread quickly to China and export began almost

immediately. Large quantities of ginseng were dug in North America in the early 1700s and shipped directly to East Asia for further processing and sale (Carlson, 1986). Anecdotal reports indicate that within 20–30 years the plant became increasingly difficult to find, although it was not extirpated from the wild (Millspaugh, 1974; Kimmens, 1975). Harvest and export quickly ended in the province of Québec (Evans, 1985; Gagnon, personal communication), and annual harvest figures dropped in the central portion of its range (central Appalachia). Nonetheless, over 60,000 kg continue to be harvested annually in the US and sold for export (Prescott-Allen and Prescott-Allen, 1986; Robbins, 2000).

P. quinquefolius was placed on Appendix II of the CITES (Convention on International Trade in Endangered Species

of Wild Fauna and Flora) list in 1973. The listing prompted the US government to create a management program with range states to ensure that federal responsibilities under CITES were satisfied (Robbins, 2000). Before export of an Appendix II species, federal authorities must determine that removal of that species will not be detrimental to its survival in the wild. In the case of *P. quinquefolius*, all states requesting export permission must file, on an annual basis, records of the previous year's harvest by weight and by collection location. The US Fish and Wildlife Service (USFWS), Office of Scientific Authority, then annually determines whether or not continued harvest of the species is detrimental to long-term survival in the wild (Robbins, 2000).

Collection of *P. quinquefolius* requires informal or formal permitting (unless the digging is done on one's property) and must be harvested in season. Opening dates vary among states and range from 1 August to 15 September (McGraw et al., 2005). Digging on national forest land requires a permit, as does harvest on state lands where permitted (harvest is usually restricted, Robbins, 2000). When collecting on private lands, written permission from the owner is necessary. However, there is evidence that some ginseng is harvested without complying with any of these regulations.

While the CITES requirements have institutionalized a framework within which states compile and submit data to USFWS managers for review, the program has struggled with multiple problems since its inception (Robbins, 2000). For example, the states receive no funding from the federal government to carry out any of the required work. Because responsibility for record keeping, submission of data to USFWS and management of wild ginseng populations does not lie with the same agencies among states, regional coordination can be complicated (Robbins, 2000). Until recently (Gagnon, 1999) there was no unifying monitoring protocol among states so data was often not comparable. Even with the design of a monitoring protocol, however, many states simply cannot or will not participate due to a lack of funding.

Managing an economically valuable species which is uncommon and widely dispersed across a geographic range is difficult. State boundaries are meaningless to species distribution but the different regulations among states further complicate any monitoring efforts. Unifying harvest practices that enhance populations of American ginseng is important if wild collection is to continue.

In the course of long-term demographic research on *P. quinquefolius* populations in the range center over the past decade, multiple types of harvesting behavior have been documented. Plants have been harvested both in and out of season (Furedi, 2004; McGraw and Furedi, 2005; Van der Voort, 2005), and removal of plants of illegal size/age has been documented (Furedi, personal communication 2000–2004; McGraw, personal communication, 2004; McGraw and Furedi, 2005). We have also documented, through observation and personal interviews (Bailey, 1999), harvest of ginseng from areas that are both legal and illegal for collection of wild plants.

Demographic research on ginseng in southern Québec (the northern margin for the species) indicated that populations there are increasing at an average rate of approximately 3% per year (Charron and Gagnon, 1991). When harvest was in-

cluded in the demographic model under varying environmental conditions, the finite rate of increase (λ) declined with increasing rates of harvest. The minimum viable population size necessary to maintain populations was estimated at 170 plants (Nantel et al., 1996), making harvesting a threat to small populations by increasing their extinction probability. Recent demographic studies of *P. quinquefolius* in the range center indicate that high densities of white-tailed deer (*Odocoileus virginianus* Zimm.) are negatively impacting long-term survival of American ginseng (McGraw and Furedi, 2005). McGraw and Furedi's (2005) estimate of minimum viable population size (under ambient white-tailed deer densities) was 800 plants. No studies have been carried out on the impacts of human harvest on *P. quinquefolius* demography in the range center.

The primary objectives of this study were to explore the potential consequences of different harvester behaviors on the population dynamics of *P. quinquefolius*, and to partition the sources of differences in population growth rates between the different harvesting behaviors using life table response experiments (LTREs). We asked three questions: (1) What are the consequences of ignoring size class limits and harvest season onset dates for population growth rate? (2) Is harvester behavior that fully complies with existing laws for important harvesting states (Kentucky, Tennessee and Virginia) adequate to sustain populations in the long-term? (3) What, if any, advantage is gained by population stewards who self-limit harvest intensity and use what is known about ginseng reproductive ecology to ensure recruitment after harvest? The null hypotheses were that any harvest would have a negative effect on population growth and that there would be no dependence of this effect on harvester behavior.

2. Methods

2.1. Study species

P. quinquefolius is a long-lived, perennial herb native to the rich, moist, deciduous forest of eastern North America (Millspaugh, 1974). It emerges in spring before full canopy leaf emergence. Individuals can live for three or more decades (Charron and Gagnon, 1991; McGraw, 2001). Ginseng progresses through a series of growth stages where leaf number is closely associated with size (Carpenter and Cottam, 1982; Charron and Gagnon, 1991; Anderson et al., 1993). A single trifoliate leaf emerges at germination (Anderson et al., 1984). Plants can retain a single leaf (with 3–5 leaflets) for multiple years (Furedi, McGraw, Van der Voort, personal observation). Two-leaf plants often flower, but rarely produce seeds (Anderson et al., 1984; Charron and Gagnon, 1991). The 2-leaf stage is typically followed by a reproductive adult period (3 or more leaves) which can begin as early as age 7 or 8 (Carpenter and Cottam, 1982; Charron and Gagnon, 1991), but may be much later. *P. quinquefolius* proliferates primarily through sexual reproduction (Schlessman, 1987), although asexual reproduction occurs rarely (Lewis and Zenger, 1982; Anderson et al., 1993; Van der Voort et al., 2003). One- to 3-seeded berries ripen from August to September and require warm and cold stratification over a period of 18–20 months, as seed embryos are immature at the time of dispersal (Hu et al., 1980; Baskin and Baskin, 1998).

Although populations were once reported to be much larger (Maxwell, 1898; Kimmens, 1975) the majority of populations have fewer than 200 individuals (Carpenter and Cottam, 1982; Lewis, 1984; Schlessman, 1985; Lewis, 1988; Charron and Gagnon, 1991; Van der Voort, 1998; McGraw and Furedi, 2005). The underground structures, the root and rhizome, are of primary interest to the harvester (and the consumer). Therefore, harvest kills the plant, although if the plant is reproductive, harvesters may facilitate reproduction by planting the seeds. Leaves are used for teas and other concoctions, but hold no value on the international market.

