

PATTERNS AND VARIABILITY IN TREE SEEDLING PHOTOSYNTHESIS:  
IMPLICATIONS FOR RECRUITMENT UNDER CLIMATE CHANGE.

by

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## ABSTRACT

Predicting future forests' structure and functioning is a critical goal for ecologists, and seedling performance under climate change will in large part determine future forest structure and composition. Seedling photosynthetic response will be key in determining if a particular species recruits enough individuals to maintain its populations. During the 2012 growing season we studied photosynthetic responses of seedlings of four dominant tree species to a wide range of environmental conditions based on temporally extensive *in situ* gas exchange measurements. Despite the large intraspecies variability in observed assimilation rates we found significant species differences in light saturated maximum assimilation rate ( $1.95 \pm 0.1415 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *Acer saccharum*,  $2.95 \pm 0.17 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *Carya glabra*,  $3.86 \pm 0.23 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *Quercus rubra*, and  $4.28 \pm 0.1972 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *Quercus velutina*) and photosynthesis under field light levels ( $1.66 \pm 0.29 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *A. saccharum* to  $3.21 \pm 0.40 \mu\text{mol m}^{-2} \text{s}^{-1}$  *Q. velutina*). Under increases in temperature, assimilation rate will likely decrease by approximately  $0.20 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *C. glabra*,  $0.21 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *Q. rubra*, and  $0.35 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *Q. velutina* in spring, but not as much or at all in summer and fall. This is likely due in part to concurrent increases in spring dark respiration rates with temperature of  $0.15 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *C. glabra*,  $0.16 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *Q. rubra*, and  $0.16 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *Q. velutina*. However, decreased stomatal conductance in response to drought was likely responsible for the observed lack of response to higher temperatures in summer and fall, as well as the lack of response of *A. saccharum* to temperature in all three seasons. We also found that, while seasonal variability exists in photosynthetic response, assimilation rate was equal in summer and fall, and that this seasonal variability was greater in the drought tolerant oak species we tested (*Q. rubra* and *Q. velutina*) than the other species (*C. glabra* and *A. saccharum*). This finding points to the

importance of field measurements in evaluating the strength of trends seen in the greenhouse.

Lastly, under projected increases in temperature and aridity, drought tolerant species may be at a competitive advantage, due to superior photosynthetic capacity under these conditions. Our findings indicate that seasonal trends in photosynthesis may be altered, and oak species may become more dominant in Northeastern forests under projected increases in temperature and aridity due to climate change.

## INTRODUCTION

Forests provide a number of ecosystem services humans are highly dependent upon (i.e., soil retention, water table replenishment, carbon sequestration, pollution mitigation, habitat for game animals and endangered species, timber, and recreation (Daily et al. 1997)), thus, assessing the future health of forests has become a major goal for ecologists. Under the current climatic trends, North American forests will be subjected to increased average temperatures, decreased average precipitation along with changes in timing of rainfall, increased environmental variability and an increased frequency of extreme events (IPCC 2007). In the long-term, these trends are predicted to lead to future changes in tree species distributional ranges (Iverson et al., 2008). But, in the short-term, and at a given location, some species may be able to acclimate to the new environment, whereas others may experience increased mortality or decreased recruitment success (Ibanez et al. 2007). Despite the major implications of such disparate responses, we do not fully understand which outcome will be more likely for most species in North America. In order to predict the future state of these forests, we will need to make accurate predictions about tree population dynamics under projected environmental conditions. In particular, understanding how recruitment of new individuals is affected by changing conditions may confer the most useful information, because this life stage will likely be the most affected by climate change (Ibanez et al. 2009).

Climate envelope models are a commonly employed (Iverson et al. 2008. McKenney et al. 2007. Hamann and Wang 2006.) and critiqued (Pearson and Dawson 2003) method for predicting future tree species distributions. However, in order to understand short-term dynamics, particularly for long-lived species with low migration rates like trees, acclimation may be a more important process than migration. And, while adult trees themselves may be fairly

good at coping with variable and non-optimum conditions over long time scales, seedlings may not. Tree seedlings typically exhibit very high mortality in comparison with other life stages, constituting a bottleneck on population growth (Harper 1977; Harcomb 1987). Seedlings cannot utilize resources, like water or nutrients, from as large a volume of soil as adult trees and also lack enough reserves to cope with sustained periods of unfavorable conditions, making their survival highly dependent upon their environment. Seedling population dynamics are correlated to adult population trends (De Steven 1994), and ultimately, if a tree species fails to recruit enough individuals over a long period of time, the population will decline.

In order to survive and further recruit to larger size classes, seedlings need to assimilate some minimum level of carbon to maintain growth (Casperson and Kobe 2001), which they use to maintain metabolic processes such as radial growth, maintenance respiration, and fine root production and leaf formation. The rate of carbon assimilation is highly dependent on environmental conditions. It is well established that light is a crucial driving factor of assimilation and growth (Burkholder 1936. Johnston 1940. Farquhar et al. 1980). Seedlings in understory environments grow more slowly than seedlings in higher light (Sack et al. 2008. Rebbeck et al. 2011). Similarly, soil moisture is important in maintaining transpiration and stomatal function, allowing the assimilation of carbon dioxide through stomata. Low soil moisture results in stomatal closure to protect leaf and whole plant xylem connectivity, leaf turgor, and internal physiologic processes, and thus prevents carbon assimilation if severe enough (Havranek and Benecke 1978), though stomatal behavior differs between species (Kubiske et al. 1996). Availability of soil resources such as nitrogen is also an important determinant of physiologic processes. Chronic nitrogen limitation may lead to sub-optimal concentrations of leaf N, potentially leading to lower amounts of Rubisco in the leaf and low

photosynthetic rates (Field and Mooney 1986). Temperature is also an important factor because it affects the rates of biochemical reactions; however, the effects of temperature on carbon assimilation may be more complex, because assimilation is the sum of multiple component processes (carbon fixation through carboxylation, electron transport and phosphorylation, and carbon release through respiration) which all have different temperature dependencies (von Caemmerer 2000). Therefore, while photosynthetic rate may increase with temperature, so will dark respiration (Man and Lieffers 1997, Dreyer et al. 2001). Furthermore, extreme high temperatures can be detrimental, actually decreasing maximum carboxylation and electron transport rates via photoinhibition (Dreyer et al. 2001.), while at the same time seedling dark respiration acclimates to sustained changes in temperature, complicating the relationship (Liang et al. 2013, Rodríguez-Calcerrada et al. 2010).

Temporal dynamics in these abiotic drivers may also limit carbon assimilation. Understory light availability, in particular, fluctuates seasonally in temperate forest environments. As canopy trees leaf out and reach maximum canopy expansion, light penetration to the understory declines, and as they lose their leaves in the fall, understory light levels increase again. A number of studies have looked at the importance of seasonal light availability in understories for seedling survival (Augspurger et al. 2005, 2008, Seiwa 1998). The early part of the growing season is critically important for seedling carbon assimilation. By constructing seasonal carbon budgets, Kwit et al. (2012) showed that for understory *A. saccharum* seedlings approximately 80% of annual assimilation was accomplished in the first 15 days of the growing season. Furthermore, in simulations, they found that seedlings leafing out 6 days earlier would have obtained 200% more carbon.

Photosynthetic processes themselves may also be highly variable, as a number of key



photosynthetic parameters vary significantly across the growing season. Net photosynthetic capacity (at saturating light  $\sim 2000 \mu\text{mol m}^{-2} \text{s}^{-1} \text{CO}_2$ ) peaked during early spring for five North American tree species (Augspurger 2005). Somewhat in contrast, for 23 temperate tree species, maximum Rubisco carboxylation rate ( $V_{\text{cmax}}$ ) and maximum electron transport rate ( $J_{\text{max}}$ ), parameters related to the maximum photosynthetic rate depending on the intracellular  $\text{CO}_2$  concentration ( $C_i$ ), were found to peak around the summer solstice, or the maximum photoperiod (Bauerle et al. 2012). Similarly, Zhu et al. (2011) found that for a single tree species, in addition to  $V_{\text{cmax}}$  and  $J_{\text{max}}$  peaking in mid-summer, dark respiration ( $R_d$ ) was highest and mesophyll conductance ( $g_m$ ) was lowest in spring, representing a potential limitation to spring assimilation. Others have found peak dark respiration in mid summer (Koniger et al. 2000). Other studies have found slightly different peak times for  $V_{\text{cmax}}$  and  $J_{\text{max}}$  in mature *Acer rubrum*, *A. saccharum* and *Nyssa sylvatica* trees (Wilson et al. 200). Thus, in order to accurately estimate seasonal carbon budgets of forest seedlings, it is important to account for this variability, and the mechanisms and drivers explaining that variability across the entire growing season in field conditions.

