# Seasonal Variation in Understory Light Near a Gap Edge and its Association with Conifer Seedling Survival in a Southern New England Forest

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**Abstract** - Forest edge-generated gradients in understory light are known to influence the survival of tree seedlings in North American deciduous forests, but the seasonality of that influence has not been investigated for the forests of southern New England. We examined the winter versus summer difference in photosynthetically active radiation (PAR) transmitted through a southern New England forest canopy in the vicinity of a large experimental canopy gap and investigated if this difference influenced the survival of *Pinus strobus* L. (White Pine) and *Tsuga canadensis* (L.) Carr. (Eastern Hemlock) seedlings along a gap–forest gradient using Kaplan-Meier survival curves and Cox proportional hazards models. The mean and the spatial distribution of winter understory PAR transmittance (%T) across the gap–forest gradient were significantly different from those of summer %T. Distance from gap edge into the forest and variability in %T during the winter months were associated with the survival of White Pine seedlings, but not with that of Eastern Hemlock seedlings, which had a constant survival probability throughout the gap–forest gradient. Summer %T was not associated with the survival of seedlings of either species. Experimentally, we found that digital fisheye canopy photos did not accurately capture the range in understory light level along a gap–forest gradient. Thus they are a poor proxy for direct PAR transmittance measurements and should be used with caution in southern New England forests, which are highly fragmented and contain many edges. Forest management actions for the conservation of White Pine should take into account winter understory light regimes rather than summer regimes.

## Introduction

Fragmentation creates edges between forested and non-forested areas that have ecological effects on the remaining forests (Butler and Wharton 2002, Harper et al. 2005). On average, 62% of forested lands in the US are located within 150 m of a human-created forest edge (Riitters et al. 2002), and, in southern New England, forest fragments are often too small to sustain many forest-dwelling species of plants, animals, and fungi (Chen et al. 1992). Still, there are many southern New England forests large enough to harbor a suite of native species and provide valuable ecosystem services that are therefore worth conserving.

Forest edges have complex influences on forest ecosystems. They change the microclimate and availability of resources such as light, soil moisture, and soil nutrients (Ashton and Larson 1996, Coates 2000, Denslow et al. 1998, Scharen-broch and Bockheim 2007) and temporarily or permanently change the dynamics of the affected forest community (Saunders et al. 1990, Turner 1996) including

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the regeneration of canopy trees (Harper et al. 2005). Southerly sun angles in the northern hemisphere generate different amounts of understory sunlight on differ-ent sides of a forest gap (Fig. 1; Canham 1989). Thus, the influence of a forest edge on the survival of tree seedlings depends on their level of shade tolerance (which is species-specific; Canham 1989), their distance from the edge (Chacón and Armesto 2005), and their cardinal location with respect to that edge (Canham et al. 1990, Coates 2000).

Experimentally created temperate forest gaps are useful for investigations of forest-edge effects (Ashton and Larson 1996). In this respect, they have an advan-tage over the forest edges created by agriculture or urban development, which may introduce many confounding variables (increase in air and water pollution, pres-ence of exotic plants and animal species, etc.) that are difficult to track and control. Although the effects of small (Sipe and Bazzaz 1995) or large forest-gap edges (Ashton and Larson 1996, Pacala et al. 1993) on survival of tree seedlings have been studied in New England forests, the understory light regime associated with those forest gaps and edges has not always been explicitly measured, making it difficult to relate seedling survival with the effects of gaps on light availability. Similarly, although the seasonality of forest understory light regimes has been described for some North American forests (Canham et al. 1990), and the seasonality of temperate forest tree seedling germination has been examined (Vranckx and Vandelook 2012), the seasonality of large forest-gap edge effects on the survival of native tree seed-lings has not been studied in southern New England forests. Furthermore, studies on the seasonality of understory light regimes (e.g., Canham et al. 1990) have relied on indirect measures of understory light such as fisheye forest canopy photographs rather than on direct measurements of understory photosynthetically active radia-tion (PAR).

We examined whether seedling distance from the edge of a large experimental forest gap, understory PAR transmittance (%T), and forest canopy openness were significant predictors of seedling survival for 2 native coniferous tree species along a gap–forest gradient in a southern New England *Quecus* (oak)–*Carya* (hickory) forest. Understanding how forest-understory light and its seasonal variation affect the survival of tree seedlings near a forest-gap edge can provide insight into how
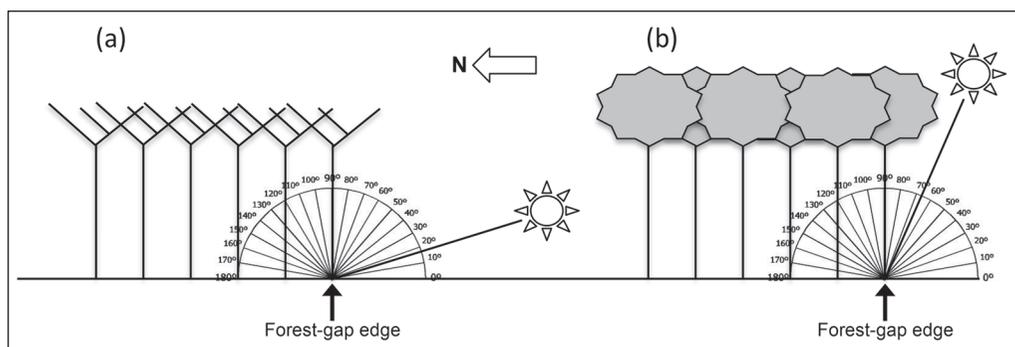


Figure 1. Canopy cover and sun angle at a south-facing forest-gap edge on (a) winter sol-stice, and (b) summer solstice in northeastern Connecticut.

forest dynamics respond to fragmentation, which could contribute to the improved management and conservation of southern New England forests. We focused this study on 2 evergreen coniferous tree species native to southern New England. *Pinus strobus* L. (Eastern White Pine, hereafter Pine) is fast-growing and shade intolerant in its natural habitat (Wendel and Clay Smith 1990). *Tsuga canadensis* (L.) Carr. (Eastern Hemlock, hereafter, Hemlock) is a slow-growing, shade-tolerant species (Canham 1989, Godman and Lancaster 1990).