2.2. Study sites

Six study populations were located in north central West Virginia in second-growth mixed mesophytic hardwoods, all of which were logged by the early part of the 20th century. All study populations were randomly located by systematic searching (see McGraw et al., 2003 for discussion of sampling this widespread but scarce understory herb). When found, individuals were marked with unique, underground tags and followed for 3 years. Aspect (4 populations were located on north-facing aspects, one on east-facing and one south-facing), slope (moderate to steep, ca. 30° to 60°, two sites had unstable soils) and elevation (ranged from 475 to 810 m) varied among populations. Detailed maps of each population were made to assist future relocation.

2.3. Annual censuses

All individuals were censused at least twice annually from 10 June to 8 July and then again (for reproductive data) from 11 August to 26 August in 1998, 1999 and 2000. Leaf and leaflet counts were made for each individual. The dimensions (length and width) of the longest leaflet of each leaf of the plant was measured. Reproductive status was recorded, including the number of buds and/or flowers present. Any signs of herbivory, disease or other unusual characteristics were noted. As with many plants, P. quinquefolius seed production is concentrated during a single period of the year resulting in a birth-pulse population (Caswell, 2001). At the August census, berries were ripe or ripening but not yet dispersed, and seed number could therefore be determined accurately.

2.4. Population Projection Matrix Models

Matrix population models project numerical change over time. They provide a theoretical basis for population management, and because most management problems involve vital rates, demographic models are essential tools in conservation and population management (Caswell, 2001). Matrix population models have been used to design management and conservation programs for species as varied as loggerhead sea turtles (Crouse et al., 1987), Furbish's lousewort (Menges, 1990), Florida manatees (Marmontel et al., 1997) and California condors (Meretsky et al., 2000), to mention just a few.

A projection matrix model specifies a matrix of transition probabilities between different classes (Table 1), from time t to t + 1, with the transition probabilities representing observed

Table 1 – Transition probability matrix (A) for Panax quinquefolius

	From stage class				
	1	2	3	4	5
To stage class					
1	a_{11}	0	a_{13}	a_{14}	a_{15}
2	a_{21}	a_{22}	a_{23}	0	0
3	0	a_{32}	a_{33}	a_{34}	a_{35}
4	0	0	a_{43}	a_{44}	a_{45}
5	0	0	a_{53}	a_{54}	a_{55}

Each element a_{ij} represents the number of size i individuals in year 2 per size j individual in year 1.
Classes are defined as: 1 = seed, 2 = seedlings and 1-leaf combined, 3 = 2-leaf, 4 = small adults (3-leaf plants with leaf area <250 cm^2) and 5 = large adults (3-leaf plants with leaf area >250 cm^2 and all 4-leaf plants).

values of survival, growth, stasis, regression in size, fertility and recruitment (Bierzychudek, 1999). This population projection equation is:

$$n(t + 1) = An(t),$$

where n is a column vector whose values represent the numbers of individuals in each class, and A is a square, non-negative matrix. Each element, a_{ij}, gives the number of size i individuals in year 2 per size j individual in year 1 (Table 1). The dominant eigenvalue of A gives the finite rate of increase (λ) of the population. When $\lambda = 1$, the population is stable in the long-term. When $\lambda < 1$, the population is declining when the stable stage distribution (SSD) is reached and when $\lambda > 1$ the population is increasing (at SSD).

2.5. Model parameterization and model development

In plants, size is often a better indicator of individual fates than age (Werner, 1975; Harper, 1977). Although leaf number was used in past ecological studies of P. quinquefolius (Carpenter and Cottam, 1982; Charron and Gagnon, 1991; Anderson et al., 1993) as a simple and convenient method of data collection, leaf area may be a more accurate parameter because it is assumed to be proportional to photosynthetic capacity. P. quinquefolius individuals with greater leaf area may reach reproductive maturity earlier and produce more seeds than smaller individuals of the same age. Leaf area has been used in other demographic models to better capture real size differences among individuals and their vital rates (Werner, 1975; Werner and Caswell, 1977; McGraw and Antonovics, 1983; McGraw, 1989; Gregg and Kéry, 2006). Recent demographic research on P. quinquefolius using a combination of leaf area and leaf number provided more accurate estimates for the vital rates and the impact of plant size on vital rates in the central Appalachians (Furedi, 2004; McGraw and Furedi, 2005). Leaf area was used to divide the 3-leaf plants into small and large adults. The decision to divide only 3-leaf plants was based on the significantly lower rate of reproduction in 2-leaf plants ($G = 567.973$, $P = 0.0001$) and the high variability in size and seed set within the 3-leaf class. Four-leaf plants produced significantly more seeds than 3-leaf plants and were categorized as large adults (ANOVA, F ratio = 139.1842, $P = 0.0001$).

Leaf length and width measurements were used to calculate leaf area based on the following multiple regression equation ($r^2 = 0.95$, N = 102):

$$LA = 4.03(LL) + 5.17(LW) + 1.38(LL * LW).$$

The equation was derived from leaflet lengths and widths, with leaf areas measured independently using a portable Li-Cor Model Li-3000A leaf area meter (n = 102). All leaf area data for 3-leaf plants used in demographic studies from 1998 to 2003 were pooled (Furedi, 2004; Van der Voort, unpublished data 2004). The mean of the annual median leaf area was 252.45 cm^2 (±4.49). The value 250 cm^2 was chosen as the cut-off between small and large adults as it was within the 95% CI of the true mean. Small adults were defined as having <250 cm^2 of leaf area. Large adults had a leaf area ⩾250 cm^2. The leaf area of all 4-leaf plants was >250 cm^2.

Kalisz (1991) and Kalisz and McPeek (1992) demonstrated the importance of quantifying the effects of seed bank dynamics, including aging of seeds, in demographic models. A large seed germination and survival study (Van der Voort, 2005) indicated that *P. quinquefolius* does possess a seed bank with seeds remaining viable for at least 5 years, as suggested by Lewis (1988). To estimate seed survival (a_{11}) and germination rates (a_{21}) required for parameter estimation of the seed class in the demographic model for *P. quinquefolius*, McGraw and Furedi (2005) used seed cage data collected from the 6 populations used for this study. The seed cages were embedded at the field sites in 2002, and checked for viability in Spring 2003 and 2004. The 2003 data were used to estimate the proportion of seeds remaining viable in the seed bank from August to May (p). The 2004 data were used to estimate the proportion of seeds remaining in the seed bank (v) and the proportion of seeds dying (Table 2). For more detail on methodology, see McGraw and Furedi (2005).