Changing climate will influence these environmental variables in a number of ways. Increasing aridity may lead to decreased average soil moisture, which could decrease seasonal carbon assimilation for tree seedlings. Similarly, increased temperature, and increased variability in temperature, with higher frequency of extreme events (IPCC 2007), could decrease seedling photosynthesis through more frequent thermal inhibition or increased total seasonal dark respiration, leading to decreased seasonal assimilation. Finally, as climate warms, many tree species will leaf out sooner in response to temperature cues, however, other tree species may not be affected or even experience abnormal budburst in response to insufficient winter chilling

(Morin et al. 2009). This will lead to changes in the timing of understory light availability, particularly if seedlings use different cues (Lechowicz 1984) or are more or less sensitive than canopy trees to temperature cues. As these responses may differ among and within species, across ontogenetic stages (seedlings vs adults) or habitats (low vs high light levels), it is crucial that we understand the processes by which seedlings determine their carbon budgets according to the environment they are exposed to.

To understand how environmental variability affects seedling carbon assimilation, and to investigate how different species may have different responses to this variability, we measured carbon assimilation rates of 78 tree seedlings across the growing season. We studied seedlings of four species that vary in growth rates, drought tolerances, shade tolerances, and successional status. Carbon assimilation data were analyzed to address the following questions: (1) How do the carbon assimilation rates of seedlings vary through the growing season in field conditions? 2) How are they affected by environmental variability, within and among seasons? And, (3) what can temporally extensive photosynthesis data tell us about future recruitment success of different species under climate change?

## METHODS

In the summer of 2012, we conducted gas exchange measurements at the E. S. George Reserve, located in the northwest corner of Livingston County, Michigan, USA (42° 28' N, -84° 00' W). The reserve is a fenced research property of the University of Michigan, and it has been maintained since 1930. The reserve is composed of reforested farmland, woodlots and pasture, with primarily Oak-Hickory forest, on kettle-kame physiography. No forest harvesting has occurred since the reserve was set aside. Soils are sandy loam to loamy sand. Average precipitation is 762 mm spread throughout the year with mean monthly temperatures ranging from -5.5°C in January to 22°C in June and July (<http://www.sitemaker.umich.edu/esgr/description>). Average growing season length is 145 days. The 2012 growing season was characterized by high drought and heat during mid-summer (Andresen, 2012). The two sites we worked on are relatively close to each other at (42.4580°, -84.0213°, ~275m a.s.l.) under Sugar Maple-Mixed Oak forest (*Acer saccharum* and *Quercus rubra*, *Q. velutina*, and *Q. alba*), and (42.4589°, -84.0120°, ~305 m a.s.l.), under Black Oak-Hickory forest (*Q. velutina* and *Carya glabra*) respectively. These sites were selected because they represent two major vegetation types in Michigan, and capture some of the topographic variation in the reserve.

In order to have a representative sample of different light conditions we measured seedling photosynthetic rates in forest research plots (5x5 m) established across natural light habitats (understory:  $10.12 \pm 0.011$  and  $10.69 \pm 0.011$  % full sunlight at site 1,  $20.97 \pm 0.032$  % full sunlight at site 2, vs gap:  $49.11 \pm 0.058$  % full sunlight at site 1,  $84.90 \pm 0.065$  % full sunlight at site 2). Seedlings of each of the four study species *Acer saccharum*, *Carya glabra*, *Quercus rubra*, and *Quercus velutina* (Table 1), were transplanted into the plots in early

summers 2009 and 2010 (McCarthy-Neumann and Ibanez 2012). We selected seedlings at two understory plots and one gap habitat plot at site 1, and from one understory plot and one gap plot at site 2 (a total of five plots). Due to low survival of seedlings in the understory at site 1, seedlings from two plots were used to obtain enough replicates. Soil samples were collected at each plot in 2009 for a comprehensive soil nutrient analysis (Appendix 1).

Forty-seven transplanted seedlings across plots and species were used in this study. In addition to the transplanted seedlings, 31 natural seedlings were located within or adjacent to plots and added to the study in July, for a total of 78 seedlings distributed across sites, light habitats, and species (Table 2). Photosynthetic measurement on a seedling was discontinued if and when it either died, or lost all its leaves ( $n = 6$ ), and at senescence. Data obtained prior to seedling mortality was used in the analysis.

#### *Data collection.*

Environmental microstations (HOBOWare, Onset computer corp. Bourne, MA) were established in both sites in the understory habitat, and measured soil moisture, temperature, and photosynthetically active photon flux every 60 minutes throughout the year. Some of the temperature data for the spring season at site 1 was lost due to equipment malfunction, however, enough remained for accurate representation of spring temperature, and the mean and standard deviation agreed well with the data from site 2. For a finer scale calibration of the soil moisture measurements, soil moisture was recorded with a soil moisture probe (Fieldsout - TDR 300 Soil Moisture Meter, Spectrum Technologies, Plainfield, IL) at each corner of the plots, at 4 points immediately adjacent to each seedling, and at 4 points immediately surrounding the HOBOWare microstation probes. This was conducted between 4 and 10 times per plot over the season, beginning in July, wherein the date and time of measurement to the nearest 30 minutes was

recorded. We used this combination of temporally extensive measurements with the data logger, and spatially extensive, manual measurements with the probe, to recreate the soil moisture environment each seedlings was exposed to during the photosynthetic measurements (Appendix 2). Hemispheric canopy photos (Rich 1990) were taken at the corner of each plot and directly above each natural seedling after full overstory canopy had developed. Photos were analyzed with the Hemiview hemispheric image analysis system (Dynamax Inc., Houston, TX) and Global Site Factor (proportion of incident global solar flux) was calculated for each plot and each natural seedling.

#### *Gas exchange.*

Photosynthesis measurements were collected with two LI-6400 Portable Photosynthesis Systems equipped with a CO<sub>2</sub> mixer assembly and the LI-02B LED red/blue light source and the LI-06 PAR sensors (Li-Cor Biosciences, Lincoln, NE). Light response curves were performed on seedlings of the four species in each plot a number of times (no less than 5, unless the seedling died) across the growing season from early may to mid-October with three seasons defined as Julian days 121-145 (spring), 172-209 (summer), and 225-297 (fall).

Measurements were taken across a range of temperatures, soil moistures, and times of day in an attempt to capture a large range of variability in environmental conditions. Observations which were clearly the result of mechanical error or non-equilibrium measurement (i.e. negative intercellular CO<sub>2</sub> concentrations) were discarded from analysis. The LI-6400 also recorded simultaneous leaf and ambient temperatures, humidity, pressure, vapor pressure deficit, ambient PAR, and the time of measurement.

For leaves smaller than the 6 cm<sup>2</sup> gasket area (< 5% of the measurements), a tracing of the leaf was made and dated at the time of measurement. Photographs of tracings were taken

next to a ruler and area of leaf tracings was subsequently estimated using ImageJ software (Schneider et al. 2012). Assimilation data was subsequently recomputed with the correct leaf areas in the LI-SIM software (Li-Cor Biosciences, Lincoln, NE).

