

Relationship between age, size, and reproduction in populations of American ginseng, *Panax quinquefolius* (Araliaceae), across a range of harvest pressures¹

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Abstract: Size-selective harvest occurs not only in some animal species in the wild, but in some plant species. *Panax quinquefolius*, a perennial plant of eastern North America, is one such species. As harvest of this species is fatal, there is potential for evolutionary change if selected traits are heritable. In this study, we compared traits potentially affected by selection among 12 populations with different harvest pressures. We used the recovery pattern of an experimentally harvested population to develop an index of harvest pressure: the proportion of seedlings and juveniles. Age was related to leaf area, symposium (stem) height, and reproduction in populations across a range of harvest indices (HI = 0.4122–0.9583). We detected variation among populations with different harvest indices in the age–leaf area relationship in 2006. A 10-y-old plant would have 30% less leaf area in a population with high harvest pressure (HI = 0.9) than in a population with low harvest pressure (HI = 0.4). Similar results were observed with symposium height in 2005 and 2006. Reproductive plants in populations with higher harvest indices had reduced seed set, likely due to Allee effects. A separate, related study showed that leaf area differences were maintained among plants from 8 populations 4 to 5 y after transplantation to a common environment. Reduced growth rates in populations with higher harvest pressure may be the outcome of appearance-mediated selection.

Keywords: evolution, harvest, life history, *Panax quinquefolius*, population differentiation.

Résumé : Comme pour la chasse d'animaux en milieu naturel, *Panax quinquefolius*, une plante vivace de l'est de l'Amérique du Nord, subit une récolte sélective en fonction de la taille. Puisque la récolte est fatale, il y a un potentiel pour un changement évolutif si les traits sélectionnés peuvent être hérités. Dans cette étude, nous avons comparé des traits potentiellement touchés par la sélection dans 12 populations subissant différentes pressions de récolte. Nous avons utilisé le patron de rétablissement d'une population récoltée expérimentalement pour développer un indice de pression de récolte : la proportion de semis et de juvéniles. L'âge de la plante était relié à l'aire de la feuille, à la hauteur de la tige et à la reproduction dans un ensemble de populations de différents indices de récolte (indices = 0.4122-0.9583). Pour 2006, nous avons détecté des variations dans la relation entre l'âge et l'aire de la feuille entre des populations ayant des indices de récolte différents. Une plante de 10 ans avait des feuilles 30 % plus petites en surface dans une population avec une pression de récolte élevée (indice = 0.9) que dans une population avec une faible pression de récolte (indice = 0.4). Des résultats similaires ont été observés pour la hauteur de la tige en 2005 et 2006. Les plantes reproductives dans les populations avec des indices de récolte plus élevés avaient un nombre réduit de graines, probablement en raison des effets d'Allee. Une étude à part, mais reliée a démontré que les différences de surface des feuilles des plantes de 8 populations ont été maintenues de 4 à 5 ans après leur transplantation dans un environnement commun. Des taux de croissance réduits dans des populations avec une pression de récolte plus élevée peuvent être le résultat d'une sélection basée sur l'apparence.

Mots-clés : différenciation de population, évolution, histoire de vie, *Panax quinquefolius*, récolte.

Nomenclature: Gleason & Cronquist, 1991.

Introduction

Rapid evolution in response to anthropogenic environmental change has been documented in a variety of wild taxa (Hendry & Kinnison, 1999; Bone & Farres, 2001; Palumbi, 2001). Humans also directly affect wild species through harvest, which can have far-reaching evolutionary effects. Mortality of harvested individuals can lead to loss of genetic diversity, and phenotypically selective harvest can lead to life history change (Ashley *et al.*, 2003). Several notable examples of such change come from commercial fisheries,

where larger fish are often selectively harvested (Law, 2000; Conover & Munch, 2002; Conover *et al.*, 2005). Life history changes often occur in directions that are not favourable to human interests, such as reduced growth rate or smaller size at reproductive maturity (Conover & Munch, 2002; Conover *et al.*, 2005). Hunting also has had evolutionary effects, leading to declines in body mass and horn size in bighorn rams (Coltman *et al.*, 2003) and probably to the increased frequency of tusklessness in African elephants (Jachmann, Berry & Imae, 1995). The strength of anthropogenic selection and the possibility of rapid evolution, even in long-lived species, have made these issues additional conservation concerns (Ashley *et al.*, 2003; Stockwell, Hendry & Kinnison, 2003).

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Animal species provide dramatic examples of the unintended evolutionary consequences of harvest. However, the number of exploited animal species is dwarfed by the number of wild plant species targeted by timber harvest or collected for medicinal use, the ornamental trade, or wild foods (Ledig, 1992; Salick, 1995; Hamilton, 2004; Ticktin, 2004). As in animal species, studies have examined the evolutionary effects of harvest in plants, including impacts on genetic diversity (Ledig, 1992; Buchert *et al.*, 1997; Rajora *et al.*, 2000; Jennings *et al.*, 2001; Cruse-Sanders, Hamrick & Ahumada, 2005) and phenotypic selection (Sokol, Greenwood & Livingston, 2004; Cornelius *et al.*, 2005; Law & Salick, 2005; Mooney & McGraw, 2007a). The majority of studies in plants have focused on timber species, probably because of their worldwide economic importance (Ledig, 1992; Buchert *et al.*, 1997; Rajora *et al.*, 2000; Jennings *et al.*, 2001; Sokol, Greenwood & Livingston, 2004; Cornelius *et al.*, 2005). Timber harvest has been generally connected with declines in genetic diversity (but see Cloutier *et al.*, 2007), and the practice of selective logging or high-grading seems to subject tree species to pressures analogous to those of fisheries (Jennings *et al.*, 2001; Sokol, Greenwood & Livingston, 2004; Cornelius *et al.*, 2005). In addition to fibre and timber uses, it is estimated that 10–18% of the world's flora, or roughly 53 000 species, are used in traditional medicine or western medicine (Hamilton, 2004).