While many studies of seedling survival, including those of Pine and Hemlock, have employed chi-square tests (e.g., Sipe and Bazzaz 1995), logistic regression, maximum likelihood, or variants thereof (e.g., Chacón and Armesto 2005, Kobe et al. 1995), these methods do not use valuable survival and mortality information regarding the timing of the mortality itself. Survival-analysis techniques such as Kaplan-Meier survival curves and Cox proportional hazards models incorporate information on the timing of mortality (Kleinbaum and Klein 2012, Mills 2011, Walters and Reich 2000), and we therefore opted to model the survival of Pine and Hemlock using survival analysis with a dataset collected on a cohort of naturally occurring seedlings over a 5-year period.

Studies have shown that for other Northeastern American temperate forest tree species such as *Acer saccharum* Marsh. (Sugar Maple), the short period of time between the end of winter and the beginning of canopy-tree leaf-out in early spring contributes the most to the overall carbon budget of seedlings in forests of Ontario, Canada (Kwit et al. 2010), and Illinois (Augspurger et al. 2005). Seedlings of deciduous species typically leaf-out earlier than their conspecific adult neighbors and take advantage of this critical period of high understory light, a phenomenon referred to as canopy avoidance. Although the 2 species we focus on in this study are evergreen, constraints on their carbon budget and survival under a mixed deciduous forest canopy are likely comparable to those of deciduous tree seedlings (Seiwa et al. 2009).

We are not aware of any study that has analyzed how the seasonality of understory light influences the survival of tree seedlings in the vicinity of large forest-gap edges in southern New England forests. We therefore asked 3 questions regarding southern New England oak–hickory forests: 1) Does understory light, measured directly as % transmittance (%T) and indirectly from canopy openness (% open sky from fisheye photos) differ significantly between winter and summer? 2) Does Pine and/or Hemlock seedling survival vary significantly across the gap–forest gradient? and, 3) Is survival significantly associated with either %T or % open sky? Specifically, (a) are the seedling responses similar for both %T and % open sky? (b) Are the responses similar in winter versus summer? and, (c) Do Pine and Hemlock differ in their patterns of survival relative to %T, % open sky, and seasons?

We predicted that (1) due to lower winter-sun angles and the presence of a large gap to the south of the edge, understory light (%T and % open sky) would be different between winter and summer; (2) Pine seedling survival would decrease from gap edge into the forest due to low shade tolerance of that species (Kobe et al. 2002, Walters and Reich 2000), but shade-tolerant Hemlock seedling survival would not be affected by distance from gap edge into the forest; and

(3) because of the canopy-avoidance phenomenon, survival of Pine and Hemlock would be more strongly associated with winter than with summer understory light levels, and both %T and % open sky would be good predictor variables of that survival for either species. We hypothesized that the influence of understory light on seedling survival would be stronger for the shade-intolerant Pines than for the shade-tolerant Hemlocks.

## Methods

### Study site

The 7800-ac Yale Myers Forest, located in the town of Eastford, CT (elevation 200 m), is owned and managed by the Yale University School of Forestry and Environmental Studies (YSFES). Our study site (41°59'2"N, 72°07'30"W) was located at the Tree Heaven Experimental Large Gap (ELG), a 110 m × 25 m artificial gap created by the Yale Forestry crew (clear-cut, including shrubs, and all slash removed) during winter 1999–2000 (Mark Ashton, YSFES, New Haven, CT, pers. comm.). The ELG has a long east–west axis and has regenerated naturally since the cut. The surrounding forest is composed of *Acer rubrum* L. (Red Maple; 42%), *Quercus rubra* L. (Red Oak; 25%), Sugar Maple (12%), White Pine (8%), *Betula lenta* L. (Sweet Birch; 7%, mostly at the margins of the gap), *Quercus velutina* Lam. (Black Oak; 5%), and Eastern Hemlock (1%) (R.C. de Gouvenain, unpubl. data). The largest and possibly the oldest trees are Red Oaks (dbh > 50 cm; age > 115 yrs; R.C. de Gouvenain, unpubl. data). At the time of this study, vegetation within the gap had an average dbh of <5 cm and was dominated by <10-year-old patchy regeneration of Sweet Birch. For the purposes of this study, we broadly defined the periods 1 October to 30 April (prior to canopy tree leaf-out) and 1 May to 30 September (after leaf-out) as winter and summer, respectively.

### Transect layout and sampling

In 2009, we established four 10 m × 40 m belt transects from randomly selected starting points along the northern edge of the ELG running perpendicular to the east–west-oriented edge. Transects ran from 10 m into the gap (hereafter, -10 m) to 30 m into the forest, following methods of McDonald and Urban (2004), with the mid-line of each transect located at least 10 m from any other transect mid-line. For each belt transect:

We tagged, numbered, and tallied by species all Pine and Hemlock seedlings, measured their height and basal diameter, and recorded the distance of each to the northern edge of the gap (negative distances for seedlings growing inside the gap, positive distances for seedlings growing inside the forest, with 0 m at the gap–forest edge). We inventoried a total of 401 seedlings—350 Pines and 51 Hemlocks.

