ORIGINAL PAPER

Alteration of selection regime resulting from harvest of American ginseng, *Panax quinquefolius*

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Abstract Replicate harvest simulations were conducted in a large natural population of *Panax quinquefolius* L. (Araliaceae) to determine the selective effects of harvest. We investigated how minimum size requirements and the influence of size on apparency to human harvesters could result in preferential removal of large plants. To determine which plants were encountered in the large population, harvesters were tracked using GPS as they searched for every legally harvestable, adult plant they could find. Plants were assigned stage-specific fitness measures based on their contributions to population growth rate (λ) under three demographically based harvest regimes: no harvest, harvest and harvest removing seeds. Plant size was codified into a size-index equal to the product of total leaf area and stem height. Heterogeneity of slopes was tested to determine if the selection gradients (β) describing the relationship between fitness and size varied among the three harvest regimes. Harvest differentially reduced the fitness of larger plants in one of four individual harvest simulations. The combined harvest simulation significantly altered the selection regime for size in the population of juvenile and adult (harvestable) plants. Seed removal by harvesters intensified fitness declines for larger plants. Because larger plants contribute most to population growth, the selective effects of harvest could result in a shift in the evolutionary dynamics of this species with significant conservation implications.

Introduction

Harvest can have unintended and often undesirable consequences for wild-harvested species. Harvest has been linked to local extinction, reduction in genetic diversity and altered population structure in exploited species (Ashley et al. 2003). When selective harvest targets heritable traits, harvest can lead to novel evolutionary changes in a wild species (Law 2001; Stockwell et al. 2003). The evolutionary consequences of selective harvest regimes have been illustrated in a variety of animal species, raising concerns about unintentional effects (Conover and Munch 2002; Ashley et al. 2003). Reductions in size at maturity and growth rate due to size-selective nets have been well documented for commercially exploited fish species (Miller and Kapuscinski 1994; Ratner and Lande 2001; Law 2001; Conover and Munch 2002). Trophy hunting has resulted in reduced horn size and body mass in bighorn sheep (*Ovis ovis*) (Coltman et al. 2003). Despite worldwide dependence on wild-harvested plants for food, fiber and medicine (Peters 2001; Ticktin 2004), the evolutionary consequences of harvest have not been investigated for a wild plant species (Lebig 1992; Bone and Farres 2001; Stockwell et al. 2003).

American ginseng (*Panax quinquefolius*) is a herbaceous perennial plant whose root is extensively harvested from the wild for export to the medicinal herb markets of Asia (Carlson 1986). Harvest of the root is fatal to the individual plant, and this subsequently impacts population size, structure and genetic diversity (Van der Voort et al. 2003; Cruse-Sanders et al. 2005). The scope of

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P. quinquefolius harvest is considerable, with the U.S. supplying an average of 60 metric tons (corresponding to 26.4–39.6 million plants) to the world market annually (Robbins 2000). The volume of root harvested annually prompted the Convention on International Trade in Endangered Species (CITES) to list *P. quinquefolius* on Appendix II in 1973 (Robbins 2000). Although *P. quinquefolius* has been successfully cultivated, wild harvest persists because wild roots are considered more potent in traditional Asian medicine and command nearly ten-times the price of cultivated roots (Carlson 1986; Robbins 2000).

There is preliminary, albeit circumstantial, evidence that harvest has led to a reduction in overall size of *P. quinquefolius* (McGraw 2001). In herbarium specimens collected over the 20th century, nine of eleven size-related traits decreased significantly while age of specimen remained consistent (McGraw 2001). Notably, this decline was most pronounced in specimens collected from Appalachian and southern states, areas that account for the largest portion of plants harvested annually (Robbins 2000; McGraw 2001). Like size reductions in other exploited species, the decline in stature of herbarium specimens of *P. quinquefolius* could be attributable to harvest if selective removal of larger individuals occurs.

Selective harvest of larger individuals could be occurring for several reasons in *P. quinquefolius*. At the time of this study, federal regulations restricted harvest to plants greater than five years in age, which can be non-destructively assessed *in situ* by counting scars on the rhizome left by the annual abscission of the stem (Anderson et al. 1993; USFWS 2002). Generally, older plants tend to be larger plants (Carpenter and Cottam 1982, Anderson et al. 1993), but regulations in most states explicitly restrict harvest to plants with three or more leaves (USFWS 2002). Plants with larger aerial parts possess larger roots (Anderson et al. 1993), which yield higher economic returns to the harvester upon sale (Robbins 2000). Many harvesters are also motivated to ensure future harvest by intentionally leaving behind smaller reproductive plants (Nantel et al. 1996). Furthermore, larger plants could also be more apparent to harvesters in the dense forest understory where *P. quinquefolius* grows. The bright red color of the ripe berries of *P. quinquefolius* have also been noted as an important visual cue for harvesters (Hufford 1997), perhaps making larger, more fecund plants especially apparent.

