

Functional Ecology

Manuscript title: Spring phenological escape is critical for the survival of temperate tree seedlings

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Data Availability Statement

Code and data used in this manuscript (i.e., for photosynthesis, survival, and growth models) are available in the Zenodo digital repository: <http://doi.org/10.5061/dryad.1c59zw3tk> (Lee & Ibáñez, 2021)

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Abstract

1. Understory plants in deciduous forests often rely on access to ephemeral light availability before the canopy closes in spring and after the canopy reopens in fall, a strategy commonly referred to as phenological escape. Although there is evidence for a relationship between understory plant phenology and demographic performance, a mechanistic link is still missing.
2. In this study, we bridged this gap by estimating annual carbon assimilation as a function of foliar phenology and photosynthetic capacity for seedlings of two temperate tree species that commonly co-occur across eastern North America. We then modeled the relationship between estimated carbon assimilation and observed seedling survival and growth.
3. Our results indicate that seedlings of both species strongly depend on spring phenological escape to assimilate the majority of their annual carbon budget and that this mechanism significantly affects their likelihood of survival (but not growth). Foliar desiccation also played a strong role in driving patterns of seedling survival, suggesting that water availability will also help shape seedling recruitment dynamics. We found only weak associations between seedling senescence in fall and annual carbon assimilation, suggesting that phenological escape in fall plays a relatively minor role in seedling demographic performance.

4. Our results indicate that spring phenological escape is critical for survival of these temperate tree species, and thus any changes to this dynamic associated with climate change could strongly impact these species' recruitment.

Keywords: *Acer saccharum*; Carbon assimilation; desiccation; foliar phenology; growth; C3 photosynthesis; *Quercus rubra*

Introduction

For understory plants growing in temperate forests, photosynthetic carbon assimilation is strongly tied to the seasonality of light availability (Heberling, Cassidy, Fridley, & Kalisz, 2019; Heberling, McDonough MacKenzie, Fridley, Kalisz, & Primack, 2019). Although plants are limited by access to light by overstory trees for most of the growing season, many understory species (including tree seedlings) have adapted to expand their leaves before the canopy closes in spring and/or maintain their leaves after the canopy has reopened in fall to gain access to direct light. This behavior, called phenological escape (Jacques et al., 2015), has been shown to allow understory species to accumulate more than half of their annual net carbon assimilation earlier in the spring before canopy closure (Heberling, Cassidy, et al., 2019; Kwit, Rigg, & Goldblum, 2010). Under current climate change, quantifying phenological escape becomes critical; with warmer springs, the rate of phenological change between the canopy and the understory, as well as among co-occurring species, could differ and consequentially impact photosynthetic performance of understory plants. Although this dynamic has received recent attention in the scientific literature (Heberling, Cassidy, et al., 2019; Heberling, McDonough MacKenzie, et al., 2019; Kwit et al., 2010), there is relatively little work investigating the potential effects that climate-driven changes to phenological escape will have on plant performance.

Previous research has found correlations between leaf out phenology and various performance metrics such as growth, survival, and fruiting (Augspurger, 2008; Routhier & Lapointe, 2002; Seiwa, 1998), but correlative studies such as these may be inaccurate if relationships are nonlinear. For example, although earlier leaf out may provide tree seedlings with increased access to light, potentially improving performance, it also places them at higher risk of death from early spring frost events (Vitasse, Lenz, Hoch, & Körner, 2014). Furthermore, correlative studies may be of little use if climate change results in non-analogue climate conditions outside of the range of variation the studies (Jackson & Williams, 2004). Therefore, a

more mechanistic understanding of the physiological mechanisms that underlie these patterns might help to develop more accurate predictions of future plant performance.

In forests, linking phenological escape of tree seedlings to demographic performance will be particularly important because of the implications for tree recruitment dynamics. Tree recruitment is a strong bottleneck that filters which individuals eventually recruit into the canopy (Grubb, 1977; Harper, 1977), and it is also the stage at which trees are most likely to experience nonrandom, directional mortality (Green, Harms, & Connell, 2014; Umaña et al., 2016). One possible approach would be to quantify performance by estimating phenological escape success via carbon status, which has been shown to be a good predictor of plant demographic success (Hlásny et al., 2011; Hoch, Siegwolf, Keel, Körner, & Han, 2013; Korol, Running, Milner, & Hunt, Jr., 1991; Lusk & Del Pozo, 2002; Piper, Reyes-Díaz, Corcuera, & Lusk, 2009). If phenological escape determines seasonal carbon assimilation (e.g., if seedlings with earlier leaf-out relative to the canopy experience greater net carbon assimilation), it will thus likely also affect tree seedling performance and consequent recruitment.

When carbon status decreases to the point where plants are no longer able to meet metabolic demand, they can succumb to death via carbon starvation (McDowell & Sevanto, 2010; Sala, Woodruff, & Meinzer, 2012). Accessing spring light via phenological escape allows understory plants rise above this threshold, but they must then avoid moving back below the threshold for the remainder of the growing season. In shady closed-canopy conditions, this often requires plants to adjust their photosynthetic capacity to minimize respiration costs. Photosynthetic capacity also acclimates to photoperiod (Bauerle et al., 2012), light availability (Peltier & Ibáñez, 2015), and temperature (Larigauderie & Körner, 1995) over the course of the growing season, and there is variability among species regarding the plasticity they exhibit (Patrick, Ogle, & Tissue, 2009). Furthermore, species differ in their photosynthetic capacity (often summarized as shade tolerance; Niinemets 2010), causing differences in carbon assimilation rates even when exposed to the same microenvironment (Walters & Reich, 1996). Warmer summer temperatures can cause disproportionately greater increases in plant respiration rates compared to increases in photosynthetic assimilation rates (Caemmerer, 2000), although there is evidence that suggests that respiration eventually reacclimates (Larigauderie & Körner, 1995; Smith & Dukes, 2013). Additionally, increases in vapor pressure deficit (VPD) associated with increased temperature may simultaneously limit photosynthetic activity by reducing

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stomatal conductance (Grossiord et al., 2020). Greater respiration costs associated with temperature and reduced photosynthetic assimilation caused by reduced light and increased VPD are therefore likely to combine to result in carbon assimilation dynamics where net change in carbon status over summer is overwhelmingly negative (Slot & Kitajima, 2015). This could potentially compromise a plant's ability to maintain a positive carbon status throughout the growing season and lead to subsequent carbon starvation (Dickman, McDowell, Sevanto, Pangle, & Pockman, 2015).

Photosynthetic activity, and thus plant carbon status, can also be affected by biotic factors. Natural enemies, such as pathogens and herbivores, can directly limit plant carbon assimilation by reducing the amount of photosynthetically active tissue (Nabity, Zavala, & DeLucia, 2009). Carbon assimilation of understory plants may also be affected by surrounding canopy trees both directly, via variation in canopy openness, and indirectly via soil-mediated mechanisms. The latter include plant-soil feedback effects (McCarthy-Neumann & Ibáñez, 2012), allelopathic effects (Gómez-Aparicio & Canham, 2008; Pellissier & Souto, 1999; Ruan et al., 2016), and soil nutrient availability (Classen et al., 2015; Phillips & Fahey, 2006), all of which have been shown to differ according to the identity of neighboring canopy trees. Therefore, a robust estimation of tree seedling carbon status will require accounting for neighborhood effects from surrounding canopy trees.

In this experiment, our goal was to evaluate the extent to which foliar carbon assimilation is associated with the performance of seedlings of two co-occurring temperate tree species (*Acer saccharum* and *Quercus rubra*) that differ in their foliar phenology, photosynthetic characteristics, shade tolerance, and response to drought. Specifically, we addressed the following questions: 1) What proportion of annual foliar carbon assimilation is accumulated during spring and fall phenological escape, and is there a difference in importance between the two seasons? 2) How does net annual carbon assimilation relate to seedling demographic performance (i.e., growth and survival)? Answers to these questions will provide a more mechanistic link between phenological escape and tree seedling performance, knowledge that will help to predict how tree recruitment will be impacted by climate change.

Methods

To address our research questions, we conducted a field experiment where we transplanted seedlings of two widely co-occurring temperate tree species near conspecific and heterospecific adults and observed their foliar phenology, photosynthetic gas exchange, survival, and growth. We estimated net carbon assimilation by combining the phenology observations with photosynthetic rates derived from the gas exchange measurements and with hourly measurements of temperature, light, soil moisture, and vapor pressure deficit. We then used generalized mixed effects models in a Cox survival model to explore how carbon assimilation affects seedling survival and growth, respectively.

Experimental Design

Study locations - This study took place at three sites in southeastern Michigan, USA: Saginaw Forest (42.270977 N, 83.806022 W), Radrick Forest (42.287083 N, 83.658056 W), and the E. S. George Reserve (42.457104 N, 84.020226 W). Forests in all three locations were established in the early 1900's following forest clearing and are currently dominated by mid- and late-successional canopy genera, such as *Acer*, *Carya*, *Prunus*, and *Quercus*. Radrick Forest and the E. S. George Reserve have relatively diverse canopies while plots in Saginaw Forest were established in former monocultures of *Acer saccharum* and *Quercus rubra*. Climate across all sites is similar, with average June-August temperatures of 22 °C, average December-February temperatures of -6 °C, and average annual precipitation of 925 mm distributed evenly throughout the year. Average canopy openness (Global Site Factor, GSF) at plots across sites was $12.6 \pm 3.5\%$ standard deviation, values characteristic of relatively closed canopies and shady summer conditions. GSF was similar across sites and between canopy species treatments (Fig. S1).

