

Population recovery following differential harvesting of *Allium tricoccum* Ait. in the southern Appalachians

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Abstract

Over 100 native herbaceous forest perennials are harvested in the United States. Management of these populations for continued survival requires information on the long-term effects of varied harvesting levels on populations of forest perennials. *Allium tricoccum* Ait. is a species that is harvested throughout its range for its edible bulb. We examined the recovery of *A. tricoccum* populations over a 5-year period following experimental harvests of different intensity to predict the number of years required to return to pre-harvest levels and to establish guidelines for sustainable harvesting. Our harvest treatments included removal of 0, 25, 50, 75, and 100% of plants within experimental plots. Treatments were repeated at three sites. Population recovery was monitored for 4 years at two sites and 7 years at one site. We found a relationship between the level of harvest and the negative impacts on populations of *A. tricoccum*, with limited population recovery in the 4 years following harvesting. We projected recovery times as a function of harvest level using a population projection model. Deterministic projections of recovery time ranged from 148 years for a 95% harvest to 2.5 years for a 5% harvest. Incorporating stochasticity into our projections increased the uncertainty in our estimates of recovery time. For example the recovery time from a 5% harvest ranged from 1 to 89 years (95% confidence limit). Based on our results, a 10% harvest once every 10 years would, on average, be a sustainable level of harvest for *A. tricoccum* in southern Appalachian forests.

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1. Introduction

More than 200 species of plants native to the United States are at risk of extinction due to collection for consumptive purposes and half of these are herbaceous forest perennials (Robbins, 1999; Kartesz, 1999). Continued over-harvesting of these plants due to a lack of management strategies based on empirical data could lead to loss of these forest resources (Chamberlain et al., 1998). Some forest perennials, such as American ginseng (*Panax quinquefolius*) and goldenseal (*Hydrastis canadensis*), have already been listed in the Convention of International Trade in Endangered Species of Wild Flora and Fauna due to over-harvesting (Robbins, 1998). Data that addresses the question of

what constitutes a sustainable harvest are critical because of the increased popularity of wild-harvested forest perennials (Robbins, 1997).

In the deciduous forests of eastern North America, *Allium tricoccum* Ait. (ramps or wild leek) is a perennial forest herb that is harvested in its entirety (leaves, bulb, and rhizome) throughout its range. As with most native forest perennials, there have been few experimental studies of population recovery following the harvesting of *A. tricoccum*. The lack of information on the effects of harvesting wild plants is a critical concern, particularly at a time of increased collections (Fuller, 1991). Without such data, increased harvesting of *A. tricoccum* may result in dramatic and long-lasting declines in wild populations.

Populations of *A. tricoccum* at its southern range limit in the southern Appalachians of North Carolina and Tennessee may already be in decline due to over-harvesting. Staff at Great Smoky Mountains National Park

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(GSMNP) began reporting in 1988 that accessible *A. tricoccum* populations were smaller and less dense than populations found in remote areas. Harvesting pressure on *A. tricoccum* populations has continued to increase. For example, in Nantahala National Forest, North Carolina (adjacent to GSMNP), the number of commercial collection permits for *A. tricoccum* increased from one permit in 1996, with a single bushel collected, to 16 permits in 2001 with 46 bushels reported as collected (Mike Wilkins, US Forest Service, personal communication). A single bushel can hold as many as 650 *A. tricoccum* plants (Dr. Jim Chamberlain, US Forest Service, personal communication). Since permits are not required for personal consumption up to one-half bushel, these collections are unrecorded making it likely that the actual harvesting pressure on *A. tricoccum* is much greater than commercial permits would indicate.

Declining populations of *A. tricoccum* at its northern range limit in southern Quebec led to studies to ascertain the cause. Nault and Gagnon (1993) used projection matrices to show that harvest rates between 10 and 15% resulted in population declines in *A. tricoccum* and that as little as a 5% harvest would be deleterious during unproductive seasons. As a result, *A. tricoccum* has been designated as a “vulnerable” species due to over-collection in Quebec (Vasseur and Gagnon, 1994). Our purpose in the current study was a similar undertaking at the southern range limit of *A. tricoccum*. We sought to examine the recovery of *A. tricoccum* populations in response to harvest intensities that ranged from 25 to 100% removal. Our specific goals were (1) to predict the number of years to recovery to pre-harvest levels from these varied levels of harvest and (2) to characterize variability in population growth rates across sites and years.