Generally, plant size is an important determinant of both the survival and fecundity components of fitness in natural populations (Werner and Caswell 1977; McGraw and Wulff 1983; Primack and Kang 1989). Total leaf area and stem height have been shown to be positively related to both reproductive output and year to year survival in *P. quinquefolius* as well (Carpenter and Cottam 1982; Lewis and Zenger 1982; Charron and Gagnon 1991;

Anderson et al. 1993). However, this dependence of fitness on plant size could be altered if selective harvest preferentially removed larger individuals. Harvesters may also commonly remove seeds present on harvested plants, which could further impact plant fitness (Cruse-Sanders et al. 2004). Anecdotal evidence suggests that seeds are likely planted in plots near the harvester's home for later extraction (USFWS 2002). Because laws in most states require seeds to be planted on site (USFWS 2002), the fate of seeds after removal is difficult to determine from harvester interviews as this would constitute illegal behavior (Bailey 1999). Nevertheless, because harvest of *P. quinquefolius* can directly target the essential components of fitness—survival and reproduction—size-selective harvest could result in novel evolutionary changes in this species.

The objective of this study was to determine if *P. quinquefolius* harvest results in alteration of the selection regime for plant size. We hypothesized that selection against larger plants could occur in the harvest simulations through the influence of minimum size restrictions or the effect of size on apparency to human harvesters. Using harvest simulations, we determined how the relationship between fitness and plant size differs in a natural population experiencing three demographically based harvest regimes: no harvest, harvest and harvest taking seeds. Alteration of the existing relationship between fitness and plant size could predict the magnitude and direction of possible evolutionary changes in *P. quinquefolius* as a result of harvest.

Methods

Study Species Natural History

American ginseng, *Panax quinquefolius* L. (Araliaceae), is a long-lived perennial herb that grows in the understory of the eastern deciduous forest. Once common, the decline of wild populations has been linked to overharvesting, increased browse by overabundant white-tailed deer, habitat loss and degradation. Plants consist of a central stem and one to four (rarely more) palmately compound leaves. Individuals are readily classified into five stage classes: seeds, seedlings (1-leaf plants), juveniles (2-leaf plants), small adults (3-leaf plants with <250 cm^2 total leaf area), and large adults (3-leaf with ≥250 cm^2 total leaf area and 4-leaf plants) (McGraw and Furedi 2005; Fig.1). Plants with two or more leaves produce an inflorescence of self-compatible flowers in mid summer (Lewis and Zenger 1983; Schlessman 1985). Flowers yield 1–3 seeded berries in late summer, which then ripen to a characteristic red color in early autumn (McGraw et al. 2005). Seeds of *P. quinquefolius* exhibit morphophysiological dormancy and remain in the soil for at least 18–22 months before

Fig. 1 Life-cycle diagram for *Panax quinquefolius* showing possible yearly (May to May) transitions in this species
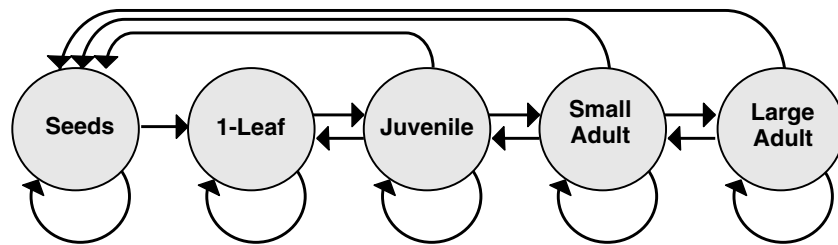
germination (Anderson et al. 1993; Baskin and Baskin 1998). The persistent soil seed bank is critical for populations to recover from harvest (Lewis 1988; Van der Voort et al. 2003).

Study Population and Plant Traits

The harvest simulations took place in a large population of *P. quinquefolius* located in a mixed deciduous forest near Morgantown, WV. The population consisted of 391 plants of all stage classes widely distributed across approximately 2 hectares. As part of an ongoing monitoring effort, each plant in the study population was cryptically labeled with an aluminum nail engraved with a unique number. Individual plants were relocated using a system of 'phototrails', which combine distances and angles with digital photographs. In May 2003, phenotypic traits were measured on each plant, including stem height, leaf number, length and width of longest leaflet per leaf. Total leaf area of each individual was determined using regression equations relating leaf number and leaflet measurements to observed leaf areas (McGraw and Furedi 2005).