Study species - We planted seedlings of two species native to and commonly co-occurring across eastern North America: late-successional sugar maple (*Acer saccharum*, Marsh.) and mid-successional northern red oak (*Quercus rubra*, L.). These two species were chosen because they differ in their shade tolerance (Crow, 1988; Lei & Lechowicz, 1990; Walters & Reich, 1996), phenological escape (Augsburger & Bartlett, 2003), and photosynthetic characteristics (Kaelke et al., 2001; Peltier & Ibáñez, 2015). *Acer saccharum* seedlings are highly shade-tolerant and are typically one of the first species in these forests to leaf out in spring whereas *Q. rubra* seedlings are only moderately shade-tolerant and leaf out later in spring, sometimes at the same time as

canopy closure. *Quercus* seedlings typically have higher maximum photosynthetic rates than *Acer* seedlings (Kaelke et al., 2001; Peltier & Ibáñez, 2015) and are also considered to be more drought tolerant (Abrams, 1990; Bahari, Pallardy, & Parker, 1985; Loewenstein & Pallardy, 1998). Adults of these species have been shown to differ in stomatal regulation (Cavender-Bares & Bazzaz, 2000; Loewenstein & Pallardy, 1998) and wood anatomy characteristics (diffuse- vs. ring-porous xylem, respectively; Roman et al. 2015), although most of these traits have not been directly measured in seedlings and may not be consistent across ontogeny (Cavender-Bares & Bazzaz, 2000). *Quercus rubra* acorns are substantially larger than *A. saccharum* seeds (Barnes & Wagner, Jr., 2004) and therefore likely confer greater initial carbon sources to first year tree seedlings.

Field experimental set-up – For three consecutive years, 2014-2016, seeds from each species sourced from multiple populations (see Table S1 in Supporting Information for seed source information) were cold-stratified and sown in a greenhouse in large tubs of potting soil (Sun Gro Horticulture; Agawam, MA, USA). Following germination and development of their first true leaves, seedlings were bare root transplanted to the field. At each site, seedlings were planted in plots established under the canopy of six adult trees, three *A. saccharum* and three *Q. rubra*; this would expose seedlings to conspecific and heterospecific soil communities. Depending on seedling availability in each year, 5-10 seedlings per target species were transplanted in separate rows extending from the base of each adult canopy tree (Table S1). In total we planted 290 *A. saccharum* seedlings and 320 *Q. rubra*.

Data Collection

Environmental data - One data recording station was established at each site to collect environmental data under the forest canopy. Each station was equipped to measure hourly temperature (°C) and relative humidity (%) using HOBO U23 Pro v2 data loggers (Onset Computer Corp., Bourne, MA, USA) and hourly soil moisture (%) and photosynthetically active radiation (PAR; $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) using HOBO Smart Sensors in combination with HOBO Micro Stations (Onset Computer Corp.). Additionally, plot-level variation in soil moisture was regularly measured using a Fieldscout TDR300 soil moisture meter (Spectrum Technologies; Aurora, IL, USA) at multiple times throughout the growing season. Plot-level variation in

midseason light availability was measured by taking hemispherical canopy photos at a height of 1 m above seedling level with a Sigma SD14 camera equipped with a Sigma 4.5 mm circular fisheye lens (Sigma Corporation, Japan) each year after the canopy at each plot had completely closed. For each photo we calculated the Global Site Factor (GSF) using Hemiview software (Delta-T Devices, Cambridge, UK), ranging from zero (fully closed canopy) to one (fully open).

Foliar phenology - We observed leaf-level dates of leaf expansion for seedlings in spring and dates of onset of seedling leaf color change, 50% leaf color change (< 50% of leaf area remains green), and leaf senescence in fall (complete abscission from the plant) beginning the year after planting and going through the end of the 2018 growing season. Seedling phenology was observed weekly in spring and fall, ending in spring when all seedlings had expanded their leaves or been declared dead and ending in fall when all seedlings had fully senesced their leaves.

Damage – Since leaf damage can affect seedling demographic performance directly by reducing photosynthetic tissue (Gerhardt, 1998; Seiwa, 1998) and indirectly through reductions in photosynthetic capacity, we observed leaf damage for all seedlings coinciding with the weekly phenology observations in spring and fall and then approximately monthly over the rest of the summer. Annual leaf damage was assessed by approximating the total percent area per leaf removed by herbivory or infected by a foliar pathogen to the nearest 5%. Herbivory damage was classified as either mammal or invertebrate herbivory. Plant infection was identified as discoloration of leaf tissue not attributable to resorption of nutrients. Plants were also monitored for foliar desiccation, which entailed having green leaves that were crisp to the touch and not photosynthetically active (determined initially via gas exchange measurements for a subset of seedlings and then visually thereafter). Importantly, we use the term “desiccation” to signify that these observations only reflect leaf-level observations, which may or may not be representative of whole plant water status.

Seedling growth and survival - Individual mortality was recorded during the phenology and damage censuses when mortality was obvious (e.g., for fully uprooted plants) or during spring of the following year if the individual did not produce new leaves. Mortality events that were

clearly unrelated to carbon assimilation dynamics (e.g., death directly resulting from squirrel or deer herbivory/uprooting) were not included in the survival analyses. Seedling height (distance from soil to apical meristem) was recorded prior to planting to account for maternal effects, which have previously been demonstrated to affect tree seedling growth and survival (Castro, 1999; González-Rodríguez, Villar, & Navarro-Cerrillo, 2011; Ibáñez, Katz, & Lee, 2017). Height growth was then measured annually thereafter at the end of each growing season. Although radial stem growth has also been strongly linked to survivorship (Martin, Canham, & Kobe, 2010), particularly for shade-tolerant seedlings such as *A. saccharum* which can persist for decades in the understory with relatively little vertical growth (Marks & Gardescu, 1998), we chose to measure height growth as it is more commonly used to categorize recruitment stages (Green et al., 2014) and is strongly correlated with light availability (Montgomery, 2004; Wagner, Madsen, & Ammer, 2009).

Carbon assimilation – We used a LI-6400 Portable Photosynthesis System equipped with a CO₂ mixer assembly and LI-02B LED red/blue light source (Li-COR Biosciences, Lincoln, NE, USA) to measure *in situ* gas exchange for a subset of transplants following spring leaf expansion and continuing through the growing season. Gas exchange measurements were taken once every two weeks in spring and fall and approximately monthly during the summer for the 2015-2017 growing seasons. We constructed *A-Ci* (at 400, 300, 200, 100, 50, 400, 400, 600, 800, 1000, 1250, and 1500 ppm CO₂) and *A-Q* curves (at 1500, 1000, 750, 500, 250, 125, 60, 30, 20, 10, and 0 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$) for each seedling, maintaining ambient humidity and temperature. Leaves smaller than the cuvette were traced in the field and leaf area was measured using ImageJ software (Schneider, Rasband, & Eliceiri, 2012). Soil moisture was measured at the individual seedling level during each measurement using the Fieldscout TDR300 Soil Moisture Meter.

Analyses

Photosynthesis

We analyzed our gas exchange data using a Bayesian adaptation of the Farquhar et al. (1980) model of C3 photosynthesis originally developed by Patrick et al. (2009) and then further modified by Peltier and Ibáñez (2015). In short, this modeling approach allowed us to estimate seasonal photosynthetic capacity at the species level that incorporates the effect of environmental

variables (i.e., light, temperature, and water availability) in the estimation of net photosynthetic activity. A detailed description of the model (along with supplemental analysis) can be found in the Supporting Information along with tables of associated parameter definitions (Table S2) and parameter posterior estimates (Table S3).

Because photosynthetic rates have been shown to vary over the course of the growing season (Bauerle et al., 2012; Peltier & Ibáñez, 2015), we estimated photosynthesis model parameters for each of the following phenophases : 1) spring period between leaf-out and the day of canopy closure; 2) summer, defined as the time between canopy closure and the beginning of seedling leaf coloration; 3) Fall 1, the time between the onset of coloration and when a specific leaf had surpassed 50% of coloration; and 4) Fall 2, measurement taken between 50% coloration and leaf senescence. Day of canopy closure in the spring was defined as the day on which the average daytime PAR (between 1000-1700 hours) dropped below $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ and then did not increase above that threshold for one week (Fig. S2, in order to rule out the possibility of low light resulting from cloudy days). Preliminary analysis did not indicate differences in photosynthetic rates based on seed source, seedling cohort, or seedling age, so these variables were not included in the analysis.

Carbon assimilation estimates

We used hourly climate data (temperature, VPD, soil moisture, and light [photosynthetic active radiation; PAR]) collected from our site-level environmental stations and simulated at the plot level (see Appendix S3 in Supporting Information for details on data simulation) into the fitted photosynthesis model and estimated hourly rates of foliar carbon assimilation for each seedling. Parameter estimates depended on the seedling species, seedling phenophase, and canopy tree species they were planted under. We then adjusted calculations according to individual leaf area, which varied over time to reflect observed reductions in leaf area caused by herbivory for individual plants. Hourly estimates of carbon assimilation were then summed over the duration of the growing season, resulting in estimations of net annual foliar carbon assimilation (Fig. 1) representing the net amount of CO_2 assimilated by seedling leaf tissue over the course of the growing season ($\text{mol CO}_2 \text{ yr}^{-1}$) for each individual (full description of this process is included in Appendix S4 in the Supporting Information). Importantly, we did not measure soil respiration or stem photosynthesis, and so this value does not reflect total seedling carbon status. However,

carbon assimilated by the stem is proportionally negligible compared to foliar assimilation (Pfan­z & Aschan, 2001), so net annual foliar assimilation is representative of gross annual carbon accumulation before accounting for belowground respiration. We then modeled the relationship between seedling foliar phenology (day of leaf out in spring or day of leaf senescence in fall) and estimated annual foliar assimilation using linear models in the *lm* package in *R* (v3.5.3) with day of event as a fixed effect.