### *Analysis*

The observed assimilation rate,  $A_{obs}$ , at a specific light level,  $Q$ , for a particular curve,  $c$ , was modeled with a Normal likelihood:

$$A_{obs_i} \sim \text{Normal}(Photom_i, \sigma^2) \quad \text{and} \\ 1/\sigma^2 \sim \text{Gamma}(0.01, 0.01)$$

In order to model observed photosynthesis in a way which incorporated the inherent variability in photosynthetic activity, we chose a simple saturating function (Figure 1a) as the process model:

$$Photom_i = A_{max_{c(i)}} * \frac{(Q_i - L_{c(i)})}{(Q_i + CF_{c(i)})} - R_{c(i)}$$

where for a particular curve  $A_{max}$  is the light-saturated maximum photosynthetic rate,  $CF$  is the half saturation point (which approximates the effect of both stomatal conductance and initial quantum yield in this model) and  $L$  and  $R$  are parameters associated with respiration of the mitochondria, hereafter referred to as dark respiration. All parameters were estimated on a curve level, with predicted half saturation point as:

$$\ln(CF_c) = \alpha_{\text{habitat type}(c)} + \beta_1 \cdot \text{soilm}_c + \beta_2 \cdot \text{soilm}_c^2 + \mu_{1_{\text{season}(c)}} * \text{Temperature}_c \\ + \mu_{2_{\text{season}(c)}} * \text{Temperature}_c^2$$

As seedlings assimilation response to light may acclimate to different light levels, we included an intercept,  $\alpha_{\text{habitat type}}$ , that varied with light habitat (understory or gap). Since assimilation rate may be controlled by soil moisture availability (via stomatal function) and

temperature (via the influence of heat on chemical reactions and vapor pressure deficit), and is inversely proportional to CF, the half saturation point was informed by these two variables. Preliminary data exploration as well as early model runs provided evidence for the quadratic relationships of both soil moisture and temperature to assimilation rate. To speed up convergence during model runs,  $\beta_1$  was restricted to negative values, indicating a positive effect of soil moisture on photosynthesis by decreasing the value of CF. Parameter  $\beta_2$  was also restricted, in this case to positive values to reflect a negative effect on assimilation, higher CF, when soil moisture values are too high. The effects of temperature were allowed to vary between seasons to investigate seasonal variation and acclimation in temperature response. Parameters were estimated from non-informative prior distributions:

$$\alpha_{\text{understory or gap}}, \beta_1, \beta_2, \mu_{1_{\text{spring, summer or fall}}}, \mu_{2_{\text{spring, summer or fall}}} \sim \text{Normal}(0, 1000)$$

The estimates for R (which is related to dark respiration) were estimated as a function of season and leaf temperature at the time of measurement as:

$$\ln(R_c) = \alpha_{\text{season}(c)} + \gamma_{\text{season}(c)} * \text{Temperature}_c$$

As with the parameter model for CF, the effect of temperature was allowed to vary by season, because many studies have shown dark respiration acclimates to long-term changes in temperature (Liang et al. 2013. Rodriguez-Calcerrada et al. 2010). Intercepts were also allowed to vary by season, and all parameters were estimated from distributions with non-informative priors:

$$\alpha_{\text{spring, summer or fall}}, \gamma_{\text{spring, summer or fall}} \sim \text{Normal}(0, 1000)$$

The curve level estimates for Amax and L were not informed by any environmental variables.

Instead, these parameters were estimated from non-informative species level prior distributions as:

$$\begin{aligned} A_{max_c} &\sim \text{Normal}(A_{maxm}, \sigma^2_{A_{max}}) & L_c &\sim \text{Normal}(LCPm, \sigma^2_{LCP}) \\ A_{maxm} &\sim \text{Uniform}(0,15) & Lm &\sim \text{Uniform}(0,1500) \\ \sigma_{A_{max}} &\sim \text{Uniform}(0,100) & \sigma_{LCP} &\sim \text{Uniform}(0,100) \end{aligned}$$

Different combinations of environmental variables, based on results from exploratory data analysis, were tried in different models. Models were evaluated by the Deviance information criterion, which penalizes overly parameterized models (Spiegelhalter et al. 2002). We ran the analyses using OpenBUGS software (Bayesian inference Using Gibbs Sampling, Spiegelhalter, Thomas, Best, and Lunn 2003). The final model was run with two chains for a ‘burn-in’ of 10,000 iterations, after which samples were monitored to assess convergence of the chains using the Brooks-Gelman-Rubin test (Gelman and Rubin 1992). After convergence was achieved, the model was run for 100,000 iterations to obtain a sufficient number of independent samples of posterior parameter estimates.

### *Model Predictions*

As part of model runs, simulations of assimilation and dark respiration rates were calculated. Assimilation was predicted in each light habitat (understory and gap) across 7 soil moisture levels (1, 5, 10, 15, 20, 25, and 30 %VWC), for each season (spring, summer, and fall). Photosynthetic photon fluxes of 280 and 600  $\mu\text{mol PAR m}^{-2} \text{s}^{-1}$  and a temperature of 25° C were used for understory and open light habitats respectively. In addition, assimilation and dark respiration (as the assimilation rate at a light level of 0  $\mu\text{mol PAR m}^{-2} \text{s}^{-1}$ ) rates in gap habitats were predicted for seasonal means (19, 28, and 18° C) and elevated (+3° C) temperatures at a light level of 600  $\mu\text{mol PAR m}^{-2} \text{s}^{-1}$ .



The effect of increased temperature on photosynthesis (ETP) was estimated by comparing the probability density functions of predicted photosynthesis under current temperature and under elevated temperature (Garrett and Zeger 2000). Comparisons are made at the average photosynthesis levels predicted at 600 PAR and gap habitat and 25% VWC, and ETP is calculated as the ratio of the areas under right side of the curves (probability of achieving a photosynthetic rate as high as the current temperature average or higher).  $ETP > 1$  indicates an increase in the probability of reaching the target rate and thus a positive effect of increasing temperature,  $ETP < 1$  indicates a decrease in probability of reaching the target and thus a negative effect of a warmer environment.

## RESULTS.

### *Environmental data*

The summer 2012 growing season was exceedingly hot and dry, in comparison with other years (Andreson 2012). Soil moisture at both sites remained low for much of the summer (midday means  $3.05 \pm 1.87$  and  $3.00 \pm 1.72$  % VWC for sites 1 and 2 respectively) and fall (midday means  $5.28 \pm 4.35$  and  $4.44 \pm 3.62$  %VWC for sites 1 and 2 respectively) and was highest in spring (midday means  $13.22 \pm 2.03$  and  $13.92 \pm 1.47$  %VWC for sites 1 and 2 respectively). Light levels in the understory were uniformly low in midseason after canopy closure (~Julian day 140 and 160 for sites 1 and 2 respectively), though fluxes were higher and more variable at site 2 (midday mean  $38.7 \pm 9.33$   $\mu\text{E m}^{-2} \text{s}^{-1}$  for day 175-200) than at site 1 (mean  $17.5 \pm 3.78$   $\mu\text{E m}^{-2} \text{s}^{-1}$  for day 175-200). Mean midday temperatures for each season (spring, summer, fall) were  $18.56 \pm 5.73$  °C,  $27.01 \pm 3.22$  °C, and  $17.62 \pm 6.06$  °C at site 1 and  $19.97 \pm 4.84$  °C,  $28.00 \pm 3.40$  °C, and  $19.03 \pm 6.37$  °C at site 2.

### *Gas Exchange*

A total of approximately 5,350 observations were taken from April 30<sup>th</sup> to October 23<sup>rd</sup> (Julian days 121-297). Observed light saturated assimilation rates showed a large amount of variability from lows near 0  $\mu\text{mol m}^{-2} \text{s}^{-1}$  to max rates of around 10  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Some evidence for species differences and seasonal differences in certain photosynthetic parameters can be observed in the raw data (Figure 1b, Appendix 3).

### *Model fits and parameter estimates*

The final model fits ( $R^2$  between predicted vs. observed) were 0.9445 for *A. saccharum*, 0.9723 for *C. glabra*, 0.9834 for *Q. rubra*, and 0.9774 for *Q. velutina*. Parameter estimates,

associated 95% credible intervals, and model variances are given in Table 3.

Within the CF parameter model, habitat specific parameters were significantly different for three of the species, *C. glabra*, *Q. rubra* and *Q. velutina*, with gap intercepts being higher than understory intercepts. Though the effects of temperature were not significantly different between seasons, it appeared that the effect of temperature in spring showed a different trend than in summer or fall. The effects of temperature followed the quadratic relationship we specified, with significant positive values for  $\mu_1$  (linear effect of temperature) and significant negative values for  $\mu_2$  (quadratic effect of temperature). The  $\mu_1$  coefficients did not vary between seasons, and within species, certain  $\mu_2$  coefficients were significantly different between seasons (Table 3).

