Respiratory response to changing temperature across trees from three latitudinal ranges in Black Rock Forest

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Abstract

Black Rock Forest in southeastern New York has undergone extensive change in terms of tree species migration and extinction. For example, studies have shown that since the early 1930's, three northern-ranged tree species became extinct and eleven tree species were introduced or had migrated from southern USA. These observations are consistent with a warming climate and rapidly accumulating biological response to that warming. This suggests that the Hudson River Valley may be an important location to study the effects of climate change on Northeastern forests. We compared a suite of physiological and leaf traits across nine tree species that have one of three distribution ranges (northern, central, and southern) and one of two leaf types (broadleaf and coniferous). Southern ranged species were found to have lower respiration energy and a higher energy of activation at a temperature of 20°C, compared to their northern and central counterparts. Analyzing carbon to nitrogen ratio, specific leaf area, and percent nitrogen by range showed evidence that southern-ranged species had higher metabolic energy. These results suggest that southern- ranged species are at a physiological advantage due to enhanced competitive ability to adjust to changing temperatures in comparison to northern and centrally ranged species. This competitive ability may result in an increase of southern-ranged tree species and a consequent decline of northern and central ranged populations as temperatures continue to increase due to global warming.

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Introduction

Global warming has become a pressing concern to all life systems on the earth due to climate increasing at an exponential rate compared to the rest of the Earth's history and also due to the biological responses to this climate change. Global surface air temperatures are projected to increase by 2.0– 5.4°C over the next century due to rising concentrations of greenhouse gases in the atmosphere, in contrast to the last 40 years where it increased by 0.2-0.3°C (Pachauri, 2007) . In the northeastern U.S. alone, air temperatures have increased over the last 30 years by 0.8°C According to the National Climatic Data Center, recent warming has been the greatest in latitudes between 40N and 70N, where a large portion of American temperate forests reside (Frumhoff, 2007).

Thus climate change is of particular importance to forests in the northeastern United States, which is warming faster than many other parts of the world. This importance is compounded by the fact that forests contain around three quarters of the earth's terrestrial biomass and thus are tightly linked with atmospheric carbon budgets(Aitken, Aitken, Yeaman, Holliday, & Wang, 2008). Each year approximately 120 Pg of carbon are sequestered by photosynthesis, while about 60 PgC is released back into the atmosphere by plant respiration (Houghton, 2007). By comparison, only about 8.4±0.5 PgC is released by fossil fuels each year which is equivalent to approximately eight times less than the amount released by plant respiration (Raich JW, 1992).

The interplay between photosynthesis and respiration is responsible for not only the individual plant's survival, but also for much of the atmospheric condition of earth (O.K. Atkin, Bruhn, Hurry, & Tjoelker, 2005). Since CO_2 is a greenhouse gas, its presence causes a positive feedback loop between terrestrial carbon cycles and global warming (Friedlingstein & Prentice, 2010). For example, warmer temperatures lead to increased respiration rates by plants, which therefore lead to increased amounts of CO_2 in the atmosphere, which then contributes to an increase in atmospheric temperature (Heimann & Reichstein, 2008). Thus, understanding how the physiological process of respiration (R) responds to and affects temperature is key in predicting species carbon capacity, atmospheric CO_2 concentrations, and regions of the Earth sensitive to global warming.

As temperatures increase, changes occur in a number of different ways in individual plant species. Physiologically, there are changes photosynthesis, respiration, and tissue growth rates; this is turn affects the plant geographically as “migration,” or a change in species’ population density and range, occurs via changing physiological rates in response to shifting climate zones (Raich JW, 1992). For example, increased temperatures seem to be shifting species’ distribution northward; this is due to increased respiration constraining plant resources and therefore affecting the species’ ability to respond to shifting temperatures (Midgley, 2007; Schuster et al., 2008).

In contrast to individual plant species, in a rapidly changing environment, or in an environment with increasing air temperature, there are three possible outcomes for forest tree populations: geographic distribution, persistence at current range via local adaptation, or extirpation (i.e. local extinction) (Aitken et al., 2008; Corlett, 2008). Geographic distribution occurs because the species moves in response to moving climate zones; local adaptation and persistence at the current range occurs because that particular species is more resilient and can survive despite a changing temperate environment; extirpation occurs because the change in environment causes the species with slow migration rates to lose its source of food and become extinct (Chuine, Belmonte, & Mignot, 2000). For example, to adapt to the changing climate several species of trees have shifted their geological range a significant distance to high altitude locations (Tjoelker, Oleksyn, Lorenc-Plucinska, & Reich, 2009). Due to this migration, in areas of rapid climate change, tree species have widened their spatial extent causing competition between native and non-native trees for critical resources such as nitrogen and carbon (Heimann & Reichstein, 2008). Tree species' ranges shifted northward a rate of 50 km per century as temperatures rose after the retreat of the Laurentide (North American) ice cap (Woodall et al., 2010). This is in contrast to tree populations today, where migration and extirpation occurs on a more rapid basis which reflects the rapidly rising temperatures(Aitken et al., 2008).

Black Rock Forest, a 1550-ha temperate forest in the northeastern United States and in the Hudson Highland region has a high dominance of oak species (Maenza-Gmelch, 1997). Oaks are a vital species to the carbon cycle because they are known to sequester large amounts of carbon in a region known to be one of the largest aboveground terrestrial carbon pools in the world (BRF). However BRF has undergone significant species distribution changes in the last 76 years where three tree species have been extirpated and succeeded by eleven new tree species that were either artificially introduced or naturally migrated (Schuster et al., 2008). This interspecies competition, for limiting resources has changed the density of a forest once dominated by oaks and therefore has also changed the carbon storage capacity of the forest. This is because different species of trees have different carbon capacities which also vary based on temperature. All of the extirpated species and a majority of the new species follow a general northward shift in range (Aitken et al., 2008; Schuster et al., 2008). This general change in a once oak-dominated species composition, particularly the northward shift in range, suggests that

BRF may be an important place to study the effects of climate change on Northeastern forests (*Global Warming*, 2013; Patterson, 2012).

As mentioned before, increasing temperatures seem to be causing the northward shift in tree distribution due to rising temperatures motivating an increase in respiration. The increase in respiration leads to a varied effect on other physiological factors which eventually lead to species range shifts. Recent models have begun to combine SDM (species distribution model) with GCM (global circulation models) to predict climate-driven species shifts (Aitken et al., 2008; Pearson & Dawson, 2003). Though some of these new models incorporate physiological variables like photosynthesis and respiration, they lack species-specific physiological data (Chuine et al., 2000; Patterson, 2012). Species-specific physiological data could help to create more accurate species distribution predictions for future climate change scenarios (Patterson, 2012).