Among the economically and culturally significant class of medicinal plants is North American ginseng, *Panax quinquefolius*. The impacts of wild harvest on this species have been investigated in multiple ways. This native forest plant is the focus of the largest international trade in medicinal plants from North America (Carlson, 1986), which warranted *P. quinquefolius*' listing in Appendix II of the Convention on International Trade in Endangered Species (CITES) in 1973 (Robbins, 2000). Although *P. quinquefolius* is cultivated, wild roots are *ca.* 10 times more valuable because they are considered more potent in Asian medicine (Robbins, 2000; USFWS, 2006). Harvest of the root is fatal to the plant, which has led authors to study how this could impact genetic diversity within populations (Cruse-Sanders & Hamrick, 2004; Cruse-Sanders, Hamrick & Ahumada, 2005). Simulated removal of just 10 to 30% of plants resulted in significant decreases in genetic diversity (Cruse-Sanders, Hamrick & Ahumada, 2005). In addition, populations in protected areas had significantly greater diversity than populations in areas open for harvest (Cruse-Sanders & Hamrick, 2004). As in other exploited species, harvest of *P. quinquefolius* is size selective, for several reasons (Mooney & McGraw, 2007a). First, harvest is limited by law to plants at least 5 y old and/or those with at least 3 leaves in most of the US states (USFWS, 2006). Unlike other herbaceous species, the age of *P. quinquefolius* plants can be estimated by counting the rhizome scars formed by the annual abscission of the stem. Second, harvesters are also likely motivated to leave behind juvenile plants, although harvester behaviour is notably difficult to ascertain (Van der Voort & McGraw, 2006). Larger plants yield more valuable roots and there is a traditional conservation ethic that could motivate some harvesters to leave behind smaller plants (Price, 1960; Van der Voort & McGraw, 2006). Third, larger

plants are more apparent to human harvesters in the dense understory where *P. quinquefolius* grows, as documented by an experimental study (Mooney & McGraw, 2007a).

For size-selective harvest to cause evolutionary changes in *P. quinquefolius* similar to those observed in animal species, the selected traits would need to be genetically based. Most methods to determine the proportion of phenotypic variation that results from genetic differences rely on growing offspring of controlled crosses to maturity, *e.g.*, offspring–parent regression (Falconer & Mackay, 1996). Because 8 y or more may be required for seeds to grow to adult plants in *P. quinquefolius*, we sought an alternative method to assess the genetic basis of the age–size relationship. Common garden experiments are a classic technique to determine if differences among populations are genetically based (Clausen, Keck & Hiesey, 1939). If carryover effects from the original environment are minimized, differences among populations that persist in the common garden can be attributable to genetic differentiation (Clausen, Keck & Hiesey, 1939). We applied this approach to *P. quinquefolius* to assess the degree to which size-related traits were genetically based.

The purpose of this study was to determine if populations of *P. quinquefolius* subjected to different harvest pressures vary in traits potentially affected by size-selective harvest. This required us to estimate the extent that harvest has taken place in our study populations. In one previous study of genetic diversity differences, populations were classified as either unprotected or protected based on their location in areas where harvest is permitted or forbidden, respectively (Cruse-Sanders & Hamrick, 2004). However, most laws guiding harvest are nearly unenforceable in practice (Robbins, 2000), and poaching from protected areas may be commonplace (van Manen *et al.*, 2005). Therefore, the protection status of a population would be, at best, an approximate indicator of harvest pressure. We developed an index of harvest pressure based on the results from an experimentally harvested population (Van der Voort *et al.*, 2003) and its recovery 10 y post-harvest. Selection on size has the potential to affect life history traits, specifically growth rate and the timing of reproduction. We compared how age relates to leaf area, sympodium (stem) height, and reproductive traits among populations with different harvest pressures.

Methods

STUDY SPECIES

North American ginseng, *Panax quinquefolius* (Araliaceae), is a perennial herb infrequently found in the understory of the deciduous forest in eastern North America (Anderson *et al.*, 1993; McGraw *et al.*, 2003). Although widespread in its distribution, it can be locally rare due to nearly 3 centuries of commercial harvest, habitat degradation, and increased browse by white-tailed deer (McGraw *et al.*, 2003; McGraw & Furedi, 2005). The life cycle of *P. quinquefolius* is structured into stage classes based upon the number of leaves. Seedlings consist of a single compound leaf for the first few years (2–5) of growth. Juvenile plants have 2 compound leaves, and adult plants

typically have 3 to 4 compound leaves (Lewis & Zenger, 1982; Charron & Gagnon, 1991; McGraw & Furedi, 2005). Plants frequently initiate flowering as juveniles, but these juveniles rarely produce seeds (Carpenter & Cottam, 1982; Schlessman, 1987). Most adult plants are reproductive, producing an umbel of small flowers at anthesis in mid-summer (Schlessman, 1985; Schlessman, 1987). Flowers of *P. quinquefolius* are self-compatible but are also visited by generalist pollinators (Schlessman, 1985). Seeds are found in fleshy berries that turn red upon ripening in late summer (McGraw *et al.*, 2005). Seeds can exhibit variable dormancy periods, but most seeds germinate in the second spring following dispersal (McGraw *et al.*, 2005; Mooney & McGraw, 2007b).

STUDY POPULATIONS

We collected data from 12 populations located in 6 states (Indiana, Maryland, New York, Pennsylvania, Virginia, and West Virginia) central to the range of *P. quinquefolius*; each population was given a 2-letter acronym to protect the details of its location (Table I). Populations occurred in the understory of mature forests on both public and private lands and were located through both field surveys and consultations with harvesters and land managers. When the populations were initially located, the areas were intensively searched to find all individuals. The populations were marked and mapped following the techniques of McGraw and Furedi (2005). That is, plants were cryptically marked with engraved nails and their locations were mapped using a “phototrail” system. The phototrail used digital photographs paired with distance and angle measurements to lead us to each plant or cluster. Detailed maps of plant clusters helped us to identify individuals when plants were closely grouped.

