



Sunfleck effects on physiology, growth, and local demography of American ginseng (*Panax quinquefolius* L.)

Alixandra Wagner, James B. McGraw*

Department of Biology, West Virginia University, Life Sciences Building, PO Box 6057, Morgantown, WV 26506-6057, USA

ARTICLE INFO

Article history:

Received 1 October 2012

Received in revised form 20 November 2012

Accepted 24 November 2012

Available online 7 January 2013

Keywords:

American ginseng

Panax quinquefolius

Sunflecks

Photosynthesis

Local demography

ABSTRACT

The light environment of the forest understory is heterogeneous, characterized by low levels of diffuse light punctuated by short periods of direct solar radiation known as sunflecks. Less well understood is the degree to which sunflecks are responsible for spatially varying performance of understory plants. We studied natural variation in the light environment, as well as physiology, growth, and microsite demographics of American ginseng (*Panax quinquefolius* L.) to test whether clustering of plants within a population was related to sunfleck variation. HOBO dataloggers were positioned in 10 clusters within a single ginseng population to measure the local understory light environment during mid-season (June 27 to August 9 2011). Photosynthesis and transpiration were measured with a Li-Cor 6400 portable photosynthesis system. Population census data were used to obtain measurements of the relative growth rate (2011–2012), seed production efficiency (2011) and seed germination (2009–2012) of plants in the same subpopulations. All measured dependent variables were regressed against the percentage of mean photosynthetic photon flux density contributed from sunflecks and mean length of the longest sunfleck. Light saturated photosynthetic rates of ginseng showed a positive linear relationship to both sunfleck characteristics, while transpiration was unaffected. The relative growth rate of established ginseng plants also had a positive linear relationship with the length of the longest sunfleck. However, germination rate was negatively affected by an increasing percentage of photosynthetic photon flux density from sunflecks. Seed production efficiency was not influenced by either sunfleck characteristic. Due to negative effects on germination, initial ginseng cluster formation is likely not associated with sunflecks, however photosynthetic and growth responses suggest that fitness effects are positive for established individuals. A spatially and temporally varying light environment is beneficial for ginseng population growth.

© 2012 Published by Elsevier B.V.

1. Introduction

The understory light environment is heterogeneous due to overstory canopy architecture, sun position, weather, and topography (Baker, 1996; Chazdon, 1988; Chazdon and Pearcy, 1991; Grant, 1997). Leaves of canopy trees absorb much of the incoming solar radiation, resulting in a diffuse understory light environment, characterized by light levels less than $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ and a low red:far-red ratio (Baker, 1996; Chazdon, 1988; Chazdon and Pearcy, 1991; Grant, 1997; Sakai et al., 2005). The diffuse light is periodically punctuated by direct light in sunflecks, causing significant heterogeneity of the understory light environment (Chazdon and Pearcy, 1991). Within sunflecks, light intensity can be 10–100-fold higher than in diffuse light, and the red:far-red ratio is higher due to the lack of filtering by canopy leaves in the wavelengths of photosynthetically active radiation (PAR: 400–700 nm; Chazdon and Pearcy, 1991).

Light can be a limiting factor of growth for understory plants (Chazdon and Pearcy, 1991), and sunflecks may play a critical role due to both the quantity and quality of light they contain (Baker, 1996; Chazdon and Pearcy, 1991; Grant, 1997). Sunflecks contribute up to 85% of the total PPFD¹ in the forest understory (Chazdon, 1988; Chazdon and Pearcy, 1991; Kursar and Coley, 1993). Sunflecks contribute up to 60% of the total daily photosynthesis of understory plants and account for up to 60% of the total carbon gain of understory plants (Chazdon, 1988; Kursar and Coley, 1993).

Sunflecks differ in duration, frequency, PPFD strength, and size due to the structure of the forest canopy (Baker, 1996; Chazdon and Pearcy, 1991). The height and flexibility of the canopy, along with the area, clustering, and arrangement of the canopy leaves are all aspects of the canopy that influence the type of sunfleck received by the understory (Baker, 1996; Chazdon and Pearcy, 1991; Oláh and Masarovičová, 1997). For example, as canopy height increases, PPFD strength and duration of sunflecks tend to decrease

* Corresponding author. Tel.: +1 304 293 0798; fax: +1 304 293 6363.

E-mail address: jmcgraw@wvu.edu (J.B. McGraw).

¹ Photosynthetic photon flux density (PPFD), Photosynthetically active radiation (PAR), Relative Growth Rate (RGR), Light saturated photosynthetic rate (A_{sat}).

(Chazdon and Pearcy, 1991; Oláh and Masarovičová, 1997). When leaves are clustered at the ends of branches sunfleck frequency is higher and as leaf area increases duration decreases (Oláh and Masarovičová, 1997). Sunflecks also usually occur in clusters due to spatial variation of the canopy (Oláh and Masarovičová, 1997).

Sunflecks have variable effects on understory plants because sunfleck strength, frequency, and duration alter the inductive state of a plant (Chazdon and Pearcy, 1986; Hull, 2002; Kursar and Coley, 1993). To utilize a sunfleck the plant must first prime its photosynthetic machinery to obtain a maximum photosynthetic rate capable of efficiently using the high levels of incoming light (Chazdon and Pearcy, 1986; Kursar and Coley, 1993; Pearcy, 2007). The induction process involves the regeneration of ribulose-1,5-bisphosphate (1,5-RuBP), activation of Rubisco, and the limiting step of stomatal opening (Hull, 2002; Kursar and Coley, 1993; Pearcy, 2007; Pearcy et al., 2004). Therefore, longer sunflecks allow time for a full inductive state to be achieved and therefore better sunfleck utilization (Chazdon and Pearcy, 1986; Kursar and Coley, 1993). Temporally clustered sunflecks are also beneficial because the previous sunfleck primes the leaf for the following sunflecks (Hull, 2002; Kursar and Coley, 1993; Pearcy et al., 2004). Once the next sunflecks do occur the plant already has a higher inductive state compared to the state it would have in diffuse light (Hull, 2002; Kursar and Coley, 1993; Pearcy et al., 2004).