Prior to the harvest simulations in August 2003, the locations of individual plants were mapped by marking each plant or cluster (plants within 5 m of each other) with a unique GPS point using a Garmin GPS V (Garmin International, Ltd. 2003). Plants that had their aboveground portion deer-browsed prior to harvest simulations were not included in the selection analyses. A total of 135 legally harvestable adult plants remained in the population, with the plants being approximately evenly divided among the large and small adult stage classes.

Harvest Simulations

The individual harvest simulations took place in late August and early September 2003, which coincided with the early part of the harvest season in West Virginia beginning August 15, 2003. Because the exceptional size of the study population warranted its protection, four volunteer 'harvesters' were recruited who could readily identify *P. quinquefolius*, but who could be trusted to keep the location of the population confidential. Flags were

placed 20 m from the last known plant on all sides of the population forming a rectangular area of 150 m×200 m; this demarcation was necessary because the harvesters had no prior experience with the population. Beginning at the same location, each harvester was given two hours to search the area unaccompanied. To test for the influence of minimum size restrictions, the harvesters were informed of state harvest criteria and asked to comply with them. Though federal law at the time of this study allowed harvest of any size of plant greater than 5 years of age, harvest is limited to plants with three or more leaves in West Virginia (USFWS 2002). The harvesters were instructed to 'harvest' all legally harvestable plants they could find by placing a flag next to the plant, but not actually digging the plant. At the end of the search period, the harvested plants were recorded and all flagging was removed. The sparse understory vegetation allowed for no trace of a previous harvester's path to remain at the site.

While searching, each harvester carried a GPS unit (Garmin GPS V, Garmin International, Inc. 2003) that recorded their location every three seconds. Following each harvest simulation, all plants were classified into one of three categories: encountered (harvested), encountered (not harvested) and not encountered. Whether or not a plant was encountered was determined by overlaying each harvester's track with the map of the plants using Erdas Imagine GIS software (Leica Geosystems Geospatial Imaging, LLC, Norcross, GA). Plants beyond 6 m of the track were considered not encountered. We determined the threshold distance by comparing the distances between harvester tracks to harvested plants; based on an average distance of approximately 4.5 m, the threshold distance of 6 m would conservatively classify plants as not encountered. These data were used to analyze selection in alternate ways (see below).

The overall efficiency or rate of harvest was determined as the number of harvestable adult plants each harvester flagged during their two-hour searches. The search efficiency of each harvester was quantified as the percentage of plants that were harvested, of those that were encountered. Differences in efficiencies between harvesters were tested using a log-likelihood test (Sokal and Rohlf 1995) in SAS JMP v. 5.1 statistical software (SAS Institute Inc., Cary, NC 2002).

Estimating Fitness

Because harvesters are unlikely to find or remove all plants (Lewis 1988; Van der Voort et al. 2003), harvest acts as an event of differential mortality in a population. Measuring fitness based on one period of differential mortality can yield important information about selection acting on phenotypic variation (Lande and Arnold 1983; Janzen and Stern 1998). However, fitness estimates based on mortality alone are insufficient because reproduction is not considered. Measuring an individual's contribution to population growth is a more biologically relevant fitness estimate because it incorporates both survival and fecundity (McGraw and Caswell 1996).

To estimate stage-specific plant fitness, we used the sample influence function (SIF_i) measured as the contribution of each individual i to the stable population growth rate (λ) (McGraw 1989; Vavrek et al. 1996, 1997). The stable population growth rate (λ), is the dominant eigenvalue for the transition probability matrix $\mathbf{A}$ (Caswell 2001). SIF_i was calculated by first removing individual i from the population, and then re-estimating the stable population growth rate (λ_{-i}). The contribution to λ of each individual was then calculated using:

$$\phi_i = n\lambda - (n-1)\lambda_{-i},$$

where n is the number of individuals in the population. The sample influence function is then calculated by:

$$SIF_i = \phi_i - \overline{\phi}$$

SIF_i provides an estimate of stage-specific fitness by incorporating the overall effect of an individual's survival, growth and reproduction on population growth; thus, a positive SIF_i value means that the individual's behavior is having a positive effect on λ and *vice versa* for a negative SIF_i value (McGraw 1989; Vavrek et al.1996).

The transition probability matrix ($\mathbf{A}$) was constructed based on transitions between stage classes observed from May 2003 to May 2004. From one year to the next an individual may grow (advance in stage), stay at the same stage, regress (decline in stage), reproduce or die (Fig. 1). The study population was censused in May of 2003 and all individuals were assigned to stage classes based on leaf number and area as above. The plants were again visited in August of 2003 to record seed production. In May of 2004, the population was censused again to observe the year to year transitions plus the appearance of new seedlings. The small percentage of plants present in 2003 but not in May of 2004 were assigned fates according to the protocols used in prior demographic studies of this species (McGraw and Furedi 2005). Seed bank dynamics were estimated from experimental seed

cages planted at the population in 2002 (McGraw and Furedi 2005).