Survival

We analyzed seedling survival using a Bayesian Bernoulli model where the probability of survival (p) for each seedling (i) to the end of the growing season in year (t), dead $Survival_{i,t} = 0$ or alive $Survival_{i,t} = 1$, is estimated with likelihood: $Survival_{i,t} \sim Bernoulli(p_{i,t})$, and process model: $logit(p_{i,t}) = \log\left(\frac{p_{i,t}}{1-p_{i,t}}\right) = \bar{\beta}X_{i,t}$. We systematically evaluated models for best fit using different combinations of eight covariates and seven categorical variables (Table S4), the latter included as random effects. Models started with an intercept (β_0) and a foliar carbon assimilation term (β_C):

$$logit(p_{i,t}) = \beta_0 + \beta_C * C_{Annual_{i,t}}$$

Where C_{Annual} is each seedling's estimated net annual foliar carbon assimilation in a given year. Values of all continuous covariates, including C_{Annual} , were standardized around their respective means. Covariates and random effects (Table S4) were then added one at a time with models being iteratively chosen based on best fit according to the area under the receiving operator characteristic curve (AUROC; Metz 1978, Murtaugh 1996). A description of the AUROC criterion is available in the Supporting Information (Appendix S5) and posterior estimates of intercepts, covariates, and random effects are available in Table S5. To avoid overparameterization of the models, either plot or site random effects, but not both, were allowed in each best-fit model. Each species was analyzed independently. The relationship between carbon assimilation and survival was estimated and plotted by using the average values of all continuous covariates (besides assimilation) and assuming that all binary covariates equal zero (see Appendix S4 in Supporting Information for further detail).

Growth

Growth measurements, standardized for each seedling i and year t were analyzed with a normal likelihood: $Growth_{i,t} \sim N(\rho_{i,t}, \sigma^2)$, limited to positive values, and process model: $\rho_{i,t} = \beta_0 + \bar{\beta}X_{i,t}$. We evaluated models for best fit using combinations of C_{Annual} and the same covariates described in the survival analysis, with the addition of a seedling random effect. Only seedlings with non-negative growth values were included in this analysis. Negative growth values were generally associated with stem die-back or deer herbivory and did not represent the realized growth of each seedling. Model selection for growth models was done based on comparisons of the Deviance Information Criterion (DIC; Spiegelhalter et al. 2002) and on goodness of fit (R^2 , predicted vs. observed), fully described in Appendix S5 in the Supporting Information. Posterior estimates of all growth model parameters are available in Table S6. Species were analyzed individually.

In both analyses, covariate parameters were estimated from non-informative normal distributions $\beta_* \sim N(0, 1000)$. Random effect parameters associated with the categorical variables were estimated from hierarchical normal distributions $\alpha_* \sim N(0, \sigma^2_{\alpha_*})$. Precision parameters ($1/\text{variance}$) were estimated from non-informative gamma prior distributions $1/\sigma^2_{\alpha_*} \sim \text{Gamma}(0.001, 0.001)$. All models were run using OpenBUGS software v3.2.3 (Lunn, Spiegelhalter, Thomas, & Best, 2009). We tracked 40,000 iterations for three Monte Carlo chains following a 30,000-iteration burn-in period. Convergence of parameters was assessed visually and by using the Brooks-Gelman-Rubin statistic (Gelman & Rubin, 1992), and models were iterated until convergence was reached. Parameter values (means, variances, and covariances) were estimated from their posterior distributions. Data and model code for all analyses are available (see Data Availability Statement).

Results

Seedling mortality rates were high for both species. Out of the 70 *A. saccharum* and 115 *Q. rubra* seedlings that survived at least one year, 27 and 94 survived to the end of the study, respectively. Data were recorded every year that a seedling was alive, however, so seedling survival models had $n = 116$ and 167 and growth models had $n = 72$ and 86 , for *A. saccharum* and *Q. rubra*, respectively. Sample sizes in the growth models were lower because growth was not measured the year a seedling died. *Quercus rubra* seedlings (146.2 ± 34.9 mm) were taller on average than *A. saccharum* seedlings (76.7 ± 14.4 mm) at the time of planting but had slightly

lower annual growth rates thereafter ($19.7 \pm 14.9 \text{ mm y}^{-1}$ and $23.7 \pm 16.1 \text{ mm y}^{-1}$, respectively). The photosynthesis models were fit using a total of 254 and 259 paired A-Q and A-Ci curves for *A. saccharum* and *Q. rubra* seedlings, respectively.

Photosynthetic capacity

Model fits for the seedling gas exchange models (R^2 , predicted vs. observed) were 0.72 for *A. saccharum* seedlings and 0.76 for *Q. rubra* seedlings. Photosynthetic parameter posterior estimates (Fig. S3) were similar to values published elsewhere for these two species (Peltier & Ibáñez, 2015). A full list of parameter posterior estimates can be found in Table S3.

We found significant differences in V_{cmax25} between the two seedling species, but the differences that were observed depended on the species of neighboring tree (Fig. S3c-d). *Quercus rubra* V_{cmax25} was consistently greater compared to that of *A. saccharum* seedlings, with significant differences in Spring and Summer when planted near mature *A. saccharum* trees and in Spring and Fall 1 when planted near mature *Q. rubra*. *Quercus rubra* V_{cmax25} did not significantly differ according to phenophase or neighbor identity. However, *A. saccharum* V_{cmax25} was significantly higher in Summer when planted near mature *Q. rubra*. Phenophase also affected *A. saccharum* seedlings when planted near mature *Q. rubra*, with significantly higher V_{cmax25} in Summer compared to Spring and Fall 1.

RuBP regeneration-limited carbon assimilation rate (J_{max25}) experienced a relatively higher degree of variation compared to V_{cmax25} (Fig. S3a-b). *Acer saccharum* seedlings planted near conspecific adults had significantly higher Spring J_{max25} and significantly lower Summer and Fall 1 J_{max25} compared to when planted near mature *Q. rubra*. *Quercus rubra* seedling J_{max25} was only significantly affected by neighbor identity in Fall 1, when J_{max25} was significantly greater when planted near mature conspecifics. Both species showed strong variation in J_{max25} associated with phenophase, but patterns tended to differ between the two canopy treatments. Rates were more consistent across phenophase when planted near adult *A. saccharum* whereas both species had significantly lower Spring J_{max25} compared to the other phenophase bins when planted near mature *Q. rubra*. In general, *Q. rubra* seedlings had higher J_{max25} compared to *A. saccharum* seedlings in Spring, Summer, and Fall 1, regardless of canopy treatment or phenophase.

Rates of dark respiration (R_{d25}) did not differ significantly by seedling or canopy species (Fig. S3e-f), but there were some significant differences associated with phenophase. Rates tended to be highest in Fall 1 and Fall 2 for both species, with the lowest respiration rates occurring in Spring and Summer. Stomatal conductance (g_{m25}) similarly did not differ significantly by seedling or canopy species (Fig. S3g-h). It only significantly differed by phenophase for *A. saccharum* seedlings planted near *Q. rubra* canopy trees, with rates in Summer that were significantly lower compared to those in Fall 1 and Fall 2.

Water Availability and VPD Effects

Soil moisture had a significant positive association (i.e., confidence intervals did not overlap 0) with J_{max25} in Spring and Summer for both species and this association was significantly negative in Fall 1 (Fig. S4). There were significant differences between species in Spring, Summer, and Fall 1 where *A. saccharum* seedling J_{max25} consistently had stronger correlations with soil moisture. VPD had significantly positive correlations with J_{max25} in Spring and Summer, but the effects in Fall 1 and Fall 2 differed between species. VPD was positively associated with J_{max25} for *Q. rubra* seedlings (significantly so in Fall 2) but negatively associated with J_{max25} for *A. saccharum* seedlings (significant in Fall 1). The effect of VPD only significantly differed by species in Fall 1 and 2.

Soil water availability had relatively weaker correlations with V_{cmax25} for both species (Fig. S5). The associations with soil moisture were significantly positive for both species in Summer and significantly negative for *A. saccharum* seedlings in Fall 1. Fall 1 was also the only season where associations with soil moisture differed between the two species. The only significant association V_{cmax25} had with VPD was for *A. saccharum* seedlings in Fall 1, which was significantly negative. There was no phenophase where the magnitude of the association differed significantly between species.

Net Annual Assimilation

Annual foliar CO₂ assimilation estimated at the individual level ranged from -0.014 to 0.364 mol CO₂ yr⁻¹ and 0.001 to 0.453 mol CO₂ yr⁻¹ for *A. saccharum* and *Q. rubra* seedlings, respectively. For *A. saccharum* seedlings, an average of 84.3% of foliar carbon was assimilated in spring, 15.9% was assimilated in summer and -0.2% was lost in fall (i.e., respiration in fall was greater

than photosynthetic assimilation for this species; Fig. 1). In contrast, an average of 52.5% of *Q. rubra* seedling annual carbon was assimilated in spring, 43.5% was assimilated in summer, and 4.0% was assimilated in fall (Fig. 1).

The correlations between estimated annual CO₂ assimilation and seedling leaf out phenology were stronger than the correlations with leaf senescence phenology for both species (Fig. 2). Day of leaf out in spring (Fig. 2a) was significantly negatively correlated with estimated annual CO₂ assimilation for *A. saccharum* (adj. R² = 0.406, p < 0.05) and *Q. rubra* seedlings (adj. R² = 0.16, p < 0.05). Day of leaf senescence in fall (Fig. 2b) negatively correlated with estimated annual CO₂ assimilation for *A. saccharum* seedlings (p = 0.33) and positively correlated with estimated *Q. rubra* assimilation (p = 0.30), but neither relationship was statistically significant.

Seedling survival

In addition to C_{Annual} , the best fit survival models for both species included covariates for presence of foliar desiccation and percent foliar damage, with the *A. saccharum* survival model also including a term for signs of deer herbivory. The effect of annual carbon was positive and significant for both species while the effects of desiccation and percent leaf damage were negative and significant (Fig. 3). Deer herbivory had a negative but non-significant effect on *A. saccharum* seedling survival (Fig. 3a). Model fit for *A. saccharum* was highest when site random effects were added and the best-fit model for *Q. rubra* survival included plot-level random effects. The models resulted in AUROC values of 0.912 and 0.891 for *A. saccharum* and *Q. rubra* seedlings, respectively. All parameter values can be found in Table S5.

