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A slow opportunist: physiological and growth responses of an obligate understory plant to patch cut harvesting

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Abstract Understory light environments change rapidly following timber harvest, and while many understory species utilize and benefit from the additional light, this response is not ubiquitous in shade-obligate species. I examined the effects of patch cut timber harvest on the physiology and growth of an obligate forest understory species to determine if disturbances via timber harvest are physiological stressors or whether such disturbances provide physiological benefits and growth increases in understory species. Forest canopy structure, along with photosynthesis, respiration, water use efficiency, stomatal conductance, and growth rates of American ginseng were quantified one summer before and two summers after patch cut timber harvest. Survival following timber harvest was lower than that observed at undisturbed populations; however, growth of survivors increased post-harvesting, with growth increasing as a function of canopy openness. Light response curves as well as photosynthesis and respiration rates indicated that plants were not well acclimated to higher light levels in the growing season after timber harvest, but rather to two growing seasons after harvest. Relative growth rate formed a positive linear relationship with maximum photosynthesis following timber harvest. My study suggests that ginseng is a "slow opportunist", because while it benefits from sudden light increases, acclimation lags at least one growing season

behind canopy changes. American ginseng is surprisingly resilient in the face of a discrete environmental shift and may benefit from forest management strategies that mimic the natural disturbance regimes common in mature forests throughout its range.

Introduction

The understory light environments of undisturbed deciduous forests are spatially and temporally heterogeneous, and are characterized by low levels of diffuse light interspersed with patches of direct light known as sunflecks (Chazdon and Pearcy 1991; Canham et al. 1994; Small and McCarthy 2002; Fournier et al. 2004; Smith and Berry 2013). Sunflecks contribute up to 80% of total photon flux density in some temperate forests, and contribute significantly to photosynthesis and carbon storage in understory plants (Horton and Neufeld 1998; Neufeld and Young 2014). Nevertheless, light remains one of the primary limiting resources in second growth, mixed mesophytic forests (Canham et al. 1990; Chazdon and Pearcy 1991; Beckage et al. 2000; Small and McCarthy 2002; Whigham 2004; Neufeld and Young 2014).

Understory light environments change rapidly following canopy disturbance. The potentially intense, yet transient sunflecks common in undisturbed forest understories become much more intense and longer lasting. Correlated with this are increases in forest floor air and soil temperatures, increases in temperature fluctuations, and decreases in both relative humidity and soil surface moisture (Liechty et al. 1992; Roberts 2004; Muscolo et al. 2014; Roberts and Gilliam 2014).

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Commercial timber harvest has been a common, recurrent form of anthropogenic disturbance throughout North American forests ever since the extensive harvest of old-growth forests in the late 1800s and early 1900s (Wyatt and Silman 2014). Timber harvesting and regeneration strategies can range from individual tree gaps caused by single-tree selection to stand replacing disturbances such as clearcutting (Lorimer and Frelich 1994; Gilliam and Roberts 1995; Roberts and Gilliam 2014). As with natural canopy disturbances, following timber harvest, patches of direct light reaching the forest understory increase in duration and intensity, and potentially increase in temporal and spatial heterogeneity (Sousa 1984; Canham 1988a, b; Small and McCarthy 2002; Roberts 2004). Although changes in the light environment following canopy disturbance can increase productivity in light-limited understory plants, these changes favor understory species in different ways. Smaller canopy gaps formed during disturbance promote the establishment and growth of shade-tolerant species, while larger canopy gaps promote shade-intolerant understory species (Prévost and Raymond 2012; Roberts and Gilliam 2014). One such shade-tolerant understory herb that may be affected by changing canopy dynamics is the ecologically, economically, and culturally valuable herb, American ginseng (*Panax quinquefolius* L.).

American ginseng is an uncommon to rare, but widespread, medicinal herb found throughout much of eastern North America (McGraw et al. 2013). Historical accounts suggest that ginseng was once abundant throughout its range, but centuries of both habitat disturbance and of overharvest for the sale of its root on the Asian traditional medicine market have resulted in decreases in range-wide abundance (McGraw et al. 2013). Prior research suggests that ginseng is pre-adapted to take advantage of the dynamic light environments of old-growth forests (Wagner and McGraw 2013). Old-growth forests are characterized by an overstory that varies in individual age, size, and species composition, and has dynamic gap formations and closures (Knohl et al. 2003; Spies et al. 2006; Manabe et al. 2009).