In addition to the observed 2003–2004 transition matrix (no harvest), each of the four harvest simulations produced two alternative transition matrices assuming two levels of harvest (harvest, harvest taking seeds). To produce the transition matrix for the first level of harvest, plants taken by harvesters were assigned a status of 'death' in 2004, since harvest is fatal to plants. For the second level of harvest, the harvested plants died and did not contribute seeds in 2003, simulating removal of seeds from the population in the transition matrix. The individual harvest simulations were also pooled to create a combined harvest simulation to represent the cumulative effect of the separate 2-hour searches. In the combined harvest simulation matrix, a plant was assigned a fate of death if removed by any of the four harvesters. Three separate fitness measures were calculated for each individual as their contributions to population growth rate (SIF_i) under three harvest regimes (no harvest, harvest, and harvest taking seeds) for each harvest simulation and for the combined harvest simulation. The SIF_i values were calculated using the software MATLAB v. 4.0 (Mathworks Inc. Natick, MA 1993).

Selection analyses

Consistent with other studies of selection operating in plant populations (Kalisz 1986; Kelly 1992; Bennington and McGraw 1995), we used a regression-based approach to determine the magnitude and direction of selection (Lande and Arnold 1983; Janzen and Stern 1998). To avoid difficulties in multiple-regression analysis resulting from highly interdependent traits (Mitchell-Olds and Shaw 1987), a single size index was calculated for each individual by taking the product of 2003 stem height and total leaf area. Size index was transformed to a standardized measure in units of standard deviations for use in the selection analyses (Lande and Arnold 1983). Outliers in the distribution of standardized size indices were identified using Mahalanobis distances in SAS JMP v. 5.1 statistical software (SAS Institute Inc., Cary, NC 2002); two exceptionally large plants (having Mahalanobis distances >4.9) were eliminated from the subsequent selection analyses.

Two separate sets of selection analyses were performed on different subsets of the overall population: one including all juvenile and adult plants, and one including only encountered adult plants. Among encountered adult plants, changes in the patterns of selection would reflect the influence of the differential apparency of larger plants to harvesters or microsite
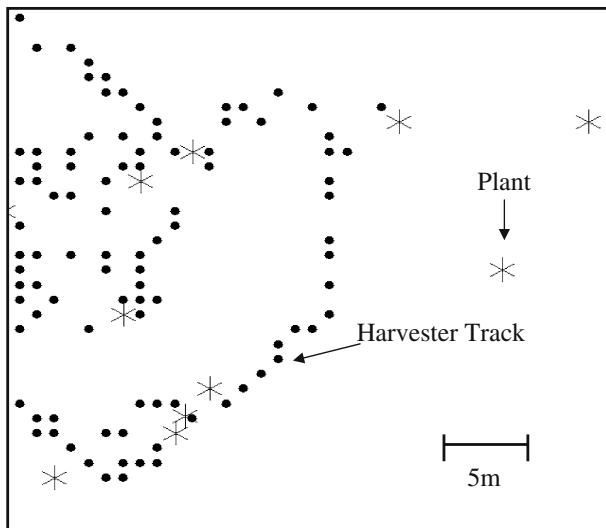
Fig. 2 Portion of harvester track overlaid with a map of plants created using GPS points dislpayed in Erdas Imagine GIS software (Leica Geosystems 1999)

effects. Specifically, adult plants not encountered by harvesters in their extensive searches may predominantly occur in difficult to access microsites (e.g. on top of a rock or under dense shrub cover). In all juvenile and adult plants, changes to the patterns of selection would occur through the combined influences of microsite, harvesting regulations and plant apparency to harvesters. Though juvenile plants are not legally harvestable, they are capable of reproduction and may have differential fitness with and without harvest.

Linear selection gradients (β) were determined from the regression of stage-specific fitness on standardized size indices of plants under each harvest regime (no harvest, harvest and harvest taking seeds). Linear selection gradients estimate the strength and direction of selection (Lande and Arnold 1983). We then used an analysis of covariance (ANCOVA) testing for heterogeneity of slopes to compare selection gradients among the three harvest regimes. Tests for variation in selection patterns were performed for each of the four harvest simulations and for the combined harvest simulation. The interaction term (Harvest Regime×Size Index) was used to determine if the selection pattern varied among harvest regimes. Non-linear models of the relationship between fitness and size-index were also analyzed for each harvest simulation to test for non-linear (stabilizing or disruptive) selection. Significance of the interaction term (Harvest Regime×Size Index^2) determined if the pattern of non-linear selection varied among harvest regimes. All statistical analyses were performed using SAS JMP v. 5.1 statistical software (SAS Institute Inc., Cary, NC 2002).

