Respiratory responses to temperature change in broadleaf trees from the northeastern US

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Abstract

Rising atmospheric temperatures appear to be driving the geographic distribution of tree species northward. The mechanism for this range shift seems to be related to increased respiration lowering the competitive ability of trees growing on the southern margin of their ranges. Current models that predict future species ranges often do not incorporate species specific physiological data for factors such as respiration, or do so in a simplistic manner. However, understanding the respiratory response of tree species will be important for accurately predicting plant growth, competitive ability and future CO_2 fluxes into the atmosphere. Northern-, centrally-, and southern-ranged tree species in the northeast United States were sampled to determine how their respiratory responses varied across temperature gradients. Northern ranged species were found to have a lower energy of activation and a higher respiration rate at environmentally realistic temperatures of 10˚C and 20˚C, compared to their central and southern counterparts. Analyzing specific leaf area and percent nitrogen by range showed evidence that northern-ranged species did not have a higher overall metabolism, but rather had a higher respiratory output due to abiotic stress. These results suggest that northern-ranged species are at a physiological disadvantage due to reduced competitive ability compared to centrally- and southern-ranged species. This reduced competitive ability among northern-ranged tree species may lead to a decline of those populations and the persistence of centrally- and southern-ranged tree species in Black Rock Forest as temperatures rise in the region.

Table of Contents

Introduction

As a result of increasing greenhouse gas concentrations in the atmosphere, global temperatures are predicted to rise between 0.3-4.8˚C over the next century (IPCC, 2013). When considering the ramifications of rising global temperatures, understanding the cycling of carbon through the terrestrial biosphere will be important because such a large pool of carbon is stored there. Each year approximately 120 Pg of carbon are sequestered by photosynthesis, while soil and plant respiration each provide an approximate 60 Pg flux of carbon back into the atmosphere (Houghton, 2007). For comparison, this 60 Pg flux of carbon from plant respiration is about seven times the amount released by fossil fuel burning (Canadell *et al.*, 2001). Nevertheless, rising temperatures due to climate change threaten to disrupt the carbon storage balance in the terrestrial biosphere. Such climate-ecosystem interactions could induce both positive and negative feedbacks that could enhance or diminish the effects of climate change (Lashof *et al*. 1997). In one positive feedback mechanism, warmer temperatures lead to increased respiration by plants and thus more CO_2 release into the atmosphere contributing to an even further increase in temperature (Heimann and Reichstein, 2008). In light of this positive feedback loop it will be important to understand how plant respiration responds to changes in temperature in order to predict net CO_2 fluxes into the atmosphere and atmospheric CO_2 concentrations in the future (Atkin and Tjoelker, 2003).

In order to predict net CO_2 fluxes from plant respiration, models will need to incorporate physiological data. Physiological data can be used to predict

competitive ability, which is related to the ratio between oxygen released by photosynthesis and CO_2 released by respiration. Photosynthesis and respiration rates increase up to an optimal temperature where rates peak (Atkin and Tjoelker, 2003). Respiration typically peaks at a higher temperature than photosynthesis, so at temperatures above the thermal optimum for photosynthesis, respiration rates continue to increase as photosynthetic rates fall (Smith and Dukes, 2013). However respiration acclimates more strongly to changes in growth temperature than photosynthesis and can show apparent acclimation of photosynthesis when only net CO_2 assimilation is considered (Way and Yamori, 2013). Therefore it will be necessary to investigate the underlying mechanisms influencing respiration in order to understand tree growth response to a changing climate. Respiratory fluxes are limited by different factors depending on temperature. At temperatures near the thermal optimum for photosynthesis, respiration is limited by substrate availability (Atkin and Tjoelker, 2003). When temperature is increased beyond the thermal optimum for photosynthesis, the rate of Rubisco deactivation rises until it exceeds the capacity of activase to promote activation (Crafts-Brandner and Salvucci, 2000). This enzymatic deactivation at temperatures above the thermal optimum for photosynthesis could inhibit growth in some tree species as temperatures rise from climate change.

Despite the importance of physiological data in predicting growth and competitive ability, many models of species distribution predictions have used non-physiological variables related to things such as soil, land use, and elevation to predict species presence or absence under climate change scenarios (Iverson and

Prasad, 1998). Although more recent models have begun to incorporate physiological variables like photosynthesis and respiration, they lack species-specific physiological data (Patterson, 2012). These models are fairly uncertain but they have predicted changes in species distributions over time that have been corroborated by field data. Such data have shown increases in air temperature leading to changes in geographic distribution. For example, there has been significant advancement of tree lines in high altitude regions in Southwest Yukon and Sierra Nevada, California (Danby and Hik, 2007b; Millar *et al.*, 2004). The full extent of tree species' range shifts due to changes in climate is unclear but historical reconstruction suggests that rates of movement during postglacial migration in the early Holocene were slower than the rates that would be needed for tree species to track 21st century climate change (McLachlan *et al.*, 2005).