Sunflecks can negatively affect some understory species (Chazdon and Pearcy, 1991; Oláh and Masarovičová, 1997). While longer sunflecks may promote maintenance of a high induction state, they can cause photoinhibition in some plants (Oláh and Masarovičová, 1997). Sunflecks with a high PFD can also cause photoinhibition (Chazdon and Pearcy, 1991). *Elatostema repens* experienced photoinhibition and reduced photosynthetic carbon gain when sunflecks were greater than $700 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Le Gouallec et al., 1990). Sunflecks also cause high leaf temperatures and wilting of leaves in some species (Chazdon and Pearcy, 1991).

While numerous studies have focused on how individual plants are affected by sunflecks, fewer have focused on the effect of sunflecks on populations (Sakai et al., 2005). Also relatively few studies have examined the effect of sunflecks on herbaceous understory plants at a community level (Gilliam and Roberts, 2003). Gilliam and Turrill (1993) found that the herb layer of a deciduous forest responded negatively to basal area and density of trees, but had no response to other variables, such as soil fertility, leading to the conclusion that canopy structure could be affecting the herbaceous layer. Vockenhuber et al. (2011) found that as canopy cover increased, herb cover and richness declined. Light availability was described as one of the factors, along with pH, and humus layer mass, that had a strong effect on herb cover (Vockenhuber et al., 2011).

For this study, we used American ginseng (*Panax quinquefolius* L.) as a model species to study effects of sunflecks on dynamics of individuals within a population. American ginseng is the premiere wild harvested medicinal plant species of the eastern deciduous forest in North America, and as such, understanding controls over population growth and decline has important economic, as well as ecological implications. American ginseng occurs in small clusters or 'subpopulations' in a heterogeneous understory light environment. One hypothesis for this clustering is that ginseng seed dispersal is limited, and therefore the clusters represent family groupings dispersed from one or a few large adults (Cruse-Sanders and Hamrick, 2004). Another possible explanation for clustering, however, is that ginseng succeeds in certain optimal understory light conditions, possibly related to the sunfleck micro-environment. Using a single population from a long-term demographic study of American ginseng, we addressed three linked questions concerning sunfleck effects on ginseng: (1) What is the range of sunfleck length and PFD that occurs within a natural

forest understory habitat? (2) Do sunflecks affect photosynthesis and transpiration? and (3) How do sunflecks affect individual plant growth and life history traits?

2. Materials and methods

2.1. Study species

American ginseng is an herbaceous, understory perennial found throughout the eastern deciduous forests of North America (Anderson et al., 1993; McGraw et al., 2003). The range of ginseng extends north into Ontario and west to the western states bordering the Mississippi River (McGraw et al., 2003). The aerial shoot of ginseng emerges in late April or early May ca. 1–2 weeks before the emergence of the tree canopy; therefore initially leaves may be exposed to high light levels (Fournier et al., 2004; Hackney and McGraw, 2001). For the majority of the growing season ginseng experiences a heterogeneous light environment of a mostly closed canopy (Fournier et al., 2004). The aerial shoot emerges from a rhizome attached to a taproot and contains 1–5 palmately compound leaves situated in a whorl (Schlessman, 1985). The aerial shoot is deciduous and from June to September photosynthate not used for tissue maintenance and reproduction is transferred below-ground to a fleshy storage root (Fournier et al., 2004; Lewis and Zenger, 1982). The flowers of ginseng are hermaphroditic and form an umbel at the juncture of the leaves (Schlessman, 1985). Ginseng reproduces mainly by seeds after a growth period of 5 or more years and almost always when it is 3- or 4-leaved (Mooney and McGraw, 2007). Seeds require a warm and cold stratification period of at least 18–20 months before germination (Lewis and Zenger, 1982). Seedlings have one leaf consisting of three leaflets and with passing years will grow in size and leaf number (Lewis and Zenger, 1982). American ginseng is a wild-harvested species and has significant economic value due to roots being highly prized in Asian traditional medicine (Robbins, 2000). Harvesting kills the whole plant, and wild populations have become scarce and hard to find at least in part due to unsustainable harvest practices (McGraw et al., 2010; Nantel et al., 1996; Robbins, 2000). In 1975 American ginseng was placed on the Appendix II of CITES (Convention on International Trade in Endangered Species).

2.2. Study site

Long-term data have been collected on the growth and life history traits of American ginseng for 30 populations distributed across seven states (Souther and McGraw, 2011). One of these populations in north central West Virginia was selected because it is 'typical' in several respects (exact location withheld due to conservation concerns). The second-growth trees that made up the canopy at the site were selectively cut in 1910, but no further cutting has occurred since that time. The canopy was composed of mixed hardwood trees (Appendix A), including sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), tulip poplar (*Liriodendron tulipifera*), beech (*Fagus grandifolia*), black birch (*Betula lenta*), and black cherry (*Prunus serotina*). Minor components included striped maple (*Acer pensylvanicum*), and basswood (*Tilia americana*). Sugar maple was the dominant tree species in terms of stems ha^{-1} and red oak was the dominant tree species in terms of basal area. The soils were acidic, well-drained, loamy sands ca. 1 m in depth. The site had southeast and northwest aspects with a mean elevation of 800 m. The forest canopy was relatively undisturbed with no major windthrow, storm damage, or defoliation events evident. Ten subpopulations of ginseng were purposely chosen to represent the range of dynamics from declining to increasing numbers over time.

2.3. Light measurement

The midseason light environment (June 27 – August 9, 2011) in each of the ginseng clusters was measured in the field using HOBO dataloggers (HOBO temperature/light pendant datalogger 64; Onset Computer, Bourne, MA, USA). HOBO dataloggers were positioned as near as possible to the center of each subpopulation. Each HOBO was fastened horizontally to a stake at a height equal to that of ginseng plants within the cluster (20–40 cm). The HOBO dataloggers recorded light levels every minute in order to have a time period short enough to capture sunflecks.

