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Population Viability Analysis of American Ginseng and Wild Leek Harvested in Stochastic Environments

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Abstract: *Many populations of threatened American ginseng (*Panax quinquefolium*) and vulnerable wild leek (*Allium tricoccum*) have declined and gone extinct because of overharvesting in Canada. We assessed the impact of harvesting on populations of these species in stochastically varying environments and estimated their extinction thresholds and minimum viable populations. With both species we used four transition matrices taken from the literature in stochastic population projections under various harvesting regimes. For American ginseng the mean population growth rate (λ) declined with increasing harvesting rate (h) according to the number of years between harvests (t_r), as $-0.54 h t_r^{-0.90}$. When plants with more than two leaves are harvested every 5 years, a harvest rate of approximately 30% was sufficient to bring the λ below the equilibrium value of 1.0. Extinction thresholds, the minimum number of plants needed to rebuild a population, varied from 30 to 90 plants, and the minimum viable population size was estimated at 170 plants. Only a dozen populations known in Canada exceed 170 plants, so most populations could not support any harvesting without serious threats to their long-term persistence. For wild leek, two harvesting strategies were identified from confiscated, illegal harvests from Gatineau Park (Québec): (1) "choosy" harvesters collect fewer but larger bulbs, and (2) "busy" harvesters collect numerous but smaller bulbs. These data allowed simulations of more-realistic harvesting strategies. The rate of the decline λ along the harvest gradient was faster for wild leek than for ginseng and varied with harvesting strategies. At harvesting rates between 1 and 8% the probability that λ falls below the equilibrium value was less than 5%. The extinction threshold of wild leek was estimated at 140–480 plants and the minimum viable population at 300–1030 plants, according to the threshold chosen. Remnant wild leek populations in Québec rarely contain more than a few hundred plants, indicating the serious threat commercial harvesting represents for this species. For both species we found that the whims of a stochastically varying environment significantly reduce sustainable harvest levels.*

Análisis de viabilidad poblacional del ginseng americano y el puerro silvestre cosechados en ambientes estocásticos

Resumen: *Muchas poblaciones del ginseng americano en peligro (*Panax quinquefolium*) y el vulnerable puerro silvestre (*Allium tricoccum*), han declinado y se han extinguido debido a una sobrecosecha en Canada. En este estudio hemos evaluado el impacto de la cosecha sobre poblaciones de estas especies en ambientes que varían estocásticamente y estimamos sus umbrales de extinción y sus poblaciones mínimas viables. Con ambas especies, usamos cuatro matrices de transición tomadas de la literatura para proyectar estocásticamente las poblaciones bajo diversos regímenes de cosecha. Para el ginseng americano, la tasa de crecimiento poblacional media (λ) declinó con el incremento de la tasa de cosecha en función del número de años entre cosechas (t_r) de acuerdo con $-0.54 h t_r^{-0.90}$. Cuando las plantas con más de dos hojas son cosechadas cada 5 años, una tasa de cosecha de aproximadamente un 30% fue suficiente para llevar a λ por debajo del valor de equilibrio de 1.0. Los umbrales de extinción, o sea el número mínimo de plantas necesario para reconstruir la población, varió entre 30 y 90 plantas y el tamaño poblacional mínimo viable fue estimado en 170 plantas. Sólo una docena de las poblaciones conocidas en Canada superan las 170 plantas, por lo tanto,*

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la mayoría de las poblaciones no podrían soportar cosecha alguna sin serias amenazas para su persistencia a largo plazo. Para el puerro silvestre se identificaron dos estrategias de cosecha a partir de cosechas ilegales confiscadas por oficiales conservacionistas en el Parque Gatineau (Québec). Los cosechadores "escrupulosos" recolectan bulbos de mayor tamaño pero en menor cantidad y los cosechadores "atareados" recolectan bulbos de menor tamaño pero en mayor cantidad. Estos datos permitieron llevar a cabo simulaciones de estrategias de cosecha más realistas. La tasa de declinación de λ a lo largo del gradiente de cosecha fue más rápida para el puerro silvestre que para el ginseng y varió de acuerdo con las prácticas de cosecha. Con tasas de cosecha que variaron entre 1 y 8%, la probabilidad de que λ caiga por debajo del valor de equilibrio fue de menos del 5%. El umbral de extinción del puerro silvestre fue estimado en unas 140–480 plantas y la población viable mínima fue estimada en unas 300–1030 plantas de acuerdo con el umbral elegido. Las poblaciones remanentes de puerro silvestre en Québec raramente contienen más de unos pocos cientos de plantas, lo que pone de relieve la seria amenaza que la cosecha comercial representa para esta especie. Encontramos que para ambas especies, los impulsos de un ambiente que varía estocásticamente reduce significativamente los niveles de cosecha sostenibles.

Introduction

It is difficult to predict how long a wild population of herbaceous plants will persist when a part of the population is regularly harvested because vital rates vary over time as they respond to varying environmental conditions. Even in habitats stable in terms of disturbance regime, relatively good seasons of growth alternate randomly with relatively bad ones. We investigated the problem of population persistence for two North American forest perennials that reach the northern limits of their distribution ranges in southern Québec: American ginseng (*Panax quinquefolium*; Araliaceae) and wild leek (*Allium tricoccum*; Liliaceae). The edible bulbs of wild leek and the medicinal roots of ginseng are currently harvested in the wild. Because these species occur in the most developed and populated areas of the southern parts of Québec and Ontario, many of their populations have disappeared because of habitat destruction (Dagenais 1985; Charron & Gagnon 1991; Couillard 1993). Recent observations estimated that 14% of known ginseng populations and 20% of known wild leek populations have disappeared in Québec (Nault & Gagnon, unpublished data). Fragmentation of mature forests has probably increased the vulnerability and accessibility of these plants.

In Canada, American ginseng is listed as rare (Argus & Pryer 1990) and occurs naturally in only a few small populations in southern Ontario & Québec (Bouchard et al. 1983; Gagnon & Charron 1987; White 1988). These populations are usually found in *Acer saccharum*-*Carya cordiformis* deciduous forest communities on rich mesic soils, now a very restricted habitat. The species has been assigned a threatened status by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; White 1988). Since 1989, export of wild American ginseng has been officially discontinued from Canada (Small et al. 1994). Under the Québec regulation on threatened or vulnerable species (Bill 108, Govern-

ment of Québec 1989), wild leek has been assigned a vulnerable status, prohibiting commercial sales (Couillard 1995). American ginseng is presently under consideration for listing as a threatened species (Lavoie 1992; Couillard 1995).

The official status designations of these plants were motivated mostly by strong indications that the size of many populations of both American ginseng and wild leek have declined and, in many places, gone extinct because of overharvesting in Canada (Dagenais 1985; White 1988). Moreover, demographic studies have shown both species to be sensitive to harvest (Charron & Gagnon 1991; Nault & Gagnon 1993). The chances are high that in many harvested populations the harvest rate had exceeded the mean growth rate until these populations reached their extinction threshold.

American ginseng and wild leek are long-lived forest herbaceous perennials with contrasting population biologies and harvesting regimes. *Panax quinquefolium* reproduces exclusively by seeds after a short prereproductive period of three years or more. Populations are typically dominated by individuals with three leaves, and the survival of these plants of intermediate size is the most critical process for population growth and maintenance (Charron & Gagnon 1991). The aerial shoots develop after the deciduous forest canopy has closed in late spring, and the leaves persist until autumn, when fruits become mature. Wild populations are scarce and difficult to locate, and the roots are highly priced on the Asian market. Diggers most likely collected roots only when seeds were ripe and planted on site the seeds of harvested plants, thus fostering recruitment. Large plants were dug out with care to keep the root intact, minimizing soil disturbance. Seedlings and juveniles were left for the next harvest because populations were revisited every 5–8 years (White 1988).

