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Source: The Journal of the Torrey Botanical Society, 145(2):109-120.
Published By: Torrey Botanical Society
https://doi.org/10.3159/TORREY-D-17-00006.1
URL: http://www.bioone.org/doi/full/10.3159/TORREY-D-17-00006.1

Journal of the Torrey Botanical Society 145(2): 109–120, 2018.

Experimental harvest and regrowth in Appalachian black cohosh (*Actaea racemosa*, Ranunculaceae) populations: Implications for sustainable management of a medicinal forest herb[1]

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Abstract. A broad range of understory forest herbs are harvested for medicinal properties, particularly from species-rich forests of the central and southern Appalachian Mountains. Many species have been collected and used for centuries with little understanding of harvest impacts, some with resulting population declines. Species valued for belowground components, such as *Actaea racemosa* L. (black cohosh), appear particularly vulnerable to harvest impacts. Between 2005 and 2011, we conducted experimental harvests on natural *A. racemosa* populations in central Appalachian oak (*Quercus* L.) forests. Responses were examined during 3 yr of moderate (33% plant removal) and intensive (66% removal) harvest treatments and up to 3 yr of regrowth, to simulate local harvesting practices and assess recovery potential. After 2 yr of moderate harvests, aboveground growth remained similar to controls. However, after 3 yr of moderate harvests or 2 yr of intensive harvests, significant declines were evident. After our third harvest year, leaf area and stem density were 65–80% lower in moderate harvest plots and 80–90% lower in intensive harvest plots, compared with controls. These differences persisted for at least 2 yr after harvests treatments ended. Curve-fitting models suggested recovery of leaf area and mean plant height to preharvest levels after 4–7 yr without further plant removal. In contrast, stem density showed little to no increase during our study period, and model projections suggested declines, rather than recovery. Thus, although individual growth metrics suggested that limited harvesting may be sustainable, results for stem density indicated little new recruitment into the population and concern for long-term population persistence. Forest herbs harvested for belowground components create particular challenges for sustainable management. Our concerns for *A. racemosa* are applicable to other economically important forest perennials in our region and worldwide and emphasize the need for continued study and monitoring to maintain viable populations and associated natural systems.

Key words: Appalachian oak forests, medicinal plants, nontimber forest products, perennial forest herbs, rhizome harvest

Nontimber forest products are increasingly recognized for their cultural and economic importance. Worldwide, an estimated 4,000–6,000 native or naturalized plant species are collected from forests for medicinal, edible, decorative, and other properties, including subsistence needs (Ticktin 2004, Vaughan *et al*. 2013). Nearly 200 species of understory herbs are harvested from North American forests for local use, sale, or export in nonprescription medicinal markets, with nearly one half of those herbs native to forests of the southern Appalachian Mountains (Greenfield and Davis 2003, Frey and Chamberlain 2016). Many of these forest herbs have been collected and used for centuries with little understanding of harvest impacts or effective management techniques. With increasing market demand and harvest pressures, recent studies suggest the potential for severe population declines in a number of eastern forest herbs (*e.g*., Rock *et al*. 2004, Albrecht and McCarthy 2006, Small *et al*. 2011, McGraw *et al*. 2013). Thus, it is essential to consider not only species preservation but also requirements for sustainable use. Specifically, there is a need to understand harvest impacts and the monitoring or management necessary to support long-term viability of target species and associated natural systems (Shackleton *et al*. 2015, Ticktin 2015).

Species life-history traits and the particular structures or organs used are important predictors

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[1] We gratefully acknowledge field assistance from undergraduate research students, volunteer citizen-scientists, and professionals throughout the region. This work was supported by the US Department of Agriculture Forest Service Southern Research Station Partnership Enhancement Initiative (12-DG-11330101-100) and by the College of Science and Technology at Radford University.

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doi: 10.3159/TORREY-D-17-00006.1

Received for publication February 2, 2017, and in revised form September 3, 2017; first published March 6, 2018.

of population vulnerability and the potential for sustainable harvest. Many Appalachian medicinal plants, such as American ginseng (*Panax quinquefolius* L.), goldenseal (*Hydrastis canadensis* L.), ramps (*Allium tricoccum* Aiton), and black cohosh (*Actaea racemosa* L.), are slow-growing, perennial herbs valued for their belowground storage organs (*e.g.*, roots, rhizomes, bulbs). Although removal of reproductive components, such as fruits or seeds, tends to have relatively little effect on long-term population viability, harvesting of belowground, perennating structures can greatly reduce clonal reproduction and result in adult mortality, making these species considerably more sensitive to harvest impacts (Castle *et al*. 2014, Ticktin 2015). For many perennial forest herbs, expansion or reestablishment is also limited by slow growth and specialized pollination, dormancy, or seed-dispersal requirements (Lezberg *et al*. 1999, Whigham 2004), and growth to harvestable size or age requires many years. As a result, populations may require decades or longer to recover from even relatively low harvest intensities (Nantel *et al*. 1996, Rock *et al*. 2004, McGraw *et al*. 2013, Ticktin 2015), creating particular challenges for sustainable management.

This study examined the impacts of experimental harvest on naturally occurring populations of *A. racemosa* (Ranunculaceae). This species is a long-lived, perennial plant, native to eastern deciduous forests and woodlands from southern Ontario to Georgia and west to Missouri (NatureServe 2015). *Actaea racemosa* tolerates a wide range of site conditions but reaches greatest abundance in moist, fertile soils and sheltered sites, particularly Appalachian cove forests (Predny *et al*. 2006). Seed-bank persistence tends to be relatively short, and morphophysiological seed dormancy and mortality of seedlings on drier sites limits population expansion from sexual reproduction (Albrecht and McCarthy 2009, 2011). More often, increases occur through clonal expansion of rhizomes and growth of rhizome fragments.