1.1. The species

A. tricoccum Ait. is a perennial spring ephemeral widely distributed in deciduous forests of eastern North America south to the southern Appalachians. Populations can be found in cove forests and northern hardwood associations throughout the southern Appalachians. Moist slopes, depressions, and streamside flats are preferred habitats in the northern extension of *A. tricoccum*'s range, whereas colluvial mountain slopes are preferred in the southern extension of its range where it grows at elevations up to about 1500 m (5000 feet) (Jones, 1979; Jones and Shildneck, 1980).

Two varieties of *A. tricoccum*, var. *tricoccum* Ait. and var. *burdickii* Hanes, have been recognized based on differences in morphology, phenology, and habitat (Jones, 1979). The geographical ranges of both varieties overlap in the southern Appalachians. *A. tricoccum* var. *tricoccum* is typically larger than var. *burdickii* and has more flowers per umbel; the petiole and flower stalk is usually red pigmented in var. *tricoccum* instead of white.

Although populations of both varieties have been described as growing together, Jones (1979) asserts that hybridization cannot occur due to a phenological barrier, that is, var. *tricoccum* typically blooms in July and var. *burdickii* blooms in June. Although Kartesz (1999) has elevated these two varieties to species level, evidence is inconclusive. For the purposes of this paper, the two varieties are combined.

2. Methods

2.1. Study sites

This study was carried out in Great Smoky Mountains National Park, in the southern Appalachian mountains of North Carolina and Tennessee, USA. Three study sites were selected in April 1989, all located in the central portion of the park at elevations between 960 m (3150 feet) and 1400 m (4500 feet) with northern aspects. Site selection was based on the following criteria: easy access for efficient sampling; an abundance of plants (at least 15 m² with no fewer than 20 plants per square meter); and, an area that is not visited regularly by harvesters.

The three sites selected for this study were Porters Creek (Site PC), Elkmont (Site EL), and Mingus Lead (Site ML). The Porters Creek site was located within an old-growth rich cove forest (Schafale and Weakley, 1990) at about 1000 m (3500 feet) in elevation. The study plots were situated on a relatively rocky north-facing slope (60%) and flat adjacent to a wet-weather drainage. The canopy was comprised of a mixture of mesophytic species, including *Tilia americana* (basswood), *Halesia tetraptera* var. *monticola* (silverbell), and *Aesculus flava* (yellow buckeye). The Elkmont site was located within a rich cove forest at about 960 m (3150 feet) in elevation. The plots were situated in a gently sloping (19%) seepage area in a secondary forest made up of *Halesia tetraptera* var. *monticola*, *Liriodendron tulipifera* (tuliptree), and *Tsuga canadensis* (eastern hemlock). The Mingus Lead site was located within an old-growth rich cove/northern hardwood transition forest (Schafale and Weakley, 1990) at about 1400 m (4500 feet) in elevation. Study plots were situated on a rocky flat (26% slope) flanked by two steep, rocky drainages. The canopy was made up of *A. flava* and *Betula alleghaniensis* (yellow birch).

Sites PC and EL contained only the red-pigmented *A. tricoccum* var. *tricoccum*, and Site ML was comprised of *A. tricoccum* var. *burdickii*.

2.2. Experimental removal

Fifteen 1-m×1-m plots were established at each site (three replicates of five treatments) for a total of 45

plots. The plots were set up in a non-linear configuration; they were arranged sequentially for ease of relocation. In April 1989, the maximum leaf width of the largest leaf of each plant in all 45 plots was measured at full leaf expansion and recorded. Leaf width was shown to be an indicator of bulb size by Nault and Gagnon (1988) and the width of the largest leaf as an estimator of plant size (Cain and Damman, 1997).

Our five treatments represented different harvest levels. Within each level, a predetermined percentage of *A. tricoccum* plants were removed from an experimental plot. The control was not manipulated. The four remaining treatments had 25, 50, 75, or 100%, of *A. tricoccum* plants removed. *A. tricoccum* plants were pulled from each plot without consideration of plant size.

In April of 1990–1993, the leaf widths of plants remaining in each of the 45 plots, as well as population recruits, were measured without further harvest. A total of 17,349 measurements were made during this 5-year period.