Obtaining species-specific data specifically related to respiration involves measuring quantitatively how the end product of respiration, CO_2, varies with temperature. It is often assumed that the relationship between plant respiration and temperature is exponential with a constant Q10, which is the proportional change in respiration with a 10°C increase in temperature — typically around 2. As a result, most simulation models assume that R responds to both short and long term changes in temperature in a fixed, exponential manner (Ryan, 1991; Will, 2000) (White et al. 2000; Cramer et al. 2001). However, a growing body of research demonstrates that the relationship between respiration and temperature is dynamic, with plant respiration often acclimating to long-term changes in temperature. Overall, neither Q10 values nor degrees of acclimation are constant; rather, both are dynamic and vary in response to the surrounding environment(O. K. Atkin & Tjoelker, 2003). Consequently, GCMs that fail to take into account such variability in Q10 and degrees of temperature acclimation of respiration are likely to result in large over-estimates of annual respiratory CO_2 release into the atmosphere and consequently over-estimate atmosphere CO_2 concentrations over longer periods of time (O. K. Atkin & Tjoelker, 2003; Loveys, Scheurwater, Pons, Fitter, & Atkin, 2002). However, the extent of acclimation varies widely between species, and the physiological mechanisms controlling respiration acclimation to temperature are still poorly understood (Loveys et al., 2002).

Thus, it is important to understand the relationship between respiration and temperature in depth, to see how it will affect earth's atmosphere as well as how or if tree species will acclimate to changing temperatures. A plant can acclimate by adjusting their metabolism to their thermal environment (Kruse, 2008). It has been theorized that there are two types of acclimation. In Type I acclimation, there are regulatory changes of existing enzymes (Atkin *et al.*, 2005). This acclimation is associated with a change in the rate of respiration primarily at moderate to high temperatures, with little or no change in respiration at low temperatures(O. K. Atkin & Tjoelker, 2003). In contrast, Type II acclimation increases the respiratory response over a wide range of temperatures and is likely the result of biochemical adjustments such as an increase in mitochondrial protein causing an increase in the overall respiratory capacity (Aitken et al., 2008; O.K. Atkin et al., 2005). Another characteristic of Type II acclimation is that is can result in respiratory homeostasis as well as an overall increase in metabolic activity by the plant; this may result in a species being able to survive and compete under increased temperatures (O.K. Atkin et al., 2005). While researching how respiration changes over temperature, Type I and Type II acclimation will be a useful lens in understanding temperature sensitivity to these physiological rates (Arkebauer, 2014).

I studied the physiological response to temperature of tree species that have northern, central or southern range limits distributed across the Hudson Highlands region of the northeastern United States. My study will focus on the respiratory response to changing temperatures in tree species of various ranges in Black Rock Forest, NY. I measured and calculated various measurements related to respiration such as R20 (respiration rate at 20°C), and Eo (parameter related to respiration activation energy), specific leaf area, carbon to nitrogen ratio (ratio of substrates over proteins), and percent nitrogen (protein indicator).

In BRF, most tree migration is northward. In the short-term, a rise in temperature increases the rate of respiration (R) and the rate of photosynthesis, releasing more CO2 into the atmosphere (Bunce, 2007). During acclimation, the rate of increase of R with temperature is reduced in plants that are used to warm environments and thus more respiration output; this is in contrast to the rate of increase of R with temperature is increased in plants that are used to colder environments and thus less respiration output. I hypothesize that because southern trees are used to warmer environments relative to other ranged trees, they would release less CO2 relative to other ranged trees. The implication of this would be that southern ranged species to have less energy (because they are respiring less) and thus prompt them northward to seek colder climates explaining the northward migration. I predict that the ability of the southern-ranged species to survive and invade to the north was due to Type II acclimation leading to increased metabolic activity and providing a competitive advantage.

Methods

Study Site

This study was conducted at Black Rock Forest, a 1550-ha research forest located in the Hudson Highlands Region of southeastern New York State, on the west bank of the Hudson River. The topography is rocky with steep slopes and elevations ranging from 110 to 450 m above sea level. The forest canopy is a mix of hardwoods comprised of about 67% oak and 33% non-oaks. Air temperatures are strongly seasonal ranging from a mean of −2.7°C in January to 23.4°C in July, and the average annual precipitation is 1,200 mm). I sampled two northern-ranged, two centrally-ranged, and four southern-ranged broadleaf tree species that grow in the forest (Table 1).

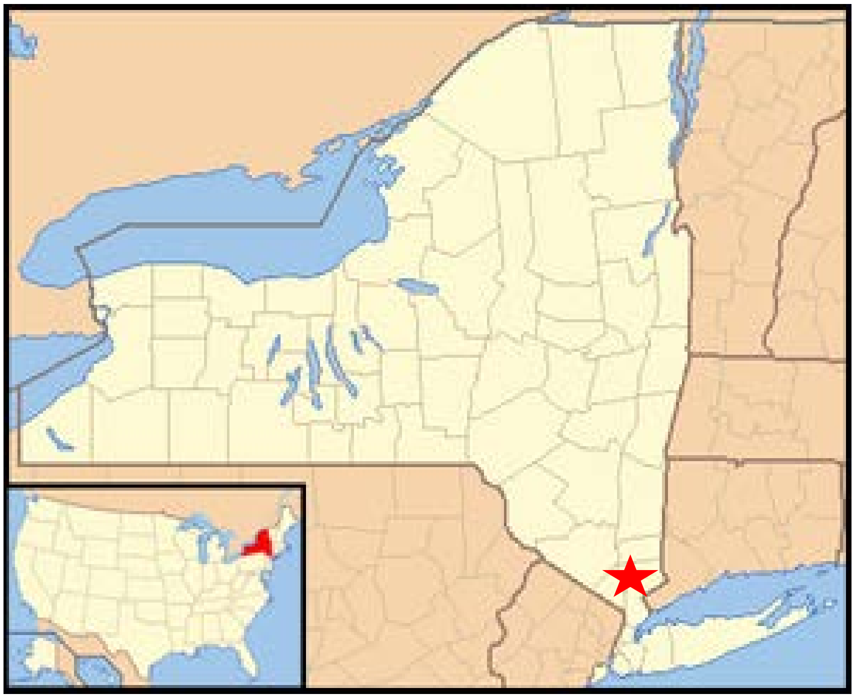
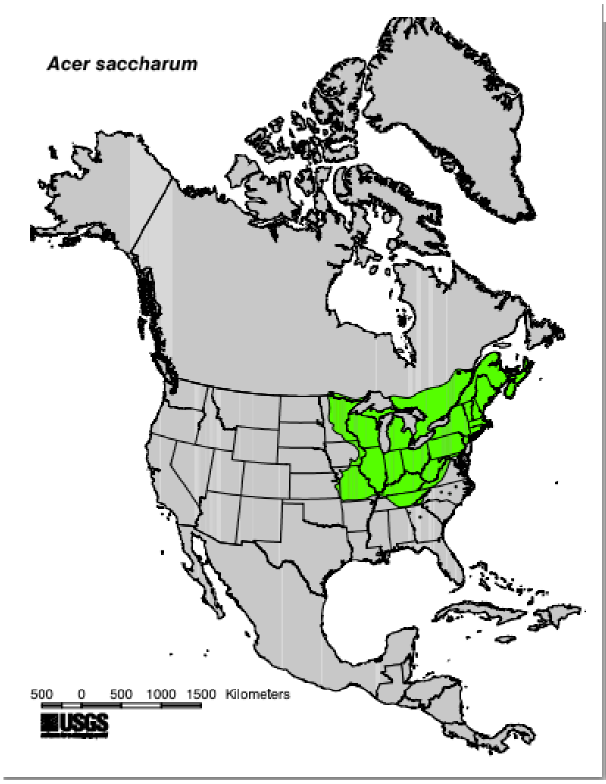