Allium tricoccum is a spring ephemeral with a short photosynthetic period. The leaves develop immediately after snowmelt, synthesize storage compounds before

the forest canopy has closed, and decay shortly afterwards (Nault & Gagnon 1988). The length of time the leaves are functional depends largely on the spring climate conditions and is reflected in year-to-year variations in vital rates (Nault & Gagnon 1988; Nault & Gagnon 1993). Slow annual growth of small-sized plants leads to a long prereproductive stage of 7 to 10 years. Most population growth and maintenance is due to vegetative propagation (Nault & Gagnon 1993). Seed production varies greatly from year to year, but input of seedlings contributes to only 1–4% of the population growth rate (Nault & Gagnon 1993). Harvesters collect, nonselectively, large volumes of wild leek bulbs with shovels, throwing away leaves and small plants and leaving the forest floor heavily disturbed. Populations are often small but easy to locate, so most harvests are of total populations and are done without any conservation measures.

Because vital rates of American ginseng and wild leek have been shown to vary over time, extinction of their remnant populations can be attributed to a combination of bioecological uncertainties, such as environmental stochasticity, and human pressures. Environmental stochasticity, the natural fluctuations in the life conditions of all individuals of a population (May 1973), is considered a major factor in many population extinctions (Shaffer 1981; Gilpin & Soulé 1986; Menges 1991, 1992; Boyce 1992; Foley 1994). In a varying environment even a population with a mean growth rate ($\hat{\lambda}$) greater than 1.0 can go extinct, providing that variance in vital rates is large enough (Lande & Orzark 1988; Menges 1992). It is thought that population sizes necessary to buffer environmental stochasticity and random catastrophes will be sufficient to protect the genetic integrity of plant populations and will prevent demographic stochasticity from driving them to extinction (Menges 1991; Lande 1993).

The relationship between environmental stochasticity, population sizes, and average time to extinction have been studied with analytical models (Goodman 1987; Lande 1993; Foley 1994). Despite the ability of these models to provide useful insights into the processes of population extinction (Belovsky 1987; Belovsky et al. 1994), they could not be used for MVP estimation with the empirical data we had.

Transition matrices constructed from empirical data have been used to perform population projections of rare and endangered plants (Fiedler 1987; Mehrhoff 1989; Menges 1990; Charron & Gagnon 1991; Nault & Gagnon 1993; Schemke et al. 1994) and in assessing the impact of harvesting (Usher 1996; Getz & Haight 1989; Pinard 1993). In a stochastically varying environment the projection of a stage-classified population is obtained by the equation $\mathbf{x}(t + 1) = \mathbf{A}_t \mathbf{x}(t)$, where the \mathbf{x} are vectors containing the number (x_i) of plants per stage class i at a given time step, and \mathbf{A}_t are observed transition matrices (Menges 1990). The transition coeffi-

cients (a_{ij}) in these matrices are the proportion of the plants of a given stage that have grown or regressed to another given stage, or remained in the same stage, between two censuses (Lefkovitch 1965). When individuals (or ramets) have been classified by size, the transition coefficients incorporate the rates of growth, survival, and fecundity. These vital rates vary over time in the same population (Menges 1992).

In theory, a great number of transition matrices \mathbf{A}_t alternate at random in a varying environment. In practice, because detailed demographic studies are time-consuming, the number of matrices \mathbf{A}_t are typically few, so stochastic population projections are performed with two or more alternated matrices having the same frequency of occurrence during the projection (Bierzychudek 1982; Caswell 1989; Cohen et al. 1983; Menges 1990) or having a frequency estimated from environmental data (Åberg 1992). This method assumes that the mean and variance of each transition coefficient in a limited set of \mathbf{A}_t matrices are representative of their mean and variance in a much larger set. These assumptions can rarely be tested because sufficiently long time series are usually lacking.

If the variance of the a_{ij} is large enough among matrices, some series of population sizes ($N(i) = \sum x_i(i)$) will fall below the extinction threshold during a stochastic projection (Menges 1992). The extinction probability of this population is the proportion of series that actually fall below this threshold within projection time (Menges 1990). By examining the relation between the starting population size $N(0)$ and this extinction probability, one can estimate the MVP (Menges 1992). This MVP is sensitive to the variance of the one-step estimates of population growth rate $\lambda(t)$ (Lande & Orzark 1988; Menges 1992), which depends on the matrix-to-matrix variance of the transition coefficients. MVP estimates will also change according to the extinction threshold chosen (Ginzburg et al. 1982).

We used stochastic projection models with previously published transition matrices of American ginseng and wild leek populations (Charron & Gagnon 1991; Nault & Gagnon 1993). Our objectives were (1) to assess quantitatively the impact of harvesting on these two species in stochastically varying environments, using the available data to run realistic harvest simulations, and (2) to estimate their population extinction threshold and minimum viable population sizes (MVP). Under natural conditions many individuals are needed to allow population growth; therefore, our models assume that the extinction threshold is the population size below which no increase of the population is possible. This definition is consistent with the property of the extinction threshold as an absorbing boundary. Extinction thresholds and associated MVP are extremely useful in population management because they help identify populations at risk and settle restoration priorities. Because our models

aimed for accurate predictions and because ginseng and wild leek have been submitted to different harvesting regimes, our treatment of each species is different.

Methods

Transition Matrices and Extinction Thresholds

For American ginseng, four transition matrices modified from Charron and Gagnon (1991) were taken (Table 1). These matrices were constructed from census data of four different populations, two populations censused for 3 years and two for 2 years. For wild leek, the four transition matrices from Nault and Gagnon (1993) were used as they appear in the original publication. They were constructed from census data of five consecutive growing seasons.

The extinction threshold is the minimum starting number of individuals (or ramets) needed to rebuild a population—to ensure a population growth rate (λ) > 1. This minimum number is a property of a given transition matrix because the transition coefficients deter-

mine the number of individuals that will go through the life cycle in a given number of years. Therefore, we computed an extinction threshold for each matrix of both species. This was done by a modified population projection algorithm in which at each matrix multiplication $A\mathbf{x}(t)$, the number of plants $x_i(t + 1)$ in a given stage i was the integer part only the figure obtained by the matrix multiplication $A\mathbf{x}(t)$. In other words, no fraction of individuals was allowed to contribute to the growth of the population as in the usual algorithm of matrix exponentiation. The starting population, $N(0)$, in which individuals were distributed according to the stable stage distribution, was changed until the growth rate of the population corresponded to the dominant eigenvalue λ of the matrix A , if its $\lambda > 1$. The lowest $N(0)$ needed to obtain this λ was the extinction threshold.