The fertility estimates for reproductive classes (a_{1j}) were calculated as follows:

$$a_{1j} = \frac{pS_j}{n_j},$$

where S_j is the total number of seeds produced by class j in year 1, n_j is the number of individuals in class j in year 1, and p is the proportion of seeds remaining viable in the soil from August until May as determined from the seed cage study (2003 data). A delayed dormancy of at least 18 months

was assumed and seeds produced in August did not germinate until one year after their first spring. The number of seeds germinating (s_g) was calculated as follows:

$$S_g = \frac{R}{0.90},$$

where R is the number of new seedling recruits found in a population in year 2 within 2 m of adult *P. quinquefolius* plants, and 0.90 is a correction factor used to adjust for uncounted seedlings beyond the 2 m search radius (90% of seedlings move less than 2 m after gravity dispersal; Van der Voort, 2005). The number of seeds remaining dormant (s_d) was needed to estimate a_{11} (seeds remaining seeds from y 1 to y 2), and was calculated as follows:

$$S_d = vpS_0 - S_g,$$

where S_0 is the actual number of seeds produced in the August prior to year 1 of the interval under consideration and v is the proportion of seeds remaining viable in the soil for 12 months as determined from the seed cage study (2004 data). Seed numbers from 1997 were needed to calculate S_0 for the first transition (1998–1999). A mean 1997 seed number was calculated by averaging seed counts from all 3 years of this study (i.e., 1998, 1999 and 2000). The elements a_{11} and a_{21} are therefore calculated as follows:

$$a_{11} = \frac{vpS_0 - S_g}{pS_0},$$
$$a_{21} = \frac{(R/0.90)}{pS_0}.$$

The formulas for a_{11}, a_{21} and fertilities (a_{1j}) used here are taken directly from McGraw and Furedi (2005).

The effect of environmental variation on seed viability in the seed cage experiments is relevant to a time period after this study was conducted. However, we assumed that the variation was representative of environmental differences in 1998–2000 as well.

Once censuses were completed, every individual was assigned to a size/stage class. The five classes in the matrix model were defined as follows: seeds (class 1), seedlings (1-leaf plants; class 2), 2-leaf plants (class 3), small adults (class 4), and large adults (class 5). Due to the low number of new seedlings, seedlings and 1-leaf plants were combined into a single class to ensure adequate parameterization. Assumptions were necessary when data were missing on individuals during the annual census periods (i.e., due to browse, harvest or some other factor). If a plant was recorded as missing for 2 years in a row, its fate was considered death in the first year it was missing. Harvest is fully destructive to an individual; a plant was considered dead if harvested. When a plant was present in years 1 and 3, but missing in year 2, class assignments were dictated by status in the first year. The number of individuals following this pattern varied among populations, but ranged from 0% to 12%, with a mean of approximately 5% per population.

Individuals present in the first two years of the study but missing in the third, were assigned to classes based on the probability of survival or death calculated from known fates of other individuals. The number of individuals that needed assignments also varied among populations in this category.

Table 2 – Seed viability estimates (p) from 2003 seed cage data, proportion of seeds remaining in the seed bank (v), and the proportion of seeds dying

Population	p	v	Dead
BO	0.958333	0.75	0.25
BS	0.905983	0.85	0.15
CR	0.931873	0.7	0.3
W2	0.948980	0.69	0.31
P4	0.949640	0.35	0.65
P5	0.918919	0.45	0.55
Mean	0.935621	0.6316667	0.3683333
SE	0.008291	0.0779066	0.0779066

Data based on McGraw and Furedi's (2005) seed cage studies.

Values ranged from 14% to 51%, with a mean of about 28%. The probability of surviving increased with size, however, large adults were 1.5 times more likely to need probability assignments. A population missing one half of the individuals for the year 3 census was browsed heavily by white-tailed deer (*O. virginianus*) early in the season. Furedi (2004) found that deer generally focused their browsing on larger *P. quinquefolius* which may explain the need for more probability assignments in this class. For adequate estimation, probability assignments were based on a mean of the 6 study populations.

Although not all transitions were possible for all individuals, plants could transition in more than one way depending on class. For example, a small adult could remain in the same class from one year to the next (stasis, a_{ij}, where $i = j$), regress in size (a_{ij}, where $i < j$), grow (a_{ij}, where $i > j$), or die. A one year time step from June to June was used to calculate the vital rates and for projecting the future size and structure of the populations.

2.6. Harvesting simulations

Estimating a rate of harvest for *P. quinquefolius* for use in harvest simulations is complicated by several factors. Personal interviews with harvesters (Bailey, 1999) indicated that harvest practices varied widely in regard to size and number of plants taken, time of harvest events, and the fate of seeds present in a population at the time of harvest. Quantifying the variability is especially difficult with a species like *P. quinquefolius* as harvesting is typically a solitary activity (or small unit of related individuals), veiled in secrecy (Bailey, 1999).

To estimate the rate of harvesting, we drew on several sources. The mean rate of harvest observed among all six populations in this study was about 3%. McGraw et al. (2003) estimated an annual rate of harvest in West Virginia of ca. 5% by extrapolating multiple estimates of *P. quinquefolius* densities from three census methods covering a wide range of aspects, elevations, management regimes and forest cover types. These low overall figures include a mixture of populations that are harvested and those that are not (probably a majority). Mooney (personal communication, 2004) conducted a harvesting experiment whereby novice "harvesters" (i.e., people who could identify *P. quinquefolius* but who were not familiar with the experimental site) were presented with an area known to contain *P. quinquefolius* and asked to flag all plants of legally harvestable size (i.e., 3-leaf and larger plants). Her estimates of harvest ranged from 16% to 37% of the total population. While the presentation of a site known to contain *P. quinquefolius* might bias the harvest rate upward, active harvesters often benefit from "cultural knowledge" passed on from a family member and/or through previous scouting episodes made throughout the year while foraging for other wild harvested products (Bailey, 1999). The experimental study population was unusually large ($n = 391$) and widely dispersed in space. Population size of *P. quinquefolius* is not well known across the state. The median population size was 5 individuals in a previous study of 43 populations containing a total of 961 plants (Van der Voort, 1998 and unpublished data). The majority of the populations (i.e., 65%) were <10 genets. McGraw and Furedi (2005) found a median of 93 individuals

in 36 populations studied in an eight-state region near the range center of ginseng from 2000 to 2004; 53% had <100 genets. A harvester encountering a small population could easily remove as much as 90% of all above-ground plant material at a site (i.e., taking all 2-leaf and larger plants). We set the harvest rate for this set of experiments at 25% as a compromise figure from the various estimates of harvest. This rate is undoubtedly within the range of actual rates experienced by those populations which are encountered by harvesters, without being extremely high or low.