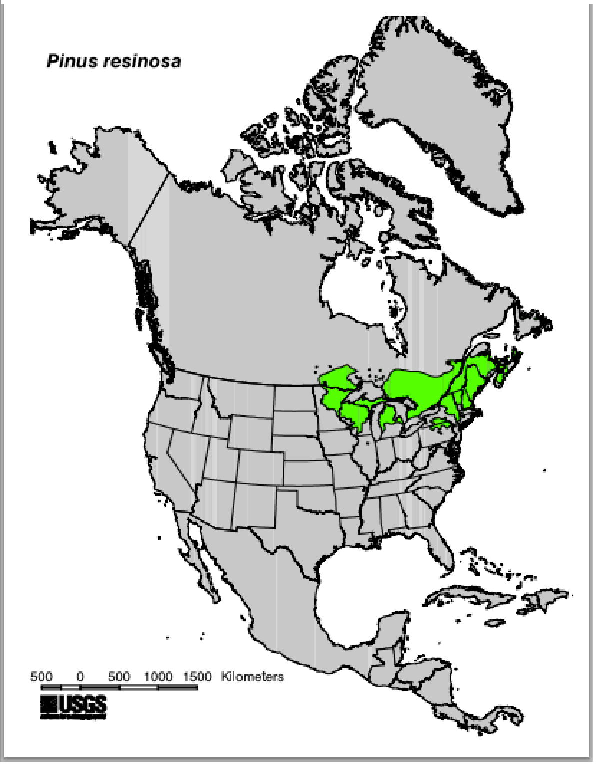
Figure 1. Map of New York State. Black Rock Forest is noted with a red star.

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

Northern	**Central**	**Southern**	
Acer sacharrum (sugar maple)	*Betula lenta* (black birch)	*Ailanthus altissima* (tree-of-heaven)	*Nyssa sylvatica* (black gum)

Pinus resinosa (red pine)	*Pinus strobus* (white pine)	*Catalpa bignonioides* (Southern catalpa)	*Carya glabra* (pignut hickory)





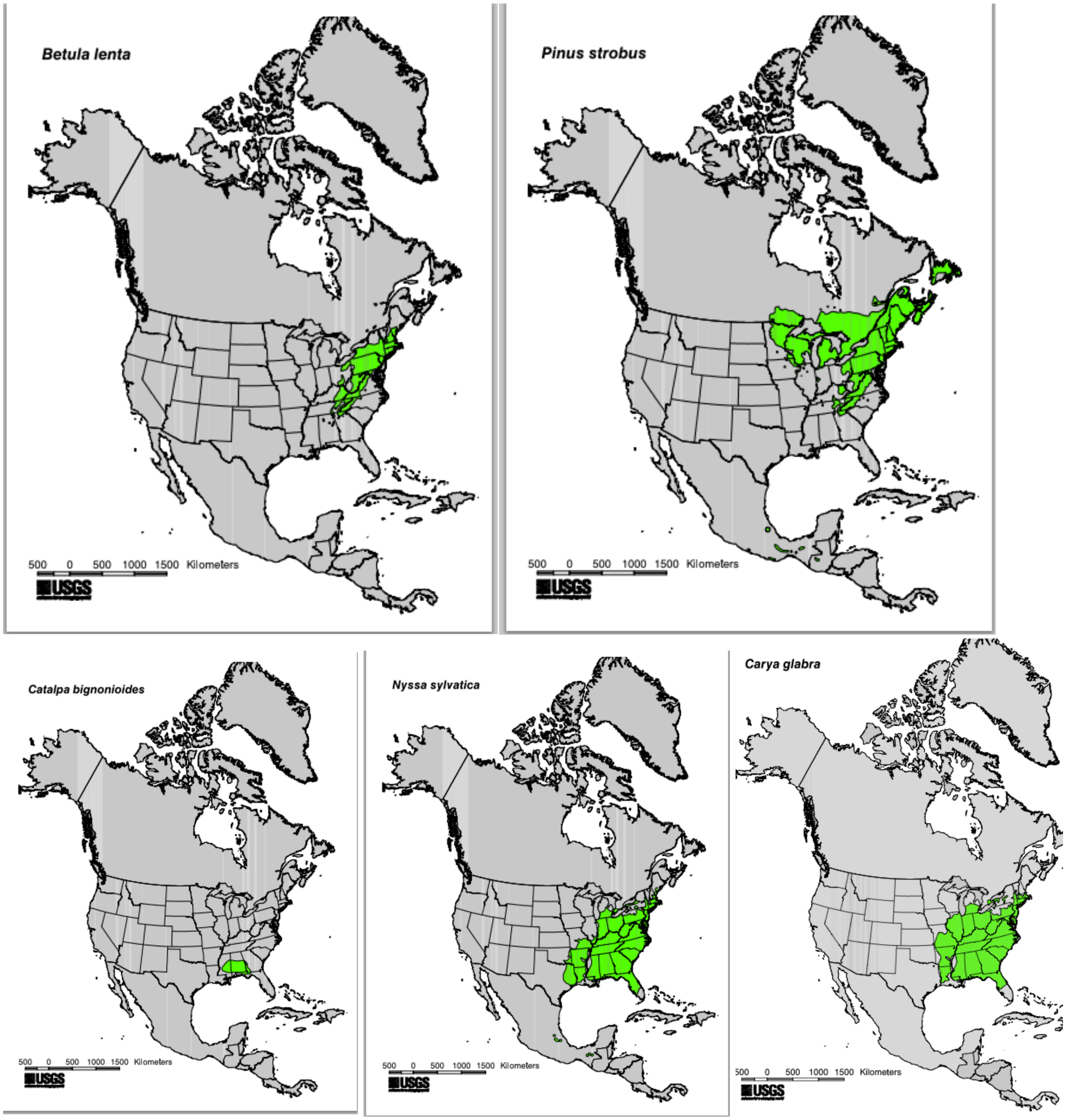


Figure 2. Current range maps for the tree species sampled. Comparison of respiratory responses to temperature were made both among species and range groupings. The range groupings are: northern (Acer sacharrum, Pinus resinosa), *central (Betula lenta, Pinus Strobus) and southern (Ailanthus altissima, Catalpa bignonioides, Nyssa Sylvatica, Carya Glabra). Ailanthus altissima* did not have a range map available *(Taken from USGS Tree Species Range Maps, 2013).*

Plant material collection

Plant collection took place in the morning hours before noon from June to August in 2012.