Wagner and McGraw (2013) determined that the maximum photosynthetic rates of American ginseng increased with greater sunfleck duration, and the percentage of mean photosynthetic photon flux density (PPFD) contributed by sunflecks. The relative growth rate of adult ginseng plants also increased as a function of both sunfleck characteristics (Wagner and McGraw 2013). The same study found that transpiration and seed production efficiency were not affected by either sunfleck characteristic, but that germination decreased as the percent of mean PPFD provided by sunflecks increased (Wagner and McGraw 2013). While carbon assimilation, growth, and reproduction of many understory species respond positively to increases in sunfleck intensity and duration, this response is not ubiquitous (Le Gouallec et al. 1990; Chazdon and Pearcy 1991; Fournier

et al. 2004; Whigham 2004). In fact, long-lasting sunflecks and sunflecks with high levels of PPFD have led to high leaf temperature, wilting, and even photoinhibition in some species (Le Gouallec et al. 1990; Chazdon and Pearcy 1991; Oláh and Masarovičová 1997). How then does the shade-adapted species, American ginseng, respond to light levels and durations that far exceed those present in sunflecks?

The known consequences of timber harvest for American ginseng are equivocal. However, one study found that American ginseng survival decreased sharply following timber harvest, with the lowest survival occurring at the most intensely harvested site (Chandler and McGraw 2015). While the direct mechanisms controlling survival were not explicitly tested, soil profile disruption or compaction through the mechanical extraction of timber was thought to be the likely cause, not physiological stress due to photoinhibition; however, the latter was not examined (Chandler and McGraw 2015). Relative growth rate increased in those individuals that survived the initial timber harvest and was greatest at the sites with the highest amount of timber extracted (Chandler and McGraw 2015). Seed production decreased initially due to desiccation of the inflorescence, but increased in the years following timber harvest (Chandler and McGraw 2015). Increases in seed production efficiency (seeds per unit leaf area), were population dependent and short-lived (Chandler and McGraw 2015). While Chandler and McGraw (2015) established the multi-faceted response of ginseng to varying intensities of timber harvest, the physiological underpinnings of the response were ignored.

Based on the results of Chandler and McGraw (2015), it is not clear whether canopy disturbances via timber harvest are physiological stressors, or whether increases in light following timber harvest provide physiological benefits, particularly in those physiological traits that directly relate to carbon accumulation. To resolve this uncertainty, I quantified the effects of canopy openness on photosynthesis, respiration, water use efficiency, and stomatal conductance of American ginseng before and after timber harvest. I further evaluated the growth response of American ginseng as a function of the changes in canopy openness and maximum photosynthesis that occurred after a harvest event. I took advantage of an existing, natural population of American ginseng that was located within a portion of a USDA experimental forest that was prescribed a patch cut timber harvest as part of a larger study.

Materials and methods

Study species

Similar to many herbs found throughout the eastern deciduous forest, American ginseng (*Panax quinquefolius* L.,

family: Araliaceae) is a widespread, long-lived perennial herb that exhibits "slow" life history patterns, including a long prereproductive period (McGraw et al. 2013). American ginseng's range is broad, extending throughout the eastern portion of the USA and into southern portions of Canada; however, natural populations are uncommon and typically consist of fewer than 200 individuals (Anderson et al. 1993; McGraw et al. 2013). Emergence from winter dormancy, elongation, and leaf expansion all occur concurrent with overstory canopy development and closure in late April and May (Lewis and Zenger 1982; Hackney and McGraw 2001; Fournier et al. 2004; McGraw et al. 2013). Seasonal aboveground growth is determinate (McGraw et al. 2013). Flowering takes place in June and July, and is followed by fruit production and ripening from July to September (Carpenter and Cottam 1982; McGraw et al. 2013). Fruits disperse in August and September, followed by plant senescence and dormancy (Lewis and Zenger 1982; McGraw et al. 2013).

Study site

American ginseng was located in a USDA experimental forest in West Virginia, USA, within the central Appalachian region of the eastern deciduous forest. A specific site identifier is withheld due to the conservation concern of American ginseng and is replaced with a non-descript identifier, 44. Site 44 had an elevation of 841 m, a mean slope of 7.7°, and was located on a north-facing slope. The experimental forest in which site 44 is located has a mean growing season of 145 days from May through October and an evenly distributed mean annual precipitation of 1430 mm (Pan et al. 1997; Schuler 2004). Site 44 was selected based on both the presence of wild American ginseng and on the anticipated harvest of timber. The timber on this second growth forest was heavily harvested in the early twentieth century (Adams et al. 2012). The land, which consisted primarily of even-aged stands, was acquired by the USDA in 1915, and silvicultural management research was initiated in 1951 when the stand was ~40 years old (Schuler 2004; Adams et al. 2012). Site 44 was prescribed a patch cut treatment. Patch cutting can represent a moderate to high level of canopy disturbance, with disturbance severity dependent on patch opening size, total area of harvest, proximity to harvest unit, and cutting cycle. The timber on site 44 had a rotation age of 65 years and was managed on a 10-year cutting cycle using small patch cutting with circular openings of about 0.162 ha with a diameter of ~45 m (Schuler 2004). Felled trees were removed from site 44 using a set of permanent skid roads that encompassed 1.85% of the total site area (USDA Forest Service, unpublished data). Skid roads were located within 50 m of the ginseng population, but were not directly over or adjacent to ginseng