In 1997, an additional 1002 leaf width measurements were collected at Site EL to test the recovery predictions made from the 1990–1993 data. The other two sites (PC and ML) were too disturbed by harvesters to be useful in this analysis. One replicate of the 75% harvest treatment was removed from the study because of a fallen tree. This gave observed data points to compare to model projections.

2.3. Data analysis and modeling

2.3.1. Summed leaf widths

We analyzed *A. tricoccum* summed leaf widths in our experimental treatments using a mixed linear model with sites considered a random effect (Pinheiro and Bates, 2000). Years were considered a fixed-effect as they were the first years of population recovery following the experimental harvesting. Leaf widths were summed across plots within replicates resulting in 225 data points (5 years by 3 sites by 3 replicates by 5 treatments). However, the Porters Creek site (PC) was harvested by Park users prior to our data collection in 1993 and, therefore, all treatments in replicate 2 and the control, 25, 50, and 75% harvested plots of replicate 3 of the PC Site were eliminated from further analyses.

We used the Box–Cox method to choose a natural log transformation to normalize these data (Weisberg, 1985). Data from 1989 were pre-treatment and so these data were used as an additional covariate describing the initial population of *A. tricoccum* prior to our experimental manipulations. Therefore the total degrees of freedom of our experimental design was 171.

2.4. Specific growth rates

We estimated the specific growth rates for each site and treatment. These were calculated as

$$R_t = \frac{L_{t+1}}{L_t} \quad (1)$$

where L_t was the total leaf width measured for a replicate in year t . The R_t were calculated for each pair of successive years for all treatments, sites, and replicates, and were always greater than zero. An R_t less than one indicated a reduction in total leaf width for the population over the time period from year t to $t+1$, while a R_t greater than one implied an increase. The R_t were used to project the time to recovery of total leaf widths at sites for different harvest levels (described in Section 2.3.3).

We analyzed the specific growth rates using a linear model. We were not able to fit a mixed model as the design matrix was not full rank and the mixed model fitting procedure could not accommodate this. Treatment and years were considered fixed-effects and sites were included in the model. We used the Box–Cox method to choose a square root transformation to normalize these data (Weisberg, 1985).

2.4.1. Population recovery

We estimated the time to recovery using a discrete, exponential model of population growth:

$$P_{t+1} = P_t R \quad (2)$$

where P_{t+1} is the population level (i.e. summed leaf widths) at time $t+1$, and R is the specific population growth rate. The population level at time T is

$$P_T = P_0 R^T \quad (3)$$

where P_0 is the initial population level. To estimate the time T for recovery given some level of harvesting, f , which represents the fraction of population not harvested (e.g. $f=1$ indicates no harvesting), we replace P_0 in (3) with fP_0 , replace P_T in (3) with P_0 , and calculate the time to recovery T :

$$T = \frac{\log(1/f)}{\log(R)} \quad (4)$$

The estimated mean recovery time calculated in this way assumes that there is the same specific growth rate (R) each year. We relax this assumption below.

We estimated the years to recovery, T , in two different ways. First, we used the estimates of specific growth rates to calculate a single estimate of R across all replicates. Due to the multiplicative nature of growth rates, the appropriate estimator of the mean growth rate was the geometric mean specific growth rate calculated across sites (s), treatments (t), and years (y):

$$G = \left[\prod_{s,t,y} R_{s,t,y} \right]^{\frac{1}{s \cdot t \cdot y}} \quad (5)$$

G was estimated to be 1.02 and, together with (4), resulted in a deterministic estimate of recovery time

from any level of harvest. In the second method, we relaxed the assumption of constant growth rate across sites and years. This was done by re-sampling from all the R 's obtained from the data on replicates at all sites, treatments, and years, projecting the population one time step using (2), and continuing this until the population was equal to or greater than the initial population level. We repeated this procedure 5000 times so as to obtain a distribution of recovery times from any level of harvest. For background on re-sampling, see Crowley (1992).

We tested the practicality of using the available specific growth rates to project *A. tricoccum* population recovery using the data collected in 1997 at Site EL. The observed specific growth rates over the 4-year period were calculated using the 1993 Site EL data from the same four treatments. These were compared to projected 4-year specific growth rates calculated from resampling the specific growth rates from the same site and treatments from 1989 to 1993.