Of particular interest in future range predictions are populations of species that lie on the so called "rear edge" or lower latitude limit of their geographic distribution. Rear edge populations are often important long-term stores of genetic diversity and foci for speciation events (Hampe and Petit, 2005). However, rear edge populations are also under higher abiotic stress, tend to have a higher mortality rate than other local species, and are under more intense interspecies competition (Aitken *et al*., 2008). Black Rock Forest, a 1550 ha oak-dominated research forest in southeastern New York State has undergone significant changes in species composition over the past 80 years. Since the 1930's, botanical surveys of Black Rock Forest have shown that three "rear edge" or northern tree species were extirpated and eleven tree species were introduced or migrated from southern USA

(Schuster *et al*., 2008). Since the 1930's, botanical surveys of Black Rock Forest have shown that three "rear edge" or northern tree species were extirpated and eleven tree species were introduced or migrated from southern USA (Schuster *et al*., 2008). The northward shift by southern species into Black Rock forest coupled with the decline of the northern "rear edge" species suggests that this forest may be an important place to study the effects of climate change on northeastern forests (Patterson, 2012).

In order to understand the persistence and extirpation of tree populations due to their relative competitive abilities, direct measurements of respiratory response to temperature must be made. Understanding respiration quantitatively involves measuring the relationship between the temperature the plant is exposed to and the amount of CO_2 released by the plant. In the past, models have represented respiration with the constant $Q_{10,}$ which is the proportional increase in respiration per 10˚C rise in temperature (O'Sullivan *et al.,* 2013). Models have assumed a constant Q_{10} of 2.0, which corresponds to respiration doubling with every 10˚C increase in temperature (White *et al.,* 2001 and Cox 2001). However, this is an oversimplification of respiration. The shape of the temperature response is dynamic and not able to be accurately modeled by an exponential function because Q_{10} varies across short-term temperature response curves (O'Sullivan *et al.*, 2013). Q_{10} was found to be lower in tissues where substrates limit respiration (Atkin and Tjoelker, 2003). Turnbull *et al.* (2005) used an Arrhenius function, which accounts for slight declines in Q_{10} with increasing temperature, to model dark respiration temperature response in temperate rainforest tree species. This model showed

more sensitivity in modeling the response of respiration to temperature, however it used a constant value for activation energy in the respiration pathway that assumed respiration was always substrate saturated. O'Sullivan *et al.* (2013) found that modified Arrhenius function where energy of activation varied inversely with temperature provided a greater degree of sensitivity in predicting the temperature dependence of respiration. Data pertaining to the temperature dependence of respiration will be crucial in creating accurate temperature response models and predicting the competitive ability of plants.

Analyzing respiration is further compounded in difficulty by the fact that plant respiration is flexible because plants are capable of adjusting their metabolism to their thermal environment (Kruse and Adams, 2008). Such adjustment is referred to as acclimation. It has been theorized that there are two types of acclimation. In Type I acclimation, Q_{10} increases with temperature. While at lower temperatures species will have a similar respiratory response compared to non-acclimated species, at higher temperatures the respiratory output of acclimated species will be increased (Atkin and Tjoelker, 2003). Type I acclimation reflects either a change in the relative amounts of individual enzymes or a change in the regulation of existing enzymes (Atkin *et al.*, 2005). In contrast, Type II acclimation increases the respiratory response for all temperatures and is likely the result of biochemical adjustments such as an increase in mitochondrial protein causing an increase in the overall respiratory capacity (Atkin and Tjoelker, 2003 and Atkin *et al.*, 2005). Type II acclimation represents a greater degree of homeostasis (Atkin and Tjoelker, 2003). This type of acclimation is likely to be accompanied by an

increase in photosynthesis due to the overall increase in metabolic activity by the plant and may be critical in species being able to survive and compete under increased temperatures (Atkin *et al.*, 2005). Type I and Type II acclimation will be a useful lens for understanding the temperature sensitivity of respiration.

I studied the respiratory response to changes in temperature for southern-, central-, and northern-ranged species relative to Black Rock Forest. Because northern-ranged species typically grow in colder environments, I hypothesized that northern-ranged species would release more CO_2 as temperature increased relative to southern-ranged species, and centrally-ranged species would be intermediate. Above the temperature optimum for photosynthesis, enzymatic deactivation of respiration pathways could inhibit growth. This would be most likely to occur in northern-ranged trees that typically grow in colder environments and may result in a lower competitive ability for those species as global temperatures rise. Furthermore, I predicted that northern-ranged species would exhibit Type I acclimation because of increased temperatures leading to higher respiratory rates without a corresponding overall increase in metabolic activity. When taken together, this trend of higher respiratory rates in northern-ranged species and a Type I acclimation response could help explain the recent decline of northern-ranged species in Black Rock Forest. Finally, I predicted that the ability of the southern-ranged species to survive and persist in new ranges further north was due to Type II acclimation leading to increased substrate production providing a competitive advantage.

Methods

The study was conducted in Black Rock Forest, a deciduous forest located in the Hudson Highlands of southeastern New York (Schuster et al., 2008). The forest is located at 41°24′ N and 74°01′ E, with elevations between 110 to 450 m above sea level (Turnbull et al. 2001). Mean annual precipitation is 1.2 meters and temperatures range from -2.7˚C in January to 23.4˚C in July (Turnbull et al. 2001). I sampled three southern-ranged, three northern-ranged, and three centrally-ranged broadleaf tree species that grow in the forest (Table 1). Range categories were created based on species range maps (Figure 1).

Table 1. Broadleaf trees that were sampled in Black Rock Forest, corresponding to each of the three categories for range (see Fig. 1).

