

Influence of temperature and nitrogen on photosynthesis in early and late successional tree species of the great lakes region: implications for forest carbon uptake

Jeannie Wilkening
University of Arizona
UMBS REU 2013

Mentors: Susan Cheng & Knute Nadelhoffer

Abstract

The interactions between forests and climate are becoming an increasingly important global processes. Therefore, forest carbon uptake, by means of photosynthesis, and the factors that affect it are important parameters for climate models. Modeling photosynthesis requires values of rate of carboxylation (V_{cmax}) and electron transport capacity (J_{max}), both of which can be derived from gas exchange measurements based on the Farquhar, von Caemmerer and Berry (FvCB) model of photosynthesis. In this study, A/Ci curve analysis was done in Northern lower Michigan for two late successional species, red oak (*Quercus rubra*) and red maple (*Acer rubrum*), and one early successional species, bigtooth aspen (*Populus grandidentata*). Samples were taken across different canopy levels and temperatures to determine the effects on photosynthetic activity. It was found that for V_{cmax} , species was not significant and canopy was only significant for red oak. For J_{max} , species was significant and canopy was significant for both red oak and red maple. Further analysis suggested that the J_{max} species differences were likely attributable to canopy differences. These results suggest the importance of canopy structure in determining the photosynthetic activity, and therefore carbon uptake, of forests. Consequently, it also implies that changes to forest composition have the potential to cause changes in the carbon uptake of the forest.

Introduction

As atmospheric carbon dioxide (CO_2) levels continue to rise and the climate continues to change, forests continue to play a critical role on the planet because they have the ability to impact climate themselves. Along with increased levels of CO_2 , climate change is expected to increase temperatures and change precipitation patterns, all

of which could affect the biogeochemical processes of forests (IPCC 2007). Climate change is expected to shift the range of various species of trees, resulting in changes to the compositions of forests. Species climate envelope models predict that as climate changes, the suitable ranges of species in the eastern United States will also shift causing some species to lose territory and others to gain territory (Iverson and Prasad 2002). Such changes to forest composition have the potential to cause serious disruptions to forest processes, including ability to sequester carbon (Scheller and Mladenoff 2004)

While these effects of climate change could have detrimental effects at the ecosystem level, they could also feed back to impact the climate even further. This is because there are a number of feedback loops between forests and climate. In particular, the carbon cycle interaction between forests and climate has the potential to play a big part in the future of forests and climate. This is because forests can act as carbon sinks, taking in CO₂ through the process of photosynthesis, and therefore can mitigate climate change to some extent (Bonan 2008). In the 1990s, it was seen that forests accounted for a global intake of 2.6 Pg of carbon a year (Bonan 2008). However, changes to forests, including changes to environmental conditions and forest composition, could have implications that affect forests' ability to accumulate carbon through photosynthesis since they are changing the conditions of these biochemical processes. Therefore, it is necessary to gain a stronger understanding of how changes to forests as part of climate change can impact the feedback between forests and climate through the process of photosynthesis.

To understand effects on photosynthesis from climatic factors, photosynthesis must be measured. The process of C₃ photosynthesis, which temperate forest tree species use to convert CO₂ and light energy into glucose, can be described using the Farquhar, von Caemmerer and Berry model (FvCB) (Farquhar et al 1980). The FvCB model models the biochemical aspects of photosynthesis, incorporating various factors that affect the rate of C₃ photosynthesis and how different compounds can act as limiting factors in the rate of CO₂ assimilation. From this model, it is possible to infer what biochemical factor limits a plant's photosynthetic capacity. The FvCB (1980) model includes the Rubisco limited portion and the RuBP limited portion of photosynthesis. The Rubisco limited portion relates to the portion of photosynthesis where the enzyme Rubisco oversees the

fixation of carbon into its organic form and is measured by the maximum rate of carboxylation (V_{cmax}). The RuBP limited portion relates to the step of photosynthesis where CO_2 is bound to the organic molecule RuBP and is measured by the maximum rate of electron transport (J_{max}), since electron transport supplies the energy for the regeneration of RuBP. These values can be determined through gas exchange measurements that measure assimilation (A), which is the CO_2 uptake by the leaf, and intercellular CO_2 concentration (C_i), which is known as an A/C_i curve (Long and Bernacchi 2003).