The negative association with desiccation was of similar magnitude to the positive association with C_{Annual} . Desiccation events were observed for six *A. saccharum* (n = 116) and 20 *Q. rubra* seedlings (n = 167) across the four years of this study, and most seedlings (92.3%) died the year foliar desiccation was recorded. Moreover, most of the desiccation events (73.1%) were recorded during the 2017 growing season. Soil moisture in 2017 was largely consistent with the other years in this study throughout most of the summer except for particularly low soil moisture in August and September (Fig. S6).

Figure 4 shows the relationship between survival probability and estimated annual foliar CO₂ assimilation (C_{Annual}) for seedlings of both species. *Quercus rubra* seedlings assimilated

more CO₂ annually than *A. saccharum* seedlings on average (symbols in Fig. 4) but had lower average probability of survival. *Quercus rubra* seedlings passed below a mean probability of survival equal to 0.5 at 0.106 mol of estimated CO₂ assimilation. This was an order of magnitude greater than the threshold for *A. saccharum* seedlings which occurred at 0.012 mol assimilation.

Seedling growth

The best fit growth models each included C_{Annual} and only one other covariate. *Acer saccharum* seedling growth was best predicted by a model that included GSF (canopy openness) whereas *Q. rubra* seedling growth was best predicted by a model that included signs of deer herbivory. All covariates were positively associated with growth for both species, but the only significant relationship was between C_{Annual} and *A. saccharum* seedling growth (Fig. 5a). The best fit *A. saccharum* growth model had a goodness of fit $R^2 = 0.504$; goodness of fit for *Q. rubra* growth was 0.456. Models for both species included seedling and plot random effects, with the *A. saccharum* model also including a year random effect and the *Q. rubra* model including random effects for seedling age and planting cohort. All parameter values can be found in Table S3.

As with probability of survival, predicted growth of *A. saccharum* seedlings with the average value of estimated annual CO₂ assimilation was greater than that of *Q. rubra* seedlings, despite the latter estimated to assimilate more CO₂ per year on average (Fig. 6). *Acer saccharum* seedlings were predicted to grow more than *Q. rubra* seedlings (23.23 ± 5.81 and 13.61 ± 28.56 mm yr⁻¹ ± s.d., respectively), but the difference was not statistically significant.

Discussion

Shifts in plant phenology have been one of the most widely reported responses of organisms to current climate change (Ibáñez et al., 2010; Menzel & Fabian, 1999; Piao et al., 2019), but few studies have addressed how differences in spring phenology affect individual performance (but see Augspurger, 2008) and what the resulting implications will be for populations and communities (Forrest & Miller-Rushing, 2010). Tree seedling phenology, carbon assimilation, and performance will be particularly important to understand with respect to forest ecosystems because survival and recruitment at this stage can act as a bottleneck determining the structure and composition of future forest canopies (Grubb, 1977; Harper, 1977). Recent studies have demonstrated that the annual carbon assimilation of temperate understory plants, including tree

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seedlings, is strongly affected by spring foliar phenology and access to light before the canopy closes (Heberling, Cassidy, et al., 2019; Heberling, McDonough MacKenzie, et al., 2019; Kwit et al., 2010), i.e., phenological escape (Jacques et al., 2015). However, it is yet unclear how differences in carbon assimilation linked to this mechanism impact the growth and survival of temperate tree seedlings.

Here, we modeled the relationship between foliar net annual CO₂ assimilation of individual tree seedlings and their demographic performance (i.e., growth and survival) for two temperate tree species that commonly co-occur across eastern North America, *Acer saccharum* and *Quercus rubra*. Furthermore, we quantified how seedling carbon assimilation is affected by spring and fall phenological escape, allowing us to directly link phenology to plant performance. We found strong relationships between estimated carbon assimilation and seedling survival but relatively weak (and likely biologically irrelevant) relationships between carbon assimilation and aboveground height growth. Seedlings of both species were found to assimilate most of their annual carbon during spring phenological escape with relatively minor contributions in fall, suggesting that capacity for phenological escape early in the growing season will play an important role in shaping future tree recruitment. Furthermore, our results suggest that studies of temperate tree seedling carbon assimilation, performance, and recruitment should concentrate on these early season dynamics and that photosynthetic capacity in midseason plays a much smaller role in influencing overall demography.

Spring leaf out date drives annual carbon assimilation

Understory plants in deciduous forests are generally limited by access to light for most of the growing season while the canopy is closed. Therefore, many species have adapted phenological escape behavior that allows them to access ephemeral periods of high light availability in spring by leafing out earlier than the canopy or in fall by senescing their leaves after the canopy (Jacques et al., 2015). Recent studies have suggested that climate change may affect the amount of carbon assimilated during phenological escape by differently affecting the phenology of understory and canopy species (Heberling, Cassidy, et al., 2019; Heberling, McDonough MacKenzie, et al., 2019), but it is as yet unexplored what effect this would have on the demographic performance of understory plants.

We found significant negative correlations between spring leaf out phenology and annual carbon assimilation for seedlings of both species (Fig. 2a), indicating that seedlings assimilated more carbon per annum the earlier they leafed out. This agrees with previous research published by Kwit et al. (2010), which found that *A. saccharum* seedlings could substantially increase their annual carbon gain with earlier leaf out relative to artificial canopy closure treatments. Although this result is intuitive, previous studies which investigated relationships between phenology and performance speculate at or assume this relationship (e.g., Augspurger, 2008; Routhier & Lapointe, 2002; Seiwa, 1998), without quantifying it. Some studies included measurements of species-level photosynthetic characteristics (e.g., Routhier & Lapointe, 2002), but not with enough detail needed to calculate the change in net carbon assimilation as a function of phenology.

In contrast, annual foliar CO₂ assimilation was not significantly correlated with leaf senescence date for either species (Fig. 2b), suggesting that fall phenological escape plays a far less important role in driving seedling carbon dynamics. This is further supported by our findings that spring foliar CO₂ assimilation on average accounted for 84.3% and 52.5% of the total annual assimilation for *A. saccharum* and *Q. rubra* seedlings, respectively, whereas fall assimilation only accounted for -0.2% and 4.0%. One possible reason for this is that timing of leaf senescence could just reflect timing of spring phenology (Fig. S7), echoing results from other research which found similar correlations (Keenan & Richardson, 2015). Alternatively, it has been recently hypothesized that leaf senescence could be driven by sink limitations (Zani, Crowther, Mo, Renner, & Zohner, 2020), where senescence occurs earlier when early- and midseason carbon assimilation is higher, but this hypothesis remains controversial because it contradicts substantial evidence from Free-Air CO₂ enrichment (FACE) experiments (Norby, 2021). Regardless of the underlying mechanism, our results suggest that phenological escape late in the growing season will have negligible effects on net CO₂ assimilation.

CO₂ assimilation affects survival more than growth

Plants rely on photosynthetic carbon assimilation to survive, grow, reproduce, and defend themselves (Mooney, 1972), and our results reflect that dependency. Survival of both species was significantly associated with net annual foliar CO₂ assimilation (Fig. 3), but the relationship between carbon and growth was only significant for *A. saccharum* seedlings (Fig. 5), and the

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relationship was weak. *Acer saccharum* seedlings were predicted to have higher overall probability of survival compared to *Q. rubra* seedlings (Fig. 4) and they also maintained > 50% mean predicted probability of survival at lower CO₂ assimilation compared to *Q. rubra*. Thus, even though *Q. rubra* seedlings assimilated more foliar CO₂ on average than *A. saccharum* seedlings (Fig. 1), their predicted probability of survival at the average value was lower (points in Fig. 4).

The differences in predicted survival probability between species could be due to a few reasons. First, our study only accounted for foliar carbon dynamics and did not account for stem or belowground carbon dynamics. Root respiration rates in temperate forests can be of similar or greater magnitude compared to foliar respiration rates (Reich, Walters, Tjoelker, Vanderklein, & Buschena, 1998), and thus could cause a dissociation between foliar carbon assimilation and seedling performance. This may be particularly true for *Q. rubra* seedlings which develop deep taproots (Wilson, Vitols, & Park, 2007) and might therefore allocate proportionally more carbon to belowground processes compared to *A. saccharum* seedlings. This is supported by previous research that has shown that 2-year-old *Q. rubra* seedlings allocated more carbon to storage than *A. saccharum*, red maple (*Acer rubrum*), or black cherry (*Prunus serotina*) seedlings on a mass basis (Canham, Kobe, Latty, & Chazdon, 1999). However, we lack the evidence needed to further support this theory in this study because we did not quantify belowground carbohydrate concentrations or mass allocation.

Additionally, our results could reflect differences in aboveground growth and respiration costs between these two species. We found consistently higher respiration rates for *Q. rubra* seedlings compared to *A. saccharum* seedlings in the parameterization of our photosynthesis models (Table S5), reflecting higher carbon costs for foliar maintenance. Further, evidence in the literature suggests that *Q. rubra* tend to have thicker leaves (i.e., lower specific leaf area) compared to *A. saccharum* (Abrams & Kubiske, 1990; Lapointe, 2001; Salifu, Apostol, Jacobs, & Islam, 2008) and that they have higher foliar C:N ratios (Midgley, Brzostek, & Phillips, 2015). These qualities provide this species with greater constitutive defense and lower palatability to insect herbivores (Throop & Lerdau, 2004), but make leaves more costly to construct. Thus, greater relative aboveground carbon costs for *Q. rubra* seedlings could make it so that this species requires greater net annual CO₂ assimilation to achieve the same probability of survival.

The higher probability of survival of *A. saccharum* seedlings may also be indicative of the higher shade tolerance reported for this species in the literature since seedlings were grown under low light conditions. Moreover, our results suggest that phenological escape may even be a critical component of shade tolerance for some species. In our study, *A. saccharum* seedlings had lower summer photosynthetic capacity, but also lower respiration costs compared to *Q. rubra* seedlings. This behavior allows seedlings to minimize carbon loss when resources are limited in the middle of the growing season (Craine & Reich, 2005). However, our results also show seedlings must accumulate a strong reserve of carbon in the spring to allow them to withstand low assimilation rates throughout the rest of the growing season (e.g., Fig. 1b; Kwit et al., 2010). Future research should investigate this dynamic further and evaluate whether phenological escape dynamics are correlated with shade tolerance in temperate deciduous forests more generally.