Since HOBO dataloggers measure light levels across a broader range of wavelengths (150–1200 nm) than that of PAR, a datalogger was calibrated against a quantum sensor Li-Cor Li-189 Light Meter (Li-Cor Inc., Lincoln NE) on a clear day. The relationship was analyzed by regression (SAS JMP 9). For values less than 26,257 lx the equation $\ln(\text{PPFD}) = 2.5323 + 0.0001158 * (\text{LUX})$ ($p < 0.0001$) was used to convert HOBO measurements of light into PPFD values (Appendix B). For values greater than 26,257 lx the linear equation $\text{PPFD} = 86.571 + 0.00657 * (\text{LUX})$ ($p < 0.0001$) was used for the conversion (Appendix B). Two different equations were used since one equation did not fit the entire curve. Lower levels of light consisted primarily of diffuse radiation that was depleted in the photosynthetically active wavelengths (400–700 nm) measured by the light meter. Therefore the linear relationship overestimated the amount of PPFD from PAR in diffuse light. A log function was better suited for lower levels of light due to the initial gradual increase in slope. A linear relationship fit better for higher levels of light because PAR made up a greater proportion of the total. While HOBO dataloggers are not designed for precise quantification of the light environment, the differences between sunfleck and non-sunfleck periods are so large, that incidents of direct sunfleck radiation were easily detectable (Appendix C).

Clear days were chosen from the data measured by the dataloggers for further use in the quantifying of sunfleck characteristics at each subpopulation. Clear days were distinguished from cloudy days by examining the time-series graphs produced by the dataloggers along with weather information and personal observation. Baseline diffuse light changes during the day were determined using quadratic regression of non-sunfleck light readings spaced at 30-min intervals vs. time (5 AM–8 PM). If there was a positive difference larger than $60 \mu\text{mol m}^{-2} \text{s}^{-1}$ between the measured light levels and the predicted diffuse light level for that time of day, the point was considered a sunfleck. The PPFD light level difference of $60 \mu\text{mol m}^{-2} \text{s}^{-1}$ was chosen based on examinations of the size of clear 'spikes' on graphs produced by the dataloggers (Appendix B) and on a previous study which considered spikes of similar magnitude ($100 \mu\text{mol m}^{-2} \text{s}^{-1}$) to be sunflecks (Chazdon and Pearcy, 1991).

Two sunfleck properties were measured for each ginseng subpopulation: (1) PPFD from sunflecks (%): the total amount of light from sunflecks divided by the total amount of light from 5:00 AM to 8:00 PM. (2) Longest sunfleck: The length of the longest sunfleck in each subpopulation. For both properties, the mean value obtained across seven clear days between June 29 and July 21 was calculated to characterize the sunfleck environment of each ginseng cluster. The variation among subpopulations was analyzed for each characteristic by ANOVA, with subpopulation as the independent variable of interest, day acting as a covariate, and the respective sunfleck characteristic as the dependent variable. All statistical analyses for light measurement were performed using SAS JMP v. 9.0.2 (SAS Institute Inc.).

2.4. Physiological measurements

Photosynthesis and transpiration were measured to determine how sunflecks affect physiological traits of ginseng. Photosynthetic

light curves, measurements of light saturated photosynthetic rates (A_{sat}), and transpiration were obtained using a Li-Cor 6400 gas-exchange system (LiCor, Inc.). For all measurements CO_2 levels were set at $390 \mu\text{L L}^{-1}$ and leaf temperature was set at 25°C . Photosynthesis was measured ($n = 4$) at 0, 50, 100, 150, 200, 300, 400, 500, 600, and $700 \mu\text{mol m}^{-2} \text{s}^{-1}$ in order to establish a photosynthetic light response curve and to determine saturating light intensity. The curve showed that photosynthesis saturated at $500 \mu\text{mol m}^{-2} \text{s}^{-1}$. Therefore, A_{sat} , and transpiration were measured at that light level (Appendix D). The light response curve was fit by Photosyn Assistant (Dundee Scientific, Dundee, UK 2000). Where possible, light saturated photosynthetic rates and transpiration were measured on two ginseng plants per subpopulation on clear days between the times of 11:00 AM and 3:00 PM in mid-July. Only plants with two or three leaves were used in the measurements. Subpopulation 9 was excluded from these measurements due to absence of two or three leaved plants. In subpopulations 13 and 36, there was only one 3-leaved plant per subpopulation. The measurements obtained for A_{sat} , and transpiration for each subpopulation were analyzed in a weighted regression (weighted by replicate number per subpopulation) against % PPFD from sunflecks and longest sunfleck using SAS JMP (v. 9.0.2; SAS Institute Inc.).

2.5. Subpopulation dynamics

Four seasons of census data (2009 through 2012) were used in this study to determine components of subpopulation dynamics. Each year, the population was visited during the spring (between May 25 and June 15) and fall (between August 5 and August 20). During the spring census, lengths and widths of the longest leaflet on each leaf were measured. Leaf area was determined by a previously developed regression equation based on these measurements. The plant was labeled as reproductive (having an inflorescence) or non-reproductive, and new seedlings were counted within a 2 m radius of every adult plant in the subpopulation. During the fall census, berries and seeds were counted on each plant.

Relative growth rate (RGR), germination rate, and seed production efficiency were measured in order to determine the effect of sunflecks on the growth and establishment of ginseng. Since ginseng plants are determinate in size within a season, we hypothesized that sunflecks would affect stored root reserves and produce larger plants in the following year. A nondestructive measure of RGR was therefore calculated for 2011–2012 based on leaf area change (McGraw and Garbutt, 1990):

$$\text{RGR}_{\text{LA}} = (\ln \text{LA}_2 - \ln \text{LA}_1) / (t_2 - t_1)$$

All 2- and 3- leaved ginseng plants present in each subpopulation from 2011 to 2012 that had not been affected by deer browse were included in the mean RGR estimate for the subpopulation. Deer browse has previously been shown to have a negative effect on individual growth, survival, reproduction and overall population dynamics of ginseng (McGraw and Furedi, 2005).

