Variable effects of timber harvest on the survival, growth, and reproduction of American ginseng (*Panax quinquefolius* L.)

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A B S T R A C T

Timber harvest is a recurrent, widespread canopy disturbance that has long-affected the eastern deciduous forest. Multi-dimensional shifts in forest dynamics occur following timbering, and while a great deal of research on tree response to timbering has been performed, far less focus has been placed on herbaceous understory response to timbering. American ginseng (*Panax quinquefolius* L.) is a long-lived, economically valuable medicinal herb believed to be adapted to the dynamic light conditions of old-growth forests. The purpose of this study was to determine if timber harvests of varying intensity had positive, neutral, or negative effects on the survival, growth, and reproduction of wild American ginseng. Hemispherical images were used to calculate the canopy openness above ginseng plants. Population census data were used to obtain measurements of survival, relative growth rate, seed production, seed production efficiency, and new seedling emergence. Changes in survival and seed production in response to timbering were analyzed using log-likelihood analyses, and the responses of relative growth rate and seed production efficiency to timbering were analyzed using nested two-way ANOVAs. Initial ginseng survival varied among sites, with lowest survival at the more intensely timbered site. Additionally, long-term survival decreased following timbering. Relative growth rate of individuals increased following timbering in both short-term and long-term analyses, with relative growth rate being greatest at sites where more tree biomass was removed. While seed production decreased the year directly following timbering, seed production increased over the three years after timbering. Both short-term and long-term effects of timbering on seed production efficiency differed among populations. While seed production increases in the years after timbering, this stimulation may not be realized due to sub-optimal germination conditions. Due both to decreases in survival following timbering and the unlikely continued increases in growth and seed production as the canopy fills in, some of these often-used timbering strategies negatively impact ginseng performance. Silvicultural strategies that mimic old-growth forest structure may be better suited for the conservation of ginseng and other similar obligate understory species.

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1. Introduction

Modern forests are the products of ecological succession that occurs after natural and anthropogenic disturbance events (Oliver, 1981; Clebsch and Busing, 1989; Seymour and Hunter, 1999). Timber harvest is a common anthropogenic disturbance that is particularly important because of its ongoing, cyclical nature and its direct effects on forest canopy structure. A great deal of research has focused on canopy disturbances created by timber harvest (Hammond et al., 1998; Fredericksen et al., 1999; Gilliam, 2002; Harrelson and Matlack, 2006; Belote et al., 2009, 2012). However, most research involving timbering has focused on the study of trees (Roberts, 2004; Gilliam, 2007). Less emphasis has been placed on the herbaceous understory, even though this stratum comprises over 80% of the plant diversity in the eastern deciduous forest (Roberts, 2004; Gilliam, 2007).

The light environments of many second growth, closed-canopy eastern deciduous forests are characterized by low levels of diffuse light punctuated by spatially and temporally heterogeneous patches of more intense sunlight referred to as 'sunflecks' (Chazdon and Pearcy, 1991; Fournier et al., 2004; Wagner and McGraw, 2013; Smith and Berry, 2013). Although sunflecks can contribute up to 60% of the daily photosynthesis of understory plants (Kursar and Coley, 1993; Chazdon, 1988), light is still the primary resource limiting productivity in the understory of relatively undisturbed forests (Chazdon and Pearcy, 1991; Beckage et al., 2000; Neufeld and Young, 2003; Whigham, 2004; Wagner and McGraw, 2013). However, following the creation of canopy gaps by timber harvest,

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patches of direct sunlight reaching the understory undergo marked increases in intensity, duration, and temporal and spatial heterogeneity (Sousa, 1984; Chazdon and Fetcher, 1984; Canham, 1988a, 1988b; Lawton, 1990; Roberts, 2004; Beaudet et al., 2004).

The growth and performance of understory species may initially increase with greater light availability (Chazdon and Pearcy, 1991; Fournier et al., 2004; Whigham, 2004). However, the large increases in canopy openness, light intensity, and light duration caused by timber harvest may exceed a threshold leading to negative performance of shade-tolerant herbaceous plants. Exposure to direct light can be detrimental to shade species, and may lead to high leaf temperature, increased water loss, and photoinhibition (Chazdon and Pearcy, 1991; Oláh and Masarovičová, 1997; Fournier et al., 2004).

In addition to the changes in the light environment, the physical extraction of timber following harvest also leads to dramatic changes in the herbaceous layer, the forest floor, and soil surface properties (Demir et al., 2007). Demir et al. (2007) found that the herbaceous cover decreased substantially on skid roads following timber harvest. Decreases in herbaceous cover on skid roads result from both the immediate mortality of individuals due to removal from, or burial underneath, the skid road and also from soil compaction. In a simulation that determined the effects of post-timbering light availability and soil compaction on forest herbs, Small and McCarthy (2002) found that *Osmorhiza claytonia* (Michx.), another shade-tolerant perennial species native to the eastern deciduous forest, experienced increased mortality and decreased growth when grown in high levels of light and compacted soils.

Some understory communities are resilient to timbering disturbance and canopy gap formation in terms of species composition and diversity; these communities are able to return to pre-disturbance composition eventually (Belote et al., 2012). However, resiliency of a community decreases as disturbance intensity increases (Roberts and Gilliam, 2003: Gilliam, 2007; Belote et al., 2012). Further, species that are encountered less frequently (i.e. rare species) are at greater risk of extirpation following disturbance (Belote et al., 2012). Observations of the herbaceous layer suggest that relatively short-lived pulses of energy generated by moderate canopy disturbances do not lead to sustained negative impacts or species composition shifts (Gilliam, 2002). Nevertheless, the extent to which timber harvest affects rare understory herbs is largely unknown.