Results

Harvest Simulations

The overall search efficiency—the number of adult plants removed during the two hour search—varied among individual harvesters (likelihood ratio=16.772, P=0.0008). The number of plants harvested during each harvest simulation ranged from 16.3% to 36.3% of the 135 adult plants in the population (Table 1). In accordance with harvest regulations, no juvenile plants were harvested during any of the simulations. However, many legally harvestable plants were never encountered during the harvest simulations. When only the encountered plants are considered, the efficiency of harvest increased, ranging from 39.4% to 57.6% of adult plants removed (Table 1), and the search efficiencies no longer varied among harvesters (likelihood ratio=6.725, P=0.0812).

Selection- All Juveniles and Adults

In the population of both juvenile and adult plants without harvest, a significant positive slope of the linear selection gradient (β=0.1450) indicated that larger plants had higher stage specific fitness than smaller plants (Table 2). There was no evidence for significant non-linear selection in the population of juvenile and adult plants ($\gamma = -0.0072$; $t = -0.22$, $P = 0.8261$).

When the population experienced harvest or harvest taking seeds, the slope of the linear selection gradients did not decline significantly in any of the individual harvest simulations (Fig. 3, Table 3). However, in the combined harvest simulation, the slope of the linear selection gradient declined significantly as the population was harvested ($F = 3.7797$, $P = 0.0233$). Removal of seeds during the combined harvest further decreased the selection gradient such that the slope not significantly different than zero ($\beta = 0.0138$; $t = 0.45$, $P = 0.6519$). Variation in non-linear selection was not detected in any harvest simulation or in the combined harvest simulation.

Selection-Encountered adults

In the population without harvest, the slope of the selection gradients (β) ranged from 0.1489 to 0.1958 for the encountered adult plants, again indicating a positive vrelationship between size-index and stage-specific fitness. In harvest simulations 2 and 4, these gradients were statistically significant and the same trends were found in simulations 1 and 3 (Table 4). Also in the combined harvest simulation, there was a positive relationship between size-index and stage-specific fitness among encountered adult plants ($\beta = 0.1738$; $t = 2.98$, $P = 0.0035$).

Table 1 Number of small and large (total leaf area >250 cm^2) adult plants in the population that were encountered and harvested, encountered but not harvested, and not encountered by the harvester (>6 m from harvester track)

Harvest Simulation	Encountered (Harvested)		Encountered (Not Harvested)		Not Encountered	Search Efficiency[a] (%)	Overall Efficiency[b] (%)
	Small	Large	Small	Large			
1	14	14	21	22	64	39.4	20.7
2	17	22	29	26	41	41.5	28.9
3	10	12	13	15	85	44.0	16.3
4	27	22	16	20	50	57.6	36.3
Combined	39	41	22	16	17	67.8	59.3

[a] Search efficiency is the percent of encountered plants harvested

[b] Overall efficiency is the percentage of plants harvested of all adults in the population

Table 2 Slopes of linear selection gradients (β) and their standard errors for the relationship between stage-specific fitness and standardized size-index of juvenile (2-leaf) and adult (3 and 4-leaf) plants across harvest simulations

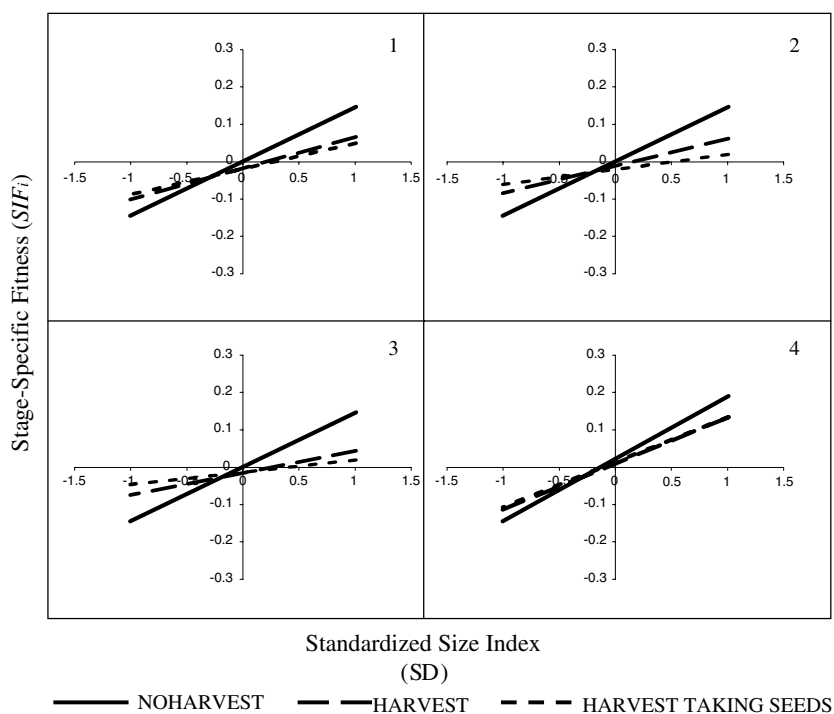| Harvest Simulation	Size Index				
	Harvest regime	β	SE	t	P-value
	No harvest	0.1450	0.0440	3.30	0.0011
1	Harvest	0.0833	0.0362	2.30	0.0223
	Harvest taking seeds	0.0681	0.0363	1.88	0.0618
2	Harvest	0.0728	0.0339	2.15	0.0327
	Harvest taking seeds	0.0400	0.0338	1.18	0.2375
3	Harvest	0.0588	0.0372	1.58	0.1150
	Harvest taking seeds	0.0326	0.0374	0.87	0.3839
4	Harvest	0.0924	0.0340	2.72	0.0071
	Harvest taking seeds	0.0848	0.0342	2.48	0.0138
Combined	Harvest	0.0418	0.0301	1.39	0.1668
	Harvest taking seeds	0.0138	0.0306	0.45	0.6519