Browsing by white-tailed deer in ginseng populations influenced the availability of plants for harvest (Furedi, 2004). Intensive, repeated censusing of all *P. quinquefolius* individuals in study populations by Furedi (2004) provided a mean rate of browse across 4 years at different dates throughout the growing season. The mean browse rate (adjusted for date) was applied to the harvester models to adjust numbers of available plants. While the browse censuses were conducted from 2000 to 2004, we assumed that the variation was representative of differences in 1998–2000.

The timing of harvest also impacts demographic rates due to differences in seed ripening and seed germinability (McGraw et al., 2005). Nearly all *P. quinquefolius* seeds in West Virginia were green (98%) at the onset of the harvest season (15 August). Green seeds germinate at a significantly lower rate than red seeds at this time (McGraw et al., 2005). Further, an experimental study showed that seeds planted 2 cm deep germinated at a rate 7.6 times higher than those scattered on the surface (McGraw, unpublished data, 2002). Seeds were also planted at 4, 6, 8 and 10 cm depths. Seeds buried at a depth of 4 and 6 cm germinated at much lower rates than the optimal 2 cm depth (37% and 66% lower, respectively). Seeds buried at 8 and 10 cm had extremely low germination rates (98% below the optimum). Adjustments for germination in relation to date of harvest were applied to the harvester type models.

The range of harvesting behaviors and extent of harvest vary across a spectrum. To explore the impact that this variability could have on population vital rates, we analyzed the effect of three classes of harvester behaviors that incorporated timing and extent of harvest and alternate fates for harvested seeds (from both red and green berries).

3. Construction of harvester models

3.1. The non-compliant harvester

The non-compliant harvest date was set at 15 June. Bailey's (1999) harvester interviews documented that non-compliant harvest occurred any time plants were found. In our simulations, non-compliant harvesters removed 25% of all 3-leaf and larger plants, and consistent with their willingness to disregard harvest season, they harvested 25% of all 2-leaf plants (an illegal size). This behavior has been observed in many populations we have monitored and is corroborated by dealers who frequently find small pre-adult roots in batches they buy from harvesters (McGraw, personal observation, 2004). There was no browse adjustment for the non-compliant harvester as harvest onset coincided with the first demographic censuses, leaving all known plants in the population available

to the harvester. Seed production of all harvested plants was set to zero, as fruits are not present in mid-June.

3.2. The compliant harvester

Compliant behavior was characterized by harvesting as soon as harvest season began on 15 August. The compliant harvester took 25% of the available 3-leaf and larger plants, and any berries on these plants were scattered on the surface of the leaf litter. To adjust for the mean rate of browsed plants at the onset of compliant harvesting, 9% of all small and large adults were randomly removed from the available plants for harvest. These individuals remained in the matrix for all calculations, however, fertilities were reduced to zero. Furedi and McGraw (2004) found that white-tailed deer generally browsed larger *P. quinquefolius*, fertility of all reproductive classes were reduced by browsing and regression to smaller classes and reduced bud set occurred with repeated browsing events on the same individuals (Furedi, 2004). Further, Furedi and McGraw (2004) documented seasonal elimination of reproductive potential (both for individuals and whole populations) in populations where complete browse occurred. We extrapolated the germination of green seeds based on a previous experiment where green and red seeds were planted at 3 different dates (McGraw, unpublished data). An adjustment was made to the germination rate in the matrix model based on the fraction of seeds that were harvested on that date. Germination was adjusted downward for the compliant harvester by multiplying a_{21} by 0.8955.

3.3. The steward

We asked whether there are optimal harvester behaviors that could positively influence population growth rate and created the steward harvester model to examine this question. The steward delayed harvest by 2 weeks to allow berry ripening (McGraw et al., 2005), harvested 25% of the 3-leaf and larger plants in the population *only* if they were fruit-bearing (i.e., the steward only took plants with berries), and always planted the berries (regardless of color) at a depth of 2 cm. Plants unavailable for harvest due to browse was set at 15%. Small and large adults were randomly removed for the analysis as outlined above for the compliant harvester. Germination of seeds for the steward was adjusted upward by multiplying a_{21} by 2.6825, taking into account the higher number of ripe seeds at the later harvest date and the increased germination due to seed burial at depth of 2 cm.

Table 3 summarizes the harvester types. The non-compliant and steward harvesters are viewed as being near the opposite ends of a spectrum of behaviors that exist, with compliant probably representing the middle of the spectrum. Undoubtedly there could be more extreme non-compliant individuals (e.g., harvesting earlier or more intensely), and stewards could be more extreme as well (e.g., harvesting fewer plants, while planting many more seeds).

3.4. Data analysis

All six populations were pooled and an average matrix was estimated for year 1 of the data set. Fewer plant fates in year 1 were estimated by probability assignments ($\cong$5%), therefore giving increased confidence in the parameters of the model for that year. To quantify the contribution of each of the estimated vital rates (i.e., the a_{ij}s) in the transition matrix to the variability in λ, life table response experiments (LTREs) were used (Caswell, 1989). Elasticities and sensitivities calculated from matrix projections predict the results of perturbations of the vital rates before they happen, but they do not tell us anything about which vital rates are actually responsible for an observed change in λ (Caswell, 1989). The decomposition analysis of an LTRE does so by combining the actual change in the a_{ij}'s with sensitivity analysis ($s_{ij} = \delta\lambda/\delta a_{ij}$). LTREs can be used for multiple comparisons of different "environmental conditions" (Knight, 2004); in this case, different types of harvesting behavior.

Table 3 – Description of three harvester types with explanation of harvest intensity and adjustments for deer browse and seed germination dependent on berry color, time of harvest and seed fate

	Non-compliant	Compliant	Steward
Season	Ignores harvest season (harvests 15 June)	Harvests in-season (15 August)	Delays harvest until greater berry ripening (1 September)
Stage	Harvests 2-leaf, small adults and large adults	Harvests only small and large adult plants. Berry color does not matter	Harvests only small and large plants *with* berries. Berry color does not matter
Intensity	Takes 25% of the 2-leaf, small adults and large adults	Takes 25% of small and large adults	Takes 25% of small and large adult plants in the population *only if* berries are present
Seed fate	N/A. Berries not present	Berries planted by scattering	All berries (i.e., red and green) planted at a depth of 2 cm
Seed adjustment	N/A	a_{21} is adjusted downward by: $a_{21} \times 0.88955$	a_{21} is adjusted upward by: $a_{21} \times 2.6825$
Browse adjustment	N/A	9% of small and large adults are browsed	15% of small and large adults are browsed

See text.