Southern	Central	Northern
Pignut hickory – *Carya glabra*	Red oak – *Quercus rubra*	Paper birch – *Betula papyrifera*
American sycamore – *Platanus occidentalis*	Chestnut oak – *Quercus prinus*	Bigtooth aspen – *Populus grandidentata*
Tulip poplar – *Liriodendron tulipifera*	Red maple – *Acer rubrum*	Quaking aspen – *Populus tremuloides*

Figure 1. Current range maps for the tree species sampled. Comparison of respiratory responses to temperature were made both among species and range groupings. The range groupings are: northern (B. papyrifera, P. tremuloides, P. grandidentata, central (Q. rubrua, A. rubrum, Q. prinus) and southern (C. glabra, L. tulipifera, P. occidentalis) (Taken from USGS Tree Species Range Maps, 2013).

Branch collection occurred in the mid morning hours. A 12 gauge semi-automatic shotgun was used to obtain samples (TriStar Sporting Arms, LTD., Missouri, USA). Branches were shot down from the top of the canopies, in order to take leaves grown in direct sunlight, because respiration rate depends on canopy

level (Ellsworth and Reich, 1993). Lower and mid-level canopy leaves tend to have a lower respiration rate and reduced temperature response compared to leaves that grow in direct sunlight (Griffin *et al.* 2002). Sampling leaves grown in direct sunlight also meant it was not necessary to quantify how much shade a given leaf was growing in. For each species, six replicate trees were sampled. After being shot off the tree, branches were immediately placed in water buckets and stems were clipped to promote water uptake. Plants were then tagged with labels and brought back to the lab for processing.

At the start of each trial, the surface area (cm^2) of each leaf sample was measured using a leaf area meter (Licor 3000C, Lincoln, USA). After measuring leaf area, fresh mass was recorded for each leaf sample and then samples were placed into the cuvette of a custom-built plant gas exchange system to measure respiration. Inside the cuvette, a wire attached to an adaptor was pressed against the lower leaf surface to measure temperature. The cuvette was covered with a dark cloth in order to stop photosynthesis and promote respiration. Using a waterbath (Julabo F25-ME, Allentown, USA) the temperature inside the cuvette was increased from 5˚C to 40˚C at a rate of 1˚C per minute. Net CO_2 release from the leaf was measured in μmol CO_2 $m^{-2}s^{-1}$ using an infrared gas analyzer (Licor 6262, Lincoln, USA). This process was repeated for each of the leaves collected from the six replicate trees for each of the nine species.

After measuring respiration, leaf samples were dried in an oven at 60˚C for two days. Dry weight values were recorded and used to calculate specific leaf area (SLA), which is the ratio of leaf area to dry mass. Leaf tissue was then ground into a

powder using a ball mill (SPEX 8000 Mixer/Mill®, New Jersey, USA). Between one and four milligrams of leaf tissue powder was placed in a tin capsule and then processed by a carbon-nitrogen flash analyzer (CE Elantech, New Jersey, USA) to acquire carbon and nitrogen ratios (CN; grams per gram of leaf tissue).

A modified Arrhenius function was used to model respiration between 5-40˚C (Equation 1). Equation 1 was adapted from O'Sullivan *et al.* (2013) and is one of seven discussed in that paper for modeling respiratory response curves by maximizing the r^2 value of the relationship between the measured and modeled data.

$$R = R_{20} e^{\frac{E_0}{g}\left(\frac{1}{T_{20}} - \frac{1}{T_a}\right)} \quad \text{(Equation 1)}$$

In this equation, E_0 represents a parameter related to the energy of activation and it defines the shape of the response curve. Because I chose a reference temperature of 20˚C, R_{20} is respiration at that temperature and T_{20} is 20. Finally g is the universal gas constant (8.314 J mol^{-1} K^{-1}) and T_a is the ambient temperature.

The solver function in Excel minimized the square of the standard deviations by adjusting E_0 and R_{20}. From the results of the temperature response fit curve, values for E_0, R_{10}, and R_{20} were compiled for each sample. Because during the growing season ambient temperatures at Black Rock Forest typically fall between 10˚C and 20˚C, those particular temperatures were chosen for analysis. In addition to E_0, R_{10}, and R_{20}, several leaf traits (leaf nitrogen, carbon to nitrogen ratio, and SLA) were tested for normality using histograms to visualize data distribution. Specific leaf area provides the mass basis for respiration and leaf nitrogen can be

used as a proxy for predicting respiration. Leaf nitrogen is indicative of the amount of protein in the leaf. More protein suggests higher metabolic activity and a higher growth cost for maintaining proteins in the leaf. In order to obtain a normal distribution, leaf nitrogen was log-transformed. After testing for normality, a one-way ANOVA with pairwise comparison of means was performed on each of the preceding factors using RStudio version 0.97.551 (RStudio, Inc, 2009-2012). The ANOVA analysis was carried out with samples grouped both by species and range. Significant differences between species and range groups were determined using Tukey contrasts. Standard error was calculated based on standard deviation.

Results

Energy of activation differed significantly between species ($p<0.0001$, $F_{9,46}=14.4$) and range ($p<0.0001$, $F_{2,53}=12.67$) (Figure 2). Northern-ranged species had an average E_0 of 52,749 $J^{-1}m^{-1}$, which was significantly lower than the energies of activation for central- and southern-ranged species (65,617 $J^{-1}m^{-1}$ and 62,501 $J^{-1}m^{-1}$ respectively). Respiration at 10˚C also differed significantly between species ($p<0.0001$, $F_{9,46}=10.39$) and range ($p<0.0001$, $F_{2,53}=19.11$; Figure 3). Respiration at 10˚C was significantly higher for northern-ranged species with an average R_{10} of 0.358 μmol CO_2 $m^{-1}s^{-1}$ compared to central- and southern-ranged species, which had average R_{10} measurements of 0.187 μmol CO_2 $m^{-1}s^{-1}$ and 0.214 μmol CO_2 $m^{-1}s^{-1}$ respectively. Similarly, respiration at 20˚C also differed significantly between species ($p<0.0001$, $F_{9,46}=9.03$) and range ($p<0.0001$, $F_{2,53}=18.19$) (Figure 4). Northern-ranged species had significantly higher rates of respiration at 20˚C with an

R_{20} of 0.846 µmol CO_2 $m^{-1}s^{-1}$ compared to their central and southern counterparts, which had average R_{20} measurements of 0.491 µmol CO_2 $m^{-1}s^{-1}$ and 0.548 µmol CO_2 $m^{-1}s^{-1}$ respectively.

