

Sugar maple (*Acer saccharum* Marsh.) provenances differ with climate of origin in survival, growth, and traits along a climate gradient: implications for the species' distribution under climate change

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DEDICATION

To all the teachers in my life, from whom I have learned so much.

ABSTRACT

Plant ranges, broadly constrained by climate, may be further shaped by interspecific interactions and intraspecific variation in growth and traits. Changing climate and species composition in plant communities lends urgency to the need to better define the factors determining species' distributions. This research seeks to determine the effects of temperature and neighbors on sugar maple (*Acer saccharum*) seedling survival, growth, biomass allocation, and functional traits, and whether this response varies with populations' climate of origin. I first examine survival and growth of forest-planted seedlings across a natural climate gradient and beyond range limits to determine whether populations' climate of origin and contrasting neighbor density and light environments affect performance. I find no evidence of climate or competition limitation beyond range margins for populations grown near their region of origin, but populations differ in survival and net growth in a manner consistent with local adaptation and contrasting growth strategies: the northern population has high survival across sites but lower mass than the southern population, which has low survival and growth facilitated by neighbors at northern sites. I then examine whether patterns of root biomass allocation of these same seedlings is affected by climate of the planting site or each populations' region of origin. I find higher root mass in southern population seedlings than in similarly sized northern population seedlings, and higher root mass fraction at colder sites in the southern (but not northern) population. Finally, I use growth chambers to examine the effects of temperature and light on growth rate and traits for three climatically distinct populations. Growth rate declines with increasing latitude of origin and is lower in the temperature treatment corresponding to the climate of origin for the southern population. High-latitude populations have low SLA and LMF, but populations do not differ in photosynthetic rates. In conclusion, I find potentially adaptive differences in populations' growth, survival, and plant traits but no direct evidence of climate or competition limitation across the range. This study highlights intraspecific variation in growth and traits, its relevance at range limits, and the need to identify whether reproductive or phenological traits also vary within species.

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INTRODUCTION

Plant species are distributed across the landscape in characteristic patterns and assemblages, and a central focus of ecology is the study of the factors determining these patterns of distribution. A species' range is a reflection of its realized niche (*sensu* Hutchinson 1957), and encompasses those abiotic conditions and biotic communities in which it can survive, grow, and reproduce. The relative contribution of biotic and abiotic factors in limiting species' ranges, however, remains an unresolved question in ecology (Gaston 2009, Sexton *et al.* 2009, Cahill *et al.* 2014).

Ranges are dynamic, and the study of the factors that limit plant ranges acquires both complexity and urgency in the face of multiple stressors such as climate change, habitat loss, and invasive species. Woody species are already shifting ranges in response to changing climate (Walther *et al.* 2005, Woodall *et al.* 2009, Boisvert-Marsh *et al.* 2014), and because species are likely to differ in their response to warming, community composition may shift as well (Shi *et al.* 2015). Furthermore, many forest ecosystems are facing increasing pressure from a host of non-native species, further altering community dynamics (Fisichelli *et al.* 2014). Species are therefore likely to face changes in both the abiotic and biotic conditions in their current distributions, and it is imperative that we better understand the factors currently maintaining range limits.

Temperature has long been recognized as a primary factor defining the range of many plant species (Salisbury 1926, Grace 1987, Woodward 1987), and the geographic extent of a species' range tends to correlate closely with climate and the species' cold tolerance (Nogués-Bravo *et al.* 2014). Low temperatures may cause mortality directly (Grace 1987, Kollas *et al.* 2014) or limit reproduction (Woodward 1990, Asselin *et al.* 2003). Temperature gradients are highly correlated with plant ranges and have been used to map range changes in prior and current episodes of climate change (*e.g.* Davis & Shaw 2001, Williams *et al.* 2004, Thuiller *et al.* 2005, McKenney *et al.* 2011). Interactions with other species also likely play a role, however, as models improve when biotic factors are added (*e.g.* Meier *et al.* 2010, Svenning *et al.* 2014), and there is evidence that species interactions can affect distributions, especially at warm-edge range margins (Bullock *et al.* 2000, Cleavitt 2004).

Range margins are a critical place to understand the dynamics of range limitation. Beyond-range transfers are a powerful tool to determine what factors may be limiting a species (*e.g.* Geber & Eckhart 2005), as we can experimentally evaluate whether there is a climate threshold beyond which survival or growth is non-sustaining, or whether the species may survive and grow beyond the range in a modified competitive environment. Species may also be locally adapted to conditions near range margins (*e.g.* McCarragher *et al.* 2011, Porter *et al.* 2013, Kreyling *et al.* 2014), and such differentiation could be critical in the species' ability to respond to climate change or other stressors that might affect the range (Oney *et al.* 2013). Therefore, any assessment of performance at range margins should compare populations from different portions of the range.

Despite the central importance of species' distribution to the field of ecology, the extent to which biotic interactions affects species' ranges remains unclear (Cahill *et al.* 2014), and there have been surprisingly few experimental studies across the range and beyond range margins (Hargreaves *et al.* 2014). Studies that examine response to environmental gradients in multiple populations are also needed (Sexton *et al.* 2009).

In my dissertation research, I seek to address the fundamental question in ecology of how climate and competition may affect a species' range. In Chapter 1, I examine growth and survival of three populations of sugar maple seedlings experimentally planted across and beyond range margins, and compare the effects of climate (differences in growth across sites) and competition (differences within and across sites between plots where understory vegetation was undisturbed or experimentally reduced). In Chapter 2, I examine patterns of root biomass allocation in these same seedlings across the climate gradient to see whether differences in growth are reflected in differing strategies of biomass allocation. In Chapter 3, I use a growth chamber experiment to compare traits and growth among three sugar maple populations under different temperature and light environments to see whether there are climate-of-origin patterns in trait response to temperature. The factors influencing plant ranges are complex, and while I do not address all potential aspects of range limitation, I do offer some insights into processes across and beyond range margins and highlight important areas for further research.

Chapter 1

Understanding range limits: effects of climate and biotic interactions on growth and survival of sugar maple (*Acer saccharum* Marsh.) along a north-south gradient

SUMMARY

Plant distributions are broadly shaped by climate, but instances where plants expand into new habitat in the absence of competitors suggest interactions with other species may also play a role in constraining ranges. The degree to which biotic factors affect range limits is unclear, however, and experimental studies that examine both biotic and abiotic factors across and beyond a species' range are needed. I examine survival and net growth in three populations of sugar maple seedlings representing a climate-of-origin gradient, experimentally planted along a north-south transect at forested sites across and beyond the species' range, grown in contrasting light and neighbor density environments. I hypothesize that sugar maple survival and net growth are constrained primarily by cold temperatures in the north and competition in the south, and expect each population's highest survival and growth to occur in its region of origin. I expect higher survival and net growth in canopy gaps than in shade, and relative to seedlings grown in undisturbed vegetation, I expect enhanced seedling survival and net growth at the southern range margin and reduced survival and net growth at the northern range margin in plots where aboveground vegetation is clipped. I find that while survival and net growth increase overall at warmer sites, survival and net growth of the locally adapted northern population at beyond-range northern sites is not reduced and is comparable to that population's performance at warmer sites. Populations differ in survival and net growth in a manner consistent with local adaptation and contrasting growth strategies: the northern population has high survival across sites but low height growth, while the southern population has greater height growth across sites but survives poorly in the north, where seedling mass is higher with neighbors. Since this study does not find beyond-range declines in survival and growth, it does not resolve the question of the relative importance of climate and competition in maintaining range limits. While warmer temperatures at beyond-range southern sites do not limit survival and net growth in the three years of this experiment, however, greater climate unpredictability could lead to changes in phenology, reproductive success, and competitive dynamics, each of which may affect the extent and location of range boundaries.

INTRODUCTION

Shifts in species distribution and changes in community composition are among the likely effects of global climate change on forest ecosystems as species respond to changes in climate through altered phenology, growth, and survival. The distributions of many plants, including woody species, are already shifting in response to changes in climate (Kullman 2002, Parmesan & Yohe 2003, Walther *et al.* 2005, Woodall *et al.* 2009, Boisvert-Marsh *et al.* 2014), and determining current range constraints is therefore critical to better predict and understand the implications of future range shifts. Ranges reflect a species' realized niche space (*sensu* Hutchinson 1957), shaped by species-specific climate tolerance and interactions with other species. The degree to which biotic factors interact with climate to shape range limits, however, remains an important unresolved question in ecology (Gaston 2009, Sexton *et al.* 2009, Cahill *et al.* 2014).

Plant range limits closely parallel broad temperature and precipitation gradients (Salisbury 1926, Grace 1987, Woodward 1987, Randin *et al.* 2013), and climate variables are therefore frequently used to approximate species' distributions (*e.g.* Pither 2003, Morin *et al.* 2007). The widely documented range shifts associated with Quaternary climate change (Davis & Shaw 2001, Williams *et al.* 2004) have led to the development of some exclusively climate-based models to predict species' distributions in response to anticipated warming (*e.g.* Walker *et al.* 2002, Thuiller *et al.* 2005, McKenney *et al.* 2011). Projected range shifts and expansion rate estimates are improved, however, when biotic factors are included as well (Araújo & Luoto 2007, Caplat *et al.* 2008, Meier *et al.* 2010, Svenning *et al.* 2014), suggesting that biotic factors may play an important role at range limits.

Greater species diversity and a more moderate climate nearer the equator led MacArthur (1972) to suggest that species' ranges are limited at high latitudes by climate and at lower latitudes by competition with other species. A trade-off between cold hardiness and growth rate has been hypothesized to constrain range limits (MacArthur 1972, Woodward & Pigott 1975, Loehle 1998, Aitken & Hannerz 2001, Koehler *et al.* 2012, Molina-Montenegro *et al.* 2012), but experimental and theoretical work has been insufficient to conclusively support or reject this hypothesis. Theory does suggest that

competition can lead to evolutionarily stable range limits across gradual environmental gradients when evolution and environmental heterogeneity are both included in models (Case & Taper 2000, Price & Kirkpatrick 2009). Few experimental studies, however, have explicitly examined both biotic and abiotic range-limiting factors across a full transect of the range (Parmesan *et al.* 2005, Sexton *et al.* 2009, Hargreaves *et al.* 2014).

Climate at high latitudes and altitudes may impose physiological constraints that shape range limits (Kreyling *et al.* 2015). Climate directly influences plant distributions through patterns of precipitation (Munson 2013) and temperature-dependent effects on plant survival and reproduction (Salisbury 1926, Grace 1987, Woodward 1987). Low temperature extremes may cause mortality through frost damage of stems and buds, especially if frost occurs during a phenologically vulnerable window such as bud-break (Inouye 2000, Augspurger 2009, Kollas *et al.* 2014). Experimental evidence for both herbaceous and woody plants suggests that species also have minimum low temperatures below which they cannot produce flowers or fertilize ovules (Woodward 1990, Asselin *et al.* 2003). Climate may also have indirect effects on range limits through temperature-mediated reduction in growth that places a species at a competitive disadvantage relative to other species (Fisichelli *et al.* 2012).

Competition, rather than climate, has been proposed as a primary range-limiting factor at low latitudes and altitudes (Dobzhansky 1950, MacArthur 1972, Kaufman 1995), given the strong pattern of increasing diversity across taxa toward the equator (Hillebrand 2004). Theory predicts competition for limiting resources is an important driver of variation in plant community structure and composition across environmental gradients (Tilman 1988), and under moderate climate conditions, range limits in species-rich communities may therefore be shaped by competition (Richardson & Bond 1991). Anecdotal evidence of competition's role at range boundaries can be found in the many species able to survive and grow in climates warmer than their equatorial range limits (Loehle 1998, Vetaas 2002) and exotic species that exceed their home-range climate envelope in island settings where competing species are fewer (Sax 2001). Experimental evidence of biotic constraints on warm-edge range margins can be found in competitive interactions for both animals (*e.g.* Gross & Price 2000, Cunningham *et al.* 2009) and

plants (e.g. Bullock *et al.* 2000, Cleavitt 2004) as well as plant-pollinator mutualisms (e.g. Moeller *et al.* 2012), though a review of warm-edge range limit studies found more support for abiotic than biotic limiting factors (Cahill *et al.* 2014).

Species' distributions may also be shaped by positive interspecific dynamics, either mutualistic or facilitative, that mitigate stressful abiotic conditions and thereby extend the realized niche (Bruno *et al.* 2003, Brooker *et al.* 2008). Fungal endophytes, for instance, allow a host grass to grow in drier regions than it would otherwise be able to occupy (Afkhami *et al.* 2014), while nurse trees at tree line facilitate the successful establishment of seedlings (Maher *et al.* 2005, Stueve *et al.* 2011). Neighboring vegetation may have a facilitative effect on seedling growth and survival by ameliorating effects of fall and spring frosts when seedlings are most vulnerable to cold damage (see Wipf *et al.* 2006), especially at northern range limits (Germino *et al.* 2002). Alternatively, surrounding vegetation could facilitate survival by ameliorating drought stress, as was found in a study of sugar maple in a variety of upland environments (Berkowitz *et al.* 1995). A study in Spain found support for both mechanisms: deciduous shrubs facilitated growth of canopy tree seedlings, protecting them from summer drought and winter frost (Gómez-Aparicio *et al.* 2008).

Facilitation and competition almost certainly occur simultaneously, though few studies explicitly examine both (but see Dickie *et al.* 2005, Montgomery *et al.* 2010, Wright *et al.* 2014). A shrub that competes with neighbors for soil nutrients and light, for example, may also facilitate neighbors by providing shade that reduces water stress. The interplay between facilitative and competitive interactions results in a continuum of net effects from strongly positive to strongly negative, and the net direction of these interactions may shift from positive to negative along environmental gradients. The stress-gradient hypothesis (Bertness & Callaway 1994, Callaway & Walker 1997) proposes that facilitation increases with environmental stress, a mechanism that may be especially important at range margins (Choler *et al.* 2001) and under conditions to which the species is not adapted (Espeland & Rice 2007). Changing climate across a species' range modulates the context in which species interact, and under increasing cold stress,

the net direction of biotic interactions may shift from competitive to facilitative (Choler *et al.* 2001, Callaway *et al.* 2002, Michalet *et al.* 2014).

Determining the degree of intraspecific genetic variation and local adaptation in populations near range margins is critical to understanding climate and competitive constraints on species' distributions. Theory suggests that local adaptation of populations at range margins is dependent on rates of dispersal and gene flow, among other factors: high gene flow from central populations may limit local adaptation at range limits (Kirkpatrick & Barton 1997), but moderate gene flow and dispersal can support local adaptation at range margins (Holt 2003). Reciprocal transplant experiments are a time-honored approach in determining intraspecific differences in response to climate and other factors (*e.g.* Hall 1932, Hiesey 1940, Eriksson & Jonsson 1986, Rehfeldt *et al.* 1999, De Kort *et al.* 2014, Welk *et al.* 2014), and such research often explicitly addresses implications for species' distributions (*e.g.* O'Neill *et al.* 2008, Wang *et al.* 2010, Vergeer & Kunin 2013, Lu *et al.* 2014). Especially valuable are beyond-range transfers using both range edge and central populations (*e.g.* Geber & Eckhart 2005), and more such studies are needed.

There is abundant evidence that plant populations adapt to climate conditions with consequent intraspecific variation in survival and growth rates (*e.g.* Rehfeldt *et al.* 1999, McCarragher *et al.* 2011, Porter *et al.* 2013, Kreyling *et al.* 2014), though in some cases populations may not occupy their optimal climate niche (see Reich & Oleksyn 2008). Intraspecific variation in growth that arises from regional adaptation to climate has been noted in common garden experiments, where plants from cold climates often grow more slowly than those from warmer sites even when grown under common warm conditions (*e.g.* Savva *et al.* 2007, Savage & Cavender-Bares 2013). There is also evidence of variation among populations in response to biotic interactions. Populations of an annual herb from contrasting light environments differed in their growth response to light competition when grown in a common garden (Dudley & Schmitt 1995), and populations of another annual herb varied in response to competition when grown with different densities of neighbors (Shaw *et al.* 1995). Under stressful conditions, facilitative interactions may dominate, and here too adaptive differences between populations may

lead to intraspecific variation in growth (Espeland & Rice 2007).

Effects of climate and competition operate at different spatial scales, and intraspecific variation in response to these factors is likely to show similar patterns. In examining the scale dependence of climate adaptation, Galloway & Fenster (2000) found adaptive differences in germination, survival, and growth of an annual legume when populations were planted 1000 km or more from the seed source but not when planted 100 km or less from the parent population. In contrast to the relatively large spatial scales required to detect intraspecific variation in response to climate, biotic interactions may not be detected beyond regional scales (Bullock 2000, Araújo & Rozenfeld 2014). In order to assess whether both biotic and abiotic factors are range-limiting, therefore, both regional and range-wide comparisons of performance are relevant.

Genetic variation is central to each species' potential to respond to ongoing changes in climate; future distributions will be shaped by species' phenotypic plasticity, mode of dispersal, and capacity to adapt in response to climate shifts (Jump & Peñuelas 2005). Tree species tend to have high levels of genetic variation within populations (Hamrick 2004), which may buffer forest species at the population level from the immediate effects of climate change (Oney *et al.* 2013). Tree species, projected to lag in their response to climate change (Iverson *et al.* 2004), may occupy current ranges for decades to come despite mismatches between species' distributions and climate optima, since long generation times constrain migration as well as adaptation (Aitken *et al.* 2008). Further research is needed to identify current constraints on tree distributions and how those limits might influence species' ability to track climate through range shifts (Renwick & Rocca 2015).

Sugar maple (*Acer saccharum* Marsh.), a widely distributed hardwood tree species native to the eastern United States, is a good candidate with which to examine the range-limiting effects of climate in the context of biotic interactions and genetic variation. Sugar maple spans a wide climate gradient and diverse forest communities, with its northern range limit coinciding with the temperate-boreal forest ecotone and its southern range limit with the mixed forests of the southeastern coastal plain (Godman *et al.* 1990). After migrating northward from southern refugia during the last glaciation,

sugar maple's geographic distribution has been stable over the past 6,000 years (Miller and Park 2009). Genetic work on sugar maple has identified regional ecotypes that display variation in tolerance to heat and drought, onset of dormancy, chilling requirements, timing of leaf flush, and growth rate (Kriebel & Gabriel 1969). Across local temperature gradients at northern margins, sugar maple grows more slowly in colder habitats (Fisichelli *et al.* 2012, Reich *et al.* 2015), and cold temperatures have been suggested as a range-limiting mechanism (Barras & Kellman 1998). At southern margins, sugar maple is limited to a small subset of the soils it occupies in other parts of its range (Godman *et al.* 1990), which could be the result of competitive interactions as well as having implications for such dynamics. Though highly shade tolerant, light competition affects sugar maple seedling survival (Hett & Loucks 1971) and growth (Canham *et al.* 1996, Beaudet & Messier 1998). In contrast to shade intolerant species, however, competition may become important (*sensu* Welden & Slauson 1986) and limiting only where abiotic stress is low and neighbor density is high (Berkowitz *et al.* 1995, Kunstler *et al.* 2011).

To determine the relative effects of abiotic and biotic factors on range limits, I conducted a three-year reciprocal transplant field experiment under natural conditions to examine the effects of climate and neighbors on sugar maple seedling survival and growth across a latitudinal transect of its range. Three populations, sourced from mid-latitude, northern, and southern portions of the range, were planted at all sites, which enabled a population-specific focus on growth and survival dynamics at and beyond range margins. The years of the experiment ranged from unusually cool and wet to hot and dry, exposing seedlings to a variety of climate conditions.

My core hypothesis was that the range of sugar maple is constrained primarily by cold temperatures in the north and competition in the south (Fig. 1-1). I hypothesized that for each of three subpopulations (from northern, central, and southern portions of the range), sugar maple seedling survival and net growth is (1) positively related to summer average and winter minimum temperatures, where each population's survival and growth increases to a locally adapted optimum and then gradually declines with further warming such that each population has highest survival and growth in its region of origin. I further

hypothesized that seedling survival and net growth is (2) reduced by understory neighbors across most of the range, especially towards southern range margins, but facilitated at the northern range margin, and (3) enhanced in canopy gaps, especially in the northern part of the range where cooler temperatures might cause high-light gaps to be less stressful for seedlings.

RESEARCH METHODS

STUDY AREA

In the western portion of its range, sugar maple (*Acer saccharum*) grows naturally from the Canadian border south to the Ozarks of Missouri (Little 1971). Sugar maple seedlings were planted at ten sites: six sites were along a north-south latitude and climate gradient spanning the species' range, while four sites were beyond the range margins in Ontario or Arkansas (Fig. 1-2). Site selection criteria were for suitable mature and relatively undisturbed forest tracts along a north south transect where a) permission to plant could be obtained, b) sugar maple was already present (if within the range), a criteria that was deemed especially important for choosing suitable sites near range margins, and where c) conditions such as elevation, slope, and soil type were otherwise as similar as possible. Beyond range margins, where sugar maple was absent from the forest, sites were chosen whose forests most closely matched the general forest type within the range.

The climate gradient spanned by this study is characterized by a 14° C spread in mean annual temperature (2.1° to 16.1° C MAT) and annual precipitation totals ranging from 701 mm in the north to 1569 mm in the south (Table S1-1). Average June/July/August (hereafter referred to as “summer”) temperatures range from 17.5° C in the north to 27.3° C in the south, while precipitation totals for June through August vary from 265 to 303 mm across sites with no clear latitudinal trend (Figure S1-1). Summer potential evapotranspiration, however, increases from 257 to 466 mm north to south, and thus the index of moisture availability (PPT/PET) at each site ranges from 1.20 to 0.62 north to south, with soil moisture decreasing further south.

At all sites, soils were classified as loams (Table S1-1), although sites varied in soil texture, soil type, and pH. Most soils were alfisols, but ultisols predominated at the two southernmost sites (ALUM and KOEN) and inceptisols (or brunisolic soils) at the three northern sites (TBAY, FORT, and DRYD). At these three northern sites, soils were shallower and underlain by glacial till and glacial lacustrine deposits, in contrast to the deep loess soils capping glacial deposits at sites in Minnesota, Iowa, and Missouri and the cherty or gravelly loams of Arkansas. Soils ranged in pH from 4.14 to 6.81, with more basic soils in the central region of the study area (Table S1-1). Most sites were located on moderate slopes (14 to 32 degrees), while northern sites (DRYD, PIKE, FORT, TBAY) had little slope (4 to 16 degrees). Site elevation was between 193 and 419 m and did not differ systematically with latitude.