Annual CO₂ assimilation was only significantly associated with height growth for *A. saccharum* (Fig. 5) and our models explained only about 50% of the variation in the data for both species. Furthermore, the predicted changes in growth were relatively small, with seedlings predicted to grow less than 1 cm in height for every additional 0.1 mol CO₂ yr⁻¹ assimilated (Fig. 6). This low amount of growth in part reflects the strongly light-limited environments that these seedlings were grown in. For example, *A. saccharum* seedlings have been recorded to grow less than a meter in height over a period of decades under closed-canopy conditions (Marks & Gardescu, 1998). Thus, it is possible that this relationship would have been better quantified using other metrics of growth such as radial stem growth, belowground growth, or total biomass (e.g., Kaelke et al., 2001; Sevillano, Short, Grant, & O'Reilly, 2016). Future studies in this area should thus account for multiple growth metrics and, when possible, investigate the extent to which using different metrics affects analysis and results.

Survival models for both species also showed significantly negative associations with desiccation and foliar damage due to pathogens and herbivory. We accounted for the negative effects that reduced water availability can have on photosynthetic performance (i.e., by directly correlating carbon assimilation rates with plot-level VPD and soil moisture, as described in Appendix S2), so this additional effect of desiccation suggests that temperate tree seedlings are additionally vulnerable to dying from hydraulic failure (McDowell et al., 2008), where plants die from catastrophic embolisms resulting from extremely negative water potentials. We did not

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collect data on xylem conductance or plant water potential as part of this study, however, so we are unable to draw substantive conclusions from these results. Similarly, leaf damage also reduced survival after accounting for reductions in photosynthetic area in our CO₂ assimilation calculations (Appendix S4), suggesting that foliar damage negatively affects performance beyond the effects associated with leaf area. We can only speculate about the mechanism underlying this effect, but one possible explanation is that foliar damage is correlated with systemic damage such as whole-plant infection that could be a contributing factor in mortality (Jain, Sarsaiya, Wu, Lu, & Shi, 2019).

Deer herbivory was important for *A. saccharum* survival and *Q. rubra* growth, but with opposite effects. Although the association between *A. saccharum* survival and deer herbivory was negative, deer herbivory had a positive association with *Q. rubra* growth, suggesting that this species grew more in response to deer herbivory events. This result, although potentially counterintuitive, is consistent with previously documented compensatory growth dynamics (McNaughton, 1983), and could reflect a potential trade-off between growth and foliar defense (Coley, 1988). However, we did not quantify nonstructural carbohydrate concentrations in this study and thus more substantive conclusions will require further research.

Water limitation and neighboring canopy tree effects

Our results suggest that spring phenological escape is the dominant driver of seedling carbon assimilation and performance, but they also suggest that water availability plays an important role. Soil moisture and VPD both affected seedling photosynthetic capacity seasonally and between species (Fig. S4-S5), with generally positive associations in Spring and Summer and negative relationships at the end of the growing season. Photosynthetic activity is thus likely to be strongly affected by water availability in summer when soil moisture is lowest. Our results also suggest that drought stress can directly affect seedling performance, as evidenced by the significant association between seedling survival and observed desiccation (Fig. 3). Although only a small proportion of seedlings (< 10% of the total) were observed to desiccate, nearly all the desiccation events took place in 2017 when soil moisture reached the lowest values recorded throughout this experiment (Fig. S6). Although this could implicate hydraulic failure as the cause of mortality for these seedlings, we did not measure plant water potentials or other metrics that would allow us to make more substantive conclusions.

We also found that seedling photosynthetic capacity was significantly affected by the identity of canopy tree species that the seedlings were planted near. Canopy tree identity strongly affected RuBP regeneration-limited carbon assimilation rate (J_{max25}) of *A. saccharum* seedlings (Fig. S3a). Values were significantly higher in spring, but lower in summer and fall for seedlings planted beneath conspecific canopy trees, suggesting that this species benefits more from phenological escape but less from growing season sunflecks compared to when planted near *Q. rubra* canopy trees. *Acer saccharum* summer respiration rates were also substantially (though not significantly) higher when planted near *Q. rubra* canopy trees, meaning that net carbon assimilation rates are especially negatively impacted by hot, droughty conditions. Our photosynthesis models accounted for temperature and soil moisture for each gas exchange observation, so it is unlikely that these results are due to differences in microenvironment between the two canopies. The underlying mechanism behind this difference is uncertain, but it is possible that some combination of inorganic nitrogen availability, concentrations of other soil nutrients, and plant-soil feedback effects could be responsible for the observed differences in seedling photosynthetic rates (Classen et al., 2015; Juice et al., 2006; Liang et al., 2020; McCarthy-Neumann & Ibáñez, 2012, 2013; McCarthy-Neumann & Kobe, 2010). However, this is speculative and future research should investigate this relationship and further explore how drought interacts with phenological escape more generally.

Conclusion

The results from this study suggest that temperate tree seedling survival is strongly associated with annual foliar CO₂ assimilation, which in turn depends on spring phenological escape. Seedlings assimilated relatively little carbon in fall compared to spring, suggesting that the timing of leaf senescence has little effect on seedling performance. Future studies should thus place an emphasis on measuring photosynthetic capacity and activity at the beginning of the growing season rather than in summer or fall. Water availability plays an important role in seedling carbon assimilation and potentially directly via hydraulic failure, but more research is needed on this topic, particularly in investigating how water availability and phenological escape interact to affect seedling performance.

Still, this study mechanistically links tree seedling phenology to survival and growth performance and will therefore allow future research to make accurate demographic projections

for these species based on climate change forecasts and estimated changes in annual carbon assimilation. The importance of spring phenological escape to net foliar carbon assimilation suggests that any changes to these dynamics resulting from climate change will have strong effects on overall seedling performance and tree recruitment. Furthermore, warmer temperatures and decreased water availability predicted for our study region (Handler et al., 2014) will make phenological escape dynamics even more important, as seedlings will need to assimilate more carbon in spring to make up for the increasing respiration costs in summer and fall. Determining whether temperate deciduous tree seedlings are capable of improving their phenological escape success is an important topic for future research and will have important implications for predictions of future forest structure and composition.

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Data Availability Statement

Code and data used in this manuscript (i.e., for photosynthesis, survival, and growth models) are available in the Zenodo digital repository: <http://doi.org/10.5061/dryad.1c59zw3tk> (Lee & Ibáñez, 2021)

References

- Abrams, M. D. (1990). Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiology*, 7(1_2_3_4), 227–238. doi: 10.1093/treephys/7.1-2-3-4.227
- Abrams, M. D., & Kubiske, M. E. (1990). Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: Influence of light regime and shade-tolerance rank. *Forest Ecology and Management*, 31(4), 245–253. doi: 10.1016/0378-1127(90)90072-J
- Augsburger, C. K. (2008). Early spring leaf out enhances growth and survival of saplings in a temperate deciduous forest. *Oecologia*, 156(2), 281–286. doi: 10.1007/s00442-008-1000-7

- Augspurger, C. K., & Bartlett, E. A. (2003). Differences in leaf phenology between juvenile and adult trees in a temperate deciduous forest. *Tree Physiology*, 23(8), 517–525. doi: 10.1093/treephys/23.8.517
- Bahari, Z. A., Pallardy, S. G., & Parker, W. C. (1985). Photosynthesis, Water Relations, and Drought Adaptation in Six Woody Species of Oak-Hickory Forests in. *Forest Science*, 31(3), 557–569.
- Barnes, B. V., & Wagner, Jr., W. H. (2004). *Michigan Trees: A Guide to the Trees of the Great Lakes Region*. Ann Arbor, MI: The University of Michigan Press.
- Bauerle, W. L., Oren, R., Way, D. A., Qian, S. S., Stoy, P. C., Thornton, P. E., ... Reynolds, R. F. (2012). Photoperiodic regulation of the seasonal pattern of photosynthetic capacity and the implications for carbon cycling. *Proceedings of the National Academy of Sciences*, 109(22), 8612–8617. doi: 10.1073/pnas.1119131109
- Caemmerer, S. Von. (2000). Biochemical models of leaf photosynthesis. In *Techniques in Plant Sciences*. Collingwood, VIC, Australia: CSIRO Publishing.
- Canham, C. D., Kobe, R. K., Latty, E. F., & Chazdon, R. L. (1999). Interspecific and intraspecific variation in tree seedling survival: Effects of allocation to roots versus carbohydrate reserves. *Oecologia*, 121(1), 1–11. doi: 10.1007/s004420050900
- Castro, J. (1999). Seed mass versus seedling performance in Scots pine: A maternally dependent trait. *New Phytologist*, 144(1), 153–161. doi: 10.1046/j.1469-8137.1999.00495.x
- Cavender-Bares, J., & Bazzaz, F. A. (2000). Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia*, 124(1), 8–18. doi: 10.1007/PL00008865
- Classen, A. T., Sundqvist, M. K., Henning, J. A., Newman, G. S., Moore, J. A. M., Cregger, M. A., ... Patterson, C. M. (2015). Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: What lies ahead? *Ecosphere*, 6(8). doi: 10.1890/ES15-00217.1
- Coley, P. D. (1988). Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia*, 74, 531–536. doi: 10.1007/BF00380050
- Craine, J. M., & Reich, P. B. (2005). Leaf-level light compensation points in shade-tolerant woody seedlings. *New Phytologist*, 166, 710–713.
- Crow, T. R. (1988). Reproductive mode and mechanisms for self-replacement of northern red

oak (*Quercus rubra*): a review. *Forest Science*, 34(1), 19–40. doi: 10.1016/S0378-1127(03)00108-7