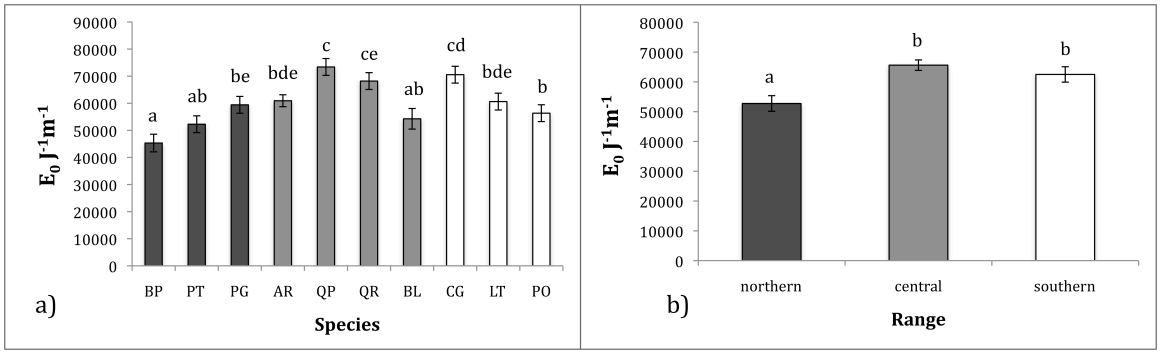

Figure 2. Energy of activation (E_0), by species (a) and range (b). Error bars represent one standard error. Means not sharing a common letter are significantly different ($p<0.05$) by Tukey contrasts. Species abbreviations correspond to species and genus names listed on range maps (figure 1).

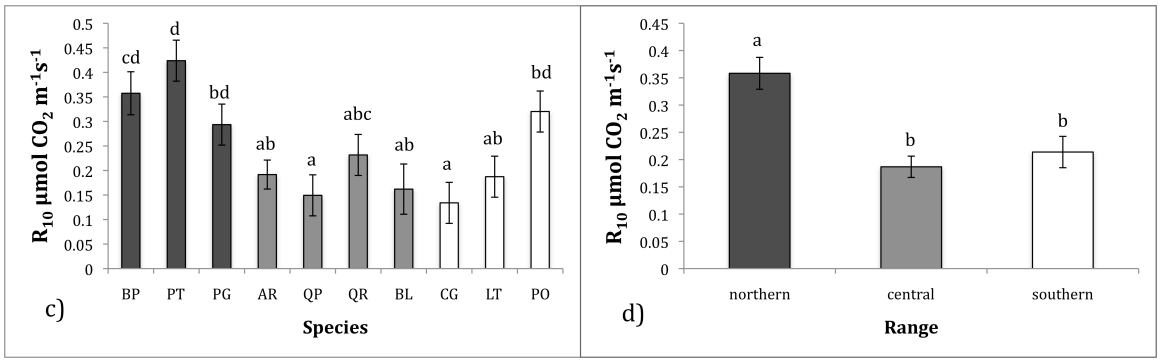

Figure 3. Respiration at 10˚C (R_{10}), by species (c) and range (d). Error bars represent one standard error. Means not sharing a common letter are significantly different ($p<0.05$) by Tukey contrasts. Species abbreviations correspond to species and genus names listed on range maps (figure 1).

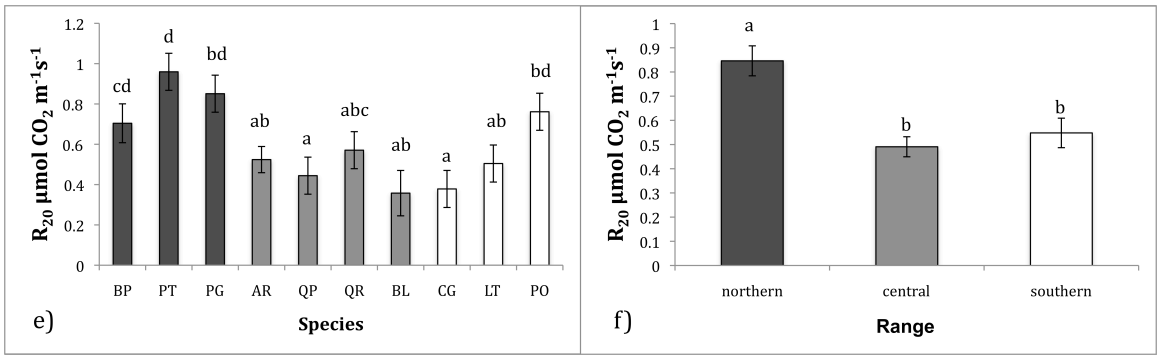

Figure 4. Respiration at 20˚C (R_{20}), by species (e) and range (f). Error bars represent one standard error. Means not sharing a common letter are significantly different ($p<0.05$) by Tukey contrasts. Species abbreviations correspond to species and genus names listed on range maps (figure 1).