MEASURING SIZE AND AGE OF PLANTS

From 2004 to 2006, the 12 populations were visited twice yearly to gather demographic data. In late May through early June, individual plants were measured and the populations were searched for new seedlings. We used several criteria to identify unmarked 1-leaved plants as new seedlings: primarily, we looked for an attached seed coat, which can persist for up to 1 y. New seedlings also tend to have distinctive morphological characteristics, including narrow leaflets and a fragile leaf petiole. Several measurements were taken on all plants: sympodium (stem) height,

length and width of longest leaflet of all leaves, and reproductive status (determined by the presence of an immature inflorescence). The leaflet length (LL) and width (LW) were used to estimate the area of each compound leaf using the following equation:

$$LA = 11.4597 + 4.5774LL - 4.5091LW + 0.5786LL \times LW \quad [1]$$

The equation used was found by regressing the leaf areas measured from 101 adults (5 leaflets per leaf) and 59 seedlings (3 leaflets per leaf) on the model containing leaflet length and width terms that yielded the best fit ($r^2 = 0.96$). The leaf areas were measured as part of previous research from 3 populations in West Virginia, which were not used in this current study (McGraw & Furedi, 2005; Mooney & McGraw, 2007b). For juvenile and adult plants, total leaf area was then estimated by adding each separate estimated leaf area. Populations were revisited in August to record fruit set and the number of seeds produced. Fruits of *P. quinquefolius* are typically either 1- or 2-seeded in the wild, which can be readily determined from fruit shape.

In *P. quinquefolius*, scars left by the annual abscission of the sympodium along the subterranean rhizome provide an estimate of age; this technique has been used previously in *P. quinquefolius*, and it is the standard set out by the USFWS to guide harvesters to comply with age restrictions (Carpenter & Cottam, 1982; Lewis & Zenger, 1982; Charron & Gagnon, 1991; Anderson *et al.*, 1993; USFWS, 2006). In July of 2005 and August of 2006, randomly selected subsets of plants in each population were aged by counting rhizome scars. Beginning at the base of the sympodium, the soil was carefully excavated from around the rhizome. Plants rarely produce 2 sympodia in a given year (Lewis & Zenger, 1982), so each scar along the rhizome was considered to be 1 y of growth. New seedlings were considered to be age zero at their appearance in the population and 1 y old if they persisted to the following census year.

POPULATION HARVEST INDEX

To develop an index of harvest history, we used data from an experimental harvest of a naturally occurring *P. quinquefolius* population (Van der Voort *et al.*, 2003). All individuals regardless of size were removed in 1996, and the area was censused from 1997 to 2001 (Van der Voort *et al.*, 2003). In the first 5 y following harvest, the population was dominated by 1-leaved seedlings and juvenile plants (Van der Voort *et al.*, 2003); therefore, we continued to census the population from 2002 to 2006 to track recovery at 10 y post-harvest. Based on this recovery pattern, we used the mean proportion of all plants that were 1-leaved seedlings and 2-leaved juvenile plants as a harvest index in the 12 study populations.

Besides harvest, other environmental factors could simultaneously affect the growth rate of individuals and the survival of adult plants. Browse by white-tailed deer is one environmental factor known to affect both growth and survival for *P. quinquefolius* (McGraw & Furedi, 2005). We tested the association between browse rates and harvest index for our 12 study populations. Plants that were browsed by white-tailed deer were identifiable by partial

TABLE I. Study populations, their locations by county, population sizes averaged from 2004–2006, and harvest indices.

Population	Location	<i>n</i>	Harvest Index
VC	Vermillion Co, IN	173	0.412
EP	Lancaster Co, PA	99	0.417
EB	Preston Co, WV	46	0.506
HP	Albany Co, NY	280	0.529
CC	Garrett Co, MD	154	0.654
LK	Franklin Co, PA	349	0.688
GB	Greenbrier Co, WV	123	0.721
TP	Albany Co, NY	62	0.724
TR	Parke Co, IN	133	0.780
PO	Bedford Co, VA	300	0.783
AD	Mercer Co, WV	75	0.849
RD	Pulaski Co, VA	129	0.958

or complete loss of aboveground parts (Furedi & McGraw, 2004). Browse rates were calculated as the mean proportion of plants that were browsed across the 3 study years. We tested the correlation between browse rate (Y_1) and harvest index (Y_2). We did not directly measure other types of environmental variation in this study. In *P. quinquefolius*, as in many other plants, seedling establishment is a portion of the life-cycle particularly vulnerable to environmental variation, e.g., low precipitation (Lewis & Zenger, 1982; Lewis, 1984). We also tested for an association between harvest index and survival of new seedlings over their first year of growth using a correlation analysis.

DATA ANALYSIS

We used full model multiple regression analysis to determine if the way size traits (Y) change with age (X_1) varies between populations with different harvest histories (X_2) (Sokal & Rohlf, 1995). Significance of the model term “Age \times Harvest Index” would indicate that the size–age relationship varied among populations with different harvest indices. We also examined how reproduction varied with age. For juvenile and adult plants, we used a logistic regression to determine how age predicts whether a plant is classified as reproductive, i.e., produces an inflorescence (Sokal & Rohlf, 1995). Among those plants classified as reproductive, we again used a logistic regression to determine if the influence of age on the probability of setting fruit varied with harvest index. Plants that were browsed by deer or otherwise missing prior to data collection for seeds were excluded from this analysis. For the subset of plants that set fruit, we examined if the number of seeds produced by a plant of a given age varied among populations with different harvest indices using multiple regression. Normality of residuals from analyses with continuous dependent variables was checked with the Shapiro–Wilk W -test; data were transformed as needed to achieve normality (Sokal & Rohlf, 1995). We performed all analyses using SAS JMP v6.0 (SAS Institute, Cary, North Carolina, USA).

COMMON GARDEN

In 2002 and 2003, a living germplasm bank for *P. quinquefolius* was created at a protected site in New York State from plants collected from wild populations in 8 states (Kentucky, Maryland, Maine, North Carolina, New York, Ohio, Tennessee, and Virginia) (R. L. Beyfuss, pers. comm.). Because it was intended as a germplasm bank rather than a common garden, the roots were planted non-randomly (in rows) and most of the plants were reproductive adults. However, the germplasm bank does minimize carryover effects from the plants’ original environments: transplants were as bare roots and they had likely acclimated to the site. In June of 2006, we measured sympodium height and leaflet size on the plants, and we also aged plants at this time using the technique described previously. Because the plot was small (5 \times 10 m), we considered the plot a “common environment” such that each individual was considered randomly placed for statistical purposes. We tested for differences among populations in sympodium height and leaf area with analysis of covariance, where age was used as a continuous covariate.