A number of factors influence the rate of photosynthesis. For instance, nitrogen has a positive interaction with photosynthesis because it makes up a significant part of the leaf material associated with photosynthesis (Wilson 2000). Additionally, it is known that the biochemical reactions of photosynthesis can be affected by light availability and temperature (Farquhar et al 1980). An understanding of how all of these factors impact photosynthesis is important since photosynthetic capacity is an important input for climate models. V_{cmax} in particular, is a critical part of Earth Systems Models (ESMs) which include the interactions between climate and forests when predicting the effects of climate change (Rogers 2013). However, there are still a number of uncertainties about how these interactions could change with the effects of climate change (Bonan 2008). One of these effects of climate change is the potential for shifts in the composition of species within forests. Therefore, this study will attempt to determine the differences in photosynthetic capacity between three tree species in Northern, lower Michigan and the potential implications that has on forest-climate interactions under climate change by asking:

1. Is there a difference between sun and shade leaves within a given species in V_{cmax} and J_{max} ?
2. How do the impacts of temperature and nitrogen content on V_{cmax} and J_{max} differ between species?

Materials and Methods

Study System

The study was conducted in a forested area at the University of Michigan Biological Station in Northern, lower Michigan (45°35'N, 84°43'W). The average temperature of this area is 5.5°C and the average precipitation is 817 mm. The mean canopy height is 22m. Canopy species include bigtooth aspen (*Populus grandidentata*), red maple (*Acer rubrum*), red oak (*Quercus rubra*), white birch (*Betula papyrifera*), eastern white pine (*Pinus strobus*), trembling aspen (*Populus tremuloides*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*) (Nave et al 2011). The three species of trees examined in the study were northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), and bigtooth aspen (*Populus grandidentata*).

Three individuals of each species were chosen for the study. Individuals were selected so they were accessible from the canopy access vehicle used during testing. For red oak and red maple, each individual had two sampling locations: a branch in the sun and a branch in the shade. For bigtooth aspen, leaves were only sampled in the sun since the crown structure results in primarily leaves in the sun, unlike the other two sampled species, which have a more extensive crown structure.

Photosynthetic Capacity

For red oak and red maple, leaves were sampled at two different canopy locations. This resulted in variation in canopy location to see if there is a relationship with between canopy location and photosynthetic capacity. Bigtooth aspen were only sampled at one canopy location since there is not as much variation in the canopy structure of these trees. All measurements were completed between 0930 and 1400 in order to capture the period of the day when leaves are most photosynthetically active. Measurements were taken across a range of temperatures ranging from approximately 25°C to approximately 30°C in order to investigate the relationship between temperature and photosynthetic capacity and how the temperature response of photosynthesis varies between species. Temperatures were spread across canopy locations and individual trees so as to evenly distribute a range of temperatures for each tree. Additionally, the sampling was designed so canopy locations and temperatures were divided evenly between morning and afternoon times throughout the day.

For each leaf, an A/C_i curve was conducted using a Li-Cor LI-6400 portable photosynthesis system. Photosynthetically active radiation (PAR) was set at 2000 $\mu\text{mol}/\text{m}^2/\text{s}$ for upper canopy leaves and 1500 $\mu\text{mol}/\text{m}^2/\text{s}$ for lower canopy leaves. These PAR values were chosen based on light response curves, which suggested these PAR levels were optimal for these species. The chamber flow rate was set to 500 mol/s and humidity was kept between 40-60%. Before beginning the curve, the leaf was allowed to acclimate to a CO₂ concentration of 400 ppm and then to 2000 ppm. The assimilation of CO₂ (A) was then measured at the following CO₂ concentrations: 2000, 1800, 1500, 1200, 800, 600, 400, 325, 250, 175, 100, and 50 ppm. The minimum waiting time for each concentration was set to three minutes and the maximum waiting time was set to five minutes.

From the A/C_i curves, values for V_{cmax} and J_{max} were derived using the method described in Sharkey et al (2007), which is based on the FvCB biochemical model of C₃ photosynthesis. The curves were fit in a way that resulted in the smallest sum of squares, but still had a reasonable mesophyll resistance (gm). Unusual points where there was evidence of an error in the readings were left out of the curve fitting analyses.