Analysis of Confiscated Wild Leek Harvests

Five confiscated samples of wild leek bulbs were obtained from the conservation division of Gatineau Park (Québec, Canada) and were used to estimate average

Table 1. Transition matrices (A_t) of four populations of American ginseng (*Panax quinquefolium*) used in stochastic projections (equation 1).^a

	Size-class ^b					
	Seed	0	1	2	3	4
Population 1, 1986–1988						
Seed	0	0	0	1.350	13.24	18.50
0	0.090	0	0	0	0	0
1	0	0.155	0.245	0	0	0
2	0	0.015	0.585	0.515	0.060	0
3	0	0	0	0.400	0.845	0.190 ^c
4	0	0	0	0.030	0.045	0.740 ^c
Population 2, 1986–1988						
Seed	0	0	0	0.595	6.535	33.59
0	0.150	0	0	0	0	0
1	0	0.250 ^d	0.525	0.055	0	0
2	0	0.015	0.385	0.430	0.030	0
3	0	0	0.040	0.440	0.770	0.105
4	0	0	0	0.025	0.170	0.855
Population 3, 1986–1987						
Seed	0	0	0	0	21.78	28.29
0	0.010	0	0	0	0	0
1	0	0.210	0.330	0	0.020	0
2	0	0	0.330	0.710	0.040	0
3	0	0	0	0.140	0.770	0.220
4	0	0	0	0	0.040	0.610 ^d
Population 4, 1986–1987						
Seed	0	0	0	0.290	11.06	25.50
0	0.060	0	0	0	0	0
1	0	0.240	0.750	0	0.020	0
2	0	0	0.150	0.730	0	0
3	0	0	0.100	0.200	0.730	0.250
4	0	0	0	0	0.140	0.750

^a Modified from Charron and Gagnon (1991).

^b 0 = seedlings; 1–4 = plants with 1, 2, 3, and ≥ 4 leaves, respectively.

^c Average a_{4-3} and a_{4-4} of all population matrices to replace the real value 0.00 obtained because no individual of class 4 was sampled in this population.

^d Correction of typographical errors found in the published matrices.

bulb size and size-structure of the harvests. The total fresh mass of each harvest was determined, and subsamples of about 200 bulbs were randomly taken to estimate the individual bulb mass. The selected bulbs were freed from remaining leaf bases, roots, and rhizomes; they were washed, oven dried at 70°C for 3 days, and then weighted to ± 0.0005 g. Because the total leaf width (TLW) defines size-classes in the matrix model (Nault & Gagnon 1993), the limits of all TLW size-classes were transformed to grams of dry bulbs. For this we used regression equations obtained for TLW and bulb dry mass from samples taken in 1984 and 1985 (Nault 1986). This classification was used to calculate the proportion of each TLW size-class in the harvested samples. The matrix model also separates the plants of a given size-class according to their reproductive status and whether or not they are issued from vegetative division. The proportion of these stages within each size-class for each censused year was taken from the data of Nault and Gagnon (1993).

Stochastic Population Projections and Harvesting Models

In stochastic population projections, transition matrices are obtained from the same population censused for more than 2 years. The ginseng matrices were obtained from different populations. We thus assumed that the site-to-site variance of the transition coefficients was representative of their year-to-year variance. This may not be entirely true, but in the absence of longer-term census data there was no alternative.

For ginseng, the environmental transition matrix, \mathbf{P}_1 , defined the random alternation of the four population matrices, \mathbf{A}_b , so that each had the same frequency and the same probability of replacing any other one. For wild leek, two environmental transition matrices were defined: \mathbf{P}_1 as above and \mathbf{P}_2 where each annual matrix had the same frequency but in which the exceptionally good growing season (represented by the 1984–1985 matrix) was always followed by a relatively bad season (represented by the 1985–1986 matrix). This alternation scenario simulated the negative carry-over effect of an exceptional season reported for this spring ephemeral (Nault & Gagnon 1993).

The projection of a stage-classified population under a post-reproduction harvesting regime is obtained by $\mathbf{x}(t + 1) = \mathbf{A}\mathbf{x}(t) - \mathbf{u}(t)$, where $\mathbf{u}(t)$ is a vector containing the number of individuals harvested in each stage class (Getz & Haight 1989). This equation defines a post-reproduction harvesting regime because each year the individuals are collected after they have grown and eventually reproduced. The equation that defines a pre-reproduction harvesting regime would be $\mathbf{x}(t + 1) = \mathbf{A}(\mathbf{x}(t) - \mathbf{u}(t))$. In a stochastically varying environment, the post-reproduction model would simply be rewritten as

$$\mathbf{x}(t + 1) = \mathbf{A}_t \mathbf{x}(t) - \mathbf{u}(t), \quad (1)$$

and the prereproduction model as

$$\mathbf{x}(t + 1) = \mathbf{A}_t (\mathbf{x}(t) - \mathbf{u}(t)). \quad (2)$$

For ginseng populations, stochastic projections used a post-reproduction harvest model (equation 1) because harvesters are reported to collect the plants when the fruits are ripe. Their bright red color makes the plants easy to locate, and the seeds can be sown on site (White 1988). In equation 1, $\mathbf{u}(t) = b\mathbf{a}\mathbf{x}(t)$, b is the harvest rate set between 0 and 0.30 corresponding to the portion of the population that is harvested; \mathbf{a} is a vector in which values of 1 identify the stage classes harvested and values of 0 identify the stage classes not harvested; and $\mathbf{x}(t)$ is a stage vector containing the number of plants per stage at time t . In the model only plants with three or more leaves were harvested, as suggested by the survey data of White (1988). Stochastic population projections were run with harvest rates of 0, 0.01, 0.05, 0.10, and 0.30, each with rotation periods of 1, 2, 3, 4, 5, 6, 7, 8, 9, and 10 years.

For wild leek, stochastic projections used a prereproduction harvest model (equation 2) because this spring ephemeral is visible only before sexual reproduction and bulb division have taken place. In equation 2, $\mathbf{u}(t) = ab\mathbf{X}(t - 1)$, \mathbf{a} is a vector containing the proportion of each stage classes found in real harvests; b is the harvest rate set between 0 and 0.20 corresponding to the portion of the population that is harvested; and $\mathbf{X}(t - 1)$ is the residual number of harvestable plants (TLW > 0.8 cm) of the previous year. The vector \mathbf{a} was determined from samples of confiscated materials. The projection was constrained so that it was not possible to harvest more ramets of a given stage than there actually were (if $u_i(t) > x_i(t)$, then $x_i(t) - u_i(t) = 0$). Stochastic population projections were run with annual harvest rates of 0, 0.01, 0.02, 0.03, 0.04, 0.05, 0.10, and 0.20, each with environmental transition matrices \mathbf{P}_1 and \mathbf{P}_2 and the two harvesting strategies. Because wild leek populations are harvested each year, all simulations were run with a rotation of one year.

With each species (and each environmental transition matrix \mathbf{P} , for wild leek), harvesting simulations used the same random sequences of matrices and were run on a time horizon of 200 years (200 iterations), thus generating a series of population sizes $N(1), N(2), \dots, N(200)$. The mean growth rate $\hat{\lambda}$ was obtained by regressing $\log_{10}(N(i))$ against time; the slope of the regression line then corresponded to $\hat{\lambda}$. This is equivalent to the numerical method of calculation of $\hat{\ln \lambda}$ given by Heyde and Cohen (1985) and Cohen (1986; in Caswell 1989, equation 8.70). The number of iterations gave a stabilized $\hat{\lambda}$. A series of one-step estimates of population growth rate $\lambda(i)$ was computed as $N(i + 1)/N(i)$. The variance of $\lambda(i)$ was computed with the standard formula for the variance of

a random variable. The 95% confidence interval of $\hat{\lambda}$ was estimated as

$$\widehat{\ln \lambda} \pm 1.96 \sqrt{\text{var}(\ln \lambda(i))/m}$$

where m = number of iterations (200; Caswell 1989).