Sites were located in mature hardwood or hardwood-dominated forests; pines were abundant at two sites (*Pinus echinata* at the southernmost site, and *P. strobus* at a centrally located site), and balsam fir (*Abies balsamea*) was present at northern sites. Forest canopies at southern sites were dominated by oaks (*Quercus alba*, *Q. velutina*, *Q. rubra*), hickories (principally *Carya ovata*), and tupelo (*Nyssa sylvatica*). Forests in the central portion of the study area were the most diverse, and were dominated by mesic hardwood species such as sugar maple (*Acer saccharum*), basswood (*Tilia americana*), black walnut (*Juglans nigra*), and slippery elm (*Ulmus rubra*), as well as oaks (*Q. alba*, *Q. rubra*). Forest canopies at sites in the northern portion of the study area were dominated by species characteristic of the boreal forest, such as quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), black ash (*Fraxinus nigra*), and balsam fir (*A. balsamea*).

The forests in which sites were located were under a variety of ownership: designated experimental forests within national forests (Ouachita National Forest, Ozark National Forest, Chippewa National Forest), state land (Wildcat Den State Park and Fish Farm Mounds State Preserve, both in Iowa), research forests under private ownership (the University of Missouri's Baskett Wildlife Research and Education Center, as well as the Pine Needles tract, owned by the Science Museum of Minnesota and managed by the St. Croix Watershed Research Center), Crown land under provincial government

management, and the woodlot of a private landowner. Forests were mature and had not been recently burned or logged, though an ice storm at one site in Arkansas a few years prior to the start of the study had thinned the forest canopy there.

EXPERIMENTAL DESIGN

To identify population-specific responses to both local and novel climate and neighbors, seedlings from three sugar maple populations were planted at each site. The populations (referred to here as northern, central, and southern) all came from the western part of the range, where sugar maple tends to be more drought-tolerant than eastern populations (Kriebel & Gabriel 1969). Within this broad regional ecotype, temperature has a greater effect on growth than precipitation (Lane *et al.* 1993), and there is evidence of genetic variation from north to south (Gunter *et al.* 2000). One-year-old field-grown seedlings were purchased from three commercial nurseries whose seed sources were sugar maple populations in Mille Lac County, MN (5.3° C MAT), Lee County, IA (11.1° C MAT), and Lincoln County, MO (12.4° C MAT), respectively (see Table S1-2 for region-of-origin climate data for each population). Seedlings, ranging in initial size from a median height of 111 mm for the central population to 327 mm for the southern population, were planted for this study in the spring of 2009 prior to leaf-out.

At each site, seedlings were planted at 48 stratified randomly selected plots within the forest interior; plots were located so that no trees >10 cm dbh occurred within 1.5 meters of plot center. To determine the effects of biotic interactions on sugar maple growth through overstory light availability and understory neighbor dynamics, plots were randomly assigned light and clipping treatments. Half the plots were located in pre-existing canopy gaps, while remaining plots were located under a closed forest canopy. In each light environment, neighbor abundance was reduced from half of the plots through annual clipping treatments, while the remaining plots were left unclipped. There were 12 replicate plots for each of 4 treatments: open canopy (gap) or closed canopy (shade) plots, with or without neighbor removal (clip or no clip), a total of 48 plots and 144 seedlings per site.

Three seedlings (one from each source population) were planted in each plot, protected from deer browsing by individual fine plastic mesh sleeves and spaced a half meter from each other and plot center. Relative abundance of herbaceous vegetation within a 1-meter radius of plot center (estimated by percent cover) and abundance of woody vegetation within a 2-meter radius of plot center (species-specific stem counts within size classes based on diameter and height) were used to characterize understory neighborhoods in each plot. In clip plots, all herbaceous understory vegetation within a 1-meter radius from plot center and all woody shrubs and saplings within a 2-meter radius of plot center were then clipped at ground level. In the remaining plots, vegetation was left intact surrounding planted sugar maple seedlings. All clip plots were clipped annually to maintain the treatment; plots where regrowth was strongest (vegetation over 15 cm covered more than 25% of the plot) were clipped twice annually, but this was necessary only at a subset of sites and plots. Clipped biomass was recorded and then removed from the plot to prevent fertilization effects from decaying biomass. Clip plots were not root trenched, as the clipping treatment was designed to reduce neighbor interactions with understory vegetation, not canopy trees.

SEEDLING MEASUREMENTS

Seedling height (from root collar to tallest branch) and root collar diameter were measured prior to planting (in the spring of 2009) and annually thereafter in mid- to late summer after growth for the season was complete. As seedling height is influenced by both stem gains and losses throughout the year, seedling stem extension (the sum of new growth on all branches) and dieback (the sum of recent mortality on all branches) were also measured annually in late summer. Seedling survival was assessed twice annually: overwintering mortality was reflected in spring survival data, and growing season mortality was captured in the mid- to late summer visit. A variety of seedling health metrics, such as leaf and stem damage due to insects, mammal herbivory, and disease, were also assessed twice annually. Phenology data on timing of leaf-out and leaf senescence were collected in spring and fall at a subset of sites by a team of trained volunteers in 2010 and 2011.

After three growing seasons and winters and before growth for the next season had commenced, all living seedlings were dug up in early spring 2012 and harvested in their entirety; they were then kiln dried at 75° C and total seedling dry mass was calculated from separate measurements of root and shoot mass. Net seedling growth over the experiment, reflected in ecological metrics such as final seedling height, diameter, and dry mass, was used rather than relative growth rate (RGR) due to the three-year interval between planting and harvest. Seedling biomass provided an integrated indicator of seedlings' growth and dieback over the course of the experiment, while seedling height is relevant to seedling performance in different light environments, as it affects success in reaching the canopy (Cole & Lorimer 2005). All analyses included initial seedling size as a covariate to account for size-related differences in growth, as populations differed in initial seedling size: median initial height and diameter were 231 and 5 mm for the northern population, 111 and 4 mm for the central population, and 327 and 7 mm for the southern population.

SITE CONDITIONS

Temperature and precipitation data for all sites in the U.S. were obtained from the PRISM Climate Group (Oregon State University, <http://prism.oregonstate.edu>, downloaded Nov. 2012); PRISM model output is based on weather station data, interpolated using local data such as elevation, and is accurate to 2 km. For the three sites in Ontario, climate data was obtained from weather stations nearest to each site via the Canadian National Climate Data and Information Archive (Government of Canada, <http://climate.weather.gc.ca>, downloaded Nov. 2012); data accuracy ranges from 15 to 24 km. Summer mean temperature was selected as the climate variable, as it is biologically relevant, explained the most variation in growth and survival data, and was highly correlated with mean annual temperature and total annual precipitation. Latitude and mean summer temperature are highly correlated, but at the northern range margin one site (TBAY) was cooler in summer (though warmer in winter) than either beyond-range site at higher latitudes due to a lake effect. Averaged over the three years of the experiment, summer temperature and precipitation and winter minimum temperature approximated

the 30-year climate normals at most sites (Table S1-3), but the first year of the experiment was cooler and wetter than average across the range, while the third year was hotter and drier and the winter was milder than average (Fig. S1-1).

Forest density and composition in the immediate vicinity of each plot was assessed using a 10-factor prism and averaged for the site. The average number of canopy species in the plot neighborhood varied across sites from 2.4 to 4.75. Total species richness of canopy trees at each site (cumulative across all plot neighborhoods) ranged from 10 to 28 species, with a median of 18 species per site; the central region was the most species diverse. On average, the three most abundant species at a site were responsible for 74% of the basal area of the forest. Average basal area varied across sites but was greatest in shade plots and at central latitudes. In gaps, average site basal area ranged from 2.9 to 4.7 m²/hectare, and in shade plots, average site basal area ranged from 3.4 to 6.6 m²/hectare. Forest canopies in the north were patchier, and the difference between the density of forest canopy surrounding gap and shade plots increased with latitude.

PLOT CONDITIONS

The herbaceous and woody components of the understory neighborhood in each plot were characterized separately. Percent cover of herbaceous vegetation varied by site and through the growing season, though there was no clear pattern across latitude. At planting time in 2009, site averages of percent herbaceous cover ranged from less than 10% to more than 90%; sites with less herbaceous cover tended to have more cover from understory woody species. In the south, the woody understory was comprised of tree species such as red maple (*Acer rubrum*), flowering dogwood (*Cornus florida*), and pawpaw (*Asimina triloba*), as well as shrubs such as blueberry (*Vaccinium sp.*), spice bush (*Lindera benzoin*), poison ivy (*Toxicodendron radicans*), and fragrant sumac (*Rhus aromatica*), while in the north, the understory was dominated by mountain maple (*Acer spicatum*), balsam fir (*Abies balsamea*), and hazelnut (*Corylus sp.*), along with northern bush honeysuckle (*Diervilla lonicera*), currant (*Ribes sp.*), and raspberry (*Rubus sp.*). At sites where it was present, sugar maple was often very abundant in the understory. Basal

area of the woody understory ranged from an average of 1.85 cm²/m² at southern and central sites to 4.95 cm²/m² at northern sites.

The clip treatment was effective in reducing the density of understory neighbors over time. Following the initial clipping, neighbor density was reduced in clip plots in subsequent years compared to unclipped plots, and annual maintenance clipping further reduced average standing biomass in plots. In 2011, clip plots averaged 17% less herbaceous vegetation prior to re-clipping than no clip plots, and with the exception of the two most southerly sites (where blueberry [*Vaccinium* spp.] was abundant and regrew vigorously), average basal area of resprouting woody stems was 78% lower in clip plots than no clip plots. At all but one site, this corresponded to a 75% to 98% reduction in biomass removed from clip plots compared to 2009. The clipping effect was least (42% reduction in biomass) at a centrally located site where the timing of the clipping treatment did not as effectively set back the primarily herbaceous understory vegetation.

Percent light reaching the understory was measured with a densiometer; readings were taken at each plot center at a height of one meter. Light environments varied from site to site, especially in gaps: site averages of percent light in gaps ranged from 9% to 36%, while average light in shade plots ranged from 4% to 10%. Compared with shade plots, gaps averaged 2.5 times more light at southern sites and 3.4 times more light at northern sites, where canopy gaps tended to be larger. At most sites, the clipping treatment increased light in both light environments compared to unclipped plots; the clipping effect on light was greatest at sites where the understory was dense and the canopy thin. Such was the case at the three most northern sites, where clip gap and shade plots had up to 2 times more light than their unclipped counterparts. Within clip treatments, however, light levels for gap and shade plots were clearly differentiated at each site: percent light in clip gaps was always higher than in clip shade plots, and likewise for unclipped plots.

STATISTICAL ANALYSIS

A preliminary multivariate analysis was used to assess correlations between latitude and three-year averages for the following climate variables: mean annual

temperature (MAT), mean annual precipitation (MAP), summer temperature, summer precipitation, summer moisture availability index, December/January/February (winter) minimum temperature, and winter precipitation. Climate variables were strongly correlated with latitude and with each other, with the exception of summer precipitation, which was not correlated with either temperature or annual precipitation. Of the climate variables, average summer temperature yielded models with the best fit for each seedling response variable; levels of significance were similar, however, with other climate variables. Given my hypotheses that both climate and competition are limiting range margins, summer temperature is well-suited for these analyses: growing season temperature has a strong effect on growth and competitive ability, and can also function as an index of climate stress through direct effects on summer growth and its correlation to winter minimum temperatures. This functional relationship between summer temperature and seedling growth yields a more meaningful interpretation of range-limiting dynamics than an analysis based on latitude, and I hereafter use this climate variable to express the latitude gradient.

Cumulative growth data were analyzed using full factorial standard least squares REML models, with log-transformed final seedling mass, height, diameter, and total stem extension as response variables and initial size as a covariate. Annual patterns in growth were also analyzed, with log-transformed annual height, stem extension, and basal diameter as response variables and the previous year's height as a covariate. In all models, plot was nested within site and both site and plot were entered as random effects in the model, an approach that addressed site-specific variation in seedling performance unrelated to the variables of interest as well as variation among the sites in understory vegetation density. Preliminary analyses indicated that continuous variables quantifying density of understory vegetation in clipped and unclipped plots, as well as differences in light levels between the light treatments, yielded results similar to models with categorical variables. Three-year average summer temperature was used as the climate variable for models with a cumulative growth response, while annual models used summer temperature data from that year. Final percent survival was analyzed with a nominal logistic model. This analysis excluded one site in the center of the range, as it

had to be harvested early. A proportional hazards model on the full dataset was also run, analyzing survival over the 35 months of the experiment. Data were analyzed with JMP Pro 9.0 statistical software (SAS Institute Inc.).

RESULTS

I found significant differences in seedling survival, growth, and phenology across the latitude and climate gradient encompassed by this experiment. The effect of summer temperature on seedling growth and survival varied by population and, to a lesser extent, canopy light availability and the presence of understory neighbors. Though my hypotheses were generally supported, performance in the south and beyond range margins was unexpectedly high, and my results do not clearly support either climate or competition as the primary range-limiting factor at the seedling stage.

Survival Response

In the full nominal logistic model for final percent survival over the three years of the experiment, all main factors (population, clip treatment, light treatment, and the three-year average of mean summer temperature) were highly significant, and there were also significant two-way interactions involving summer temperature (Table 1-1). Averaged across sites, survival was highest for northern population seedlings, while seedlings from the central population had the lowest survival. As hypothesized, a higher proportion of seedlings survived to the end of the experiment in clipped than in unclipped plots (55% vs. 47%), and survival was higher in gaps than in shade (58% vs. 44%). Survival also increased with temperature, with highest overall survival at southern sites.

As hypothesized, each population's survival increased with mean summer temperature, but in contrast to my hypothesis, northern and central populations showed no evidence of a plateau or decline in survival beyond their region of origin, though southern and central populations did have a more strongly positive survival response to temperature than the northern population (Fig. 1-3a). Consistent with hypothesis (1), northern populations survived better at northern sites than the other populations, while the southern population had highest survival at southern sites (Fig. 1-3a), resulting in a

significant interaction between population and summer temperature ($\chi^2 = 51.7$, $df = 2$, $p < .0001$).

Population-specific seasonal patterns in mortality were apparent from differences between northern and southern populations in the timing and proportion of seedlings that died from one time step to the next (Table S1-4). Summer mortality, measured as the proportion of seedlings that died between spring and summer visits, was generally low across the range for both populations. Winter seedling mortality (the proportion that died between the summer visit and the following spring) of the southern population at northern sites, however, was two- to four-fold higher than for the northern population in the first year. This is consistent with my hypothesis that populations would show evidence of local adaptation and decreasing survival with distance of climate transfer, though the northern population did not show a similar decline in survival at southern sites.

Survival patterns in the contrasting light environments closely mirrored my hypotheses (Fig. 1-1c): survival was higher overall in gaps, and the positive effect of gaps was greatest at northern sites (Fig. 1-4a). Survival did not statistically differ between gap and shade plots at the two southernmost sites (Fig. 1-4a), leading to a significant interaction between summer temperature and light treatment in the nominal logistic model ($\chi^2 = 5.3$, $df = 1$, $p < .05$).

A full proportional hazards model was used to examine how treatment effects on survival varied with time (Fig. 1-5). All main effects remained significant, and the effect of the clipping and light treatments on survival increased through time. The interaction between population and mean summer temperature remained significant, but there was no longer a significant light treatment \times mean summer temperature interaction (data not shown).

Growth Response

Cumulative seedling growth was analyzed with a variety of response variables: final seedling height, mass, diameter, and total stem extension. Of these, seedling height is most directly proximate to a young tree's ability to reach the canopy and become a

reproductive individual. I therefore focus first on final seedling height, then address differences among growth models.

As hypothesized, the populations differed in their height response to the temperature gradient (Fig. 1-3b), though the central population performed poorly across the range and neither the northern nor central populations showed the hypothesized plateau or decline in growth response at the highest temperatures. In the full linear mixed effects model for final seedling height, initial seedling height was highly significant as a covariate, but there were no significant differences in height between populations once initial height had been taken into account (Table 1-1). There was, however, a significant population \times mean summer temperature interaction ($F_{2,568} = 8.15, p < .001$): height of the southern population showed a strong positive response to increasing mean summer temperature and performed best at southern sites, consistent with hypothesis (1), while seedlings from the northern and central populations showed a much weaker positive height growth response to increasing temperatures (Fig. 1-3b).

Light availability had a strong effect on height growth, as hypothesized, both as a main effect and through interactions with clip treatment ($F_{1,330} = 2.91, p < .1$), mean summer temperature ($F_{1,426} = 3.67, p < .1$), and a three-way clip treatment \times light treatment \times mean summer temperature interaction ($F_{1,388} = 2.84, p < .1$) [Table 1-1]. Final seedling height was greater on average in gap than in shade plots, and the difference in height between gap and shade was greatest at northern sites (Fig. 1-4b), as hypothesized (Fig. 1-1c). At northern sites, the clip treatment narrowed the difference between light treatments: in the shade, seedlings were taller in the clip treatment, while in gaps, seedlings were shorter in the clip treatment (Fig. 1-4b). At southern sites, in contrast, there was little difference in height among the clip and light treatments.

Final seedling height for the northern and southern populations was on average strongly positively correlated with final survival across temperature, clip and light treatments, while for the central population, final height and survival were only weakly correlated (Fig. 1-6). For the southern population, this reflects both higher survival and growth at southern than northern sites. Though the northern population had a much more muted response to the latitude gradient, height and survival remained linked via site-

specific differences in overall performance. The central population, on the other hand, had poor performance across sites, and even at sites where it survived well, its height growth was less than that of the other populations.

My hypotheses were supported across growth metrics, and results for the main effects were largely consistent among all growth models (Table 1-1). In each of the full linear mixed effects models for growth, light treatment was a highly significant main effect: seedlings were not only taller in gaps but also had greater mass, basal diameter, and total stem extension. For all growth metrics except final seedling height, sugar maple performance differed significantly among the populations: after taking initial differences in size into account, southern seedlings still had greater mass, basal diameter, and total stem extension than seedlings from northern or central populations. As a main effect, the clipping treatment was non-significant for seedling height, but it had a highly significant effect on seedling mass and basal diameter and a moderately significant effect on stem extension, all of which increased in clip plots as hypothesized. Summer temperature was largely non-significant as a main effect in growth models, though it had a marginally significant effect on seedling basal diameter, which increased with warmer temperatures.

The population \times mean summer temperature interaction was the only one significant across most growth models, though the degree of effect varied. In addition to seedling height, the interaction was moderately significant for stem extension ($F_{2,594} = 4.45, p < .05$) and seedling mass ($F_{2,557} = 2.79, p < .1$): consistent with the results for height, the southern population also had greater mass and more stem extension, especially at warmer sites. The interaction was non-significant, however, for basal diameter.

The clipping treatment is associated with statistically significant differences in final seedling mass across populations and temperature (population \times clip treatment [$F_{2,523} = 3.22, p < .05$], population \times clip treatment \times mean summer temperature [$F_{2,560} = 3.05, p < .05$]), partially supporting hypothesis (2) [Fig. 1-7]. Though not hypothesized, clipping response varied among populations: reducing understory neighbors had a positive effect on mass of seedlings from northern and central populations but a negative effect on seedlings from the southern population. Across a temperature gradient, both warmer temperatures and the clip treatment increased seedling mass of the northern and

central population, though for the central population the positive effect of clipping was greatest at colder sites. Only the southern population showed the hypothesized switch from a negative to positive effect of clipping, as seedling mass was reduced by clipping at colder sites and enhanced at warmer sites.

Annual Patterns in Growth and Survival

Seedling responses to experimental conditions, expressed in final percent survival and cumulative growth variables, could reflect either a consistent response across the three years of the experiment or a response that varied in strength or direction across years. To address this, I analyzed annual survival and growth responses, using the same basic model but substituting annual summer mean temperatures for the three-year average and the previous years' size as a covariate.

Survival patterns did indeed change across the years of the experiment. Mortality was greatest in the first year, and while population had a significant effect on survival in every year, the strength of the effect declined successively every year (Table S1-5). The effect of mean summer temperature on survival was significant in the first two years of the experiment, but not the final year. The effect of the clipping and light treatments, on the other hand, increased over time.

Seedling growth response was largely consistent over the experiment, but response to clipping and temperature differed by year (Table S1-6). The clip treatment had an initial negative effect on seedling height in the planting year, and seedling stem extension was positively affected by clipping only at southern sites; the positive overall effect of clipping on final basal diameter and stem extension did not become significant until the second or third year of the experiment, respectively. Mean summer temperature had a significant positive effect on seedling growth in two of the three years; the effect was non-significant in the hot, dry summer of 2011.

The population \times summer temperature interaction for height growth noted across the three years of the study was also significant for annual height and stem extension in both 2009 and 2010 (but not 2011) when each year was analyzed independently. An interaction between summer temperature and light environment, significant for final

seedling height, was significant only in 2010, where both height and extension were lower in shade plots, especially at cold sites. The three-way interaction between population, clip treatment, and summer temperature was significant only for final seedling mass and not for any annual growth variable.

Two interactions, clip treatment \times light treatment and clip treatment \times light treatment \times mean summer temperature, were significant in the analysis of final seedling height but not in any year of the experiment. A population \times light treatment \times mean summer temperature interaction, on the other hand, was significant in 2009 and 2010 for stem extension and in 2011 for height but was not significant in the analysis of cumulative growth, though it was consistent with population by temperature and temperature by light interactions in final growth models. Southern and central populations both responded to warmer temperatures with increased extension or height, but especially in shade plots: in gap plots, extension or height remained relatively constant across sites. The northern population, on the other hand, had a weak, non-significant response of stem extension to temperature and no change in the relative performance of seedlings in gap and shade plots across sites.

Phenology Response

Phenology data on spring leaf expansion and fall leaf senescence, collected in 2011 from a northern site (PIKE) and southern site (KOEN), revealed differences in populations' response to seasonal cues as well as growing season length across sites (Table 1-2). The northern population leafed out faster in spring and had full-sized leaves earlier than the southern population, while in the fall, the northern population senesced earlier than the southern population. This pattern was supported in both years and at all sites where phenology was measured (2010 data not shown). Though volunteers missed the critical leaf-out window at PIKE in 2011, the incomplete results are consistent with the overall trend. At the southern site, the northern population's growing season (calculated from completion of leaf-out to initiation of senescence) was about six weeks longer than at the northern site, mostly due to earlier leaf-out in spring. The southern population's growing season at the southern site was even longer, but as only 57% of

seedlings from the southern population had initiated leaf senescence when surveyed, the full length of its growing season is unknown. At the northern site, the southern population kept its leaves at least two weeks longer than the northern population, though conditions were no longer favorable for growth. At another northern site, snow-covered southern seedlings with green leaves were observed in mid-November, suggesting full senescence might not have been achieved by that population at northern sites prior to winter onset.