Carbon to nitrogen ratio differed significantly between species ($p<0.0001$, $F_{9,46}=12.02$) and by range ($p<0.05$, $F_{2,53}=4.13$) (Figure 5). Northern-ranged CN ratio was significantly lower than centrally-ranged, however southern-ranged species were intermediate (22.4, 26.4, and 23.0 respectively). The log of leaf nitrogen differed significantly by species ($p<0.0001$, $F_{9,46}=8.32$) but not by range ($p=0.05151$, $F_{2,53}=3.14$) (Figure 6). Northern-ranged species had back transformed mean leaf nitrogen percent by mass of 8.96%, while central had a mean of 6.43% and southern had a mean of 8.32%. Specific leaf area (SLA) ratio differed significantly between species ($p<0.0001$, F-statistic: 9.106 on 9 and 46 DF) but not by range ($p=0.267$, F-statistic: 1.354 on 2 and 53 DF) (Figure 7).

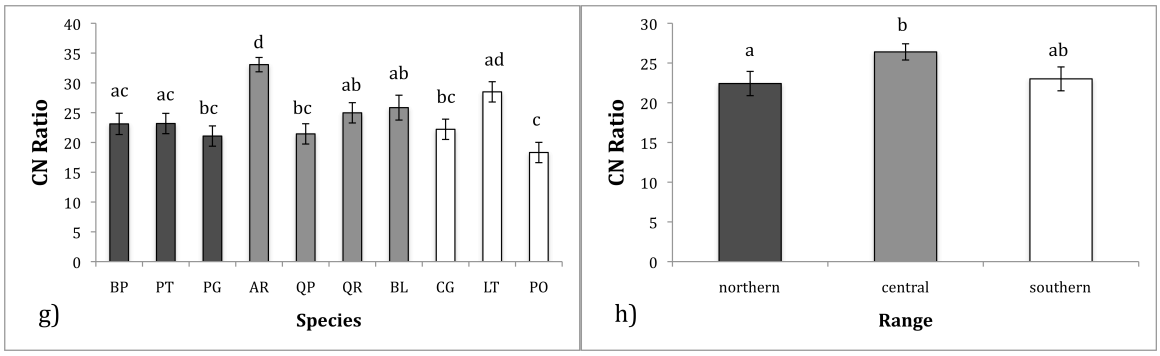

Figure 5. Carbon to nitrogen ratio by species (g) and range (h). Error bars represent one standard error. Means not sharing a common letter are significantly different ($p<0.05$) by Tukey contrasts. Species abbreviations correspond to species and genus names listed on range maps (figure 1).

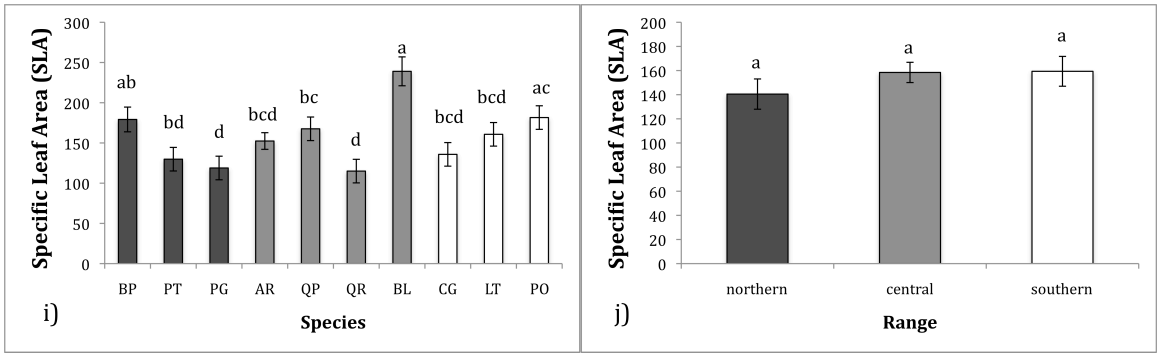

Figure 6. Specific leaf area (SLA) by species (i) and range (j). Error bars represent one standard error. Means not sharing a common letter are significantly different ($p<0.05$) by Tukey contrasts. Species abbreviations correspond to species and genus names listed on range maps (figure 1).

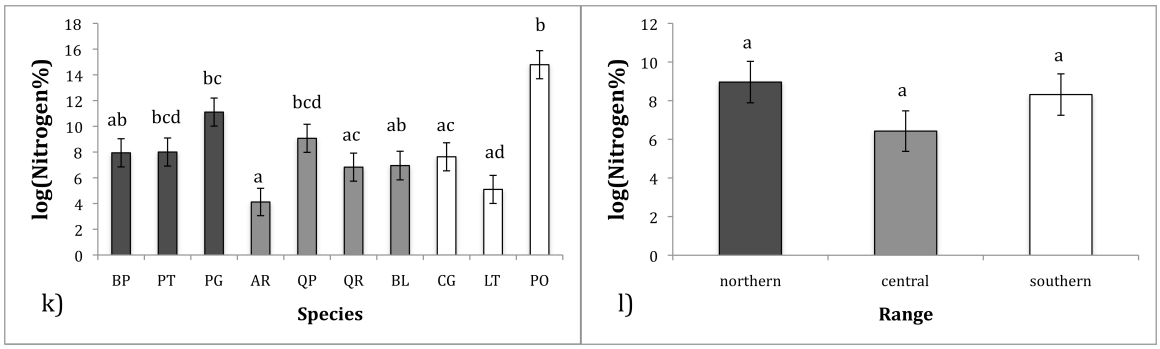

Figure 7. Log of percent nitrogen by species (k) and range (l). Error bars represent one standard error. Means not sharing a common letter are significantly different ($p<0.05$) by Tukey contrasts. Species abbreviations correspond to species and genus names listed on range maps (figure 1).