- Dickman, L. T., McDowell, N. G., Sevanto, S., Pangle, R. E., & Pockman, W. T. (2015). Carbohydrate dynamics and mortality in a piñon-juniper woodland under three future precipitation scenarios. *Plant, Cell and Environment*, 38(4), 729–739. doi: 10.1111/pce.12441
- Farquhar, G. D., Caemmerer, S. Von, & Berry, J. A. (1980). A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta*, 149, 78–90. doi: 10.1007/BF00386231
- Forrest, J., & Miller-Rushing, A. J. (2010). Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1555), 3101–3112. doi: 10.1098/rstb.2010.0145
- Gelman, A., & Rubin, D. B. (1992). Inference from interative simulation using multiple sequences. *Statistical Science*, 7(4), 457–511. doi: 10.1214/ss/1177011136
- Gerhardt, K. (1998). Leaf defoliation of tropical dry forest tree seedlings - Implications for survival and growth. *Trees - Structure and Function*, 13(2), 88–95. doi: 10.1007/PL00009741
- Gómez-Aparicio, L., & Canham, C. D. (2008). Neighbourhood analyses of the allelopathic effects of the invasive tree *Ailanthus altissima* in temperate forests. *Journal of Ecology*, 96(3), 447–458. doi: 10.1111/j.1365-2745.2007.01352.x
- González-Rodríguez, V., Villar, R., & Navarro-Cerrillo, R. M. (2011). Maternal influences on seed mass effect and initial seedling growth in four *Quercus* species. *Acta Oecologica*, 37(1), 1–9. doi: 10.1016/j.actao.2010.10.006
- Green, P. T., Harms, K. E., & Connell, J. H. (2014). Nonrandom, diversifying processes are disproportionately strong in the smallest size classes of a tropical forest. *Proceedings of the National Academy of Sciences*, 111(52), 18649–18654. doi: 10.1073/pnas.1321892112
- Grossiord, C., Buckley, T. N., Cernusak, L. A., Novick, K. A., Poulter, B., Siegwolf, R. T. W., ... McDowell, N. G. (2020). Plant responses to rising vapor pressure deficit. *New Phytologist*, 226(6), 1550–1566. doi: 10.1111/nph.16485
- Grubb, P. J. (1977). The Maintenance of Species-Richness in Plant Communities : The Importance of the Regeneration Niche. *Biological Reviews*, 52(4), 107–145. doi:

10.1111/j.1469-185X.1977.tb01347.x

- Handler, S., Duveneck, M. J., Iverson, L., Peters, E., Scheller, R. M., Wythers, K. R., ... Ziel, R. (2014). Michigan forest ecosystem vulnerability assessment and synthesis: a report from the Northwoods Climate Change Response Framework project. In *General Technical Report NRS-129*. Newtown Square, PA. doi: 10.2737/NRS-GTR-129
- Harper, J. L. (1977). *Population Biology of Plants*. London, UK: Academic Press.
- Heberling, J. M., Cassidy, S. T., Fridley, J. D., & Kalisz, S. (2019). Carbon gain phenologies of spring-flowering perennials in a deciduous forest indicate a novel niche for a widespread invader. *New Phytologist*, 221(2), 778–788. doi: 10.1111/nph.15404
- Heberling, J. M., McDonough MacKenzie, C., Fridley, J. D., Kalisz, S., & Primack, R. B. (2019). Phenological mismatch with trees reduces wildflower carbon budgets. *Ecology Letters*, 22(4), 616–623. doi: 10.1111/ele.13224
- Hlásny, T., Barcza, Z., Fabrika, M., Balázs, B., Churkina, G., Pajtik, J., ... Turčáni, M. (2011). Climate change impacts on growth and carbon balance of forests in Central Europe. *Climate Research*, 47(3), 219–236. doi: 10.3354/cr01024
- Hoch, G., Siegwolf, R. T. W., Keel, S. G., Körner, C., & Han, Q. (2013). Fruit production in three masting tree species does not rely on stored carbon reserves. *Oecologia*, 171(3), 653–662. doi: 10.1007/s00442-012-2579-2
- Ibáñez, I., Katz, D. S. W., & Lee, B. R. (2017). The contrasting effects of short-term climate change on the early recruitment of tree species. *Oecologia*, 184(3), 701–713. doi: 10.1007/s00442-017-3889-1
- Ibáñez, I., Primack, R. B., Miller-Rushing, A. J., Ellwood, E., Higuchi, H., Lee, S. D., ... Silander, J. A. (2010). Forecasting phenology under global warming. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1555), 3247–3260. doi: 10.1098/rstb.2010.0120
- Jackson, S. T., & Williams, J. W. (2004). Modern analogs in quaternary paleoecology: Here today, gone yesterday, gone tomorrow? *Annual Review of Earth and Planetary Sciences*, 32(1), 495–537. doi: 10.1146/annurev.earth.32.101802.120435
- Jacques, M. H., Lapointe, L., Rice, K., Montgomery, R. A., Stefanski, A., & Reich, P. B. (2015). Responses of two understory herbs, *Maianthemum canadense* and *Eurybia macrophylla*, to experimental forest warming: Early emergence is the key to enhanced reproductive output.

- American Journal of Botany*, 102(10), 1610–1624. doi: 10.3732/ajb.1500046
- Jain, A., Sarsaiya, S., Wu, Q., Lu, Y., & Shi, J. (2019). A review of plant leaf fungal diseases and its environment speciation. *Bioengineered*, 10(1), 409–424. doi: 10.1080/21655979.2019.1649520
- Juice, S. M., Fahey, T. J., Siccama, T. G., Driscoll, C. T., Denny, E. G., Eagar, C., ... Richardson, A. D. (2006). Response of sugar maple to calcium addition to northern hardwood forest. *Ecology*, 87(5), 1267–1280. doi: 10.1890/0012-9658(2006)87[1267:ROSMTC]2.0.CO;2
- Kaelke, C. M., Kruger, E. L., Reich, P. B., Kaelke, C. M., Kruger, E. L., & Reich, P. B. (2001). Trade-offs in seedling survival, growth, and physiology among hardwood species of contrasting successional status along a light- availability gradient. *Can. J. For. Res*, 31, 1602–1616. doi: 10.1139/cjfr-31-9-1602
- Keenan, T. F., & Richardson, A. D. (2015). The timing of autumn senescence is affected by the timing of spring phenology: implications for predictive models. *Global Change Biology*, 21(7), 2634–2641. doi: 10.1111/gcb.12890
- Korol, R. L., Running, S. W., Milner, K. S., & Hunt, Jr., E. R. (1991). Testing a mechanistic carbon balance model against observed tree growth. *Canadian Journal of Forest Research*, 21, 1098–1105. doi: 10.1139/x91-151
- Kwit, M. C., Rigg, L. S., & Goldblum, D. (2010). Sugar maple seedling carbon assimilation at the northern limit of its range: the importance of seasonal light. *Canadian Journal of Forest Research*, 40(2), 385–393. doi: 10.1139/X09-196
- Lapointe, L. (2001). How phenology influences physiology in deciduous forest spring ephemerals. *Physiologia Plantarum*, 113(2), 151–157. doi: 10.1034/j.1399-3054.2001.1130201.x
- Larigauderie, A., & Körner, C. (1995). Acclimation of leaf dark respiration to temperature in alpine and lowland plant species. *Annals of Botany*, Vol. 76, pp. 245–252. doi: 10.1006/anbo.1995.1093
- Lee, B. R., & Ibáñez, I. (2021). *Data and code for “Spring phenological escape is critical for the survival of temperate tree seedlings.”* Dryad. doi: 10.5061/dryad.1c59zw3tk
- Lei, T. T., & Lechowicz, M. J. (1990). Shade adaptation and shade tolerance in saplings of three *Acer* species from eastern North America. *Oecologia*, 84, 224–228. doi:

10.1007/BF00318275

- Liang, X., Zhang, T., Lu, X., Ellsworth, D. S., BassiriRad, H., You, C., ... Ye, Q. (2020). Global response patterns of plant photosynthesis to nitrogen addition: A meta-analysis. *Global Change Biology*, 26(6), 3585–3600. doi: 10.1111/gcb.15071
- Loewenstein, N. J., & Pallardy, S. G. (1998). Drought tolerance, xylem sap abscisic acid and stomatal conductance during soil drying: A comparison of young plants of four temperate deciduous angiosperms. *Tree Physiology*, 18, 421–430.
- Lunn, D., Spiegelhalter, D. J., Thomas, A., & Best, N. (2009). The BUGS project: Evolution, critique and future directions. *Statistics in Medicine*, 28, 3049–3067. doi: 10.1002/sim.3680
- Lusk, C. H., & Del Pozo, A. (2002). Survival and growth of seedlings of 12 Chilean rainforest trees in two light environments: Gas exchange and biomass distribution correlates. *Austral Ecology*, 27(2), 173–182. doi: 10.1046/j.1442-9993.2002.01168.x
- Marks, P. L., & Gardescu, S. (1998). A case study of sugar maple (*Acer saccharum*) as a forest seedling bank species. *Journal Of The Torrey Botanical Society*, 125(4), 287–296.
- Martin, P. H., Canham, C. D., & Kobe, R. K. (2010). Divergence from the growth-survival trade-off and extreme high growth rates drive patterns of exotic tree invasions in closed-canopy forests. *Journal of Ecology*, 98(4), 778–789. doi: 10.1111/j.1365-2745.2010.01666.x
- McCarthy-Neumann, S., & Ibáñez, I. (2012). Tree range expansion may be enhanced by escape from negative plant-soil feedbacks. *Ecology*, 93(12), 2637–2649. doi: 10.1890/11-2281.1
- McCarthy-Neumann, S., & Ibáñez, I. (2013). Plant-soil feedback links negative distance dependence and light gradient partitioning during seedling establishment. *Ecology*, 94(4), 780–786.
- McCarthy-Neumann, S., & Kobe, R. K. (2010). Conspecific and heterospecific plant-soil feedbacks influence survivorship and growth of temperate tree seedlings. *Journal of Ecology*, 98(2), 408–418. doi: 10.1111/j.1365-2745.2009.01620.x
- McDowell, N. G., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., ... Yepez, E. a. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, 178(4), 719–739. doi: 10.1111/j.1469-8137.2008.02436.x
- McDowell, N. G., & Sevanto, S. (2010). The mechanisms of carbon starvation : how , when , or does it even occur at all? *New Phytologist*, 186, 264–266. doi: 10.1111/nph.12154