Actaea racemosa is sold in the US and European markets for nonprescription treatment of menopausal and premenstrual symptoms and has been listed as a top-10 selling herbal supplement since 2002 (Predny *et al*. 2006, AHPA 2012). Despite that, more than 98% of *A. racemosa* commercial sales derive from natural populations rather than cultivated sources. From 1997 to 2005, more than 1 million kilograms of *A. racemosa* rhizomes were harvested from eastern US forests, exceeding harvest of all other medicinal species monitored by the American Herbal Products Association (Silver Spring, MD). Surveys of southern Appalachian nontimber forest product buyers indicated that the largest quantities of *A. racemosa* were obtained from forests of eastern Kentucky and southwest Virginia (Kruger and Chamberlain 2015). Although *A. racemosa* is classified as "apparently secure" throughout its native range (N4; NatureServe 2015), field experiments have demonstrated that populations are sensitive to harvest impacts and have limited postharvest recovery (Small *et al*. 2011). In a vulnerability assessment of North American medicinal herbs, Castle *et al*. (2014) rated harvest effects on *A. racemosa* as particularly high because it is collected for roots and rhizomes. Today, this species is listed as "at-risk" by United Plant Savers (2014), and global declines of 10–30% are predicted over the next decade unless harvest pressures are alleviated through increased cultivation (NatureServe 2015).

Effectively managing *A. racemosa* and other commercially important nontimber forest products requires an understanding of population responses to the range of harvest intensities, frequencies, and recovery periods currently in practice. This study simulated local harvest practices on naturally occurring *A. racemosa* populations to assess short- and long-term experimental harvest impacts and the potential for population persistence and regrowth. We expanded on earlier studies of *A. racemosa* populations in central Appalachia to consider effects of repeated annual harvests and regrowth in subsequent years and to propose management approaches to support long-term persistence. Finally, we sought to improve methods of assessing postharvest recovery for this and other economically important eastern forest herbs.

Materials and Methods. Study Sites and Field Methods. Harvest experiments were conducted in naturally occurring *A. racemosa* populations in George Washington-Jefferson National Forest, Augusta County, VA (38°26′33.52″N, 79°15′51.80″W). Elevation of the study sites was approximately 1,190 m, with moderately steep (26–32%) southeast-facing (approximately 130°) slopes. The vegetation is classified as Appalachian oak (*Quercus* L.) forest (Stephenson *et al*. 1993), dominated by a canopy of *Quercus rubra* L., *Acer* *rubrum* L., *Betula lenta* L., *Prunus serotina* Ehrh., and occasional *Tsuga canadensis* (L.) Carriere, with sporadic subcanopy or shrub-layer *Hamamelis virginiana* L. and ericaceous species (*Kalmia latifolia* L., *Vaccinium* spp., and *Pieris floribunda* (Pursh) Benth. & Hook. f.). These secondary forests are generally older than 100 yr and developed after broad-scale logging and occasional livestock grazing or burning in the late 1800s and early 1900s. Today, stands are relatively even-aged or two-aged after the loss of the American chestnut (*Castanea dentata* (Marshall) Borkh.) in the 1930s (Stephenson *et al.* 1993).

In June 2005, a 100-m transect was established along the upper contour of the study area, with a minimum 3-m buffer from the road edge (FS-85, minimal-use gravel) and was designated as Site 1. Twelve subtransects were established at random starting points along the main transect. Each subtransect was 45 m long and orthogonal to the main transect. Three 2- × 5-m sample plots were located randomly along each subtransect and assigned to one of three experimental harvest treatments: 0% (control), 33%, or 66%. Harvest intensities were selected in consultation with industry representatives, harvesters, and others familiar with regional harvesting practices and followed harvest regimes of a parallel harvest study in North Carolina. (Small *et al.* 2011). This layout resulted in 12 plots per harvest treatment and a total of 36 plots at Site 1. To expand sampling and monitoring efforts, two additional 100-m transects were established in neighboring forest stands in June 2007 and June 2009 and designated Site 2 and Site 3, respectively. Locations for subtransects and plots in Sites 2 and 3 were established following the same methods as those used in Site 1, adding 12 sample plots per treatment at each site.

In each plot, *A. racemosa* stem density and the distance of each stem from the main and subtransects were measured. Foliage height was measured for each plant, from the ground surface to the top of the main canopy of leaves, excluding flowering or fruiting peduncles. Because the vegetative canopy of *A. racemosa* is generally elliptical, foliage area was calculated as follows: $(PI \times D_1 \times D_2)/4$, where D_1 was one of two perpendicular measurements of the foliage diameter, beginning with the longest dimension. Petioles branching aboveground or originating from the same location along a rhizome was measured as single stems; petioles branching originating from discrete locations along underground rhizomes was measured as separate stems.

Experimental harvests were designed to mimic procedures used by regional harvesters. After measuring aboveground growth, the number of plants to be harvested was determined, based on the total number of stems in the plot and the assigned harvest treatment. The largest plants were selected for harvest, based on measured crown dimensions. However, every effort was made to avoid severing or splitting rhizomes. If one or more smaller stems were attached to the same rhizome and harvesting that plant would severely affect the rhizome or exceed the total number of stems designated for harvest, the next largest plant in the plot was selected. All aboveground and belowground plant materials (shoots, rhizomes, roots) were excavated as completely as possible for each harvested plant. It is important to note, however, that rhizome fragments often remain in the soil after harvesting, with natural disintegration of rhizome connections. These vegetative propagules are likely to be important sources for postharvest regeneration of *A. racemosa*, as observed in *Hydrastis canadensis* (van der Voort *et al.* 2003, Albrecht and McCarthy 2006).