In a series of transition matrices there is often one matrix that stands out from the others because of unusually bad or good growing conditions during the census interval. The frequency of this unusual matrix can be modified in distinct population projections to explore the sensitivity of the growth rate to the frequency of this matrix. Therefore, harvesting simulations were repeated with a mean matrix in which transition coefficients are average values of those in the four matrices. Mean matrices are defined as $\bar{A} = \sum b_i A_i$, where A_i is one of the observed population matrices and b_i is the frequency of probability of occurrence of that matrix such that $\sum b_i = 1$. The dominant eigenvalue of this matrix \bar{A} corresponds to the growth rate μ of the population ($\mu = \lambda_1^{\bar{A}}$); the value of $\hat{\lambda}$ defined above should be close to μ (Caswell 1989). The most different matrices were of ginseng population three (the lowest λ) and for wild leek of 1984-1985 (the highest λ). For each harvest rate the frequency b_i of the unusual matrices was successively set at 0.25, 0.1, 0.05, and 0.01, representing a chance of occurring every 4, 10, 20, and 100 years.

The growth rate of a population harvested annually (μ_b) can be predicted from the mean matrix as

$$\mu_b \approx (1 - \sum b_i e_i) \mu_0, \quad (3)$$

where b_i is the annual harvest rate of size class i , e_i is the sum of the elasticity values of size class i , and μ_0 the growth rate of the population when not harvested. Elasticity values give the proportional change in μ resulting from a proportional change in any given transition coefficient (a_{ij}) of the mean matrix (de Kroon et al. 1986). With ginseng, calculation of predicted μ_b excluded the elasticity associated with fecundity (first row of the elasticity matrix) because it is assumed that harvesters leave the fruits on site (White 1988). If equation 3 is used with any single matrix A , the growth rate μ is replaced by λ_1^A .

For both species (and each environmental transition matrix P , for wild leek) 50 stochastic population projections of 100 years were run without harvesting. Each projection used a different random sequence of matrices and generated a random series of growth rates $\lambda(1)$, $\lambda(2)$, ..., $\lambda(100)$. From each series of $\lambda(i)$ we computed a corresponding series of population sizes $N(i)$ with the formula $N(i+1) = \lambda(i)N(i)$. The number of simulated years during which the values of $N(i)$ stayed above the extinction threshold is an estimate of the population persistence. The extinction probability was computed as the proportion of simulated series of $N(i)$ having a persistence lower than 100 years. By changing the starting population size, $N(0)$, simultaneously for all 50 series

of $N(i)$, we determined the lowest $N(0)$ needed to have an extinction probability 0.05 (± 0.01) over 100 years. This $N(0)$ was the minimum viable population (MVP). The different values of $N(0)$ ranged from the extinction threshold to 2000, with increments of one individual when the right (smaller) range of $N(0)$ had been identified. All simulations were run with the spreadsheet software EXCEL 3.0 (Microsoft Corporation 1991, Redmond, Washington).

Results

Size Structure of Confiscated Wild Leek Harvests

The analysis of samples of confiscated wild leek harvests revealed two harvesting strategies: a strategy of "choosy" harvesters and a strategy of "busy" harvesters (Fig. 1). The choosy types harvested plants mostly in the largest size-classes, with a peak at size class 5 (ramets with two leaves, each 3-5 cm wide). Four confiscated samples out of the five analyzed presented this strategy. These samples weighed from 2.3 to 8 kg (fresh mass) and contained between 550 and 2000 bulbs. The busy type seemed less selective, harvesting more broadly and more rapidly, collecting a greater quantity of middle-sized ramets (size-class 4: one large or two small leaves; Fig. 1). A single confiscated harvest representing the busy type contained more plants (8.8 kg, 3600 bulbs) and debris than the average in the choosy type of harvest. Using the total fresh mass of the bulbs (85 kg) harvested by the 16 illegal harvesters, the average dry mass of one bulb (3.5 g) and a dry-to-fresh mass ratio of 1:4, we estimated the total confiscated harvest of 1993 to be 25,000 ramets in Gatineau Park.

Mean Population Growth Rate

For ginseng the slope of the linear decline of the mean population growth rate ($\hat{\lambda}$) along the gradient of harvest pressure varied according to the rotation period (Fig. 2). The relationship between the rate of decline of $\hat{\lambda}$ and the rotation period is an exponential function described by the following equation:

$$\hat{\lambda}_b = \hat{\lambda}_0 - 0.54 b t_r^{-0.90}, \quad (4)$$

where λ_b is the mean growth rate under harvesting rate b , t_r is the rotation period in years, b is the harvesting rate, and λ_0 is the mean growth rate of the population when not harvested. Note also that $\hat{\lambda}$ tended toward the growth rate μ of the mean matrix \bar{A} , as expected (Table 2; Caswell 1989). This growth rate μ increased as the frequency of a bad growing season decreased (Table 3). But even if it occurred only once every 100 years, the population could not survive an annual harvest rate higher than 10%.

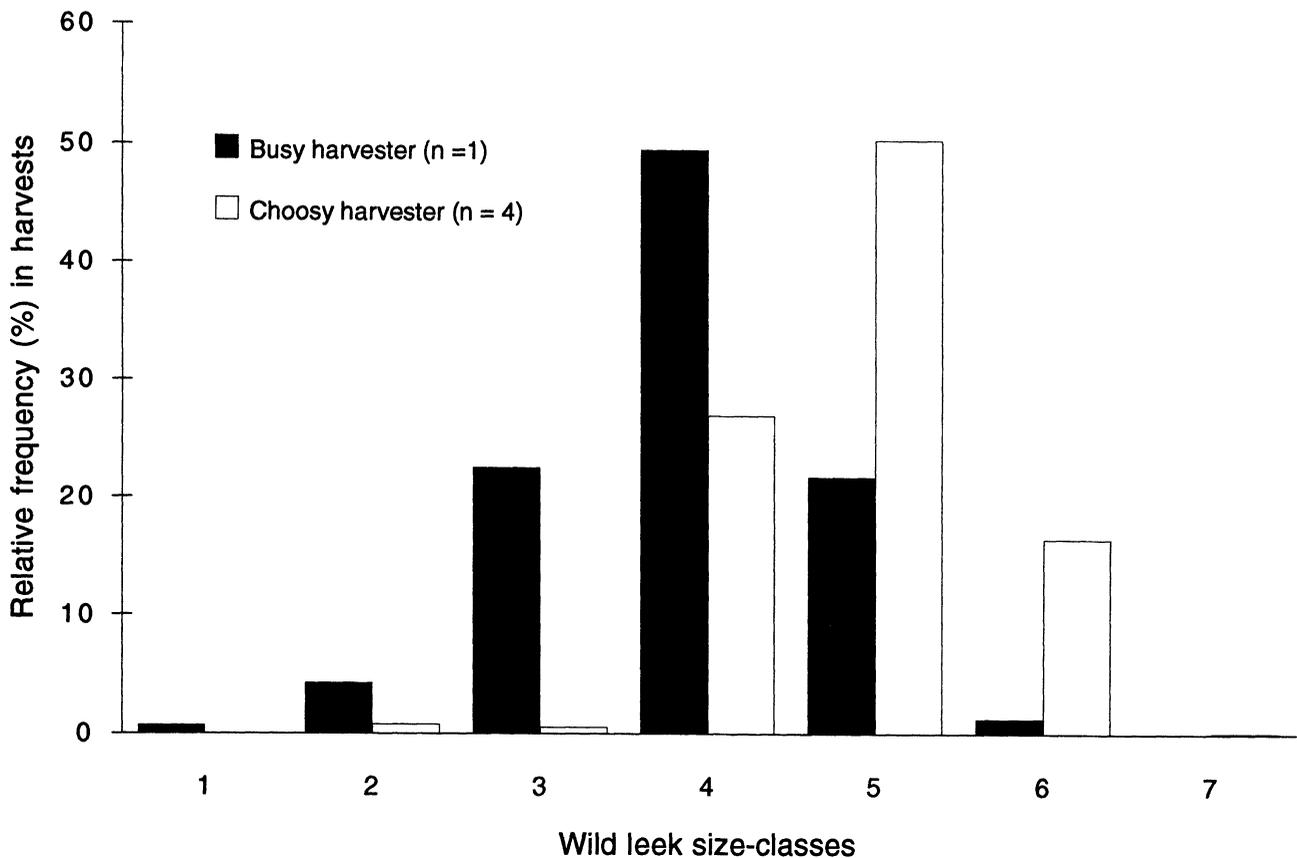


Figure 1. Comparison of the size distribution of wild leek (*Allium tricoccum*) plants harvested according to the harvesting strategies "choosy" or "busy." The size-classes are based on total leaf width (cm) as follows: 1: ≤ 0.8 ; 2: 0.9–2.0; 3: 2.1–3.8; 4: 3.9–6.5; 5: 6.6–10.0; 6: 10.1–15.0; 7: > 15.0 .