DISCUSSION

While a species' distribution broadly maps the abiotic conditions of its fundamental niche, both models and experimental work suggest that at least in certain cases, a species' range reflects a realized niche further defined by biotic interactions (Bullock *et al.* 2000, Cleavitt 2004, Araújo & Luoto 2007, Wisz *et al.* 2013, Bulgarella *et al.* 2014). As rapidly changing climate causes abiotic niche conditions to shift geographically, this may lead not only to a disconnect between a species' fundamental niche and its distribution but also cascading effects from changing species distributions and novel interactions (Wisz *et al.* 2013). Additionally, species often exhibit genetic variation across the range, and it is important to examine performance of populations from different parts of the range to better understand range-wide and range-limiting dynamics (Kreyling *et al.* 2014, Lu *et al.* 2014). Complicating efforts to understand species' potential distribution shifts is the lack of beyond-range transplant studies that examine potential biotic as well as abiotic range-limiting factors under natural conditions and for multiple populations (Hargreaves *et al.* 2014). This experiment, designed to address these gaps, showed population-specific responses at northern and southern range margins that emphasize the importance of both broad climate tolerance and local adaptation in conjunction with biotic interactions.

Range-limiting factors at the northern margin

The strong correspondence between species distributions and climatic thresholds, particularly at high latitudes and altitudes, has been well documented in the literature (Salisbury 1926, Grace 1987, Woodward 1987, Randin *et al.* 2013). Beyond-range

transplant experiments are one of the best ways to detect the limiting effect of climate (Hargreaves *et al.* 2014), but despite transplanting seedlings several hundred kilometers north of the range boundary, I found only very modest declines in either survival or growth for the northern population. Towards the species' northern margin, seedlings with origins from central and southern portions of the range had marked declines in survival and (for the southern population) in growth, suggesting climate limitation among these populations. The northern population, however, appeared to be locally adapted and its survival and growth was only very slightly lower at the lower temperatures found at and beyond the northern range margin. These seedlings were able to persist at beyond-range sites where winter minimum temperatures averaged 1° Celsius colder than the northernmost within-range sites. Successful sugar maple regeneration was also noted in a stand where summers were cooler than either of the beyond-range transplant sites (R. Putnam, personal observation).

The high survival rate of sugar maple seedlings beyond the northern range margin, coupled with strong recruitment near the northern range edge, raises the possibility that the current distribution of sugar maple does not reflect the climate tolerance of the species, either due to dispersal limitation (*e.g.* Samis & Eckert 2009, Marsico & Hellman 2009), recent climate warming (*e.g.* Doak & Morris 2010), or both (*e.g.* Engler *et al.* 2009). Current northern range margins of sugar maple do not seem to be maintained by lack of dispersal, however, as northward distributional shifts of sugar maple saplings have been noted in Quebec over the past thirty years, though with an estimated migration rate of 0.4 km/year, dispersal likely limits the rate at which sugar maple distribution responds to changes in climate (Boisvert-Marsh *et al.* 2014). Seed predation by small mammals has also been posited as a potential constraint at northern range margins, potentially reducing dispersal distance (Kellman 2004, Brown & Vellend 2014).

While transplant experiments often yield evidence of climate limitation through direct effects on survival (*e.g.* Klimeš & Doležal 2010, Vergeer & Kunin 2013), a species may be able to survive experimental transplanting beyond range limits yet be climate-limited in its distribution (Salisbury 1926, Vetaas 2002) if its envelope of climate

tolerance exceeds its distribution (*e.g.* Van der Veken *et al.* 2007). As elsewhere, the northern range limit of sugar maple has experienced warmer temperatures in recent decades, especially in winter (data not shown), but during this study, average summer and winter minimum temperatures at the range margin either approximated or were lower than twentieth-century averages, with the exception of the final winter, which was much warmer than average (Table S1-7). Sites beyond the northern range margin showed similar summer and winter temperature patterns over the three years of the study (Fig. 1-1a,c), which suggests that the conditions under which seedlings survived and grew during the experiment were in line with the twentieth-century climate conditions under which sugar maple trees at the cold northern range limit established and matured. Rare climate events can have a significant effect on plant distributions (Giesecke *et al.* 2010), however, and occasional climate extremes could play a role in limiting sugar maple's northern range boundary.

Though direct effects of rare climate events on sugar maple survival cannot be excluded as a possible range-limiting factor, high survival of sugar maple seedlings beyond the northern range margin, also noted in other beyond-range transplant studies of the species (Kellman 2004, Brown & Vellend 2014), suggests the possibility that the northern extent of the range could be constrained at least in part by biotic factors. Climate can limit ranges through indirect effects on metabolism and growth (Angert 2006), and it is possible that sugar maple is outcompeted at its northern range margin by faster-growing boreal species. The northern range margin could also be maintained by a suite of interacting factors, such as temperature, interspecific competition, and herbivory. Sugar maple is preferentially favored over many boreal species by deer, and height growth is less responsive to warmer temperatures when browse pressure is high (Fisichelli *et al.* 2012), a dynamic that is further exacerbated by slower growth under cooler versus warmer temperatures (Reich *et al.* 2015) and by slower growth relative to other boreal species (Fisichelli *et al.* 2015). This study does not directly address sugar maple growth relative to other species, and further research should examine whether climate-mediated growth responses shift the balance of competitive interactions at range margins.

Climate could also be limiting the distribution through its effects on processes such as flowering or fertilization (Woodward 1990). Evidence of climate limitation for sugar maple at other life stages, however, is scant. Kellman (2004) measured lower germination of sugar maple seeds experimentally planted beyond range limits than for those within the range, but this was attributed to seed predation, and survival of germinants beyond the range exceeded within-range survival. At the furthest extent of the native distribution, there is no evidence of reproductive limitation in sugar maple; in these disjunct stands, recruitment is high and matches that within the range (Graignic *et al.* 2014, R. Putnam, *personal observation*).

Though sugar maple reproduction remains high at range margins, it is also possible that the northern margin reflects a climate threshold beyond which reproductive success declines sharply. High latitudes are characterized by growing seasons that are both cool and short; under such conditions, reproductive timing becomes critical. In a study of cocklebur, experimental transfers across a latitude gradient found that locally adapted populations at range margins reproduced earlier than populations elsewhere in the range (Griffith & Watson 2005), suggesting that reproductive timing is a key constraint at northern margins. Models incorporating phenology to predict survival and reproductive success in trees (see Chuine & Beaubien 2001) predict that sugar maple and many other species are limited in the north by lack of sufficient degree days for fruit maturation (Morin *et al.* 2007). Experimental tests of these predictions for long-lived woody species are difficult, however; this study did not measure reproductive success of northern marginal populations.

Range-limiting factors at the southern margin

Range margins at low latitudes and altitudes, lacking cold temperatures as a limiting constraint, have been hypothesized to be limited instead by biotic interactions such as competition (MacArthur 1972, Kaufman 1995, Loehle 1998). Alternatively, it has been suggested that the lack of cold temperatures to meet chilling requirements might itself be limiting (Cannell & Smith 1986, Sykes *et al.* 1996, Guilbault *et al.* 2012). In a recent comprehensive literature review on the range-limiting dynamics at warm-edge

margins (Cahill *et al.* 2014), no broadly shared constraint emerges: while there is evidence to support competition as the primary mechanism (*e.g.* Bullock *et al.* 2000, Cleavitt 2004, Dickinson *et al.* 2007), other studies support climate limitation through a variety of mechanisms (*e.g.* Macias *et al.* 2006 [aridity], Offord 2011 [frost damage, heat stress], Guilbault *et al.* 2012 [chilling requirements]). Few studies explicitly examine both biotic and abiotic limiting factors, but of those that do, there is some support for both having a range-limiting effect (*e.g.* Bruelheide 2003, Hara 2010).

Contrary to both these and my own hypotheses, however, I found no evidence to support either competition or climate limitation at sugar maple's southern range edge: survival and growth of seedlings from all populations remained high beyond the southern range margin. Neither the clipping treatment of understory vegetation nor canopy gaps significantly enhanced survival or growth at southernmost sites, suggesting that competition from neighbors did not limit performance of sugar maple seedlings. The experiment spanned years with above- and below-average temperature and precipitation, but annual analyses of seedling growth within sites and across years did not show a consistent growth response to increases in either temperature or precipitation, nor were variations in seedling survival across years linked to these weather patterns (results not shown). High survival and growth at beyond-range southern sites occurred even in the summer of 2011, which was the warmest summer at these sites of the past 40 years (Fig. S1-1a).

As was suggested for the northern range margin, high beyond-range survival and growth of sugar maple seedlings does not exclude the possibility of competitive limitation: species with higher growth rates relative to sugar maple competing for canopy openings (see Yetter & Runkle 1986) could contribute to maintaining southern range margins. The effect of neighbors on target seedlings can also be positive at an early life stage but negative at another; for example, neighbors might facilitate seedling establishment but reduce reproductive fitness of mature plants (Stanton-Geddes *et al.* 2012).

While this study indicates that sugar maple seedlings can survive and grow beyond the southern range limit, at least under the subset of climate conditions

experienced during the three years of the experiment, the possibility of limitation in another life stage remains. Range limit models that incorporate both climate and phenology predict that sugar maple, along with other tree species, may be limited by lack of adequate chilling in the southern part of the range, causing them to be slow to break dormancy and late to flower, exposing immature fruits to frost damage in fall (Morin *et al.* 2007). I have no experimental data on flowering beyond the southern range margin, but in weekly phenology surveys in the spring of 2011, bud-break of seedlings was not delayed relative to other understory species, and the majority of seedlings in all populations had fully expanded leaves before the canopy closed (R. Putnam, *personal observation*).

Climatic constraints on germination could be another potential range-limiting mechanism for the species, as the seed requires one to three months of stratification under moist, near-freezing conditions for optimal germination (Godman *et al.* 1990). Germination of sugar maple seeds experimentally planted beyond the southern range limit in fall of 2010 was high, more than double the germination rate of those planted at sites within the range (R. Putnam, unpublished data), and it suggests that at least in some years, winters beyond the range limit are sufficiently cool to support germination of sugar maple seed. Rapid spring warming, however, can severely limit germination (Godman *et al.* 1990), and it is possible that the range is constrained by a combination of episodic germination success and dispersal limitation associated with a patchy distribution at the southern range edge.

Biotic Interactions

Interactions between species can have strong effects on the local distribution of plants, thereby influencing species' distribution at a broader scale (Wiszniewski *et al.* 2013); understanding these dynamics is becoming increasingly important, especially in the context of changing climate (Bruehlheide 2003, HilleRisLambers *et al.* 2013). Biotic interactions may restrict the range of an inferior competitor (*e.g.* Miller & Silander 1991, Gifford & Kozak 2012), expand the realized niche of a species through facilitative or mutualistic interactions that mitigate stressful abiotic conditions (*e.g.* Choler *et al.* 2001,

Afkhami *et al.* 2014), or both (Cleavitt 2004). I expected interactions between seedlings and understory vegetation to shift across the range from competitive in the south to facilitative in the north. Instead, I found only modest (though significant) levels of competition across the range; only the southern population experienced a facilitative benefit from understory neighbors beyond the northern range margin.

Seedling growth was higher on average in clipped than in unclipped plots, and while the intensity of competition (*sensu* Welden & Slauson 1986) between seedlings and understory vegetation varied from site to site and among populations, the overall intensity of competition was relatively constant across the range for two of the three populations. At and beyond the southern range margin, where I hypothesized clipping would have an especially positive effect, I found no evidence to support competition as a range-limiting factor. While the lower neighbor densities achieved by clipping generally had a positive effect on seedlings, clipping had a negative effect on growth for the southern population at northern sites, which I attribute to abiotic stress. To fully assess the importance of competition at range margins, however, I would need site-specific quantitative measures of competition in the absence of abiotic stress; while a few studies have measured competition importance along gradients (Damgaard & Fayolle 2010, Kunstler *et al.* 2011), this approach has not been applied to range limits of woody species.

Canopy trees also affected resource availability and abiotic stress, and differences between canopy gaps and the closed canopy were reflected in patterns of seedling survival and growth. I focus here on the effects of light environment rather than belowground resources, as a review of root competition in forests found that for understory individuals, belowground competition with canopy trees is of secondary importance to light competition at all but the most xeric and nutrient poor sites (Coomes & Grubb 2000). Seedlings had higher survival and growth in gaps than in shade, but this effect was strongest at and beyond northern range margins. Since light is an important resource, the relative decline in performance in southern gaps is suggestive of increasing stress; water loss, leaf temperatures, and photoinhibition have all been found to increase with higher light (Niinemets & Valladares 2004), and are likely increasing along the temperature gradient as well.

The ultimate measure of competitive success is not short-term survival and growth but the rate at which individuals reach the canopy and reproductive maturity relative to other species competing for the same canopy openings. Growth of sugar maple seedlings in unclipped plots was fairly high beyond both northern range margins (for the northern population) and southern range margins (for all populations). Without considering the growth of competing species, however, the slight differences in growth between clipped and unclipped plots cannot be fully interpreted. The assemblage of potential competitors differs between within-range and beyond-range forest communities, and it is possible that sugar maple may be competitively excluded from the canopy beyond current range margins, despite growth rates similar to within-range sites.

Growth of heterospecific seedlings was not measured in this experiment. There is, however, some evidence in the literature to suggest that sugar maple may face competitive limitation at and beyond range margins. In the southern part of its range, Yetter and Runkle (1986) found that while sugar maple was among the five most abundant canopy tree species in the understory at several sites in North Carolina, its growth rate in canopy gaps was the second lowest of those species. At the temperate-boreal forest ecotone at the northernmost extent of sugar maple's range in Minnesota, height growth of sugar maple saplings is significantly lower than that of balsam fir (*A. balsamea*), an abundant competitor typical of boreal forests (Fisichelli *et al.* 2015). A possible mechanism for the difference in growth is the temperature-dependent effects on leaf nitrogen for the two species, which declined with temperature for sugar maple but not for balsam fir (Fisichelli *et al.* 2015).

Though reducing understory vegetation density did not substantially enhance beyond-range seedling survival or growth, the effect of neighbors nonetheless changed with latitude. The stress gradient hypothesis predicts that facilitative interactions between species will outweigh competitive dynamics under stressful conditions (Bertness & Callaway 1994, Choler *et al.* 2001, Callaway *et al.* 2002). I found evidence to support this hypothesis at three of the four northernmost sites, where seedlings from the southern provenance had higher final dry mass in unclipped plots, suggesting this population experienced a net facilitative effect of neighbors at these sites. Neighbors may ameliorate

the seedling microclimate by reducing vapor pressure deficit (VPD) (*e.g.* Muhamed *et al.* 2013) or by moderating temperature and irradiance extremes (*e.g.* Castro *et al.* 2004), and where these stresses are limiting, such interactions may lead to a net positive effect on growth. The facilitative effect of neighbors for the southern population, where seedlings were growing furthest from their native region, was in contrast to the response of northern and central seedlings at these sites, which had higher final mass in clipped plots, suggesting net competitive interactions with neighbors predominated for these populations.

It has been suggested that facilitative interactions are especially important for provenances that are least adapted to local conditions (Espeland & Rice 2007), and the southern population's response at northern sites supports this hypothesis. Though the northern population was arguably equally ill-adapted to typical conditions at the southernmost sites, mean summer temperatures in 2009 were cooler than average across the latitude gradient (Fig. S1-1): thus, even at beyond-range southern sites, the northern population adjusted to transplanting under conditions typical of within-range sites, while at northern sites the abnormally cool summer further exacerbated the climate disconnect experienced by the southern population. Although some studies have suggested facilitation may play an important role at range limits in ameliorating marginal conditions (Germino *et al.* 2002, Castro *et al.* 2004), I did not find support for this, as the local (*e.g.* northern and southern) populations did not exhibit evidence of a net facilitative effect from neighbors when planted at northern and southern range boundaries.

Population insights

There is a long history of using reciprocal transplant experiments to understand differences in population response to the environment (*e.g.* Hall 1932, Hiesey 1940, Eriksson & Jonsson 1986, Hamann *et al.* 1998, Rehfeldt *et al.* 1999) and the implications of this variation in determining range limits (*e.g.* Levin & Clay 1984, Geber & Eckhart 2005). Across-range transfers highlight the degree to which populations are plastic in their response (Eckhart *et al.* 2004, Reich & Oleksyn 2008), though adaptation at range limits also occurs and may be rapid (Woodward 1990, Davis & Shaw 2001). Several

authors recently have emphasized the need to study range-limiting effects of both biotic and abiotic factors at the population, rather than species, level, with a particular focus on range margins (Sexton *et al.* 2009, Hargreaves *et al.* 2014). I found population-level differences in response to conditions across the range and at range margins, suggesting that genetic variation among populations has implications for both range-wide performance and dynamics at range boundaries.

This study's inclusion of provenances from different parts of the range highlighted population differences and underscored the importance of using multiple populations to understand range constraints. Although overall sugar maple survival was positively correlated with temperature, which would seem to support climate limitation in the north, seedling sensitivity to temperature varied by population. Southern and central populations had high mortality at northern sites that was associated with cold winter minimum temperatures, and, for the central population, low growth rate as well. The northern population, however, had low mortality across the range, and even at a site more than 200 km north of the species' continuous distribution, 60% of seedlings from the northern provenance survived. The northern population of sugar maple thus appears to be differentiated from more southerly populations in key, if not yet fully understood, attributes that influence the current extent of the northern range margin.

Clinal variations in growth and survival were apparent in each population, but the populations also exhibited differing overall growth and survival strategies. Of the three populations, southern seedlings consistently had highest net growth, even at the coldest sites where its survival was poor (Fig. 1-7). The northern population, on the other hand, was characterized by lower net growth across sites, but its survival was generally high and was less affected by cold temperatures. The central population was intermediate in its responsiveness to the summer temperature gradient: it had the low net growth of the northern population and the temperature-dependent survival of the southern population. Of the three populations, the central one consistently had both the lowest survival and growth across sites. Whether this general underperformance in both growth and survival was due to the small initial size of seedlings or the particular characteristics of this population, or both, is impossible to know. Regardless, it is important to keep this poor

performance in mind when comparing the three populations' differential responses to the temperature gradient across sites.

The patterns of intraspecific variation in net growth and survival that I observed between northern and southern populations are consistent with what I would expect to find if there were a tradeoff between cold hardiness and growth rate such as has been proposed as a range-limiting mechanism (MacArthur 1972, Woodward & Pigott 1975, Loehle 1998, Aitken & Hannerz 2001, Koehler *et al.* 2012). The southern, but not the northern, population had a steep decline in survival with increasing latitude driven by winter mortality. Summer mortality of southern seedlings was generally low across the range, but winter mortality was high in the northern half of the range and beyond range margins, and there, few southern seedlings survived beyond the first winter. First-year winter survival of northern population seedlings was two to four times higher than the southern population in the northern part of the range. Of the seedlings that survived, the southern population consistently had higher net growth than the northern population across sites, and though plants from both populations were larger at warmer sites, this was especially true of the southern population.

There could be alternative explanations for the observed differences in growth and survival patterns between northern and southern populations. It has recently been suggested that the apparent tradeoff between cold hardiness and growth rate among willow species is driven by differing phenological cues for budburst, growth, and cold acclimation across the range that lead to differences in growth and survival (Savage & Cavender-Bares 2013). In botanic gardens, species from warmer climates were phenologically delayed in their response to environmental cues relative to species native to the climate, leading to predicted costs due to a shorter season for growth (Zohner & Renner 2014). Phenology constraints have been proposed as a range-limiting mechanism (Chaine 2010, Chapman *et al.* 2014), and there is some evidence for intraspecific variation as well in the timing of phenological processes such as leafing out and leaf abscission (Chaine *et al.* 2000, Morin *et al.* 2009, Vitasse *et al.* 2013).

High mortality among southern seedlings at northern sites could therefore potentially be explained not by lack of cold hardiness *per se* but by a mismatch between

environmental cues and phenology. Seedlings from the southern population leafed out slightly later in spring than northern seedlings and held their leaves longer in the fall (Table 2). A mismatch in phenology cues could cause a seedling to partially or fully miss the spring window before the canopy closes, which has been experimentally shown to have highly negative effects on growth and survival of sugar maple seedlings (Augspurger 2008). Later leaf senescence in the fall exposes leaves to freezing damage, and in willows is associated with higher loss of nitrogen due to poor nitrogen retranslocation (Weih 2009). Thus it is possible that seedlings from the southern population were losing the opportunity for carbon gain in the spring and experiencing added costs with holding leaves later in fall, a combined effect that may have reduced growth and survival at northern sites.

Low net growth of the northern population, especially notable relative to the southern population's growth at southern sites, could also be a consequence of a functionally shorter growing season, not just lower potential maximum growth rate (see Chapter 3). Leaf abscission for seedlings from the northern population occurred much earlier in the fall than for the southern population (Table 1-2). Sugar maple is photosynthetically active in the fall prior to leaf senescence and accumulates carbon in root and stem tissue even after cessation of height growth (Horowitz *et al.* 2009), and the northern population's lower total growth may thus be due in part to a lesser ability to capitalize on the long growing season at southern sites.

While I do not measure reproductive fitness in this study, differences in net growth and survival among the populations suggest at least some degree of local adaptation: at both northern and southern range margins, the local population was taller and survived better than the other populations. This is consistent with previous genetic work on sugar maple (Kriebel & Gabriel 1969) and has implications for the species' response to climate change. Oney *et al.* (2013) proposed that intraspecific variation may buffer the effects of climate change, and my results support that suggestion. Southern range margins are generally considered especially vulnerable as the climate warms (Aitken *et al.* 2008), but the southern population had high survival and growth beyond current range margins, even during two warmer-than-average summers. Though the

northern population had lower growth, its high survival under climate “warming” conditions simulated by across-range transplanting suggests that the northern population may also fare better than predicted with climate change.

Possible Study Limitations

The lack of strong evidence to support either climate or competition constraints on the range of sugar maple raises the possibility that either some other factor is responsible for limiting the range or that climate or competition are in fact constraining the range in some way that was not measured or characterized. I first address other possible factors that have been proposed as range-limiting for this or other species, and then revisit competition and climate and discuss ways one or both might yet be limiting ranges.

While biotic stressors such as disease or insect herbivory are often considered of primarily local importance, the ability of exotic species in nonnative habitat to expand beyond their native niche, as suggested by the enemy release hypothesis (Keane & Crawley 2002), indicates that the range-limiting effects of pathogens, insects, and other herbivores may be underestimated (Mitchell & Power 2003, DeWalt *et al.* 2004, McCarthy-Neumann & Ibañez 2012, Gundale *et al.* 2013). A study on sugar maple’s fungal seed pathogens, however, found similarly low levels of seed loss in forests dominated by conspecifics and heterospecifics (Kotanen 2007). While a variety of insects and leaf pathogens attack young sugar maple (Gardescu 2003), I did not find any consistent patterns in levels of foliar insect and disease damage across sites, and the effects were not correlated with seedling growth (data not shown).