Aboveground growth measures and experimental harvests were conducted annually for a consecutive 3 yr, beginning with the year of plot establishment (Site 1: 2005–07, Site 2: 2007–09, Site 3: 2009–11). Harvest effects were assessed in the year after each experimental harvest treatment. To assess postharvest population recovery, annual measurements of foliage height, foliage area, and stem density continued in harvest and control plots through 2011. All growth measures and experimental harvests were conducted in June of each year.

DATA ANALYSIS. Because our primary objectives were to examine harvest impacts and postharvest recovery, plots initially lacking *A. racemosa* were excluded from analysis. Final data sets included 25 plots at Site 1 (0% control, 8 plots; 33% harvest, 9 plots; and 66% harvest, 8 plots), 26 plots at Site 2 (8, 9, and 9 plots, respectively), and 28 plots at Site 3 (11, 7, and 10 plots, respectively). Foliage area, stem density, and mean and maximum plant height were compared across harvest treatments (0, 33, and 66%; fixed effect) for preharvest, final harvest, and 1 and 3 yr of recovery, using one-way multivariate ANOVA (MANOVA) tests. Depen-

Table 1. Comparison of *Actaea racemosa* plant size and abundance measures across harvest treatments. Harvest impacts were assessed in the year after experimental harvest treatments. Comparisons made within sites and years only. Multivariate ANOVA Site 1 (S1): d.f. = 6,40; Site 2 (S2): d.f. = 6,42; Site 3 (S3): d.f. = 6,46. Individual ANOVAs Site 1: d.f. = 2,22; Site 2: d.f. = 2,23; Site 3: d.f. = 2,25. Bold values are significant, and superscript denotes significant planned comparisons between harvest treatment (33 and 66% harvests) and control groups.

	Site 1			Site 2			Site 3		
Dependent variable	Wilks λ	*F* ratio	*P*	Wilks λ	*F* ratio	*P*	Wilks λ	*F* ratio	*P*
Preharvest year (S1: 2005, S2: 2007, S3: 2009)	0.940	0.21	0.971	0.540	2.52	**0.036**	0.660	1.77	0.127
Foliage area					0.44	0.651			
Stem density					1.17	0.328			
Maximum height					1.62	0.220			
Final harvest year (S1: 2008, S2: 2010, S3: 2011)	0.488	2.87	**0.020**	0.354	4.77	<**0.001**	0.351	5.28	<**0.001**
Foliage area		7.83	**0.003**^{33,66}		16.45	<**0.001**^{33,66}		9.80	<**0.001**^{66}
Stem density		4.43	**0.024**^{66}		9.34	**0.001**^{33,66}		7.04	**0.004**^{66}
Maximum height		0.87	0.433		2.29	0.123		0.26	0.771
Recovery yr 1 (S1: 2009, S2: 2011)	0.450	3.27	**0.010**	0.381	4.35	**0.002**			
Foliage area		7.80	**0.003**^{33,66}		16.31	<**0.001**^{33,66}			
Stem density		4.32	**0.026**^{33,66}		8.93	**0.001**^{33,66}			
Maximum height		0.50	0.614		3.86	**0.036**^{66}			
Recovery yr 3 (S1: 2011)	0.664	1.52	0.198						

dent variables were checked for significant intercorrelation ($P < 0.05$); mean height was removed from MANOVAs for weak multicollinearity. *Subtransect* was treated as a random effect in the preliminary analyses, which was not significant and was, therefore, removed in later analyses. Planned orthogonal contrasts were used to compare individual harvest treatments in significant MANOVAs.

Changes in response variables were analyzed over time using adjusted, repeated-measures ANOVAs, with *plot* as the subject factor, *year* as the repeated measure (within-factor, fixed effect), and *harvest treatment* as the grouping variable (between-factor, fixed effect). Equality of within-subject covariance matrices (circularity or sphericity) is an assumption of all within-subject *F* tests, including repeated-measures ANOVA, indicating equal variance of differences among assessed populations (von Ende 2001). Circularity was assessed among treatments using Box's M test, and Greenhouse-Geisser adjusted probabilities were used to avoid inflated *F* statistics because of lack of circularity. Following recommendations of von Ende (2001), multivariate, repeated-measures analyses were conducted and compared with univariate results. Both sets of tests produced equivalent results, so only univariate results are presented. Dependent variables were transformed as needed to meet normality and variance assumptions. For significant fixed effects, *a priori*, planned comparisons were used to compare responses at each site for: control *vs*. harvest treatments, preharvest *vs*. subsequent years, and final harvest *vs*. final recovery year. Tests were conducted in JMP Pro 11 (SAS Institute, Cary, NC) and NCSS 9 Statistical Software (NCSS, LLC, Kaysville, UT).

To generalize trends across years, harvest response and recovery trends were examined using global nonmetric multidimensional scaling (NMS) ordination with Sørenson distance in PC-ORD 6 (McCune and Mefford 2011). Mean and maximum height, foliage area, and stem density data for each plot were used in the ordination analysis. In addition, pooled data (pooled across sites by treatment year [*e.g.*, preharvest, harvest yr 1]) were used to calculate differences between treatment groups and controls and analyzed for best-fit curves. Scatter plots and r^2 values from generalized linear model curve-fitting procedures were used to determine the linear or nonlinear model (up to second-order polynomial) that best fit temporal trends in each response variable.