Within the R parameter model, related to dark respiration, at least two of the intercepts associated with season were different from each other for all species except *A. saccharum*, for whom all three seasons were similar. For *C. glabra*, all three season intercepts were significantly different, and for the two oak species, the intercepts for spring and summer were different from each other, but the intercept for fall was not significantly different from either spring or summer. All coefficients associated with temperature were significantly different from zero, some positive as expected but a few were negative, and for all species the coefficient differed significantly between at least two seasons (see Table 3).

Amax parameters (maximum photosynthetic rate at saturated light levels; Table 3) varied between  $1.95 \pm 0.1415 \mu\text{mol m}^{-2} \text{s}^{-1}$  (*A. saccharum*) and  $4.28 \pm 0.1972 \mu\text{mol m}^{-2} \text{s}^{-1}$  (*Q. velutina*), Parameter L (point within the light gradient at which assimilation and respiration rates are similar; Table 3) ranged between  $3.92 \pm 0.420 \mu\text{mol PAR m}^{-2} \text{s}^{-1}$  for (*A. saccharum*) and  $13.14 \pm 1.042 \mu\text{mol PAR m}^{-2} \text{s}^{-1}$  (*Q. velutina*) reflecting the shade tolerance range among the species. For

both Amax and L parameters, species ranged from largest to smallest as *Q. velutina*, *Q. rubra*, *C. glabra*, and *A. saccharum*, with significant differences between all species except the two oaks (Figure 2).

### *Model Predictions*

Predictions from the simulations showed that for all species, average photosynthetic assimilation rate was lower in understory plots ( $280 \mu\text{mol PAR m}^{-2}\text{s}^{-1}$ ) than in gap plots ( $600 \mu\text{mol PAR m}^{-2}\text{s}^{-1}$ ), though the credible intervals overlapped (simulations not shown, but also see Figure 4). Assimilation rates increased with soil moisture for *A. saccharum* and *C. glabra* at low soil moistures and for *Q. rubra* at all soil moistures. However for *Q. velutina* assimilation decreased with increasing soil moisture. For all four species the magnitude of the effect was very small (Table 3, simulations not shown). Spring assimilation decreased by approximately  $0.20 \mu\text{mol m}^{-2}\text{s}^{-1}$  for *C. glabra*,  $0.21 \mu\text{mol m}^{-2}\text{s}^{-1}$  for *Q. rubra*, and  $0.35 \mu\text{mol m}^{-2}\text{s}^{-1}$  for *Q. velutina* with an additional 3 degrees temperature. *A. saccharum* showed little or no response to temperature (Figure 3). This decrease in photosynthesis with increasing temperature did not take place during the summer or fall for either of *C. glabra* or *Q. rubra*, but was still evident to a lesser extent in summer for *Q. velutina*. Though not significant, seasonal variation in predicted mean assimilation rates for the *Quercus* species was found (Figure 4), with summer assimilation rates being higher than spring assimilation rates. Similar trends across seasons were seen in *C. glabra* and *A. saccharum*, though the magnitude of the variation was smaller (Figure 4). *A. saccharum* had significantly lower assimilation rates than either of the oak species in summer and fall, but not in spring. Within all four species, predicted assimilation rates were very similar in summer and fall.

Predicted dark respiration in spring for each of the two *Quercus* species ( $2.50 \pm 0.41$

$\mu\text{mol m}^{-2} \text{s}^{-1}$  for *Q. rubra* and  $2.06 \pm 0.39 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *Q. velutina*) was higher (non-overlapping 95% credible intervals) than the summer rates. This difference was significant for *Q. rubra*, and marginally significant for *Q. velutina* (Figure 3). Predicted mean summer and fall dark respiration rates for the two *Quercus* species were essentially equal ( $0.90 \pm 0.35$  and  $0.92 \pm 3.485 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *Q. rubra* and  $0.58 \pm 0.38$  and  $0.57 \pm 0.38 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *Q. velutina*). In the other two species, this same trend of high dark respiration rates in spring ( $0.48 \pm 0.28 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *A. saccharum* and  $1.39 \pm 0.31 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *C. glabra*) and low, similar dark respiration rates in summer and fall ( $0.072 \pm 0.26$  and  $0.086 \pm 0.26 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *A. saccharum* and  $0.45 \pm 0.31$  and  $0.48 \pm 0.31 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *C. glabra*) was apparent. Species also showed different dark respiration responses to temperature. Predicted mean dark respiration was most sensitive to increased temperature in spring, with increases in dark respiration rates of  $0.15 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *C. glabra*,  $0.16 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *Q. rubra*, and  $0.16 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *Q. velutina* at temperature  $3^\circ\text{C}$  above the seasonal average. Dark respiration in *A. saccharum* did not respond to increases in temperature. Predicted dark respiration did not respond significantly to the elevated temperature scenarios in the other two seasons for any of the four species.

The effect of elevated temperature scenarios on photosynthesis (ETP) was predominately negative for all species (Table 4, Figure 5). There were very small increases in the probability of reaching current photosynthesis rates at elevated temperatures for *A. saccharum* in spring (+2%) and summer (+4%) and *C. glabra* in summer (+2%). In all other combinations of species and season, effects were negative, with %changes in probability of reaching current photosynthesis rates at elevated temperature ranging from 10% to 59%.

## DISCUSSION.

To better understand how different North American tree species may respond to climate change, we investigated the relative importance and impacts of natural environmental and seasonal variability on seedling carbon assimilation under field conditions. We found evidence that assimilation rates vary seasonally, but do not peak in mid-summer, as previously reported, most likely due to decreased stomatal conductance in response to drought, with seedlings having identical rates in summer and fall. Seasonal variability was most significant in drought tolerant species (particularly the two *Quercus*), perhaps due to less severe effects of drought on these species. Temperature had little effect on assimilation rates or dark respiration rates in summer and fall, contrary to expectations, indicating stomatal conductance may play a role in the response. Dark respiration increased with temperature in fall, and was likely responsible for the decrease of assimilation with temperature in spring. Finally we found that drought-tolerant species, particularly the two *Quercus*, had superior photosynthetic rates even in understory light habitats, though *C. glabra* had comparable but lower mean rates. Because assimilation rates are important determinants of growth and survival, these *Quercus* species may become more competitive under projected climate change.

### *Effects of Light habitat*

Assimilation response to light habitat, canopy or gap, was somewhat complex, representing the interaction of multiple components describing the photosynthetic process. Examining the predictions for assimilation rates in both understory and gap habitats, predicted mean rates were consistently higher in gaps for any given temperature, season, and soil moisture combination for all four species. However, the intercepts for CF were actually higher for gap plants than understory plants, implying lower light use efficiency in the gaps, as assimilation rate

reaches its half-maximum rate at a higher light level. This means that, for at least three species, the two *Quercus* and *C. glabra*, seedlings have significantly lower quantum yields (that is, the instantaneous response to light at low levels) in gaps. This response is likely due to acclimation to the habitat in which they are growing. Though we did not measure leaf nitrogen or leaf area, this likely indicates less investment in and partitioning of nitrogen to expensive leaf proteins (chlorophyll and thylakoid proteins) for light capture and higher electron transport efficiency per unit chlorophyll in gap plots where light is more abundant (Evans 1989. Evans and Poorter 2001).

### *Effects of temperature*

For all species except *A. saccharum*, the effect of higher temperature on assimilation rate was found to vary seasonally, having no effect in summer and fall and a negative effect in spring. This effect of temperature during the spring is most likely due (at least in part) to the concurrent increase in dark respiration with temperature. The lack of response in both assimilation and dark respiration in the drier seasons (summer and fall) is likely due to the stomata closing in response to high vapor pressure deficit (VPD) (Ellsworth and Reich 1992). With increased seasonal temperatures comes increased evaporation demand, and thus stomata close at higher vapor pressure deficits to limit water loss (Oren et al. 1999), leading to lower assimilation rates as well as reduced metabolic activity and thus lower dark respiration. However the observed pattern is also consistent with acclimation behavior, as dark respiration is known to increase with temperature on short time scales and acclimate over longer time scales (Rodríguez-Calcerrada et al. 2010. Liang et al. 2013. Tjoelker et al. 1999). It is not possible with this model to determine how much of the change in seasonal sensitivity in dark respiration to temperature is due to stomatal versus acclimation processes (via changes in leaf N and carbohydrate concentration as

in Tjoelker et al. 1999). Most likely it is both processes acting simultaneously. Future work using models which explicitly quantify stomatal conductance will hopefully allow us to parse out the relative contribution of these two processes. It is likely that the response of assimilation is mostly driven by dark respiration, and the decrease in sensitivity as the season progresses is at least in part due to decreased stomatal conductance.