Canopy leaves were collected from six replicate mature trees from nine species categorized into four groups (Southern-ranged, Northern-ranged, Centrally-ranged, and Newly Introduced). In total, seven broad-leaved tree species and two conifer species were used in this study. A 12-gauge semi-automatic shotgun (TriStar Sporting Arms, LTD., Missouri, USA) was used to shoot down branches grown in direct sunlight from six replicate trees per day. Once the branches fell to the ground, they were placed in a bucket of water where the stem was pruned for optimal water uptake. Plants were then tagged with their appropriate labels and brought back to the lab for processing.

Leaf traits

Leaves were sampled off a main branch, freshly weighed, and run through a leaf area meter used to acquire the projected leaf area (cm^2). Leaves were then placed into separate coin envelopes and dried in an oven at 60°C for two days. Dry weight values (mg) and leaf area (cm^2) were used to calculate specific leaf area (SLA) which is the ratio of leaf area to dry mass. After drying from 5 to 8 hours, leaves were ground into powder using a ball mill (SPEX 8000 Mixer/Mill®, New Jersey, USA). Two to four milligrams of dried leaf powder were then weighed into tin capsules and then run through a carbon-nitrogen flash analyzer (CE Elantech, New Jersey, USA) to acquire carbon and nitrogen ratios of the dry mass (CN ratio; grams per gram of leaf tissue).

Temperature Response of Respiration

An instrument was built and used to measure the response of respiration to changing temperature by stimulating a changing, yet controlled temperature environment. Freshly collected canopy leaves were placed in a darkened, temperature-controlled cuvette attached to a circulating water bath which was used to control the temperature. Dry air was passed through the cuvette at a flow rate of 0.45 L/hr and into an LI-800 infrared gas analyzer (LI-COR, Lincoln, Nebraska) or IRGA which measured the flux of CO_2 out of the leaf as it was heated from 5°C to 35°C as seen in Figure 1.

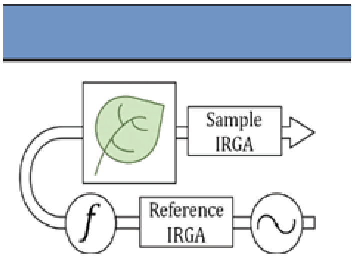


Figure 1. Leaf was placed in darkened, temperature controlled cuvette. Dry CO2 passed through the cuvette at a rate of 0.45 L/hr where it went into the IRGA (infrared gas analyzer). The flux of CO2 was measured between temperatures 5°C to 35°C.

The Q10, or the temperature sensitivity at a reference temperature, for each leaf was calculated from 5°C to 35°C using the equation:

$$Q_{10} = \left(\frac{R_2}{R_1} \right)^{\left(\frac{10}{T_2 - T_1} \right)} \quad \text{(Equation 1)}$$

R1 and R2 are the rates of respiration at temperatures T1 and T2, respectively. The temperature response of respiration was modeled using a polynomial fit equation that assumes that reaction rate increases exponentially with temperature (Ryan, 1991; Tjoelker, 1999):

$$R = R_{20} e^{\frac{E_0}{g}\left(\frac{1}{T_{20}} - \frac{1}{T_a}\right)} \quad \text{(Equation 2)}$$

E0 represents a parameter related to the energy of activation that is temperature adjusted, G is the ideal gas constant(8.314 J mol-1 K-1), T20 is the reference temperature which is 20°C in this model, and Ta is the average ambient temperature on the day each leaf collected was collected. These equations were used to visually represent Q10 and respiration response to changing temperature through graphical representation. From the results of the temperature response fit curve, values for E_0 and R_{20} were compiled for each sample.

Data Analysis and Statistics

The square of the standard deviations was minimized by manipulating E_0 and R_{20} using the solver function in Excel. From the results of the temperature response fit curve and how the data compared to the model fit, values for E_0 and R_{20} were compiled for each sample. In addition to E_0 and R_{20}, several leaf traits (leaf nitrogen, carbon to nitrogen ratio, and SLA) were tested for normality using histograms to visualize data distribution. Leaf nitrogen is indicative of metabolic activity and the amount of protein in the leaf. Carbon to nitrogen ratio is a ratio of substrate over proteins; this indicates how much ATP or energy is needed to support the activities of the cell or in other words supply over demand. Specific leaf area (SLA) provides the mass basis for respiration and leaf nitrogen can be used as a proxy for predicting respiration. In order to obtain a normal distribution, leaf nitrogen, CN Ratio, SLA, and R20 was log-transformed while E0 was square-root 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

Respiration at 20℃ differed significantly between species ($p<0.0001$) and range ($p<0.0001$) (Figure 3). Southern-ranged species had significantly lower rates of respiration at 20℃ with an R_{20} of 0.120 µmol CO_2 $m^{-1}s^{-1}$ compared to their central counterparts, which had average R_{20} measurement of 1.009 µmol CO_2 $m^{-1}s^{-1}$ respectively. Northern-ranged species had an R_{20} of 0.434 µmol CO_2 $m^{-1}s^{-1}$ which was lower than their southern counterparts but not significantly. Energy of activation differed significantly between species ($p<0.0001$) and range ($p<0.0001$) (Figure 4). Southern-ranged species had an average E_0 of 87,546 $J^{-1}m^{-1}$, which was significantly higher than the energy of activation for centrally-ranged species (37,480 $J^{-1}m^{-1}$). Northern ranged species had an activation energy of 59,527 $J^{-1}m^{-1}$ but this value was not significantly different than the E_0 of central and southern ranged species.

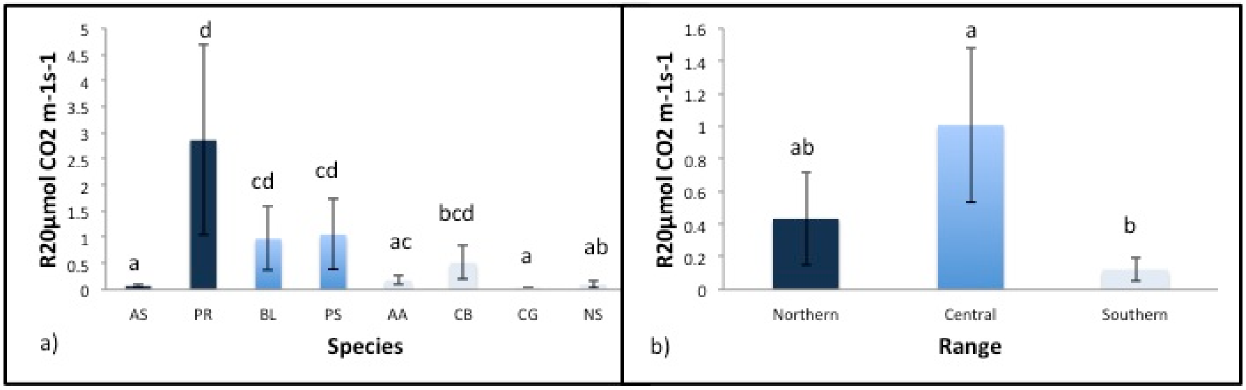


Figure 3. Respiration at 20℃ (R_{20}), by species (a) and range (b). Error bars represent one standard error. Means not sharing a common letter are significantly different ($p<0.05$) by Tukey contrasts. Species abbreviations correspond to species and genus names listed on range maps (figure 2).