subpopulations. The particular cutting cycle analyzed in this work occurred after the 2013 growing season in late fall, and I classified this treatment as an intermediate-level canopy disturbance. I obtained maximum temperature (°C) and precipitation (mm) data from a nearby weather station for each day within the 2013, 2014, and 2015 growing seasons (Menne et al. 2012). A one-way ANOVA was performed to determine if maximum daily temperature varied among growing seasons, and a Tukey–Kramer HSD post hoc test was used to determine differences in means. A one-way Welch's ANOVA was used to compare precipitation among growing seasons, as transformations did not improve normality.

Canopy environment

Hemispherical images of the sky were taken above each individual or small subpopulation of tightly aggregated individuals in July–August of each growing season to quantify the changes in canopy structure that occurred following timber harvest. Due to the short stature of the plant, the canopy is defined as the understory, mid-story, and tree canopy vegetation that extends greater than 20 cm aboveground, which is near the mean height of a ginseng plant (Chandler and McGraw 2015). Hemispherical photographs were taken on overcast days from a position 20 cm above the soil surface with the top of the photograph oriented northward. A Canon EOS Rebel T2i equipped with a 180° fisheye lens (Sigma 4.5 mm F2.8 EXDC) was used to capture the 18MP images. The canopy cover was analyzed for 54 images using Gap Light Analyzer software (Frazer et al. 1999) to determine percent canopy openness, defined as the percentage of open sky visible beneath the forest canopy. Percent canopy openness is determined by partitioning pixels into "sky" and "non-sky" categories and calculating the distribution of sky based on pixel categories (Frazer et al. 1999). While some studies indicate that PPFD and photosynthetically active radiation are not correlated with percent canopy openness under very low light conditions (Whitmore et al. 1993; Machado and Reich 1999), the majority of canopy openness values in the present study exceeded the low light levels reported in these studies. Further, other studies have established linear relationships between canopy openness and mean daily percent PPFD under higher light levels, as well as between canopy openness and global radiation (combined percentage of diffuse and direct beam total season radiation) (Machado and Reich 1999; McCarthy and Robison 2003).

Ginseng census, growth, and reproduction

Thirty-four ginseng plants were located on site 44 the spring before timber harvest and were censused for three

growing seasons (2013–2015). Individuals were labeled using a subterranean tag to ensure accurate identification for each census period. Census data were collected twice annually: once in the spring to assess plant emergence and leaf area, and once in the fall to assess reproduction. Data collected included plant emergence (Y/N), leaf number, length and width of the longest leaflet on each leaf (cm), reproductive status (Y/N), and number of seeds.

Individual survival was determined using plant emergence data. New seedlings were considered dead if they did not re-emerge in the growing season after germination, while older plants were considered dead if they did not emerge for two consecutive growing seasons. The 2-year observation period was necessary because established individuals with damaged shoots or roots may lie dormant for one growing season and re-emerge the following season (Farrington et al. 2009). A G test was performed to determine if the mortality rates at population 44 differed from the expected mean mortality rate calculated from 12 undisturbed populations. A logistic regression was performed to determine if the canopy openness in the summer following timber harvest (2014) affected the survival probability.

Individual leaf area was calculated using a regression equation based on the allometric relationship between leaf area and length and width of the longest leaflet on the leaf (Souther and McGraw 2011). Individual leaf areas were summed to yield the total leaf area for each plant. The changes in leaf area of an individual over time, relative growth rate (RGR_{LA}), was calculated based on changes in plant leaf area between growing seasons using the formula (McGraw and Garbutt 1990):

$$RGR_{LA} = \frac{(\ln LA_2 - \ln LA_1)}{(t_2 - t_1)}.$$

Leaf area of an individual ginseng plant in the present growing season is determined by carbon storage in the prior growing seasons. Therefore, any growth effect of timber harvest that occurred during the dormant season (late fall, 2013) would not be manifest in the 2013–2014 interval, but rather in the 2014–2015 interval. Accordingly, the change in leaf area from 2013 to 2014 represents RGR_{LA} before timber harvest (BT), while the change in leaf area from 2014 to 2015 represents RGR_{LA} after harvest (AT). A paired t test was used to compare relative growth before timber harvest (RGR_{BT}) to after timber harvest (RGR_{AT}). The relative growth rate from 2013 to 2015 was also calculated to determine if there was a net increase in size over the entire study. While the paired t test may reflect the mean change in RGR_{LA} in response to light, this measurement could overlook subtle variations in RGR_{LA} present before and after the timber harvest. To determine if RGR_{LA} changed as a function of variation in canopy openness in either transition period, two regressions were performed, one with relative growth rate before timber harvest (RGR_{BT}) regressed on percent canopy openness before timber harvest (2013), and a separate one relating the same variables after timber harvest (2014).