Our results do suggest that seedlings may not be able to assimilate as much carbon under increased temperature. An alternative representation of the effects of temperature on photosynthesis is presented in Table 4 and Figure 5. By comparing the posterior probability density functions associated with model predictions of mean assimilation, we can make inferences about the probabilities of observing different photosynthetic rates under different conditions (as the ratio of the probabilities of a given event taking place under different conditions). Using this method, *C. glabra*, *Q. rubra*, and *Q. velutina* all have decreased probabilities of reaching their mean rate from model predictions when the seasonal average temperature is increased by 3° C. This means that the seedlings of these species would likely assimilate less carbon under projected increases in temperature. The effects are particularly large in spring, where the percent change in probabilities of reaching current levels are 45% lower for *C. glabra* and *Q. rubra*, and 59% lower *Q. velutina*. The outlier here is *A. saccharum*, which seems essentially unaffected by a 3 °C increase in temperature, except perhaps in fall. This may reflect drought intolerance traits. Closure of stomata under high temperatures (and thus potentially high VPD's) represents a strategy to conserve water, and this is what our assimilation rates for *A. saccharum* may have represented, a shut down of the stomata with very low photosynthetic activity even in spring. This may explain the lack of response to temperature differences in any season for this species. Lastly, when interpreting the results for *A. saccharum*,



it is important to emphasize the small sample size of *A. saccharum* individuals in gap habitats (n=3), all of which were natural seedlings (all planted seedlings in this habitat had died).

### *Seasonal variability*

Understanding the seasonal variability associated with photosynthetic parameters may lead to better understanding of seasonal carbon budgets as well as improved accuracy in larger scale carbon models. We found significant seasonal variability in both assimilation rates and dark respiration, though our assimilation results disagreed in some ways with previous studies. While we did find assimilation to be lowest in spring, we did not find peak photosynthetic activity at mid summer or maximum photoperiod, as other researchers have (Bauerle et al. 2012, Zhu et al. 2011), though we were looking at ambient assimilation rate, not specifically  $V_{max}$  or  $J_{max}$ . This discrepancy is likely due to the fact that we conducted our measurements *in situ*. Unlike many studies, we have measured photosynthesis under ambient conditions, rather than non-resource limiting greenhouse conditions. We also were looking at seedlings, which are more vulnerable to environmental fluctuations than adult trees (as in Zhu et al. 2011) or saplings (as in Bauerle et al. 2012). This same pattern in seasonal variability of low photosynthetic capacity in spring with similar rates in summer and into fall has been observed in other field studies of adult trees (Wilson et al. 2001). This pattern implies that, while under ideal conditions leaves may present a peak of photosynthetic activity in midsummer, this may not occur in field conditions, especially under a drought. Even if plants may have higher photosynthetic ability in midsummer, any increase in assimilation rate could have been countered by decreased stomatal conductance, as this is also the driest part of the summer. Furthermore, if this seasonal trend of midsummer maximum assimilation is indeed operating in natural ecosystems, it may be suppressed by projected increases in aridity and precipitation variability, making it difficult to

scale up observed photosynthetic activity in larger carbon cycle models. However, it's important to note that our model does not explicitly account for stomatal conductance, and thus, these results must be interpreted with some caution.

### *Species Differences*

Lastly, photosynthetic traits differed among the study species, which may have significant implications for recruitment processes in these forests. *Q. velutina* and *Q. rubra* have the highest light saturated maximum assimilation rates, as well as the highest assimilation rates under most conditions, despite having the highest dark respiration rates. In the understory habitat, all four species had comparable photosynthetic rates in spring, and it was also in this season that assimilation was the most impacted by temperature for both *Quercus* species and *C. glabra*, yet the mean rates for *A. saccharum* were still the lowest. *A. saccharum* was relatively insensitive to temperature increases, but this pattern is likely the result of the drought impact across seasons and not of a lack of response to warmer conditions. That *A. saccharum* had non-zero assimilation rates in mid summer implies that in infrequent drought years, *A. saccharum* and other shade tolerant, drought intolerant species may persist in the understory, but with assimilation rates that would make them poor competitors if drought years become increasingly frequent.

### *Conclusions*

Results from our model predictions showed that under all the conditions observed over the growing season, the oak species had higher mean assimilation rates, despite exhibiting the largest increases in dark respiration with increased temperature. Though these assimilation rates were within the upper range of predicted assimilation rates for *C. glabra*, they were significantly

higher than *A. saccharum* assimilation in summer and fall. Furthermore, even small differences in assimilation rates, if compounded over multiple seasons, may lead to significant, exponential differences in resource acquisition and growth, and thus competitive ability. This could have large implications for successional processes in secondary oak forest, and the resilience of late successional *A. saccharum* dominated forests, particularly if *Quercus* dark respiration acclimates to projected increases in temperature. Thus, although responses to different environmental variables are highly variable and appear to vary somewhat across the growing season, different species may respond differently to projected increases in temperature and aridity, and oaks may become more dominant in North American Eastern forests at the expense of less drought tolerant, slower growing species like *A. saccharum*.

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TABLES

*Table 1.* Study species, drought and shade tolerances, and relative growth rates (from Barnes and Wagner, 2004).

Species (code)	Drought tolerance	Shade tolerance	Growth
<i>Acer saccharum</i> (Acsa)	low	tolerant	very slow
<i>Carya glabra</i> (Cagl)	high	intermediate	slow
<i>Quercus rubra</i> (Quru)	moderate-high	intermediate	moderate
<i>Quercus velutina</i> (Quve)	high	intolerant	moderate

*Table 2.* Seedlings per habitat and curves measured per season used in the study. Spring, summer, and fall measurements correspond to Julian days 121-145, 172-209, and 225-297 respectively.

Species	Understory	Open	Spring	Summer	Fall
Acsa	9	3	11	37	20
Cagl	11	13	35	65	35
Quru	6	12	21	53	36
Quve	10	14	34	86	61

Table 3. Final model parameter estimates and 95% credible intervals. 95% credible intervals that do not overlap zero indicate significance. The “x” symbol indicates parameters which were restricted to either positive or negative values. Different letters indicate statistically significant differences between habitats (a,b) or seasons (c,d,e) for a species.