We made 2 measurements of photosynthetically active radiation (PAR) 10 cm above each seedling (hereafter, seedling PAR) with a LI-COR® quantum sensor and data logger (Li-Cor, Lincoln, NE) between 10:00 am and 2:00 pm on overcast days 6 times during the study period (3 times each in the winter and summer months). We recorded synchronous PAR measurements (hereafter referred to as base PAR)

in an open field with another quantum sensor and data logger. To avoid spatial or temporal bias, we randomly chose starting points for yearly PAR measurements among the 4 transects. We calculated percent transmittance (%T) of PAR through the forest canopy above each seedling as:

%T = (seedling PAR / base PAR) x 100%

We took 1 hemispherical fisheye canopy photo between 10:00 am and 2:00 pm on overcast days with a Nikon D700 fitted with a Sigma 8-mm lens held 10 cm above each seedling 6 times during the study period (3 times each in the winter and summer months), and analyzed the images using the software GLA (Frazer et al. 1999) to calculate % open sky, a measure of forest canopy openness above each seedling.

We collected data annually for a period of 5 years (total study length = 60 months), except %T and % open sky, which we measured in 2009, 2010, and 2013. We recorded all dead seedlings and defined survival time for any seedling as the time from the beginning of the study in 2009 to the time it was found dead. Seedlings alive at the end of the study were counted as censored in the survival analyses. We analyzed the growth of these seedlings in a separate study.

To control for the potential confounding effect of seedling size and/or age on survival in this study, we selected 32 of the 350 inventoried Pine seedlings using stratified random sampling at the end of the 5-y study (2 seedlings per 10-m distance interval per transect) and either collected a core (for seedlings ≥2 cm diameter at base) or a stem basal cross-section (for seedlings <2 cm diameter). Any seedling located within a YSFES research plot was not sampled; instead we sampled the closest seedling outside any such plot. Hemlock seedlings were not numerous enough to be subsampled for size and age. We mounted and sanded Pine cores and cross-sections on wood bases, and counted rings under a dissecting microscope.

### Data analysis

We calculated the average of the measurements of %T for each seedling taken on a given sampling date. We employed R (R Core Team 2014) and a Wilcoxon Mann-Whitney test to graphically and statistically analyze the difference between average understory %T in winter and summer. We compared linear least-squares regression models and nonlinear exponential models to each other and to a null model with slope = 0 using Akaike information criterion (AIC) to analyze the association between winter or summer understory %T and distance from the gap–forest edge, and between winter or summer % open sky and distance, respectively. Following Hilborn and Mangel (1997) and Logan (2010), a model with a smaller AIC (by a |difference| > 2) was designated as the model that best fit our data. Using the subsample of 32 Pine seedlings that had been aged, we analyzed the association of Pine seedling diameter and age with distance to gap edge using linear regression models.

We analyzed survival data using the IBM SPSS® statistical package and employed Kaplan-Meier (KM) survival analysis to analyze time-to-death data on Pine and Hemlock seedlings that were grouped according to their distance from the gap edge (groups 1–4 corresponded to seedlings located between -10 m and 0

m, 0 m and 10 m, 10 m and 20 m, and 20 m and 30 m, respectively). This analysis considered the possible differences (1) between the 2 species and (2) within each species between distance groups. Differences in survival distribution among groups were tested with the log-rank (Mantel-Cox) test following Kleinbaum and Klein (2012).

To analyze the effects of predictor variables on seedling survival, we employed an extension of the Cox proportional hazards model (hereafter, Cox model) to allow for time-dependent covariates as predictors in the model. The baseline hazard, also referred to as the failure or risk probability, gives the instantaneous conditional probability that a seedling will die at a given time, given that the individual has survived up to that time. Relative to the baseline hazard, we can quantify how a covariate (either fixed or time-segmented) in the predictive model affects the hazard rate. We employed the forward, stepwise, logistic regression (LR) method to evaluate which predictor variables in the model affected the hazard rate of seedlings, and the Wald parametric test to test for the significance of the variables entered in the model. Regression coefficients from the model revealed the magnitude of the effect a given variable had on the hazard rate of the seedlings. The extended Cox model is as follows:

$$h(t,X[t]) = h_o(t)\exp(\Sigma_{i=1}^{p1}\beta_i X_i + \Sigma_{j=1}^{p2}\beta_j X_j[t]),$$

where $t$ = time, $X(t)$ is the vector of predictors that are modeled at time $t$, $h_o$ is the baseline hazard, and the exponential term includes both time independent ($X_i$) and time-segmented ($X_j t$) covariates (Kleinbaum and Klein 2012, Mills 2011). We considered %T and % open sky over each seedling to be time-segmented covariates since they change primarily because of internal characteristics of the forest. We also explicitly factored in distance as a time-independent variable in the Cox models to calculate the contribution of understory light seasonality on seedling survival after controlling for the effect of distance.

Due to improper programing of the LI-COR® datalogger during our measurements of base PAR in the summer of 2013 for 2 of the 4 belt transects, we tested how robust our survival models would be to the removal of the summer 2013 %T measurements. We ran a test model with the data from the 2 unaffected belt transects with all 3 summer %T segments (2009, 2010, and 2013), and without the 2013 summer %T measurement; in both cases, the $\beta$ coefficient exhibited the same negative effect on the hazard, suggesting that survival analysis models were sufficiently robust to remove summer 2013 %T data from the analysis.