Results

EXPERIMENTAL HARVEST

As of 10 y post-harvest, the experimentally harvested population had not recovered its stage distribution, which was originally dominated by reproductive adults. The population consisted of 21.7% seedlings and juvenile plants prior to harvest in 1996, but in 2006 62.5% of the population remained in these stages (Figure 1).

HARVEST INDEX AND AGE

Among the 12 study populations, we observed a mean of 46 plants across the monitoring period in the smallest population (EB) and a mean of 349 plants in the largest population (LK). The mean proportion of seedlings and juveniles (Harvest index) ranged between 0.4122 for the VC population and 0.9529 for the AD population (Table I). In addition, 3 incidences of harvest were observed during the census period. Following the August census of 2004 and prior to the May census of 2005, 31% of plants were harvested from the AD population and 14% of the plants were harvested from the CC population. Similarly, following the August census of 2005 but prior to May of 2006, 18% of plants were harvested from the EB population. In each population, shallow holes were present at the locations of missing plants and their cryptic markers were missing or displaced. These populations had different numbers of individuals in each stage class prior to harvest, but harvest reduced the number of adult plants in all population (Figure 2). Correspondingly, the proportion of seedlings and juvenile plants (Harvest index) increased by 0.1148, 0.1479, and 0.0354 in the year following harvest for the AD, CC, and EB populations, respectively. Transition of plants among stages caused some variation in how harvest index reflected the number of adult plants harvested. For example, germination resulted in 72 new seedlings in the CC population in 2005, which elevated harvest index in addition to the removal of adults. In 2006, 2 y following harvest for

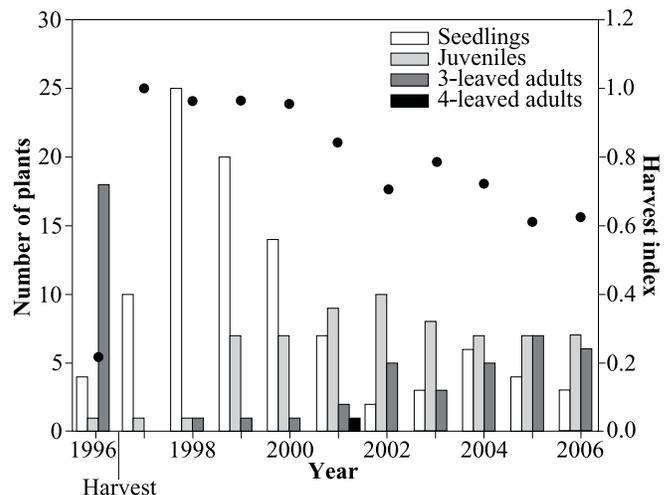


FIGURE 1. The numbers of plants observed in 4 stage classes in an experimentally harvested population from prior to harvest (1996) to 10 y after harvest (2006). The harvest index (solid circles) was calculated as the proportion of seedlings and juvenile plants.

populations AD and CC, there were still fewer adults than prior to harvest.

Altogether, we collected age data for 683 plants among the 12 study populations using rhizome scars. The fewest plants ($n = 18$) were aged in the smallest population (EB), while the most plants ($n = 85$) were aged in the largest population (LK). In all populations, we observed new seedlings over the study period, which added to the total age observations. Relatively few plants were observed that were greater than 20 y of age ($n = 23$), and these occurred entirely in populations with lower harvest indices. To ensure that the relationship of age to size and reproduction would be evenly characterized across harvest indices, we excluded plants

greater than 20 y of age from the subsequent analyses. The number of plants in the youngest age class, new seedlings, did not show similar patterns with respect to harvest index. The number of new seedlings ranged from 3 (EB and RD) to 77 (CC). The populations with the fewest seedlings had both low (EB) and high (RD) harvest indices. Among the 301 new seedlings observed, there was no association between survivorship over their first year of growth and the harvest index of their population ($r = -0.1657, P = 0.5884$). The average proportion of plants that were browsed by white-tailed deer was not associated with harvest index ($r = 0.2348, P = 0.4871$).

LEAF AREA

Slightly different numbers of plants were used in the analyses among years (2004, 2005, 2006), as some plants were browsed prior to data collection and more plants were censused in most populations as the monitoring period continued (Table II). Leaf area displayed a non-linear relationship with age ($b_{age*age} = -3.106, t = -4.69, P < 0.0001$); therefore, we used a square-root transformation to linearize leaf area data in subsequent analyses. As expected, age was a positive predictor of leaf area for plants across all populations in all years of study (2004: $b = 0.2133$; 2005: $b = 0.3148$; 2006: $b = 0.2640$). Plants in populations with higher harvest indices had significantly smaller leaf areas in all years of study (2004: $b = -7.1881$; 2005: $b = -2.9312$; 2006: $b = -2.2517$). In 2006, the relationship between age and leaf area varied among populations with different harvest indices (Figure 3a). Specifically, a 10-y-old plant would have a leaf area of 120 cm² in a population with a low harvest index (HI = 0.4), but a plant of the same age would have a leaf area of 88 cm² in a population with a high harvest index (HI = 0.9).