Leaf Chemistry and Area

After each A/C_i curve was completed, the leaf was then collected and leaf area without the petiole was measured using a Li-Cor 3100 Area Meter. The leaf was then dried in a Grieve 343 model oven at 60°C for at least 3 days. The dry mass of the leaf was then measured without the petiole. The leaf was then ground using a ball mill. Samples were then analyzed using a Costech Analytical CHN analyzer attached to a Finnigan Delta Plus XL isotope ratio mass spectrometer to determine the nitrogen content of the leaf and the nitrogen isotope content.

Statistics

Statistical analyses were then conducted to determine what correlations, if any, were present between canopy location, leaf temperature, nitrogen content and photosynthetic capacity. An analysis of covariance (ANCOVA) was conducted first between canopy layers for red oak and red maple to determine if there is a significant

difference between canopy layers within species in the temperature responses of J_{max} and V_{cmax} . In the ANCOVA analysis, canopy layer was included as the independent variable and either V_{cmax} or J_{max} was included as the dependent variable. Both temperature ($^{\circ}C$) and nitrogen mass per standard leaf area (N/SLA) ($g^2\ cm^{-2}$) were included as covariates. Further ANCOVA analysis was then done to see if there are significant differences between species, this time using species as the independent variable. These species ANCOVA analyses were then followed by a Tukey Test to compare species regressions individually. Further ANCOVA analyses were then conducted if canopy was shown to be significant in earlier analyses. For these analyses, species, further divided by canopy level, was used as the independent variable. Once again this was followed by a Tukey Test to compare species and canopy regressions individually.