Fig. 3 Predicted values of stage specifc fitness (SIF$_i$) for adult and juvenile plants in each harvest simulation (1–4) under three harvest regimes (no harvest, harvest, harvest taking seeds)

Table 3 Results of ANCOVA testing for heterogeneity of slopes among three harvest regimes in the population (no harvest, harvest, and harvest taking seeds) for the elationship of stage-specific fitness to size-index of both juvenile and adult plants

Harvest simulation	Source	df	MS	F	P-value
1	Harvest Regime (HR)	2	0.0301	0.0809	0.9223
	Size-Index (SI)	1	7.1520	19.2556	<0.0001
	HR×SI	2	0.4037	1.0870	0.3378
	Error	729	0.3714		
2	Harvest Regime (HR)	2	0.0276	0.0802	0.9230
	Size-Index (SI)	1	5.4134	15.7266	<0.0001
	HR×SI	2	0.7025	2.0408	0.1307
	Error	729	0.3442		
3	Harvest regime (HR)	2	0.0192	0.0501	0.9511
	Size-Index (SI)	1	4.5503	11.8518	0.0006
	Regime×SI	2	0.8427	2.1949	0.1121
	Error	729	0.3839		
4	Harvest regime (HR)	2	0.0391	0.1127	0.8935
	Size-Index (SI)	1	8.4533	24.3810	<0.0001
	HR×SI	2	0.2613	0.7536	0.4710
	Error	729	0.3467		
Combined	Harvest regime (HR)	2	0.0174	0.0566	0.9450
	Size-Index (SI)	1	3.2763	10.6405	0.0012
	HR×SI	2	1.1637	3.7794	0.0233
	Error	729	0.3079		

Table 4 Slopes of linear selection gradients (β) and their standard errors for the relationship between stage-specific fitness and size-index of encountered adult plants among three harvest regimes (no harvest, harvest and harvest taking seeds)

Harvest simulation	Harvest Regime	β	SE	t	P-value
1	No harvest	0.1510	0.0835	1.81	0.0749
	Harvest	0.0942	0.0535	1.76	0.0828
	Harvest taking seeds	0.0497	0.0575	0.87	0.3900
2	No harvest	0.1958	0.0705	2.78	0.0067
	Harvest	0.0585	0.0434	1.35	0.1809
	Harvest taking seeds	0.0126	0.0441	0.29	0.7757
3	No harvest	0.1489	0.0891	1.67	0.1013
	Harvest	−0.0075	0.0457	−0.12	0.9080
	Harvest taking seeds	−0.0764	0.0691	−1.11	0.2742
4	No harvest	0.1860	0.0737	2.52	0.0136
	Harvest	0.1317	0.0485	2.71	0.0081
	Harvest taking seeds	0.1168	0.0500	2.34	0.0219
Combined	No harvest	0.1738	0.0584	2.98	0.0035
	Harvest	0.0174	0.0242	0.72	0.4747
	Harvest taking seeds	0.0216	0.0228	0.95	0.3499

Harvest significantly reduced the slope of the selection gradients describing the relationship between size-index and stage-specific fitness for harvest simulation 2, and again this decline was exacerbated when harvesters removed seeds (Table 5, Fig. 4). A similar trend ($0.05 < P < 0.10$) towards an altered pattern of selection was also observed for harvest simulation 3, and this was also significant for the combined harvest simulation.