	Acsa		Cagl	
Parameter	Mean $\pm$ SD	95% CI	Mean $\pm$ SD	95% CI
<u>Model</u>				
variance	0.29 $\pm$ 5.07	-	0.092 $\pm$ 2.10	-
<u>CF</u>				
habitat	1.64 <sup>a</sup> $\pm$ 0.50	(0.65–2.62)	2.55 <sup>a</sup> $\pm$ 0.019	(2.53 – 2.57)
$\alpha$ understory				
habitat	1.51 <sup>a</sup> $\pm$ 0.49	(0.53–2.46)	3.13 <sup>b</sup> $\pm$ 0.0092	(3.11– 3.13)
$\alpha$ gap				
soil moisture				
$\beta_1^x$	-0.041 $\pm$ 0.024	(-0.093 – -0.0039)	-0.00060 $\pm$ 0.00068	(-0.0025– -0.00015)
soil moisture				
$\beta_2^x$	0.0033 $\pm$ 0.00087	(0.0018–0.0050)	9.7*10 <sup>-7</sup> $\pm$ 1.0*10 <sup>-6</sup>	(7.4*10 <sup>-8</sup> – 3.7*10 <sup>-6</sup> )
Temperature				
$\mu_1$ spring	0.11 <sup>c</sup> $\pm$ 0.039	(0.015–0.18)	0.075 <sup>c</sup> $\pm$ 0.015	(0.060 – 0.092)
Temperature				
$\mu_1$ summer	0.1555 <sup>c</sup> $\pm$ 0.039	(0.071–0.24)	0.095 <sup>c</sup> $\pm$ 0.0091	(0.077 – 0.11)
Temperature				
$\mu_1$ fall	0.10 <sup>c</sup> $\pm$ 0.043	(0.0097–0.18)	0.033 <sup>c</sup> $\pm$ 0.0053	(0.020 – 0.044)
Temperature				
$\mu_2$ spring	-0.0015 <sup>c</sup> $\pm$ 0.00083	(-0.0030– 0.00046)	-0.0012 <sup>c</sup> $\pm$ 0.00052	(-0.0019 – -0.00070)
Temperature				
$\mu_2$ summer	-0.00296 <sup>c</sup> $\pm$ 0.00085	(-0.0048– -0.0012)	-0.0018 <sup>c</sup> $\pm$ 0.00030	(-0.0024 – -0.0012)
Temperature				
$\mu_2$ fall	-0.0012 <sup>c</sup> $\pm$ 0.00093	(-0.0028– 0.00090)	0.00063 <sup>d</sup> $\pm$ 0.00020	(0.00021 – 0.0011)
<u>R</u>				
season				
$\alpha$ spring	-0.011 <sup>c</sup> $\pm$ 0.30	(-0.61 - 0.57)	-2.49 <sup>c</sup> $\pm$ 0.071	(-2.56 – -2.42)
season				
$\alpha$ summer	-2.64 <sup>c</sup> $\pm$ 31.63	(-67.66 – 55.32)	-63.58 <sup>d</sup> $\pm$ 13.88	(-91.68 – -40.22)
season				
$\alpha$ fall	-2.89 <sup>c</sup> $\pm$ 31.62	(-59.97 – 63.65)	-10.39 <sup>c</sup> $\pm$ 2.73	(-16.81 – -7.68)
Temperature				
$\gamma$ spring	-0.039 <sup>c</sup> $\pm$ 0.017	(-0.076 – -0.0046)	0.093 <sup>c</sup> $\pm$ 0.0051	(0.087 – 0.098)
Temperature				
$\gamma$ summer	-24.76 <sup>d</sup> $\pm$ 18.49	(-69.23 – -0.88)	1.52 <sup>d</sup> $\pm$ 0.33	(0.97– 2.19)
Temperature				
$\gamma$ fall	-24.14 <sup>d</sup> $\pm$ 18.05	(-69.32 – -1.00)	0.23 <sup>c</sup> $\pm$ 0.066	(0.16– 0.39)
<u>Amax</u>				
mean	1.95 $\pm$ 0.14	(1.67 – 2.23)	2.95 $\pm$ 0.17	(2.62 – 3.29)
variance	1.34 $\pm$ 7.62	-	3.74 $\pm$ 29.47	-
<u>L</u>				
mean	3.93 $\pm$ 0.42	(3.12 – 4.77)	6.77 $\pm$ 0.63	(5.60 – 8.07)
variance	0.063 $\pm$ 0.0023	-	22.91 $\pm$ 14.54	-

continued.

Parameter	Quru		Quve	
	Mean $\pm$ SD	95% CI	Mean $\pm$ SD	95% CI
<u>Model</u>	0.087	-	0.14 $\pm$ 3.92	-
variance	$\pm 1.85$			
<u>CF</u>				
<i>habitat</i>	3.05 <sup>a</sup> $\pm$ 0.054	(2.92 – 3.16)	2.85 <sup>a</sup> $\pm$ 0.11	(2.64 – 3.00)
$\alpha$ understory				
<i>habitat</i>	3.52 <sup>b</sup> $\pm$ 0.040	(3.46 – 3.61)	3.47 <sup>b</sup> $\pm$ 0.11	(3.28 – 3.65)
$\alpha$ gap				
<i>soil moisture</i>	-0.015 $\pm$ 0.011	(-0.044 – -0.058)	-0.0058 $\pm$ 0.0060	(-0.023 – -0.00024)
$\beta 1^x$				
<i>soil moisture</i>	0.00052 $\pm$ 0.00035	(0.000051 – 0.0013)	0.0011 $\pm$ 0.00032	(0.00066 – 0.0019)
$\beta 2^x$				
<i>Temperature</i>	0.048 <sup>c</sup> $\pm$ 0.013	(0.025 – 0.075)	-0.0025 <sup>c</sup> $\pm$ 0.018	(-0.036 – 0.032)
$\mu 1$ spring				
<i>Temperature</i>	0.047 <sup>c</sup> $\pm$ 0.010	(0.027 – 0.066)	0.034 <sup>c</sup> $\pm$ 0.012	(0.011 – 0.059)
$\mu 1$ summer				
<i>Temperature</i>	0.064 <sup>c</sup> $\pm$ 0.0098	(0.046 – 0.084)	0.064 <sup>c</sup> $\pm$ 0.010	(0.046 – 0.082)
$\mu 1$ fall				
<i>Temperature</i>	-0.00055 <sup>c</sup> $\pm$ 0.00036	(-0.0013 – 0.00014)	0.0014 <sup>c</sup> $\pm$ 0.00060	(0.00027 – 0.0025)
$\mu 2$ spring				
<i>Temperature</i>	-0.00012 <sup>c</sup> $\pm$ 0.00031	(-0.00070 – 0.00051)	0.00051 <sup>c</sup> $\pm$ 0.00031	(-0.00010 – 0.0011)
$\mu 2$ summer				
<i>Temperature</i>	-0.00081 <sup>c</sup> $\pm$ 0.00032	(-0.0014 – -0.00022)	-0.00078 <sup>d</sup> $\pm$ 0.00023	(-0.0012 – -0.00033)
$\mu 2$ fall				
<u>R</u>				
<i>season</i>	-1.23 <sup>c</sup> $\pm$ 0.053	(-1.33 – -1.14)	-2.92 <sup>c</sup> $\pm$ 0.29	(-3.28 – -2.55)
$\alpha$ spring				
<i>season</i>	-30.64 <sup>d</sup> $\pm$ 16.72	(-70.27 – -10.87)	-6.02 <sup>d</sup> $\pm$ 0.92	(-8.30 – 4.44)
$\alpha$ summer				
<i>season</i>	-0.15 <sup>cd</sup> $\pm$ 31.12	(-59.23 – 61.39)	-0.36 <sup>cd</sup> $\pm$ 30.17	(-61.50 – 55.88)
$\alpha$ fall				
<i>Temperature</i>	0.060 <sup>c</sup> $\pm$ 0.0025	(0.055 – 0.065)	0.13 <sup>c</sup> $\pm$ 0.011	(0.11 – 0.14)
$\gamma$ spring				
<i>Temperature</i>	0.70 <sup>d</sup> $\pm$ 0.39	(0.24 – 1.61)	0.12 <sup>c</sup> $\pm$ 0.022	(0.084 – 0.18)
$\gamma$ summer				
<i>Temperature</i>	-25.69 <sup>e</sup> $\pm$ 18.40	(-68.85 – -1.36)	-25.10 <sup>d</sup> $\pm$ 18.14	(-21.83 – -1.13)
$\gamma$ fall				
<u>Amax</u>				
mean	3.86 $\pm$ 0.23	(3.41 – 4.30)	4.28 $\pm$ 0.20	(3.89 – 4.66)
variance	5.46 $\pm$ 39.84	-	6.87 $\pm$ 64.68	-
<u>L</u>				
mean	10.43 $\pm$ 1.093	(8.374 – 12.67)	13.14 $\pm$ 1.042	(11.16 – 15.24)
variance	92.42 $\pm$ 392.0	-	126.3 $\pm$ 821.7	-

*Table 4.* Effect of temperature on photosynthesis (ETP), changes in the probability of reaching a target rate, i.e., predicted photosynthetic rates at current conditions, under a climate scenario where seasonal temperature increases by 3C. ETP > 1 indicates an increase in the probability of reaching the target rate and thus a positive effect of increasing temperature, ETP < indicates a decrease in probability of reaching the target and measures the negative effect of a warmer environment.