American ginseng (*Panax quinquefolius* L.) is one rare herbaceous species whose densities and long-term population dynamics may be altered by timber harvest, especially if such disturbances are frequent and intense (Wagner and McGraw, 2013). Due to the high demand for its root on the Asian market, ginseng is the premier medicinal, non-timber forest product in the United States (McGraw et al., 2010, 2013). Ginseng is a widespread, long-lived perennial herb that exhibits the 'slow' life history of many understory herbs present throughout the eastern deciduous forest (McGraw et al., 2013). Historic accounts suggest that ginseng was once far more abundant than it is today; corroborating evidence includes an approximate threefold decrease in annual ginseng export from the mid 1800s to the late 1900s (Carlson, 1986; Robbins, 1998). Overharvesting of ginseng is often described as the primary cause of reduced population size (Carlson, 1986; Nantel et al., 1996; Robbins, 1998; McGraw, 2001; McGraw et al., 2010). However, extensive changes in ginseng habitat also occurred during this time period, primarily through changes in canopy structure due to timber harvest (Charron and Gagnon, 1991). The presence of wild populations of ginseng following the widespread timbering that occurred in the late 1800s and early 1900s suggest that ginseng is capable of surviving under sparse canopies. Additionally, the presence of ginseng in the closed canopy, second-growth forests common throughout eastern North

America today suggests that ginseng is capable of surviving under a dense canopy. Although ginseng may be able to survive in these two extremes of canopy structure, ginseng performance is likely to be suboptimal at either end of this disturbance spectrum.

Wagner and McGraw (2013) investigated a suite of ginseng physiological and growth characteristics in an intact second growth eastern deciduous forest, and they hypothesized that ginseng is pre-adapted to the dynamic light environments of old growth forests (Wagner and McGraw, 2013); forests characterized by an overstory that varies in age, size, and species composition, and by temporally and spatially heterogeneous canopy gap formations and closures (Knohl et al., 2003; Spies et al., 2006; Manabe et al., 2009; Wagner and McGraw, 2013). Although some aspects of American ginseng performance may benefit from smaller inputs of light energy from sunflecks (Wagner and McGraw, 2013), the effects of sudden, large canopy openings caused by timber harvest are unknown.

While research has been conducted to determine how different types of disturbances affect populations of American ginseng (McGraw and Furedi, 2005; Van der Voort and McGraw, 2006; Mooney and McGraw, 2009; Souther and McGraw, 2011), it is important to understand how an anthropogenic disturbance type such as timber harvest affects a full suite of ginseng performance metrics so that sustainable, economically-viable forest management strategies can be developed. The purpose of this study was to determine if timber harvest events typical of the eastern deciduous forest negatively affect the survival, growth, and reproduction of wild American ginseng. Based on the research performed by Wagner and McGraw (2013), which suggested that increased energy from sunflecks enhances the performance of ginseng, and based on observations of ginseng performance following canopy disturbance of varying intensities, we hypothesized that: (1) ginseng survival and performance would vary depending on timber harvest intensity; and (2) initial rates of ginseng survival following timber harvest would decrease, but the growth and reproduction of the individuals that did survive would increase.

2. Materials and methods

2.1. Study sites

Five study sites containing wild populations of American ginseng were located within the Appalachian region of the eastern deciduous forest. The timber on each of these second growth forest sites was cut during the study period, however due to the opportunistic nature of this type of work, sites differed in the type of timber harvest implemented, and in the date of the timber harvest (Fig. 1).

Specific site locations and names are sensitive due to the economic and conservation values of American ginseng, therefore site identifiers have been replaced with generic labels. The first site (CAB) was located within a state forest in southern West Virginia. The timber at CAB was removed using a 12″ (30.5 cm) diameter limit harvest, and was performed in Winter 2011–2012. The second site (LAW) was located on privately owned land in southwestern Virginia. The timber on this site was also extracted in Winter 2011–2012 using a selection cut where the majority of valuable trees were extracted. The third research site (WY) is privately owned, and is also located in southwestern Virginia. The timber at WY was extracted using a selection cut, and like the previous two sites, cutting occurred in Winter 2011–2012. The remaining two research sites (F27 and F18) were located at higher elevation in central West Virginia. The timber at F27 was removed using an 18″ (45.7 cm) diameter limit cut in Fall 2012, while the timber on F18 was removed using a patch clearcut in Fall 2013. These five sites varied in land-use history, aspect, elevation, and slope (Fig. 1).

Site Characteristics				Year				
Population	Initial N	Aspect	Mean Slope	Elev. (m)	Pre-2011	2011	2012	2013	2014

Site characteristics / Year grid (Fig. 1)

Population	Initial N	Aspect	Mean Slope	Elev. (m)	Pre-2011	2011	2012	2013	2014
CAB	84	0°	9.5°	373		LA $\xrightarrow{RGR_{bc}}$ SP	LA $\xrightarrow{RGR_{ac1}}$ SP HP	LA $\xrightarrow{RGR_{ac2}}$ SP HP	LA SP HP
LAW	291	300°	16.2°	663	LA $\xrightarrow{RGR_{bc}}$ SP	LA $\xrightarrow{RGR_{bc}}$ SP	LA $\xrightarrow{RGR_{ac1}}$ SP HP	LA $\xrightarrow{RGR_{ac2}}$ SP HP	LA SP HP
WY	38	280°	28°	908	LA $\xrightarrow{RGR_{bc}}$ SP	LA $\xrightarrow{RGR_{bc}}$ SP	LA $\xrightarrow{RGR_{ac1}}$ SP HP	LA $\xrightarrow{RGR_{ac2}}$ SP HP	LA SP
F27	80	168°	16°	689			LA $\xrightarrow{RGR_{bc}}$ SP HP	LA $\xrightarrow{RGR_{ac1}}$ SP HP	LA SP HP
F18	33	355°	7.7°	841				LA $\xrightarrow{RGR_{bc}}$ SP HP	LA SP HP