Discussion

The evidence for selection favoring large individuals in the population without harvest is in accord with previous observations of the life history of *P. quinquefolius*. The components of the size-index (total leaf area and stem height) are known to be significant positive predictors of both seed production and year to year survival in *P. quinquefolius* (Carpenter and Cottam 1982, Lewis and Zenger 1982; Charron and Gagnon 1991, Anderson et al. 1993). The magnitudes were also consistent with the median of published standardized selection gradients (0.16) reported for quantitative traits in other wild species (Kingsolver et al. 2001). The selection regimes operating in all juveniles and adults as a whole, and encountered adults in this population were all remarkably similar. Previous studies of the variation in selection across life cycle stages have

Table 5 Results of ANCOVA testing for heterogeneity of slopes among three harvest regimes (no harvest, harvest, and harvest taking seeds) of the relationship of stage-specific fitness to size-index of encountered adult plants

Harvest simulation	Source	df	MS	F	P-value
1	Harvest regime (HR)	2	0.9472	3.1046	0.0470
	Size-Index (SI)	1	2.0200	6.6207	0.0108
	HR × SI	2	0.1794	0.5879	0.5564
	Error	204	0.3051		
2	Harvest regime (HR)	2	0.4074	1.4992	0.2251
	Size-Index (SI)	1	2.2000	8.0962	0.0048
	HR × SI	2	0.8415	3.0967	0.0468
	Error	273	0.2717		
3	Harvest Regime (HR)	2	0.0698	0.2498	0.6180
	Size-Index (SI)	1	1.5683	5.6100	0.0045
	HR × SI	2	0.6619	2.3676	0.0973
	Error	144	0.2796		
4	Harvest regime (HR)	2	0.7390	2.5422	0.0807
	Size-Index (SI)	1	5.3306	18.3389	<0.0001
	HR × SI	2	0.1123	0.3864	0.6799
	Error	249	0.2907		
Combined	Harvest regime (HR)	2	0.2108	1.1249	0.3258
	Size-Index (SI)	1	1.8813	10.0387	0.0017
	HR × SI	2	0.9906	5.2858	0.0055
	Error	369	0.1874		

Fig. 4 Predicted values of stage specific fitness (SIF_i) for adult plants encountered in each harvest simulation (1–4) under three harvest regimes (no harvest, harvest, harvest taking seeds)
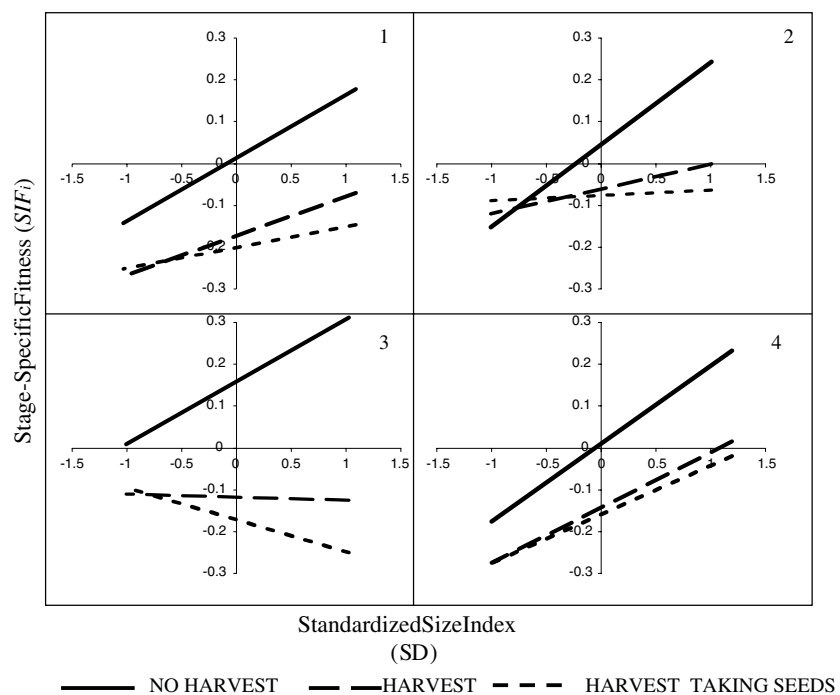
found gradients to mostly vary in magnitude (Kelly 1992); however measurement of selection at later life stages can be dramatically influenced by previous episodes of differential mortality (Bennington and McGraw 1995).

Individual harvesters did not significantly affect the selection regime present in the population of juvenile and adult plants. Nevertheless, the direction of the change was consistent across harvest simulations, suggesting insufficient numbers of harvested plants to detect differences.

Corroborating this was the observation that the fitness advantages of larger plants declined significantly in the combined harvest simulation. Though reported rates of harvest are limited, the combined harvest simulation may be more realistic for several reasons. In one published observation of harvest, diggers were able to remove all but one plant they found in the population (Lewis 1988). High prices can encourage harvesters to allocate more time to searching (Bailey 1999), likely more than the two hours

used in this study. The size of the study population meant that large proportions of plants were never encountered, thus diluting the overall effects of individual harvesters. Given the above issues, the results of this study do not exclude the contribution of legal minimum size restrictions to selective harvest of *P. quinquefolius*.