I wanted to compare changes in RGR_{LA} observed at population 44 to changes in RGR_{LA} at nearby (<20 km away) undisturbed control populations named "29" and "30" to ensure that observed changes in RGR_{LA} at population 44 were a function of the timber harvest and not of typical year-to-year variation. There was no recent history of ginseng harvest at site 44 or at the two long-term research populations. One-leaved individuals comprised ~50% of the total population size at all three populations. Juveniles (two-leaved) comprised ~30, 20, and 40%, and adults (three- and four-leaved) 20, 30, and 10% at populations 44, 29, and 30, respectively. The relative growth rate of individuals within populations 29 and 30 did not differ, and as such, the data from these two populations were pooled into one control for this study. A two-way ANOVA was performed to determine if growth differed between the harvested population (44) and the control populations (control) over the period before (2013–2014) and after (2014–2015) the timber harvest event, and a Tukey–Kramer HSD post hoc test was used to determine differences in means.

Seed production is generally positively related to total leaf area (McGraw et al. 2013) but this relationship can be altered by changes in the light environment and by the changes in internal resource availability that follow canopy disturbance (Schlessman 1985). A two-way ANOVA without replication was used to determine if the number of seeds produced by each reproductive individual present in the population differed in the growing seasons before (2013) and following (2014, 2015) the timber harvest.

Physiological measurements and analyses

Light response curves were constructed from photosynthesis measurements made with a Li-Cor 6400XT portable gas exchange system (Li-Cor, Lincoln, NE, USA) to determine how increases in light caused by the patch cut affected gas exchange. Physiological measurements were made each growing season (2013–2015) for each two- and three-leaved individual in the population. I observed no four-leaved individuals on site 44. Although an absence of large individuals is often indicative of harvest, harvest was not observed throughout the study. In accordance with Wagner and McGraw (2013), one-leaved individuals were excluded from all physiological measurements. Measurements were taken in mid-season (mid-July to early August) on clear days between 11:00 a.m. and 3:00 p.m. Net photosynthesis was measured at nine PPFD levels: 0, 100, 300, 500, 700, 900, 1100, 1300, and 1500 μmol m^{-2} s^{-1}; CO_2 levels were set at 390 μmol CO_2 mol^{-1}, and cuvette temperature was set at 25 °C.

Light response curves were fit and parameter estimates were established using a non-rectangular hyperbola model (Landflux.org 2016; Marshall and Biscoe 1980), and values for maximum photosynthetic rate (A_{max}) and dark respiration were derived from the model fits. Five separate mixed models were used to determine if A_{max}, respiration, photosynthetic water use efficiency (A_n/E), intrinsic water use efficiency (A/g_s), and stomatal conductance (g_s) were greater in the growing seasons following timber harvest, and Bonferroni post hoc analyses ($\alpha = 0.0167$) were used to determine differences in means. The use of mixed models offers several important advantages over other standard statistical analyses (e.g., ANOVA, regression). The model incorporates all available repeated data, including those for subjects who are missing some or all follow-up values and can incorporate the correlation which occurs with replicate observations (Laird and Ware 1982; Singer 1998; Singer and Willet 2003). An increase in A_{max} following timber harvest would indicate that plants utilize and benefit from the additional light, while stress may be manifested as increases in respiration and stomatal closure, and decreases in water use efficiency. Two regressions were performed to determine if the growth of individuals as a function of A_{max} was stimulated after timber harvest relative to before harvest, where RGR_{BT} was regressed on A_{max} before timber harvest (2013), and RGR_{AT} was regressed on A_{max} after harvest (2014).

Results

Daily maximum temperature (°C) did not differ between the 2013 (24.29 ± 0.36) and 2014 (24.37 ± 0.38) growing seasons, but was slightly higher in 2015 (25.59 ± 0.39; $F_{(2,433)} = 3.6565$, $p = 0.0266$). A one-way Welch's ANOVA indicated that precipitation (mm) did not differ among growing seasons ($F_{(2,287)} = 0.0026$, $p = 0.9974$).

Canopy openness varied over the 3-year study period (Fig. 1). Mean canopy openness increased from 17% (± 0.89) in the growing season prior to timber harvest (2013) to 36% (± 2.63) in the growing season directly after harvest (2014): a relative increase of 112%. However, as expected, canopy openness decreased to 28% (± 2.84) for two growing seasons after the timber harvest (2015) due to growth release of understory and mid-story herbs and woody plants.