## Results

### Winter versus summer understory %T

Mean understory percent transmittance (%T) was significantly higher in the winter (69.0%) than in the summer (30.6%) (Wilcoxon Mann-Whitney W = 153436.5, $P < 2.2 \times 10^{-16}$; Fig. 2). Frequency distribution of winter %T was normally distributed (Fig. 3a, b), but summer %T measurements were highly skewed (Fig. 3c, d). Winter understory %T was negatively associated with distance from gap edge

(winter %T = 78.55 × exp[-0.009 × distance]), from an average of about 82% in the gap to 60% in the forest understory (Fig. 4a). Summer understory %T was also nonlinearly and negatively associated with distance from gap edge (Summer %T = 42.91 × exp[-0.026 × distance]) from an average of about 50% in the gap to 23% in the forest understory (Fig. 4b).

**Winter versus summer canopy cover**

Winter % open sky was linearly and negatively associated with distance along the gap–forest transects (winter % open sky = 73.4 × -0.25 × distance; Fig. 4c), but summer % open sky was not significantly associated with distance along the same transects (summer % open sky = 32.53; Fig. 4d). Thus, during both the winter and summer months, percent transmittance (%T) was a more accurate measurement of the spatial heterogeneity in understory solar radiation that reached each seedling than % open sky. Percent open sky was (1) weakly associated with distance in gap–forest transects in the winter, (2) constant along the same transects in the summer, and (3) affected by small gaps in the summer (high % open-sky data points across distance in Fig. 4d); thus, we did not include % open sky as a predictor variable of survival in our analysis.
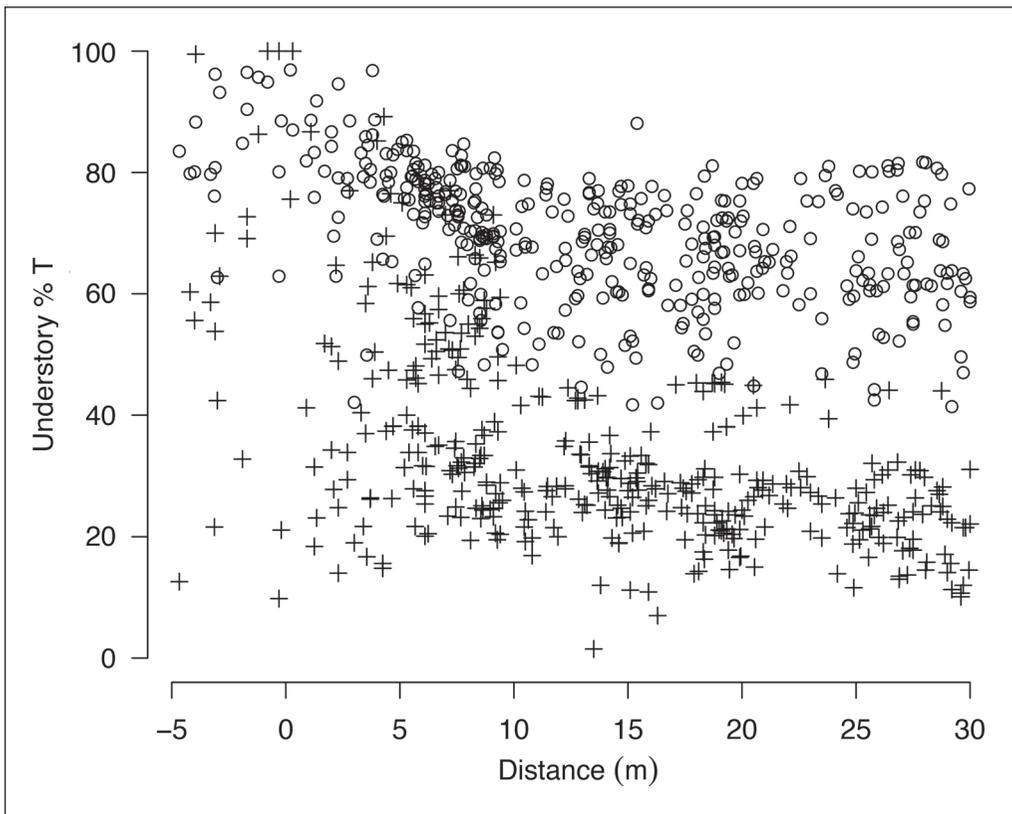


Figure 2. Winter (○) versus summer (+) %T as a function of distance from gap edge. Each point represents the 60-month average %T above each of the 401 Pine and Hemlock seedlings combined, for each season.

### Seedling survival – Kaplan-Meier survival curves

KM models revealed a significant difference among the distance-stratified survival curves for Pine seedlings between groups 2 and 4 (but not between any other group pair), with higher survival for seedlings in distance group 2 (closer to the gap) than for those in group 4 (log-rank test $P = 0.006$; Table 1, Fig 5a). However, KM models of Hemlock seedling survival stratified by distance groups revealed no significant pairwise differences in the cumulative survival probabilities among distance groups (Table 1, Fig. 5b), suggesting that all Hemlock seedlings had the same survival probability regardless of distance from the gap edge. In addition, there was no significant difference between the survival distributions of Hemlock and Pine seedlings paired by distance group (Table 2).