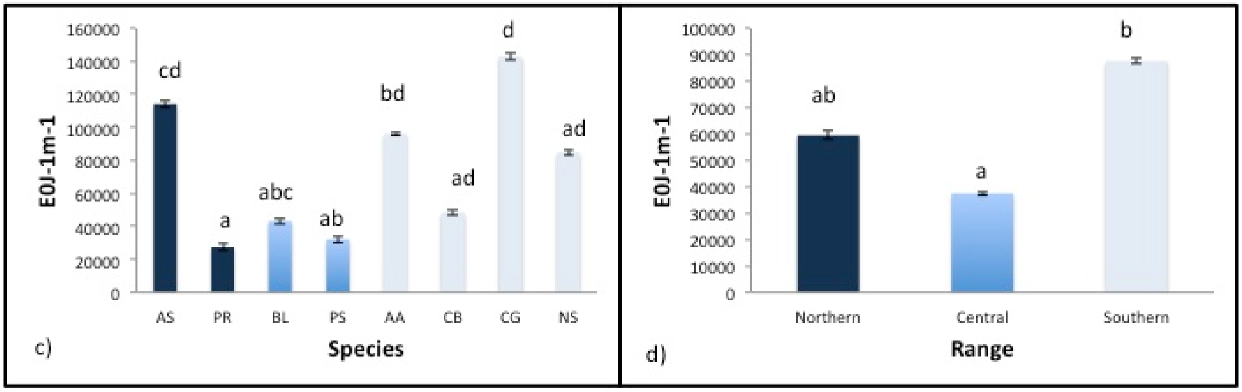


Figure 4. Energy of activation (E0), by species (c) and range (d). Error bars represent one standard error. Means not sharing a common letter are significantly different (p<0.05) by Tukey contrasts. Species abbreviations correspond to species and genus names listed on range maps (figure 2).

Carbon to nitrogen ratio differed significantly between species (p<0.0001) and by range (p<0.05) (Figure 5). Southern-ranged CN ratio (16.8) was significantly lower than northern- and central-ranged CN ratio (34.8 and 27.3 respectively). Specific leaf area (SLA) ratio differed significantly between species (p<0.0001) and by range (p<0.05) (Figure 6). Southern-ranged SLA (21.8) was significantly higher than northern- and central- ranged SLA (9.5 and 7.9 respectively). The log of leaf nitrogen differed significantly by species (p<0.0001) and by range (p<0.05) (Figure 7). Southern-ranged species had back transformed mean leaf nitrogen percent by mass of 2.65% which was significantly higher than the northern mean of 1.29% and the central mean of 1.71%.

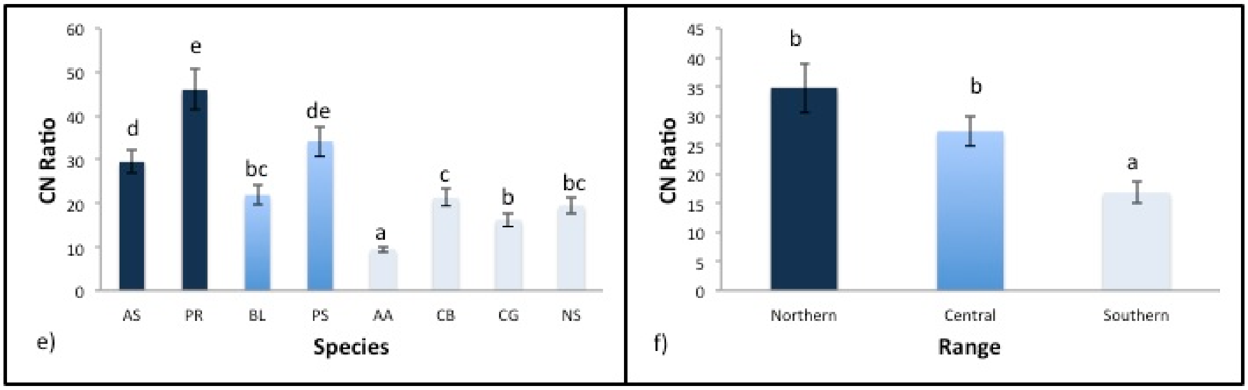


Figure 5. Carbon to nitrogen ratio by species (e) and range (f). Error bars represent one standard error. Means not sharing a common letter are significantly different (p<0.05) by Tukey

contrasts. Species abbreviations correspond to species and genus names listed on range maps (figure 2).

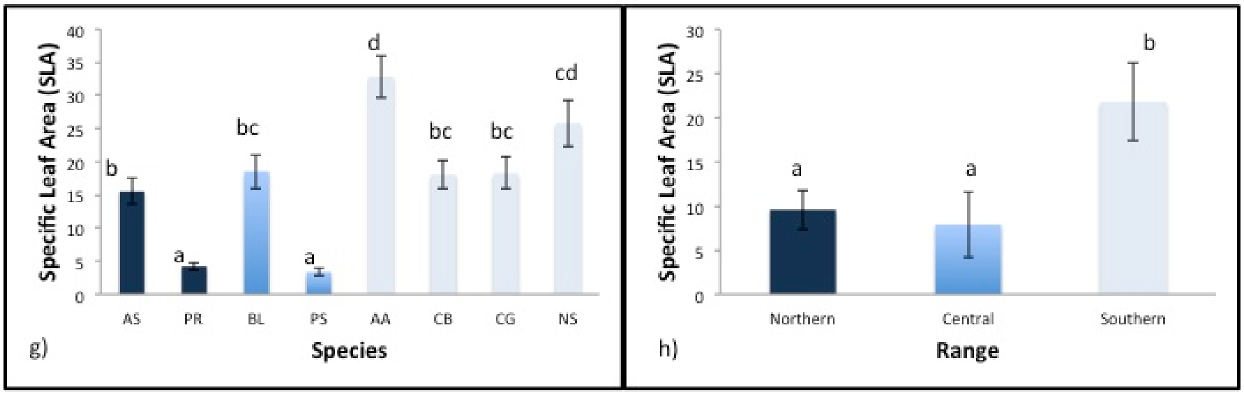


Figure 6. Specific leaf area (SLA) by species (g) and range (h). Error bars represent one standard error. Means not sharing a common letter are significantly different ($p<0.05$) by Tukey contrasts. Species abbreviations correspond to species and genus names listed on range maps (figure 2).