Survival, growth, and reproduction

At 22%, the mortality observed at population 44 was greater than the expected mortality at 12 undisturbed populations across American ginseng's range ($G = 7.286$, $p < 0.05$; data taken from Souther and McGraw 2011).

Fig. 1 Example of hemispherical images taken above the same plant in the summer before timber harvest (**a**; 2013), the summer after timber harvest (**b**; 2014), and two summers after timber harvest (**c**; 2015). These and other hemispherical images were used to calculate canopy openness above each individual or small aggregation of individuals each growing season

Nevertheless, a logistic regression indicated that variation in canopy openness directly after timber harvest (2014) did not affect the probability of survival ($\chi^2 = 0.17$, $p = 0.6759$).

There was a marked increase in relative growth rate among individuals following the timber harvest ($t = 4.35$, $p = 0.0002$). Plants grew significantly faster after timber harvest ($RGR_{LA} = 0.62 \pm 0.11$) than before timber harvest ($RGR_{LA} = -0.234 \pm 0.05$). Further, there was a net
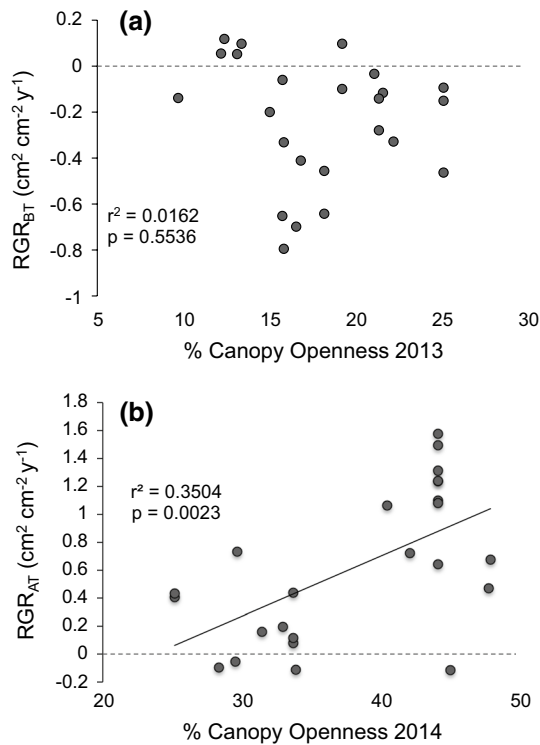
Fig. 2 Linear regressions showing relative growth rate (RGR) of American ginseng as a function of variation in percent canopy openness in **a** the growing season before timber harvest (2013; RGR$_{BT}$) and **b** the growing season after timber harvest (2014; RGR$_{AT}$)
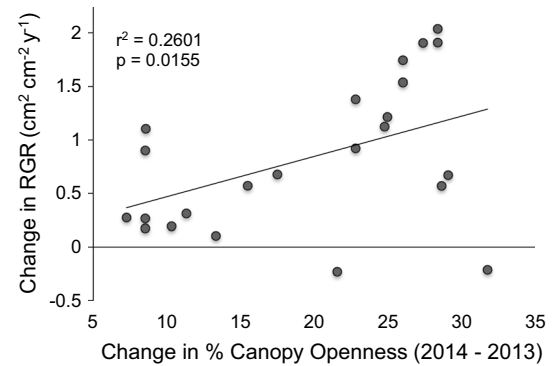

Fig. 3 Linear regression showing change in relative growth rate after the timber harvest compared to before the timber harvest as a function of the change in percent canopy openness between the growing season prior to timber harvest (2013) and the growing season directly following timber harvest (2014)
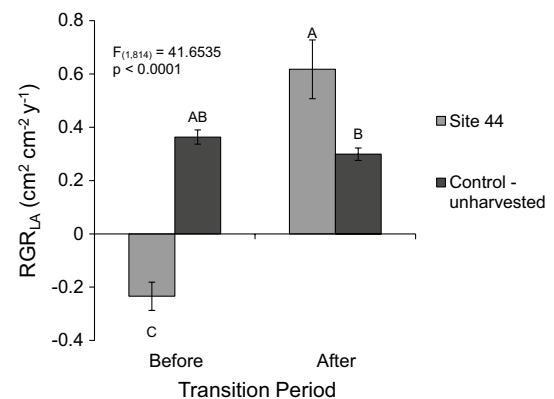