### Seedling survival – Cox proportional hazards model

For Pine, increasing winter %T significantly decreased the baseline hazard rate for seedlings ($P = 0.049$) by 1.9% for every unit of %T, and increasing distance from the gap significantly increased the hazard rate ($P = 0.015$) by 4.1% for
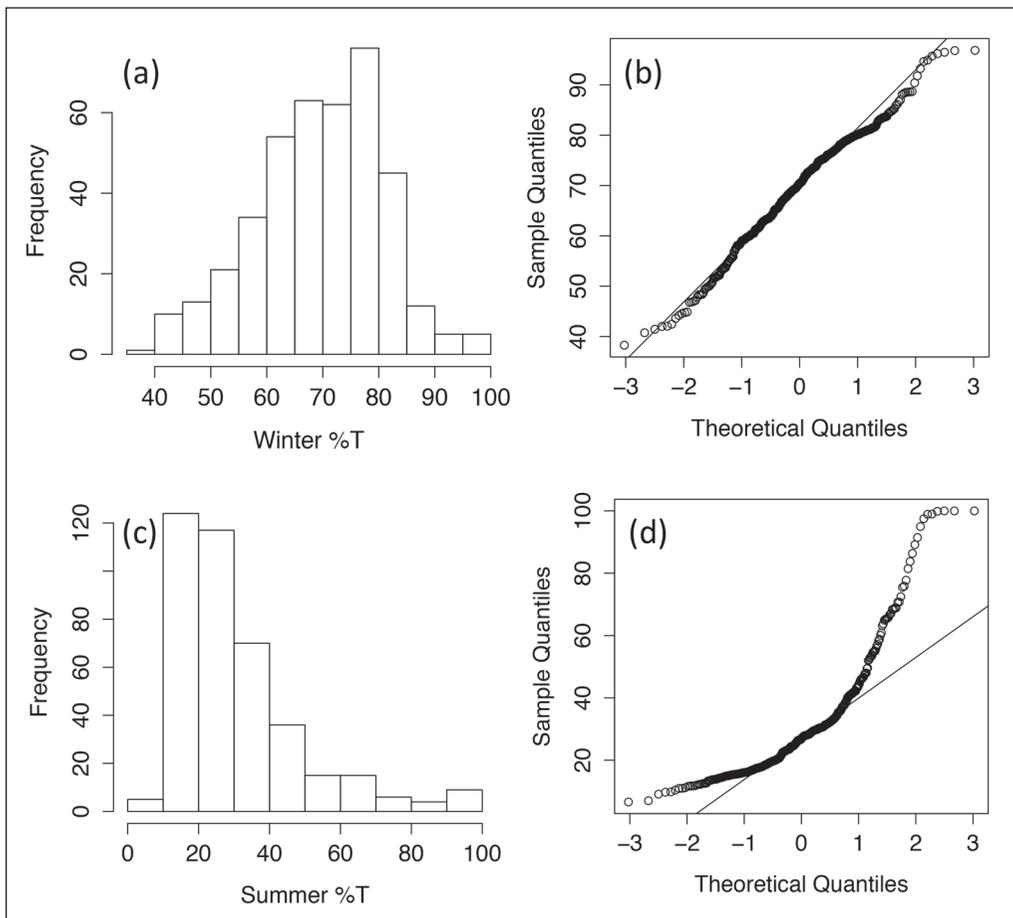


Figure 3. (a) Histogram and (b) quantile versus quantile (Q–Q) plot of winter %T data; (c) histogram and (d) Q–Q plot of summer %T data.
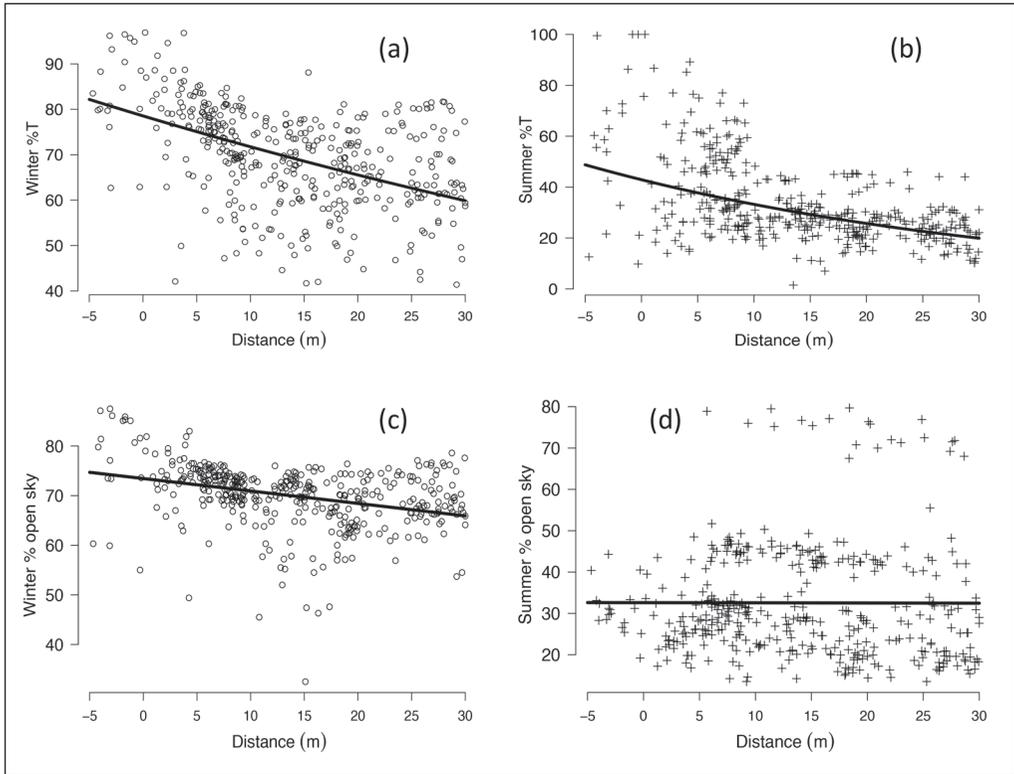
Figure 4. (a) Winter and (b) summer understory %T as a function of distance from gap edge, with fitted exponential models (black lines). (c) Winter and (d) summer % open sky as a function of distance from gap edge, with fitted linear regression models (black lines). Each point represents the 60-month average winter or summer %T and average winter or summer % open sky above each of the 401 Pine and Hemlock seedlings combined.