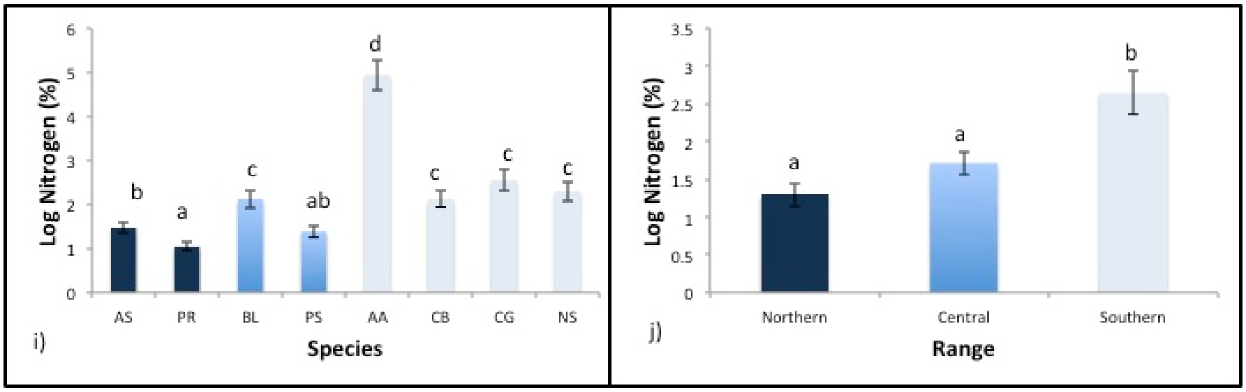


Figure 7. Log of percent nitrogen by species (i) and range (j). Error bars represent one standard error. Means not sharing a common letter are significantly different ($p<0.05$) by Tukey contrasts. Species abbreviations correspond to species and genus names listed on range maps (figure 2).

CN Ratio was significantly negatively correlated with E_0 and positively correlated with R_{20} ($p<0.05$ and $p<0.01$) (Figure 8). A linear trendline was added to the data and the R^2 value was 0.24 and 0.63 respectively. SLA was also significantly positively correlated with E_0 and negatively correlated with R_{20} ($p<0.05$ and $p<0.01$) (Figure 9). A linear trendline was added to the data and the R^2 value was 0.19 and 0.42 respectively. Leaf nitrogen was significantly positively correlated with E_0 ($p<0.05$) and negatively correlated with R_{20} ($p<0.05$) (Figure 10). A linear trendline was added to the data and the R^2 value was 0.12 and 0.24 respectively.

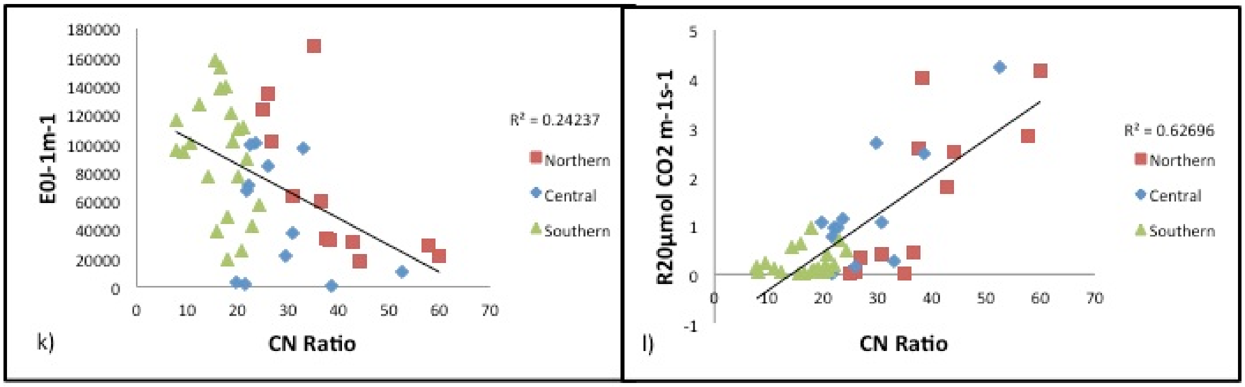


Figure 8. CN Ratio correlation with E0 (k) and R_{20} *(l). A linear trendline is shown with* R^2 *value displayed.*

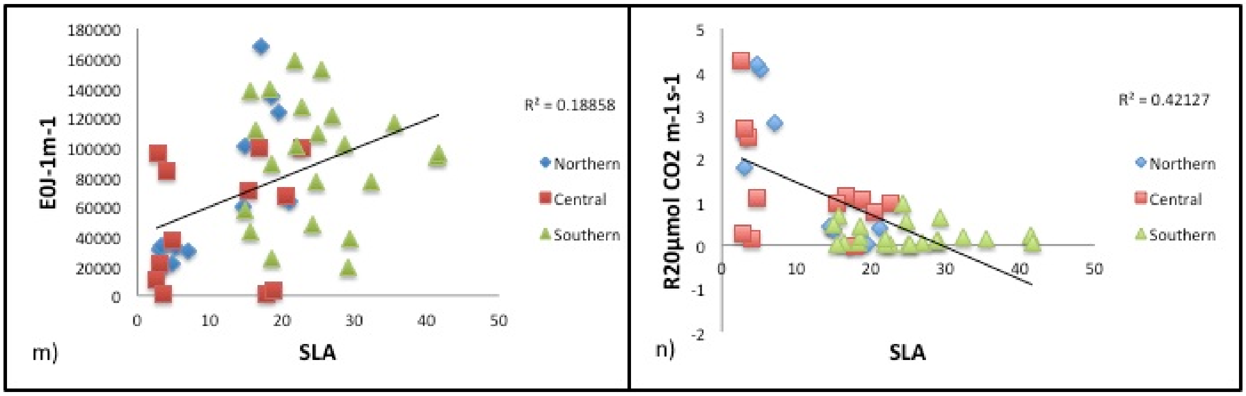


Figure 9. SLA correlation with E0 (m) and R_{20} *(n). A linear trendline is shown with* R^2 *value displayed.*

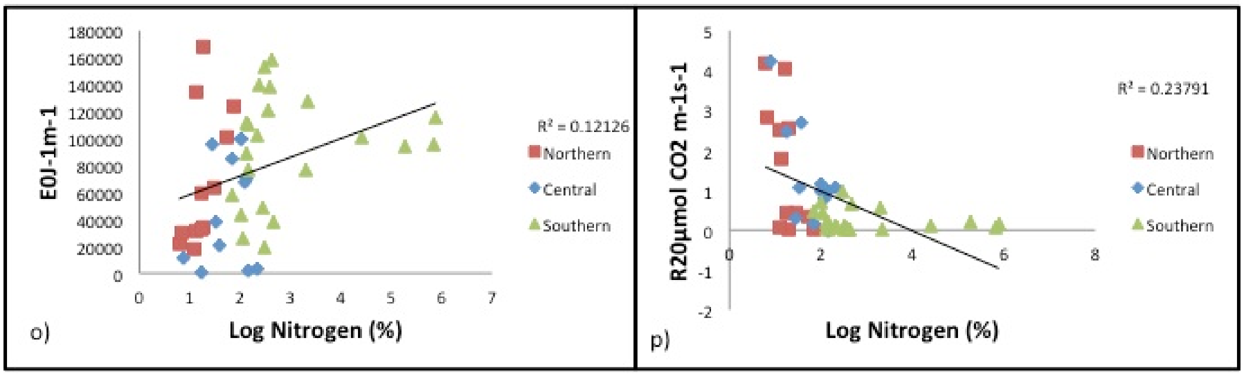


Figure 10. Leaf nitrogen correlation with E0 (o) and R20 *(p). A linear trendline is shown with* R^2 *value displayed.*

The above results may be heavily influenced by the presence of coniferous species in the central and northern groups, which makes up 2 species out of 8 that this study is composed of. The other six species are broadleaf species. *Pinus strobus* and *pinus resinosa* are noted to have the highest rates of respiration and the lowest rates of activation energy (Figure 3 and 4).