The most prominent declines in the slopes of linear selection gradients in the individual harvest simulations occurred in the population of encountered adult plants. The removal of seeds exacerbated the selective effects of harvest by further decreasing the fitness advantages of larger plants. Though the decline of slopes was consistent across simulations, the small number of adults removed may again explain the lack of widespread significance for these declines. Nonetheless, in at least one harvest simulation, selective harvest resulted from the differential removal of large adults that were encountered. This result suggests that the selective harvest of large plants was influenced by the contribution of size to apparency. Ripe, red berries are a noted visual cue for harvesters (Hufford 1997), which could additionally heighten the increased apparency of larger, more fecund plants. Though few berries were ripe at the time of the harvest simulations, this is realistic as start of legal harvest season in the majority of states occurs before berry ripening (McGraw et al. 2005). Harvests occurring when berries are ripe would be expected to strengthen our conclusion that the size-fitness relationship is altered by harvest.

Selection operating through apparency to human harvesters is most equivalent to studies of evolution of weed species in response to weeding pressures (Barrett 1983; Kadereit and Briggs 1985; Briggs et al. 1992). Like the selection observed in this study, selection imposed by weeding results from unintentionally selective mortality. Unlike typical artificial selection, changes effected by unintentional selection often occur in unanticipated or unwanted directions from the perspective of the human selective agent. For example, hand weeding of rice fields resulted in *Echinochloa crus-galli* genotypes that mimic shoots of crop seedlings and 'escape' removal (Barrett 1983). Similarly, unintentional selection created by preferentially removing larger ginseng plants would favor smaller plants, perhaps with less valuable roots.

In contrast to unintentional selection, selective harvest regimes in wild harvested animal species have generally resulted from intentional size-selectivity to increase economic yield or comply with well-intentioned conservation regulations (Rowell et al.1989; Miller and Kapuscinski 1994; Ratner and Lande 2001; Conover and Munch 2001). Selective harvest of plants is perhaps most similar to the practice of 'high-grading' in commercial timbering, which has been speculatively linked to changes in exploited tree species in temperate and tropical forests (Lebig 1992).

Intentionally selective harvest could also be a factor during wild harvest of *P. quinquefolius*. Harvesters could be motivated to deliberately leave small harvestable-sized plants behind for several reasons; for example, diminishing economic returns for the time invested in freeing relatively small roots from the soil. Systematically leaving behind small plants in combination with minimum size requirements and the influence of apparency could actually increase the fitness of small plants relative to that of large plants.

Though this study reports evidence for size-selective harvest, many other factors are important to consider before harvest can be considered a force in the evolution of *P. quinquefolius* populations. Namely, variation in total leaf area and stem height must be related to underlying heritable variation. Furthermore, harvest of *P. quinquefolius* is also subject to the 'tragedy of the commons' such that harvesters are motivated to leave no plants behind in a population, regardless of size or existing laws. This intensity of harvest can threaten population persistence (Nantel et al. 1996; Van der Voort et al. 2003), and thus population extinction could preclude a response to selection. The ability of a wild population to respond to anthropogenic selective pressures is ultimately a function of both genetic and demographic factors and can be difficult to predict (Burger and Lynch 1995; Gomulkiewicz and Holt 1995). Nevertheless, the decrease in the fitness advantage of larger plants has the potential to alter the size distribution in harvested populations.

In a long-lived perennial plant such as *P. quinquefolius*, reduced or lost selective advantage may also affect traits beyond those directly associated with size. Studies in other plant species have illustrated the ability of selection on a specific character to influence other traits or life-history events through phenotypic or genetic correlations (Kalisz 1986; Kelly 1992; Bennington and McGraw 1995). In harvested populations of *P. quinquefolius*, growth to larger size classes may no longer be favored, as allocation to growth would come at additional costs to survival and/or reproductive output. Because larger plants contribute disproportionately to population growth, smaller, less fecund plants would have additional consequences for population persistence. More complex indirect effects may be important as well in harvested populations. Altered fitness costs for reproduction at later stages may favor enhanced seed production by reproductive juvenile plants, which typically act only as pollen donors in the population (Schlessman 1987). Some evidence exists for this type of life-history change; in a study of 21 populations in four states, a higher proportion of juvenile plants were reproductive in unprotected populations versus protected populations (Cruse-Sanders and Hamrick 2004). Altogether, these examples illustrate the potentially far-reaching effects of human interaction with natural populations. Alteration of selection patterns due to harvest as

observed in this study could result in a significant shift in the evolutionary dynamics for this species.

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