Results. HARVEST RESPONSE. Preharvest plant size and density were similar across treatments (Table 1; Fig. 1). Although MANOVA results suggested preharvest differences among treatments at Site 2, individual response variables did not

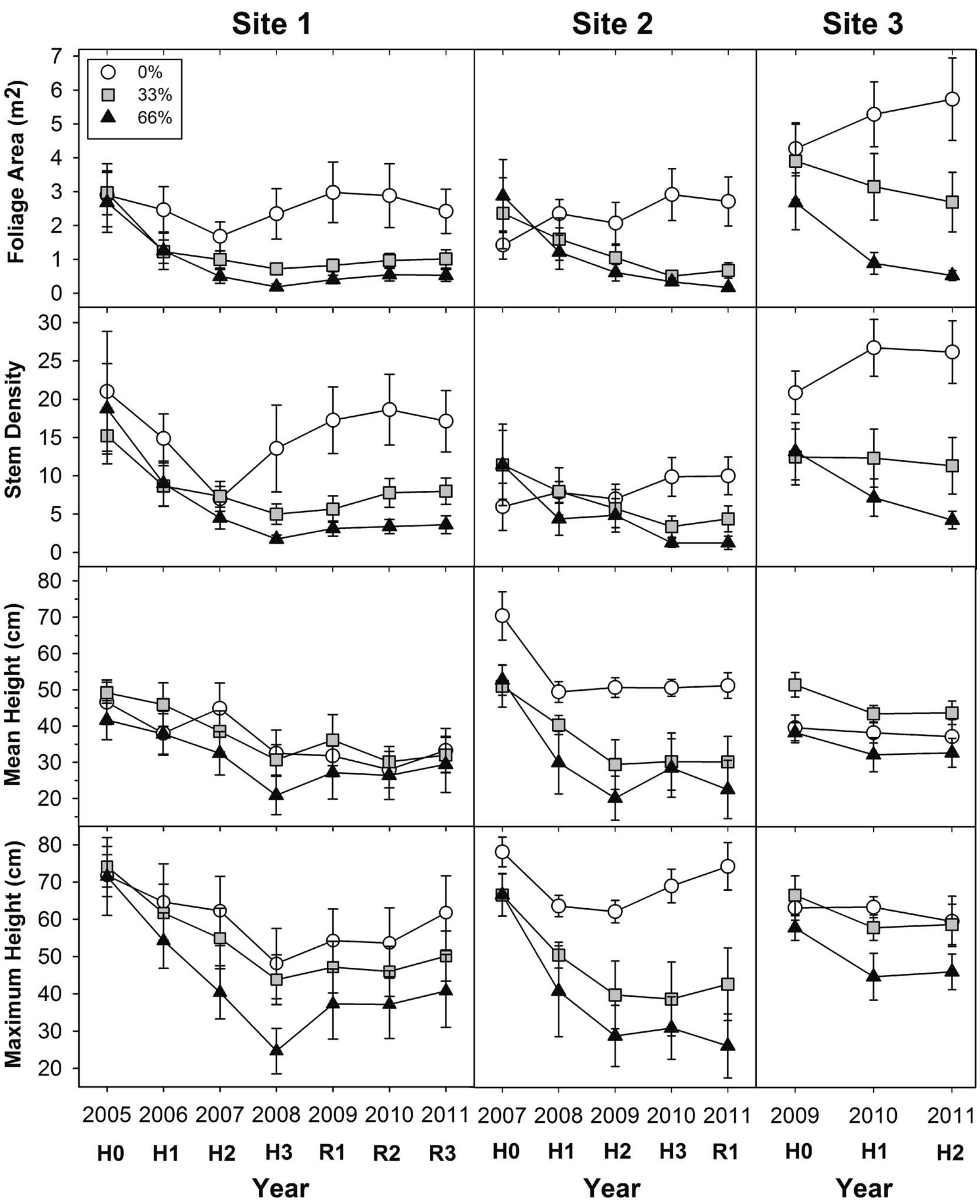

FIG. 1. Changes in height, foliage area, and stem density for *Actaea racemosa* populations after 3 yr of experimental harvest and subsequent regrowth. Means ± SEs shown. Plant measures conducted immediately before application of harvest treatments. H0 = preharvest year, H1 = harvest yr 1, R1 = recovery yr 1, and so forth.

differ significantly. After 2–3 yr of experimental harvests, most growth measures had declined significantly (preharvest *vs*. final harvest), and harvest × year (H × Y) interactions were evident at all sites (Table 2; Fig. 1). After the final year of harvest, intensive harvest plots (66% harvest) had 80–90% less foliage area and stem density than control plots (all sites; Table 1; Fig. 1). With 3 yr of moderate harvests (33%) foliage area was 70–80% less (Sites 1 and 2), and stem density was

Table 2. Changes in *A. racemosa* growth measures across sample periods and harvest treatments. Values are *F* ratios (Greenhouse-Geisser adjustment for within-factor and interaction effects) and d.f. from repeated-measures ANOVAs. Superscript denotes significant planned comparisons for harvest treatment (0, 33, or 66%) or year (preharvest versus final harvest [H], recovery yr 1 [1], or recovery yr 3 [3]).