Seed production efficiency was calculated by dividing the number of seeds produced by the leaf area of the respective ginseng for each subpopulation for 2011. Leaf area was used to account for the fact that as leaf area increases so does seed production of American ginseng (Schlessman, 1985).

Germination rate was calculated as the number of seedlings in each subpopulation in 2011 and 2012 divided by the number of seeds produced by each subpopulation in 2009 and 2010. The 2-year time-delay was included because seeds lie dormant in the soil for a minimum of 2 years prior to germinating; A 4-year study with seed cages showed that more than 70% of seeds germinated after two winters at this site (McGraw, unpublished data). Since

seed viability of counted seeds is nearly 100% and more than 90% of seeds are dispersed within 2 m of the parent plant (McGraw and Furedi, 2005), we inferred that germinated seedlings (2011 + 2012)/seeds produced (2009 + 2010) was a good integrated estimate of effective germination rate for a subpopulation.

All measurements were analyzed using regression in SAS JMP (v. 9.0) against % PPFD from sunflecks and longest sunfleck. Mean relative growth rate and seed production efficiency values for each cluster were weighted by sample size. Germination rate in a subpopulation was weighted by the total number of seeds.

3. Results

The mid-season understory light environment varied widely among subpopulations of ginseng due to spatial variation in sunflecks (Fig. 1). The contribution of sunflecks to total PPFD ranged from 4% to 35.6% ($F = 19.94$, $p < 0.0001$). The length of the longest sunfleck varied from ca. 2 min to as high as 10 min ($F = 7.04$, $p < 0.0001$). At the low end of both scales (subpopulations 9, 26, 28, and 32), the common canopy factor was the presence of *Fagus grandifolia* (Appendix A), a species known to cast dense shade. The majority of the sunflecks, especially sunflecks of longer duration, occurred in the afternoon from 1:00 PM to 3:00 PM for each subpopulation; this span includes solar noon for mid-season at the latitude of the site. The two sunfleck characteristics were correlated with each other ($r = 0.9610$, $p < 0.0001$). The highest % PPFD contribution and the longest sunfleck both occurred in the same subpopulation (ID = 13), as did the lowest % PPFD contribution and shortest duration of the longest sunfleck (ID = 32; Fig. 1).

Light saturated photosynthetic rate of ginseng had a positive linear relationship with both % PPFD from sunflecks ($p = 0.0268$) and length of the longest sunfleck ($p = 0.0352$; Fig. 2A and B). The increase in A_{sat} from the lowest to the highest sunfleck microenvironments was nearly 50%. Transpiration rate was not affected by either % PPFD contribution ($p = 0.6395$) or sunfleck duration ($p = 0.5902$; Fig. 2C and D).

Consistent with the enhanced photosynthetic response, mean relative growth rate of individuals on a leaf area basis showed the same tendency across subpopulations over a 1 year period (2011–2012; Fig. 3). The positive linear relationship to long-term growth was slightly greater for maximum sunfleck duration than for percent PPFD contribution from sunflecks ($p = .0323$ vs. $p = .0606$). Both regressions suggest a minimum sunfleck threshold is required before a mean growth in leaf area is possible since both regression lines crossed the x -axis (Fig. 3); plants declined in size below the threshold. No change was observed in seed production efficiency (seeds per unit leaf area) as a function of sunfleck microenvironment characteristics: % PPFD contribution ($p = 0.6713$) and longest sunfleck ($p = 0.8223$) (Fig. 4).

In contrast to the photosynthetic and growth patterns, germination rate had a negative linear relationship with % PPFD from

sunflecks ($p = 0.0252$; Fig. 5A). The germination response to sunfleck duration showed a similar trend ($p = 0.0735$; Fig. 5B). Germination varied from ca. 50% at the low end of the PPFD range to near 0 at the high end.

4. Discussion

4.1. Sunfleck patterns

The understory light environment showed a large degree of heterogeneity, as expected for a deciduous forest containing a mixture of mature trees. Sunflecks were present, and their duration as well as contribution to the overall light available to the understory, varied spatially, which can be seen by the variation of the sunfleck characteristics among the subpopulations, each having a unique combination of canopy tree species. This result meshes with those of other studies that have shown the overhead canopy having a large influence on the types of sunflecks received by the understory (Baker, 1996; Fladeland et al., 2003; Oláh and Masarovičová, 1997; Sakai et al., 2005). Despite measuring the sunfleck environment over several weeks in midseason, with associated changes in sun angle and intensity, sunfleck patterns within a subpopulation were consistent over time and significantly different among patches on the forest floor. Similar results were found by Young and Smith (1980) who concluded that sunflecks are relatively predictable day to day at a specific site through a season when excluding variations due to weather. Notably, the sunfleck variation in the studied forest was not due to large gap formation due to death of or defoliation of large trees; rather, variation appeared due to minor branch breakage or loss of scattered small canopy trees through density-dependent thinning, as well as variation in canopy architecture among tree species.

4.2. Ginseng responses to sunfleck patterns

The midseason light environment of a subpopulation affected the light saturated photosynthetic rates of plants in subpopulations, such that those plants exposed to more sunflecks were better able to respond at higher light intensities. It is possible that increased sunfleck frequency and duration would be correlated with diffuse light penetration, making it difficult to disentangle those effects; however this correlation was not significant ($r = .3545$, $p = .3149$). Photosynthetic acclimation to varying light exposure is commonly observed, though not ubiquitous (Ellsworth and Reich, 1992; Leakey et al., 2003; Montgomery and Givnish, 2008; Neufeld and Young, 2003; Nobel et al., 1975; Watling et al., 1997; Yin and Johnson, 2000; Young and Smith, 1980). Plants can acclimate to a light environment in numerous ways to allow for more efficient capture and use of light (Bailey et al., 2000; Ernstsen et al., 1997; Katahata et al., 2005; Walters and Horton, 1994). Plants can increase or decrease the number of chloroplasts produced per unit