Results

Photosynthetic Differences Within Canopy

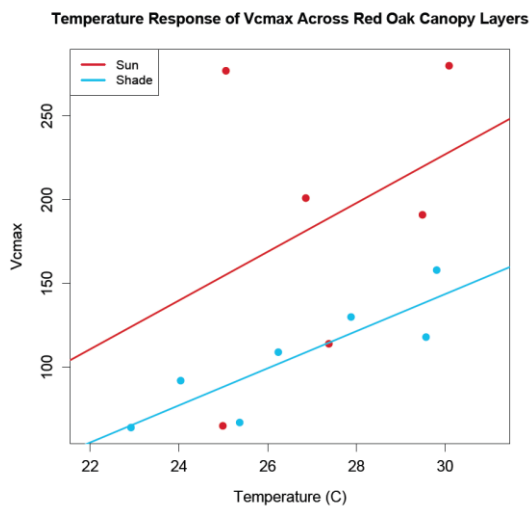


Fig 1. Temperature response of V_{cmax} across shade and sun leaves of red oak

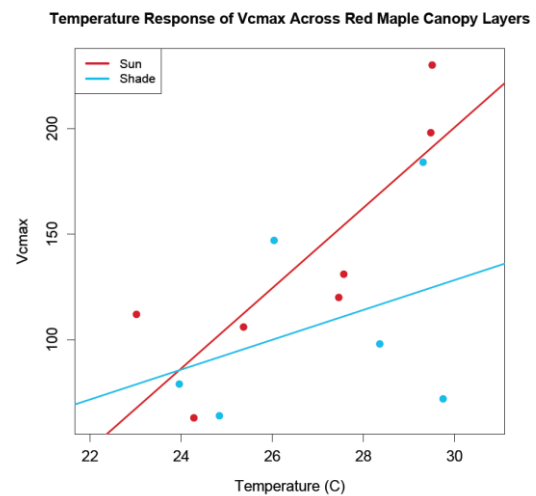


Fig 2. Temperature response of V_{cmax} across shade and sun leaves of red maple

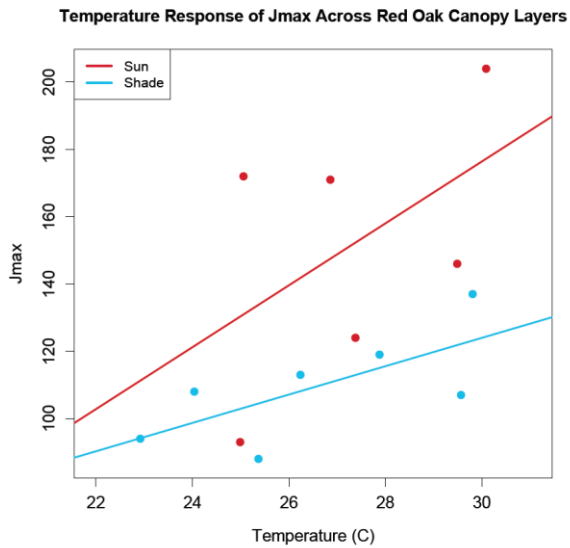


Fig 3. Temperature response of Jmax across shade and sun leaves of red oak

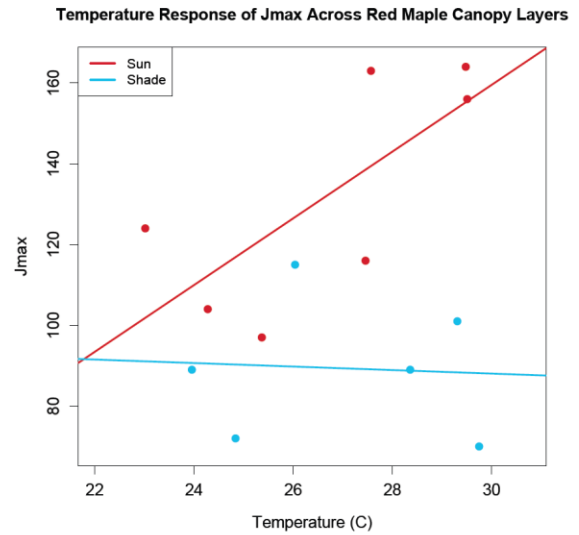


Fig 4. Temperature response of Jmax across shade and sun leaves of red maple

For V_{cmax} , the results of the ANCOVA showed canopy to be a significant variable ($p=0.032$) for red oak with sun values being higher than shade values (Fig 1). Temperature was also found to be significant for Red Oak ($p=0.039$). For V_{cmax} in red maple, canopy was not significant ($p=0.198$), but temperature was significant ($p=0.039$) (Fig 2). For J_{max} , canopy was significant in red oak ($p=0.029$) (Fig 3) and red maple ($p=0.007$) (Fig 4).

Photosynthetic Differences Across Species

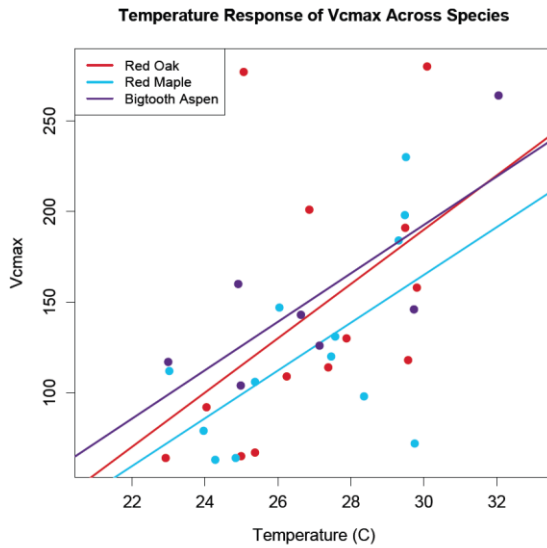


Fig 5. Temperature response of V_{cmax} across species as a whole

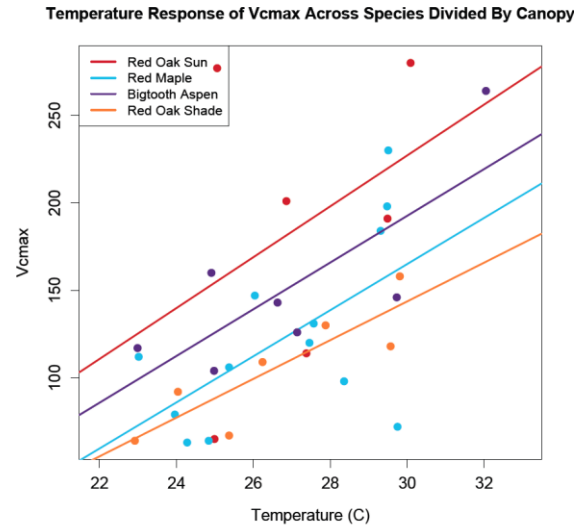


Fig 6. Temperature response of V_{cmax} across species with red oak divided by canopy