Deer herbivory has been suggested as one potential factor contributing to regeneration failure of sugar maple at a site in the southern part of the range (Belden & Pallardy 2009) and high browse pressure from deer at the boreal forest ecotone is especially limiting for temperate species (Fisichelli *et al.* 2012). In extreme cold climates where growth rates are temperature limited, ungulate herbivory can restrict trees from areas where they would otherwise be able to grow (Speed *et al.* 2010). At the landscape

scale in more moderate climates, however, deer density does not appear to be correlated with reproductive success of sugar maple (Didier & Porter 2003).

At range margins, where the landscape may become functionally fragmented into smaller pockets of suitable habitat, species may have increased difficulty establishing in a suitable environment (Bahn *et al.* 2006, Lohmus *et al.* 2014). Even in the absence of an environmental gradient, stable range limits can emerge if the distribution of suitable habitat on the landscape becomes so patchy that dispersal can't overcome the distance (Keitt *et al.* 2001). I intentionally selected beyond-range sites that were as similar to within-range sites as possible, and thus my results do not necessarily reflect the general suitability of beyond-range forests for sugar maple.

Despite my efforts to choose sites that were similar, the planted sugar maple seedlings survived and grew on soils that varied in acidity (Table S1-1) and fertility. Only soil pH was measured in this study, but the reduction in bioavailability of soil nutrients and increase in uptake of toxic metals on acidic soils is well understood (St. Clair & Lynch 2005). Though sugar maple is sensitive to acidic soils and observed declines in sugar maple health in the northeastern United States have been linked to calcium and magnesium deficiencies (St. Clair *et al.* 2008), evidence from this study shows that soils are not directly limiting the western portion of sugar maple's range either through poor survival or attenuated growth. Drought, freeze/thaw cycles, and defoliation by insects or deer can all compound nutrient stress (St. Clair *et al.* 2008), however, and nutrient stress is one of many factors that could combine to limit sugar maple under otherwise marginal conditions.

The latitude transect selected for this study captured a strong temperature gradient, but the moisture gradient is less clearly associated with latitude. The experiment did, however, span both wetter-than-average and drier-than-average years (Fig. S1-1b), and coupled with similar variation in temperature across years (Fig. S1-1a), it is likely that seedlings experienced soil water stress in at least some years of the experiment. Sugar maple seedling growth has been shown to be higher at moist, rich sites (Walters & Reich 1997), and drought has been associated with sugar maple dieback and decline (Kolb & McCormick 1993). Soil moisture data was not collected in this experiment, but

in models, sugar maple's western range boundary is driven by soil water stress (Walker *et al.* 2002) though its overall distribution is only very weakly influenced by soil moisture (Chuine & Beaubien 2001).

Belowground competition for soil water and nutrients between planted sugar maple seedlings and understory neighbors, though not manipulated, might have been important; in some species, the strongest competition occurs belowground (Cahill 2002). This experiment manipulated neighboring plants through aboveground biomass removal; the degree to which belowground interactions were affected by this treatment remains unknown. Vegetation removal enables only the net effect of neighbors to be determined and does not allow above- and belowground processes to be distinguished (Montgomery *et al.* 2010), and the full extent of biotic interactions occurring at sites across the range may therefore have been masked by concurrent above- and belowground interactions in opposing directions. When above- and belowground competition were examined separately for red maple (*Acer rubrum*) and five other woody species in forest understory and gaps, however, belowground neighbor interactions consistently had either a negative or neutral effect on seedlings (Montgomery *et al.* 2010). The competitive effect I observed is therefore likely conservative and may well underestimate the magnitude of neighbor interactions.

Plots were not root trenched, a manipulation that would have reduced belowground interactions with canopy trees. A root trenching experiment of sugar maple and other species in Quebec found no effect on sapling height or diameter growth, which was attributed to the overriding importance of light competition (Ricard *et al.* 2003). Another experiment found root trenching had a positive effect on seedling height and mass at low light but did not affect survival or biomass distribution between shoots and roots (Machado *et al.* 2003), while a review of root trenching experiments concluded that light limits seedling growth at sites with rich moist soils and root trenching has a positive effect on growth primarily on drier, nutrient-poor soils (Coomes & Grubb 2000). These studies suggest that while belowground competition with overstory individuals can affect seedling growth, light competition is of primary importance in the forest understory.

Unlike range limit studies of herbaceous plants, the timespan from germination to reproductive maturity for woody plants is not conducive to ecological experiments. An important caveat to this study is the possibility that the factors limiting sugar maple's distribution, whether climate, competition, or some combination of factors, constrain a life stage other than the seedling. Perhaps most importantly, this study could not address flowering or the production of fertile seed, processes that could be limiting the distribution either through direct climate limitation or through phenology (Morin *et al.* 2007). If fecundity was low or sporadic at range margins, sugar maple might be unable to maintain a population beyond current range margins.

Demographic processes offer another way to think about range-limiting dynamics (Holt *et al.* 2005), as the realized niche of plants is achieved through local patterns of dispersal, germination, and mortality (Gaston 2009). In this study I have been focused on spatial variation of deterministic factors and their effects on a subset of demographic parameters. However, temporal or demographic stochasticity could also limit distributions, particularly if population size or growth rate at range limits was low or the availability of suitable habitat was limited (Holt *et al.* 2005). This study was not designed to quantify either of these sources of variability, but these factors may play a role in constraining the distribution of some species (Villellas *et al.* 2013), especially in the context of changing climate (Nabel *et al.* 2013).

CONCLUSION

Climate change presents a variety of potential challenges for plants; changing patterns of temperature, precipitation, and their attendant effects on growth, survival, and phenology may affect patterns of distribution and lead to novel assemblages of competitors. Examining plant survival and growth responses to climate in the context of biotic interactions such as competition and facilitation, as well as other biotic interactions such as pathogens that were not addressed in this study, is therefore critical. I found sugar maple seedling survival and growth varied clinally across the range and beyond range margins, with the nature and strength of effects strongly influenced by the latitude of population origin.

Though direct evidence of climatic or biotic constraints at either range margin was limited, it is plausible that both climate and biotic factors may impose constraints that are beyond the scope of this study to detect. Climate-mediated effects on phenology and growth may shift the competitive balance between species (Savage & Cavender-Bares 2013, Rawal *et al.* 2014), which in turn has the potential to influence species' distributions (Chuine & Beaubien 2001). Future range limit studies should examine changes in phenology and reproductive success at range margins and characterize the performance of the focal species relative to that of other competitors at range margins.

The natural forest environment of this experiment sets it apart from many range-limit studies (reviewed by Hargreaves *et al.* 2014) and enables a nuanced examination of biotic interactions with canopy and understory plants across a climate gradient. Seedling performance in this ecologically realistic context not only gives important insight into regeneration dynamics under a range of abiotic conditions but also potential responses to changing climate. This study suggests that while warmer temperatures themselves may not limit survival and growth directly, greater climate unpredictability could lead to changes in phenology, reproductive success, and competitive dynamics that would have implications for the extent and location of range boundaries.

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TABLES AND FIGURES

TABLE 1-1 The effects of population (northern, central, and southern origin), clip treatment (clipped or unclipped aboveground vegetation), light treatment (shaded understory or canopy gaps), and temperature (ten transplant sites spanning a 10.5° C difference in average summer temperature) on survival (nominal logistic model) and log-transformed seedling mass, diameter, height, and cumulative stem extension (linear mixed effects models) over a three-year period. In the mixed-effects models, both site and plot (nested within site) were entered as random effects to account for site-specific variation in seedling performance unrelated to temperature. Seedling mass, diameter, and height measurements were made at the end of the experiment; summer temperature (June/July/August) data, obtained from the PRISM Climate Group of Oregon State University and the Canadian National Climate Data and Information Archive, was averaged over the three years of the experiment. Log-transformed initial height was used as a covariate for all response variables but final diameter, where log-transformed initial diameter was used instead. Significance levels: $P < .0001$ (****), $P < .001$ (***), $P < .01$ (**), $P < .05$ (*), $P < .1$ (+)

Model Factor	Survival $\chi^2 = 410.01$ N = 1293	Mass $R^2 = .783$ N = 714	Diameter $R^2 = .795$ N = 772	Height $R^2 = .647$ N = 770	Extension $R^2 = .705$ N = 770
Population	****	****	****	-	****
Clip treatment	***	****	***	-	*
Light treatment	****	****	****	****	****
Temperature (3yrAv_JJA_MeanTemp)	****	-	+	-	-
Population x Clip	-	*	-	-	-
Population x Light	-	-	-	-	-
Population x Temperature	****	+	-	***	*
Clip x Light	-	-	-	+	-
Clip x Temperature	-	-	-	-	-
Light x Temperature	*	-	-	+	-
Population x Clip x Light	-	-	*	-	-
Population x Clip x Temperature	-	*	-	-	-
Population x Light x Temperature	-	-	-	-	-
Clip x Light x Temperature	-	-	-	+	-
Initial size covariate	-	****	****	****	****

TABLE 1-2 Spring and fall phenology data from two sites: the southern site (KOEN) was just beyond the continuous distribution of sugar maple, while the northern site (PIKE) was near the northern range margin. The date of each visit (DayCount) is given in number of days from Jan. 1. Phenology data is based on a subset of seedlings at each site: at KOEN, $N = 20$, 16, 19 (northern, central, and southern populations), and at PIKE, where no central seedlings survived and southern seedlings survived poorly, $N = 22$, 5 (northern, southern populations). At both sites, the northern population leafed out slightly before the southern population, but the southern population retained green leaves in the fall well after the northern population had senesced and consequently had a longer growing season, especially at the southern site. Initiation of spring leaf-out was measured from the first discernible changes in buds and complete when most leaves on an individual were extended and full size. Fall senescence was initiated with changes in leaf color and complete following full leaf abscission.

Spring Leaf-out 2011							
Site	DayCount	Northern population		Central population		Southern population	
		Initiated	Completed	Initiated	Completed	Initiated	Completed
KOEN	80	0%	0%	0%	0%	5%	0%
	87	50%	0%	12%	0%	11%	0%
	103	100%	65%	100%	19%	100%	29%
	110	100%	94%	100%	59%	100%	90%
PIKE	126	91%	0%	-	-	80%	0%
	140	100%	100%	-	-	100%	100%

Fall Leaf Senescence 2011							
Site	DayCount	Northern population		Central population		Southern population	
		Initiated	Completed	Initiated	Completed	Initiated	Completed
PIKE	265	5%	0%	-	-	0%	0%
	279	86%	36%	-	-	20%	0%
	293	100%	95%	-	-	100%	0%
KOEN	304	100%	89%	100%	29%	57%	5%

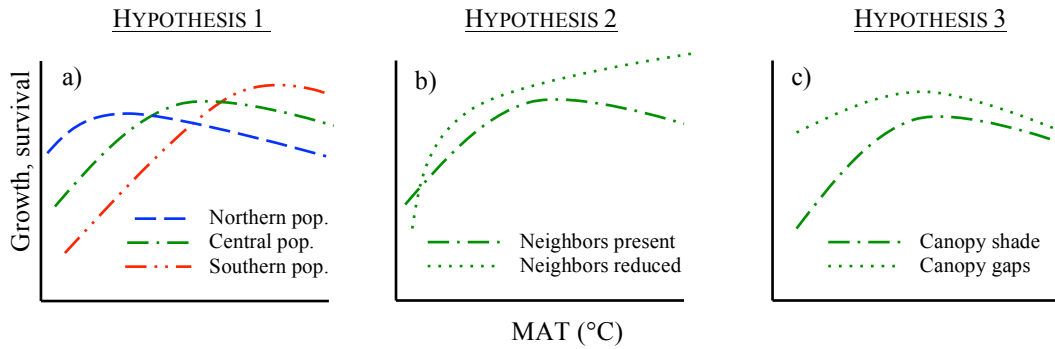


FIGURE 1-1 I hypothesized that for each of three subpopulations (from northern, central, and southern portions of the range), sugar maple seedling survival and net growth is (1) positively related to average summer temperature and winter minimum temperature, where each population's survival and net growth increases to a locally adapted optimum and then gradually declines with further warming such that each population has highest survival and growth in its region of origin. I further hypothesize that seedling survival and net growth is (2) reduced by understory neighbors across most of the range, especially towards southern range margins, but facilitated at the northern range margin, and (3) enhanced in canopy gaps, especially in the northern part of the range where cooler temperatures might cause high-light gaps to be less stressful for seedlings. Hypotheses 2 and 3 are here illustrated with the central population but similar patterns are expected across populations. As average summer (June-July-August) and winter (December-January-February) minimum temperatures are both highly correlated with mean annual temperature (MAT), I illustrate these hypotheses using MAT.

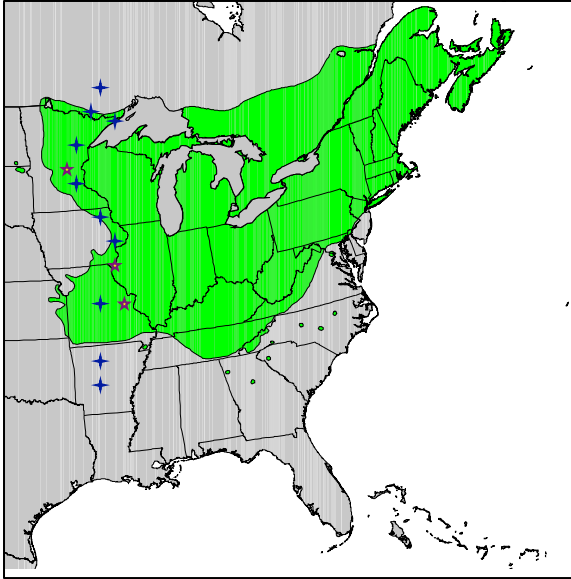


FIGURE 1-2 Range map for sugar maple (*Acer saccharum*), adapted from Little (1971). In the western portion of its range, sugar maple can be found from southern Missouri to the Minnesota/Ontario border. Seedlings were planted at ten sites along a north-south transect of the western edge of the species' range and beyond range margins to the north and south. Four-pointed stars indicate planting sites, and five-pointed stars mark the county of seed origin for each population.

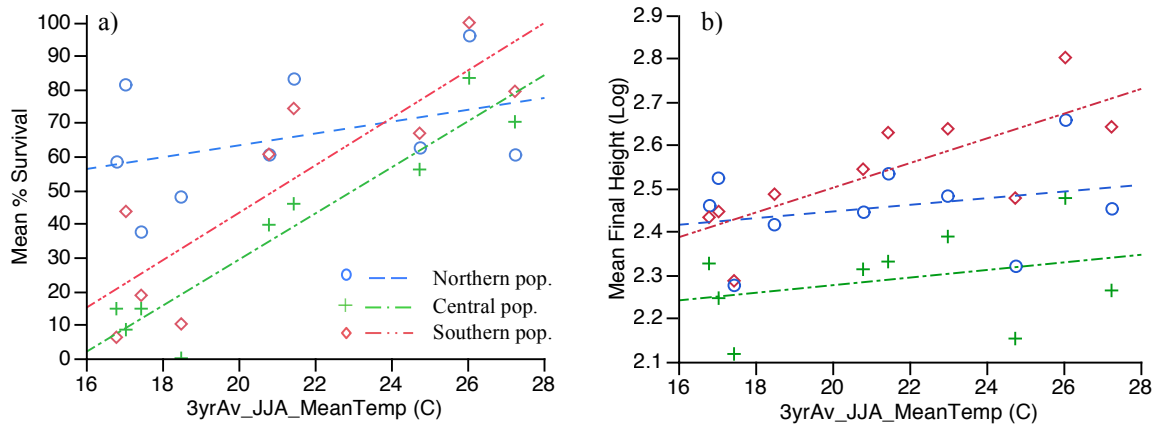


FIGURE 1-3 Final percent survival (a) and final height (b) of seedlings across sites. Both seedling survival and final height are positively correlated with summer temperature, increasing at warmer (lower latitude) sites. At northern sites, the northern population out-survived (but did not substantially outgrow) the southern population, while at southern sites the southern population both outgrew and out-survived the northern population, though differences in survival were less marked. Other growth metrics (not shown) such as total stem extension, final stem diameter, and final seedling mass showed similar patterns to height, but the southern population had higher growth than the northern population even at the coldest sites.

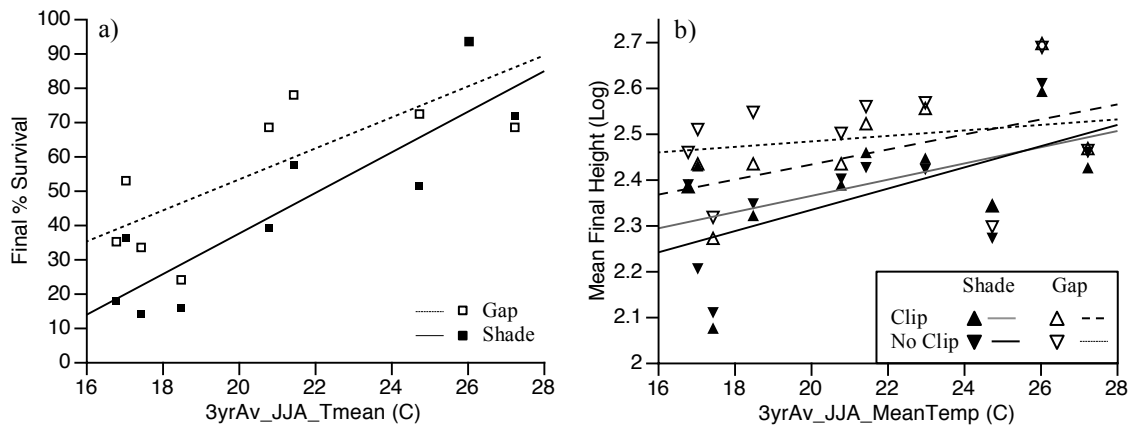


FIGURE 1-4 Final percent survival (a) and final height (b) of seedlings across sites, separated by light treatment (a,b) and clip treatment (b). For both survival and net growth, differences between light treatments (shaded and open symbols) were greatest at northern (colder) sites. The clipping treatment, however, reduced the difference in height between seedlings in gaps and shade at northern sites: seedlings in gaps grew less in clipped plots, while seedlings in the shade grew more in clipped plots.

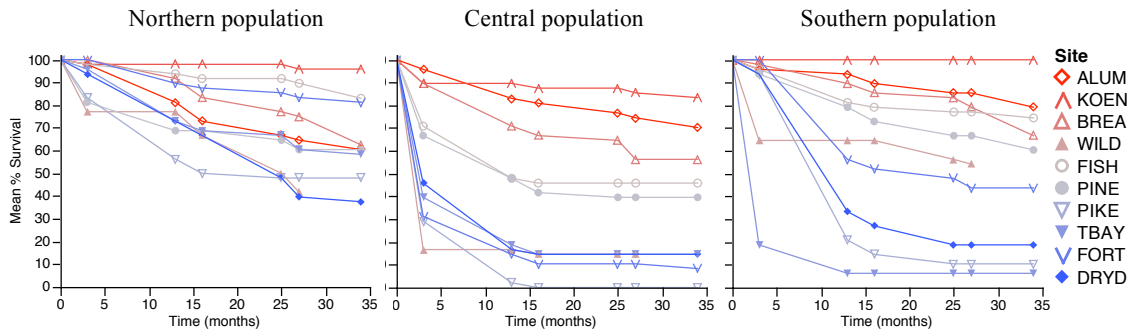


FIGURE 1-5 Percent survival over time for the northern, central, and southern populations, separated by site. Each site has a unique symbol and is listed from southern to northern latitudes (top to bottom). One centrally located site (WILD) was harvested early, so no data is available for the last time step. Survival declines over time at most sites, but is lowest at northern sites and most mortality occurred in the first year, whereas mortality at southern sites was more constant across years.

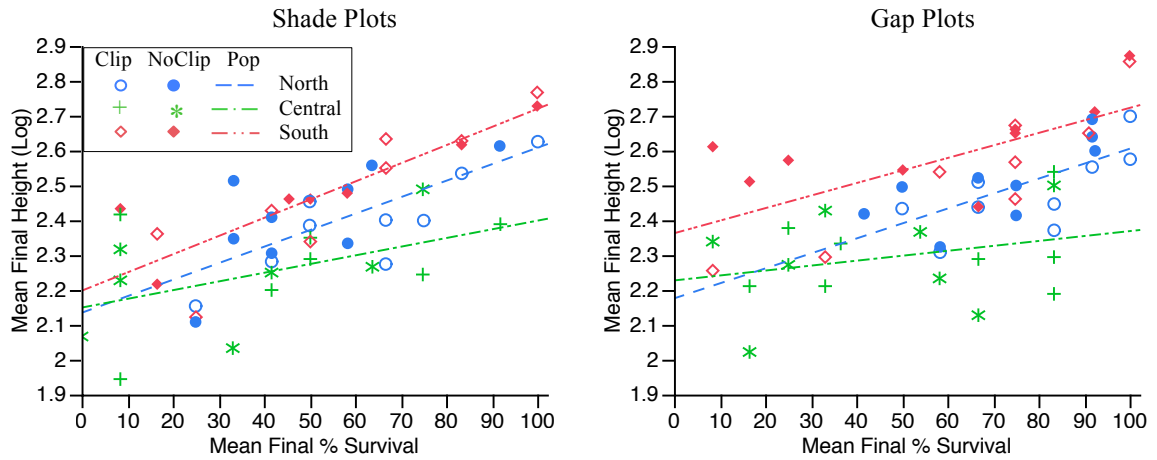


FIGURE 1-6 The relationship between seedling final height and survival for the northern, central, and southern populations in shade and canopy gaps. Final height and survival are strongly correlated for northern and southern populations: taller seedlings survived better, and the relationship between height and survival was more strongly positive in shade than in gaps. The central population had poor performance across sites and grew less than other populations even at sites where it had high survival.

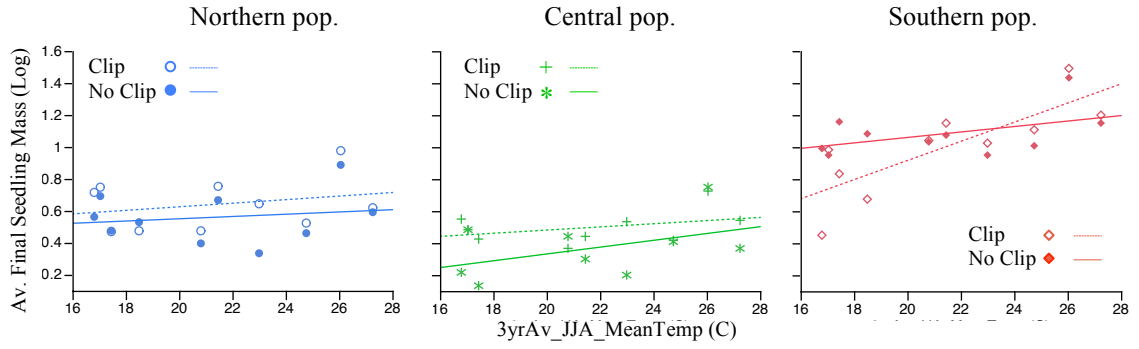


FIGURE 1-7 Seedling mass across sites for the northern, central, and southern populations, separated by clip treatment. Northern and central populations have higher mass in clip plots, while the southern seedling has higher mass in unclipped plots at northern sites and in clipped plots at southern sites.