3. Results

3.1. Summed leaf widths

Our experimental harvesting treatments reduced *A. tricoccum* summed leaf widths over the period of 1990–1993 (Table 1; P -value < 0.0001) with the magnitude of the effect related to the degree of the initial population reduction. The estimated main effects of the treatments (on the log scale) were -0.48 for a 25% reduction in initial population, -0.74 for 50% reduction, -1.31 for 75% reduction, and -1.52 for 100% reduction, with all of these effects significantly different from 0 (P -values < 0.05). There was not a year:treatment interaction (P -value = 0.94) indicating that there was not significant recovery of the populations in the 4 years following the harvesting treatments (Fig. 1; 1990–1993). The initial level of the *A. tricoccum* populations prior to harvesting interacted with the treatments (Table 1;

Lo:Treatment P -value = 0.03) so that the initial summed leaf width was positively related to subsequent summed leaf width in all treatments except the 100% removal treatment. This was reasonable because the initial population size should be positively related to subsequent recovery except when the initial population is completely removed (i.e. the 100% removal treatment).

The random site effect had a standard deviation of 0.28 with estimated effects of -0.21 , 0.39, and -0.18 for sites PC, EL, and ML. The effect sizes were of a similar magnitude to estimated year effects (which were 0.29, 0.40 and 0.30 for 1991, 1992, and 1993) but were substantially smaller than treatment effects. This suggests that variability in recovery in the years immediately following harvesting is similar to spatial variability across sites.

3.2. Specific growth rates following harvesting

Specific growth rates (R 's) were significantly different across treatments and years (Fig. 2; P -values = 0.001 and < 0.001 , respectively, Table 2), with no treatment:year interaction on specific growth rates (P -value ~ 1). The estimated treatment effects on specific growth rate (on the transformed scale) were 0.035 for a 25% reduction in initial population, 0.027 for 50% reduction, 0.063 for 75% reduction, and 0.11 for 100% reduction, with only the latter two effects significantly different from zero (P -values < 0.05). The ordering of these effects indicates that populations more severely reduced by harvesting had greater subsequent growth rates. The estimated year effects were for 0.23 for 1990, 0.13 for 1991, and 0.001 for 1992, with the former two effects significantly different from 0 (P -values < 0.001). Thus, growth rates were higher in the years immediately following harvesting, declining as the populations recovered. These results suggest a simple logistic model of population recovery might be justified with population growth rate declining as the population level increases.

3.3. Population recovery

The deterministic estimates of the projected recovery time ranged from ~ 148 years for a 95% harvest to 2.5 years following a 5% harvest (Fig. 3). While the mean of the stochastic estimates were similar to the deterministic results (Fig. 3), the stochastic estimates of recovery time included much greater variability in the projected recovery time. For example, the deterministic estimate of recovery time following a 20% harvest was 11 years compared to the mean stochastic estimate of 18 years. However, the 95% confidence interval on the stochastic interval included estimates that ranged from 1 to 150 years (Fig. 4).

Table 1
ANOVA table of the mixed linear model fit to summed leaf widths (log transformed)

Term	Numerator df	Denominator df	F-value	P-value
Intercept	1	156	438.75	< 0.0001
Lo (initial summed leaf widths)	1	156	0.064	0.80
Treatment	4	156	9.62	< 0.0001
Year	3	156	8.01	0.0001
Lo:Treatment	4	156	2.93	0.03

The treatments were 25, 50, 75, and 100% removal of *A. tricoccum* plants along with an unmanipulated control. Pre-treatment data was collected in 1989 and subsequent plant responses to experimental manipulations were monitored in 1990–1993.