Discussion

As hypothesized, the northern-ranged tree species released more CO_2 at both reference temperatures of 10˚C and 20˚C. However, there was not a significant difference between the respiratory responses of the centrally- and southern-ranged trees. This could potentially be due to the original range categories selected. Although each of the centrally-ranged species do have a distribution extending further north than the southern-ranged species, the majority of the range of the centrally-ranged species still lies south of Black Rock Forest. In contrast, the bulk of the geographic range for the northern species is north of the forest. The designation of only two range categories, northern and southern, might be appropriate for future work with the species used in this study.

The mechanisms that determine species ranges are still unclear; however there have been hypotheses about the underlying processes driving biogeographic distributions. Central to many of these hypotheses is "Rapoport's rule" which predicts that the latitudinal range of species increases from low to high latitudes

(Stevens, 1989). Greater climatic variability, lower competition, and lower energy availability at high latitudes compared to low latitudes provide a framework for explaining Rapoport's rule (Morin and Chuine, 2006). The outcomes of these latitudinal gradients in defining species ranges are driven by abiotic stress (Morin and Chuine, 2006). Climate change may increase abiotic stress in some species more than others and lead to changes in geographic distributions of tree species.

The significantly higher R_{10} and R_{20} values for northern-ranged species suggest that more energy is being expended by maintenance respiration in response to abiotic stress from climate change. Because the allocation of photosynthates first goes to meet the respiration requirements of existing biomass, there is a trade off between abiotic stress and growth and competitive ability (Pederson, 1998; Morin and Chuine, 2006). Northern-ranged species could be at a physiological disadvantage along the rear edge of their margin because of more energy being allocated for maintenance respiration leaving less energy for growth and competition. This finding is consistent with Loehle (1998) suggesting that the southern margins of tree species ranges are determined by competitive ability. It was also suggested that the northern margins of ranges are determined by cold-tolerance, which could explain the expansion of southern-ranged trees northward into Black Rock Forest as temperatures rise from climate change.

Nevertheless, the higher R_{10} and R_{20} values for northern-ranged species could reflect an increase in overall metabolic activity at all temperatures and may be unrelated to competitive ability. However the evidence for Type I acclimation in northern-ranged species makes this explanation unlikely. The significantly lower E_0

for northern-ranged species could potentially be from regulatory changes in existing enzymes lowering the energy barrier for the respiration pathway indicating Type I acclimation. There was no significant difference in percent nitrogen by range category. Higher percent nitrogen is indicative of more proteins in the leaf and is a proxy for overall metabolic activity. More protein would increase the amount of substrate available in the leaf for respiration and thus indicate Type II acclimation. However, because percent nitrogen was not higher among northern-ranged species, it is more likely that the significantly higher respiration rates were due to regulatory changes in enzymatic activity or Type I acclimation.

Further evidence of Type I acclimation in northern-ranged species comes from the specific leaf area results. Specific leaf area is the amount of surface area on a leaf per unit of dry mass and because leaves are the primary organs for photosynthesis in plants, a higher SLA value indicates an elevated ability to capture light. It was found that dark respiration positively correlated with both SLA and photosynthesis across both biomes and functional groups (Reich *et al.*, 1997). Typically a higher value for SLA indicates a higher rate of respiration, not due to stress but due to overall increased metabolic function. However, the results of this study found that there was no difference in SLA by range group. If the significantly higher respiration rates in northern-ranged species were due to increased overall metabolic activity, the SLA for northern-ranged species would be correspondingly higher and would be evidence of Type II acclimation. Similarly, if the SLA for southern-ranged species were significantly higher than the other range categories, there would be evidence of Type II acclimation in those species. However, because

SLA did not differ by range category, the results of this study are inconclusive in testing the hypothesis that southern-ranged species are exhibiting Type II acclimation.

Significantly higher respiratory rates without corresponding significantly higher percent nitrogen and SLA together suggest that northern-ranged populations in Black Rock Forest are undergoing Type I acclimation. Because Type I acclimation suggests that more energy is being allocated to maintenance respiration, northern-ranged populations in Black Rock Forest may have a reduced competitive ability leading to their decline on the rear-edge.

Implications

Climate change is likely to drive an ongoing change in species composition in Black Rock Forest. If rear edge populations of northern ranged tree species are under increased abiotic stress due to climate change, it could impede their ability to compete in the northeast US. Furthermore if the northern margins of southern-ranged tree populations are determined by cold tolerance, rising temperatures due to climate change could expand the extent of southern species ranges northward. In other words, it may become warm enough for southern-ranged species to persist at higher latitudes. These changes on the margin are consistent with a predicted northward shift in tree species ranges over the next century (Morin *et al.*, 2008).

One species range prediction model shows *Betula papyrifera* moving out of Black Rock Forest (Figure 8). Although there have been numerous studies predicting range shifts due to climate change, the respiration parameters in these

species range shift predictions do not use species-specific data. Such species-specific respiration data will allow for more accurate models to be made.