Fig. 1. Characteristics of each population are listed on the left, including initial population size (growing season prior to timber harvest). For each population, a jagged vertical line indicates the timing of the timber harvest. Remaining symbols indicate recorded data. LA represents leaf area, SP represents seed production, HP represents the collection of hemispherical photographs, and RGR_x represents the calculation of relative growth rate. RGR_{bc} represents the RGR prior to the cut, RGR_{ac1} represents the RGR one year after the cut, and RGR_{ac2} represents RGR two years following the cut. F18 was excluded from pre- vs. post-cut analyses of survival and RGR due to the late date of cutting, however some variables could be included for this population, effectively increasing replication, so it is included in those analyses. Likewise, WY, F27, and F18 were excluded from some measures of reproduction due to small sample size and/or late date of cutting, however data from these populations were included for more short-term analyses.

Nevertheless, the geographic spread and abiotic and biotic characteristics of these sites are representative of many wild American ginseng populations.

Three of the sites used in this study (CAB, F27, F18) were selected based upon anticipated timber harvest and based on the presence of wild ginseng within the stand. Ginseng census data on these sites were collected in the year prior to and the years following each respective timber harvest. While the timber on two of the sites (LAW and WY) was harvested without our prior knowledge, these were sites having a long history of annual ginseng censusing (up to 13 years), allowing for a unique opportunity to observe the long-term effects of canopy disturbance on ginseng plants.

2.2. Canopy environment

Hemispherical images were used to quantify changes in canopy structure following timber harvest. When observing canopy openings in this study, the canopy we are referencing is the canopy above a typical-sized ginseng plant. As such, it is important to note that our definition of canopy refers to the understory, mid-story, and tree canopy. For each population, hemispherical photographs were taken on overcast days using a digital camera (Canon EOS Rebel T2i) with a 180-degree fisheye lens (Sigma 4.5 mm F2.8 EX DC). The camera was situated pointing vertically upward on a tripod ca. 20 cm above the ground, the height of a typical adult ginseng plant. Images were taken directly above each individual ginseng plant in the population or if individuals were tightly clustered, at the center of the cluster. Images were then analyzed using Gap Light Analyzer (GLA) software (Frazer et al., 1999). Specific site characteristics (slope, aspect, and geographic location) as well as North American averages of solar constant, cloudiness index, beam fraction, and clear-sky transmission coefficient were used to parameterize the GLA program. Gap Light Analyzer processes hemispherical images by partitioning pixels into "sky" and "non-sky" categories, and then calculating the distribution of sky brightness based on these pixel categories (Fournier et al., 2004), yielding an estimate of percent canopy openness.

2.3. Census

Ginseng plants were labeled using a subterranean tag so that each individual could be unequivocally identified each census year. For each population, census data were collected twice annually; once in the spring and once in the fall. Data collected on each individual included the presence or absence of the individual, the number of leaves, leaflet arrangement (typically 3–7 leaflets per leaf), stem height (cm), leaflet lengths (cm), leaflet widths (cm), reproductive status (Reproductive: Y/N), and number of seeds.

Survival was determined yearly for every individual in each population. Two criteria were used to establish death of an individual: (1) new seedlings were considered dead if they did not re-emerge one growing season after their initial emergence; (2) all other individuals were considered dead if they did not emerge for two consecutive growing seasons. The waiting period was necessary because if plant tops are damaged, the plant may re-emerge one year later after being dormant for a growing season.

The leaf area of each individual was calculated using a previously established regression equation based on the allometric relationship of leaf area to leaflet width and leaflet length (Souther and McGraw, 2011; Wagner and McGraw, 2013). Relative growth rate (RGR_{LA}), the change in leaf area of an individual over time, was calculated based on the changes in total leaf area from year-to-year using the formula:

$$RGR_{LA} = \frac{(lnLA_2 - lnLA_1)}{(t_2 - t_1)}$$

Leaf area of a ginseng plant in the given year is determined by nutrient acquisition and carbon storage of the year prior. Therefore, the effects of a dormant-season timber harvest event on ginseng leaf area would not be evident in the first growing season directly following the cut, but rather in the second. Because of this, we included the year in which the cut occurred as a 'before cut' year when making RGR comparisons.

To assess reproduction, we determined whether each individual produced seeds and counted the total number of seeds at the fall

census. In addition, we measured seed production efficiency; the number of seeds produced by an individual per unit leaf area. Total plant leaf area is related to total seed production (Schlessman, 1985), but efficiency may also be affected by changes in light level, and subsequent changes in internal resource availability.

2.4. Analyses

2.4.1. Canopy openings

Since the intensity of cutting varied among populations, the canopy openness above ginseng plants was estimated for the year before and the years following timber harvest to quantify the overstory change due to timber harvest. For two sites in which the timing of the cut was known in advance (F27 and F18), canopy characteristics were characterized both prior to and following timber harvest. However, at three sites (CAB, LAW, WY) images were not captured prior to timber harvest because harvest implementation was not known in advance (Fig. 1). For CAB and LAW, a forested reference site was located ca. 100 m from the original site to compare the cut site to an uncut reference. No reference site with similar aspect and slope was available for WY, and thus WY was removed from this analysis.

2.4.2. Survival

To determine whether survival prior to cutting differed from survival after cutting (three-year survival prior, compared to two-year survival after cutting), a loglikelihood analysis was performed. Two populations (LAW and WY) were used in this analysis because of available pre-cutting long-term census data.

