Warming Climates, Changing Forests: Temperature Tolerances of Trees and Carbon Dynamics in Northeastern Temperate Forests

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Abstract

Extensive botanical surveys and long term plots have shown that since the early 1930's, Black Rock Forest, located in the Hudson Highlands of New York, three tree species were extirpated and seven were gained. These results are consistent with a warming climate and suggest the Hudson River Valley may be an important location to study the effects of climate change on Northeastern forests. Classic global vegetation and species distribution models primarily use species presence/absence or presence only distribution with preferred environmental parameters to predict range distributions of plant communities under increasing CO2 regimes, and thus climate warming. Although these models have begun to incorporate physiological data (photosynthesis, stomatal response, and respiration), they lack a sophisticated parameterization of species-specific physiological characteristics and complex interactions within plant communities. More experimentation is necessary to validate assumptions regarding the mechanisms behind tree species responses to climate change and narrow the variability of model outputs. During the summer of 2012, I explored the physiological mechanisms for species tolerance to increasing temperatures and considered the potential effects on the carbon storage capacity of forest trees under the predicted warmer climates of the coming century.

Author's Note

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1. Plant Responses to Climate Change

Climate change forecasts predict global surface air temperature increases of $2.0 - 5.4^{\circ}$ C over the next century (Pachauri, 2007). In the Northeast U.S., temperatures have already increased by 0.8° C in the last 30 years (Frumhoff et al. 2007). Temperatures of this magnitude may seem subtle, but the effect has made an impact on our ecosystems and its inhabitants. Historical records in Northern Europe, dated as early as the 1700's, have documented migrations and range expansions for plant, insect, and bird species. For example, butterflies in England have been seen to move northward in warmer summers that have succeeded mild winters (Ford, 1945; Parmesan, 2006). Unfortunately for plants, responses to increasing air temperatures are not as simple, as they are sessile organisms, relying on seed dispersal to migrate to areas of climatic tolerance and successful establishment and reproduction for a thriving population.

Plant communities' response to the predicted increases in air temperature will be observed through changes in geographic distribution (Aitken et al., 2008; Corlett, 2008; Loarie et al., 2009)), persistence at current range *via* local adaptation (Aitken et al., 2008), or extirpation (i.e. local extinction) (Aitken et al., 2008; Corlett, 2008). Several studies have observed significant movement of tree-lines to high-altitude regions as well as increases in tree density in higher elevations over time (Aitken et al., 2008; Danby & Hik, 2007a, 2007b; Millar et al. 2004). The advantage of living on high slopes includes a slower rate of migration necessary to displace oneself to track temperature tolerances. Unfortunately, plants on low slopes require higher rates of migration where large displacements are necessary to track climate change (Loarie et al., 2009).

Global vegetation models (GV) and species distribution models (SDMs) have shown that 1 km y⁻¹ migration rates for plants may be necessary in regions of rapid climate change (Aitken et al., 2008). However, fossil records and molecular evidence show that tree species may be moving slower than what current models predict (Pearson, 2006). Research indicates that the species tolerance will be critical in determining whether a tree will be able survive given the rate of regional warming. The tolerance of a species to extreme climate conditions is a measure of the persistence of a species and their ability to locally adapt to a changed environment (Midgley, Thuiller, & Higgins, 2007). Persistence is particularly important for species that lie on the "rear edge" of their geographic range, where their persistence is necessary to maintain genetic diversity and promote the evolution of their species (Hampe & Petit, 2005). Species at the margins of their migratory range are under high abiotic stress, such as interspecific competition due to low relative fecundity and population density (Aitken et al., 2008). Unfortunately, if plants have low tolerances to increasing temperatures, they will not be able to adapt fast enough to the low residence time of the current climate, thereby risking lower fitness and possible extinction (Loarie et al., 2009). However, species with high tolerances can acclimate via physiological processes or exhibit inherent life history traits that allow them to persist under changing climate conditions. Further study on species tolerances is critical in forecasting plant community shifts where the implications may result in tree species survival and persistence or extirpation.