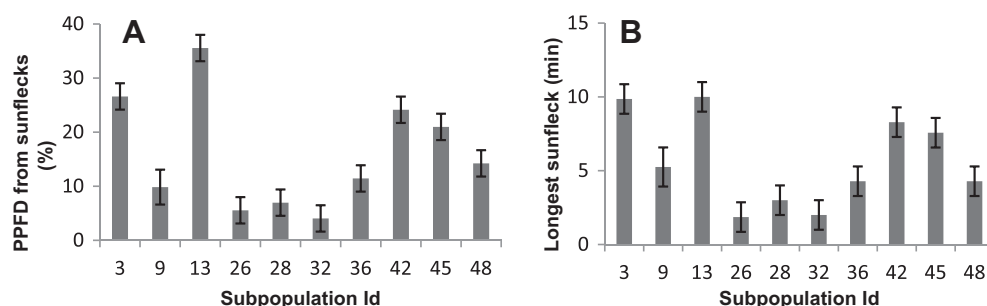


Fig. 1. Mean sunfleck characteristics (± 1 s.e.) in 10 subpopulations of the local population (A) mean percentage of PPFD per day from sunflecks (B) mean length of the longest sunfleck.

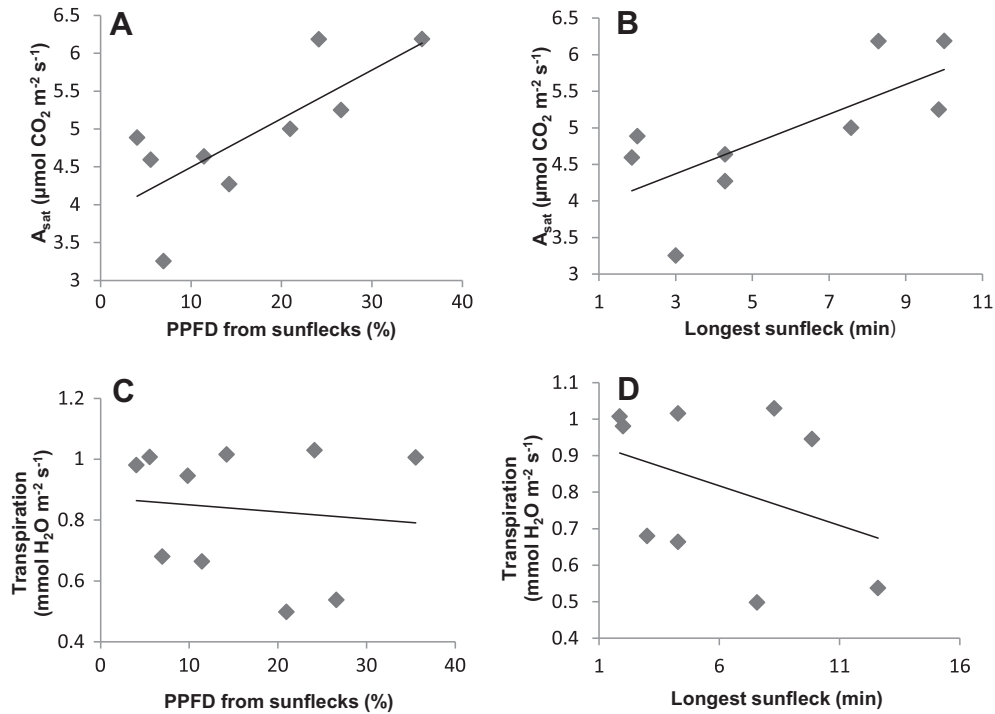


Fig. 2. The effect of sunflecks on mean photosynthetic capacity (A and B) and transpiration rate (C and D) in 9 subpopulations of ginseng.

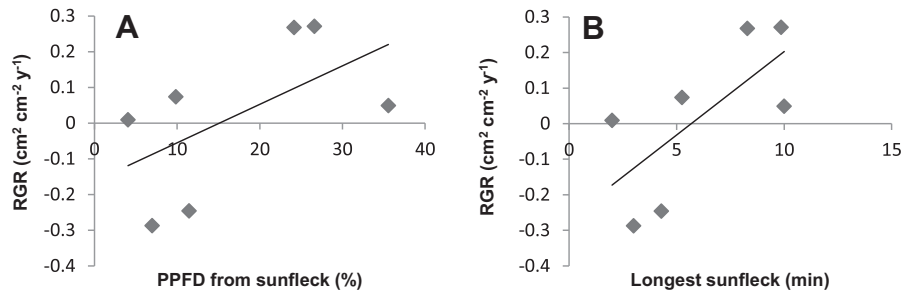


Fig. 3. The effect of sunflecks on the relative growth rate (RGR; 2011–2012) based on leaf area of 10 subpopulations of American ginseng in relation to (A) mean percentage of PPFD from sunflecks per day and (B) mean longest sunfleck duration per day.

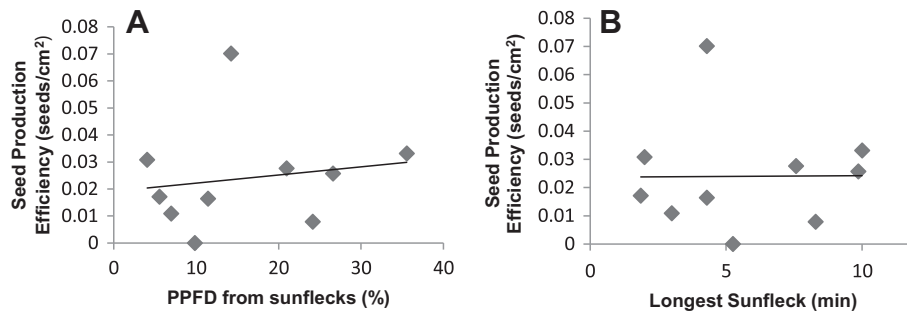


Fig. 4. The effect of sunflecks on seed production efficiency (number of seeds produced per unit leaf area of ginseng) in 10 subpopulations of American ginseng with relation to (A) mean percentage of PPFD from sunflecks per day (B) mean longest sunfleck duration per day.