To determine whether survival in the first year following timber harvest (AC_1) differed among populations (LAW, F27, WY, and CAB), a loglikelihood analysis was performed. Each of these populations experienced a unique silvicultural treatment, and while there were other differences among the sites, the magnitude of the differences in logging practices was very likely a contributing factor to survival differences.

2.4.3. Relative growth rate (RGR)

To determine if the shift in relative growth rate caused by cutting (one year before vs. one year after timbering) differed among four populations (LAW, WY, CAB F27), a two-way nested ANOVA was performed with population and time-relative-to-timbering as the main effects, and individual nested within population. The main effect of time-relative-to-timbering (BC vs. AC_1) was the primary term of interest in the model.

We then wanted to determine if relative growth rate prior to cutting differed from relative growth rate after cutting (three years before vs. two years after timbering) on two sites for which we had long-term growth data (LAW and WY). For each individual, the natural log of leaf area was regressed over the year, and the overall RGR for the time periods before timbering and after timbering was calculated as the slope of the line. A two-way nested ANOVA was performed with population and time-relative-to-timbering (three years before timbering vs. two years after timbering) as the main effects and individual nested within population. As with the previous analysis, time-relative-to-timbering was the variable of interest.

2.4.4. Seed production, seed production efficiency (SPE), and new seedling emergence

To determine if the proportion of flowering individuals producing seeds differed the year prior to and the year after timber harvest, a log-likelihood analysis was performed using all five populations (Fig. 1). A second log-likelihood analysis was performed comparing the proportion of flowering individuals producing seeds at CAB and LAW the year before timbering (BC) and three

years after timbering (AC_1, AC_2, and AC_3) to determine if seed production varied for multiple years after a timbering event

Using only individuals that produced seeds, a two-way nested ANOVA was performed to determine if there were short-term (the two years surrounding the timbering event) differences in the seed production efficiency, and if so, if this effect differed among populations. The LAW, F27, F18, and CAB populations were used in this study. A Tukey–Kramer HSD post hoc test was used to determine differences in means.

A second analysis of seed production efficiency took advantage of the early cutting date in two of the populations (CAB and LAW) to determine if there was a difference in seed production efficiency over multiple pre- and post-cut years (one year prior to cut and three years after cut), and if so, if this effect differed between populations. A two-way nested ANOVA was performed with time-relative-to-timbering and population as main effects, and individual was nested within population.

In order to determine if new seedling emergence was affected by timber harvest and to separately determine if new seedling emergence depended upon population, a 2-way ANOVA without replication was performed with time period (before cut and after cut) and population as the main effects. A Tukey–Kramer HSD post hoc test was used to determine differences in means.

3. Results

3.1. Canopy openings

As expected, pre-cut/reference canopy openness above ginseng plants was lower than all years following timbering for each population (Fig. 2), and patterns in canopy openness varied among populations. At CAB, which had a 12″ (30.5 cm) diameter limit cut, canopy openness above ginseng plants increased by 81% in the season following timbering relative to the reference, but decreased the two years following. A similar pattern was observed at F27, which had an 18″ (45.7 cm) diameter limit cut. In the first year after the cut at F27, canopy openness increased 133% relative to pre-cut, however, the absolute canopy openness (21%) was still the lowest of any population in the year after the cut. In the first year after timbering, the canopy at LAW (selection cut) was only opened up by 10% relative to the reference, but remained open in the years following timbering, likely due to additional cuts that were occurring in the vicinity. The canopy above ginseng plants at F18 (patch clearcut) was opened by 112% following timbering, leading to a ginseng canopy that was more open than all other populations (36%), but the late cut date on F18 precluded additional canopy analyses.

3.2. Survival

The effect of timbering on survival did not differ between populations (LAW and WY); $\chi^2_{\text{time-relative-to-cut} \times \text{population}} = 2.75$, $p = 0.6011$). However, for both populations survival did decrease in the two years after timber harvest (Fig. 3; $\chi^2_{\text{time-relative-to-cut}} = 15.47$, $p = 0.0038$) with the probability of survival decreasing from ca. 90% the year before cut to ca. 75% two years after cut.

The proportion of individuals surviving the first year following timber harvest (AC_1) differed among populations (Fig. 4; $\chi^2_{\text{population}} = 41.138$, $p < 0.0001$). The lowest post-cut survival was from CAB, one of the populations that incurred the most intense timber harvest. In fact, the proportion of individuals surviving one year after timbering at CAB was ca. half that of all other populations.