An 'ambient' matrix was created from the estimated average matrix by removing harvest altogether. Harvested plants were reassigned fates according to their class affiliation in the year of harvest. In other words, if a large adult was harvested, it was reassigned to the large class (i.e., class 5) for the creation of the 'ambient' matrix. This followed the protocol for fate assignments described earlier. The majority of the harvested plants were in the large adult class and seed production of the harvested individuals was high. In Comparison Set I, each of the harvester types was compared to the 'ambient' matrix. In Comparison Set II, three additional comparisons were made: compliant-non-compliant, steward-non-compliant and steward-compliant, for a total of 6 LTREs.

The different harvesting type matrices were created by applying the rates of harvest, browse and germination adjustments outlined above to the data set 10 separate times to create 10 different matrices for each scenario. The mean matrix was determined to produce the non-compliant, compliant and steward scenario matrices, respectively. Each model can be summarized:

$$\lambda_{\text{ScenarioA}} - \lambda_{\text{ScenarioB}} \cong \sum (a_{ij\text{ScenarioA}} - a_{ij\text{ScenarioB}})s_{ij}.$$

The summed terms give an indication of the relative contribution of each parameter. The s_{ij}'s were the sensitivities of the average matrix created using the 2 matrices being compared (e.g., $\lambda_{\text{ScenarioA}} + \lambda_{\text{ScenarioB}}/2$ for the generic example above).

MATLAB (Mathworks, Version 4.0) was used for all calculations for the demographic analyses including estimation of standard errors, which were calculated using jackknifing.

4. Results

4.1. Effects of harvester type on demography

As expected, mortality of large and small adults varied greatly among simulations. In the absence of harvesting (i.e., 'ambient'), large adult mortality was very low (2% per year; Fig. 1). Mortality of class 5 plants was highest in the non-compliant simulation (27%), followed by compliant (25%) and then steward (17%; Fig. 1). Class 3 (2-leaf) plants, were only removed in the non-compliant simulation. Mortality in this class was 30% for the non-compliant simulation and 7% in the other three simulations. Stasis and growth of small adults was also altered by harvesting (Fig. 1). Fertility was also greatly reduced in the presence of harvesting (Fig. 1). The non-compliant simulation had the largest reduction (25% lower than 'ambient'). There were also very large differences in the rate of germination among the harvester classes (Fig. 1). These will be discussed in detail in the LTRE analysis.

4.2. Effects of harvester type on population growth rate

Estimates of population growth rates (λ) in the four scenarios varied (Fig. 2). The non-compliant harvester population was estimated to be declining by 15% per year ($\lambda = 0.8522$, ±0.0229), while the compliant harvester population was estimated to be declining by 8% per year ($\lambda = 0.9236$, ±0.0199). This same population under the steward simulation was estimated to be increasing by 4% per year ($\lambda = 1.0412$, ±0.0195).

In the absence of harvest (i.e., 'ambient'), the population was also increasing by ca. 4% ($\lambda = 1.0389$, ±0.0173; Fig. 2).

Elasticity analysis of the four populations indicated that small changes in the proportion of plants remaining in the same class (i.e., stasis across classes) had the greatest relative effect on population growth rate (Table 4). Stasis of large plants (a_{55}) had the highest elasticity for three of the four simulations (all but non-compliant, where stasis of 2-leaf plants, a_{33}, was higher). Survival in the seed bank class (a_{11}) had a substantial effect on population growth rate in all but the 'ambient' matrices. Small changes in the proportion of germinating seeds (a_{21}) also affected λ in all simulations.

4.3. LTRE analysis

Depending on the comparison, varying numbers of the 17 vital rates were affected by harvesting. Only those parameters that had substantial differences in the vital rates and the sensitivity of λ to changes in those vital rates will be discussed. All comparisons are listed in Tables 5 and 6.

4.4. Comparison Set I

In the first set of comparisons, all three harvester types were compared to the 'ambient' (no harvest) matrix.

Thirteen of 17 vital rates differed between the non-compliant and 'ambient' matrices (Table 5). Change in the rates of stasis of large and small adults and 2-leaf plants accounted for the 3 highest contributions to the λ difference between the two matrices. Lower stasis of large adults (a_{55}) in the non-compliant matrix accounted for nearly half of the reduction in λ seen in the non-compliant simulations. The illegal harvest of 2-leaf plants was second in importance, accounting for 16% of the reduction. The change in all fates of 2-leaf plants accounted for 28% of the reduction in λ. Even though population growth rate had a relatively low sensitivity to the fertility of large adults, the change in the vital rate (a_{15}) was very large (the highest change in Δa_{ij} among all six comparisons). The lower fertility of large adults in the non-compliant matrix accounted for 8% of the reduction in λ.

Change in rates of stasis of large and small adults accounted for the two highest contributions to the difference between the compliant and 'ambient' matrices (Table 5). Lower stasis of large adults (a_{55}) accounted for over half (61%) of the reduction in λ in the compliant simulations. Less stasis of small adults (a_{44}) accounted for 10% of the reduction while less growth of small adults into the large adult (a_{54}) class accounted for 9% of the reduction in λ. Despite the fact that the population growth rate was most sensitive to germination of seeds, λ was little affected by it because Δa_{21} was very small between the compliant and 'ambient' matrices.