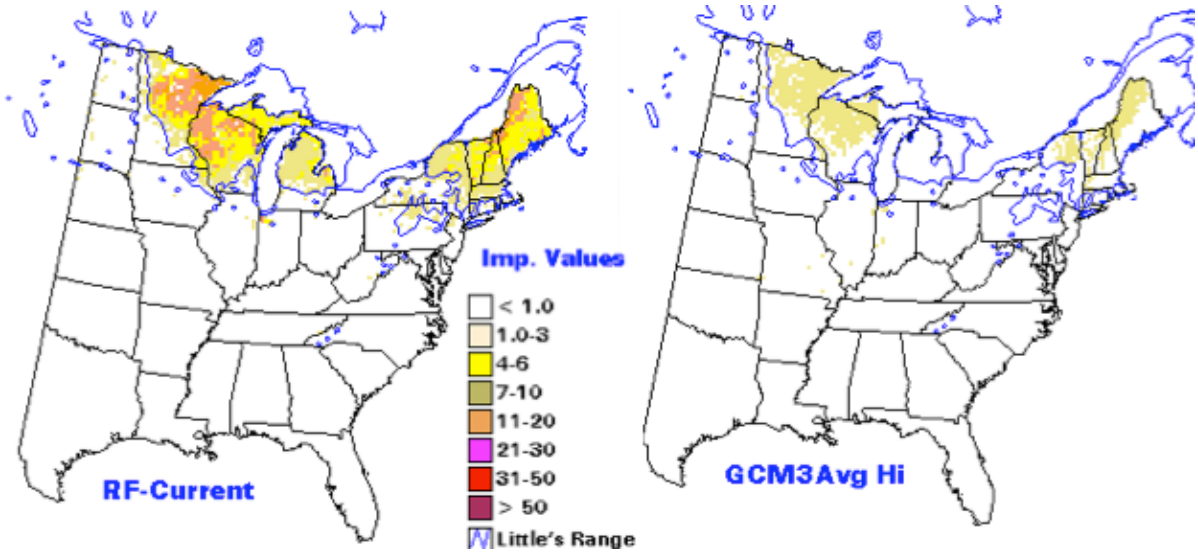

Figure 8. Current species range distribution (left) and predicted future range based on an average of three climate change models (right) for Betula papyrifera (Iverson and Prasad, 2002).

Accurate models are important because changing species composition will have effects on the overall dynamics of broadleaf forests across temperate latitudes. Particularly, shifting species distribution could cause large-scale changes in the amount of CO_2 that the forest respires. If the carbon storage capacity of northeastern forests is lowered, increased CO_2 release could lead to positive feedback loops in the terrestrial biosphere. Furthermore, on an ecosystem level, changes in tree species composition could lead to a cascade of ecological consequences. Changes in canopy density could drive changes in understory growth and microbial soil composition. As plant species composition changes, animal population levels may be influenced by changes in habitat or food availability. Finally, when making future range predictions, the ability for tree species to migrate

across fragmented habitats will be crucial in determining their future geographic ranges.

Recommendations

Significantly more physiological data is needed in order to make models that accurately predict species range changes. Additional respiratory response to temperature curves for more species would help to illuminate differences between range groups, particularly for northern species. Because forest canopy in Black Rock Forest is primarily composed of *Quercus rubra* and *Acer rubrum*, a study with more replicates comparing only the respiratory response to temperature of those two species could be useful. It could shed light on the shift away from primarily *Quercus rubra* and towards the increasing dominance of *Acer rubrum*. In order to assess the acclimation of respiratory response to temperature more directly, a longitudinal cross-section of samples of a single species could be taken. Comparing samples grown in a range of thermal conditions would allow for the direct comparison of respiration rates at a single temperature in a single species. Another potential future area of research could be a cross-region comparison of respiratory response to temperature. Comparing the northeast United States to other boreal forests across the globe would provide valuable insight into where and how broadleaf tree species range changes are occurring.

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References

Aitken, S. N., Yeaman, S., Holliday, J. a., Wang, T., & Curtis-McLane, S. (2008). Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, *1*(1), 95–111.

Atkin, O. K., & Tjoelker, M. G. (2003). Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in plant science*, *8*(7), 343–51.

Atkin, O. K., Bruhn, D., Hurry, V. M., & Tjoelker, M. G. (2005). The hot and the cold: unravelling the variable response of plant respiration to temperature. *Functional Plant Biology*, *32*(2), 87.

Canadell, J. G., Que, C. Le, Conway, T. J., Gillett, N. P., Houghton, R. A., Marland, GreggRaupach, M. R., Field, C. B. (2007). Contributions to accelerating atmospheric CO 2 growth from economic activity , carbon intensity , and efficiency of natural sinks. *PNAS*, *104*(47), 18866–18870.

Cox, P. M. (2001). Description of the " TRIFFID " Dynamic Global Vegetation Model. *Hadley Centre Technical Note*, (January).

Crafts-Brandner, S. J., & Salvucci, M. E. (2000). Rubisco activase constrains the photosynthetic potential of leaves at high temperature and CO2. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(24), 13430–5.

Danby, R. K., & Hik, D. S. (2013). in Southwest Evidence of Recent Treeline Yukon from Aerial Photographs Dynamics. *Arctic*, *60*(4), 411–420.

Ellsworth, D.L. & Reich, P. B. (1993). Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia*, (96), 169–178.

Griffin, K. L., Turnbull, M., & Murthy, R. (2002). Canopy position affects the temperature response of leaf respiration in Populus deltoides. *New Phytologist*, *154*(3), 609–619.

Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: the rear edge matters. *Ecology letters*, *8*(5), 461–7.

Heimann, M., & Reichstein, M. (2008). Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature*, *451*(7176), 289–92.

Houghton, R. a. (2007). Balancing the Global Carbon Budget. *Annual Review of Earth and Planetary Sciences*, *35*(1), 313–347.

Intergovernmental Panel on Climate Change. (2013). Climate change 2013: The physical science basis. New York, NY. Retrieved December 7, 2013, from http://www.climatechange2013.org/images/uploads/WGI_AR5_SPM_brochure.pdf

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.

Kruse, J., & Adams, M. a. (2008). Three parameters comprehensively describe the temperature response of respiratory oxygen reduction. *Plant, cell & environment*, *31*(7), 954–67.

Lashof, D. A., Deangelo, B. J., Saleska, S. R., & Harte, J. (1997). Terrestrial Ecosystem Feedbacks to Global Climate Change. *Annual Review of Energy and the Environment*, 75–118.

McLachlan, J. S., Clark, J. S., & Manos, P. S. (2005). Molecular Indicators of Tree Migration Capacity Under Rapid Climate Change. *Ecology*, *86*(8), 2088–2098.

Millar, C. I., Westfall, R. D., Delany, D. L., King, J. C., & Graumlich, L. J. (2004). Response of Subalpine Conifers in the Sierra Nevada, California, U.S.A., to 20th-Century Warming and Decadal Climate Variability. *Arctic, Antarctic, and Alpine Research*, *36*(2), 181–200.

Morin, X., & Chuine, I. (2006). Niche breadth, competitive strength and range size of tree species: a trade-off based framework to understand species distribution. *Ecology letters*, *9*(2), 185–95.

Morin, X., Viner, D., & Chuine, I. (2008). Tree species range shifts at a continental scale : new predictive insights from a process-based model. *Journal of Ecology*, (96), 784–794.

O'Sullivan, O. S., Weerasinghe, K. W. L. K., Evans, J. R., Egerton, J. J. G., Tjoelker, M. G., & Atkin, O. K. (2013). High-resolution temperature responses of leaf respiration in snow gum (Eucalyptus pauciflora) reveal high-temperature limits to respiratory function. *Plant, cell & environment*.

Patterson, A. E. (2012). Warming Climates, Changing Forests: Temperature Tolerances of Trees and Carbon Dynamics in Northeastern Temperate Forests. *Consilience: The Journal of Sustainable Development*, *9*.

Pedersen, B. S. (1998). Modeling tree mortality in response to short- and long-term environmental stresses. *Ecological Modeling*, *105*(2-3), 347–351.

Prasad, A. M., L. R. Iverson., S. Matthews., M. P. (n.d.). A Climate Change Atlas for 134 Forest Tree Species of the Eastern United States. *Northern Research Station, USDA Forest Service, Delaware, Ohio*. Retrieved May 5, 2013, from http://www.nrs.fs.fed.us/atlas/tree

Prentice I.C., Farquhar G.D., Fasham M.J.R., Goulden M.L., Heimann M., Jaramillo V.J., Kheshi H.S., Le Quere C., S. R. J. & W. D. W. R. (2001). The carbon cycle and atmospheric carbon dioxide. In Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. In K. M. & C. A. J. J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai (Ed.), (pp. 183–237). Cambridge, UK.: Cambridge University Press.

Reich, P. B., Ellsworth, D. S., Vose, M., & Volin, J. C. (1997). Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. *Oecologia*, *114*, 471–482.

Schuster, W. S. F., Griffin, K. L., Roth, H., Turnbull, M. H., Whitehead, D., & Tissue, D. T. (2008). Changes in composition, structure and aboveground biomass over seventy-six years (1930-2006) in the Black Rock Forest, Hudson Highlands, southeastern New York State. *Tree physiology*, *28*(4), 537–49.

Smith, N. G., & Dukes, J. S. (2013). Plant respiration and photosynthesis in global-scale models: incorporating acclimation to temperature and CO 2. *Global Change Biology*, *19*(1), 45–63.

Stevens, G. (1989). The Latitudinal Gradient in Geographical Range: How so Many Species Coexist in the Tropics. *The American Naturalist*, *133*(2), 240–256.

Turnbull, M. H., Whitehead, D., Tissue, D. T., Schuster, W. S., Brown, K. J., & Griffin, K. L. (2001). Responses of leaf respiration to temperature and leaf characteristics in three deciduous tree species vary with site water availability. *Tree physiology*, *21*(9), 571–8.

Turnbull, M. H., Tissue, D. T., Griffin, K. L., Richardson, S. J., Peltzer, D. a, & Whitehead, D. (2005). Respiration characteristics in temperate rainforest tree species differ along a long-term soil-development chronosequence. *Oecologia*, *143*(2), 271–9.

USGS Digital Representations of Tree Species Range Maps from "Atlas of United States Trees" by Elbert L. Little, Jr. (and other publications). (2013). Retrieved May 5, 2013, from http://esp.cr.usgs.gov/data/little/

Way, D. a, & Yamori, W. (2013). Thermal acclimation of photosynthesis: on the importance of adjusting our definitions and accounting for thermal acclimation of respiration. *Photosynthesis research*.

White, A., Cannell, M. G. R., & A.D., F. (2000). The high-latitude terrestrial carbon sink : a model analysis. *Global Change Biology*, (6), 227–245.