3.3. Relative growth rate (RGR)

Among individuals present both one year before and one year after timber harvest, there was a marked increase in RGR after
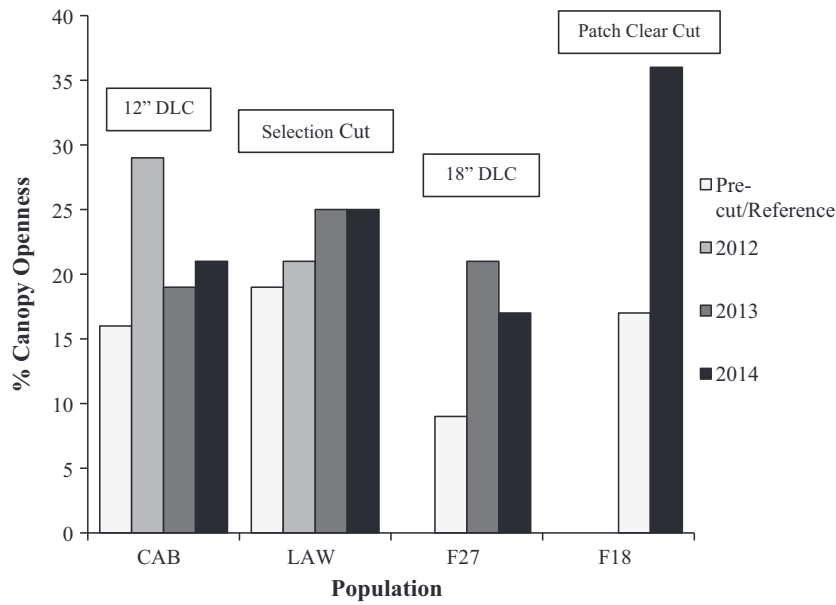
Fig. 2. Canopy openness as measured by hemispherical images taken above the American ginseng plants at four populations: CAB [12″ (30.5 cm) diameter limit cut], F27 [18″ (45.7 cm) diameter limit cut], LAW (selection cut), and F18 (patch clearcut).
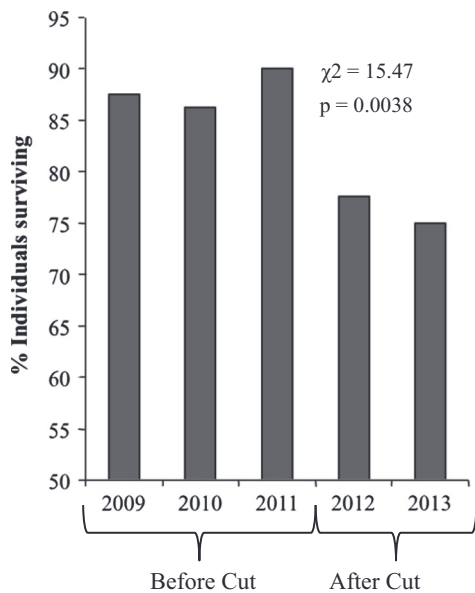

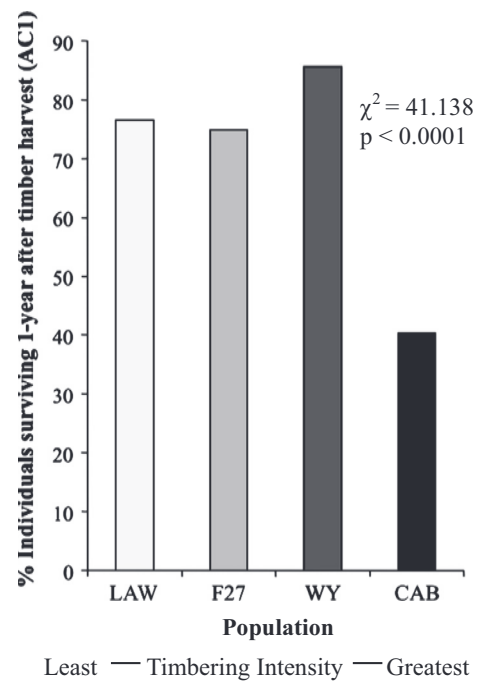**Fig. 3.** The proportion of individuals surviving in two of the long-term ginseng populations (LAW and WY).

Fig. 4. The proportion of individuals surviving the first year after timber harvest at four ginseng populations.

timbering (Fig. 5a; F_{cut} = 60.02, $p < 0.0001$). Additionally, as with the proportion of individuals surviving one year after timber harvest, mean RGR varied among populations (Fig. 5b; $F_{population}$ = 9.19, $p < 0.0001$). Nevertheless, the effect of timber harvest on RGR did not depend on the population from which the ginseng plants originated ($F_{cut \times population}$ = 0.59, $p = 0.6252$).

In accordance with the increase in short-term RGR following timber harvest, the long-term RGR of individuals from the LAW and WY populations also depended on the time period relative to timber harvest (Fig. 5c; $F_{time-relative-to-cut}$ = 11.69, $p = 0.0011$). Mean relative growth rate of individuals was over three times greater in the two years following timber harvest as it was in the three years prior to timber harvest.