SYMPODIUM HEIGHT

In all years, sympodium height increased significantly with age, as expected (2004: $b = 0.4325$; 2005: $b = 0.5863$; 2006: $b = 0.5452$). In 2004 and 2005, sympodium height varied significantly with harvest index (2004: $b = -3.0556$; 2005: $b = -4.7585$); both slopes indicated that sympodium heights were smaller in populations with high harvest indices. In 2005 and 2006, the age-sympodium height relationship varied significantly with harvest index. Sympodium height increased more with age in populations with lower harvest indices (Figure 3b). In 2005, a 10-y-old plant would be 15 cm in height in a low harvest index population (HI = 0.4), whereas a plant of the same age would be 12 cm

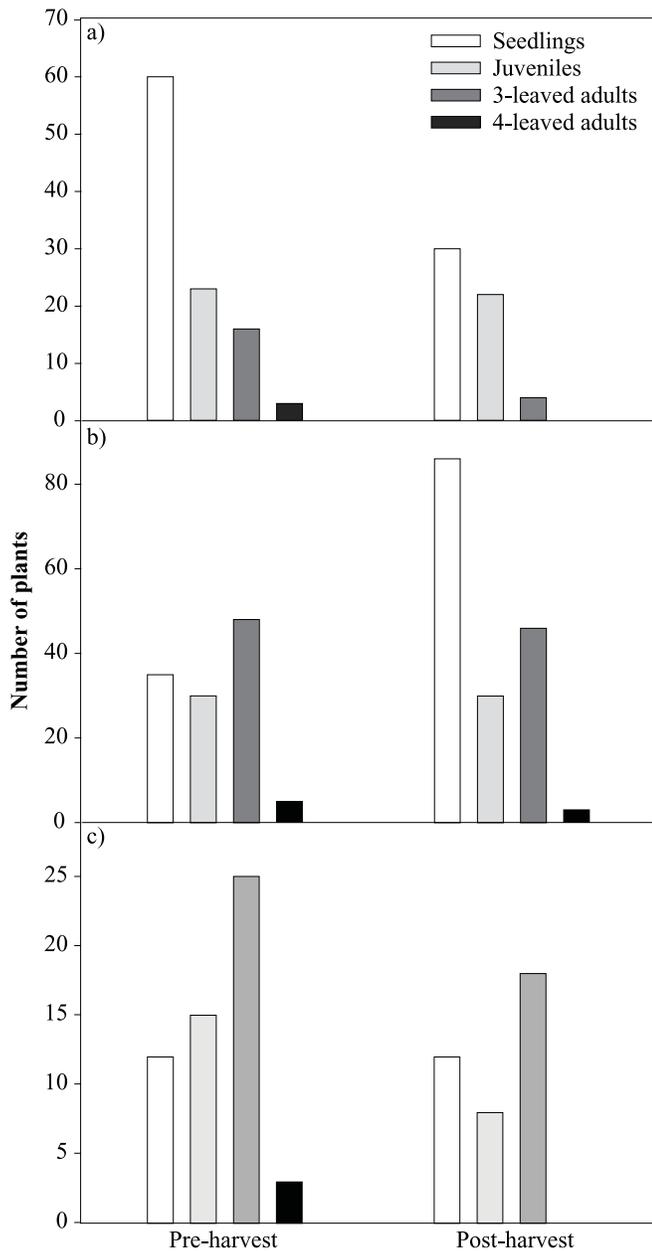


FIGURE 2. The proportions of plants among stage classes (seedlings, juveniles, and adults) in AD (a), CC (b), and EB (c) populations before and after harvest events.

TABLE II. Results from regression of leaf area (square root transformed) on age and harvest index for 3 study years.

Year	<i>n</i>	Model term	<i>F</i> -ratio	<i>P</i> -value
2004	454	Age	307.599	< 0.0001
		Harvest Index	12.330	0.001
		Age × Harvest index	0.505	0.478
		Age	660.714	< 0.0001
2005	536	Harvest Index	6.130	0.014
		Age × Harvest index	0.258	0.612
		Age	908.905	< 0.0001
		Harvest Index	6.756	0.010
2006	650	Age × Harvest index	10.739	0.001

in height in a high harvest index population (HI = 0.9). In 2006, a 10-y-old plant would be 15 cm in height in a low harvest index population (HI = 0.4), whereas a plant of the same age would be 13 cm in height in a high harvest index population (HI = 0.9). Detailed results of the multiple regression analyses are presented in Table III.

REPRODUCTION

In every year of the study, age significantly influenced the likelihood that a juvenile or adult plant would produce an inflorescence (Table IV). The probability of flowering consistently increased with age (2004: $b = 0.0989$; 2005: $b = 0.2491$; 2006: $b = 0.2550$). The likelihood of flowering did not vary significantly with harvest index in any year. A trend in 2004 suggested that as harvest index increased, the frequency of juvenile and adult plants being classified as reproductive declined ($b = -1.4393$). Harvest index did not alter the age–flowering relationship in any year of study.

In addition to deer browse, we observed one other environmental factor that accounted for many flowering plants not producing fruit. Stink bugs (Pentatomidae) destroyed and scattered fruits at the VC population in 2004 and 2005 and at the HP population in 2005. We did not include fruit-set data from these populations for these years in the final analyses because we could not accurately determine if fruits were present on plants prior to predation.

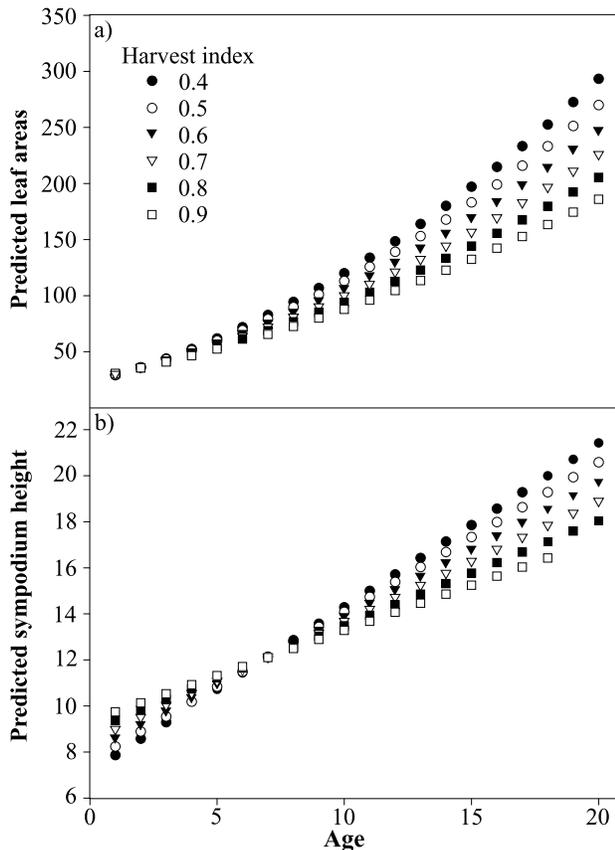


FIGURE 3. The predicted leaf areas (a) and sympodium heights (b) of plants aged 1 to 20 y in populations across the observed range of harvest indices (0.4 to 0.9). Depicted results are from regressions performed on data collected in 2006.