With an annual harvest rate of 10% the $\hat{\lambda}$ of the wild leek population has a 95% chance of falling between 0.972 and 1.026 for all harvesting strategies and environment alternations (Fig. 3). The main difference among simulations was between harvesting strategies. This difference increased along the gradient of harvest pressure (Fig. 3). With a harvest rate of 20% the maximum impact (lowest $\hat{\lambda}$) was that of a choosy harvester when a good growing season was always followed by a bad one (P_2). The minimum impact was that of a busy harvester with the environmental transition matrix P_1 . With harvesting rates below 5% the differences were less pronounced. The frequency of an exceptionally good reproduction year did not alter greatly the decline of the population growth rate along the gradient of harvest pressure (Table 4).

Extinction Threshold and Minimum Viable Populations

The extinction thresholds of American ginseng populations vary with the deterministic growth rates set by their transition matrices (Table 5). Among the four populations studied by Charron and Gagnon (1991), population 1 was very close to its extinction threshold. It was

not possible to compute an extinction threshold for population 3 because its deterministic growth rate (λ) was less than 1. The MVP for this set of matrices, using an extinction threshold of 91 (560 including seeds; Fig. 4), was estimated at 172 plants (1068 including seeds). We estimated that a population of 172 has a probability of extinction of 0.04 over 100 years. Moreover, populations that fell below 91 in the simulations did so within 4 years, otherwise they persisted for 100 years. Beyond 4 years the sizes reached by the simulated populations were too large to have a chance of falling below 91, even if the $\lambda(t)$ were less than 1.0 more than 1 year in a row.

If the plants were distributed as the stable stage distribution associated with the mean matrix, a population of 172 plants would have 55 plants with more than two leaves (Fig. 4). None of the populations studied by Charron and Gagnon (1989) reached this number (Table 5). Only three populations in Québec are presently known to have more than 500 plants, but most populations have less than 50 (Nault & Gagnon, unpublished data). In Ontario the average number of plants in known populations was estimated as 10 to 20 plants (White 1988).

The extinction thresholds of the wild leek populations also vary with the deterministic growth rate set by the

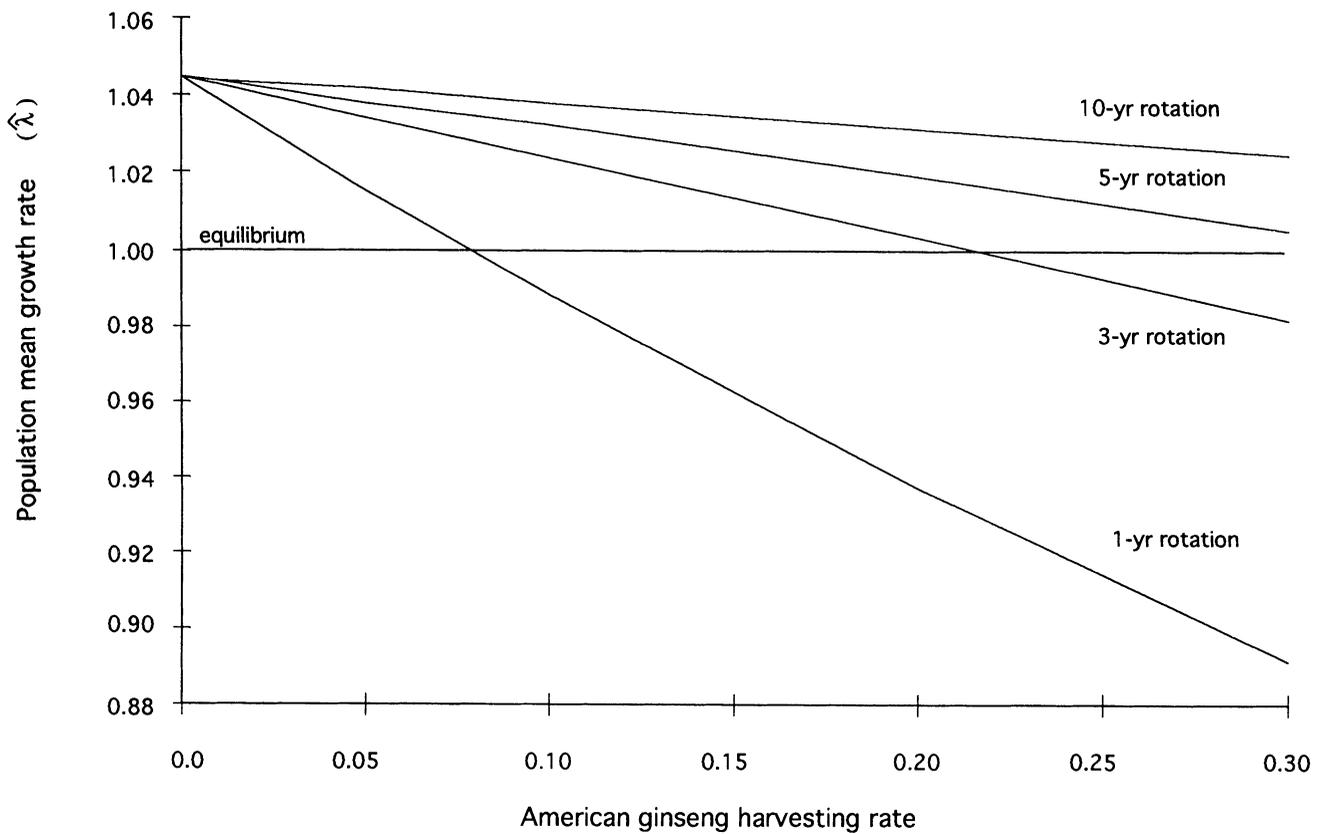


Figure 2. Decline of the mean growth rate ($\hat{\lambda}$) of a population of American ginseng (*Panax quinquefolium*) on the harvesting gradient for different rotation periods. Mean growth rates ($\hat{\lambda}$) were computed from 200-year stochastic projections using four transition matrices.

annual transition matrix (Table 5). The MVP for this population was estimated around 300 or 1000 individuals, depending on whether we used an extinction threshold of 140 (set by the mean matrix) or 482 (set by the matrix

Table 2. Mean growth rates ($\hat{\lambda}$ and μ) of an American ginseng (*Panax quinquefolium*) population under different harvest rates, in a stochastic environment, simulated with the four population matrices of Table 1.