SUPPLEMENTAL INFORMATION

TABLE S1-1 Summary annual climate data (calculated from 30-year climate normals, 1971 - 2000) and soil characteristics for each site. Climate data were obtained from the PRISM Climate Group of Oregon State University (for the seven sites in the United States) and the Canadian National Climate Data and Information Archive (for the three sites in Ontario, Canada). Soil texture and pH were measured in the lab from soil samples collected at each site in 2011.

Site	Latitude Longitude	MAT (°C)	Total Ann PPT (mm)	Ann. Moisture Avail.	Soil texture	Soil pH
Jessieville, Arkansas (ALUM)	34.8 <i>N</i> / 93.0 <i>W</i>	16.1	1569	1.80	Loam	4.14
Jasper, Arkansas (KOEN)	36.0 <i>N</i> / 93.2 <i>W</i>	14.4	1196	1.49	Silt loam	4.62
Ashland, Missouri (BREA)	38.7 <i>N</i> / 92.2 <i>W</i>	12.5	1023	1.35	Silt loam	4.8
Muscatine, Iowa (WILD)	41.5 <i>N</i> / 90.9 <i>W</i>	10.3	912	1.30	Silt loam	6.54
New Albin, Iowa (FISH)	43.5 <i>N</i> / 91.3 <i>W</i>	7.8	853	1.35	Sandy loam	6.81
Marine-on-St. Croix, Minnesota (PINE)	45.2 <i>N</i> / 92.8 <i>W</i>	7.2	815	1.28	Sandy loam	6.75
Cass Lake, Minnesota (PIKE)	47.3 <i>N</i> / 94.5 <i>W</i>	3.9	670	1.19	Loam	5.1
Neebing, Ontario (TBAY)	48.3 <i>N</i> / 89.4 <i>W</i>	2.5	712	1.39	Sandy loam	5.18
Fort Frances, Ontario (FORT)	48.8 <i>N</i> / 93.4 <i>W</i>	2.9	721	1.33	Sandy loam	4.55
Dryden, Ontario (DRYD)	49.9 <i>N</i> / 92.3 <i>W</i>	2.1	701	1.31	Sandy loam	4.53

TABLE S1-2 Climate-of-origin data for the three populations in this field experiment, based on 30-year climate normals (1981-2010) obtained from the PRISM Climate Group of Oregon State University. Moisture availability (PPT/PET) was calculated using equations from Thornthwaite (1948). Seedlings were purchased from three nurseries whose seed sources were sugar maple populations in Mille Lacs County, MN, Lee Co., IA, and Lincoln Co., MO (north, central, and south populations, respectively).

Population	Latitude	Elevation (m)	Annual			Summer (June/July/August)		
			Temp _{mean} (° C)	PPT _{total} (mm)	Moisture Avail.	Temp _{mean} (° C)	PPT _{total} (mm)	Moisture Avail.
North	45.90453	368	5.3	781	1.34	19.3	322	0.88
Central	40.61227	176	11.3	978	1.34	23.7	329	0.77
South	39.02523	179	12.6	1031	1.36	24.3	290	0.67

TABLE S1-3 Summary climate data (average summer temperature, summer precipitation, and winter minimum temperature, with standard deviations) for each site, comparing climate normals (1971 – 2008) and the years of the experiment (2009 – 2011). Actual temperatures experienced by seedlings during the growing season are likely somewhat cooler, as seedlings were in the understory and most were shaded to some degree, even in gaps. Climate data were obtained from the PRISM Climate Group of Oregon State University (for ALUM, KOEN, BREA, WILD, FISH, PINE, and PIKE) and the Canadian National Climate Data and Information Archive (for TBAY, FORT, and DRYD).

Latitude (°N)	Site	Prior to Experiment (1971- 2008)			During Experiment (2009-2011)		
		Mean JJA Temp (°C) (SD)	Mean JJA PPT (mm) (SD)	Mean DJF Tmin (°C) (SD)	Mean JJA Temp (°C) (SD)	Mean JJA PPT (mm) (SD)	Mean DJF Tmin (°C) (SD)
34.8	ALUM	25.90 (0.86)	102.60 (30.02)	0.68 (1.42)	27.34 (1.70)	101.06 (12.36)	0.49 (1.45)
36.0	KOEN	24.58 (0.88)	85.16 (22.02)	-2.71 (1.73)	25.96 (1.76)	75.97 (26.92)	-2.84 (1.74)
38.7	BREA	24.45 (0.97)	99.94 (38.63)	-5.15 (1.97)	24.99 (1.66)	120.65 (28.37)	-5.47 (2.12)
41.5	WILD	23.00 (0.96)	105.66 (38.99)	-8.27 (2.40)	23.15 (1.55)	140.88 (56.22)	-8.95 (2.51)
43.5	FISH	21.45 (0.95)	112.93 (36.86)	-11.17 (2.78)	21.73 (1.65)	124.25 (57.25)	-11.32 (3.15)
45.2	PINE	20.68 (1.01)	111.31 (30.32)	-13.64 (2.81)	20.51 (1.40)	118.31 (16.51)	-13.97 (3.49)
47.3	PIKE	18.72 (1.10)	95.15 (23.74)	-17.96 (3.08)	18.46 (1.51)	92.10 (31.49)	-17.60 (3.78)
48.3	TBAY	16.22 (0.93)	79.90 (20.50)	-18.24 (2.67)	16.82 (1.75)	74.77 (12.08)	-17.27 (3.36)
48.8	FORT	17.48 (1.13)	97.34 (29.91)	-19.10 (3.30)	17.04 (1.43)	87.14 (35.29)	-20.07 (4.47)
49.9	DRYD	17.56 (1.24)	96.02 (23.26)	-19.78 (2.76)	17.46 (1.43)	88.24 (34.72)	-18.23 (3.97)

TABLE S1-4 Seasonal patterns in seedling mortality for northern and southern populations at each site, illustrated by the proportion of seedlings that died from one time step to the next. Northern and southern populations have similar rates of summer mortality (those that died between spring and summer visits) but differ in winter mortality (those that died between the summer visit and the following spring visit), especially at northern sites, where the southern population had high winter mortality. Seedlings at WILD had to be harvested early, so mortality is not available for winter 2011.

Site	Northern Population						Southern Population					
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
	2009	2009	2010	2010	2011	2011	2009	2009	2010	2010	2011	2011
ALUM	0.02	0.17	0.10	0.09	0.03	0.06	0.04	0.02	0.04	0.05	0	0.07
KOEN	0.02	0	0	0	0.02	0	0	0	0	0	0	0
BREA	0	0.08	0.09	0.08	0.03	0.17	0.02	0.09	0.05	0.02	0.05	0.16
WILD	0.23	0	0.14	0.25	0.17	-	0.35	0	0	0.13	0.04	-
FISH	0.02	0.04	0.02	0	0.02	0.07	0.04	0.15	0.03	0.03	0	0.03
PINE	0.19	0.15	0	0.06	0.06	0	0.06	0.16	0.08	0.09	0	0.09
PIKE	0.17	0.33	0.11	0.04	0	0	0.06	0.78	0.3	0.29	0	0
TBAY	0.04	0.24	0.06	0.03	0.09	0.03	0.81	0.67	0	0	0	0
FORT	0	0.10	0.02	0.02	0.02	0.03	0	0.44	0.07	0.08	0.09	0
DRYD	0.06	0.22	0.09	0.28	0.17	0.05	0.06	0.64	0.19	0.31	0	0

TABLE S1-5 The effects of population (northern, central, and southern origin), clip treatment (clipped or unclipped aboveground vegetation), light treatment (shaded understory or canopy gaps), and temperature (ten transplant sites spanning a 10.5° C difference in average summer temperature) on log-transformed annual and final seedling survival in nominal logistic models. Summer temperature (June/July/August) data was obtained from the PRISM Climate Group of Oregon State University and the Canadian National Climate Data and Information Archive; three-year average summer temperature was used for the final survival model. The previous year's log-transformed height was used as a covariate for annual models, and log-transformed initial height was used as a covariate for the final survival model. Significance levels: $P < .0001$ (****), $P < .001$ (***), $P < .01$ (**), $P < .05$ (*), $P < .1$ (+).

Model Factor	2009	2010	2011	2012	Final
	$\chi^2 = 337.14$ N = 1439	$\chi^2 = 528.82$ N = 1333	$\chi^2 = 105.50$ N = 857	$\chi^2 = 46.30$ N = 711	$\chi^2 = 410.01$ N = 1293
Population	****	****	***	+	****
Clip treatment	-	*	**	+	***
Light treatment	**	****	+	+	****
Temperature	****	****	-	-	****
Population x Clip	-	-	-	-	-
Population x Light	+	-	-	-	-
Population x Temp.	**	****	-	-	****
Clip x Light	-	+	-	-	-
Clip x Temp.	-	-	-	-	-
Light x Temp.	-	**	-	-	*
Pop. x Clip x Light	-	-	-	**	-
Pop. x Clip x Temp.	-	-	+	-	-
Pop. x Light x Temp.	-	-	-	*	-
Clip x Light x Temp.	-	-	-	+	-
Log prev. year's size	**	*	****	***	-

TABLE S1-6 The effects of population (northern, central, and southern origin), clip treatment (clipped or unclipped aboveground vegetation), light treatment (shaded understory or canopy gaps), and temperature (ten transplant sites spanning a 10.5° C difference in average summer temperature) on log-transformed annual seedling height, stem extension, and diameter in linear mixed effects models (data on diameter was not collected in 2009). Summer temperature (June/July/August) data was obtained from the PRISM Climate Group of Oregon State University and the Canadian National Climate Data and Information Archive. The previous year's log-transformed height (for height and extension models) or log-transformed diameter (for diameter models) was used as a covariate for annual models. Significance levels: $P < .0001$ (****), $P < .001$ (***), $P < .01$ (**), $P < .05$ (*), $P < .1$ (+).

Model Factor	2009		2010			2011		
	Height R ² = .82 N = 1333	Extens. R ² = .22 N = 1339	Height R ² = .79 N = 847	Extens. R ² = .52 N = 868	Diam. R ² = .84 N = 896	Height R ² = .85 N = 769	Extens. R ² = .64 N = 770	Diam. R ² = .83 N = 768
Population	-	****	-	****	***	***	****	****
Clip treatment	*	-	-	-	*	-	**	*
Light treatment	-	-	****	****	***	****	****	***
Temperature	****	**	*	+	*	-	-	-
Population x Clip	-	-	-	-	-	-	-	-
Population x Light	-	-	-	****	-	-	-	-
Population x Temp.	****	****	****	****	-	-	-	-
Clip x Light	-	-	-	-	-	-	-	-
Clip x Temp.	-	**	-	+	-	-	-	-
Light x Temp.	-	-	+	****	-	-	-	-
Pop. x Clip x Light	-	-	-	-	-	-	-	*
Pop. x Clip x Temp.	-	-	-	-	-	-	-	-
Pop. x Light x Temp.	-	+	-	***	-	*	-	-
Clip x Light x Temp.	-	-	-	-	-	-	-	-
Log prev. year's size	****	****	****	***	****	****	****	****

TABLE S1-7 Average temperature over the three years of the experiment compared to 20th century averages for mean annual temperature (MAT), mean summer temperature (June/July/August), and mean winter minimum temperature (December/January/February) at International Falls, MN (48.5917° N, 93.4053° W), a location at the current northern range limit of sugar maple that occurs along this study’s latitudinal transect. Differences in yearly temperature metrics that exceeded one standard deviation from the long-term mean are given in bold: summer 2009 was over 2° C cooler, 2010 was warmer overall, and 2011 had winter minimum temperatures over 6° C warmer than the long-term average. Historical climate data for the past century were obtained from the PRISM Climate Group of Oregon State University; no corresponding dataset is available for sites beyond the range limit.

	Summer Mean Temp.			Winter Mean min. Temp.			Mean Annual Temp.		
	Average 1900-1999: 17.61° C (1.06)			Average 1900-1999: -19.76° C (2.70)			Average 1900-1999: 2.88° C (0.99)		
<i>Year of Experiment</i>	<i>2009</i>	<i>2010</i>	<i>2011</i>	<i>2009</i>	<i>2010</i>	<i>2011</i>	<i>2009</i>	<i>2010</i>	<i>2011</i>
Temperature (°C)	15.27	17.93	17.73	-19.67	-20.6	-13.53	2.1	4.1	3.3
Av. temperature diff. (°C)	-2.34	0.32	0.12	0.11	-0.84	6.23	-0.78	1.22	0.42

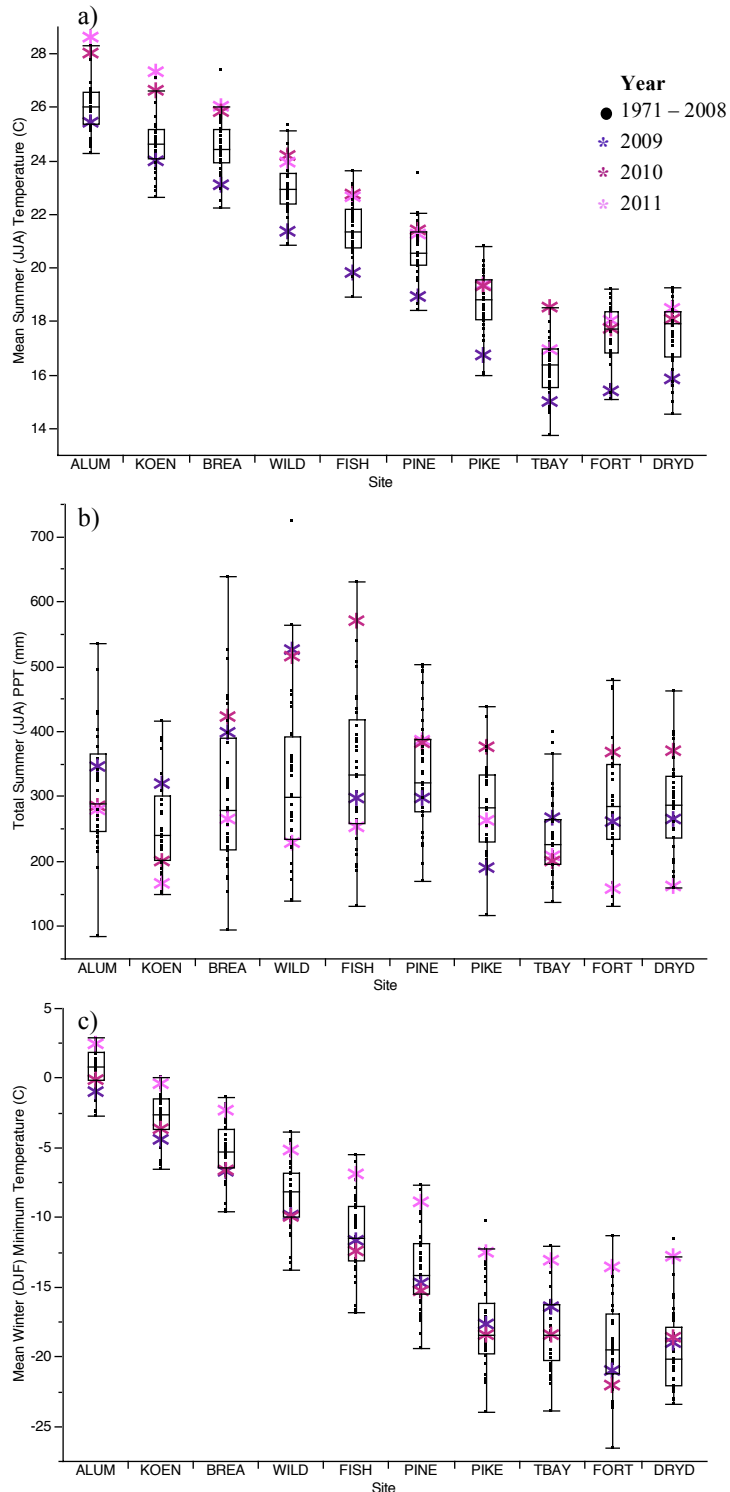


FIGURE S1-1 Climate normals (1971 – 2008) and climate for years of experiment (2009 – 2011) for (a) mean summer temperature, (b) mean summer precipitation, and (c) mean winter minimum temperature for each of the planted sites (arranged south to north, left to right). Box plots show quantiles and outliers.

Chapter 2

Root biomass fraction of forest-planted sugar maple (*Acer saccharum* Marsh.) seedlings varies with climate of population origin across a latitude gradient

SUMMARY

Relative biomass distribution to above- and belowground plant organs is expected to reflect allocation to the most limiting resource, but because belowground biomass is difficult to measure, root allocation patterns across climate and resource gradients remain poorly understood. I examine root biomass in three populations of sugar maple seedlings representing a climate-of-origin gradient, experimentally planted at forested sites along a north-south transect spanning the species' range and at sites beyond range margins. I also examine the effect of contrasting light levels and neighbor density by comparing root mass of seedlings grown in shaded understory and canopy gaps, and those with surrounding aboveground vegetation reduced ("clip" plots) or undisturbed ("no clip" plots). After accounting for differences in seedling size, I expect higher root mass in seedlings from cold region-of-origin populations and those grown at high-latitude sites, in canopy gaps, and surrounded by higher densities of neighbors, all environments where I hypothesize belowground resources will be more limiting than light. I also expect populations from lower latitudes to have more plasticity in root biomass across environments than populations from high latitudes. In contrast to my expectations and many other studies, I find higher root biomass in the low-latitude (southern) population, a potentially adaptive difference that could indicate soil nutrient and/or water limitation in its region of origin. The southern population also has more plasticity in root biomass distribution, increasing root biomass at cold high-latitude sites. I do not, however, find a biologically significant effect of neighbor density or light environment on root biomass distribution. I conclude that biomass distribution to roots may vary along broad temperature and resource gradients but is not responsive to changes in local resource environment once plant size is taken into account. Plasticity of root biomass appears to vary among populations, and high plasticity may allow the southern population to cope with increasingly variable growing conditions under climate change. Because I used allometric analyses, this research is able to distinguish between differences in biomass distribution due to size and those that are the result of plasticity or selection.

INTRODUCTION

The effect of resource and climate gradients on plant biomass allocation has been an enduring focus of ecological research and theory. Carbon distribution to above- and belowground plant tissues, which directly influences plant resource uptake and growth, can be viewed as a reflection of growth constraints across environmental gradients, as I expect plants to preferentially allocate biomass to enhance acquisition of the most limiting resource (Bloom *et al.* 1985). Biomass allocation may therefore vary across habitats and resource environments (Poorter *et al.* 2012), yet patterns of belowground biomass distribution remain poorly understood, especially in a natural growing environment across multiple sites (Smithwick *et al.* 2014). Determining how root biomass shifts across large-scale latitude and temperature gradients will contribute to basic foundations of ecological knowledge and also has implications for understanding potential responses to climate change.

Clinal variation in soil temperature across latitude gradients directly influences root processes, affecting root growth and respiration as well as rates of nutrient and water uptake (Pregitzer *et al.* 2000). Several studies have found an inverse relationship between root biomass fraction and temperature (Fan *et al.* 2009, Luo *et al.* 2012, Poorter *et al.* 2012, Reich *et al.* 2014), but while shifts in biomass allocation with temperature are apparent from data aggregated across species and biomes, the extent to which individual species change allocation patterns in response to temperature is unclear. Co-occurring tree species may vary in root traits (Comas & Eissenstat 2009) and in their response to temperature (Lee *et al.* 2007), and intraspecific populations from contrasting climates may differ in root mass fraction (Oleksyn *et al.* 1992). Additionally, species from habitats of contrasting quality may differ in plasticity of biomass allocation (Atkin *et al.* 2006). Among woody species, however, such plasticity may be limited at the seedling stage by developmental constraints (Gedroc *et al.* 1996, Lohier *et al.* 2014), and in a review of biomass allocation across species and environments, Poorter *et al.* (2012) concluded that morphology tends to be more plastic than allocation. Further research is needed on root biomass allocation patterns at the species level to determine whether and how species may shift biomass allocation in response to a temperature gradient.

At a local scale, plants may also plastically shift biomass allocation in response to changing availability of resources such as light (Givnish 1988, Portsmouth & Niinemets 2007), nutrients (Müller *et al.* 2000, Hodge 2004), and soil moisture (Hertel *et al.* 2013). In low-light environments, plants may allocate less biomass to roots (Reich *et al.* 1998), especially for shade-intolerant species (Walters *et al.* 1993), which tend to demonstrate greater plasticity in biomass allocation than shade-tolerant species (Gunton *et al.* 2010). In response to belowground resources, root growth often increases where soil nutrients or moisture are limiting (Müller *et al.* 2000, Kozłowski & Pallardy 2002). Plants grown with high neighbor densities under field conditions or where nitrogen was limiting exhibited larger root biomass fractions, but this effect disappeared in enriched environments, suggesting a plastic biomass allocation response to soil resource availability (Gleeson & Tilman 1994, Berendse & Möller 2009). Whether belowground biomass allocation is plastic in response to both temperature and neighbor density, however, has not been examined on a regional scale.

Intraspecific genetic variation across latitude gradients has been noted for a wide array of both above- and below-ground plant traits (De Frenne *et al.* 2013). There is conflicting evidence on whether and how populations differ in patterns of belowground biomass allocation, however, despite a consistent trend for species' proportional root biomass allocation to increase with latitude across large geographic scales (*e.g.* Fan *et al.* 2009, Luo *et al.* 2012, Reich *et al.* 2014). Within some species, studies have found higher root allocation relative to shoots or needles in populations originating from cold northern latitudes (Oleksyn *et al.* 1992, Maron *et al.* 2007, De Frenne *et al.* 2012) or high altitudes (Oleksyn *et al.* 1998, Johnston & Pickering 2004), while other studies have found the opposite pattern (Reinartz 1984, Montesinos-Navarro *et al.* 2011, Matías *et al.* 2014). Common garden experiments that span latitude gradients are an important yet under-utilized tool for examining intraspecific responses to temperature in the context of interacting environmental factors (De Frenne *et al.* 2013). Further research is needed on intraspecific variation in biomass allocation and how climate of origin influences distribution of biomass, if at all.