2. Regional Climate Effects on Plant Communities

Regional climate effects on natural communities has not only affected species distribution directly, but has been linked with increased forest disturbance (e.g. fires and disease) impacting future forest composition (Pachauri, 2007). In a previous review article, Schuster et al. (2008) summarized changes in forest composition at Black Rock Forest (BRF) over a seventy-six year time period. They found that three tree species were extirpated. One of these species, the American elm (Ulmus americana L.), was once dominant in northeastern U.S. forests but declined in numbers due to Dutch elm disease (Ophiostoma ulmi (Buism.) Nannf.). Introduced to North America from the Netherlands and spread by the native elm bark beetle (Hylurgopinus rulipes Eich.; (Gibbs, 1981; Schuster et al., 2008)), Dutch elm disease nearly eradicated the BRF American elm population after 1949. Accounts of paper birch (betula papyrifera Marsh.), a northern-ranged tree species whose southern margin occurs at BRF, were rare in the 1930's, with only one individual documented in 2003. Black spruce (Picea mariana (Mill.) B.S.P.), a northern-ranged conifer once located in high-elevation wetlands failed to reproduce and survive and was last documented as present in the forest in 1949 (Schuster et al., 2008). These extirpated species provide evidence to the direct and indirect effects of climate change that will continue to have profound impacts on plant community composition.

There is no doubt that compositional changes have occurred at BRF over the past seventy-six years. However, these changes are not anything new. Paleoecological records from sediment cores at BRF's Sutherland Pond have collected thousands of years of vegetation profiles. Sediment cores are cylinders of compacted soil and mud that have preserved fallen pollen grains, seeds, conifer needles, and charcoal. These macrofossils fall to the bottom of lakes or ponds, accumulate, and are covered with soil deposits over time creating a series of layers that correspond with a certain period in the surrounding environment's history. Sediment cores collected at BRF date as far back as the Younger Dryas, a "cold snap," which occurred approximately 11,600 - 13,000 years before present (ypb) (Maenza-Gmelch, 1997a, 1997b, 1997c; Peteet, 2000). The earliest pollen records show a dominance in herbaceous and shrub species, indicating a tundra-like climate (Maenza-Gmelch, 1995; Peteet, 2000). Around 12,500 ybp increases in pollen influx and organic deposition suggest a climactic warming period in which a "mixed boreal coniferous-temperate deciduous woodland" dominated the forest (Maenza-Gmelch, 1995). The warming period was succeeded by the Younger Dryas cold snap, which lasted over 1500 years and featured spruce, fir, and alder as the dominating tree species. The transition from the Younger Dryas to the Holocene occurred over 50-70 years with average July temperatures increasing 3-4°C (Peteet, 2000) provoking the establishment and the expansion of tree species that make up our current northern hardwood-conifer forests.

Although we continue to observe plant community shifts several thousand years later, accelerated increases in air temperature and short residence times of local or regional climates have narrowed the opportunity for plants to track ecological niches (Aitken et al., 2008; Iverson, Schwartz, & Prasad, 2004; Loarie et al., 2009). The extirpation of three tree species at BRF has been succeeded with the establishment of eleven tree species, which have either been planted (*Acer saccharum*

Marsh.), migrated naturally, or been introduced anthropogenically over the past thirty years (eight of the eleven species shown in Table 1). The majority of these introduced species have a southern-range distribution in which BRF lies at their northern margin. The remainders are non-native to North America and are regarded as invasive in their habit (tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle), and white poplar (*Populus alba* L.)) (Schuster et al., 2008). Mitigated through climate change, the migration of southern tree species and persistence of those that were introduced *via* planting have been deemed successful at changing the forest species richness, bringing about larger implications for regional and global cycles.

3. Plant Community Shifts and Forest Carbon Storage

Currently, the Hudson Highland's region has a high dominance of oak species, which are known to sequester large amounts of carbon (Schuster et al., 2008) in a region known to be one of the largest aboveground terrestrial carbon pools in the world (Pederson, 2004). However, various factors, such as insect outbreaks, severe droughts, and extensive forest clearings in the surrounding Hudson Highlands region have resulted in the mortality of dominant tree species and have controlled the long-term biomass and carbon dynamics of BRF since the late 1940's (Schuster et al., 2008). One of the most influential factors influencing the sequestration of carbon at BRF involves shifts in tree species composition. Oak species have inherent physiological and physical traits that contribute to their long-term persistence in northeast U.S. forests. However, declining oak recruitment (due to increased deer browsing and competition) and periodic landscape disturbances threaten the forest's carbon storage potential. Introduced or migrant tree species that are successful at establishment and reproduction as a product of climate change may negatively influence carbon storage capacity changing the forest into a source of carbon dioxide perpetuating warmer atmospheric temperatures. In addition, the replacement of both young and mature oaks with migrant or introduced species could reduce the set of important ecosystem services oak-dominated forests provide (Schuster et al., 2008). Researching the physiological capacities of trees under a warming climate, interspecific competition of species and tolerance to environmental disturbance is crucial in our understanding of how these factors will affect forest composition and forest carbon storage.