Variable	Harvest rate (%) ^a				
	0	1	5	10	30
λ	1.045	1.039	1.016	0.988	0.892
$\text{var}(\lambda_i)^b$	0.0831	0.0826	0.0811	0.0795	0.0759
$\text{var}(\ln(\lambda_i))$	0.0806	0.0810	0.0829	0.0855	0.0973
μ	1.045	1.039	1.016	0.989	0.892
predicted μ_b^c	1.045	1.040	1.018	0.992	0.888

^a Harvest rates represent the percentage of plants harvested in size-classes 3 (three leaves) and 4 (\geq four leaves)

^b Variance computed with the standard formula of the variance of a random variable.

^c The growth rate of a population harvested annually (μ_b) can be predicted by $\mu_b \approx (1 - \sum h_i e_i) \mu_0$, where h_i is the harvested rate of size class i , e_i is the sum of the elasticity values of size class i (excluding the values for reproduction), and μ_0 is the population growth rate of the mean matrix with no harvesting ($= 1.045$).

with the lowest λ ; Table 5; Fig. 4). If the individuals were distributed as the stable stage distribution associated with the mean matrix, a population of 303 or 1032 plants (502 or 1705 individuals including seeds) would have 209 or 713 plants of harvestable size (leaves more than 0.8 cm wide; Fig. 3). Remnant wild leek popula-

Table 3. Growth rate (μ_b) of an American ginseng (*Panax quinquefolium*) population under different harvest rates, simulated with mean matrices^a computed with four different probabilities of an unusually bad year.

Probability ^c	Harvest rate (%) ^b				
	0	1	5	10	30
0.25	1.045	1.039	1.016	0.989	0.892
0.10	1.072	1.067	1.043	1.015	0.914
0.05	1.082	1.076	1.052	1.023	0.922
0.01	1.089	1.082	1.059	1.030	0.927

^a $A = \sum b_i A_i$, where the A_i are population transition matrices and each b_i is the frequency or probability of occurrence of a population matrix such that $\sum b_i = 1$.

^b Harvest rates represent the percentage of plants harvested in size-classes 3 and 4.

^c The probability (b_3) is the frequency of an unusually bad year as represented by the matrix of population 3 (see Table 1).

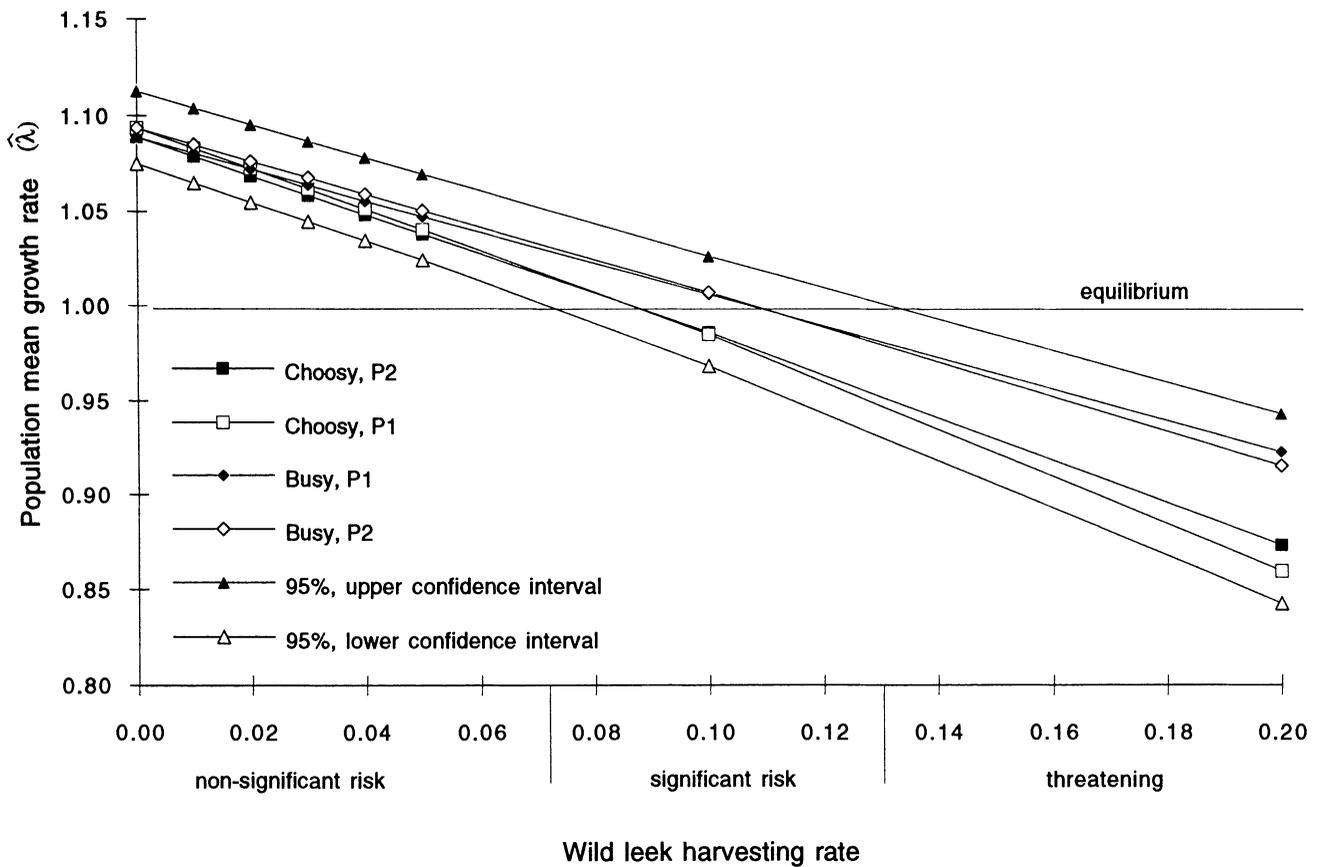


Figure 3. Decline of the mean growth rate ($\hat{\lambda}$) of a population of wild leek (*Allium tricoccum*) on a harvesting gradient for two harvesting strategies, each simulated using environmental transition matrix P_1 and P_2 . Harvesting strategies are based on size-structure of harvests. The “choosy” type harvested plants mostly in the largest size classes, and the “busy” type harvested more broadly with a greater quantity of middle-sized plants (Fig. 1).

tions in Québec are typically sparse and rarely contain more than a few hundred plants.

The estimated MVP of wild leek was not much influenced by the environmental transition matrix used, but the shape of the extinction probability curve, as it declines along $X(0)$, differed between environmental transition matrices (Fig. 4). Extinction probabilities were higher when projections were made with environmental transition matrix P_2 . Also, the curves were steeper when the extinction threshold was set lower (Fig. 4). We estimated that all calculated wild leek MVP have an extinction probability of 0.06 over 100 years. As for ginseng, wild leek populations that went below the extinction threshold in the simulations did so very early (within 3 years); otherwise they persisted for 100 years.

Discussion

Impact of Harvesting Ginseng and Wild Leek

There are some indications that many harvesters of American ginseng collect all the large plants (two leaves

or more) they can find (Lewis 1984). A survey of 29 harvesters of American ginseng in Ontario revealed that most respondents follow conservation measures such as harvesting late in the season, sowing the seeds, leaving the younger plants, and rotating their visits (White 1988). Despite such measures, mean collected root mass has decreased constantly (White 1988). In Québec the importance of harvesting is unknown (Gagnon & Charron 1987).