Discussion

As hypothesized, the southern-ranged tree species released the least amount of CO_2 at R20. While the southern-ranged R20 was significantly lower, there was not a significant difference between the R20 rates of the centrally- and northern-ranged trees. The significantly higher R20 values for northern- and central-ranged species suggest that more energy is being expended by maintenance respiration in response to the biological stress from trying to adapt to a new climate range due to global warming (Wullschleger S.D., 1992). Because of more energy being allocated for maintenance respiration leaving less energy for growth and competition, northern- and central- ranged species could be at a physiological disadvantage.

The significantly lower R20 values for southern-ranged species could reflect a regulatory change in existing enzymes lowering the energy barrier for the respiration pathway indicating Type I acclimation. However the evidence for Type II acclimation in southern-ranged species makes this explanation unlikely. The significantly higher E_0 for southern-ranged species could potentially be because southern trees are used to warmer environments relative to other ranged trees and thus are acclimating to colder temperatures(L. Rustad, 2001); warm-grown plants acclimating to colder temperatures have shown to be less responsive to temperature and consequently have a larger E0 (Loveys et al., 2002).

Further evidence of Type II acclimation in southern-ranged species comes from the specific leaf area and percent nitrogen results. Specific leaf area is the amount of surface area on a leaf per unit of dry mass and thus a higher SLA value indicates an elevated ability to intercept light. This is important because the leaf is the primary vehicle of photosynthesis and is powered in part by sunlight. It was found that dark respiration positively correlated with both SLA and photosynthesis across both biomes and functional groups (Reich, 1997). Typically a higher value for SLA indicates a higher rate of respiration, not due to stress but due to overall increased metabolic function. A proxy for overall metabolic activity is percent nitrogen due to nitrogen being indicative of more proteins in the leaf which then go on to contribute to metabolic activity.

Southern-ranged species showed the highest rates in both percent nitrogen and SLA. High SLA is typically correlated with high percent nitrogen, which indicates increased metabolic activity as well as more proteins, which then correlates to high respiration due to the cost of maintaining those proteins. However, the correlation between percent nitrogen and respiration accounted for 23% of the variance in a negative direction (high percent nitrogen tended to correlate with low respiration rates), showing the exact opposite trend than what is expected from literature. In addition, while southern-ranged species show the highest rates of percent nitrogen and SLA, they also show the lowest rates of respiration. This can be explained through the different pathways an increase in percent nitrogen can take: an increase in percent nitrogen indicates more protein which in turn increases the amount of substrate available in the leaf not only for respiration but also for photosynthesis. This is because nitrogen is partitioned between both chloroplasts and mitochondria, which are consequently reflected in differences in the rates of photosynthesis and dark respiration (Makino A. & B., 1991). According to Patterson (2013), the southern ranged species had the highest rates of photosynthesis; this data in conjunction with the fact that southern ranged species had the lowest rates of respiration imply that the high level of protein activity (indicated by the significantly high percent nitrogen) is mostly partitioned for photosynthesis, leaving less for metabolic energy for respiration. Thus, significantly higher SLA and percent nitrogen make it more likely that the significantly lower respiration rates were due to biochemical adjustments such as an increase in chloroplast protein, indicating Type II acclimation.

As the leaf traits reflect the geographical origin of the species, range-specific leaf morphology gives further insight in explaining patterns in leaf traits (CN ratio, SLA, and percent nitrogen) and thus, acclimation type as well. As southern ranged species had the highest rate of SLA, they also tend to have the thinnest leaves (the higher the SLA or the higher the ‘leaf area to dry mass ratio’ is, the thinner the leaf is). Thin leaves are less expensive (per unit surface area with potential for light interception) for plants to produce. This is because every cell has the potential to respire at the same rate but not every cell can photosynthesize at the same rate due to light only shining upon the top layer of cells. Thus, thin leaves (higher SLA) are more energetically efficient in comparison to thick leaves (lower SLA) due to the increased ratio of cells with the potential for light interception. This is seen in the correlation between R_{20} and SLA, which accounted for 42% of the variance of R_{20}; southern ranged species clustered on the bottom right of the trendline, demonstrating its Type II acclimation traits in tending to have high SLA and low respiration.

The correlation between respiration and CN Ratio accounted for 63% of the variance of R20. This strong correlation seems to indicate that respiration is controlled by the supply of respiratory substrates (which CN Ratio measures). Thin leaves tend to have low CN Ratio while thick leaves tend to have high CN Ratio. Thus, as expected, the thin leaves of southern ranged species clustered at the lower left part of the trendline, with low CN Ratio and low respiration. These traits were also indicative of Type II acclimation.

Southern leaves have high N, high SLA, and low CN. As mentioned before, as warm-grown plants southern leaves are acclimated to higher temperature and are therefore less responsive to a change in the temperature when it enters colder climates. EO is a quantification of how responsive R is to a change in temperature; therefore we see these relationships among EO and leaf traits: the correlation between activation energy (E0) and CN Ratio, SLA, and log percent nitrogen accounted for 24%, 18%, and 12% of the variance of E0 respectively. Southern species seem to be the most scattered range among the three correlation graphs, demonstrating visually that the southern range is the least responsive to a change in temperature through the wide range of E0 values.

Thus, the range-specific leaf morphology (thin leaves) that provides the physiological backing to significantly high percent nitrogen, high SLA, and low CN Ratio found in southern ranged tree species all suggest a Type II acclimation. Because Type II acclimation suggests increased overall metabolic activity, southern- ranged populations may have an enhanced competitive ability compared to other ranged species, leading to their advance in Black Rock Forest.

Implications

This research allowed us to collect physiological information for many species that have little to no published data. Once analyzed this data will allow us to see how each species will respond to changing temperature and environment, and thus see which species will adapt the best. Due to tree migration and changing species density in forests, the carbon storage capacity will also change. By predicting which species will adapt the best, we can also predict the changing carbon capacity of the forest based on individual carbon capacities of different tree species. Further research on the physiological response across a range of temperatures will help us determine what species can best acclimate, physiologically, to this region's changing climate, how community composition will change, and what the impacts will be on the global carbon cycle under future warmer conditions.

Accurate species distribution models that predict how species will respond to temperature is important so scientists can know which species requires mitigation steps to be taken to prevent extirpation. In addition, shifting species distribution could cause large-scale changes in the amount of CO_2 that the forest respires and cause the forest to become either a carbon sink or source. This would also affect the local lifesystems and species; if the tree population changes then this would most likely have an effect on available resources in the forest, thereby affecting and transforming the animal, fungi, and microbacterial populations as well.