Unlike the likelihood of flowering, age did not consistently predict the likelihood that a flowering plant would set fruit (Table V). In 2005 and 2006, the probability of fruit set increased significantly with age across all populations (2005: $b = 0.1806$; 2006: $b = 0.1102$). Though the slope was also positive ($b = 0.0715$), age was not a significant predictor of fruit set in 2004. The likelihood of a flowering plant producing fruits was significantly less in populations with higher harvest indices in 2004 and 2006 (2004: $b = -3.5027$; 2006: $b = -6.7732$). Harvest index had no significant effect on the probability of fruit set in 2005, but the relationship between age and fruit set varied among populations with different harvest indices in this year. Specifically, the predicted likelihood of a reproductive plant setting fruit increased less with age among populations with high harvest indices ($HI > 0.6$; $b = 0.18429$) than in populations with low harvest indices ($HI < 0.6$; $b = 0.8763$). Relatively few plants ($n = 17$) in low harvest index populations were

TABLE III. Results from regression of sympodium height on age and harvest index for 3 study years.

Year	<i>n</i>	Model term	<i>F</i> -ratio	<i>P</i> -value
2004	454	Age	97.928	< 0.0001
		Harvest index	5.814	0.016
		Age × Harvest index	1.003	0.317
2005	537	Age	229.387	< 0.0001
		Harvest index	15.286	0.000
		Age × Harvest index	5.266	0.022
2006	653	Age	300.699	< 0.0001
		Harvest index	0.262	0.609
		Age × Harvest index	12.046	0.001

TABLE IV. Results from logistic regression of reproductive status (presence/absence of inflorescence) on age and harvest index for juvenile and adult plants observed for 3 study years.

Year	<i>n</i>	Model term	Likelihood-ratio χ^2	<i>P</i> -value
2004	411	Age	11.985	0.001
		Harvest index	3.259	0.071
		Age × Harvest index	0.271	0.603
2005	405	Age	44.953	< 0.0001
		Harvest index	2.582	0.108
		Age × Harvest index	1.912	0.167
2006	374	Age	50.293	< 0.0001
		Harvest index	0.078	0.780
		Age × Harvest index	0.916	0.338

TABLE V. Results from logistic regression of fruit set (yes/no) on age and harvest index for reproductive plants over three study years; observations exclude plants that were browsed or otherwise missing prior to collection of data in August of each year.

Year	<i>n</i>	Model term	Likelihood-ratio χ^2	<i>P</i> -value
2004	144	Age	2.51	0.113
		Harvest index	4.74	0.029
		Age × Harvest index	0.62	0.431
2005	179	Age	13.63	0.000
		Harvest index	0.58	0.446
		Age × Harvest index	3.87	0.049
2006	168	Age	4.39	0.036
		Harvest index	22.63	< 0.0001
		Age × Harvest index	3.73	0.055

observed in 2005 due to seed predation in populations VC and HP. As a result, the relationship between age and the likelihood of fruit set was less significant in low harvest index populations ($\chi^2 = 2.93$, $P = 0.0868$) than in high harvest index populations ($\chi^2 = 14.56$, $P = 0.0001$). In 2006, there also was a trend for the age–fruit set relationship to vary with harvest index. The likelihood of a reproductive plant setting fruit increased significantly with age in populations with harvest indices less than 0.6 ($b = 0.1560$, $\chi^2 = 7.17$, $P = 0.0074$). However, in populations with high harvest indices (> 0.6), the likelihood of setting fruit did not increase significantly with age ($b = 0.0270$, $\chi^2 = 0.24$, $P = 0.6218$).

Within the subset of reproductive plants that set fruit, age was not a consistent predictor of the number of seeds (Table VI); only in 2004 was there a trend that suggested the number of seeds increased with age ($b = 1.2209$). In both 2005 and 2006, the number of seeds produced was significantly less in populations with higher harvest indices (2005: $b = -3.1557$, 2006: $b = -2.4636$). In 2006, for example, a reproductive plant in a population with a low harvest index (0.4) would produce 1.6 seeds, while a reproductive plant in a population with a high harvest index (0.9) would produce 0.38 seeds. The relationship of age to number of seeds produced by reproductive plants did not vary with harvest index in any year of study.

COMMON GARDEN

From the 8 populations, 29 transplanted individuals emerged in 2006. When age was used as a continuous covariate, there were significant differences in leaf area among the populations ($F = 3.1263$, $P = 0.0213$). The largest difference in leaf area was between 3-leaved adult plants from North Carolina (382.3 ± 51.7 cm², mean \pm SE) and Ohio (156.8 ± 44.5 cm²). We also found a trend for sympodium height to vary among plants originating from the 8 different populations ($F = 2.882$, $P = 0.0694$).

Discussion

Harvest events can have profound effects for targeted species, but they do not necessarily extirpate populations. For *P. quinquefolius*, the distribution of individuals among stage classes remained skewed towards seedlings and juvenile plants 5 y after the experimental harvest (Van der Voort *et al.*, 2003). As of 10 y post-harvest, the population con-

tinued to be dominated by seedlings and juvenile plants. The fact that stage structure has not recovered to pre-harvest levels is likely due to the intensity of the experimental harvest, *i.e.*, all aboveground plants were removed (Van der Voort *et al.*, 2003). Had the experimental harvest followed regulations such that juveniles and seedlings were left behind, we would expect recovery of stage distribution to occur more rapidly, as illustrated by demographic simulations (Van der Voort & McGraw, 2006). As it was conducted, we have mostly tracked the growth of individuals from seeds, although one juvenile plant escaped harvest by having no aboveground portion in 1996 (Van der Voort *et al.*, 2003). Some of the seedlings that emerged in the first spring following harvest had reached adult size by 2006; however, germination later in the study period and the persistence of juvenile plants has prolonged the impact of harvest on the stage distribution. If environmental conditions persist and no additional harvest events occur, we would likely see the original stage distribution eventually return. However, harvest repeated on a regular (1–5 y) basis would continue to affect stage distribution.