Intraspecific variation may extend to plasticity among populations (Ackerly *et al.* 2000, Des Marais *et al.* 2013), including plasticity to belowground biomass allocation (Bell & Sultan 1999). Differences in plasticity among populations could be due in part to evolutionary constraints such as limited gene flow and stressful abiotic conditions reducing plasticity in populations near range margins (Kirkpatrick & Barton 1997, Colautti *et al.* 2010). Among populations, plasticity may covary with growth rates (Crick & Grime 1987, Grassein *et al.* 2010), and relative growth rate in turn tends to vary with a population's altitude (Jia *et al.* 2010) or latitude of origin (Li *et al.* 1998, Miyazawa & Lechowicz 2004, Koehler *et al.* 2012). Although reciprocal transplant experiments have a long history and are powerful tools for describing variation among populations (*e.g.* Hall 1932, Hiesey 1940, Rehfeldt *et al.* 1999, De Kort *et al.* 2014), few studies have explored population differences in root traits across multiple common gardens (but see Santamaria *et al.* 2003, De Frenne *et al.* 2012). Consequently, there is only limited data on plasticity of root traits across natural environmental gradients.

An additional limitation of prior attempts to describe plasticity in belowground biomass allocation lies in conflating ontogenetically-influenced differences in allocation with phenotypic plasticity. Differential rates of growth among plants in experimental treatments may cause substantial size variation among same-aged plants. It has been repeatedly noted that biomass allocation changes with plant size and ontogeny (Troughton 1956, Evans 1972, Coleman *et al.* 1994, Reich 2002), and that proportional comparisons of root and shoot biomass between treatments may inflate or misrepresent the treatment effect (McConnaughay & Coleman 1999, Reich 2002). Allometric analyses are therefore the preferred approach for distinguishing between changes in root mass fraction due to experimental conditions (“true plasticity”) and those that are a function of size (Reich 2002, Weiner 2004). Despite this, few studies that measure both above- and below-ground biomass employ an allometric approach, and further research is needed on this front.

Sugar maple (*Acer saccharum* Marsh.), a shade-tolerant species common to mesic hardwood forests of the eastern and central United States (Godman *et al.* 1990), was selected to investigate root allocation across a latitude gradient and potential intraspecific

variation in response to climate, light environment, and neighbor density. Sugar maple's range spans a climate gradient typical of many hardwood species that characterize eastern forests in the United States, and genetic variation in the species has been identified for potentially relevant traits such as heat and drought tolerance, onset of dormancy, chilling requirements, timing of leaf flush, and growth rate (Kriebel & Gabriel 1969).

Furthermore, among hardwood tree species, sugar maple's root morphology is well-suited for root studies in a natural setting, as its shallow roots relative to many deep-taprooted species (Pallardy & Rhoads 1993) make excavating forest-planted seedlings easier.

To determine how root mass fraction might change across a latitude and climate gradient and whether there are intraspecific differences in patterns of root biomass allocation, I conducted a reciprocal transplant experiment at ten sites along a north-south transect of sugar maple's range encompassing a 14 °C MAT gradient. Three populations, originating from mid-latitude, southern, and northern portions of the range, were planted at all sites under natural forest conditions and differing levels of light and neighbor density. At the conclusion of three growing seasons, I harvested all living sugar maple seedlings and measured root and shoot dry mass fractions.

Temperature gradients may affect the availability of soil resources both directly and indirectly: evapotranspiration increases with temperature, leading to drier soils and potential water limitation in warm regions, while the rate of plant processes such as water and nutrient uptake can be temperature-limited in cold regions, functionally reducing soil resource availability (Lambers *et al.* 1998). While temperature limitation places a constant constraint on resource availability that would favor higher investment in roots, water limitation in periodically dry environments may be interspersed with pulses of water availability better captured by plasticity in root morphology than root biomass (Padilla *et al.* 2014). Across broad temperature gradients, evidence suggests roots comprise a higher proportion of total plant biomass at higher latitudes (Fan *et al.* 2009, Luo *et al.* 2012, Poorter *et al.* 2012, Reich *et al.* 2014), and I therefore expect that seedlings at the coldest sites will have a higher fraction of biomass in roots.

Higher root mass fractions are often found in populations originating from colder regions (Oleksyn *et al.* 1998, Maron *et al.* 2007, De Frenne *et al.* 2012), and populations from high altitudes or latitudes also tend to have lower growth rate (Darychuk *et al.* 2012, Koehler *et al.* 2012) and conservative functional trait values (Díaz *et al.* 2004, Wright *et al.* 2005). Plasticity in biomass distribution, on the other hand, is hypothesized to be higher in populations that occupy more variable environments, are resource-acquisitive and have higher growth (Grassein *et al.* 2010). I expect a greater proportion of biomass distributed to roots in the slower-growing northern population and higher plasticity in biomass distribution in the southern population, patterns consistent with local adaptation to resource availability and growing conditions in their region of origin.

Biomass allocation to roots may also shift in response to the availability of above- and belowground resources. Consistent with theory that predicts greater allocation to the most limiting resource (Bloom *et al.* 1985), root mass fraction tends to decrease at high levels of soil nutrients and water and increase in high irradiance environments (Poorter *et al.* 2012). I therefore expect root mass fraction to increase with neighbor density and in canopy gaps. Among studies that account for seedling size, however, there is only limited evidence of shifts in allocation in response to water and nutrients (Reich 2002), and I have no clear *a priori* expectation of the degree of effect understory light levels or competition would have on patterns of biomass distribution in an allometric analysis.

RESEARCH METHODS

Sugar maple seedlings from subpopulations originating from northern, central, and southern portions of its range (Table S1-2) were planted at sites across a north-to-south transect of the species' range and beyond range margins (Fig. 2-1) as part of an experiment examining the effects of climate and local understory competition on seedling performance and potential constraints on range limits (see Chapter 1). Young sugar maple were purchased as one-year-old field-grown seedlings from three commercial nurseries whose seed sources were sugar maple populations in Mille Lac County, MN (5.3° C MAT), Lee County, IA (11.1° C MAT), and Lincoln County, MO (12.4° C MAT).

The northern, central, and southern populations thus spanned the westernmost extent of sugar maple's distribution (Fig. 2-1) and a 7.1° C range in MAT.

The latitude and climate gradient encompassed by the planting sites is characterized by a 14° C range in mean annual temperature (2.1° to 16.1° C MAT) and 868 mm range in total annual precipitation (701 to 1569 mm north to south). Average June/July/August (hereafter referred to as “summer”) temperatures over the past three decades range from 17.5° C in the north to 27.3° C in the south, while precipitation totals for June through August vary from 265 to 303 mm across sites, with no clear latitudinal trend (Fig. S2-1). Average soil moisture availability over a 30-year period is also relatively even across sites: the site-specific index of moisture availability (PPT/PET) ranges from 0.63 to 0.88 on average, with slightly greater soil moisture availability at higher latitudes (Fig. S2-1). Conditions in the three years of this experiment generally tracked climate normals closely, though total precipitation (and consequently, soil moisture availability) were notably higher in the central portion of the range than the long-term average (Fig. S2-1).

Seedlings from all three populations were planted at all sites in the spring of 2009. Of the ten sites at which seedlings were planted, six encompassed a north-south transect of sugar maple's range on the western edge of the species' distribution and two each were located beyond the northern and southern range margins, in Ontario and Arkansas, respectively. Data from only eight sites were used for this paper, however, because at two northern within-range sites (PIKE and TBAY) the number of surviving seedlings from central and southern populations was insufficient for statistical analyses. Initial seedling size differed among populations: those from the southern population had the greatest height and root collar diameter, while the central population had the least. Roots were trimmed to 25 cm prior to planting, and most seedlings had roots that required trimming.

Seedlings were planted in a natural setting within forests that had not been recently logged or burned. Each plot had a seedling from each of the three populations; seedlings were grown in individual fine plastic mesh sleeves to reduce damage from deer browse. Plots were randomly located within a stratified experimental design, and were evenly divided between those located in small canopy gaps within the forest interior and

those under the closed forest canopy. In each light environment, half the plots received an annual clipping treatment in a 2-m radius of planted seedlings to reduce the aboveground density of understory vegetation, while in the remaining plots seedlings were grown in the naturally occurring understory vegetation matrix. Because belowground competition was neither directly manipulated nor quantified, the clip treatment achieved only a reduction in aboveground neighbor interactions and neighboring vegetation likely influenced seedlings to some extent in both clipped and unclipped plots.

After three complete growing seasons, seedlings were dug up by hand in the spring of 2012 before growth commenced; consequently, seedling mass in this study does not include photosynthetic tissue. The majority of roots were successfully unearthed, and while fine and coarse roots were not measured separately, both were present. Most seedlings had essentially clean roots at harvest, as the majority of the harvest was done under dry conditions and most sites had sandy or silt loam soils. Those seedlings that were harvested under wet conditions were rinsed in the field (if the mud was excessive) and further soil was removed after air-drying. Seedlings were then kiln dried at 75° C, and dry mass of roots and shoots were recorded separately. Within-population variation in the size of the seedlings, all same-aged, enabled an allometric analysis of how the distribution of biomass to roots shifts with seedling size. This experiment does not address changes in allometry over time, however, as all seedlings were collected in a single harvest.

Climate data used for analyses were obtained from the PRISM Climate Group (Oregon State University, <http://prism.oregonstate.edu>, downloaded Nov. 2012) for sites in the United States, while for the three sites in Canada, climate data was gathered from weather stations nearest to each site via the Canadian National Climate Data and Information Archive (Government of Canada, <http://climate.weather.gc.ca>, downloaded Nov. 2012). PRISM model output is based on weather station data, interpolated using local data such as elevation, and is accurate to 2 km; Canadian weather station data accuracy ranges from 15 to 24 km.

STATISTICAL ANALYSIS

Seedling root biomass was analyzed using an allometric approach that accounts for potential variation in biomass distribution with plant size. In all models, log-transformed dry mass of roots was the response variable and log-transformed dry mass of non-photosynthetic shoots was included as a predictor. Analyses employed a standard least squares mixed model (REML) approach; both site and plot (nested within site) were entered as random effects to account for site-specific variation in seedling performance unrelated to the climate gradient.

The distribution of research sites was explicitly designed to encompass a temperature gradient and address hypotheses on temperature effects on root allocation; I therefore focused my analyses on temperature. While my hypotheses of seedling performance across the temperature and latitude gradient are linked to moisture availability, a model with temperature alone was superior to models including both climate variables, based on AIC values. I used summer (June/July/August) average temperature rather than mean annual temperature, as the former reflects conditions during the growing season when the majority of tissue allocation occurs.

Analyses initially included three-way interactions, but as none were significant, these were dropped from the model. There were only five sites where more than ten seedlings of all three populations were present (ALUM, KOEN, BREA, FISH, and PINE), so most models were run on a subset of the data that included just northern and southern populations at the aforementioned sites as well as two sites (WILD and FORT) where the central population survived poorly but the southern population had more than ten surviving seedlings. The full model (with population, temperature, log shoot mass, clip treatment, light treatment, and interactions) showed differences in allocation between clip and light treatments that, while significant, were too small to interpret in a biologically meaningful manner, and as there was no significant interaction with either clip or light treatments, these effects were dropped from subsequent models. The simplified model (population, temperature, log shoot mass, and interactions) was then run for two populations (northern and southern) and eight sites (including DRYD, where the southern population had nine surviving seedlings). In addition, the simplified model was run for all

three populations with the subset of five sites where seedlings from the central population were present in sufficient numbers. All analyses excluded two sites (PIKE and TBAY) where only the northern population had more than eight seedlings that survived to the conclusion of the experiment. Data were analyzed with JMP Pro 9.0 statistical software (SAS Institute Inc.).

RESULTS

Population origin affected patterns of root biomass distribution, both as a main effect and through interactive effects with climate at planting sites (Table 2-1). The populations differed significantly in root mass fraction ($F_{1,365} = 233$, $P < .0001$) but opposite that which I had hypothesized: seedlings from the southern population consistently had higher root mass than similarly-sized northern population seedlings (Fig. 2-2a, 2-3, 2-4, 2-5, 2-6). Moreover, in an analysis of the five sites where all three populations were present, the central population had intermediate root allocation: at a given shoot mass, it had less root mass than the southern population but more than the northern population (Fig. 2-2b). Though the populations differed in average initial seedling size, these population differences in proportional biomass distribution are robust, as analyses took size differences into account.

The difference between populations in allometric patterns of root mass distribution was greatest at northern sites: at the southernmost site, northern and southern population with similar shoot mass had approximately equal root mass, while at more northern sites, southern population seedlings had significantly more root mass than similarly-sized seedlings from the northern population (population \times temperature interaction, $F_{1,330} = 14.0$, $P = .0002$, Table 2-1; Fig. 2-3, 2-4). This underscores the importance of looking at biomass distribution patterns at the population level, as populations' significantly different responses to temperature may be obscured at the species level.

The allometric relationship between root and shoot mass also changed across sites (temperature \times shoot mass interaction, $F_{1,477} = 12.8$, $P < .001$, Table 2-1), as the slope became less strongly positive at more northern sites (Fig. 2-3). Changes in both slopes

and intercepts across sites indicates plasticity in the allometric relationship between shoot and root mass; as hypothesized, the southern population exhibited greater plasticity and distributed more biomass to roots at colder sites, regardless of seedling size (Fig. S2-2). Marginally significant differences between populations in the allometric trajectory of how root mass changed with size (population \times shoot mass interaction, $F_{1,388} = 3.7$, $P < .1$) reflect a slightly different allocation strategy in the southern population, which was rootier in general than the northern population but especially at smaller seedling sizes (Fig. 2-2a).

The proportional distribution of biomass to shoots and roots across latitude were consistent with the allometric analyses. When seedlings from the northern and southern populations were compared in the 25th, 50th, and 75th percentiles for shoot mass across sites, the southern population consistently had a greater proportion of biomass in roots than the northern population, while within-population comparisons across size percentiles highlighted the decreasing proportion of biomass distributed to roots as seedling size increased (Fig. 2-6). Comparisons of the two populations at the mean shoot mass for each site also consistently show a greater fraction of total seedling mass distributed to roots in southern population seedlings (Fig. 2-5), with differences more pronounced at colder sites. On a dry mass basis, southern seedlings allocated between 67% and 84% of total (non-photosynthetic) mass to roots, while northern seedlings allocated between 55% and 66% to roots. In across-site comparisons of seedlings at a common size (shoot mass), the proportion of biomass distributed to roots was highest at southern sites for the northern population and at northern sites for the southern population (Fig. 2-4).

Other models yielded results similar to the main model. Light environment and competition from understory neighbors were included in early models, but while both clipping and light treatments had statistically significant effects on root allocation (Table S2-1), the effects were tiny (Fig. S2-3) and not biologically interpretable, nor were there significant interactions involving either factor. A model including all three populations at a subset of sites had almost all of the significant effects of the main model, though there was no significant shoot mass by temperature interaction (Table S2-2). In addition, temperature was marginally significant as a main effect ($F_{1,3} = 6.1$, $P < .1$), while the

interaction between population and temperature was less significant than in the main model ($F_{2,338} = 3.2, P < .05$).

DISCUSSION

Root biomass fraction was expected to shift clinally with temperature, since both growing conditions and the degree to which certain resources are limiting often change across latitude and temperature gradients. While multi-species analyses indicate that root biomass tends to increase as temperature decreases across a broad regional to global scale (Vogel *et al.* 2008, Fan *et al.* 2009, Luo *et al.* 2012, Poorter *et al.* 2012, Reich *et al.* 2014), I found no evidence that temperature across a latitude gradient consistently affects root biomass fraction of sugar maple seedlings at the species level. Instead, I found intraspecific variation in the degree to which biomass distribution patterns shifted with temperature: only the southern population responded in a manner consistent with global patterns, showing greater proportional root biomass at cold northern sites.

If variation in proportional root mass distribution among populations were to mirror that of global biogeographic patterns, I would hypothesize lower root biomass in southern than northern populations, but in contrast to this expectation, I found that regardless of seedling size, southern seedlings had higher root mass than northern seedlings across all sites, while seedlings from the central population had intermediate patterns of proportional root mass. Though evidence of higher proportional root mass in a warmer-origin population has also been found in a perennial herb (Reinartz 1984) and in young Scot's pine seedlings (Matías *et al.* 2014), my findings are somewhat surprising, as they contradict both global patterns (most recently, Reich *et al.* 2014) and also numerous other studies that have measured population differences in root biomass fractions across a range of latitude origins (*e.g.* Cannell & Willett 1976, Li *et al.* 1998, Maron *et al.* 2007, De Frenne *et al.* 2012, Woods *et al.* 2012). My results raise the possibility that for some species, temperature may be indirectly influencing genetic variation and resulting population-level differences in root biomass allocation through effects on soil resources.

Potentially adaptive differences in root biomass between populations such as I observed between southern and northern populations could arise from regional

differences in soil resources. Plants tend to increase the proportion of roots relative to aboveground biomass under less fertile conditions (Reich 2002, Kobe *et al.* 2010), and within a species, populations originating from regions with low-nutrient soils may have a higher proportion of biomass in roots in both nutrient-rich and nutrient-poor soils than populations from sites where nutrients are not limiting (Burgess *et al.* 2015). While I did not directly measure soil nutrients in this study and thus cannot assess the degree to which soil fertility varies from north to south at the western edge of sugar maple's range, it has been noted that sugar maple tends to be restricted to certain soil types in the southern part of its range (Godman *et al.* 1990).

Soil moisture is another resource that may vary geographically, and though there is little evidence of shifts in biomass distribution in response to water availability after accounting for plant size (Reich 2002), a few studies have found genetic variation in biomass allocation patterns that match soil moisture differences in the populations' regions of origin, with higher proportion of roots in genotypes from regions with lower soil moisture (Richter *et al.* 2012, Kuster *et al.* 2013). While there is little difference in average annual moisture availability among populations' regions of origin, there are seasonal and inter-annual differences in soil moisture experienced by northern and southern source populations (Tables S2-1, S2-4). For sugar maple, the higher root mass of southern population seedlings may allow this drought-sensitive species to survive periodic low soil moisture, which occurs more frequently at the southern edge of its range (Table S2-3).

Genetic variation among plant populations may lead not only to differing patterns of biomass distribution but also differences in the degree of plasticity they express in response to temperature and resource gradients. The southern sugar maple population, whose seedlings had higher root biomass at northern than southern sites, showed greater plasticity in root biomass than seedlings from the northern population, whose proportional root biomass stayed relatively constant across sites when similarly-sized seedlings were compared. Evidence of higher plasticity of roots in the southern population, which had a higher relative growth rate potential than the northern population (see Chapter 3), is consistent with interspecific comparisons that suggest higher plasticity

in roots (Crick & Grime 1987) and leaf traits (Grassein *et al.* 2010) for species with rapid resource capture and growth strategies. Similarly, an intraspecific comparison of native and invasive populations found that for one of two species studied, invasive genotypes had higher plasticity and growth than native genotypes in the non-native range (Lamarque *et al.* 2015). Very few studies examining plasticity in biomass distribution have used an allometric approach, however (but see Troughton 1961, Ledig *et al.* 1970), which is critical in differentiating true plasticity from shifts in biomass that are a function of size rather than environment *per se* (Reich 2002, Weiner 2004). This study, which took a quasi-allometric approach and controlled for size when comparing seedling root biomass, supports the conclusion that differences among populations in biomass distribution to roots and the plasticity of those responses go beyond size-dependent effects.

Experiments across latitudinal gradients offer important insights on the effects of temperature (De Frenne *et al.* 2013), but interpreting results from such experiments is also implicitly challenging, as these gradients encompass multiple covarying environmental factors such as soil moisture availability and photoperiod. In this case, it seems likely that the plasticity in proportional root biomass distribution expressed by southern population seedlings at northern sites was in response to temperature rather than a water availability gradient: seedlings showed significant shifts in root biomass across the five northernmost sites where summer temperature, but not the three-year average of soil moisture availability, varied clinally. Evidence from other studies further suggests that there is little change in relative biomass distribution in response to water stress, with root biomass remaining either unchanged during drought (Hibbs *et al.* 1995, Kreyling *et al.* 2008) or, where significant effects do occur, declining with plant size (Weißhuhn *et al.* 2011, Arndal *et al.* 2014, but see Asseng *et al.* 1998, Taeger *et al.* 2015). Average summer temperature at the northern sites where the southern population exhibited greatest plasticity in root biomass was 7° C colder than that population's region of origin, and the southern population's conservative pattern of biomass allocation at these sites was likely due to this temperature difference between the climate of origin to which it was adapted and experimental growing conditions.

Photoperiod varies with latitude and, though it is correlated with temperature, has effects on plant growth independent of temperature (Troughton 1961). In field settings, however, there is convincing evidence that temperature interacts with photoperiod cues in growth cessation and bud set (*e.g.* Rohde *et al.* 2011), and in some species, temperature seems to be the primary factor influencing growth cessation (Heide 2011). Sugar maple, which has determinant growth, is more strongly influenced by temperature than photoperiod in the timing of bud break and subsequent growth (Olmstead 1951). Evidence suggests that any effects of photoperiod on the proportion of biomass allocated to roots versus shoots are species-dependent and, more importantly, short-term and not compounding (Cannell & Willett 1976, Burdett & Yamamoto 1986). Furthermore, Troughton (1961) found that photoperiod affected the allometric relationship between roots and shoots only when day-length was less than 12 hours. For all these reasons, it is reasonable to conclude that the differences among populations in proportional root mass distribution across a latitude gradient are influenced more by temperature (and/or moisture) than differences in photoperiod.

One potential way that adaptive differences in response to temperature might be expressed is through variation in patterns of biomass allocation among populations, but prior to this experiment there has been very little experimental evidence of this. One study found population differences in the responsiveness of root length to a greenhouse warming treatment (Matías *et al.* 2014), but several other studies that looked for shifts in root biomass of provenances across a temperature gradient failed to find a significant interaction between temperature and latitude of population origin, whether using experimentally manipulated temperature treatments (Richter *et al.* 2012, Kuster *et al.* 2013) or multiple common gardens (De Frenne *et al.* 2012). None of these studies, however, used an allometric analysis to distinguish between the effects of size differences ('apparent plasticity', McConnaughay & Coleman 1999) and true plasticity. Without accounting for differences in seedling size, population differences across treatments do not constitute evidence of true plasticity (Reich 2002, Weiner 2004).