3.4. Seed production, seed production efficiency (SPE), and new seedling emergence

Among all five populations, the proportion of flowering individuals that produced seeds decreased the year after timber harvest (χ^2_{cut} = 10.917, $p = 0.0010$). Approximately 50% of all flowering plants present in the populations one year before timbering produced seeds, while only 33% of flowering plants produced seeds the year following timber harvest. In the separate, long-term analysis of seed production at two populations (CAB and LAW), the proportion of flowering individuals producing seeds was dependent
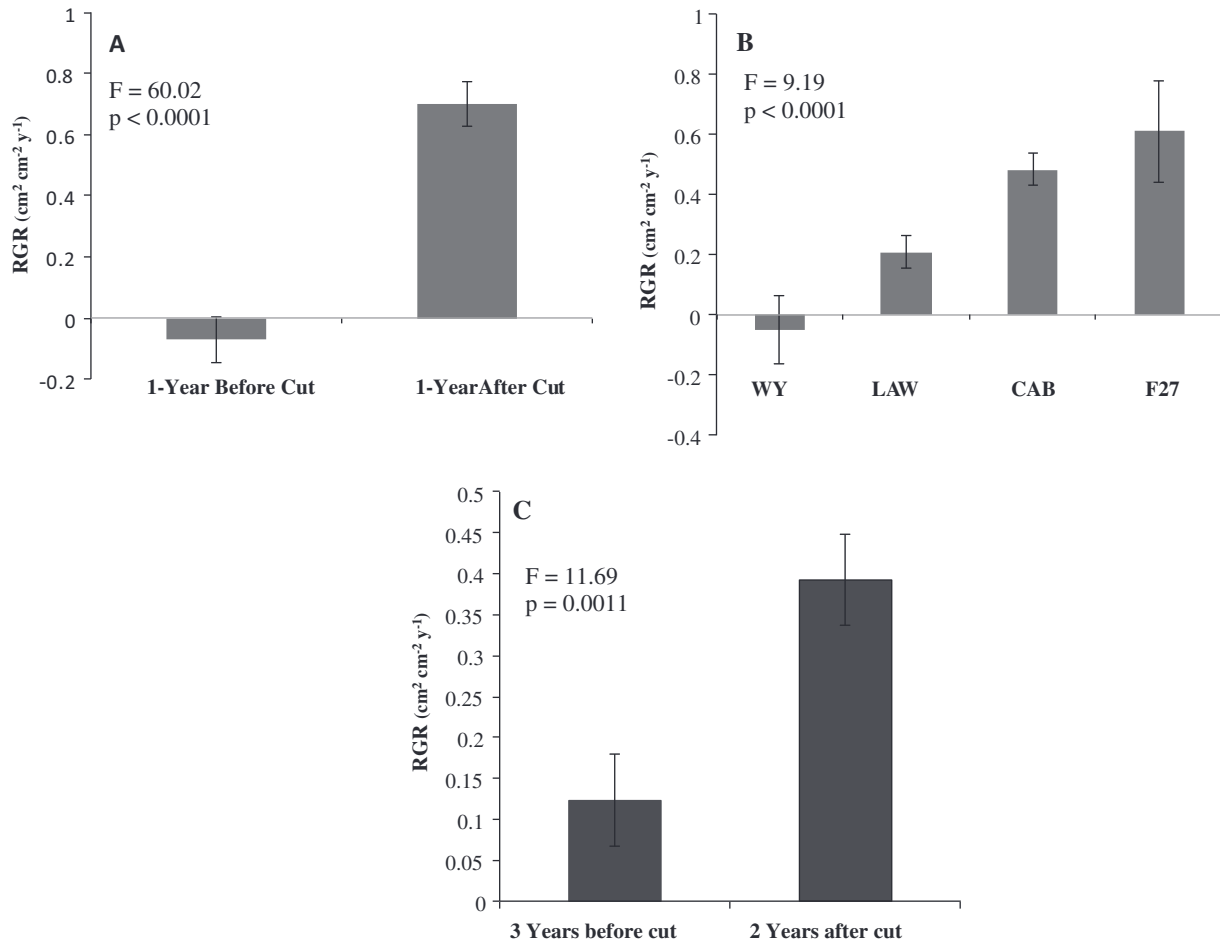
Fig. 5. (A) Relative growth rate (RGR) of individuals present both one year before and one year after the timber harvest at four populations (WY, LAW, CAB, and F27) (B) Relative growth rate of individuals in four populations, independent of the timbering events. (C) Relative growth rate three years before cut and two years after cut at two long-term populations (LAW and WY).

on the year relative to timber harvest (Fig. 6; $\chi^2_{\text{year-relative-to-cut}}$ = 38.216, $p < 0.0001$). Similar to the result obtained in the previous short-term analysis of SPE, the proportion of flowering individuals producing seeds declined the year following timber harvest in these long-term populations. However, the proportion of flowering individuals producing seeds increased each year following, and three years after timbering, the proportion of individuals producing seeds surpassed the pre-timbering value.

The short-term effect of timber harvest (one year before and one year after) on seed production efficiency depended upon the population (Fig. 7A; $F_{\text{cut} \times \text{population}}$ = 4.6924, $p = 0.0051$). The SPE at two of the populations (F27 and CAB) increased markedly the year following timber harvest, while SPE at LAW and F18 remained unchanged. Likewise, the long-term analysis of seed production efficiency in the CAB and LAW populations showed a differential effect of time-relative-to-timbering and population on seed production efficiency (Fig. 7B; $F_{\text{time-relative-to-cut} \times \text{population}}$ = 3.5543, $p = 0.0159$). The seed production efficiency (SPE) at CAB increased by ca. 40% the first year after timber harvest (AC_1) and decreased to pre-timbering SPE rates by the third year after timber harvest (AC_3). Meanwhile, no change in SPE was seen in the LAW population in any of the years following timbering.

Among all populations, new seedling emergence was reduced by ca. 70% following timbering events ($F = 5.92$, $p = 0.0333$). In addition, populations differed in seedling emergence rates ($F = 6.96$, $p = 0.0048$) with the greatest number of new seedling emergence occurring at LAW, and the least at WY.
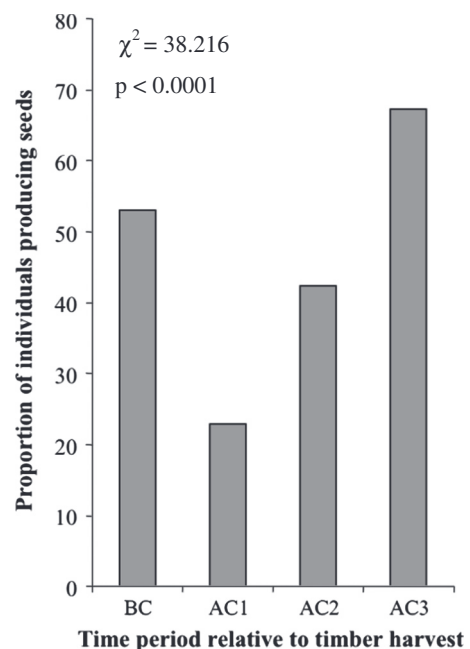