Dependent variable	Harvest	Year	H × Y
Site 1: 2005–2011			
Foliage area	4.67*^{,66}	9.10***^{,H,1,3}	1.88^{a}
Stem density	2.72^{a}	8.22***^{,H,1,3}	2.21*
Mean height	0.39	4.31*^{,H,1,3}	0.31
Maximum height	0.52	4.55*^{,H,1,3}	0.40
d.f. (each test)	2,132	6, 32	12,132
Site 2: 2007–2011			
Foliage area	4.12*^{,33,66}	8.22***^{,H,1}	8.66***
Stem density	2.45^{a}	6.83***^{,H,1}	10.42***
Mean height	3.40*^{,66}	5.54**^{,H,1}	1.60
Maximum height	3.35*^{,33,66}	5.52**^{,H,1}	1.77
d.f. (each test)	2,92	4,92	8,92
Site 3: 2009–2011			
Foliage area	7.03**^{,66}	12.96***^{,H}	11.04***
Stem density	6.65**^{,33,66}	6.27**^{,H}	5.94***
Mean height	1.84	1.29	0.65
Maximum height	1.35	1.33	1.92
d.f. (each test)	2,50	2,50	4,50

^{a} $P \leq 0.10$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

65% lower (Site 2). Harvest response at Site 3 was only assessed for 2 yr after initial harvests. At that site, moderate harvest and control plots showed no significant differences in *A. racemosa* growth parameters.

The NMS ordination results illustrate temporal changes and experimental harvest impacts in *A. racemosa* populations (Fig. 2). The ordination was best fit with a two-axis solution, based on the NMS scree plot and Monte Carlo randomization test ($P < 0.05$, final stress = 3.41, final instability < 0.0001, 58 iterations). Axis 1 accounted for more than 80% of the variation in the data and was positively correlated with plant vigor (maximum height $r = 0.98$, mean height $r = 0.88$, foliage area $r = 0.75$, stem density $r = 0.66$). Axis 2 was also positively correlated with stem density ($r = 0.98$), foliage area ($r = 0.90$), and maximum height ($r = 0.61$). Control plots clustered high on Axis 1 for all sample years, indicating consistently robust plants. Plots subjected to 33 and 66% harvests decreased gradually along Axis 1 from the preharvest to the third harvest year, indicating progressively smaller and/or fewer plants. Harvest response was particularly pronounced in the intensive harvest treatment, which showed the greatest separation of plots across the ordination. After 3 yr of 66% harvesting, plots were positioned low on Axes 1 and 2, indicating markedly smaller plants and reduced stem density relative to earlier years or control plots.

HARVEST RECOVERY. *Actaea racemosa* populations on Sites 1 and 2 were reexamined in subsequent years, to assess population recovery. We found persistent differences between harvest and control plots for at least 2 yr after experimental harvests ended. Final harvests were conducted in 2007 at Site 1 and in 2009 at Site 2, and population responses measured the following year (Harvest yr 3). In "recovery year 1" (Site 1, 2009; Site 2, 2011), we saw little evidence of increasing plant size or reestablishment, with plant measurements in harvest treatments continuing to diverge from control plots (Table 1; Fig. 1). Foliage area and stem density remained 80–95% less in intensive harvest plots than in control plots. Moderate harvest plots also showed little recovery, with 55–75% less leaf area and stem density than in control plots. By "recovery year 3" (assessed only at site 1), *A. racemosa* growth no longer differed significantly between control and harvest treatments, suggesting some degree of population recovery. Examination of temporal changes, however, suggests persistent harvest effects. Repeated-measures ANOVAs showed significant differences in all measured growth variables for preharvest *vs.* final-harvest year, as well as at 1 and 3 yr of recovery (Table 2). The NMS ordination results also suggested limited population recovery (Fig. 2, 33% and 66% harvests). In both moderate and intensive harvest treatments, Axis 1 scores for plots increased during recovery yr 2 and 3, as compared with harvest yr 3. These plots showed the greatest similarity (overlapping of points) to harvest yr 2, suggesting increased plant vigor (larger, more numerous) but failure to recover to preharvest or control plot levels.

Aggregate differences (across study sites) between control and treatment plots suggest that *A. racemosa* harvest response and recovery is nonlinear (Fig. 3). All vegetative growth measures declined in response to experimental harvesting. Foliage area and plant height (mean and maximum) typically were lowest after the final harvest year (H-3) or first recovery year (R-1). In subsequent years, those growth measures increased gradually to our final year of sampling (R-3).