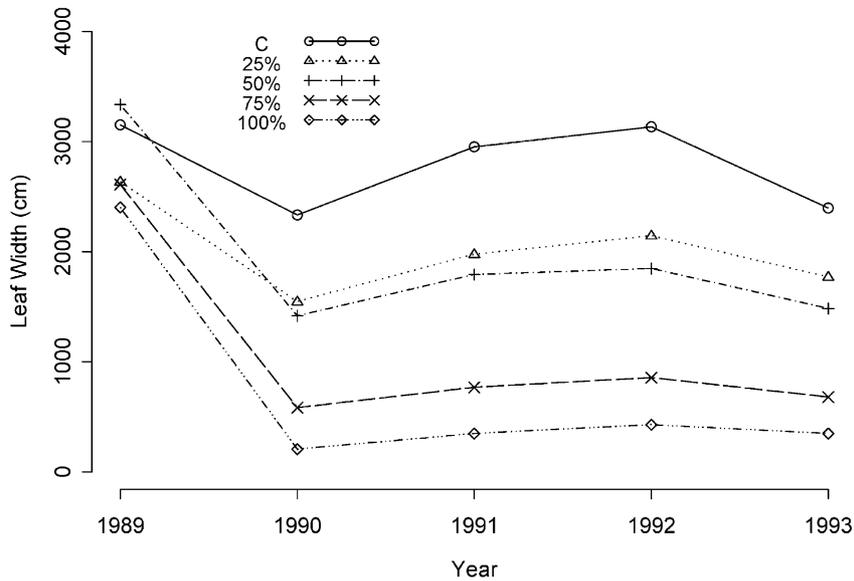


Fig. 1. Total leaf widths summed across replicates and sites. The 1989 points represent pre-treatment levels prior to harvests made in the same year.

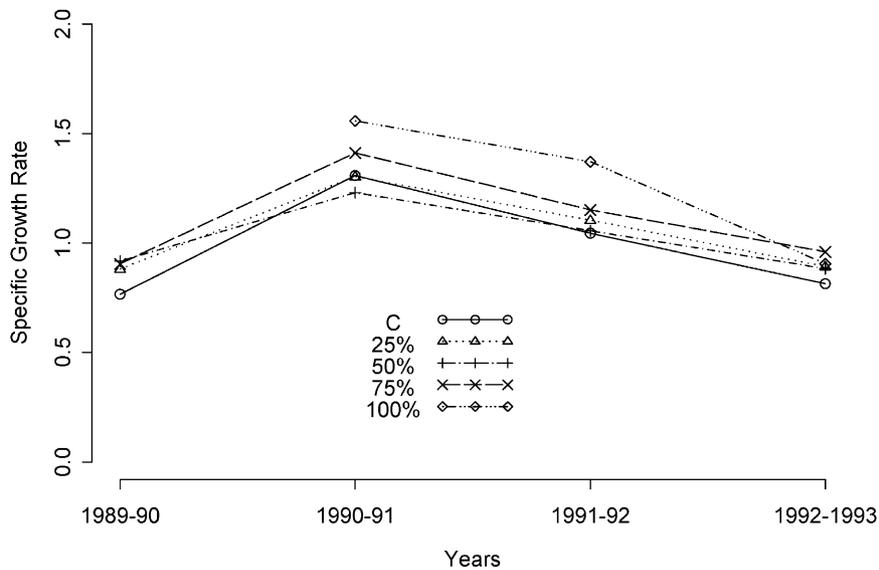


Fig. 2. Specific growth rates calculated across replicates and sites using Eq. (1). The 1989–1990 points correspond to the growth rates from the harvest levels in 1989 to the 1990 census. A growth rate for the 100% removal treatment could not be calculated in 1989–1990 as this would mean dividing by 0 [see Eq. (1)] in text.

Table 2
ANOVA table of a linear model fit to specific growth rates (square root transformed) for summed leaf widths calculated for all replicates and years using Eq. (1) in the text

Term	Numerator df	Denominator df	F-value	P-value
Treatment	4	163	4.74	0.001
Year	3	163	30.4	<0.0001

observed in a sample of 14 (since there were 14 field observations) contained all 14 observed data points, indicating that the results from our simple model were not significantly different from the observed growth rates.

4. Discussion

Our projected growth rates from 1993 to 1997 were similar to the observed growth rates at Site EL (Fig. 5). The 95% confidence interval from the bootstrapped simulation on the minimum and maximum growth rates

A sustainable harvest is one in which plant products can be harvested indefinitely from a limited area with little impact to the populations being harvested (Peters, 1996). We found that even a single 25% experimental