Fig. 6. The proportion of individuals that produced seeds each year relative to timbering at two of the long-term populations (CAB and LAW).
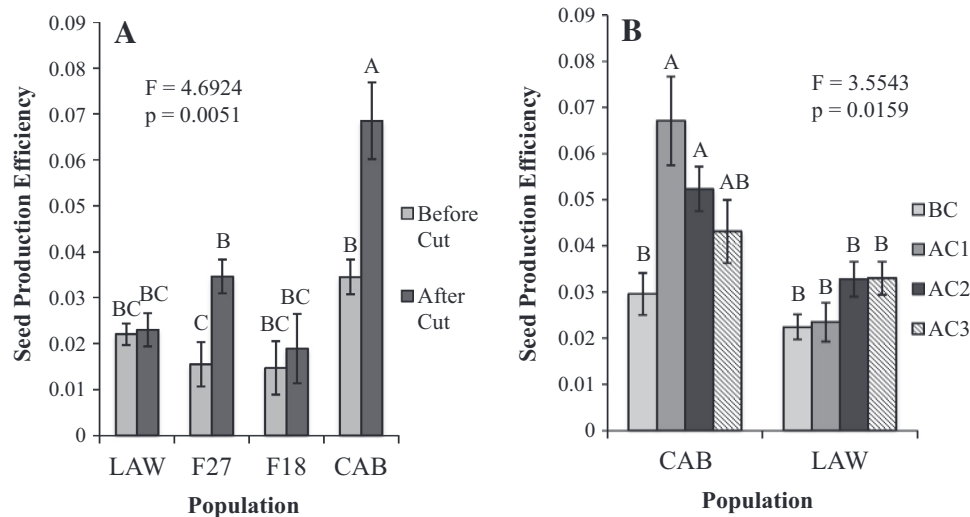
Fig. 7. (A) Short-term differential effects of timber harvest and population on seed production efficiency. (B) Long-term differential effects of timber harvest and population on seed production efficiency (BC – before cut, AC_1 – one year after cut, AC_2 – two years after cut, AC_3 – three years after cut).

4. Discussion

In the absence of disturbance, American ginseng survival rates tend to be high (Charron and Gagnon, 1991). In fact, a separate study showed that the average survival probability of juvenile and adult ginseng plants in twelve undisturbed ginseng populations was 87% (data taken from Souther and McGraw, 2011). In the present study, the average proportion of individuals surviving in all populations was only 69% the year after timbering, and 76% two years after timbering in two of the long-term populations (LAW and WY). These results indicate that, in general, timber harvest negatively impacts survival of American ginseng. Additionally, the amount of canopy removed and mode of timber extraction impacts ginseng survival with survival being lower at highly disturbed sites.

Based on field observations, the disturbance to the forest floor that resulted from timber harvest led to significant mortality in places where the soil profile was destroyed or compacted by equipment. Skid roads that are placed on cut sites to facilitate movement of timber result in the displacement and compaction of soil, and Demir et al. (2007) noted a reduction in herbaceous cover on skid roads. Furthermore, forest floor damage and the resulting plant mortality can occur simply by moving the timber across the ground during extraction, especially if the harvest is performed during a time period when the soil profile is easily disturbed (i.e. when soil is not frozen). Mortality of entire ginseng clusters within populations due to soil disturbance was observed on multiple sites throughout this study.

The relative growth rate of surviving ginseng plants increased markedly in the years following timber harvest, and this increase was likely due to the sudden increase in light availability once the canopy was opened. Greater canopy openness would stimulate photosynthesis, leading to greater carbon storage and overall increases in leaf area the following year (Wagner and McGraw, 2013), although tests to support this mechanism were not performed. Though increases in light are beneficial to plant growth to some critical level, Oláh and Masarovićová (1997) determined that long-duration sunflecks lead to photoinhibition in some plant species. In the present study, observations of thickened leaves and chlorosis following timber harvest indicate that the ginseng plants were stressed, but the continued increases in relative growth rate two years following timber harvest suggest that net carbon assimilation across a growing season was not reduced. Wagner

and McGraw (2013) found that ginseng growth rate increased with increases in both the percent photosynthetic photon flux density from sunflecks and the duration of the longest sunfleck. The results of the present study support these earlier findings (Wagner and McGraw, 2013), and suggest that ginseng growth is stimulated by increases in light caused by canopy openings. However, it is important to note that other changes in ginseng habitat following timbering, such as nutrient availability and soil moisture, could have also affected ginseng performance.

Although ginseng mortality can be high following timbering, subsequent increases in incident photosynthetically active radiation and leaf area may lead to positive gains in the belowground portion of the surviving ginseng plants. Anecdotal evidence obtained from ginseng harvesters suggests that in the years following timbering, occasionally very large plants may be found a few years after heaving cutting. Such increases in root size could be economically beneficial since roots are sold by weight. However, it is unclear whether the increase in root mass of the surviving portion of ginseng plants is enough to offset losses due to mortality.

Initial observed decreases in ginseng seed production were likely caused by desiccation of ginseng inflorescences (flowering clusters) due to the higher light, lower humidity, and higher temperatures at the forest floor in the first growing season following timbering. The leaf area of ginseng increased following timber harvest, and although not observed in the first growing season after timbering, increases in seed production probability eventually followed suit, as was expected with increased plant size (Schlessman, 1985).

While in some cases the seed production efficiency increased after timbering, the increases were population dependent, and were not long-lived. We propose that the increases in seed production efficiency at CAB and not at LAW can be explained at least in part by the fact that far more tree biomass was removed from CAB. As a result, the biological demand for nitrogen decreased and decomposition likely increased (as reviewed by Roberts and Gilliam, 1995), leading to a larger pulse of nitrogen available for uptake by other plants at CAB.