Because so few studies have taken an allometric approach in examining plasticity in root biomass, it is difficult to determine the generality of my results. It may be that

plasticity of biomass distribution among populations in response to temperature is uncommon if there is an easier or less costly way for plants to shift resource acquisition (such as by shifting the morphology of leaves or roots, *e.g.* specific leaf area or specific root length, or increasing the nutrient uptake potential of roots by allocating to cellular nutrient uptake mechanisms) than at the coarse level of above- and belowground biomass distribution (Ryser & Eek 2000, Reich 2002, Hill *et al.* 2006). Alternatively, plasticity of biomass distribution in response to temperature gradients may happen only when plants are exposed to a broader temperature gradient than is usually experimentally tested. Further study is needed to better understand whether and how plasticity of biomass distribution operates across large-scale temperature gradients.

The proportional root biomass response of individual species to temperature gradients has been inconsistent among studies, in contrast to the general global pattern of greater root biomass at colder sites. Several studies using experimentally or passively warmed outdoor chambers (raising temperatures 2 to 5 °C above ambient) failed to find a direct effect of temperature on roots or on proportional biomass distribution (Richter *et al.* 2012, Kuster *et al.* 2013, Taeger *et al.* 2015), in line with the results from this large-scale common garden study. Those studies that found a significant effect of temperature on roots are conflicting: some found a positive effect (Buchwal *et al.* 2013, Matías *et al.* 2014) while others detected a negative effect of warmer temperature on roots (Way & Sage 2008, De Frenne *et al.* 2012). It seems, therefore, that it is premature to use the broad regional relationship between root biomass and temperature as a predictor of root biomass dynamics at the species level.

There are several possible explanations for why species seem to differ in the direction and degree to which plants shift biomass distribution to roots across temperature gradients. Broad global patterns often emerge only across very large gradients; the synthesis of Reich *et al.* (2014), for instance, spans over 40 °C MAT. Across a narrower range of temperature, species-level relationships between biomass and temperature could be opposite that of the overall trend yet still fit within the range of variation encompassed by the global relationship between temperature and biomass allocation. Global patterns may therefore be driven by interspecific, rather than intraspecific, differences in response

to broad temperature gradients. Species patterns also do not capture the complexity of intraspecific variation among populations, which could have opposing patterns of biomass distribution responses to temperature.

This study found no significant effect of either the light or neighbor density treatments on root biomass, in keeping with a number of other studies that compared plants of similar sizes rather than ages. Theory predicts that higher neighbor density and more intense competition for belowground resources should lead to greater root mass (Bloom *et al.* 1985), but because competition affects plant size which in turn affects biomass distribution, size-dependent differences in root mass represent only “apparent” plasticity (Huang *et al.* 2009). Several studies in addition to this one have found no effect of neighbor density on biomass distribution to roots after plant size is taken into account, whether the competition was aboveground (Casper *et al.* 1998), belowground (Cahill 2003), or both (Troughton 1956). There is also evidence to suggest that the degree of root allocation response of seedlings to competition from surrounding understory neighbors may depend more on site fertility and soil nutrient limitation than neighbor density: Berendse and Möller (2009) found that after accounting for size, the proportion of mass allocated to roots increased only at lower levels of nitrogen.

In a review of biomass allocation patterns across light environments, plants grown in high light generally had greater root mass fraction than plants in low light (Poorter & Nagel 2000), but under an allometric approach this pattern is less clear (Reich 2002). Consistent with my results, several studies have found that after accounting for size, root mass of woody seedlings did not change across light environments (Ledig *et al.* 1970, Philippot *et al.* 1991, Chen 1997, Chen & Klinka 1998). Even among studies that controlled for plant size and found higher root allocation under high light environments, the direction and significance of the effect depended on the species (Rice & Bazzaz 1989, Walters *et al.* 1993, McConnaughay & Coleman 1999). It is possible that leaf biomass, absent from this analysis due to early seedling harvest, could affect carbon allocation to roots and that seasonal differences among populations might emerge in response to light environments. It seems, however, that root biomass is less sensitive to light environment,

and adjustments in shoot and leaf morphology, though not measured in this study, may better characterize plants' response to light.

CONCLUSION

The degree to which plants plastically adjust biomass allocation in response to the environment has long been debated (*e.g.* Thornley 1972, Bloom *et al.* 1985, McConnaughay & Coleman 1999, Reich 2002, Poorter *et al.* 2012, Freschet *et al.* 2013). This study, which found shifts in biomass allocation across environments only within populations and no consistent pattern of plasticity at the species level, suggests that there may be costs to adjusting biomass allocation to roots that in many cases exceed the benefits of such plasticity. Instead, a plastic response in biomass allocation may be selected for only in populations occupying highly variable or resource-rich environments. As one of only a handful of studies to gather data on the plasticity of root biomass allocation across natural environmental gradients, this paper points to the need for additional research on allocation to roots within species and along resource gradients that co-vary with latitude.

The scope and rate of climate change provides another compelling reason to better understand the extent of plasticity in root biomass allocation, as global change is likely to affect plant roots in a multitude of ways (Norby & Jackson 2000). Predicted shifts in patterns of precipitation and an increasing incidence of drought may affect plant root dynamics (Hanson & Weltzin 2000, Olmo *et al.* 2014), as may changes in soil nutrient cycling and availability associated with climate change (BassiriRad 2000, Carrillo *et al.* 2014). The effects of climate change on plants may be expressed through phenotypic plasticity in traits as well as evolution (Franks *et al.* 2014), and determining the plasticity of belowground allocation across naturally existing resource gradients therefore offers one window into how species may respond to ongoing climate change.

Though differences in biomass allocation response to environmental gradients have been noted both among species (*e.g.* Portsmouth & Niinemets 2007, Grassein *et al.* 2010) and within species (*e.g.* Montesinos-Navarro *et al.* 2011, Matías *et al.* 2014), it is difficult to make conclusions about allocation plasticity without accounting for

differences in plant size (Weiner 2004). Allometric analyses of biomass allocation are uncommon, but both this study and others that account for plant size (*e.g.* Reinartz 1984, Fu *et al.* 2013) have noted within-species variation in the degree of plasticity, with environment causing trait variation above and beyond ontogenetic differences. Further allometric analyses such as this one are critical to clarify the degree to which changes in biomass allocation in response to the environment are truly plastic, not merely size-dependent, and to determine the extent of such plasticity.

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TABLES AND FIGURES

TABLE 2-1 The effects of population (northern and southern origin) and temperature (8 transplant sites spanning a latitude gradient with a 14 °C range in MAT) on log-transformed seedling root mass, accounting for differences in shoot mass ($R^2 = .901$, $N = 486$). In this mixed-effects model, both site and plot (nested within site) were entered as random effects to account for site-specific variation in seedling performance unrelated to temperature.

Fixed effect	df	<i>F</i>	<i>P</i>
Population	1, 365	232.8	<.0001
Shoot mass (log)	1, 474	923.5	<.0001
Population x Shoot mass	1, 388	3.7	.0542
Temperature (3yrAv JJA mean)	1, 6	0.0	.9241
Population x Temperature	1, 330	14.0	.0002
Shoot mass x Temperature	1, 477	12.8	.0004

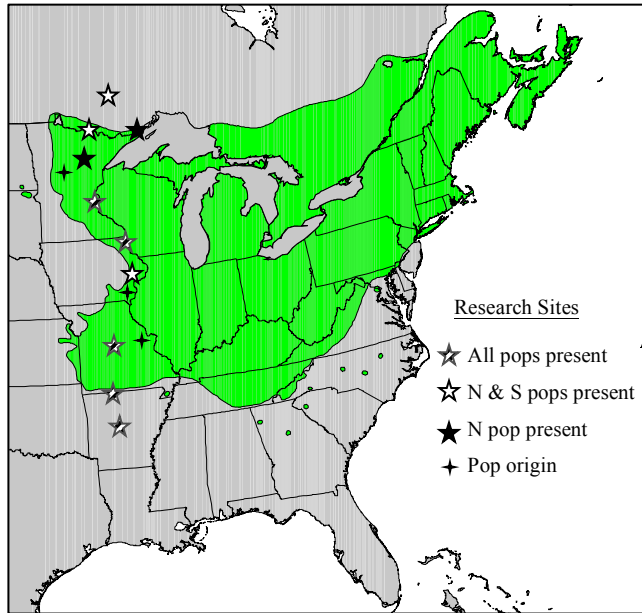


FIGURE 2-1 Range map for sugar maple (*Acer saccharum*), adapted from Little (1971). In the western portion of its range, sugar maple can be found from southern Missouri to the Minnesota/Ontario border. Seedlings were planted at ten sites along a north-south transect of the western edge of the species' range and beyond range margins to the north and south. For the purposes of this study, a population was considered "present" at a site when more than eight seedlings survived to harvest. By this criterion, eight sites had both northern and southern seedlings and five sites had all three populations that survived to final harvest. The counties of seed origin for the three populations (north, central, and south) are also indicated.

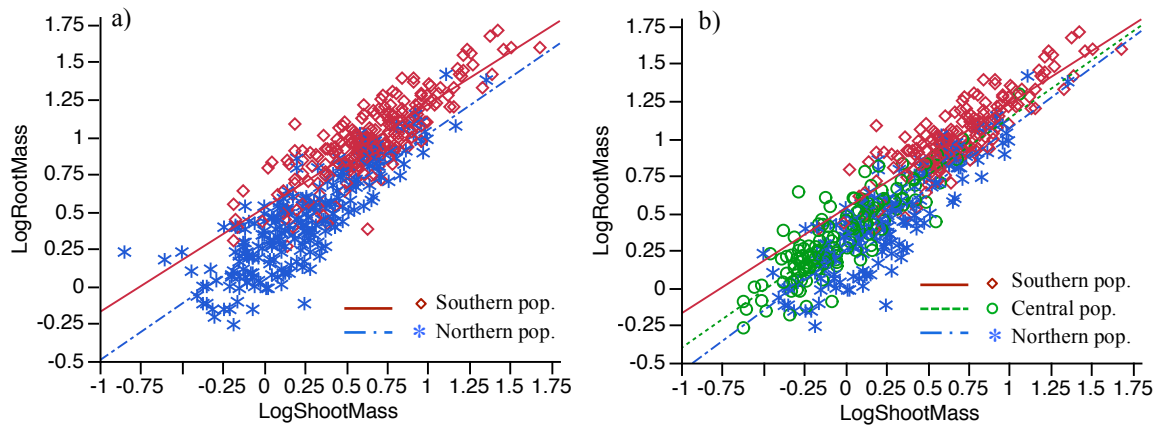


FIGURE 2-2 Comparisons of the allometric relationship between root and shoot mass (log transformed) for the southern and northern populations (a) and those populations plus the central population (b) for seedlings were grown along a latitude and temperature gradient. At the eight sites where southern and northern seedlings were present (ALUM, KOEN, BREA, WILD, FISH, PINE, FORT, DRYD), seedlings from the southern population had higher root mass than similarly sized seedlings from the northern population (a), while at the subset of sites where all three populations were present (ALUM, KOEN, BREA, FISH, PINE), the central population showed an intermediate level of root biomass distribution (b): seedlings from the central population had less roots than similarly sized southern population seedlings but more than the northern population.

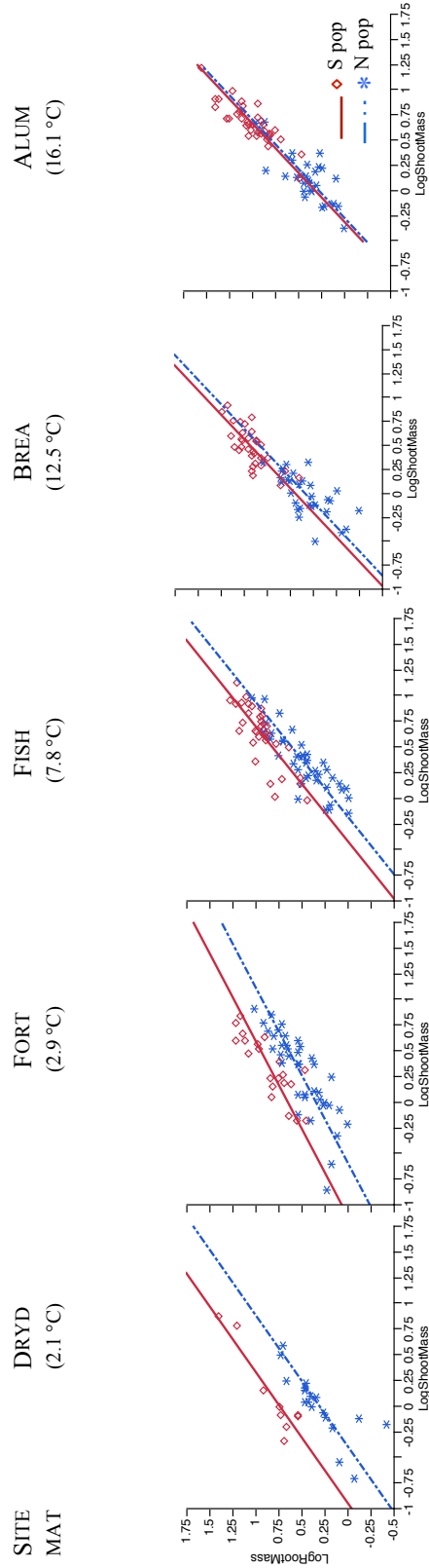


FIGURE 2-3 Across sites spanning a latitude and temperature gradient (south to north, left to right), the difference in the allometric relationship of root mass to shoot mass (log transformed) between populations increased with latitude. Across sites, seedlings from the southern population had higher root mass at a given shoot mass than northern seedlings, but this difference was greatest at cold northern sites. Within each site, slopes for the populations were constrained to be parallel to better illustrate the interaction between temperature and population.

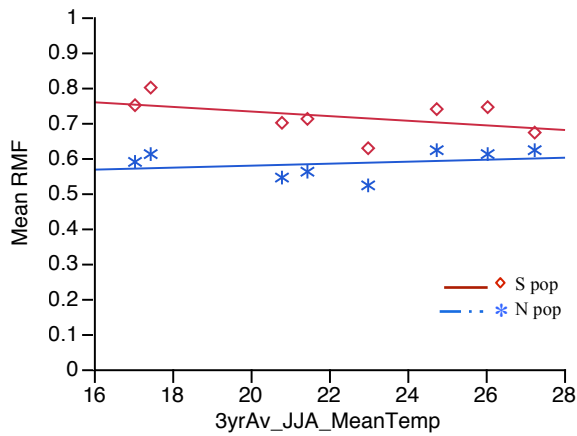


FIGURE 2-4 Mean root mass fraction (RMF) of southern and northern populations along the gradient in average summer (June/July/August) temperature spanned by the eight sites where both populations were present, illustrating a significant interaction between populations and the temperature of planting sites (see Table 3-1). For this figure, mean shoot biomass (calculated from pooled data across sites and populations) was used to determine population-specific root mass from best-fit lines of the biomass data at each site. At a common shoot mass, populations differed in average RMF; the southern population consistently had a higher RMF, though the difference between populations is lowest at the warmest sites. While RMF exhibits site-specific variation, RMF tended to increase at colder sites in the southern population and decrease at colder sites in the northern population.

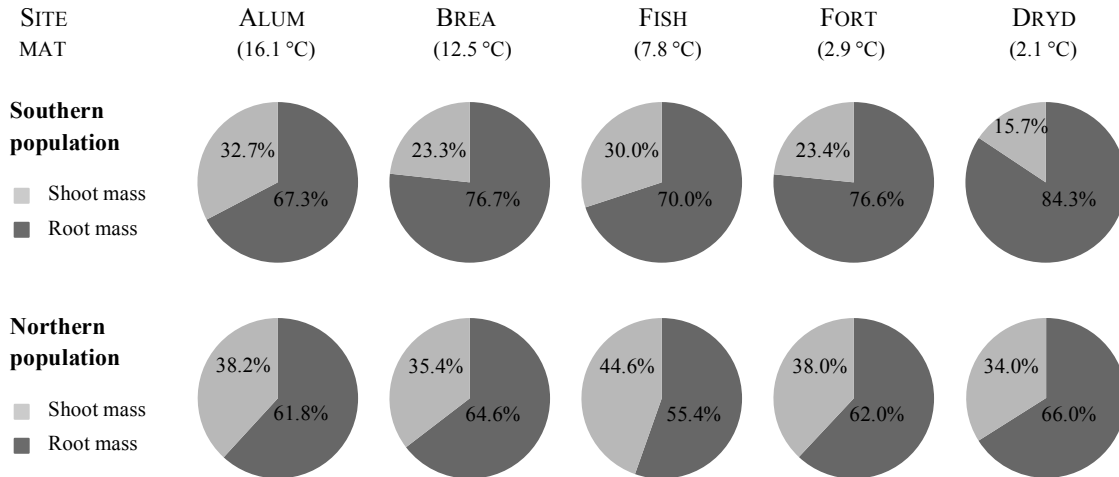


FIGURE 2-5 Southern and northern populations differ in the relative distribution of biomass to roots versus non-photosynthetic shoots, where site-specific mean shoot biomass (pooled across southern and northern populations) was used to determine population-specific root mass from best-fit lines of the biomass data at each site; five sites are shown here (from south to north, left to right). Southern seedlings consistently had a larger proportion of their total mass in roots than northern seedlings, though the contrast between populations was least at the southernmost site and greatest at the northernmost site. Changes in the proportion of root biomass between populations and across sites reflect plasticity, and comparisons of populations' site-specific mean shoot biomass indicate that populations differ in root allocation even in a common site environment. Biomass distribution between populations at each site was very similar to that shown above when the site-specific *population* mean (*i.e.* where seedling shoot size differed between populations) was used instead of the site mean.

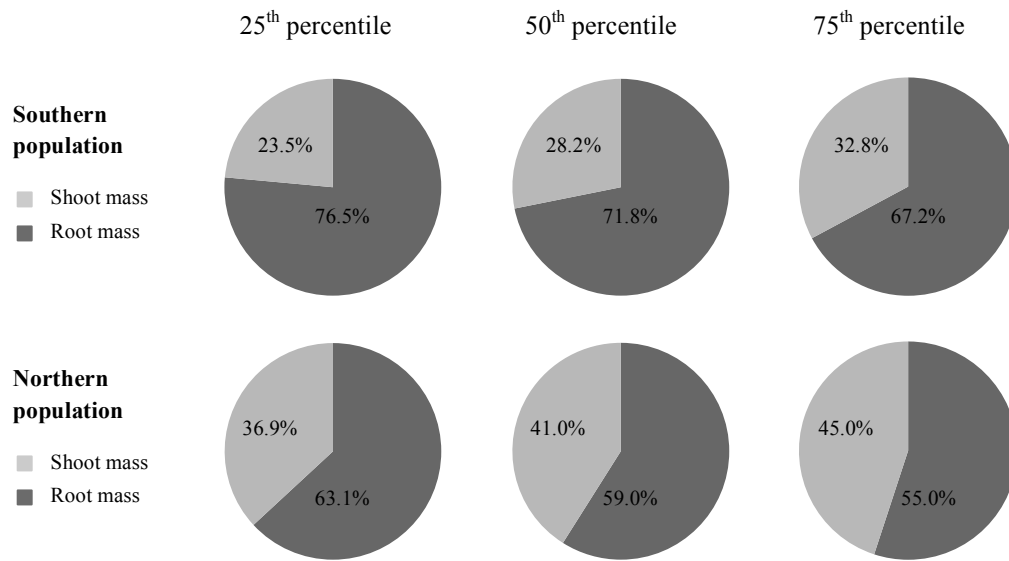


FIGURE 2-6 Comparison of percent root mass in southern and northern seedlings with the same shoot mass at the 25th, 50th, and 75th quartiles for size (quartiles determined from pooled data across all sites and both populations). Southern seedlings have more biomass in roots than the northern population, and both populations have proportionately more roots when smaller.

SUPPLEMENTAL INFORMATION

TABLE S2-1 A mixed effects model with population (northern and southern origin), clip treatment (clipped and unclipped understory), light treatment (shaded canopy and canopy gaps), temperature (7 transplant sites across a latitude gradient), and two-way interactions on seedling root mass, accounting for differences in shoot mass ($R^2 = .897$, $N = 459$).

Fixed effect	df	<i>F</i>	<i>P</i>
Population	1, 357	210.4	<.0001
Clip treatment	1, 237	4.3	.0401
Light treatment	1, 251	4.7	.0303
Shoot mass (log)	1, 441	743.2	<.0001
Temperature (3yrAv JJA mean)	1, 5	0.3	.6365
Population x Clip	1, 330	0.7	.3878
Population x Light	1, 335	0.6	.4307
Population x Shoot mass	1, 380	2.4	.1325
Population x Temperature	1, 318	8.1	.0048
Clip x Light	1, 244	0.0	.9309
Clip x Shoot mass	1, 418	0.9	.3353
Clip x Temperature	1, 270	0.0	.8328
Light x Shoot mass	1, 424	1.6	.2059
Light x Temperature	1, 282	0.5	.4839
Shoot mass x Temperature	1, 442	9.8	.0019

TABLE S2-2 The effects of population (northern, central, and southern origin) and temperature (5 transplant sites spanning a latitude gradient with a 8.9 °C range in MAT) on seedling root mass, accounting for differences in shoot mass ($R^2 = .918$, $N = 494$). In this mixed-effects model, both site and plot (nested within site) were entered as random effects to account for site-specific variation in seedling performance unrelated to temperature.

Fixed effect	df	<i>F</i>	<i>P</i>
Population	2, 392	71.4	<.0001
Shoot mass (log)	1, 331	901.3	<.0001
Population x Shoot mass	2, 409	3.2	.0429
Temperature (3yrAv JJA mean)	1, 3	6.1	.0885
Population x Temperature	2, 388	3.2	.0422
Shoot mass x Temperature	1, 443	2.4	.1194

TABLE S2-3 Frequency and degree of cumulative summer (June/July/August) soil moisture deficit over the past 115 years at the two sites (BREA and PIKE) whose climate matches that of the southern and northern populations' regions of origin. There is a higher frequency of summers with moisture deficit exceeding 200 mm at the southern than the northern site. Moisture deficit is calculated by the difference between potential and actual evapotranspiration; moisture deficit is greater than zero in years where potential evapotranspiration is greater than precipitation. Climate data were obtained from the PRISM Climate Group of Oregon State University.