Table 1. Log-rank test statistic ($\chi^2$) and *P*-value for pairwise comparison of White Pine (PIST; lower-left of matrix diagonal) and of Eastern Hemlock (TSCA; upper-right of matrix diagonal) seedling cumulative survival KM curves among distance groups, sample size (*n*), and number of recorded mortality events. Group 1 = -10–0 m, group 2 = 0–10 m, group 3 = 10–20 m, and group 4 = 20–30 m.

| Distance group | Distance group 1 | | 2 | | 3 | | 4 | | *n* (TSCA) | # of mortality events (TSCA) |
|---|---|---|---|---|---|---|---|---|---|---|
| | $\chi^2$ | *P* | $\chi^2$ | *P* | $\chi^2$ | *P* | $\chi^2$ | *P* | | |
| 1 | | | 0.333 | 0.564 | 0.927 | 0.336 | 0.398 | 0.528 | 4 | 0 |
| 2 | 0.066 | 0.797 | | | 0.829 | 0.363 | 0.004 | 0.950 | 12 | 1 |
| 3 | 0.827 | 0.363 | 3.383 | 0.066 | | | 1.126 | 0.289 | 14 | 3 |
| 4 | 1.753 | 0.186 | 7.703 | 0.006 | 1.011 | 0.315 | | | 21 | 2 |
| *n* (PIST) | 13 | | 134 | | 124 | | 79 | | | |
| # of mortality events (PIST) | 1 | | 13 | | 21 | | 19 | | | |

every meter away from the gap edge into the forest. Cox models of summer %T and distance data revealed that distance significantly increased the hazard rate of Pine seedlings ($P = 0.003$) by 4.8% for every meter away from the gap edge, but variation in summer %T did not significantly affect the hazard rate (Table 3). For
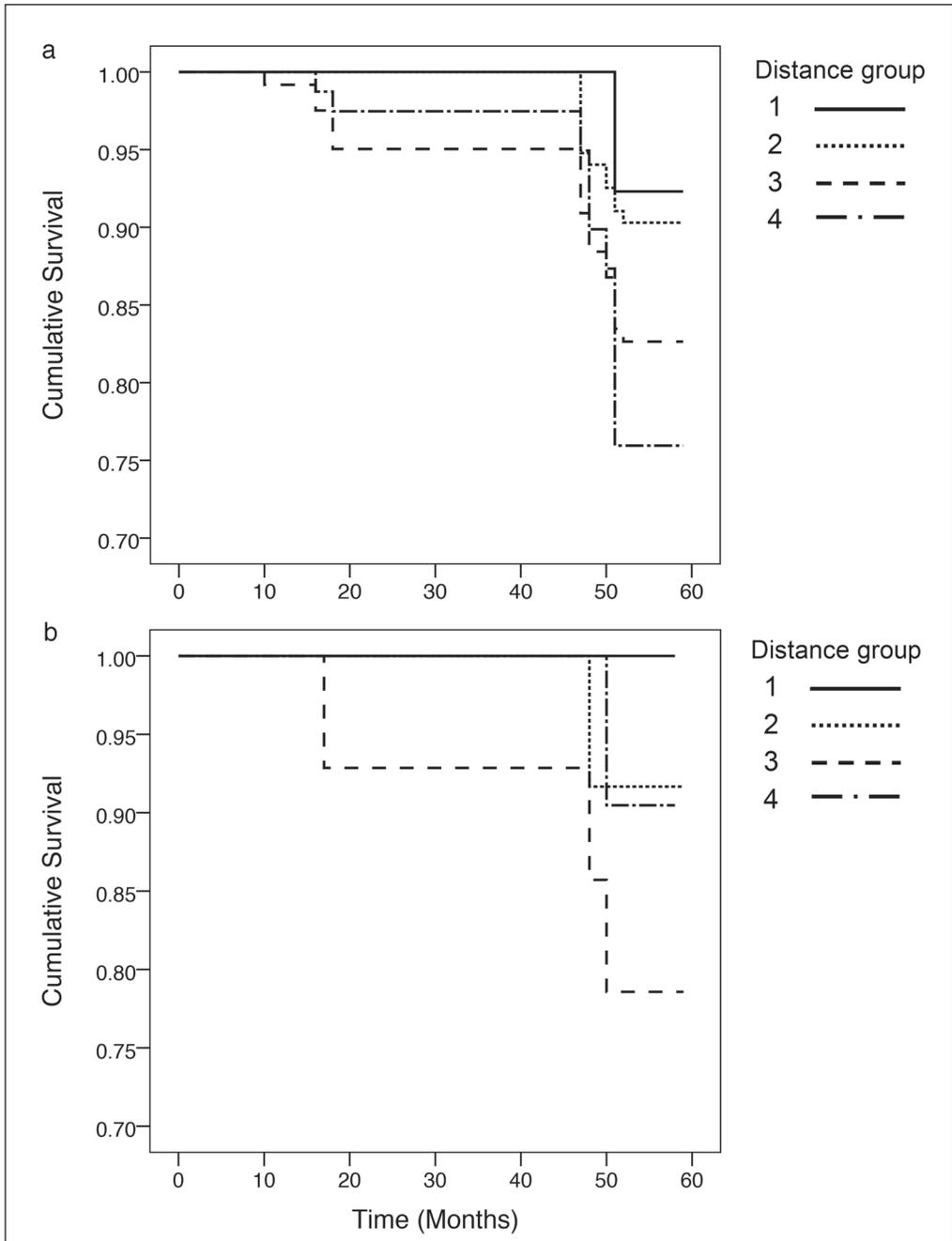


Figure 5. (a) White Pine and (b) Eastern Hemlock Kaplan-Meier seedling-survival curves in each of the 4 distance groups (see Table 1 and text for description of groups).