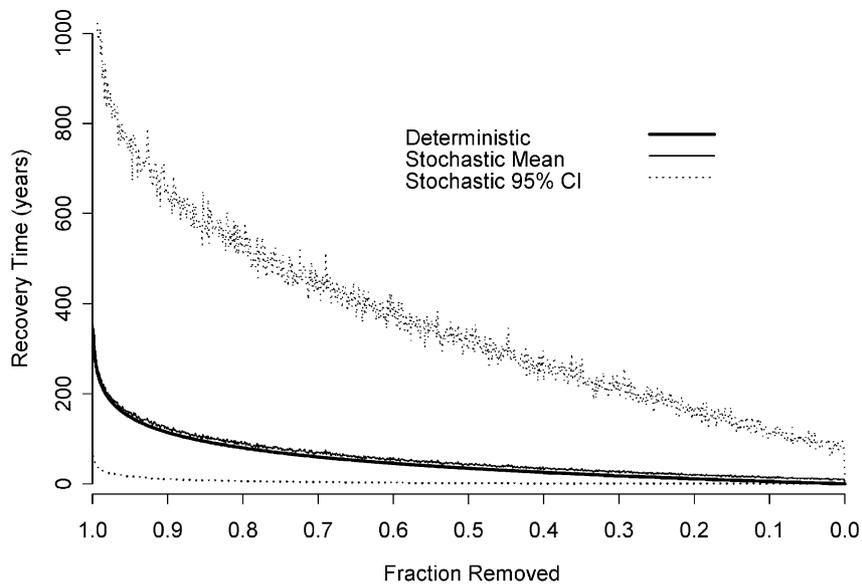


Fig. 3. Time to recovery (e.g. return to pre-harvest total leaf width) as a function of harvest intensity. The solid curve shows the deterministic estimate from Eq. (4) assuming a single, fixed specific growth rate each year [estimated using Eq. (5)]. The stochastic estimates were obtained from 5000 simulations using re-sampled specific growth rates.

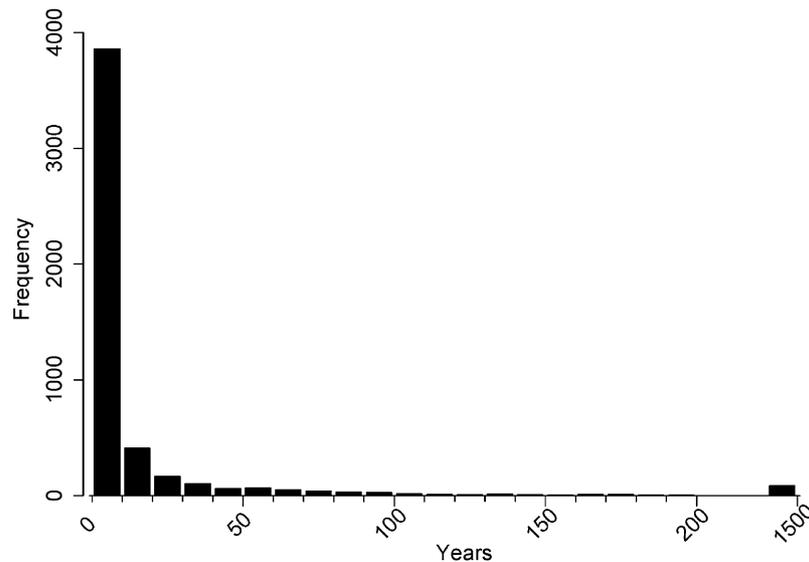


Fig. 4. Simulated distribution of recovery time to pre-harvest total leaf width following a 20% harvest. Recovery times were obtained from 5000 simulations using re-sampled specific growth rates.

harvest was detrimental to populations of *A. tricoccum* at its southern range limit as our plant populations did not recover from this level of harvesting in the 4 years of our study. A simple population model based on our data projected the mean recovery time from a 25% harvest to be approximately 22 years. Our results are consistent with Nault and Gagnon (1993) who predicted that a 10–15% harvest was detrimental to northern populations of *A. tricoccum*. Together these studies clearly indicate that at the northern and southern range limits, harvesting is not sustainable except at very modest levels. There is virtually no information on populations in the interior

of these range limits with which to assess harvesting impacts.