The maximum sustainable rate of harvest on any population is the rate at which the $\hat{\lambda}$ falls below the equilibrium value of 1.0. For ginseng populations the maximum rate of annual harvest would be a little more than 5% (Table 2). Because of the variance in $\lambda(i)$, however, the growth rate of a population under this harvesting pressure still has a chance of falling temporarily below the equilibrium. This sustainable harvest rate is about three times lower than the maximum value of 15.8% estimated previously under the assumption of a favorable and unchanging environment (Charron & Gagnon 1991).

The gradient of harvesting rates on a wild leek population can be divided into three ranges of rates for which the risk that the $\hat{\lambda}$ will drop below 1.0 is nonsig-

Table 4. Growth rate (μ_b) of a wild leek (*Allium tricoccum*) population under different harvest rates, simulated with mean matrices^a computed with four different probabilities of an unusually good year.

Probability ^c	Harvest rate (%) ^b							
	0	1	2	3	4	5	10	20
Choosy harvesters								
0.25	1.091	1.081	1.071	1.061	1.051	1.040	0.988	0.873
0.10	1.082	1.072	1.062	1.052	1.042	1.032	0.982	0.875
0.05	1.078	1.069	1.059	1.049	1.040	1.030	0.980	0.877
0.01	1.076	1.066	1.057	1.047	1.037	1.028	0.979	0.878
Busy harvesters								
0.25	1.091	1.083	1.075	1.066	1.058	1.050	1.009	0.925
0.10	1.082	1.074	1.066	1.057	1.049	1.041	1.002	0.923
0.05	1.078	1.070	1.062	1.054	1.046	1.039	0.999	0.923
0.01	1.076	1.068	1.060	1.052	1.044	1.036	0.998	0.923

^a $\bar{\mathbf{A}} = \sum b_i \mathbf{A}_i$, where the \mathbf{A}_i are population transition matrices and each b_i the frequency or probability of occurrence of each matrix, such that $\sum b_i = 1$.

^b Harvest rates are expressed as the percentage of plants harvested in a whole population, according to size distributions shown in Fig. 1.

^c The probability (b_i) is the frequency of an exceptionally good year as represented by the matrix of 1984–1985 (see Nault & Gagnon 1993).

nificant (< 5%); significant (> 5%, < 95%); and threatening (> 95%). If we set the maximum sustainable harvest rate at the upper limit of the nonsignificant risk range, it would be less than 8% (Fig. 3). This is about two times lower than the 15% maximum rate estimated previously under the assumptions of an unchanging environment and a harvest strategy in which collected plants are uniformly distributed in the largest size-classes (Nault & Gagnon 1993).

The strategies used by wild leek harvesters have a significant impact on population maintenance. The busy harvesters, when collecting the same number of plants as the choosy ones, had less impact. This is because the busy type of harvester collected more in the small size-classes, in which plants are known to contribute less to population growth according to the elasticity matrices (Nault & Gagnon 1993). But because the busy harvesters collect more plants than the average choosy harvesters, they would have a greater overall impact.

For wild leek the slope of the declining curve of $\hat{\lambda}$ along the gradient of harvesting pressure ranged from -0.83 to -1.09 (Fig. 3). These slopes are steeper than that of -0.51 obtained with a ginseng population harvested annually (Fig. 2). Therefore, simulated annual harvests had more impact on wild leek than on ginseng populations. The greater sensitivity of wild leek to harvest may be due to prereproduction harvests of large plants in a population that maintains its number mostly by bulb division of these large plants. High elasticity values are concentrated in large size-classes in wild leek (Nault & Gagnon 1993), compared to ginseng in which high elasticity values are more evenly distributed among size-classes (Charron & Gagnon 1991). Because wild leek is visible only in spring, the only conservation measure would be to delay bulb harvest until the end of the photosynthetic season, when bulbs are filled with re-

serves (usually at the end of May in Québec; Nault & Gagnon 1988). The number of bulbs necessary to obtain the same mass would then be greatly reduced.

Implications for Conservation

The MVP for both studied species is about twice the size of their corresponding extinction thresholds. We cannot tell if this is a general trend, but such a similarity between these two different species was unexpected. This simple ratio, if general, could become a convenient rule of thumb.

Table 5. Extinction thresholds ($N_t(0)$ and $N_p(0)$), population sizes (N_{obs}), and deterministic growth rates (λ) computed for each matrix of American ginseng (*Panax quinquefolium*) and wild leek (*Allium tricoccum*).

Species	Matrix	$N_t(0)^a$	$N_p(0)^b$	N_{obs}^c	λ
Ginseng	1 (1986–1988) ^d	529	87	60–80	1.055
	2 (1986–1988) ^d	146	30	75–76	1.170
	3 (1986–1987)	—	—	75–76	0.880
	4 (1986–1987)	560 ^e	89	128–132	1.050
Wild leek	1984–1985	132	77	1640	1.130
	1985–1986	797 ^e	479	2628	1.024
	1986–1987	191	113	2319	1.106
	1987–1988	156	93	3710	1.100
	1984–1988 ^d	234 ^e	139	3026	1.091

^a $N_t(0)$ is the total starting population distributed as the stable stage distribution associated with each individual matrix.

^b $N_p(0)$ is the number of plants (= $N_t(0)$ – number of seeds) according to the stable stage distribution.

^c N_{obs} is the number of plants observed during censuses (minimum and maximum for the ginseng). For ginseng, N_{obs} are from exhaustive censuses; for wild leek, N_{obs} are from a subsample of 18 m² of a much larger population ($N_{obs} \approx 10^6$).

^d Mean matrices.

^e Numbers used to compute the minimum viable populations (MVP).