- McNaughton, S. J. (1983). Compensatory Plant Growth as a Response to Herbivory. *Oikos*, 40(3), 329–336. Retrieved from <https://www.jstor.org/stable/3544305>
- Menzel, A., & Fabian, P. (1999). Growing season extended in Europe. *Nature*, 397(6721), 659. doi: 10.1038/17709
- Metz, C. E. (1978). Basic principles of ROC analysis. *Seminars in Nuclear Medicine*, 8(4), 283–298. doi: 10.1016/S0001-2998(78)80014-2
- Midgley, M. G., Brzostek, E., & Phillips, R. P. (2015). Decay rates of leaf litters from arbuscular mycorrhizal trees are more sensitive to soil effects than litters from ectomycorrhizal trees. *Journal of Ecology*, 103(6), 1454–1463. doi: 10.1111/1365-2745.12467
- Montgomery, R. (2004). Relative importance of photosynthetic physiology and biomass allocation for tree seedling growth across a broad light gradient. *Tree Physiology*, 24(2), 155–167. doi: 10.1093/treephys/24.2.155
- Mooney, H. A. (1972). The Carbon Balance of Plants. *Annual Review of Ecology and Systematics*, 3(1), 315–346. doi: 10.1146/annurev.es.03.110172.001531
- Murtaugh, P. A. (1996). The statistical evaluation of ecological indicators. *Ecological Applications*, 6(1), 132–139. doi: 10.2307/2269559
- Nabity, P. D., Zavala, J. A., & DeLucia, E. H. (2009). Indirect suppression of photosynthesis on individual leaves by arthropod herbivory. *Annals of Botany*, 103(4), 655–663. doi: 10.1093/aob/mcn127
- Niinemets, Ü. (2010). A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. *Ecological Research*, 25(4), 693–714. doi: 10.1007/s11284-010-0712-4
- Norby, R. J. (2021). Comment on “Increased growing-season productivity drives earlier autumn leaf senescence in temperate trees.” *Science*, 371(6533), eabg1438. doi: 10.1126/science.abg1438
- Patrick, L. D., Ogle, K., & Tissue, D. T. (2009). A hierarchical Bayesian approach for estimation of photosynthetic parameters of C3 plants. *Plant, Cell and Environment*, 32(12), 1695–1709. doi: 10.1111/j.1365-3040.2009.02029.x
- Pellissier, F., & Souto, X. C. (1999). Allelopathy in Northern Temperate and Boreal Semi-Natural Woodland. *Critical Reviews in Plant Sciences*, 18(5), 637–652. doi: 10.1080/07352689991309423

- Peltier, D. M. P., & Ibáñez, I. (2015). Patterns and variability in seedling carbon assimilation: implications for tree recruitment under climate change. *Tree Physiology*, 35(1), 71–85. doi: 10.1093/treephys/tpu103
- Pfanz, H., & Aschan, G. (2001). *The Existence of Bark and Stem Photosynthesis in Woody Plants and Its Significance for the Overall Carbon Gain. An Eco-Physiological and Ecological Approach*. 62, 477–510. doi: 10.1007/978-3-642-56849-7_19
- Phillips, R. P., & Fahey, T. J. (2006). Tree species and mycorrhizal associations influence the magnitude of rhizosphere effects. *Ecology*, 87(5), 1302–1313. doi: 10.1890/0012-9658(2006)87[1302:TSAMAI]2.0.CO;2
- Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., ... Zhu, X. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*, 25(6), 1922–1940. doi: 10.1111/gcb.14619
- Piper, F. I., Reyes-Díaz, M., Corcuera, L. J., & Lusk, C. H. (2009). Carbohydrate storage, survival, and growth of two evergreen *Nothofagus* species in two contrasting light environments. *Ecological Research*, 24(6), 1233–1241. doi: 10.1007/s11284-009-0606-5
- Reich, P. B., Walters, M., Tjoelker, M., Vanderklein, D., & Buschena, C. (1998). Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. *Functional Ecology*, 12(3), 395–405. doi: 10.1046/j.1365-2435.1998.00209.x
- Roman, D. T., Novick, K. A., Brzostek, E. R., Dragoni, D., Rahman, F., & Phillips, R. P. (2015). The role of isohydric and anisohydric species in determining ecosystem-scale response to severe drought. *Oecologia*, 179(3), 641–654. doi: 10.1007/s00442-015-3380-9
- Routhier, M. C., & Lapointe, L. (2002). Impact of tree leaf phenology on growth rates and reproduction in the spring flowering species *Trillium erectum* (Liliaceae). *American Journal of Botany*, 89(3), 500–505. doi: 10.3732/ajb.89.3.500
- Ruan, X., Pan, C. De, Liu, R., Li, Z. H., Shu-Ling, L. I., Jiang, D. A., ... Wang, Q. (2016). Effects of climate warming on plant autotoxicity in forest evolution: a case simulation analysis for *Picea schrenkiana* regeneration. *Ecology and Evolution*, 6(16), 5854–5866. doi: 10.1002/ece3.2315
- Sala, A., Woodruff, D. R., & Meinzer, F. C. (2012). Carbon dynamics in trees: Feast or famine? *Tree Physiology*, 32(6), 764–775. doi: 10.1093/treephys/tpr143

- Salifu, K. F., Apostol, K. G., Jacobs, D. F., & Islam, M. A. (2008). Growth, physiology, and nutrient retranslocation in nitrogen-15 fertilized *Quercus rubra* seedlings. *Annals of Forest Science*, 65(1), 101–101. doi: 10.1051/forest:2007073
- Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9(7), 671–675. doi: 10.1038/nmeth.2089
- Seiwa, K. (1998). Advantages of early germination for growth and survival of seedlings of *Acer mono* under different overstorey phenologies in deciduous broad-leaved forests. *Journal of Ecology*, 86(2), 219–228. doi: 10.1046/j.1365-2745.1998.00245.x
- Sevillano, I., Short, I., Grant, J., & O'Reilly, C. (2016). Effects of light availability on morphology, growth and biomass allocation of *Fagus sylvatica* and *Quercus robur* seedlings. *Forest Ecology and Management*, 374, 11–19. doi: 10.1016/j.foreco.2016.04.048
- Slot, M., & Kitajima, K. (2015). Whole-plant respiration and its temperature sensitivity during progressive carbon starvation. *Functional Plant Biology*, 42(6), 579–588. doi: 10.1071/FP14329
- Smith, N. G., & Dukes, J. S. (2013). Plant respiration and photosynthesis in global-scale models: Incorporating acclimation to temperature and CO₂. *Global Change Biology*, 19(1), 45–63. doi: 10.1111/j.1365-2486.2012.02797.x
- Spiegelhalter, D. J., Best, N. G., Carlin, B. P., & Van Der Linde, A. (2002). Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society. Series B: Statistical Methodology*, 64(4), 583–616. doi: 10.1111/1467-9868.00353
- Throop, H. L., & Lerdau, M. T. (2004). Effects of nitrogen deposition on insect herbivory: Implications for community and ecosystem processes. *Ecosystems*, 7(2), 109–133. doi: 10.1007/s10021-003-0225-x
- Umaña, M. N., Forero-Montaña, J., Muscarella, R., Nytech, C. J., Thompson, J., Uriarte, M., ... Swenson, N. G. (2016). Interspecific functional convergence and divergence and intraspecific negative density dependence underlie the seed-to-seedling transition in tropical trees. *The American Naturalist*, 187(1), 99–109. doi: 10.1086/684174
- Vitasse, Y., Lenz, A., Hoch, G., & Körner, C. (2014). Earlier leaf-out rather than difference in freezing resistance puts juvenile trees at greater risk of damage than adult trees. *Journal of Ecology*, 102(4), 981–988. doi: 10.1111/1365-2745.12251
- Wagner, S., Madsen, P., & Ammer, C. (2009). Evaluation of different approaches for modelling

individual tree seedling height growth. *Trees - Structure and Function*, 23(4), 701–715. doi: 10.1007/s00468-009-0313-4

Walters, M. B., & Reich, P. B. (1996). Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology*, 77(3), 841–853.

Wilson, E. R., Vitols, K. C., & Park, A. (2007). Root characteristics and growth potential of container and bare-root seedlings of red oak (*Quercus rubra* L.) in Ontario, Canada. *New Forests*, 34(2), 163–176. doi: 10.1007/s11056-007-9046-7

Zani, D., Crowther, T. W., Mo, L., Renner, S. S., & Zohner, C. M. (2020). Increased growing-season productivity drives earlier autumn leaf senescence in temperate trees. *Science*, 370(6520), 1066–1071. doi: 10.1126/science.abd8911

Figures

Figure 1: Average tree seedling net foliar CO₂ assimilation estimates (\pm 95% Confidence Intervals) for spring, summer, and fall. Panels on the right show examples of (b) additive CO₂ assimilation and (c) average daily assimilation rates for representative *A. saccharum* (blue, circles) and *Q. rubra* (yellow, triangles) individuals.