Due to global warming, climate change is likely going to continue to drive change in species composition in Black Rock Forest. Adjusting for warming temperatures, there is a predicted northward shift in tree species ranges over the next century (Morin, 2006). If southern-ranged species are more capable to acclimating to a change in temperature than their northern and central counterparts, than continued climate change could drive the range of southern species northward. If southern- ranged species continue to head north, enabled by their Type II acclimation advantage, northern and central ranged tree species will continue to be under abiotic stress due to competing for depleting resources.

Recommendations

Due to the dearth of published data on these species, significantly more physiological data is needed. This study only samples two or four species from each range, but future studies will need to sample many more to make adequate models that accurately predict species range changes. In particular, additional data on respiratory responses to changing temperatures would help to clarify the physiological differences between different ranged populations, particularly with the southern-ranged species. Also, due to the inherently different leaf morphologies present in coniferous and broadleaf species, it is recommended that the two different leaf type species would not be included in the same study and rather, would be studied separately. This is because coniferous and broadleaf species demonstrate significantly different measurements in leaf traits due to the considerable influence of leaf morphology on physiological processes (Abrams & Kubiske, 1990).

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List of references

Abrams, M. D., & Kubiske, M. E. (1990). Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: Influence of light regime and shade-tolerance rank. *Forest Ecology and Management, 31*(4), 245-253.

Aitken, Sally N., Aitken, Sally N., Yeaman, Sam, Holliday, Jason A., & Wang, Tongli. (2008). Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary applications, 1*(1), 95-111. doi: 10.1111/j.1752-4571.2007.00013.x

Arkebauer, R. (2014). *Respiratory responses to temperature change in broadleaf trees from the northeastern US.* (B.A.), Columbia University, New York, NY.

Atkin, O. K., & Tjoelker, M. G. (2003). Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science, 8*(7), 343-351. doi: Doi 10.1016/S1360-1385(03)00136-5

Atkin, O.K., Bruhn, D., Hurry, V.M., & Tjoelker, M.G. (2005). Evans Review No. 2: The hot and the cold: unravelling the variable response of plant respiration to temperature. *Functional Plant Biology, 32*(2), 87-105. doi: http://dx.doi.org/10.1071/FP03176

Bunce, J. A. (2007). Direct and acclimatory responses of dark respiration and translocation to temperature. *Annals of Botany, 100*(1), 67-73. doi: Doi 10.1093/Aob/Mcm071

Chuine, I., Belmonte, J., & Mignot, A. (2000). A modelling analysis of the genetic variation of phenology between tree populations. *Journal of Ecology, 88*(4), 561-570. doi: Doi 10.1046/J.1365-2745.2000.00468.X

Corlett, R. (2008). Plant Mobility and Climate Change. *Faculty of Science research* , 1-2.

Friedlingstein, P., & Prentice, I. C. (2010). Carbon-climate feedbacks: a review of model and observation based estimates. *Current Opinion in Environmental Sustainability, 2*(4), 251-257. doi: Doi 10.1016/J.Cosust.2010.06.002

Frumhoff, P. C., Mccarthy, J. J., Melillo, J. M., Moser, S. C., & Wuebbles, D. J. . (2007). Confronting Climate Change in the U.S. Northeast: Science, Impacts, and Solutions. *Synthesis report of the Northeast Climate Impacts Assessment (NECIA).*

Heimann, M., & Reichstein, M. (2008). Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature, 451*(7176), 289-292. doi: Doi 10.1038/Nature06591

Houghton, R. A. (2007). Balancing the global carbon budget. *Annual Review of Earth and Planetary Sciences, 35*, 313-347. doi: Doi 10.1146/Annurev.Earth.35.031306.140057

Kruse, J. J. (2008). Three parameters comprehensively describe the temperature response of respiratory oxygen reduction. . *Plant, cell & environment, 31*(7), 954-967.

L. Rustad, J. Campbell, G. Marion, R. Norby, M. Mitchell, A. Hartley, J. Cornelissen, J. Gurevitch,. (2001). A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia, 126*(4), 543-562.

Loveys, B. R., Scheurwater, I., Pons, T. L., Fitter, A. H., & Atkin, O. K. (2002). Growth temperature influences the underlying components of relative growth rate: an investigation using inherently fast- and slow-growing plant species. *Plant Cell and Environment, 25*(8), 975-987. doi: Doi 10.1046/J.1365-3040.2002.00879.X

Maenza-Gmelch, T. E. (1997). Vegetation, climate, and fire during the late-glacial–Holocene transition at Spruce Pond, Hudson Highlands, southeastern New York, USA. *Journal of Quaternary Science, 12*(1), 15-24.

Makino A., & B., Osmond. (1991). Effects of Nitrogen Nutrition on Nitrogen Partitioning between Chloroplasts and Mitochondria in Pea and Wheat. *Plant Physiology, 96*(2), 355-362.

Midgley, G. F., Thuiller, W., & Higgins, S. I. . (2007). *Chapter 11: Plant Species Migration as a Key Uncertainty in Predicting Future Impacts of Climate Change on Ecosystems : Progress and Challenges*. Berlin, Heidelberg, New York.

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), 185-195.

Pachauri, R. K. (2007). Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. 104.

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*(1), 160-171.

Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography, 12*(5), 361-371. doi: Doi 10.1046/J.1466-822x.2003.00042.X

Raich JW, Schlesinger WH. (1992). The global carbon-dioxide flux in soil respiration and its relationship to vegetation and climate. *Chem. Phys Meteor, 44*, 81-99.

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.

Ryan, M. G. (1991). Effects of Climate Change on Plant Respiration. *Ecological Applications, 1*(2), 157-167. doi: Doi 10.2307/1941808

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), 537-549.

Tjoelker, M. G., Oleksyn, J., Lorenc-Plucinska, G., & Reich, P. B. (2009). Acclimation of respiratory temperature responses in northern and southern populations of Pinus banksiana. *New Phytologist, 181*(1), 218-229. doi: Doi 10.1111/J.1469-8137.2008.02624.X

Will, R. (2000). Effect of different daytime and night-time temperature regimes on the foliar respiration of Pinus taeda: predicting the effect of variable temperature on acclimation. *Journal of Experimental Botany, 51*(351), 1733-1739. doi: Doi 10.1093/Jexbot/51.351.1733

Woodall, C. W., Oswalt, C. M., Westfall, J. A., Perry, C. H., Nelson, M. D., & Finley, A. O. (2010). Selecting tree species for testing climate change migration hypotheses using forest inventory data. *Forest Ecology and Management, 259*(4), 778-785. doi: Doi 10.1016/J.Foreco.2009.07.022

Wullschleger S.D., Norby R.J., Gunderson C.A. (1992). Growth and maintenance respiration in leaves of Liriodendron tulipifera L. exposed to long-term carbon dioxide enrichment in the field. *New Phytologist, 121*(4), 515-523.