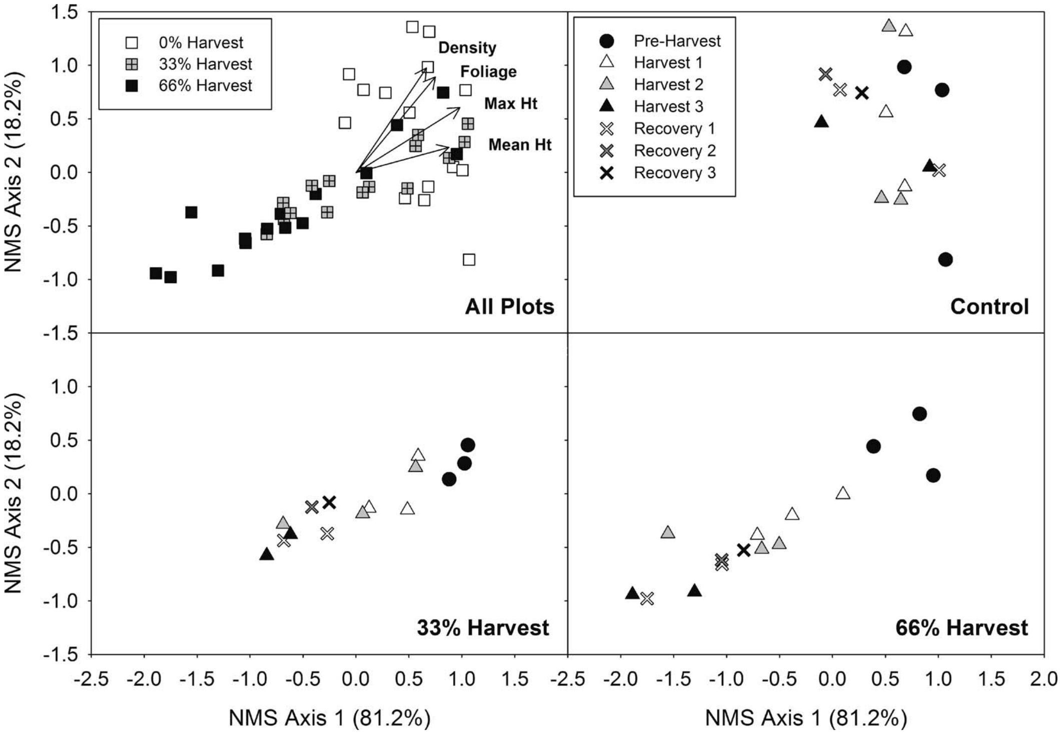

FIG. 2. Nonmetric multidimensional scaling (NMS) ordination of *A. racemosa* harvest plots. Mean values for each response variable (foliage area, stem density, plant height, maximum plant height) calculated within treatment year (preharvest or individual harvest or recovery years), harvest intensity (0, 33, or 66% harvest), and study site (Sites 1, 2, or 3) for NMS analysis. Vectors represent the strength and direction of correlation between axes and growth response variables.

Overall trends in foliage area and plant height from preharvest through final recovery in aggregated data sets were best fit by quadratic functions (Table 3; Fig. 3), with quadratic regression models suggesting recovery of foliage area and maximum plant height to preharvest conditions after 4.3–4.5 yr of recovery (8.3–8.5 yr from the start of our study) in both 33% and 66% harvest treatments. Recovery of mean height to preharvest levels was estimated to occur after approximately 7 yr of recovery (33% harvest = 6.8 yr; 66% harvest = 7.1 yr). Unlike other growth measures, the number of plants per plot (stem density) continued to diverge from control plots, with no evidence of recovery after experimental harvests ceased (Fig 3). Stem density trends for both harvest treatments were best fit by logarithmic functions, suggesting continued declines and lack of new recruitment into these populations (Table 3).

Discussion. Earlier harvest and monitoring efforts at this site emphasized the need for longer-term studies (Small *et al.* 2011). Our previous work found significant reductions in all *A. racemosa* growth measures after 2–3 yr of intensive harvests (66% plant removal). However, effects of moderate harvest intensities (33% removal) were unclear, with plant sizes and stem densities intermediate between, and not significantly different from, control or intensive harvest treatments. In addition, no recovery was evident after 1 yr without harvest. Our current study expanded on that research by examining 3 yr of experimental harvests, followed by 3 yr of potential recovery. Harvest responses also were compared on a third, newly established site. This extended evaluation provided a clearer picture of harvest effects on surviving plants and regrowth. Although control plots showed year-to-year variation, plants remained relatively robust across the 7-yr study period. In contrast, plants in harvested populations were consistently smaller and less abundant. As in our earlier study, severe declines were evident after 3 yr of intensive harvest (80–