Fig. 4 Differential effects of time period relative to timber harvest year (Before: 2013–2014, After: 2014–2015) and treatment (harvested vs. control) on the relative growth rate of American ginseng (±SE). Means connected by the same letters are not significantly different

increase in growth over the entire study period (RGR$_{15-13}$ = 0.135). Regression analyses indicated that the relative growth rate did not vary as a function of canopy openness before the timber harvest (Fig. 2a), but formed a positive linear relationship with canopy openness following the timber harvest (Fig. 2b). Additionally, greater increases in canopy openness directly after harvesting resulted in greater increases in growth (Fig. 3). The two-way ANOVA indicated that individual growth differed between the harvested and control sites before and after the timber harvest event ($F_{(1,814)} = 41.65$, $p < 0.0001$; Fig. 4). Mean growth rate at population 44 was far lower before timber harvest (2013–2014) than the growth rate at comparable, undisturbed control populations over the same time period (Fig. 4). However, this pattern is reversed after the timber harvest (2014–2015), and mean growth rate at population 44 after harvest was approximately twice that of the control populations over the same time period (Fig. 4).

Although increases in relative growth rate were observed following the timber harvest, the same was not true for seed production. A two-way ANOVA without replication indicated that there was no difference in the mean number of seeds produced by reproductive individuals among pre-harvest and post-harvest years ($F_{(2,14)} = 0.0218$, $p = 0.9785$).

Physiological response

There were no differences in maximum photosynthetic rate (A_{max}) in the growing seasons directly before (2013) and after (2014) timber harvest (Table 1a). However, A_{max} increased by ~69% in two growing seasons following timber harvest (2015) relative to the growing season before timber harvest (2013; Table 1a). Similar patterns are depicted in the mean light response curves that were created only with data from individuals that were present in the population for each of the three growing seasons (Fig. 5).

Respiration was greater in the growing season directly after timber harvest (2014) compared to both the growing season before harvest (2013) and following harvest (2015; Table 1b). However, respiration rates pre-timber harvest (2013) and two growing seasons post-timber harvest (2015)

Table 1 Results of mixed models comparing (a) maximum rate of photosynthesis, (b) respiration rate, (c) photosynthetic water use efficiency, (d) intrinsic water use efficiency, and (e) stomatal conductance one growing season before timber harvest (2013), one growing season after timber harvest (2014), and two growing seasons after timber harvest (2015)

Variable	$F_{(2,\,28)}$	p	Growing season	Mean ($\pm$SE)
(a) A_{max}	9.423	0.001*	2013	3.763 ($\pm$0.172)
			2014	4.951 ($\pm$0.691)
			2015	6.393 ($\pm$0.618)
(b) Respiration	7.767	0.002*	2013	0.343 ($\pm$0.032)
			2014	0.616 ($\pm$0.076)
			2015	0.340 ($\pm$0.068)
(c) WUE$_{photo}$	1.082	0.353	2013	3.731 ($\pm$0.139)
			2014	3.618 ($\pm$0.317)
			2015	4.268 ($\pm$0.546)
(d) WUE$_{intrinsic}$	2.271	0.122	2013	60.205 ($\pm$2.703)
			2014	66.431 ($\pm$5.884)
			2015	52.259 ($\pm$5.202)
(e) Stomatal conductance	19.719	<0.0001*	2013	0.055 ($\pm$0.013)
			2014	0.065 ($\pm$0.024)
			2015	0.117 ($\pm$0.034)

Bonferroni post hoc analyses were utilized separately for each variable to compare means among growing seasons

* significant p values

Fig. 5 Mean light response curve ($\pm$SE) depicting A_{net} at each of five levels of PPFD (0, 100, 300, 500, and 700) per year for each individual whose physiological measurements were obtainable in all of the three growing seasons. Data points from greater PPFD values are excluded, as A_{net} within years did not vary significantly at these levels

did not differ (Table 1b). No differences in photosynthetic water use efficiency (WUE$_{photo}$; Table 1c) or intrinsic water use efficiency (WUE$_{intrinsic}$; Table 1d) were observed throughout the study period. Stomatal conductance was greater in two growing seasons after the timber harvest (2015) relative to both the growing season prior to (2013) and following (2014) timber harvest (Table 1e).

Relative growth rate did not change as a function of the variation in A_{max} before timber harvest (Fig. 6a). However, relative growth rate tended to form a positive linear relationship with A_{max} following harvest (Fig. 6b). These results were consistent with the response of growth to percent canopy openness (Fig. 2a, b). While growth rate did not vary with canopy openness and maximum rate of photosynthesis before the timber harvest (Figs. 2a, 6a), growth rate formed a positive linear relationship with both variables following timber harvest (Figs. 2b, 6b).