From aging nearly 700 plants in 12 wild populations, we observed relatively few plants older than 20 y of age. Several previous studies present comparable results. Nearly all of the 211 plants aged by Lewis (1984) in a New York State population were less than 21 y old, with one exceptional 43-y-old plant. In Missouri, Lewis and Zenger (1982) found no plants with more than 18 stem abscission scars on the rhizome. Carpenter and Cottam (1982) found no plants older than 23 y of age among the 3 populations they examined in Wisconsin. Results from these previous studies suggest that older plants (> 20 y of age) are uncommon throughout much of the range of *P. quinquefolius*. When we consider these older plants in our data set, a relationship with stage distribution emerges that is consistent with the effects of harvest. Every population with a proportion of seedlings and juveniles less than 0.75 had at least 1 plant 20 y of age or greater among those plants we aged. In contrast, no plants of this age group were found in the 4 populations with harvest indices greater than 0.75.

Explanations other than harvest could be developed that would yield the impacts on age and stage structure we observed. For example, recent establishment by seed would create “young” populations dominated by seedlings and juveniles. In *P. quinquefolius*, it has been suggested that wild populations are derived from seeds deliberately planted by harvesters (Grubbs & Case, 2004). However, several genetic studies have failed to detect evidence of this phenomenon in wild populations (Boehm *et al.*, 1999; Schluter & Punja, 2002; Grubbs & Case, 2004). Molecular markers reveal extensive differentiation between wild populations and high inbreeding estimates within wild populations (Cruse-Sanders & Hamrick, 2004; Grubbs & Case, 2004). This pattern is consistent with the effects of repeated bottlenecks as would result from harvest events (Cruse-Sanders & Hamrick, 2004; Cruse-Sanders, Hamrick & Ahumada, 2005), rather than the establishment of populations from highly diverse cultivated populations (Boehm *et al.*, 1999; Schluter & Punja, 2002; Grubbs & Case, 2004). Although it is unlikely that our study populations were established by

TABLE VI. Results from regression of number of seeds (ln transformed) on age and harvest index for those reproductive plants that produced any seeds in each study year.

Year	<i>n</i>	Model term	<i>F</i> -ratio	<i>P</i> -value
2004	68	Age	3.293	0.074
		Harvest index	2.714	0.104
		Age \times Harvest index	0.001	0.972
2005	117	Age	2.383	0.125
		Harvest index	23.041	< 0.0001
		Age \times Harvest index	0.213	0.645
2006	108	Age	1.780	0.185
		Harvest index	23.594	< 0.0001
		Age \times Harvest index	0.454	0.502

humans, animal seed dispersers could aid in colonization of new habitats. However, such dispersal agents are unknown in *P. quinquefolius*, as the predominant consumer of seeds—white-tailed deer—destroy the seeds in the process (Furedi & McGraw, 2004). Repeated browse by white-tailed deer could also lead to the effects on age and stage distribution we observed. Browsed plants often regress to a smaller stage class in the following year, and repeated browse can cause mortality (McGraw & Furedi, 2005). In *Trillium catesbaei*, another understory perennial that may be aged, a highly browsed population had fewer older plants than populations with less browse (Jenkins, Webster & Rock, 2007). We found no evidence of a relationship between harvest index and current levels of deer browse. Other types of environmental disturbance—for example, disease outbreak or prolonged drought—could mimic the effects of harvest on age and stage distribution. Given the observational nature of our data, we cannot entirely discount these possibilities.

We directly observed the effects of harvest in 3 of the 12 study populations during the 3-y monitoring period. In every instance, fewer plants were harvested from the populations than were removed in the experimental harvest (Van der Voort *et al.*, 2003); nevertheless, harvest increased the proportions of seedlings and juvenile plants in the following year(s). Differences among populations with varying harvest histories have been observed by previous studies (Cruse-Sanders & Hamrick, 2004; Kauffman, 2006). The populations in areas open to harvest observed by Cruse-Sanders and Hamrick (2004) had significantly higher proportions of seedlings and juveniles than populations in legally protected areas (Cruse-Sanders & Hamrick, 2004). Comparisons between frequently and infrequently harvested sites in North Carolina reveal similar impacts on stage structure (Kauffman, 2006). In addition, reproductive adult plants were older in the infrequently harvested sites than in the frequently harvested sites (Kauffman, 2006). Based on these results and the long-term effects on population structure observed from the experimental harvest, we believe that the proportion of seedlings and juveniles reveals the “fingerprint” of harvest pressure.

We have determined the relationship between age and size in populations across a range of harvest pressures, thereby examining the evidence for changes that would fit the predictions of harvest-induced evolutionary change. Plants in populations with higher harvest indices consistently had smaller leaf areas, and at least in 2006, the age–leaf area relationship varied with harvest index. The nature of this variation followed the predictions of harvest-induced evolutionary change in that plants grew slower in harvested populations. The fact that this effect was only detectable in 2006 may relate to sample size, as fewer plants were observed in previous years. Alternatively, year to year variation in environmental conditions may have influenced our ability to detect differences. For example, particularly “good” years may allow even slow-growing plants to attain large sizes. In terms of sympodium height, we also found evidence of plants growing slower in populations with higher harvest indices in 2005 and 2006. At any given age, plants in populations with higher harvest indices had significantly reduced sympodium heights. In

a related experimental study, *P. quinquefolius* plants with greater leaf areas and sympodium heights had reduced fitness when their population experienced harvest (Mooney & McGraw, 2007a). Notably, this fitness difference occurred because large adult plants were simply more apparent to the human harvesters (Mooney & McGraw, 2007a). Sympodium height is likely an important component of apparency in the often dense understory where *P. quinquefolius* grows. The reduced sympodium heights are similar to results from herbarium specimens of *P. quinquefolius* collected from 1900 to 2001 (McGraw, 2001). Of the 11 measured traits, sympodium height along with peduncle height showed the largest declines, 25.8% and 42.7%, respectively (McGraw, 2001). These declines were linked to harvest as they were most pronounced in specimens from regions of intensive harvest, but simultaneous environmental factors could not be discounted (McGraw, 2001).