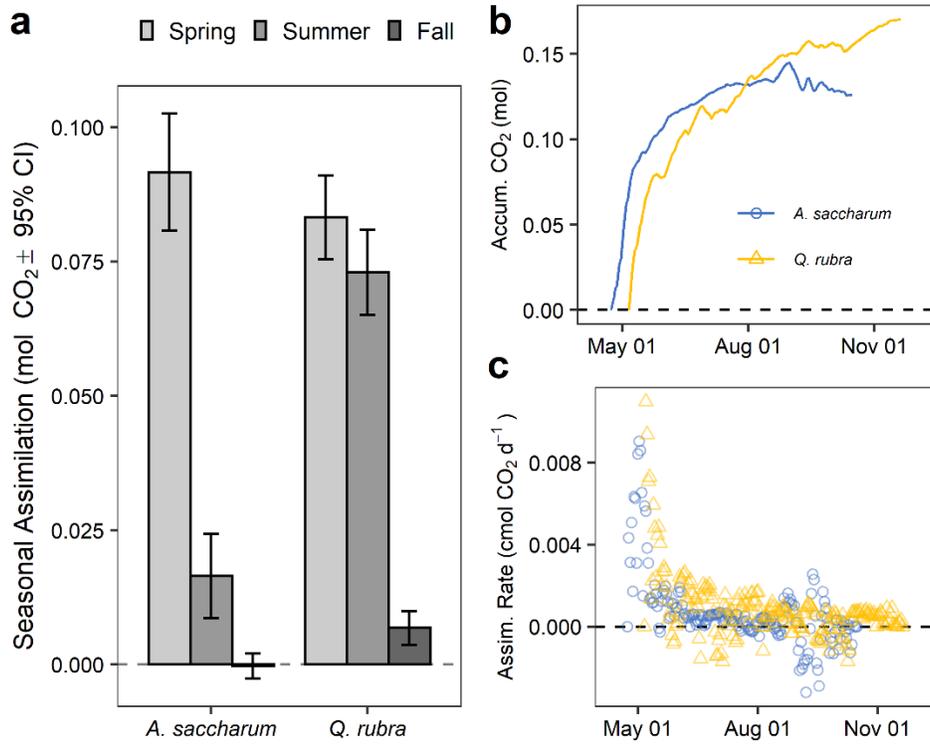


Figure 2: Relationships between estimated net annual CO₂ assimilation and a) day of leaf out or b) day of leaf senescence. Blue lines and symbols represent the trends for *A. saccharum* seedlings and yellow lines and symbols represent trends for northern *Q. rubra* seedlings. Symbol shading indicates whether seedlings were planted under *A. saccharum* (filled) or *Q. rubra* (empty) canopy trees.

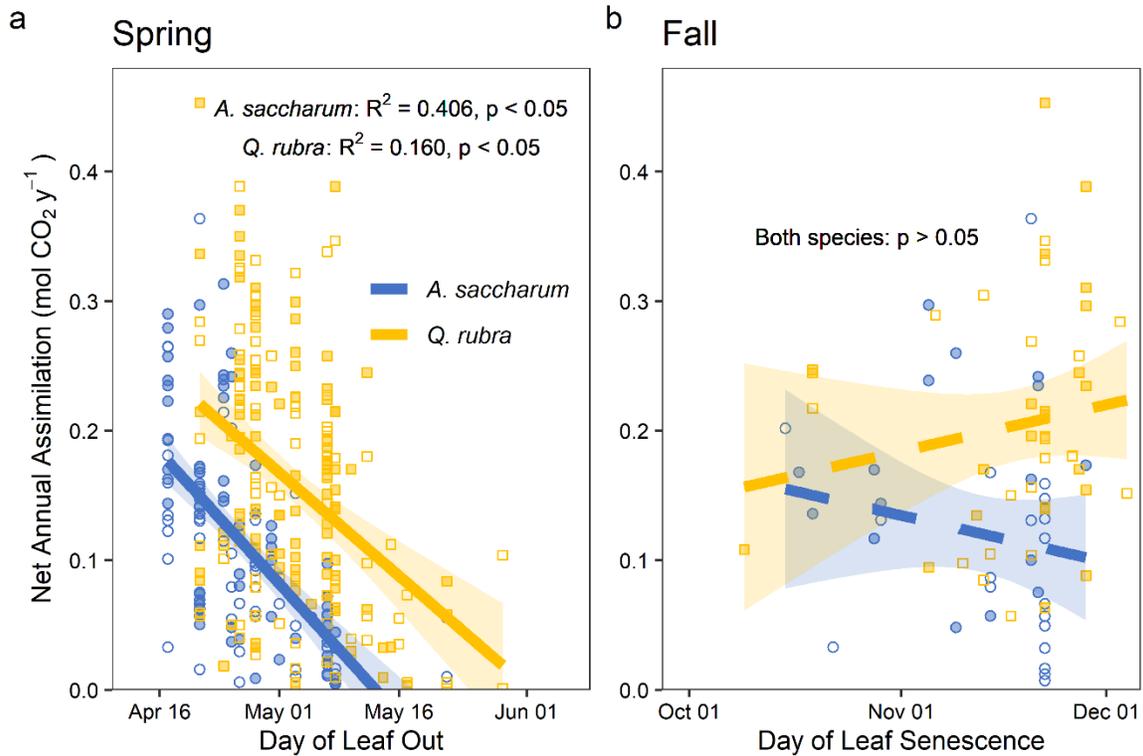


Figure 3: Posterior estimated means and 95% credible intervals (CI) for survival model parameters for (a) *A. saccharum* and (b) *Q. rubra* seedlings. Asterisks indicate parameter estimates that are significantly different from zero.

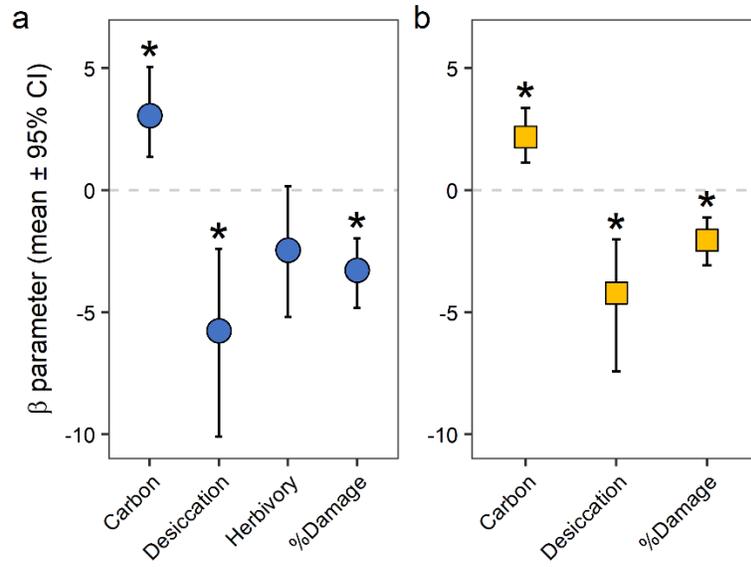


Figure 4: Predicted probability of survival (lines; mean \pm 95% predictive intervals) as a function of estimated annual foliar CO₂ assimilation for *A. saccharum* (blue) and *Q. rubra* seedlings (yellow). Points represent the probability of survival for seedlings with the average estimated assimilation for each species.

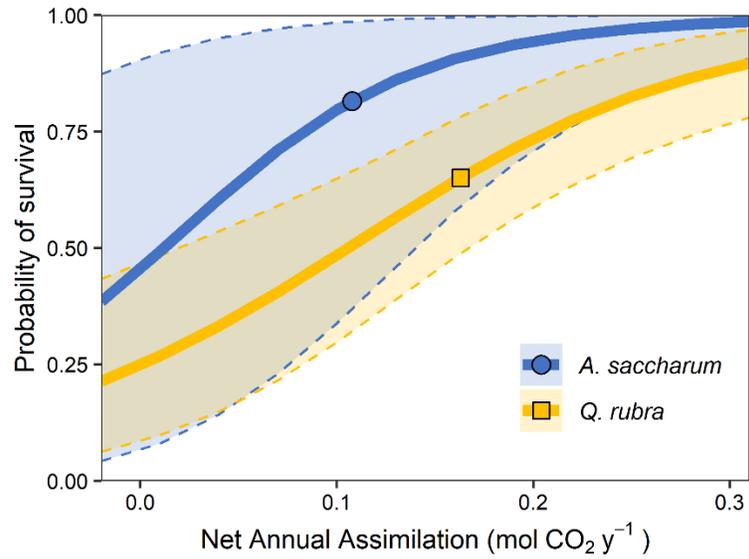


Figure 5: Posterior estimated means and 95% credible intervals (CI) for growth model parameters for (a) *A. saccharum* and (b) *Q. rubra* seedlings. Asterisks indicate parameter estimates that are significantly different from zero.

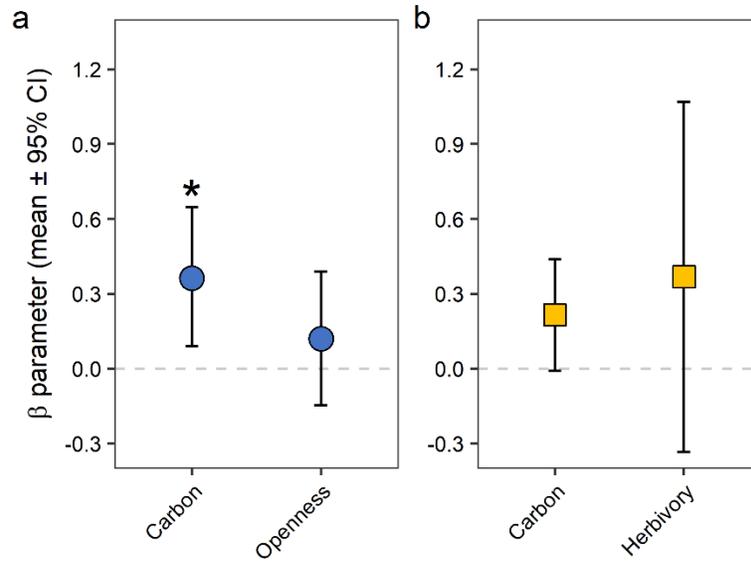


Figure 6: Predicted height growth (lines; mean \pm 95% predictive intervals) as a function of estimated annual foliar CO₂ assimilation for *A. saccharum* (blue) and *Q. rubra* seedlings (yellow). Points represent the predicted growth for seedlings with the average estimated assimilation for each species.