We found that the magnitude of spatial variability in population parameters (e.g. summed leaf widths) across sites was similar to temporal variability across years, but both of these sources of variability were smaller than the treatment effects. Nevertheless, inclusion of this added variability into projections of population recovery substantially increased the uncertainty in time to population recovery (Fig. 3) and emphasizes the need for studies that span across sites and years. The year and treatment effects on specific growth rates also suggest

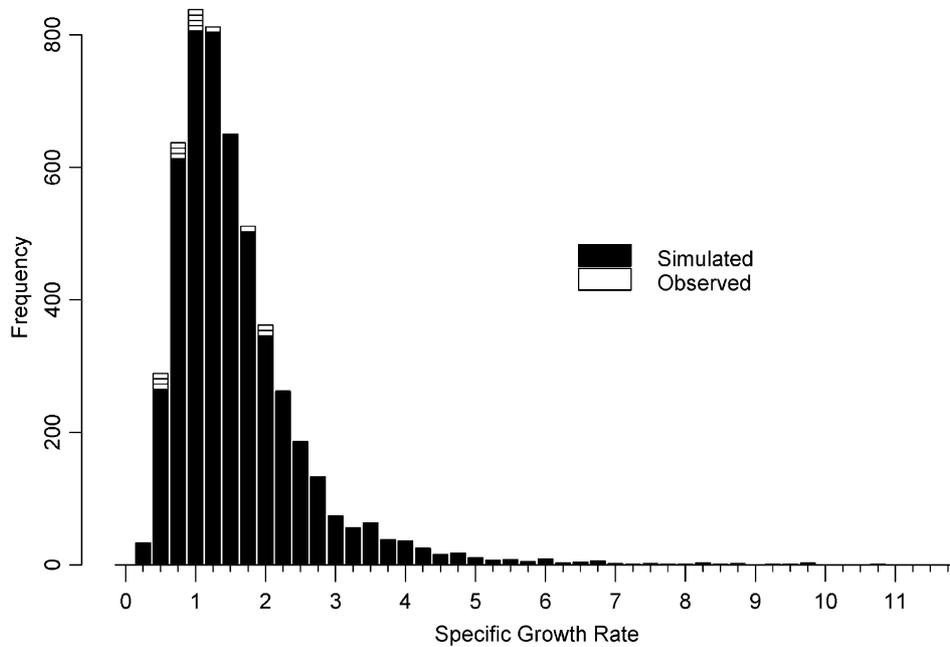


Fig. 5. Projected specific growth rates over the 4 years from 1993 to 1997 compared to observed growth rates for Site EL. Simulated specific growth rates of total leaf width over 4 years were obtained by re-sampling specific growth rates from site EL. Each unfilled bar indicates one observed 4-year specific growth rate for a total of 14 data points shown.

that population recovery may be density dependent. Higher specific growth rates occurred following higher levels of harvesting, and specific growth rates declined as recovery proceeded.

Our results on time to population recovery should be viewed as conservative because harvesting occurred only once in a 5-year period. Actual harvesting of *A. tricoctum* populations is not restricted to a one-time harvest. Anecdotal evidence in Great Smoky Mountains National Park suggests repeated harvesting in a given location over a number of years until the population is depleted. *A. tricoctum* populations in Canada have declined to extinction due to over-harvesting (Nantel et al., 1996). Based on our results, the sustainable harvest level of a local population, e.g., the plants at a particular site, of *A. tricoctum* near the southern limit of distribution is 10% or less once every 10 years. This ensures an approximately 85% probability that the population would recover by the next harvest. This is not equivalent to a complete harvest of 10% of the sites every 10 years, which would lead, on average, to overall population decline.

In our study, we removed plants of all sizes but in reality, harvesters of *A. tricoctum* are more likely to collect larger plants. This may leave few plants to propagate through bulb division, which is the predominate mode of population growth for *A. tricoctum* (Nault and Gagnon, 1993). Differential selection of only larger plants will likely have a more negative impact on population recovery than collection of plants of all sizes, even if the same total biomass is removed (Nantel et al.,

1996). In addition to directly testing the impact of harvest levels in the middle portion of *A. tricoctum*'s range, we also recommend studies to test the effect of differential size selection during harvesting on population recovery.

Finally, we recommend improved monitoring of harvests and greater enforcement of harvest limits. In southern Appalachian national forests, for example, a collection permit is not required for harvesting of *A. tricoctum* if collection is for personal consumption under one-half bushel. We suggest that permits be required even in these circumstances and that there be greater enforcement of collection limits. This is called for since low levels of harvesting can have long lasting impacts on *A. tricoctum* populations.

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