Species	Spring		Summer		Fall	
	ETP	% change	ETP	% change	ETP	% change
Acsa	1.02 0	+2%	1.04 0	+4%	0.910	-10%
Cagl	0.560	-45%	1.02 0	+2%	0.880	-12%
Quru	0.540	-45%	0.850	-15%	0.890	-11%
Quve	0.412	-59%	0.610	-49%	0.840	-16%

FIGURES

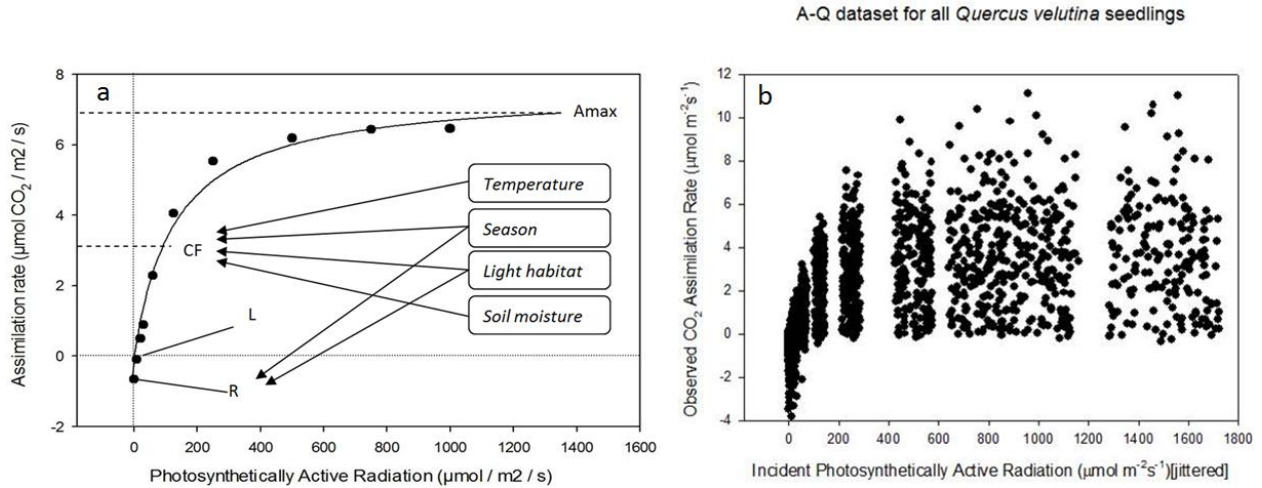
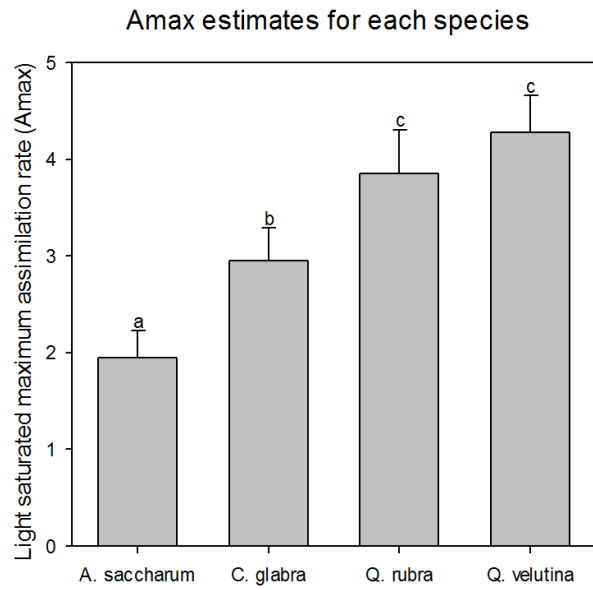
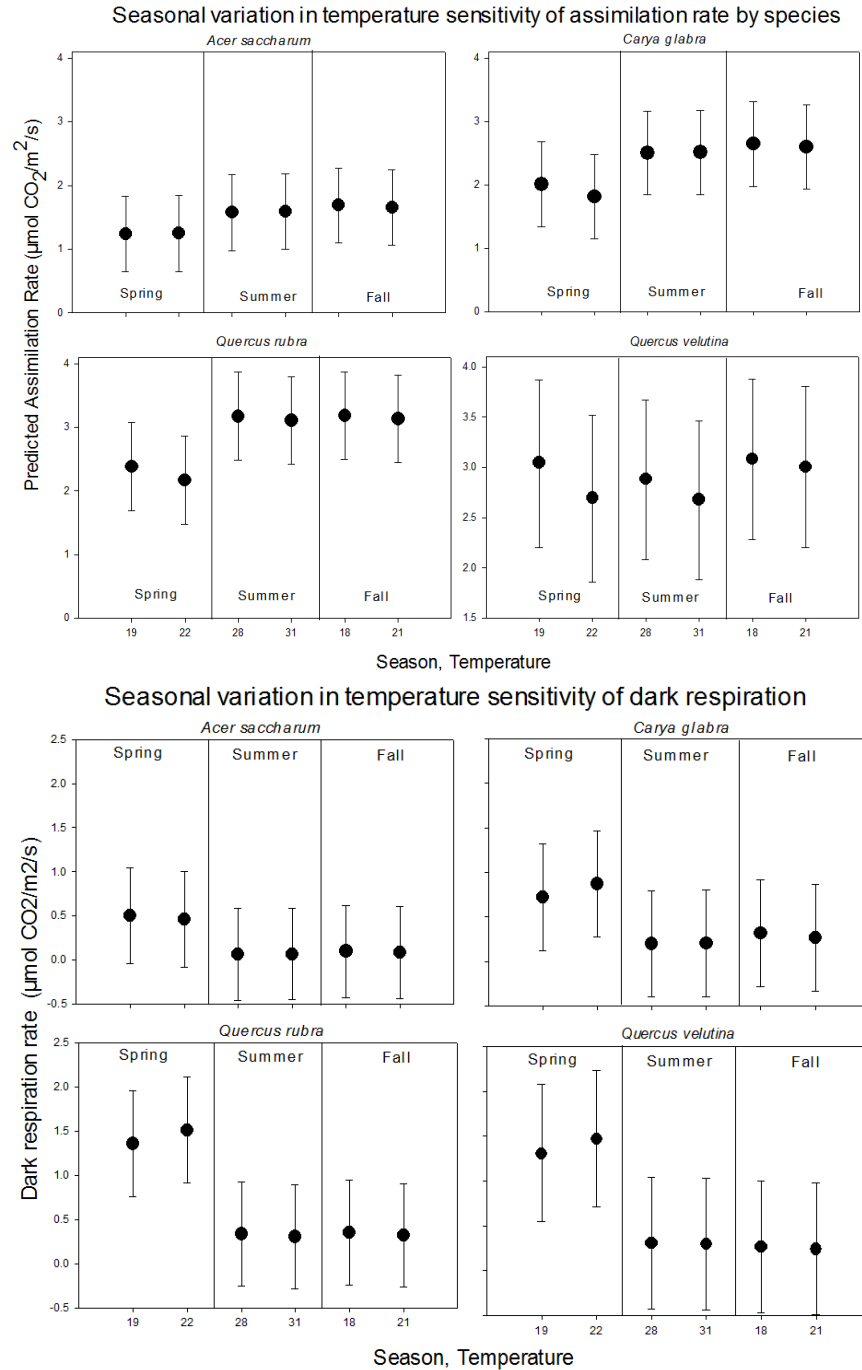


Figure 1. (a) Conceptual representation of the species level assimilation model, showing how each parameter is related to each portion of one light curve for *Q. velutina*, and which environmental parameters inform which photosynthetic parameters. (b) Light curve dataset for *Q. velutina* showing variability in observed photosynthesis. Light levels have been jittered.



*Figure 2.* Light saturated maximum photosynthetic rate estimates for each of the four species, means (bars) and 95% upper credible interval (whiskers). Lowercase letters indicate statistically different estimates.



*Figure 3.* Predicted photosynthetic assimilation rate at 600  $\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$  (top panels) and dark respiration rate (as assimilation rate in darkness) (bottom panels), means (circles) and 95% credible intervals (whiskers) in spring, summer, and fall at seasonal mean temperature (19, 28, 18° C) and elevated temperature (+3° C :22,28, and 21° C) in gap habitats. Species names listed above each plot. Soil moisture is held constant at 25% VWC.