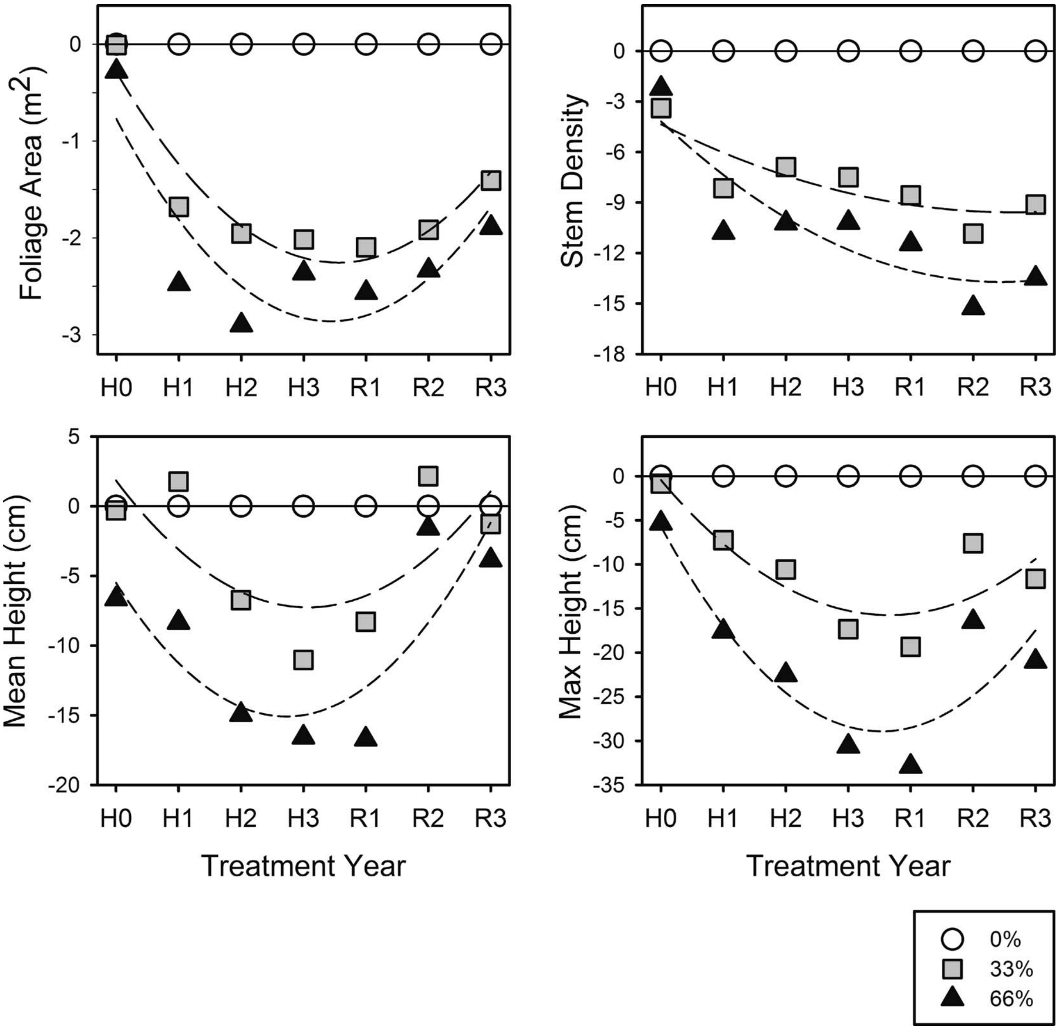

FIG. 3. Differences between *A. racemosa* harvest treatment responses and controls. Data pooled by treatment year (H0 = preharvest, H1 = harvest yr 1, R1 = recovery yr 1, and so forth) across the three study sites. Preharvest through final recovery year trends for foliage area and height measures best fit by nonlinear, quadratic models; trends in stem density best fit by logarithmic models (Table 3).

Table 3. Best-fit curvilinear regression equations for difference data (harvest treatments relative to controls) over time. Data pooled by treatment year across all study sites. (See Fig. 3.)

Dependent variable	Curve-fitting equation	R^2
Foliage area		
33% harvest	$y = 0.156x^2 - 1.423x + 0.981$	0.895
66% harvest	$y = 0.178x^2 - 1.578x + 0.629$	0.739
Stem density		
33% harvest	$y = -2.935 \ln(x) - 4.210$	0.756
66% harvest	$y = -5.402 \ln(x) - 3.938$	0.811
Mean height		
33% harvest	$y = 0.968x^2 - 7.872x + 8.745$	0.480
66% harvest	$y = 1.294x^2 - 9.633x + 2.837$	0.660
Maximum height		
33% harvest	$y = 1.151x^2 - 10.698x + 9.113$	0.730
66% harvest	$y = 1.870x^2 - 16.930x + 9.400$	0.784

90% less aboveground growth than in unharvested plots), with results supported at our third study site. Unlike previous work, extended monitoring also showed clear effects of moderate harvest intensities after 3 yr (65–80% less foliage area and stem density than unharvested plots).

Differences between harvest and control plots persisted for at least 2 yr after harvests ended. In the first recovery year, *A. racemosa* populations showed little increase in plant size or density in either harvest treatment. Rather, the poorest aboveground growth typically occurred after the third harvest year or first recovery year. After 3 yr of recovery, density and growth increased but remained below preharvest and control levels. Curve-fitting models suggest that plant growth (*i.e.*, foliage area, plant height) is likely to recover to preharvest levels after 4–7 yr without further plant removal. Similar trends were observed at each site, but these estimates should be interpreted cautiously (representing aggregated trends across sites and only one to two sites in recovery years). Our results for foliage area and plant height suggest that limiting harvest intensity or duration is important for sustainable management. Although 2 yr of 33% rhizome removal did not significantly reduce aboveground growth (relative to control), a third year of moderate or intensive harvesting, or 2 yr at high intensity, caused significant declines in both plant size and density. Thus, removal of no more than 33% of the population or harvesting for no more than a consecutive 2 yr, followed by a recovery period, may be sustainable at this site. Rock *et al.* (2004) similarly suggest that only low harvest levels can be sustained in *A. tricoccum*. Those authors recommended removal of less than 10% of the population annually during a 10-yr period. Others suggest that continued monitoring and active postharvest management is important for successful reestablishment (*e.g.*, Sinclair *et al.* 2005, McGraw *et al.* 2013, Ticktin 2015).

Although relatively few harvest studies have been conducted on *A. racemosa*, our results are generally consistent with studies of other perennial forest herbs. Many species show declines in aboveground and belowground growth and reproduction in the years immediately after harvests and require many years for full recovery. At high harvest intensities or frequencies, recovery is often limited, and some researchers question the ability of populations to return to preharvest levels. For example, Van der Voort *et al.* (2003) found average *Panax quinquefolius* and *Hydrastis canadensis* plant size to be less in the first growing season after harvests. Stature increased with increasing recovery period, but it was unclear whether populations would continue to decline with repeated harvests. Likewise, Sanders and McGraw (2005) found *H. canadensis* leaf area to be just one third of preharvest levels after 2 yr of postharvest recovery. Albrecht and McCarthy (2006) suggested that *H. canadensis* requires multiple years to recover to preharvest levels. Their field experiments showed significant increases in plant height, leaf size, and reproductive output after 4 yr (*vs.* 2 yr) of recovery, although results were inconsistent across sites. These declines in leaf area and other aboveground measures have important implications for postharvest recovery because those measures tend to be strongly correlated with overall plant growth and reproductive output. In harvested *P. quinquefolius* populations, decreased leaf area and stem height have been associated with decreased rhizomes and overall plant growth and reduced seed set (Mooney and McGraw 2009). Similarly, spikenard (*Nardostachys grandiflora* DC.), a Himalayan forest perennial harvested for medicinal rhizomes, showed reduced growth and fecundity after harvesting, particularly at higher intensities (Ghimire *et al.* 2008). If responses are similar in *A. racemosa*, then our observed declines in foliage area and plant height suggest simultaneous reductions in reproductive output and rhizome accretion for several years after harvests.