Hemlock, neither winter %T and distance, nor summer %T and distance significantly affected the hazard rate for seedlings (Table 3).

## Seedling age and size as a function of distance

Mean Pine seedling age was 11 years (± 3, range = 7–19) and mean basal diameter was 1.74 cm (±1.27, range = 0.43–5.54 cm). Seedling age was not associated with either seedling diameter or distance from gap ($P = 0.14$, $R^2 = 0.046$, and $P = 0.28$, $R^2 = 0.008$, respectively), However, Pine seedling diameter was negatively associated with distance from gap edge ($P = 0.004$, $R^2 = 0.256$), suggesting that seedlings closer to the gap had grown faster than seedlings further into the forest.

## Discussion

### Seasonality of understory %T and canopy cover

The significant difference we found in understory %T between winter and summer, with higher understory %T recorded in the winter throughout the gap–forest transects despite lower sun angles, has also been observed in forests of southern Ontario (Gildner and Larson 1992, Kwit et al. 2010) and North Carolina (Lopez et al. 2008), as well as in other temperate deciduous forests of the world (Kawarasaki and Hori 2001). However, our study revealed that not only is the average understory %T different between the 2 seasons, but its spatial distribution along a gap–forest gradient is also different. This result is clearly associated with the effect of the gap, which affects the %T distribution up to about 10 m inside the forest from the gap edge, but with a steeper gap–forest light gradient in the summer than in the winter within these first 10 m inside the forest from the gap edge.

Table 2. Pooled sample size (*n* pooled), log-rank test statistic ($\chi^2$) and *P*-value for comparison of cumulative survival KM curves between White Pine and Eastern Hemlock seedlings within the same distance groups pooled across all 4 transects, and survival data pooled across species.

| Distance group | *n* pooled | $\chi^2$ | *P* |
|---|---|---|---|
| 1 | 17 | 0.308 | 0.579 |
| 2 | 146 | 0.023 | 0.879 |
| 3 | 138 | 0.154 | 0.695 |
| 4 | 100 | 1.965 | 0.161 |

Table 3. *β* (regression coefficient), standard error (SE), and *P*-value for each Cox model predictor variable (distance from the gap edge and %T) for each species. A negative *β* indicates a decrease in the baseline hazard as the value of the predictor variable increases; conversely, a positive *β* denotes an increase in the baseline hazard as the value of the predictor variable increases.

| | White Pine | | | | Eastern Hemlock | | | |
|---|---|---|---|---|---|---|---|---|
| | Winter | | Summer | | Winter | | Summer | |
| | Distance | %T | Distance | %T | Distance | %T | Distance | %T |
| *β* | 0.041 | -0.019 | 0.048 | -0.001 | 0.011 | -0.014 | 0.003 | -0.009 |
| SE | 0.017 | 0.009 | 0.016 | 0.008 | 0.044 | 0.032 | 0.057 | 0.028 |
| *P* | 0.015 | 0.049 | 0.003 | 0.888 | 0.802 | 0.651 | 0.962 | 0.733 |

Our study revealed that canopy cover (% open sky), estimated using digital hemispherical (fisheye) photos taken above each seedling was fairly constant along gap–forest transects, which ran contrary to our prediction that canopy cover would be low in the gap and near the gap edge. This finding can be attributed to the fact that the Tree Heaven ELG was already 9 years old at the beginning of this study and had started to regenerate with fast-growing tree species such as Sweet Birch that had grown to ~1.5 m tall in 2009, overtopping some of the Pine or Hemlock seedlings growing in and at the edge of the gap. We were unable to measure the thickness of the canopy cover over each seedling from fisheye-photo measurements of canopy cover, and therefore unable to discriminate between seedlings in the forest that were covered by multiple layers of leaves, and seedlings in the gap that were covered by only few layers of leaves that transmitted more sunlight. So, although fisheye photographic measurements of canopy cover have been found useful as proxy measurements of understory light in studies where large forest gaps were not included (Kobe et al. 1995), others such as Canham et al. (1994) have found it difficult to rely solely on this technique without complementing it with direct PAR measurements using quantum sensors. For this study, direct measurement of percent transmittance using quantum sensors gave a more accurate estimation of the sunlight reaching each seedling, especially in the summer. The use of fisheye canopy photos as an estimate of sunlight transmittance in southern New England should therefore be used only in undisturbed forests.

**Seedling survival**

Given the documented shade tolerance of Hemlock and the shade intolerance of Pine, we expected the mortality of Eastern Hemlock seedlings to be lower than that of White Pine seedlings, but we found no significant differences in KM survival curves between the 2 species at any distance from the gap edge. Due to the small sample size available for Hemlock, a potential Type II error may also have led to this finding. Death of only 1 Hemlock seedling in our sample overly influenced the step sizes in the Hemlock KM curves. Cox models benefited from a larger overall sample size since the cohort-mortality data were not divided into distance groups, and revealed that there was indeed a difference in mortality between the 2 species.