Although canopy removal is stimulating seed production and in some cases seed production efficiency, the effects of this stimulation may not be realized due to low seed germination rates. While germination rates were not directly accounted for in this study, it was found that new seedling emergence decreased significantly following timber harvest. Wagner and McGraw (2013) found that

ginseng seed germination had a negative linear relationship to both sunfleck duration and % PPFD from sunflecks. The inverse relationship of seed germination and light was attributed to two possible, yet contradictory, causes. First, growth of other plants in the area was being stimulated by sunflecks, and these plants were overtopping ginseng seeds, leading to light levels too low to induce germination (Wagner and McGraw, 2013). Second, seeds present in areas of high sunfleck activity were desiccating due to higher incident light (Wagner and McGraw, 2013). In the present study, increases in herb- and shrub-layer cover and desiccation of seeds was observed following timbering. Moreover, American ginseng seed banks are not long-lived (Charron and Gagnon, 1991; Cruse-Sanders and Hamrick, 2004). As a result, we do not expect that the majority of seeds in the seed bank will be viable long enough to make a large contribution to population size once germination conditions improve.

In their study of short-term understory response to timbering, Fredericksen et al. (1999) determined that increases in ground- and shrub-layer cover occur following timbering, and that the cover of these strata increase with increasing timber harvest intensity. Our results that quantify the mean changes in canopy openness above ginseng plants in the years before and after timbering support the findings of Fredericksen et al. (1999) in that the ground- and shrub-layer canopies at the intensely harvested CAB population filled in more densely in the years following timbering than the less intensely-cut sites (LAW and F27). As the ground- and shrub-layers begin filling in after a timbering event, ginseng plants and other similar herbaceous species will be overtopped and heavily shaded, and it is possible that growth and seed production may decline as a result. Therefore it is doubtful that the stimulation of growth and reproduction caused by timbering will persist for a long period of time following a timbering event.

Studies have found that short-term understory diversity is typically not affected by timber harvest (Fredericksen et al., 1999; Belote et al., 2012; Duguid and Ashton, 2013), but may be affected by site-specific characteristics such as resource availability and heterogeneity (Fredericksen et al., 1999; Duguid and Ashton, 2013). While richness and diversity of forests can remain unchanged following timber harvest, this maintenance may be the result of influxes and/or increases in ruderal species rather than the retention of the mid- to late-successional species that were originally on the site (Meier et al., 1995; Small and McCarthy, 2002; Duguid and Ashton, 2013). As a result, biodiversity measures that do not make distinctions about the nature of diversity (i.e. early successional species vs. late successional species) do not accurately account for the retention of rare species like American ginseng and other similar herbs following timber harvest. The site-specific nature of herbaceous response to timber harvest makes in-depth studies of species' response to varying timber harvest techniques necessary (Roberts and Gilliam, 1995), and the present study provides an understanding of the fate of American ginseng following varying types (intensities) of timbering. To our knowledge, the present study is the first to examine in detail survival, growth, and reproductive responses of a single, long-lived, economically valuable herbaceous plant species to timber harvest in the eastern deciduous forest.

Chamberlain et al. (2013) determined that in eighteen states in the eastern United States, the annual revenue value of wild ginseng (ranging from $26.9 million to $43.4 million) is significantly less than the annual stumpage value of hardwood timber extracted from these same states ($1.27 billion). Nevertheless, American ginseng is an important source of supplemental income in rural Appalachia (Chamberlain et al., 2013). Additionally, the habitat of American ginseng is shared by many other herbaceous species that are harvested for their medicinal qualities such black cohosh (*Actaea racemosa* L.), bloodroot (*Sanguinaria canadensis* L.), and goldenseal (*Hydrastis canadensis* L.). All of these medicinal, herbaceous species are important both in terms of their impacts on annual income in Appalachia and on forest biodiversity (Chamberlain et al., 2013). The insights gained concerning the response of American ginseng to timber harvest translate to these similar understory herb species, and allow predictions to be made about the response of these other economically-valuable species to timbering events.

Timber harvest strategies typical of many privately owned woodlots in the eastern deciduous forest are driven primarily by the economic value of timber products. In West Virginia's recent past, for example, the majority of timber harvests were not based in silvicultural theory, but instead consisted of large-scale removals of sawtimber-size trees through diameter-limit harvesting (Fajvan et al., 1998). American ginseng is believed to be adapted to the spatial and temporally heterogeneous light environments typical of old growth forests (Wagner and McGraw, 2013). Therefore, theoretically, ginseng populations could benefit from silvicultural management techniques that minimize forest floor disturbance and mimic old-growth canopy structure. These types of timbering will perhaps be less detrimental to the initial survival of American ginseng and other similar understory herbs, and may allow for increases in growth and seed production due to spatially heterogeneous increases in light availability.

5. Conclusions

Based on the results of this study, growth of individual American ginseng plants may benefit from the formation of canopy gaps caused by timber harvest, but harvest needs to be performed in a manner that preserves the soil profile and increases the initial chances of ginseng survival. While seed production increases following timber harvest events, the germination rates may actually decrease due to the excess light availability in the understory (Wagner and McGraw, 2013), minimizing the effect of this reproductive stimulation. Some current silvicultural strategies such as single-tree selection and group selection mimic the structure of old-growth forests (Lorimer and Frelich, 1994; Goebel and Hix, 1996); environments to which American ginseng and perhaps other understory shade-species are adapted. These silvicultural strategies that mimic old growth forest structure are perhaps a good fit for land managers who have multi-dimensional goals involving continued production of valuable timber, maintenance of forest biodiversity, and conservation and stewardship of ecologically and economically valuable understory herbs such as American ginseng.

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