Individual plant metrics suggest that long-term (limited) harvesting of *A. racemosa* can be sustained; however, results for stem density were less encouraging. Even 3 yr after harvest treatments ended, stem density in both moderate and intensive treatments remained well below control and preharvest levels, with logarithmic models suggesting long-term declines rather than recovery. Harvesting appeared to stimulate growth in surviving individuals, likely through reduced competition, but without recruitment of new individuals. Thus, apparent "recovery" more likely reflects increased growth of survivors rather than population expansion. The presence (or absence, as we see here) of seedlings and juveniles in populations of long-lived species, such as forest perennials, provides important information about regeneration potential (Franco and Silvertown 2004, Mooney and McGraw 2009). If this interpretation is correct, our results suggest only limited recovery of *A. racemosa* after harvesting and potential threats to the long-term persistence of those populations.

Disturbance influences may also be important in understanding harvest response. *Actaea racemosa* occurs most often in rich, fertile, and moderate- to high-pH soils (NatureServe 2015) but tolerates a broader range of habitats than many economically important forest perennials (*e.g.*, *H. canadensis*, *P. quinquefolius*, *A. tricoccum*) and may be found in relatively open, disturbed sites (*e.g.*, Small and McCarthy 2002). Noted disturbances our at study sites include *Tsuga canadensis* (an occasional, mixed-canopy, dominant plant) needle and branch loss because of the hemlock woolly adelgid, occasional gypsy moth defoliation, white-tailed deer herbivory, and competition from invasive plants. Deer populations in Augusta County, VA, and surrounding counties in Virginia have been estimated at more than 12 km^{-2}. However, the Virginia Department of Game and Inland Fisheries describes deer populations in Augusta County as at or below environmental capacity and impacts on public and private lands as relatively low because of ample hunting and habitat (VDGIF 2015). We observed relatively little evidence of deer browse on *A. racemosa* and other understory species in our study plots. Our main transects also lie in close proximity to a limited-use gravel road. Nonnative, invasive plants and aggressive grasses occur frequently along the road edge but were relatively uncommon in our plots. However, influences of increased light availability and altered species composition because of insect disturbance, deer browse, and invasive plant competition will be important to monitor in the future as potential influences on *A. racemosa* recovery.

Limited understanding of species used as nontimber forest products, particularly their responses to harvesting, contributes to unsustainable use. Assessing sustainability and developing effective management protocols is challenging given the range of species and plant components used (Ticktin 2015). In addition, products harvested for underground perennating organs (*e.g.*, roots, rhizomes, bulbs), bark, or entire plants tend to be particularly difficult to manage (compared with those harvested for flowers or fruits) because extraction leads to direct plant mortality, reduced genetic diversity, and shifts in population age or stage structure toward juvenile plants and negatively affects population persistence (Mooney and McGraw 2009, Ticktin 2015). Long-lived and slow-growing species, such as forest herbs are particularly sensitive to changes in age- or stage-specific survival, especially loss of adults or reproductively mature individuals (Franco and Silvertown 2004, McGraw *et al.* 2013). Thus, our concerns for recovery and sustainable harvest of *A. racemosa* are applicable to many eastern forest herbs and extend worldwide to other nontimber forest products (*e.g.*, Mulligan and Gorchov 2004, Silvertown 2004, Gaoue *et al.* 2011).

Relationships between aboveground and belowground plant components are also poorly understood, particularly as needed to effectively estimate belowground biomass from aboveground characteristics. Despite that, aboveground measures most often are used to assess plant recovery and belowground biomass accretion in these species (Piper 1989, Chamberlain *et al.* 2013, Small *et al.* 2014). Both aboveground and belowground structures are important to plant growth and potential for recovery after disturbance or expansion into new environments, particularly in long-lived species (Lezberg *et al.* 1999, Donohue *et al.* 2000). Like many studies of root-based forest products, we used leaf area and other aboveground metrics, along with root biomass, to assess harvest impacts. These indirect measures clearly are preferred over destructive measures for evaluating population regrowth. However, this practice underscores the importance of continued research to understand aboveground and belowground biomass relationships for use in forest product inventories and assessment of population health and conservation status.

Lastly, ecological research on nontimber forest products has focused primarily on population dynamics in individual species, with little attention to harvest effects on community structure or ecosystem services. Studies in these areas suggest that these broader-scale considerations are also essential for sustainability (Ticktin 2004; 2015). In eastern deciduous forests, understory herbs typically comprise the largest component of forest diversity and contribute to ecosystem productivity, nutrient retention, and overstory composition far more than would be expected given their relative size and biomass (Small and McCarthy 2003, Gilliam 2007). Overharvesting of perennial forest herbs has the potential to affect broader processes, ranging from nutrient cycling, competitive interactions, and susceptibility to herbivores and invasive species to effects on associated insect, avian, and small mammal populations (Ticktin 2004, Gilliam 2007, McGraw *et al*. 2013, Muller 2014). Thus, improved understanding and effective management are necessary to minimize impacts on economically important, native plant populations and to support long-term viability of target species and associated ecosystems.

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