When V_{cmax} was compared across the across species, it was found that species was not significant ($p=0.342$), but temperature ($p<0.001$) and N/SLA ($\text{g}^2 \text{cm}^{-2}$) ($p<0.001$) were significant. When species were compared again, this time with red oak canopy layers split since canopy was a significant variable for red oak, it was seen that species and canopy combined were significant ($p=0.022$). Temperature ($p<0.001$) and N/SLA ($p=0.014$) were also significant. When specific species and canopy combinations were compared individually in the Tukey Test, it was seen that only oak sun and oak shade were significantly different ($p=0.028$).

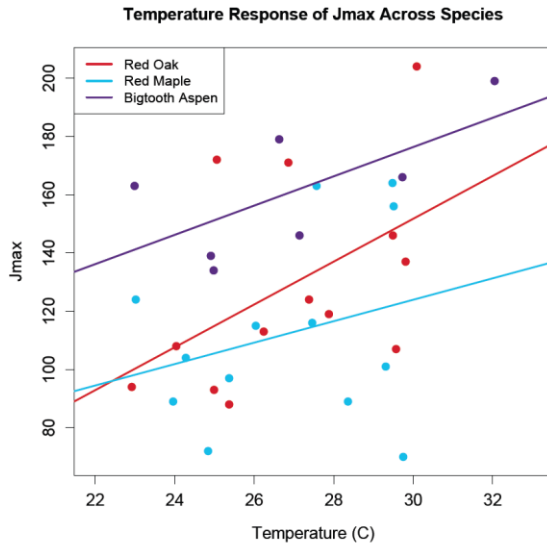


Fig 7. Temperature response of Jmax across species as a whole

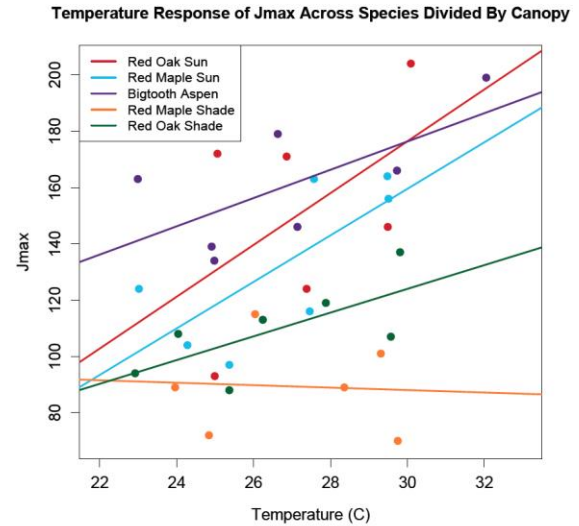


Fig 8. Temperature response of Jmax across species with red oak and red maple divided by canopy

When comparing across species for Jmax, species was significant ($p=0.001$). N/SLA ($p=0.001$) and temperature ($p=0.004$) were also significant. When species were compared individually, red oak and bigtooth maple were significantly different from one another ($p=0.028$) as were red maple and bigtooth aspen ($p=0.028$). When species and canopy were both used to divide the samples, species and canopy combined ($p<0.001$) were significant as was temperature ($p=0.001$). When individual species and canopy locations were compared, the Tukey Test showed maple sun and maple shade ($p=0.009$), aspen sun and maple shade ($p<0.001$), oak sun and maple shade ($p<0.001$), oak shade and aspen sun ($p=0.002$), and oak sun and oak shade ($p=0.033$) were significantly different from one another.

Discussion

Photosynthetic Differences Within Canopy

Based on the results of the intra-species comparisons, canopy was shown to be a potentially important factor for both Jmax and Vcmax. Significant differences were seen in the canopy of red oak for both Vcmax and Jmax and in red maple for Jmax, with the

photosynthetic parameters being higher in the sun leaves than compared to the shade leaves of the same species. These results seem to support the differences in maximum rates of photosynthesis (A_{max}) observed across canopy positions in previous studies (Bassow and Bazzaz 1998, Turnbull et al. 2001).