leaf area (Bailey et al., 2000). The rates of Rubisco activation and deactivation can also be adjusted to light (Ernstsen et al., 1997). *Ocimum basilicum* had slower deactivation rates of Rubisco when grown under fluctuating light environments than when in a shade

environment, allowing for the sequential higher levels of light to be efficiently utilized (Ernstsen et al., 1997). Overall levels of Rubisco present are dependent on light (Bailey et al., 2000). Changes in chlorophyll a/b ratio can occur over a season, allowing for

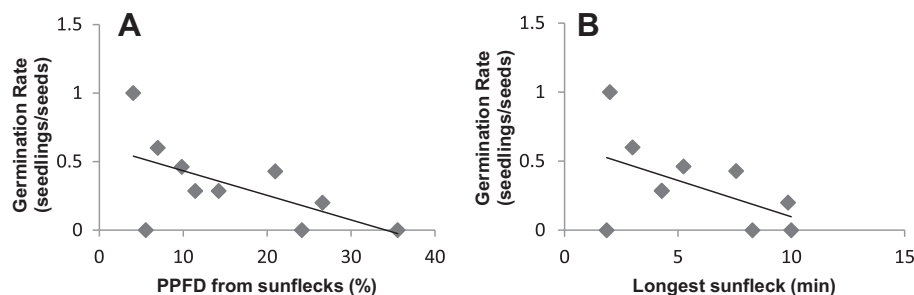


Fig. 5. The effect of sunflecks on germination rate (the number seedlings from 2011 to 2012 per number of seeds produced from 2009 to 2010) in 10 subpopulations of American ginseng with relation to (A) mean percentage of PPFd from sunflecks per day (B) mean longest sunfleck duration per day.

differences in light harvesting (Katahata et al., 2005). Also changes in the ratio of photosystem II to photosystem I occur to allow acclimation to different light quality (Walters and Horton, 1994). A previous study examining the effect of the understory light environment on ginseng found differences in the maximum quantum yield of photosystem II due to the understory light environment (Fournier et al., 2008). Also, as PPFd decreased due to the closing of the canopy the ratio of chlorophyll a/b in ginseng decreased (Fournier et al., 2008).

The lack of response of transpiration to the understory sunfleck environment may be due to the spring emergence of ginseng leaves in a more uniform light environment prior to canopy tree leafout. Stomatal size and densities might therefore have been similar among subpopulations despite later midseason light environment differences. There is still a possibility that the rate of stomatal opening and closure, and therefore transpiration, would differ among subpopulations. Perhaps the differences in light environment were simply not enough to cause stomatal closure. Alternatively, in the year of measurement soil moisture may have been adequate throughout the growing season, given that rainfall was substantial and frequent throughout the period (Appendix E).

One of the most remarkable findings of this study was that the sunfleck microenvironment, measured over a single midseason period (44 days), predicted leaf area change of individual ginseng plants from 1 year to the next. The light measurements probably reflected long-term differences in light environment, both earlier and later in the season, and therefore resulted in more or less stored reserves to support the next year's growth. The demonstrated relationship suggested that if there was not enough light input from sunflecks, plants would decline in size, and above a threshold they would increase. As survival, growth, and reproduction have been shown to be strongly size-dependent in ginseng (Charron and Gagnon, 1991), such growth changes, if sustained, likely pre-sage the eventual fate of entire clusters. While we used linear regression to establish the functional relationship between growth rate and sunflecks, and a plausible causative mechanism exists (greater carbon assimilation due to enhanced photosynthesis), explanations other than light variation are also possible. For example, different canopy tree species were associated with the lower sunfleck levels. Trees such as red oak (*Quercus rubra*), red maple (*Acer rubrum*), and white ash (*Fraxinus americana*) have a high amount of sunfleck occurrence in their understory, while more shade tolerant trees, such as hemlock (*Tsuga*), beech (*Fagus grandifolia*), and sugar maple (*Acer saccharum*) have lower amounts of sunflecks (Canham et al., 1994). These tree species affect soil properties below their canopies as well as the light environment, through differential leaf decomposition, leaf litter accumulation, and root properties such as depth and nutrient uptake rates (Finzi et al., 1998). These other effects of specific canopy trees could alter ginseng growth as well, but they were unmeasured in this study.

The negative effects of sunflecks on ginseng germination are somewhat difficult to interpret since the light environment of the seeds was not measured (dataloggers were placed at adult plant height). If additional sunflecks in a patch stimulated more growth of competing herbaceous plants, ginseng seeds may have actually been more shaded in high sunfleck than in lower sunfleck microenvironments. Alternatively, higher exposure to sunflecks may have dried out the seeds, resulting in greater mortality than in low sunfleck environments. Whatever the cause of lower germination, our results suggest that the understory light environment that is good for adult plant growth may not be good for offspring recruitment.

The understory light environment has been described as a possible control for distribution and abundance of the understory herb layer (Tomita and Seiwa, 2004). The above results support that idea and help explain the spatial distribution of ginseng across the forest floor due to influence from the sunfleck environment. Established ginseng populations may likely be found under canopies where sunflecks contribute to the light environment. The greater amounts of PAR from the sunflecks allow for more growth in the ginseng that are present. The high presence of sunflecks will not be beneficial for the germination of ginseng, especially under canopies that allow a high % PPFd and long durations of sunflecks. Therefore, new subpopulations of ginseng may be established in areas that have less of a sunfleck presence. Seedling establishment is a vulnerable stage in a plant's life cycle, so seed dispersal and the presence of a suitable light habitat are important in the establishment of new subpopulations or possibly populations, depending on length of dispersal (Goode and Allen, 2009). After establishment further growth could be aided by treefall or other disturbances that can open up a canopy. These patterns are evidence that the 'dynamic mosaic' (Neufeld and Young, 2003) light environment exerts a temporally varying influence on understory plants such as ginseng.

Numerous disturbances can open up the forest canopy and stimulate understory plant growth. Within the 30 censused ginseng populations in our larger set of populations studied, ice storms and subsequent branch breakage, lightning strikes killing part or all of tree crowns, wind damage causing partial crown or total tree death, and herbivory by defoliating insects (gypsy moth/tent caterpillars) have all caused canopy openings above ginseng clusters. Such disturbances will likely benefit existing patches of ginseng plants. Our study site had none of these major disturbances, so caution is in order before extrapolating our results to larger canopy gaps.