The effects of increased germination (due to seed planting in the steward simulations) in the steward-'ambient' simulations contributed 58% to the increase in λ, despite all the other changes between the matrices being negative (due to harvest – Table 5). Even with the lower rate (38%) of stasis of large adults (a_{55}) and a 10% reduction in fertilities of large adults (a_{15}) in the steward matrix, λ was slightly higher than that of the 'ambient' matrix.
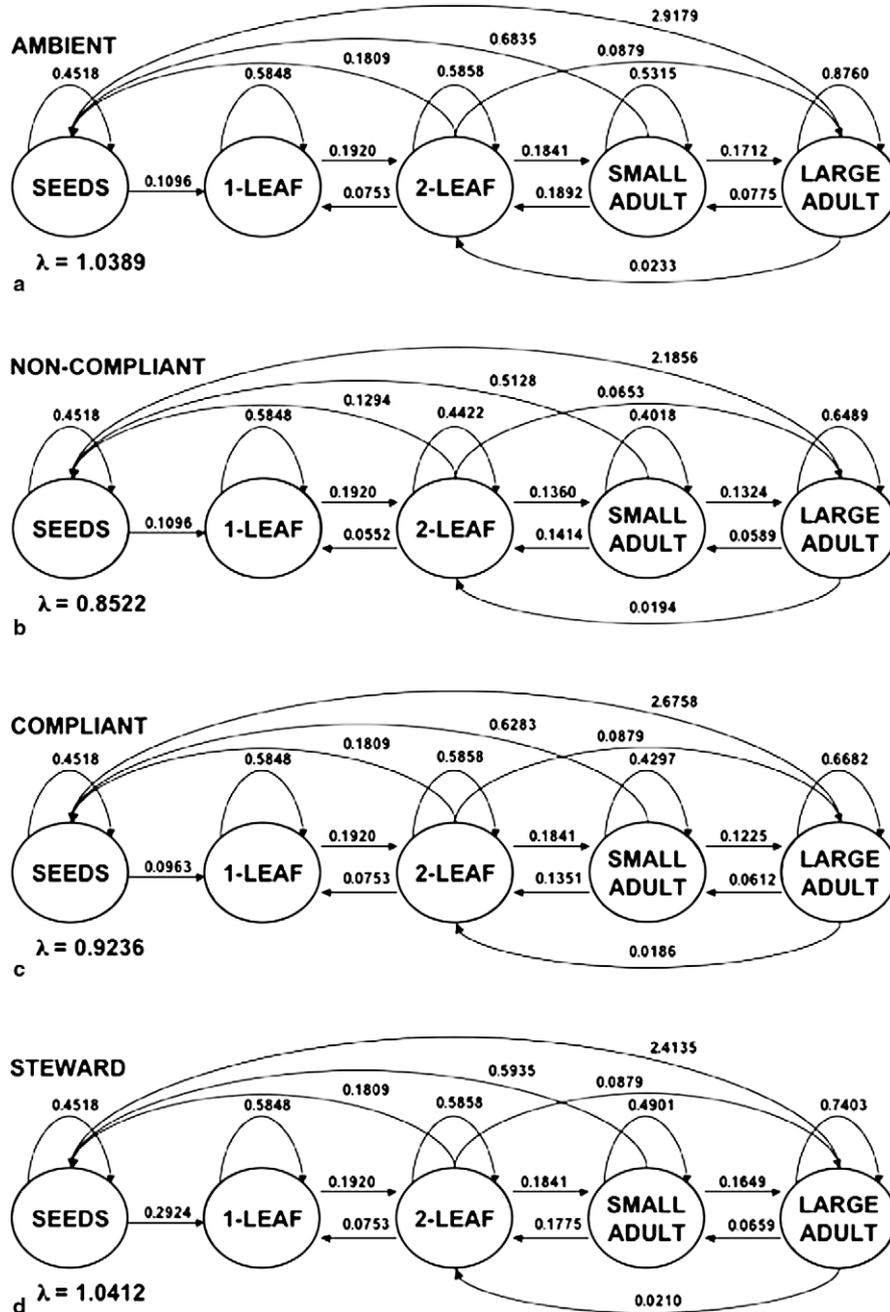
Fig. 1 – Life cycle diagram of *Panax quinquefolius* showing the five classes (seeds, seedlings and 1-leaf plants, 2-leaf plants, small adults and large adults) and all possible transitions between classes when (a) all plants were included in the calculation of a mean ambient matrix (i.e., no harvesting), when (b) the non-compliant harvester treatments were applied, when (c) the compliant harvester treatments were applied and (d) when the steward harvester treatments were applied. The probabilities of transitioning from one class to another (a_{ij}) are indicated by the numbers above each arrow.

4.5. Comparison Set II

The compliant ($\lambda = 0.9236$)–non-compliant ($\lambda = 0.8522$) comparison was of particular interest because it quantified the positive effect of existing regulations, or conversely, the negative effect of breaking those laws. The top three contributors to the lower λ in compliant vs. non-compliant simulations were differences in fates of 2-leaf plants (Table 6). These changes were present due to the illegal harvest of 2-leaf

plants in the non-compliant regime. The change in all fates of 2-leaf plants accounted for 81% of the reduction in λ in the non-compliant matrix. The lower fertility of large adults in the non-compliant matrix accounted for 15% of the reduction in λ. The largest change in a vital rate was in the fertility of large adults (a_{15}). Although λ had a low sensitivity to this parameter, the large Δa_{15} resulted in an impact on λ. Even though population growth rate was most sensitive to the germination of seeds, the difference between the matrices in a_{21}
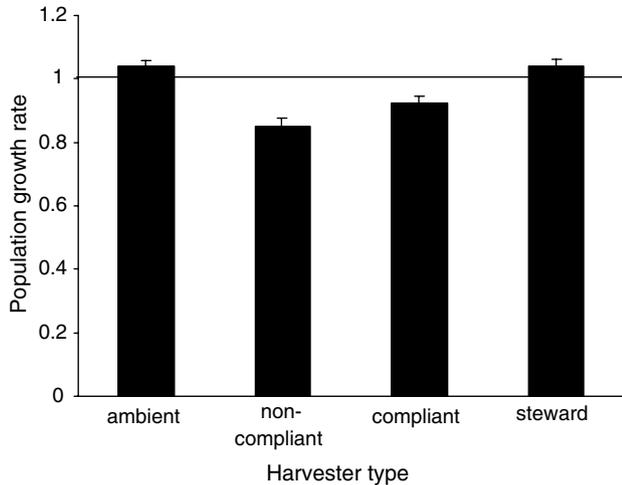
Fig. 2 – The population growth rate (and 95% confidence intervals from the mean s.e. of 10 jackknifed mean matrices for each harvest type) of a single population of *Panax quinquefolius* under four varying conditions of harvest. When $\lambda = 1$, the population is stable, when $\lambda > 1$, the population is increasing and when $\lambda < 1$, the population is declining.

Table 4 – Elasticities (e_{ij}s) corresponding to the mean matrices for harvester type under four varying conditions of harvesting: ambient (no harvest), non-compliant, compliant and steward

Size at time $t + 1$	Size at time t				
	Class 1	Class 2	Class 3	Class 4	Class 5
Ambient					
Class 1	0.0425	–	0.0027	0.0053	0.0469
Class 2	0.0549	0.0783	0.0059	–	–
Class 3	–	0.0608	**0.1087**	0.0186	0.0047
Class 4	–	–	0.0409	0.0625	0.0188
Class 5	–	–	0.0347	0.0358	**0.3780**
Non-compliant					
Class 1	0.0810	–	0.0060	0.0089	0.0569
Class 2	0.0718	**0.1773**	0.0093	–	–
Class 3	–	0.0811	**0.1037**	0.0125	0.0026
Class 4	–	–	0.0413	0.0459	0.0101
Class 5	–	–	0.0395	0.0301	**0.2222**
Compliant					
Class 1	0.0680	–	0.0066	0.0101	0.0543
Class 2	0.0710	**0.1457**	0.0135	–	–
Class 3	–	0.0844	**0.1847**	0.0188	0.0033
Class 4	–	–	0.0456	0.0470	0.0084
Class 5	–	–	0.0408	0.0251	**0.1726**
Steward					
Class 1	0.0653	–	0.0094	0.0121	0.0636
Class 2	0.0851	**0.1192**	0.0079	–	–
Class 3	–	0.0930	**0.1454**	0.0174	0.0026
Class 4	–	–	0.0523	0.0550	0.0095
Class 5	–	–	0.0435	0.0322	**0.1865**

Elasticity values reflect the proportional effect of small changes in each a_{ij} on λ. The matrix elements having the greatest effect on population growth rate are in bold.

was very small and therefore the impact on projected population growth was small as well.