Discussion

Consistent with previous findings, the survival rate of this population was lower than rates observed at other, undisturbed populations (Chandler and McGraw 2015). One mechanism that leads to decreased survival following
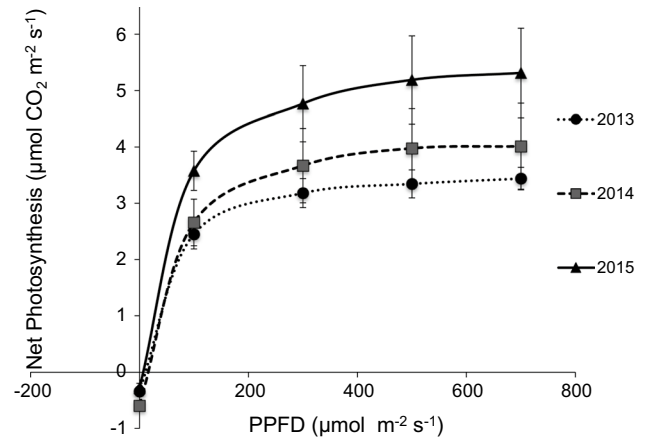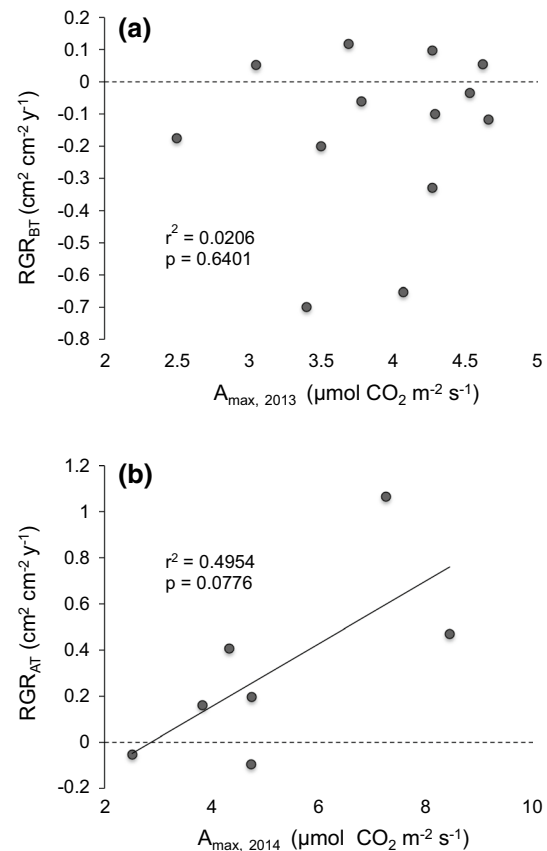

Fig. 6 Linear regressions illustrating relative growth rate (RGR) of American ginseng as a function of maximum photosynthetic rate (A_{max}) in **a** the transition period prior to timber harvest (RGR$_{BT}$) and **b** the transition period following timber harvest (RGR$_{AT}$)

timber harvest is the destruction and compaction of the soil profile that results both from the formation of skid roads and also from the physical dragging of timber across the soil (Chandler and McGraw 2015). Population 44 is located in a USDA research forest where care is taken to minimize soil disturbance during timber extraction through the use of minimal, permanent skid roads. As a result, the survival reported in this study was likely higher than would occur on a typical timber harvest on private lands (Chandler and McGraw 2015). Another mechanism that could lead to a decrease in American ginseng survival is potential increases in herbivory via white-tailed deer (*Odocoileus virginianus*) after timber harvest (Campbell et al. 2004; McGraw et al. 2013). However, herbivore damage did not increase in population 44 following harvest. Additionally, there were no increased signs of pathogen or fungal damage to individuals within population 44 following the timber harvest (Chandler, personal observations). Aboveground vegetative damage caused by the growth of *Galium* sp. was observed in one subpopulation of American ginseng, two growing seasons after timber harvest (2015), but the damage did not contribute to decreased survival in this study.

The net increase in relative growth rate from 2013 to 2015, the growth stimulation beyond that of the control populations, and the positive linear relationship of growth rate to canopy openness all indicate that the canopy disturbance led to growth greater than typical year-to-year variation. The observed increase in growth rate after timber harvest follows the results of Chandler and McGraw (2015). However, the decrease in size between 2013 and 2014 (pre-timber harvest) was puzzling, and a similar trend was not observed in Chandler and McGraw (2015). A decrease in growth before timber harvest (2013–2014) may be attributed to the interaction of numerous factors including low light availability, aspect, slope, nutrient availability, and surface soil moisture. Drought stress can influence leaf expansion; however, a comparison of maximum daily temperature as well as precipitation taken from a nearby weather station indicated that there was no difference in either metric between the 2013 and 2014 growing seasons. Nevertheless, a more open canopy the spring after timber harvest (2014) resulted in increased light and presumably in decreased soil surface moisture, though not directly measured. While seed production did not differ before and after timber harvest in this study, reproduction in American ginseng is strongly size dependent (Schlessman 1985; Charron and Gagnon 1991), and as the leaf area of individuals in the population increase, short-term increases in seed production are predicted to follow.