For changes we observed to be attributable to an evolutionary response to selective harvest, a significant portion of the observed phenotypic variation would need to be genetically based. From the common garden study, even with a low sample size, we observed that plants from different states maintained different leaf areas and probably sympodium heights 3–4 y after transplantation. For this observed variation among populations to be attributable to genetic differentiation, carryover effects from their original environment would need to be minimal. When the common garden technique is used, it is assumed that carryover effects in transplants and seeds diminish over time (Gallagher *et al.*, 1988; Thompson, McNeilly & Gray, 1991; Fischer & Matthies, 1998; Montalvo & Ellstrand, 2001). In our study, we would expect carryover effects to have declined over time, despite the fact that whole roots were transplanted. Using age as a covariate allowed us to account for its particular influence on plant size, but we cannot entirely rule out confounding positional effects as plants were planted in rows. Assuming relatively little environmental variation across the small plot, our results indicate at least in some broad sense heritability for leaf area and sympodium height in *P. quinquefolius*. Evidence is sometimes weak for high heritability of plant size traits (Antlfinger, Curtis & Solbrig, 1985; Stratton, 1992; Geber & Griffen, 2003), but stem height and the components of leaf area have shown the ability to rapidly respond to selection in many plant species subject to environmental change (Bone & Farres, 2001).

The results we observed in terms of reproduction also suggest potential far-reaching effects of harvest in *P. quinquefolius*. For the age–reproduction relationship in general, we see that age is a reliable predictor of flowering across years but not necessarily for the probability of fruit production or the numbers of seeds. Our ability to detect the effect of age was likely influenced by sample size; missing plants reduced the observations available for fruit production analyses, and the fact that many plants produced no seeds further reduced the observations available for seed number analyses.

Besides sample size, environmental factors could reduce the influence of age on plant reproductive success: cold or wet weather could reduce pollinator visitation (Bergman, Molau & Holmgren, 1996), and water availability

may limit reproduction in drought years (Lewis & Zenger, 1982). Sample size likely also affected our ability to detect variation in how age predicts reproduction among populations with different harvest indices. Nevertheless, we found evidence in both 2005 and 2006 for the probability of fruit set to increase less with age for plants in populations with high harvest indices. Reduced fruit set and numbers of seeds could be the result of pollen limitation in harvested populations as a consequence of there being fewer reproductive plants; this Allee effect was demonstrated in *P. quinquefolius* by an experimental study whereby increased seed production occurred at higher plant densities (Hackney & McGraw, 2001). In fisheries studies, similar reductions in density by harvest have resulted in fecundity changes that are independent of phenotypic selection (Law, 2000; Conover *et al.*, 2004).

The changes we observed mirror those of exploited fish stocks, but harvest-induced evolutionary change in fisheries can be complicated by simultaneous environmental variation (Rijnsdorp, 1993). Low-quality environments might reduce growth rates of plants regardless of the effects of selection on size. In *P. quinquefolius*, harvesters might preferentially target populations in marginal habitats if populations in high-quality habitats have been overexploited. Previous work has found some evidence of this phenomenon: field searches of sites identified as likely habitat by GIS models failed to find *P. quinquefolius* more often than other understory herbs (van Manen *et al.*, 2005). We did not measure environmental variation directly, but rather examined the survival of new seedlings in their first year of growth. New seedlings of forest perennials can be particularly sensitive to environmental variation, *e.g.*, edge effects. In another understory perennial, *Trillium camschatcense*, seedling recruitment was negatively affected by edge effects in forest fragments (Tomimatsu & Ohara, 2004). The higher temperatures and reduced soil moisture associated with edges can reduce seedling survival for understory perennials (Bruna, 2002). Unlike growth rate, seedling survivorship showed no association with harvest index. Overall, this suggests that variation in environmental quality does not underlie the differences in growth rates we observed.

The scope of wild harvest worldwide suggests that our results may have parallels in other species (Hamilton, 2004). Although slower growth of trees left behind by selective timber harvest has been documented (Sokol, Greenwood & Livingston, 2004), analogous results for herbaceous plant species are less common. In a study of *Saussurea laniceps* (Himalayan snow lotus), the authors found smaller flowering individuals in harvested areas relative to protected areas (Law & Salick, 2005); because age was not included in their analyses, individuals may have been flowering at smaller sizes or harvested populations may simply have consisted of younger plants. Weeding pressure is also analogous to selection through harvest, although the intention from the human perspective is different. Life history changes have been brought about by weeding; for example, in the annual *Senecio vulgaris*, plants in well-kept gardens developed faster but stayed smaller than plants from unmanaged sites (Kadereit & Briggs, 1985; Briggs *et al.*, 1992). Evidence for selective harvest in other plant species would indicate that the effects we observed may be more widespread. For

example, specimens of *Dioanaea muscipula* (Venus' fly trap) confiscated from harvesters had significantly larger petioles and traps than plants left behind (Luken, 2005). Conscious or unconscious selection of specific phenotypes by human harvesters is likely in many plants targeted for wild harvest (Salick, 1995).

Changes in growth rate as an evolutionary consequence of harvest could have far-reaching effects in *P. quinquefolius*, which could extend to other harvested plant species. For example, allocation to roots could be reduced if smaller leaf areas or reduced sympodium heights limit light interception and photosynthesis. Indeed, mean root mass has decreased since these data were collected by the USFWS in compliance with CITES (USFWS, 2006). Reductions in root sizes would affect harvesters directly: they might need to collect more roots to achieve reasonable economic returns or they might find that harvesting is no longer worth their efforts. Similar diminishing returns have also been characteristic of overharvested fisheries, where decreases in age-at-maturity also result in smaller fish (Law, 2000). Although exploitation typically ranks behind habitat destruction and invasive species as threats to native plant species (Wilcove *et al.*, 1998), our results suggest that wild harvest can have evolutionary impacts with potentially negative consequences. Overall, our results extend observations from animal species to plants, which represent a significant portion of the worldwide biodiversity used by humans.

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