Fourteen of 17 vital rates differed in the steward vs. non-compliant comparison, all of which positively contributed to the difference in the projected high rate of growth for the steward matrix (Table 6). The greatest change was in the parameter a_{21}, germinating seeds, and population growth rate was very sensitive to this vital rate. The increased germination of seeds in the steward matrix (37%) accounted for over one third of the increase in λ. Similar to the previous comparison (compliant-non-compliant) the stasis of 2-leaf plants contributed substantially to the difference in the projected population growth rate of the steward (18%). The change in fates of all 2-leaf plants accounted for 31% of the increase in λ.

In the steward-compliant comparison, fewer changes were observed between the matrices that contribute to the difference in the estimated population growth of the two harvester types (Table 6). The increased rate of germination (a_{21}) accounted for nearly three quarters (72%) of the increase in λ. The Δa_{21} in this matrix combined with the high sensitivity of the population growth rate to the transition, resulted in the highest contribution (i.e., $\Delta \lambda$) of the comparisons in Comparison Set II.

5. Discussion

In the first set of comparisons (three harvester types compared to the 'ambient,' no-harvest matrix), neither the non-compliant nor the compliant harvester had an opportunity to compensate for the loss of seeds due to harvesting. The non-compliant harvester eliminated all reproductive potential from the individuals that were taken in June. Total seed loss from a population was also potentially higher for the non-compliant model because the number of plants harvested in June was greater (i.e., no browse adjustment was made for the non-compliant harvester). The compliant harvester reduced germination of all seeds present at the time of harvest because germination rates are lower on 15 August than 1 September (McGraw et al., 2005), and seeds were not buried.

The consequences of ignoring size class limits and harvest season onset date for population dynamics of *P. quinquefolius* are large, suggesting that these regulations, if followed, would partially protect the resource. Wild ginseng populations in the non-compliant model were expected to decline at an average rate of approximately 15% per year when the stable stage distribution (SSD) is reached, a rate that would rapidly drive a population to extinction. The non-compliant harvester removed 2-leaf plants (class 3). All of the LTRE comparisons with the non-compliant harvester indicated that stasis and growth of class 3 individuals contributed substantially to the difference in the projected population growth rates among populations. Initially, increasing the proportion of 2-leaf plants remaining 2-leaf plants and growing into larger stages would have the largest effect on λ.

Compliance with current federal and state regulations, if it is only marginal compliance as with our compliant harvester scenario, does not appear to be adequate to ensure the sustainability of harvest of *P. quinquefolius*. The compliant model simulations showed that such populations were expected to decline at an average rate of approximately 8%

Table 5 – Comparison Set I – Life table response experiment (LTRE) for three harvester type comparisons to the mean ambient matrix (no harvesting) for *Panax quinquefolius*

Parameter	Comparison								
	Non-compliant-ambient			Compliant-ambient			Steward-ambient		
	Δa_{ij}	s_{ij}	$\Delta\lambda$	Δa_{ij}	s_{ij}	$\Delta\lambda$	Δa_{ij}	s_{ij}	$\Delta\lambda$
a_{11}	0	0.1231	0	0	0.1205	0	0	0.1296	0
a_{21}	0	0.5504	0	−0.0133	0.6130	−0.0082	0.1828	0.3808	0.0696
a_{22}	0	0.1887	0	0	0.1846	0	0	0.1834	0
a_{32}	0	0.3509	0	0	0.3757	0	0	0.4369	0
a_{13}	−0.0515	0.0242	−0.0012	0	0.0236	0	0	0.0332	0
a_{23}	−0.0201	0.1080	−0.0022	0	0.1200	0	0	0.0976	0
a_{33}	−0.1436	0.2008	−0.0288	0	0.2442	0	0	0.2326	0
a_{43}	−0.0481	0.2480	−0.0119	0	0.2391	0	0	0.2732	0
a_{53}	−0.0226	0.4622	−0.0104	0	0.4308	0	0	0.4839	0
a_{14}	−0.1707	0.0110	−0.0019	−0.0552	0.0113	−0.0006	−0.0900	0.0146	−0.0013
a_{34}	−0.0478	0.0910	−0.0043	−0.0541	0.1175	−0.0064	−0.0117	0.1023	−0.0012
a_{44}	−0.1297	0.1124	−0.0146	−0.1018	0.1150	−0.0117	−0.0414	0.1201	−0.0050
a_{54}	−0.0388	0.2095	−0.0081	−0.0487	0.2073	−0.0101	−0.0063	0.2127	−0.0013
a_{15}	−0.7323	0.0196	−0.0144	−0.2421	0.0184	−0.0045	−0.5044	0.0230	−0.0116
a_{35}	−0.0039	0.1629	−0.0006	−0.0047	0.1903	−0.0009	−0.0023	0.1607	−0.0004
a_{45}	−0.0186	0.2011	−0.0037	−0.0163	0.1863	−0.0030	−0.0116	0.1887	−0.0022
a_{55}	−0.2271	0.3749	−0.0851	−0.2078	0.3357	−0.0698	−0.1357	0.3343	−0.0454

Table 6 – Comparison Set II – Life table response experiment (LTRE) with results for a pairwise comparison of three harvester types of Panax quinquefolius