This summer, I studied the physiological response to increasing temperature of tree species (i.e. species tolerances) that have northern or southern range limits distributed across the Hudson Highlands region of the northeastern United States. Through quantitative observational and experimental tests, this research seeks a better understanding of what species will be best able to physiologically acclimate to the region's changing climate, how plant community composition is likely to change, and what the impact of these changes could be on the global carbon cycle under future warmer conditions.

4. Black Rock Forest Study Site

This study was conducted at the Black Rock Forest, a 1,550 ha preserve located in the Hudson Highlands Region of southeastern New York State. The

forest encompasses a mixed hardwood forest with a canopy comprised of about 67% oak and 33% non-oaks (Schuster et al. 2008). Red oak (*Quercus rubra* L.) and chestnut oak (*Quercus prinus* L.) dominate the canopy, while the understory is dominated by red maple (*Acer rubrum* L.). Sugar maple (*Acer saccharum* Marsh.), black birch (*Betula lenta* L.), and yellow birch (*Betula alleghaniensis* Britt.) make up a significant composition of the forest as well. 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 (NOAA, 2000).

BRF is the site of extensive long-term research with data on species replacements over the last 80 years. First colonized by English settlers in 1700, the forest has been repeatedly logged with some portions converted to agriculture and pastureland until it was abandoned around 1900. In 1928, the forest became a research forest, and in 1989 BRF was bought from Harvard and established as part of a consortium of local educational and research institutions (Schuster et al., 2008). Columbia University's membership as part of the BRF Consortium made our research possible during the summer of 2012.

5. Data Collection

Researchers and BRF staff collected canopy leaves from six replicate mature trees from ten species that were categorized into four groups (Southern-ranged, Northern-ranged, Centrally-ranged, and Newly Introduced; Table 1). A pole pruner or line saw are common and inexpensive tools used to retrieve branch samples. However, canopy heights in mature forests reach well over 100 ft., requiring unconventional methods for the acquisition of intact tree branches. Scientists sometimes use industrial equipment such as cherry-pickers as a lift to reach high branches. In extreme cases, scaffolding may be installed for long term projects. Unfortunately, these methods are often consuming and expensive. One method that is commonly employed is the "Shot-gun" method, where a shot-gun is used to sever branches off canopy trees that are inaccessible with the use of traditional tools. Although the method requires a few hours of safety training and target practice, the method can be efficient and moderately inexpensive.

The use of a 12-gauge semi-automatic shotgun (TriStar Sporting Arms, LTD., Missouri, USA) was implemented 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. Leaf porosity, a measure of leaf conductance to water vapor (used to infer more general environmental response of gas exchange including CO_2 uptake) was recorded (Image 2). Plants were then tagged with their appropriate labels and brought back to the lab for processing.

Southern-ranged species	Northern-ranged species
Angiosperms Quercus velutina Carya glabra Carya ovata Liriodendron tulipifera Nyssa sylvatica Platanus occidentalis Gymnosperm Pinus rigida	Angiosperms Acer saccharum Gymnosperms Picea glauca Larix laricina Pinus resinosa
Newly Introduced ca. 1930	Centrally-ranged species
Angiosperms Catalpa bignonioides Ailanthus altissima Populus abla Crataegus crus-galli Morus rubra Populus deltoides Ulmus rubra	Angiosperms Betula lenta Quercus rubra Quercus prinus Gymnosperm Pinus strobus

Table 1. Temperate tree species that naturally occur at the BlackRock Forest, Cornwall, NY. Species ranges categorized by thenative ranges specified in the USDA Forest Service Sylvics Manuals(http://www.na.fs.fed.us).



Image 1. The shotgun method is employed to retrieve canopy tree branches.



Image 2. Porosity measurements were conducted in the field.