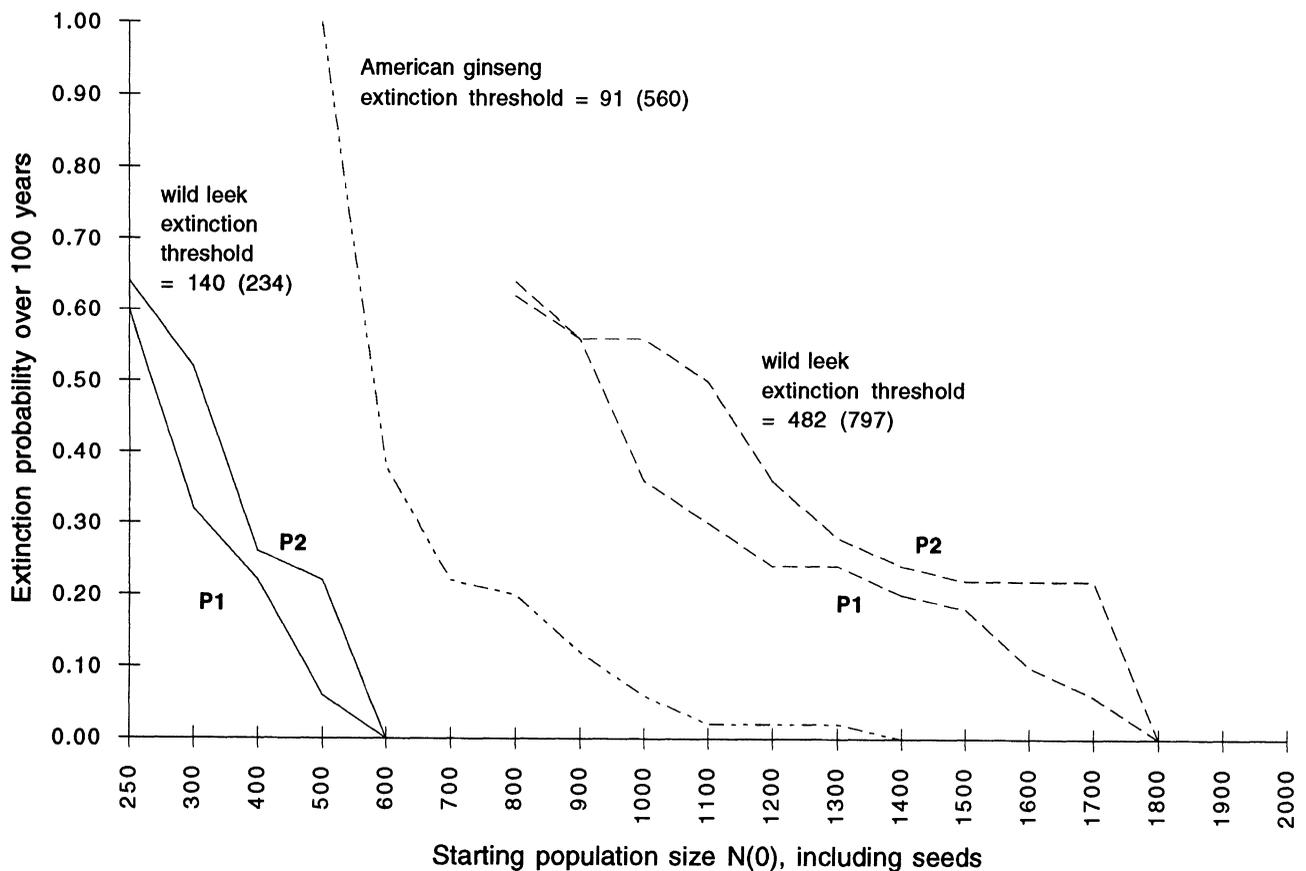


Figure 4. Extinction probability over 100 years for populations of American ginseng (*Panax quinquefolium*) and wild leek (*Allium tricoccum*) as a function of starting population size. P_1 and P_2 are different environmental transition matrices. Figures in parentheses represent total population numbers, including seeds.

For American ginseng the results of harvesting simulations and MVP estimation suggest that most small, isolated populations found in Québec and Ontario are too small to support any harvesting. Populations above MVP may not support more than very low harvesting rates on a long rotation period. For instance, with an annual harvesting rate of 10% persistence T (in years) above MVP increases as the logarithm of $X(0)$ $T = 116 \log_{10}(X(0)) - 349$. This means that even a population of 485 plants (3000 individuals when including seeds) would go below its MVP in less than 100 years.

Our results show that increases in the harvesting rotation period are beneficial for ginseng populations. With the average rotation period of 5 years (White 1988), a harvest rate of 30% would give a mean growth rate of 1.007 with a 95% confidence interval of 0.967–1.049 (Fig. 2). Most reproductive plants are found in age classes 4–7 years and older, and seeds have a dormancy of 1.5 years (Charron 1989), so we expect that seeds produced during harvest year will reach reproductive size 7 years later. Also, in 5 years only a small proportion of juveniles will reach a size large enough to yield rela-

tively good seed crops. Therefore, rotation longer than 5 years would be more prudent. At such a low sustainable level, however, harvesting of wild roots of ginseng can hardly generate a reasonable income.

The sowing of seeds is also likely to be beneficial. Charron and Gagnon (1991) showed that, with a probability of seedling recruitment higher than 20%, all populations studied reached a $\lambda > 1$. Using a germination rate of 34% (half of the rate obtained in an experimental garden; Charron 1989) in the four transition matrices, the $\hat{\lambda}_0$ in equation 4 increased from 1.045 to 1.186. This would allow, in theory, an annual harvest rate of up to 30%. Therefore, sowing seeds would be an efficient method of enhancing the viability of existing wild populations in Canada. But because these calculations are based on “mature” populations and because only older plants produce a large number of seeds, there is reason to be even more conservative.

Large populations of wild leek seem able to support low harvesting rates (below 8%). For a population containing 10,000 plants of TLW > 0.8 cm, however, this represents only 800 bulbs per year, a collection typical

of a single, choosy harvester. With an annual harvest rate of 20% ($\lambda = 0.873$), persistence above MVP increases as the logarithm of $X(0)$: $T = 17\log_{10}(X(0)) - 48$. Regulations over the number of harvestable plants, in relation to population size, would be difficult to enforce.

It appears likely that many populations of both wild leek and American ginseng in Québec have declined and even disappeared because of overharvesting. Since the 1930s American ginseng has been cultivated in Canada. Today the species is cultivated mostly in southwestern Ontario and southern British Columbia (Small et al. 1994). In this last province, the net income for the sales of ginseng roots on the Asian market reached \$28 million (Canadian) in 1993 (Schreiner 1994).

In 1983 commercial trade of wild leek bulbs in Québec was estimated to be worth from \$290,000 to \$580,000 (Canadian) per year (Dagenais 1985). The official designation of the species as vulnerable in Québec will allow harvests for personal use only and will lead to legal actions on commercial retailers. Cultivation of wild leek would decrease the harvesting pressure on wild populations because cultivated plants would meet the same market demands as those taken by collectors. Production costs would be higher, however.

In a context of commercial production, efforts should be taken to protect and improve the viability of remnant wild populations of both species as living gene banks. It is hoped that the commercial value of the species will make these efforts more appealing to various levels of government as well as private interests. Ginseng and wild leek could contribute to public awareness about plant conservation in Canada because these species possess high cultural, educational, and ecological value. Ginseng has a long history of medicinal use, both by Asian and American cultures. Wild leek was also used by aboriginal peoples of Canada and is a well-known spring ephemeral. With their foliage developing immediately after snowmelt, wild leek plants play an important ecological role by capturing soil nutrients that might otherwise be lost from the site (Muller 1978).

Limitations of the Harvesting Models and Extinction Probability Estimates

Our conclusions may appear extremely conservative because they do not stem from results of experimental harvests and because of almost unavoidable gaps in knowledge. For both species the effect of plant density on vital rates is unknown; the models we used did not explicitly incorporate density dependence. Density dependence in matrix population models for the perennial herb *Viola fimbriatula* gave population trajectories with undamped oscillations when the density function was discontinuous (Solbrig et al. 1988, 1990). Such a behavior would increase extinction risk. In any case, the incorporation of a realistic and explicit nonlinearity in a projec-

tion model requires a lot of data (Ginzburg et al. 1990). Most probably, transition coefficients derived from field observations on natural populations already incorporate density effects, but to an unknown extent.

Because of lack of relevant data, our stochastic projections did not include random catastrophes, which can represent a major risk for populations (Menges 1991; Lande 1993; Mangel & Tier 1994). Sugar maple stands on rich mesic soils are the typical habitat for both species. Small-scale disturbances, such as windthrows, may occur in these forests and can possibly damage whole patches of forest herb populations. The distribution of such environmentally caused catastrophes for a given population is hard to estimate (Foley 1994). Another major cause of population extinction for both species in southern Canada has been habitat conversion or destruction by development. Legal designation of wild leek as vulnerable in Québec should decrease this kind of catastrophe.

Despite these knowledge gaps, we think our approach has much to offer and has reduced the uncertainty about the effects of harvesting wild leek, American ginseng, and other organisms in stochastic environments. When organisms are harvested it should be remembered that the whims of a stochastically varying environment significantly reduce sustainable harvest levels. Harvesters usually seek large, mature individuals. Yet, the population viability of most iteroparous forest herbs and woody plants studied so far appears to depend highly on the survival of mature individuals (Silverton et al. 1993). This may be particularly true at the northern limit of the distribution of ginseng and wild leek because more-variable or -rigorous climatic conditions lead to more-episodic recruitment.

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