Parameter	Comparison								
	Compliant-non-compliant			Steward-non-compliant			Steward-compliant		
	Δa_{ij}	s_{ij}	$\Delta\lambda$	Δa_{ij}	s_{ij}	$\Delta\lambda$	Δa_{ij}	s_{ij}	$\Delta\lambda$
a_{11}	0	0.1472	0	0	0.1538	0	0	0.1488	0
a_{21}	−0.0133	0.6226	−0.0083	0.1828	0.3817	0.0698	0.1961	0.4126	0.0809
a_{22}	0	0.2451	0	0	0.2315	0	0	0.2213	0
a_{32}	0	0.3862	0	0	0.4410	0	0	0.4680	0
a_{13}	0.0515	0.0364	0.0019	0.0515	0.0491	0.0025	0	0.0463	0
a_{23}	0.0201	0.1540	0.0031	0.0201	0.1217	0.0024	0	0.1284	0
a_{33}	0.1436	0.2425	0.0348	0.1436	0.2319	0.0333	0	0.2714	0
a_{43}	0.0481	0.2424	0.0117	0.0481	0.2826	0.0136	0	0.2656	0
a_{53}	0.0226	0.4706	0.0106	0.0226	0.5279	0.0119	0	0.4889	0
a_{14}	0.1155	0.0150	0.0017	0.0807	0.0187	0.0015	−0.0348	0.0189	−0.0007
a_{34}	−0.0063	0.0998	−0.0006	0.0361	0.0885	0.0032	0.0424	0.1108	0.0047
a_{44}	0.0279	0.0997	0.0028	0.0883	0.1078	0.0095	0.0604	0.1084	0.0065
a_{54}	−0.0099	0.1936	−0.0019	0.0325	0.2015	0.0065	0.0424	0.1995	0.0085
a_{15}	0.4902	0.0205	0.0100	0.2279	0.0256	0.0058	−0.2623	0.0237	−0.0062
a_{35}	−0.0008	0.1368	−0.0001	0.0016	0.1208	0.0002	0.0024	0.1388	0.0003
a_{45}	0.0023	0.1367	0.0003	0.0070	0.1472	0.0010	0.0047	0.1358	0.0006
a_{55}	0.0193	0.2655	0.0051	0.0914	0.2750	0.0251	0.0721	0.2501	0.0180

per year (at SSD). In contrast, under the steward model wild ginseng populations were expected to increase at an average rate of approximately 4% per year when the stable stage distribution was reached. The steward behavior results in a 12% difference in the projected population growth rate between the two models. The $\Delta\lambda$ between the two matrices is not trivial, particularly when much of the difference can be explained by the increase in a single parameter, a_{21} (germination of seeds). Results of these experiments suggest that stewardship behavior could dramatically impact population growth rates of wild *P. quinquefolius*. Seed planting at a depth of 2 cm, combined with a later harvest season, could cause declining ginseng populations to increase.

While ginseng harvest seasons were devised to ensure berry ripening, there is no clear geographic pattern to the season onset dates (McGraw et al., 2005). However, the recent amendment by the West Virginia legislature which reset harvest onset to the 1st of September is encouraging and may foment more widespread unification. Wild ginseng populations are widely dispersed geographically; many populations will not experience harvest in a given year. Drawing on wildlife models where no-take limits are imposed regionally in areas with especially high rates of harvest (to provide rest time for population recovery), ginseng harvest could be closed on a countywide basis for set time periods (Bailey, 1999).

Any attempt to ensure sustainable harvest of wild *P. quinquefolius* will fail without further targeted research. We need additional estimates of minimum viable population size for ginseng throughout its range. The two existing estimates (Charron and Gagnon, 1991, of 170 individuals and McGraw and Furedi, 2005, of 800 genets) were made from data collected ca. 15 years apart and from different geographic regions (i.e., the northern margin of the species range and in the range center, respectively). Charron and Gagnon know of only one dozen populations >170 individuals in southern Quebec and McGraw and Furedi know of only 2 populations >800 genets in the center of the range. Small populations with low intrinsic rates of increase are especially susceptible to the negative effects of harvest (Pfab and Scholes, 2004). Our understanding of the dynamics of population recovery following harvest is also limited to two field studies (Lewis, 1988; Van der Voort et al., 2003).

American ginseng is one of dozens of wild-harvested species that are regulated. In the case of ginseng, 'regulation' is almost a misnomer, however. A loose and regionally variable set of regulations exist simply because *P. quinquefolius* is listed on Appendix II of CITES. While ginseng digging requires a permit, for example, a US$10 fee provides access to over 400,000 ha of national forest land in West Virginia (i.e., the Monongahela National Forest) for one season. Attempts to monitor the behavior of harvesters on such vast tracts of land is not realistic. The ginseng dealer is a key player in the management of ginseng. When a dealer chooses not to purchase a root, s/he is reacting to the incentives of the market (i.e., the dealer's decision is based on whether s/he can sell a specific root on the market). Recent changes in CITES regulations (e.g., minimum age requirements for roots), have forced dealers into the position of accepting/rejecting material after making a judgement on the age of the root collected by the harvesters. Roots that are too young, theoretically, will be denied export and a dealer does not want to be left with a quantity of unmarketable roots. Dealers increasingly therefore play a critical role in regulating ginseng. They could also fill a key position in dissemination of information about enhancing wild ginseng populations. Appropriate educational materials and workshops combined with effective dissemination outlets (e.g., dealers, hunting and outdoor magazines, materials circulated with hunting licenses and regulations, workshops conducted through state extension agencies, etc.) would provide a good venue for harvest regulation changes.

Non-compliant harvesters exist in reality and they can "break the rules" more dramatically than defined in the model. For example, all individuals in populations may be removed (Bailey, personal communication, 1995–1998), and digging may occur earlier than 15 June in some areas (Furedi, personal observation, 2000–2003). The harvesting rate of 25% set for these simulations had strong negative impacts on the projected population growth rates for the non-compliant and compliant harvesters. Even greater negative effects would be expected with higher rates of harvest. Diggers whom we would characterize as stewards, sometimes remove fewer large adults than prescribed in the model (Bailey, personal communication, 1995–1999). The variability in harvester types devised for this study falls within the realm of possible behaviors for diggers. Unfortunately, the frequency of harvesters along the behavioral continuum is unknown, suggesting an important gap in our understanding of the harvest dynamics. Our results strongly suggest that only by having a predominance of 'stewards' will ginseng be sustainably harvested. Regulation changes, e.g. harvest season changes that align seasons with seed ripening phenology (McGraw et al., 2005) could go a long way toward making 'compliant' harvesters into better stewards. However, it is difficult to force compliant harvesters to plant seeds in an optimal manner on a site, which the LTRE analysis shows is an important component of the 'steward' strategy. Therefore any move toward improved sustainability of harvest must include a strong educational component that shows how stewardship is in the best long-term interest of each harvester.

Because ginseng harvest regulations are difficult to enforce, and harvesters may benefit in the short-term by breaking the rules, the ginseng resource may be subject to the 'tragedy of the commons' (Hardin, 1968). If an individual knows that her/his neighbor may remove whatever plants s/he may choose to leave behind (to enhance population growth, for example), why not harvest all the available plants oneself? To evaluate the likely success of promoting sustainable harvester behavior, we must know more about harvesters, their incentives for digging and their long-term interest in maintaining a wild ginseng trade.

Acknowledgements

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