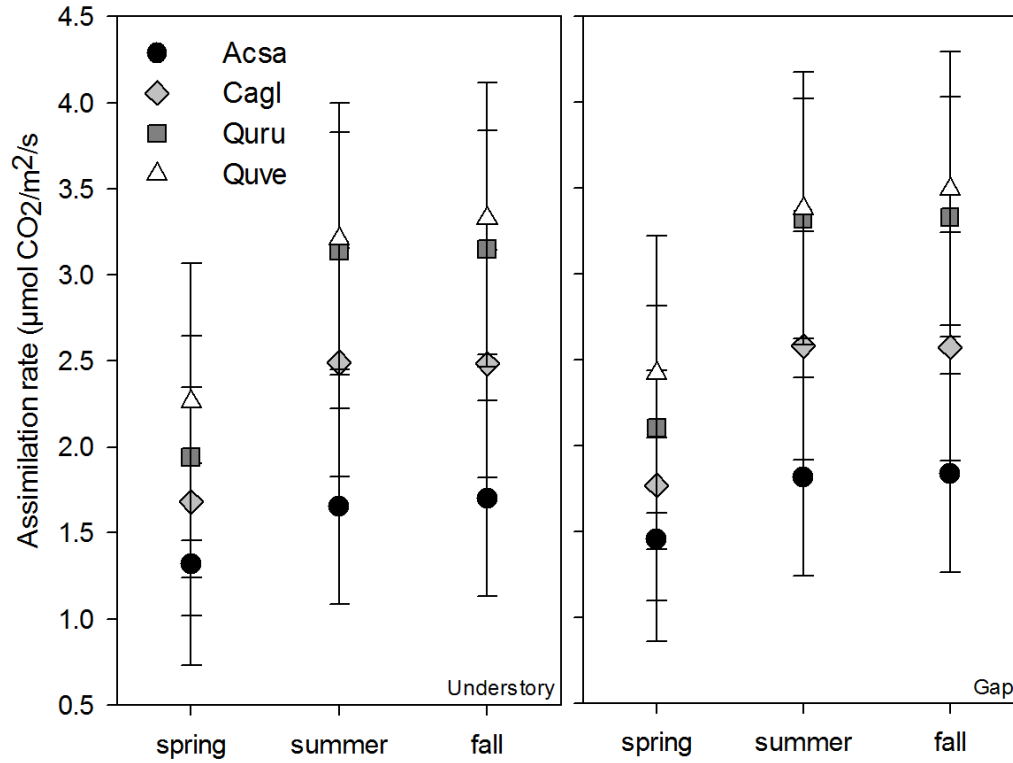
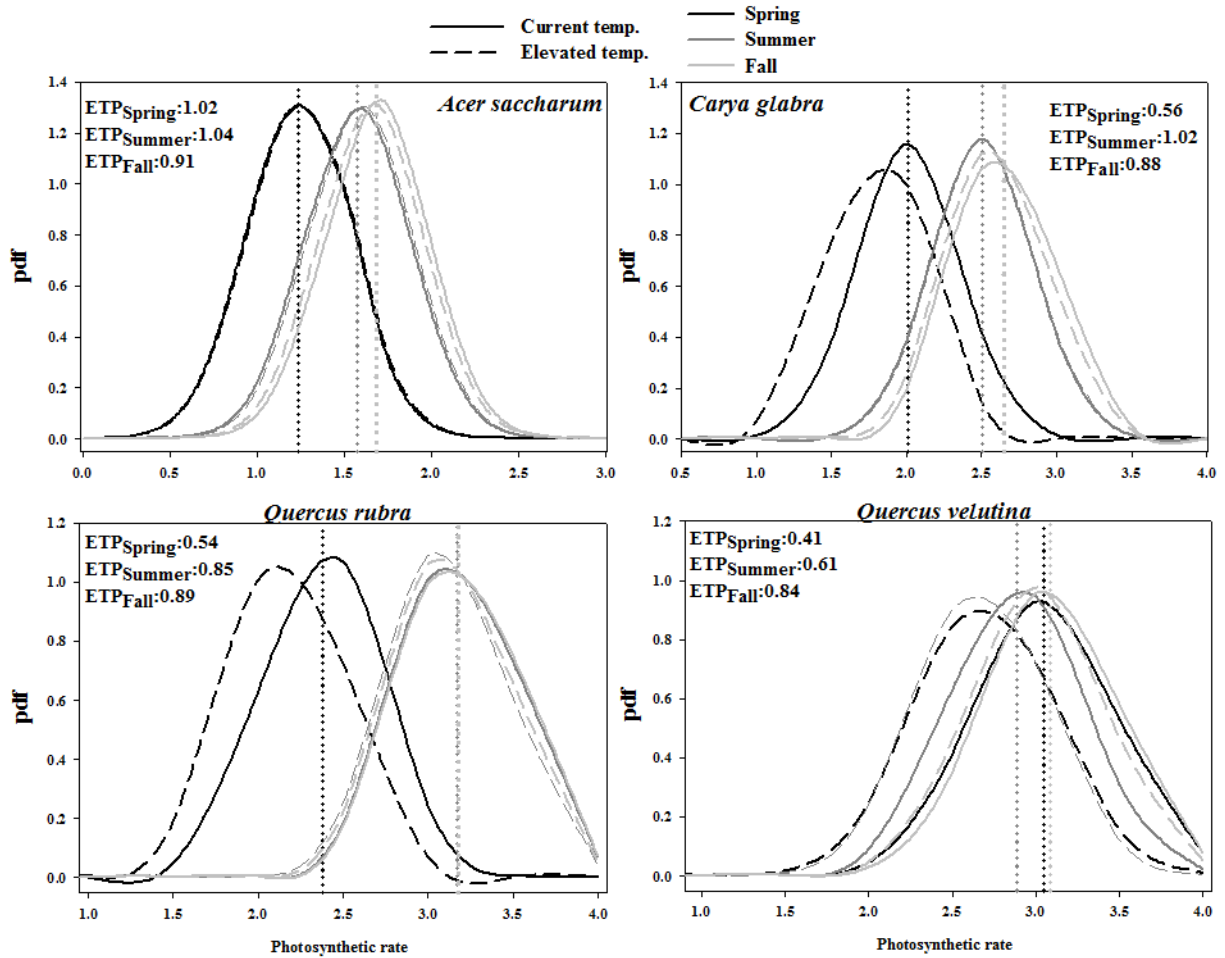


Figure 4. Predicted mean photosynthetic assimilation rates (circles) and 95 % credible intervals (whiskers) by species for each season in understory (light level  $280 \mu\text{mol PARm}^{-2} \text{s}^{-1}$ ) and gap (light level  $600 \mu\text{mol PARm}^{-2} \text{s}^{-1}$ ) habitats at 15% VWC and  $25^\circ \text{C}$ . Black circles correspond to *A. saccharum*, light gray diamonds *C. glabra*, dark grey squares *Q. rubra*, and white triangles *Q. velutina*



*Figure 5.* Posterior probability density functions of predicted photosynthesis under current temperature (solid line) and under elevated temperature (+3° C, dashed lines) and effect of temperature on photosynthesis (ETP). ETP > 1 indicates an increase in the probability of reaching the target rate, ETP < indicates a decrease in probability of reaching the target rate. Comparisons are made at the average photosynthesis levels predicted at 600  $\mu\text{mol PARm}^{-2} \text{s}^{-1}$ , habitat and 25% VWC.

*Appendix 1. Summary soil nutrient data by plot (2009)*

Site	Plot	Total N (mg/L)	Phosphorous
1	Understory	0.0402	28.30632
1	understory	0.0439	20.12796
1	Open	0.0222	66.80426
2	Understory	0.01675	8.842422
2	open	0.0378	19.4753

*Appendix 2. Soil moisture sub-model.*

Fine scale soil moisture data was fit to the HOBO microstation soil moisture data with individual seedling regressions. All parameters had non-informative prior distributions. The subsequent fit was used to predict soil moisture for individual seedlings at the specific time photosynthetic measurements were taken.

*Likelihood:*

Soil moisture  $\sim$  normal( $\mu_{\text{seedling}}, \sigma^2$ )

$1/\sigma^2 \sim$  gamma(0.01, 0.01)

*Process:*

$\mu_{\text{seedling}} = \alpha_{\text{seedling}} + \beta_{\text{seedling}} * \text{moisture}_{\text{site}}$

Appendix 3. Light curve datasets for each species.

Data points for all light curves (assimilation versus light level) used in the analysis for this study. Light levels have been jittered to better visualize the variability in the data at a given light level.