A comparison of the mean light response curves prior to harvest (2013) and one growing season after harvest (2014) indicated that the individuals were only partially acclimated to the higher light levels caused by timber harvest (Fig. 5), a pattern that may be generally applied to many understory herbs that overwinter underground and re-emerge concurrent with tree canopy emergence. Acclimation in the first season after timber harvest was minimal because some aspects of leaf morphology were already pre-formed based on environmental conditions and carbon storage in 2013, the growing season before the harvest event. Individuals displayed signs of stress the growing season after timber harvest (2014), which included reddened leaves presumably from adaxial accumulation of anthocyanins, higher respiration, and early senescence (Neufeld and Young 2014). The second year following timber harvest (2015), plants produced leaves that were better acclimated to high light levels as a result of greater exposure to higher light and greater carbon storage during the 2014 growing season. Although not directly measured, these well-acclimated leaves likely had greater stomatal density than the leaves produced in both 2013 and 2014, as evidenced by greater stomatal conductance in the 2015 growing season.

American ginseng may be aptly classified as a "slow opportunist". Delayed acclimation to higher light is a consequence of American ginseng having determinate growth and pre-formed leaves, and results in a consistent time lag behind canopy changes. Similar herbs such as *Sanguinaria canadensis L.* and *Trillium grandiflorum* have "slow" life histories and produce a single flush of leaves per growing season (Lubbers and Lechowicz 1989; Marino et al. 1997; Neufeld and Young 2014), and may likewise exhibit delayed acclimation to changes in canopy structure. By the time acclimation occurs in these plants, the understory and mid-story close in due to growth release of saplings and ruderal species, leading to increased resource competition. It is possible that the lag inherent in these understory herbs limits the duration and magnitude of growth stimulations following canopy disturbance. Similarly, shade-tolerant trees experience a lag time in response to gap formation due to prolonged suppression and slow growth under dense shade (Canham 1989). Nevertheless, signs of acclimation to higher light levels such as increased maximum rate of photosynthesis and increased growth rate indicate that American ginseng is an opportunist that benefits from rapid, discrete increases in light availability.

This study suggests that increases in canopy openness lead to increases in carbon acquisition and subsequent growth of American ginseng; however, an analysis of a full spectrum of canopy openness was impractical and not explored. Nonetheless, it is doubtful that physiological and growth parameters would remain positive at both the lowest and the highest levels of canopy openness. The more probable relationship of these parameters to canopy openness is parabolic with peak stimulation at some intermediate level of canopy openness.

Little is known about the state of the herbaceous layer in the eastern deciduous forest prior to the early 1900s when widespread timber harvests removed all but ~0.09% of old-growth forests (Davis 1993; Leverett 1996; Wyatt and Silman 2014). Researchers have quantified the response of herbaceous communities to timber harvest, but confounding factors preclude broad conclusions and generalizations (Duffy and Meier 1992; Fredericksen et al. 1999; Gilliam 2002; Neufeld and Young 2014). Less research has focused on the physiological and growth response of herbaceous species to timber harvest disturbances. A separate study suggested that moderate to severe timber harvests are detrimental to the population maintenance of American ginseng (Anderson et al. 1993). However, the same study did not directly quantify the response of American ginseng to timber harvest, but rather tallied the number of their populations that had incurred timber harvests in recent history (Anderson et al. 1993). The results of Anderson et al. (1993) are partially refuted in the current study and in Chandler and McGraw (2015). In fact, the results of this study and others suggests that ginseng may still be light limited in the absence of canopy disturbances (Chandler and McGraw 2015, 2016), and the growth of American ginseng and other similar understory herbs is stimulated by intermediate-intensity timber harvests. Nevertheless, care must be taken when extrapolating these results to other types of timber harvest that vary greatly in intensity and geographic extent.

Increases in individual and population growth following natural canopy disturbances may be mirrored in anthropogenic disturbances, especially if such disturbances are management-based practices that mimic the natural disturbance regimes of old-growth forests. Single-tree selection and group selection are two silvicultural strategies that mimic old-growth forest structure (Lorimer and Frelich 1994; Goebel and Hix 1996), and the careful implementation of these management techniques may enhance ginseng performance (Chandler and McGraw 2015). Such strategies would serve the dual purpose of providing economically valuable timber and of stimulating growth of rare understory herbs such as American ginseng, a herb that is surprisingly resilient in the face of rapid environmental shift.

Author contribution statement JLC conceived, designed, and executed this study and wrote the manuscript. No other person is entitled to authorship.

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