4.3. Conclusions

Based on the overall results this study, a spatially and temporally heterogeneous canopy would likely provide the optimal light environment for establishment and growth of ginseng. It seems likely that species such as ginseng were well-adapted to the heter-

ogeneous light regime of old growth forests caused by the presence of varying tree age, size, and species composition, and a dynamic light environment with repeated gap formation and closure (Knohl et al., 2003; Manabe et al., 2009; Spies et al., 2006). If this is true, forest management practices that create such variable light environments would also be beneficial to understory plant populations such as ginseng (Liira and Kohv, 2010). Because of the complex response of different life history stages, one should not expect such a 'healthy' understory to consist of continuous dense populations. Instead, spatially and temporally dynamic patches of plants will be sustained over time.

Acknowledgments

We thank Zach Bradford, Jen Chandler, Amy Hruska, and Jessica Turner for their help on this project in the field and in the lab. We also thank previous census crews who gathered the plant size data from 2009 to 2012. In addition, we thank Kenneth Smith for his assistance with the Li-Cor 6400. Susan Raylman, Richard Thomas, and William Peterjohn provided helpful comments on the sampling protocols, measurements and manuscript. This project was funded by the Henry W. Hurlbutt Memorial Endowment and by NSF Grants DEB-0613611 and DEB-1118702 to JBM.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2012.11.038>.