Although our KM and Cox models confirmed our prediction that Hemlock seedlings should have similar survival functions regardless of distance from the gap edge into the forest, Cox models revealed that distance was a significant predictor of survival of White Pine in both winter and summer. Because seedling basal diameter was negatively associated with distance from gap, Pine survival at our study site may be a function of both distance from gap and seedling growth rate, as observed in other studies (e.g., Kobe 2006). This finding confirms that White Pine has a narrow environmental niche at the regeneration stage (Seiwa 2007) and is predominantly adapted to high-light microenvironments. This relationship between growth rate and survival deserves further investigation, and we will address it in a separate study.

Cox Models also indicated that winter %T variability explained some of the variability in Pine mortality, underscoring the importance of understory light levels when

the canopy trees were still devoid of leaves for the survival of White Pine seedlings. Kobe et al. (1995) also observed differences in mortality between juvenile Hemlock and Pine trees in Connecticut and Michigan mixed forests with the probability of survival remaining fairly flat for Hemlock across a 0.1-to-100 understory %T range, while Pine exhibited a steep decrease in its probability of survival below 10%T. White Pine seedlings may need at least 20% of full sunlight to survive (Wendel and Clay Smith 1990). In our study, all of the sampled seedlings (both Pine and Hemlock) received at least 20% transmittance of full sunlight in the winter, but only 2/3 of the seedlings (most of those Pine) received that exposure in the summer, explaining why winter understory light is important for White Pine seedling survival. Light levels are similarly critical to the survival of many deciduous tree seedlings in North American forests (Augspurger 2008, Augspurger and Bartlett 2003). For Eastern Hemlock, neither winter %T and distance, nor summer %T and distance significantly affected the hazard rate for the seedlings. To our knowledge, our study is the first to characterize the importance of understory light seasonality for seedling-stage survival of a coniferous tree species in a New England deciduous forest.

Other environmental factors or biotic interactions that we did not measure may also explain some of the variability in survivorship of White Pine along our gap-to-forest transects (see Dovčiak et al. 2001). Forest-gap soils are typically warmer, contain more moisture, and have higher nitrogen concentrations than surrounding forest soils (Scharenbroch and Bockheim 2007), and the survival of seedlings of several tree species, including White Pine, has been associated with the interaction of light levels and physical and chemical properties of soils (Walters and Reich 2000). Nitrogen is typically the most limiting resource in forest soils, and N availability and assimilation are strongly correlated with the relative growth rate of conifers (Walters and Reich 2000) and thus could influence their survival. McKenna (2007) analyzed soils from within and around another Yale Myers Forest ELG located 2.5 km south of the Tree Heaven ELG for N levels 2 y after the gap creation, and found that they contained higher N concentrations at the center of the gap than in the surrounding forest. It is likely that similar soil-N gradients existed at our study site 2 y after its establishment, which may have influenced Pine regeneration in and around the gap as a function of distance from the gap edge, as was indicated by our Cox proportional hazards models results.

Root competition from other species in the forest, on the gap edge, and in the gap could also be partly responsible for the spatial variability in White Pine mortality we observed, as noted in other studies (Dovčiak et al. 2001, Matonis et al. 2011, Parker et al. 2009, Pitt et al. 2009, Yeaton 1978). Frozen soils in the winter can reduce photosynthesis by Eastern Hemlock (Hadley 2000) and may also contribute to a differential survival response of the 2 species to understory light in the winter. Finally, herbivory and especially deer browsing likely played a role in seedling mortality at our study site as it does in other northern hardwood forests (Saunders and Puettmann 1999, Ward et al. 2000), but the few instances of browsing we observed were spatially dispersed and therefore unlikely to differentially affect seedling mortality along the gap-to-forest gradient.

Notwithstanding those other possible explanatory variables, our KM and Cox models suggested that at least some of the variability in Pine seedling survival at our study site was explained by distance from the gap and by winter understory sunlight transmittance. Thus, for White Pine just as for deciduous tree species, seedling survival appears to depend more on photosynthesis and carbon assimilation during the October–April half of the year than during the May–September half, despite the lower sun angles during winter months. Preliminary results suggest that, for Pine at least, seedling-growth rate may also be a predictor of survivorship. Our findings suggest that management actions designed to either re-introduce or conserve existing White Pine populations in southern New England deciduous forests should monitor and/or manage for understory light levels based on winter light measurements, rather than on summer light measurements.

## Conclusion

Numerous environmental variables and biotic interactions affect the survival of tree seedlings in northeastern hardwood forests, but understory light is especially critical for seedlings of many North American tree species. In this study, we showed that both the transmittance of sunlight through a southern New England forest canopy to the forest floor, and the spatial distribution of that sunlight in the vicinity of a forest gap, are significantly different in the winter than in the summer months. While Eastern Hemlock seedling survival was not associated with either distance from the gap or variation in understory sunlight transmittance, the survival of White Pine seedlings was associated with both, but only in the winter months for understory light transmittance. This finding suggests that, just as seedlings of deciduous tree species often rely on critical pre-canopy tree leaf-out understory light levels for survival, seedlings of shade-intolerant coniferous species such as White Pine also rely mostly on winter light transmittance through an open forest canopy for survival. Experimentally, we also found that proxy measurements of light levels via the analysis of digital fisheye canopy photos did not accurately describe understory light levels in and near a regenerating 10-year-old gap in a southern New England forest. Direct rather than indirect measurements of winter understory light should be used to tailor management actions designed to re-introduce or conserve Pine populations. The association between White Pine seedling growth rate and survival warrants further study.

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