Image 3. Photosynthetic measurements were made using the Licor[®] 6400.

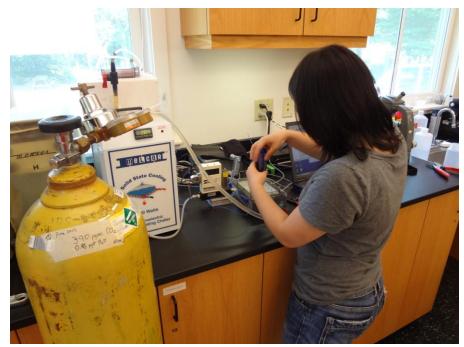


Image 4. Leaf respiration measurements were conducted on a leaf from each branch sampled.

In the lab, fully expanded leaves were chosen for measurement and allowed to acclimate to room temperature prior to the first measurement. Six leaves were then sampled off the main branch, freshly weighed, and run through a leaf area meter used to acquire the leaf area (cm²). A healthy leaf (still attached to the main branch) was selected and inserted into a portable photosynthesis machine (Licor[®], Nebraska USA) to measure net photosynthetic rates at three temperatures (16, 23 (ambient), and 29°C) over eleven CO₂ levels (1000, 740, 650, 550, 450, 350, 250, 150, 75, 50, 25 µmol) (Image 3). Once data were collected, the leaf's area (cm²) and weight (mg) were recorded.

Concurrently, one leaf from the six previously sampled leaves was placed in the cuvette of a respiratory system where CO_2 expelled from the leaf was continually measured as the temperature inside the respiratory system increased from 5 to 35°C (Image 4). The leaf used in the Licor[®] as well as the remaining five leaves removed from the main branch were placed into separate coin envelopes and dried in an oven at 60°C for two days. Leaves that were dried in the oven were ground into powder using a ball mill, which is a cylindrical device used to grind or mix materials (SPEX 8000 Mixer/Mill[®], New Jersey, USA). Two to four milligrams of dried leaf powder were then placed into tin capsules where they were then run through a carbonnitrogen flash analyzer (CE Elantech, New Jersey, USA) to acquire carbon and nitrogen grams per unit of leaf tissue.

Preliminary data exploration has revealed interesting patterns related to physiological capabilities of migrating plant populations. Further statistical analysis performed over the next several months will test whether net photosynthetic and respiratory rates are species specific and if native/historic species ranges dictate physiological ability to acclimate to increasing temperatures.

6. Future Research Plans and Conclusions

Future experiments that are conducted under laboratory conditions will be necessary to determine baseline measurements of tree physiological capabilities in a controlled environment without competitors. Our lab proposes to study trees seedlings, which are earlier in their life stage than the mature trees sampled in our field study. Our aim is to test whether seedling growth temperatures dictate physiological ability to acclimate to increasing temperatures (assess local adaptation potential for each species). Seedlings will not be considered physiologically identical to mature trees or indicative of mature tree response, but rather will provide information related to how physiological capacity may influence forest regeneration and species migration as affected by temperature. The parallel field and lab study presented and proposed will quantify tree species that have little to no published data. The data collected from this research will enable us to rank/categorize species best able to acclimate to rising temperatures, forecast community composition using SDMs, and evaluate carbon storage potential under various temperature scenarios.

Continued study on thermal tolerances and acclimation potential of plant species to increasing temperatures is critical for assessing which species will flourish under projected environmental conditions and which species may struggle to adapt if migration to preferred niches is failed. Future research will enable scientists and policy makers to identify regions most affected by climate change and designate protected areas large enough to contain moving climates (Loarie et al., 2009). Slowing climate change through reduced emissions is the optimal way to ensure plants are able to migrate to suitable environments (Huntley, 1991). However, assisted migration or recolonization efforts may be necessary to prevent local extinction of some plant species (Huntley, 1991). Given the rapid pace of moving climates, ex situ conservation programs, such as The Millenium Seed Bank Project, an international conservation project coordinated by the Kew Royal Botanic Gardens, have been instituted to collect and cryopreserve seeds from around the world (Kew Royal Botanic Gardens, 1996). As scientists fill gaps in the current understanding of plant responses to climate change, policy makers will be better equipped to employ innovative conservation strategies that will increase the likelihood of plant survival and maintain compositional and functional diversity in plant communities around the world.

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