References

- Anderson, R.C., Fralish, J.S., Armstrong, J.E., Benjamin, P.K., 1993. The ecology and biology of *Panax quinquefolium* L. (Araliaceae) in Illinois. *Am. Midl. Nat.* 129, 357–372.
- Bailey, S., Walters, R.G., Jansson, S., Horton, P., 2000. Acclimation of *Arabidopsis thaliana* to the light environment: the existence of separate low light and high light responses. *Planta* 21, 794–801.
- Baker, N.R., 1996. *Photosynthesis and the Environment*, New York.
- Canham, C.D., Finzi, A.C., Pacala, S.W., Burbank, D.H., 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Can. J. For. Res.* 24, 337–349.
- Charron, D., Gagnon, D., 1991. The demography of northern populations of *Panax quinquefolium* (American ginseng). *J. Ecol.* 79, 431–445.
- Chazdon, R.L., 1988. Sunflecks and their importance to forest understory plants. *Adv. Ecol. Res.* 18, 1–63.
- Chazdon, R.L., Pearcy, R.W., 1986. Photosynthetic responses to light variation in rainforest species I. Induction under constant and fluctuating light conditions. *Oecologia* 69, 517–523.
- Chazdon, R.L., Pearcy, R.W., 1991. The importance of sunflecks for forest understory plants. *Bioscience* 41, 760–766.
- Cruse-Sanders, J.M., Hamrick, J.L., 2004. Spatial and genetic structure within populations of wild American ginseng (*Panax quinquefolium* L., Araliaceae). *J. Heredity* 95, 309–321.
- Ellsworth, D.S., Reich, P.B., 1992. Leaf mass per area, nitrogen content and photosynthetic carbon gain in *Acer saccharum* seedlings in contrasting forest light environments. *Funct. Ecol.* 6, 423–435.
- Ernstsen, J., Woodrow, I.E., Mott, K.A., 1997. Responses of Rubisco activation and deactivation rates to variations in growth-light conditions. *Photosynth. Res.* 52, 117–125.
- Finzi, A.D., Canham, C.D., Van Breemen, N., 1998. Canopy tree-soil interactions within temperate forests: species effects on pH and cations. *Ecol. Appl.* 8, 447–454.
- Fladeland, M.M., Ashton, M.S., Lee, X., 2003. Landscape variations in understory PAR for a mixed deciduous forest in New England, USA. *Agric. For. Meteorol.* 118, 137–141.
- Fournier, A.R., Gosselin, A., Proctor, J.T.A., Gauthier, L., Khanizadeh, S., Dorais, M., 2004. Relationship between understory light and growth of forest-grown American ginseng (*Panax quinquefolium* L.). *J. Am. Soc. Hort. Sci.* 129, 425–432.
- Fournier, A.R., John, T.A., Khanizadeh, S., Gosselin, A., Martine, D., 2008. Acclimation of maximum quantum yield of PSII and photosynthetic pigments of *Panax quinquefolium* L. to understory light. *J. Ginseng Res.* 32, 347–356.
- Gilliam, F.S., Roberts, M.R., 2003. *The Herbaceous Layer in Forests of Eastern North America*, New York.
- Gilliam, F.S., Turrill, N.L., 1993. Herbaceous layer cover and biomass in a young versus a mature stand of a central Appalachian Hardwood Forest. *Bull. Torrey Bot. Club* 120, 445–450.
- Goode, L.K., Allen, M.F., 2009. Seed germination conditions and implications for establishment of an epiphyte *Aechmea bracteata* (Bromeliaceae). *Plant Ecol.* 204, 179–188.
- Grant, R.H., 1997. Partitioning of biologically active radiation in plant canopies. *Int. J. Biomet.* 40, 26–40.
- Hackney, E., McGraw, J.B., 2001. Experimental demonstration of an Allee effect in American ginseng. *Cons. Biol.* 15, 129–136.
- Hull, J.C., 2002. Photosynthetic induction dynamics to sunflecks of four deciduous forest understory with different phenologies. *Int. J. Plant Sci.* 163, 913–924.
- Katahata, S., Naramoto, M., Kakubari, Y., Mukai, Y., 2005. Photosynthetic acclimation to dynamic changes in environmental conditions associated with deciduous overstory phenology in *Daphniphyllum humile*, an evergreen understory shrub. *Tree Phys.* 25, 437–445.
- Knohl, A., Schulze, E., Kolle, O., Buchmann, N., 2003. Large carbon uptake by an unmanaged 250-year-old deciduous forest in Central Germany. *Agric. For. Meteorol.* 118, 151–168.
- Kursar, T.A., Coley, P.D., 1993. Photosynthetic induction in shade-tolerant species with long and short-lived leaves. *Oecologia* 93, 165–170.
- Le Gouallec, J.L., Cornic, G., Blanc, P., 1990. Relations between sunfleck sequences and photoinhibition of photosynthesis in a tropical rainforest understory herb. *Am. J. Bot.* 77, 999–1006.
- Leakey, A.D.B., Press, M.C., Scholes, J.D., 2003. Patterns of dynamic irradiance affect the photosynthetic capacity and growth of dipterocarp tree seedlings. *Oecologia* 135, 184–193.
- Lewis, W.H., Zenger, V.E., 1982. Population dynamics of the American ginseng *Panax quinquefolium* (Araliaceae). *Am. J. Bot.* 69, 1483–1490.
- Liira, J., Kohv, K., 2010. Stand characteristics and biodiversity indicators along the productivity gradient in boreal forests: defining a critical set of indicators for the monitoring of habitat nature quality. *Plant Biosyst.* 144, 211–220.
- Manabe, T., Shimatani, K., Kawarasaki, S., Aikawa, S., Yamamoto, S., 2009. The patch mosaic of an old-growth warm-temperate forest: patch-level descriptions of 40-year gap-forming processes and community structures. *Ecol. Res.* 24, 575–586.
- McGraw, J.B., Furedi, M.A., 2005. Deer browsing and population viability of a forest understory plant. *Science* 307, 920–922.
- McGraw, J.B., Garbutt, K., 1990. Demographic growth analysis. *Ecology* 71, 1199–2004.
- McGraw, J.B., Sanders, S.M., Van der Voort, M., 2003. Distribution and abundance of *Hydrastis Canadensis* L. (Ranunculaceae) and *Panax quinquefolium* L. (Araliaceae) in the central Appalachian region. *J. Torrey Bot. Soc.* 130, 62–69.
- McGraw, J.B., Souther, S., Lubbers, A.E., 2010. Rates of harvest and compliance with regulations in natural populations of American ginseng (*Panax quinquefolium* L.). *Nat. Areas J.* 30, 202–210.
- Montgomery, R.A., Givnish, T.J., 2008. Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: dynamic photosynthetic responses. *Oecologia* 155, 455–467.
- Mooney, E.H., McGraw, J.B., 2007. Effects of self-pollination and outcrossing with cultivated plants in small natural populations of American ginseng, *Panax quinquefolium* (Araliaceae). *Am. J. Bot.* 94, 1677–1687.
- Nantel, P., Gagnon, D., Nault, A., 1996. Population viability analysis of American ginseng and wild leek harvested in stochastic environments. *Cons. Biol.* 10, 608–621.
- Neufeld, H.S., Young, D.R., 2003. Ecophysiology of the herbaceous layer in temperate deciduous forests. In: Gilliam, F., Roberts, M. (Eds.), *The Herbaceous Layer in Forests of Eastern North America*, Oxford University Press, pp. 38–90.
- Nobel, P.S., Zaragoza, L.J., Smith, W.K., 1975. Relation between mesophyll surface area, photosynthetic rate, and illumination level during development for leaves of *Plectranthus parviflorus* Henckel. *Plant Phys.* 55, 1067–1070.
- Oláh, R., Masarovičová, E., 1997. Responses of CO₂ uptake, chlorophyll content, and some production features of forest herb *Smyrniolium perfoliatum* L. (Apiaceae) to different light conditions. *Acta Phys. Plant.* 19, 285–293.
- Pearcy, R.W., 2007. Responses of plants to heterogeneous light environments. In: Pugnaire, F., Valladares, F. (Eds.), *Functional Plant Ecology*, second ed. CRC Press, pp. 213–246.
- Pearcy, R.W., Krall, J.P., Sassenrath-Cole, G.F., 2004. Photosynthesis in fluctuating light environments. *Photosyn. Environ.* 5, 321–346.
- Robbins, C.S., 2000. Comparative analysis of management regimes and medicinal plant trade monitoring mechanisms for American ginseng and goldenseal. *Cons. Biol.* 14, 1422–1434.
- Sakai, T., Saigusa, N., Yamamoto, S., Akiyama, T., 2005. Microsite variation in light availability and photosynthesis in a cool-temperate deciduous broadleaf forest in central Japan. *Ecol. Res.* 50, 537–545.
- Schlessman, M.A., 1985. Floral biology of American ginseng (*Panax quinquefolium*). *Bull. Torr. Bot. Club.* 112, 129–133.
- Souther, S., McGraw, J.B., 2011. Evidence of local adaptation in the demographic response of American ginseng to interannual temperature variation. *Conservation Biol.* 25, 922–931.
- Spies, T.A., Hemstrom, M.A., Youngblood, A., Hummel, S., 2006. Conserving old-growth forest diversity in disturbance-prone landscapes. *Conserv. Biol.* 20, 351–362.
- Tomita, M., Seiwa, K., 2004. Influence of canopy tree phenology on understory populations of *Fagus serratata*. *J. Vegetation Sci.* 15, 379–388.

- Vockenhuber, A., Scherber, C., Langenbruch, C., Meißner, M., Seidel, D., Tschardtke, T., 2011. Tree diversity and environmental context predict herb species richness and cover in Germany's largest connected deciduous forest. *Persp. Plant Ecol. Evol. Syst.* 13, 111–119.
- Walters, R.G., Horton, P., 1994. Acclimation of *Arabidopsis thaliana* to the light environment: changes in composition of the photosynthetic apparatus. *Planta* 195, 248–256.
- Watling, J.R., Ball, M.C., Woodrow, I.E., 1997. The utilization of lightflecks for growth in four Australian rainforest species. *Funct. Ecol.* 11, 231–239.
- Yin, Z., Johnson, G.N., 2000. Photosynthetic acclimation of higher plants to growth in fluctuating light environments. *Photosyn. Res.* 63, 97–107.
- Young, D.R., Smith, W.K., 1980. Influence of sunlight on photosynthesis, water relations, and leaf structure in the understory species *Arnica cordifolia*. *Ecology* 61, 1380–1390.