Photosynthetic Differences Across Species

For V_{cmax} , species does not appear to have a significant impact. This is in line with the idea that within plant functional types (PFT) V_{cmax} does not vary greatly (Rogers 2013). For J_{max} , species was significant. Bigtooth aspen had significantly higher values of J_{max} than compared to both red oak and red maple. In terms of succession, the early successional bigtooth aspen had higher J_{max} values than the late successional red oak and red maple. When species were divided by canopy, species combined with canopy was significant. Individual comparisons showed that sun leaves, regardless of species, were different from shade leaves, regardless of species. Within sun leaves and shade leaves, however, there were no significant differences between species. This suggests that the difference seen between bigtooth aspen and red oak and red maple when whole species were compared was probably due to the fact that bigtooth aspen consisted only of sun leaves. It also suggests that canopy is ultimately a more important factor than species. However, species could still be indirectly significant since species can differ in crown structure and nitrogen content and both nitrogen and canopy position were significant factors for J_{max} .

This importance of canopy structure in differences in photosynthetic parameters implies that succession could impact forest carbon uptake through changes in the canopy structure as species change. It also indicates that models that take into account the relationships between canopy structure and photosynthetic parameters will be better able to predict changes that could occur with forest carbon uptake in the future.

Acknowledgements

I would like to thank Susan Cheng and Knute Nadelhoffer for their mentoring throughout the project, Mary Anne Carroll and Dave Karowe for their leadership of the Research Experience for Undergraduates (REU) program, Jim le Moine for support

throughout the project, Jennifer Croskrey for conducting the chemical analysis for the project, John Menz for being a great safety buddy, the Forest Ecosystem Study Group for advice and support, the University of Michigan Biological Station, the National Science Foundation, and my fellow REU students for their friendship, support, and enthusiasm throughout the program. This research was funded by the University of Michigan Biological Station REU program generously funded by the National Science Foundation.

References

- Bazzaz, B. and. (1998). How Environmental Conditions Affect Canopy Leaf-Level Photosynthesis in Four Deciduous Tree Species HOW ENVIRONMENTAL CONDITIONS AFFECT CANOPY LEAF-LEVEL PHOTOSYNTHESIS IN FOUR DECIDUOUS TREE SPECIES. *Ecology*, 79(8), 2660–2675.
- Bonan, G. B. (2008). Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science (New York, N.Y.)*, 320(5882), 1444–9. doi:10.1126/science.1155121
- Farquhar, G., Caemmerer, S. Von, & Berry, J. A. (1980). A Biochemical Model of Photosynthetic CO₂ Assimilation in Leaves of C₃ Species. *Planta*, 90, 78–90.
- IPCC, 2007: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Iverson, L. R., & Prasad, A. M. (2002). Potential redistribution of tree species habitat under five climate change scenarios in the eastern US. *Forest Ecology and Management*, 155(1-3), 205–222. doi:10.1016/S0378-1127(01)00559-X
- Long, S. P., & Bernacchi, C. J. (2003). Gas exchange measurements, what can they tell us about the underlying limitations to photosynthesis? Procedures and sources of error. *Journal of experimental botany*, 54(392), 2393–401. doi:10.1093/jxb/erg262
- Nave, L. E., Gough, C. M., Maurer, K. D., Bohrer, G., Hardiman, B. S., Le Moine, J., ... Curtis, P. S. (2011). Disturbance and the resilience of coupled carbon and nitrogen cycling in a north temperate forest. *Journal of Geophysical Research*, 116(G4), G04016. doi:10.1029/2011JG001758
- Rogers, A. (2013). The use and misuse of V_{c,max} in Earth System Models. *Photosynthesis research*. doi:10.1007/s11120-013-9818-1
- Scheller, R. M., & Mladenoff, D. J. C. A. C. D. C. N. P. W. S. L. (2005). A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA. *Global Change Biology*, 11(2), 307–321 ST – A spatially interactive simulation o. doi:10.1111/j.1365-2486.2005.00906.x
- Turnbull, M., Whitehead, D., Tissue, D., Schuster, W., Brown, K., Engel, V., & Griffin, K. (2002). Photosynthetic characteristics in canopies of *Quercus rubra*, *Quercus prinus* and *Acer rubrum* differ in response to soil water availability. *Oecologia*, 130(4), 515–524. doi:10.1007/s00442-001-0842-z