Degree of moisture deficit	Summer (June/July/August) moisture deficit frequency (# years), 1900 – 2014	
	Southern site	Northern site
0 – 100 mm	24	53
101 – 200 mm	50	55
201 – 300 mm	32	7
> 300 mm	9	0

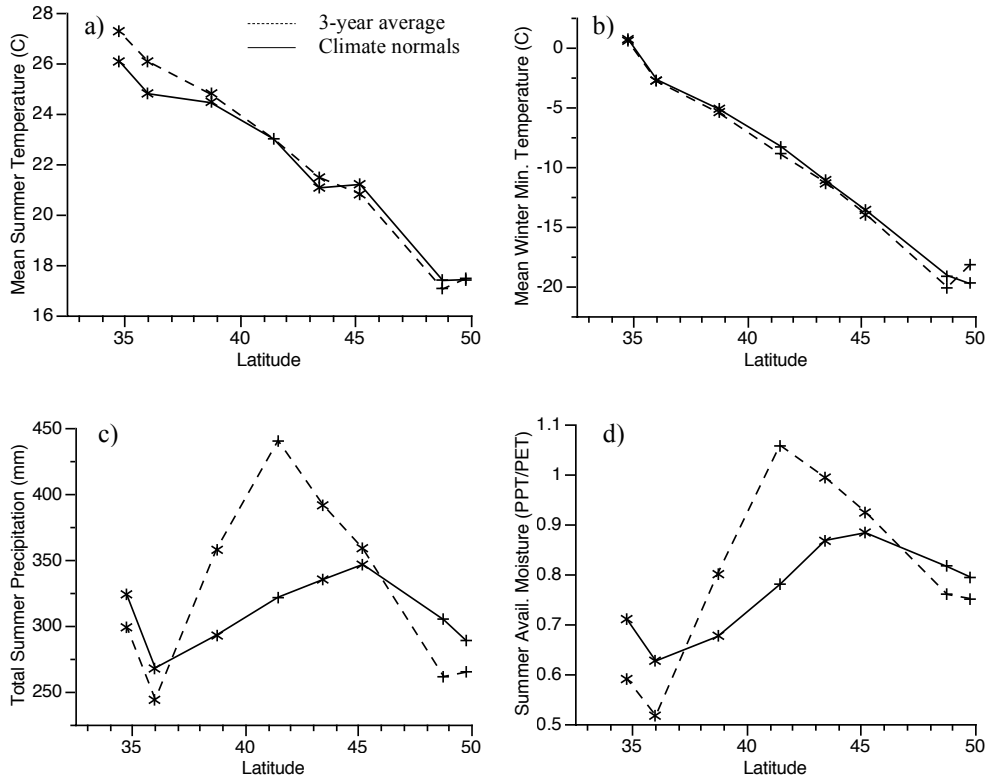


FIGURE S2-1 Comparisons of weather data averaged over the three years of the experiment (dashed line) and 30-year climate normals (solid line) for average summer (June/July/August) temperature (a), average winter (December/January/February) minimum temperature (b), total summer precipitation (c), and summer available soil moisture (d) at each of the sites. For analyses comparing northern and southern populations, all eight sites (indicated by + or *) were used, while five sites (indicated by *) were used for analyses that included the central population. Climate data were obtained from the PRISM Climate Group (for ALUM, KOEN, BREA, WILD, FISH, and PINE) and the Canadian National Climate Data and Information Archive (for FORT and DRYD).

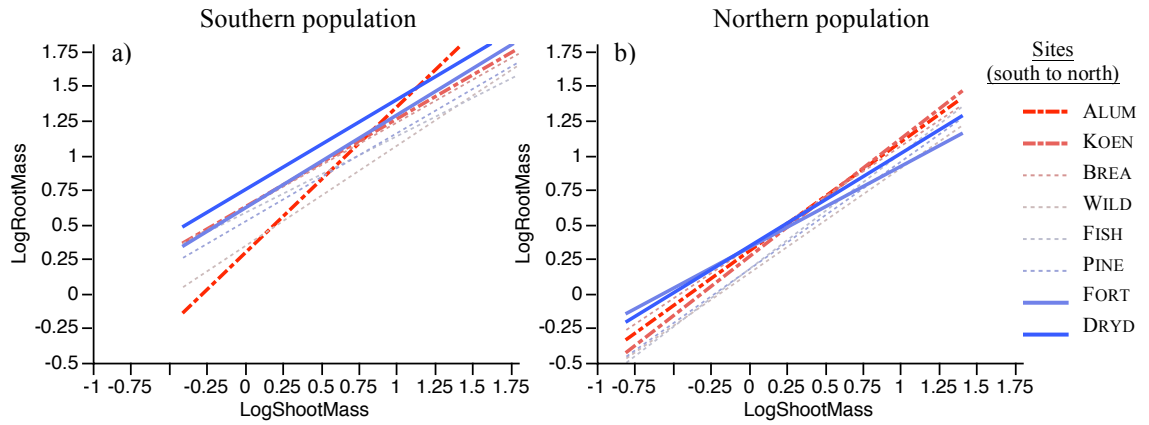


FIGURE S2-2 Site-specific allometric relationships for the southern (a) and northern (b) populations. Bold trend lines indicate beyond-range sites (in the north, FORT and DRYD; in the south, ALUM and KOEN). The southern population has higher root mass for a given shoot mass, but also exhibits more plasticity in root mass across sites, with highest root mass relative to shoot mass at the northernmost site.

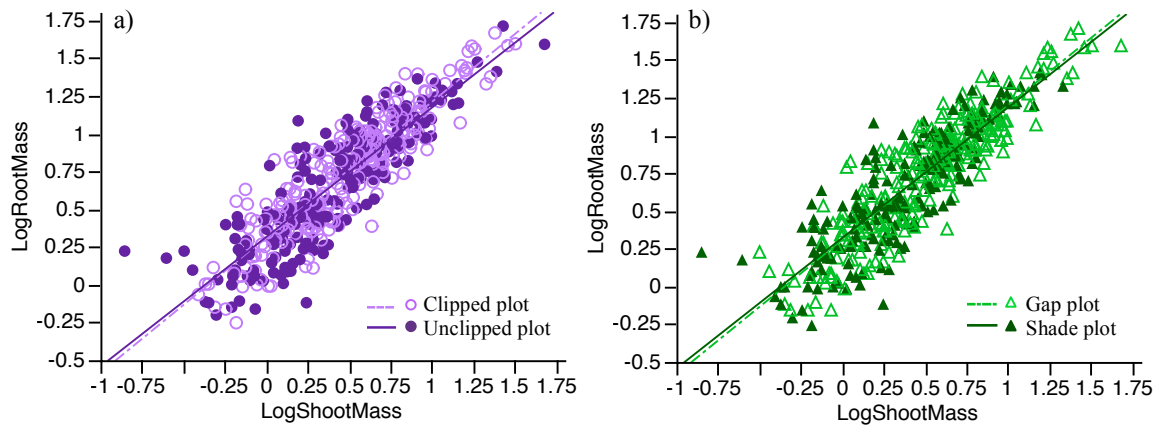


FIGURE S2-3 The effects of (a) clip treatment and (b) light treatment in an allometric analysis of root mass are statistically significant, but differences in intercept and slope between these treatments are so slight as to be likely biologically meaningless. Furthermore, the effects of these treatments do not change across a latitude gradient, between populations, or over the range of sizes measured in this experiment.

Chapter 3

**Variable trait response to temperature in sugar maple (*Acer saccharum* Marsh.)
seedlings despite consistent differences in growth among provenances**

SUMMARY

Plant growth is directly affected by functional traits such as leaf morphology, leaf chemistry, photosynthetic rate and biomass allocation. Both plant growth and traits tend to vary broadly with temperature: plants with conservative growth and associated traits predominate in colder environments and plants with higher growth and resource-acquisitive traits tend to be found in warm regions. Few studies, however, have examined whether climatically distinct populations within a species differ in trait responses to temperature and light. I examine plant growth and leaf traits in three populations of sugar maple seedlings representing a climate-of-origin gradient, experimentally planted in climate-controlled growth chambers under contrasting temperature and light treatments. I expect higher relative growth rate (RGR) and associated traits (SLA, LMF, A_{\max}) at 31° than 25° C, lower RGR, SLA, and LMF in the cold-origin (northern) population, and a decline in RGR, SLA, and LMF in the northern population under the warming treatment. I also expect greater plasticity in the warm-origin (southern) population's response to increasing light availability (higher RGR and A_{\max} , lower SLA, LMF, and leaf N). In contrast to my hypothesis, I find higher RGR at 25° C, perhaps due to greater respiration costs in seedlings grown at the warmer temperature. I find lower RGR and trait values (for SLA, LMF, and leaf N) in the northern population, as expected, but the two southern populations do not vary consistently in trait values along a climate-of-origin gradient, nor is there a consistent pattern of population differences in growth and trait response to temperature or light. Other studies suggest SLA and A_{\max} have a greater influence on RGR than LMF, but in this study A_{\max} did not significantly differ across populations and growth temperatures. In conclusion, I find intraspecific variation in traits and growth in response to temperature but only limited evidence that such variation is geographically structured along a climate-of-origin gradient.

INTRODUCTION

Functional traits may provide a common denominator in the plant world with which to understand variation in plant growth within and across species and environments. Intraspecific variation in trait expression may reflect both plastic responses to local growing conditions such as temperature and light and adaptation to large-scale climate differences across its range (López *et al.* 2010, Garzón *et al.* 2011, Wellstein *et al.* 2013), yet relatively few studies have assessed whether geographically distinct populations differ in trait plasticity (Oleksyn *et al.* 1998, Fajardo & Piper 2011, Grady *et al.* 2013). Evidence that populations' growth response to temperature may vary with region of origin (*e.g.* Koehler *et al.* 2012, De Frenne *et al.* 2013, De Kort *et al.* 2014, Lu *et al.* 2014) suggests more research is needed to assess the degree to which populations across a species' range differ in functional trait values and temperature response.

Functional traits (*sensu* Violle *et al.* 2007) are inextricably tied to plant growth: the relative growth rate (RGR) of a plant is, by definition, the product of its specific leaf area (SLA), leaf mass fraction (LMF), and net assimilation rate (NAR) (Evans 1972). Plants show remarkable convergence in trait correlations across biomes, suggestive of general trade-offs along a “plant economics spectrum” (Freschet *et al.* 2011, Reich 2014), though individual species may differ somewhat from global patterns (Niinemets 2015). Functional traits span a continuum of expression ranging from resource-conservative to resource-acquisitive, reflecting the trade-offs that constrain plant growth and characterize differing plant growth strategies (Reich 2014). Species with conservative traits and lower growth tend to be associated with cold environments, while plants with resource-acquisitive traits and higher growth more frequently predominate in warmer regions (Díaz *et al.* 2004, Wright *et al.* 2005). These patterns of functional trait expression across regional and global temperature gradients (*e.g.* Wright *et al.* 2005, Zhang *et al.* 2015), however, are primarily driven by species turnover across communities (Cornwell & Ackerly 2009, Meng *et al.* 2015) and may not reflect species-specific variation in trait-environment relationships (Grady *et al.* 2013, Niinemets 2015).

Intraspecific variability in trait expression is increasingly recognized as an important component of overall trait diversity in communities and along regional

environmental gradients (Albert *et al.* 2010b, Fajardo & Piper 2011, Laforest-Lapointe *et al.* 2014, Carlucci *et al.* 2015). The degree of trait plasticity expressed among populations and across growing environments has implications for species coexistence (Albert *et al.* 2010b), and may mediate the response of species and communities to stressors such as climate warming (Garzón *et al.* 2011, Oney *et al.* 2013). I set out to determine whether species-level traits and growth respond to warming as I would expect given global patterns, and the extent to which populations differ in trait and growth responses to temperature and light along a climate-of-origin gradient.

To address these questions, I measured seedling growth and traits under experimental warming and varying light levels for three populations of sugar maple (*Acer saccharum* Marsh.), a highly shade-tolerant species common to the cool temperate forests of northeastern United States (Godman *et al.* 1990). Genetic analyses have identified several regional ecotypes that differ in growth rate as well as tolerance to heat and drought (Kriebel & Gabriel 1969); differences in growth among populations (McCarragher *et al.* 2011) suggest that associated functional traits may also vary with region of origin. In the northern portion of its range, warming enhanced sugar maple growth and photosynthesis (Reich *et al.* 2015), but growth and trait response to warming has not been examined across populations. Though shade tolerant, sugar maple is also responsive to changes in light availability, exhibiting greater morphological plasticity than other similarly shade-tolerant species (Beaudet & Messier 1998).

Size and growth rate of many plant species are enhanced by moderate increases in temperature and irradiance, though the degree and direction of the temperature effect may depend on the species' location in its climate envelope and whether temperature or some other factor is most likely limiting metabolism and growth (Reich & Oleksyn 2008). Experimentally warmed plants of species that are not near their upper heat tolerance have higher RGR (Stirling *et al.* 1998, De Swart *et al.* 2006, Campioli *et al.* 2013), mass (Tjoelker *et al.* 1998), and height (Oke & Wang 2015), while higher irradiance levels are also associated with increased RGR (Portsmouth & Niinemets 2006), mass (Robakowski *et al.* 2005), and height (Beaudet & Messier 1998). Under experimental warming, photosynthetic rate (A_{\max}), SLA, and/or LMF increase (Higuchi *et al.* 1999, Xu *et al.*

2012, Liang *et al.* 2013, Possen *et al.* 2015), and leaf nitrogen tends to decline (An *et al.* 2005, Sardans *et al.* 2008). For light-limited plants, higher irradiance increases A_{\max} but is associated with decreases in SLA, leaf nitrogen, and LMF (Portsmouth & Niinemets 2006). I might therefore expect light levels to affect growth primarily through higher rates of photosynthesis, while warming might enhance growth both through higher rates of photosynthesis and changes in leaf morphology (Table 3-1). Alternatively, I might find a modest or uneven trait response to warming: species vary in their response to temperature, and other studies have failed to find a temperature response in SLA (Medek *et al.* 2007), A_{\max} (Niu *et al.* 2008), LMF (Loveys *et al.* 2002), or leaf N (Hudson *et al.* 2011) for at least one of the examined species, or found the opposite temperature effect (*e.g.* declining SLA with temperature, Hudson *et al.* 2011).

Within a species, the relative growth rate of climatically distinct provenances may vary, even when experimentally grown under common conditions (*e.g.* Ching & Hinz 1978, Kerr & Niles 1998, Vitasse *et al.* 2009). Differences in growth rate among populations may be associated with intraspecific variation in cold hardiness: as cold hardiness increases, RGR tends to decline (Darychuk *et al.* 2012, Koehler *et al.* 2012), and due to lower growth rates and earlier growth cessation, cold-adapted northern populations also tend to have less height growth than southern populations (Oleksyn *et al.* 2001). In sugar maple, a common garden study found intraspecific variation in growth rates consistent with local adaptation to climate (McCarragher *et al.* 2011), and I would therefore expect growth rates to be inversely related to populations' latitude of origin (Table 3-1).

Intraspecific differences in growth along a climate-of-origin gradient might arise from geographically structured genetic variation in functional traits (McKown *et al.* 2014). Populations originating from warmer, low-altitude regions often have higher SLA (Kao & Chang 2001, Fajardo & Piper 2011) and LMF (Ran *et al.* 2013) and lower leaf nitrogen (Gornall & Guy 2007, Wu *et al.* 2014) and A_{\max} (Benowicz *et al.* 2000, Gornall & Guy 2007), and I might expect similar patterns of differentiation in trait values between northern and southern sugar maple populations (Table 3-1). Other studies, however, have found a lack of population differentiation in A_{\max} (Teskey & Will 1999)

and evidence that the degree or direction of climate origin's effect on traits may vary among species for traits such as LMF and SLA (De Swart *et al.* 2006, Vitasse *et al.* 2014, Rosbakh *et al.* 2015), so I might find instead that populations are not differentially adapted in this subset of functional traits.

Populations might be distinguished not only by adaptive differences in functional traits and growth rate but also by variation in the plasticity of their response to experimental warming or reciprocal transfer common garden experiments; few studies, however, have attempted to assess intraspecific plasticity in temperature or light response. Limited evidence suggests that low-latitude populations may be more responsive to warming than high-latitude populations in RGR (Odland *et al.* 2003) or height growth (De Frenne *et al.* 2011). Though the former study did not examine functional traits and the latter found no evidence of differences among populations in SLA with warming, temperature-induced intraspecific plasticity in growth suggests there may be corresponding variation among populations in trait response to temperature. I expect growth rate, height, and mass of southern sugar maple populations to be more responsive to temperature than the northern population, combined with greater SLA and/or LMF under warming in southern populations (Fig. S3-1). In contrast, I expect similar temperature responses in A_{\max} and associated leaf nitrogen among populations, for while species may vary in plasticity of A_{\max} in response to temperature (Atkin *et al.* 2006), intraspecific comparisons of provenances reveal similar levels of plasticity in adjusting A_{\max} in response to temperature (Teskey & Will 1999, Robakowski *et al.* 2005). Population differences in response to light have been noted for SLA (Robakowski *et al.* 2005) and LMF (Soustani *et al.* 2014). Though populations in these studies were not clearly differentiated along a temperature-of-origin gradient, I hypothesize that greater growth in the southern population will be associated with greater plasticity in traits in response to changes in irradiance (Fig. S3-2).

RESEARCH METHODS

Two-year-old sugar maple seedlings, commercially grown from three seed provenances (mature populations in Minnesota, Missouri, and Tennessee), were

purchased from nurseries in 2011. The geographic extent spanned by these populations (Fig. S3-3) was associated with a 5° C difference in mean summer (June/July/August) temperature between northern (Minnesota) and southern (Missouri and Tennessee) regions of origin (Table 3-2). The bare-root seedlings were kept dormant until planting time in May, then established in 6.23-liter plastic pots filled with field soil (approximately 40% sand, 60% loam) and grown for five months in eight temperature-controlled growth chambers. Each chamber contained ten seedlings from each of the three populations. At the time of planting, an additional ten representative seedlings from each population were measured, kiln-dried at 75° C, and dry mass of roots and shoots were recorded (seedlings were dormant, so leaves were not present). Height, diameter, and biomass data from this subset were used to estimate initial mass of the planted seedlings, for which there were only height and diameter measurements.

Growth chambers, each containing 10 seedlings per population, were assigned temperature and light treatments; there were 2 replicate chambers of each treatment combination, and 20 seedlings per population for each of four treatments. Half the chambers had day/night temperatures of 31/19 °C, consistent with average summer temperatures in Missouri and Tennessee, while the remaining chambers, with day/night temperatures of 25/13 °C, were more typical of summer temperatures in Minnesota (Table 3-2). Seedlings in all chambers were watered every four days (250 mL per pot), and a 14-hour photoperiod was maintained throughout the experiment.

Multiple layers of woven and knitted shade cloth were used in each chamber to simulate the shade conditions characteristic of the forest understory. Light was first reduced a week after planting (around the time of leaf-out), and three weeks after planting, shade cloth layers were adjusted to create light levels approximating 1 - 2% of total daily flux (or 7 - 14 micromols/m²/sec) in low-light chambers and 4 - 6% of total daily flux (or 27 - 44 micromols/m²/sec) in higher-light (though still shaded) chambers. Due to seedling architecture and density, as well as variability in the transmissivity and positioning of shade cloth, chambers tended to be shadier and the gradient of light achieved somewhat broader than the target. While light gradients between the two treatments overlapped, low-light chambers had median seedling light levels of 5.2

micromols/m²/sec, and the median seedling light level in higher-light chambers was 15.7 micromols/m²/sec (Table S3-1).

In late July, photosynthesis was measured for a subset of seedlings. Measurements were made at saturated light (500 PAR) and ambient growing temperature (either 25° or 31° C) on fully expanded, non-senescent leaves using an LI-6400XT (LiCOR). Leaves selected for photosynthesis and subsequent analysis were representative for the plant in size, position on the plant, and degree of shading. Leaf punches from those seedlings were kiln dried and weighed, then SLA was calculated and samples were analyzed for carbon and nitrogen content. In August and October, light levels at a representative leaf were measured for each seedling; for the subset of seedlings with a sampled leaf, light measurements were made at that leaf. In October, light was also measured at each seedling's maximum height. An AccuPAR LP-80 (Decagon Devices) was used for all light measurements. Seedlings were harvested in mid-October, prior to senescence, kiln dried at 75° C, then weighed, with the dry mass of each seedling component (leaves, shoots, and roots) recorded separately.

STATISTICAL ANALYSIS

A variety of response variables pertaining to seedling growth, allocation, leaf chemistry, morphology, and photosynthesis were analyzed to evaluate seedling performance across populations and in response to temperature and light treatments. All analyses used standard least squares mixed models and an REML approach, and temperature and light treatment terms, nested within growth chamber, were entered as a random effect in every model to account for chamber-specific variation in seedling performance.

Response variables associated with seedling growth included relative growth rate and log-transformed seedling mass and seedling height. In calculating RGR, final seedling mass was adjusted to exclude leaf mass, as initial mass was of dormant, leafless seedlings. Among potential response variables for dry mass, seedling mass yielded the best-fit model, though shoot, root, and leaf mass models were similar. Biomass allocation also had several potential response variables; of these, leaf mass fraction had the greatest

response to population, light, and temperature. Response variables for leaves included specific leaf area, percent leaf nitrogen, and photosynthetic rate at maximum light (500 PAR) and ambient growing temperature. Photosynthetic rate was also measured on seedlings at a common temperature (25° C) for seedlings grown at both 25° and 31° C, as well as at 30 PAR, but none of the factors in either of these models were significant. Statistical models included a full factorial of the following predictors: population, temperature treatment, and a continuous light variable: either LogLeafLight (for SLA, leaf nitrogen, and photosynthesis models) or LogMaxLightMeas (for all other models). Leaf light was measured at sampled leaves shortly after photosynthesis measurements and leaf sample collection and was therefore considered the most appropriate light variable for leaf-level processes at that point in time; maximum light measured, on the other hand, captured peak light availability for a seedling but was specific neither to a particular leaf nor to a time of harvest. Because seedling size can have a substantial effect on growth-resource relationships (MacFarlane & Kobe 2006), all models also included a size covariate: log-transformed initial height at time of leaf-out yielded best-fit models for final height, percent leaf nitrogen, and photosynthetic rate, while all other models used log-transformed initial diameter as the size covariate. Data were analyzed with JMP Pro 9.0 statistical software (SAS Institute Inc.).

RESULTS

POPULATION DIFFERENCES

Intraspecific variation was present in almost every seedling metric I examined: seedling growth, allocation, leaf morphology, and leaf chemistry all differed significantly among populations, and only photosynthetic rate did not show statistically significant variation among populations (Table 3-3). As hypothesized, seedling growth was highest in the southernmost (TN) population, whether measured as relative growth rate, seedling mass, or seedling height (Fig. 3-1). Biomass allocation to leaves was consistent with hypotheses, with higher LMF in the TN than the MN population (Fig. 3-2c,g), but higher root mass fraction (RMF) in the MO than MN populations suggests that allocation

patterns do not closely follow a climate-of-origin gradient (Fig. S3-4). Differences among populations in leaf morphology were partially consistent with hypotheses: the MN population had the lowest SLA, as hypothesized, but the MO population had the highest (Table 3-3, Fig. 3-2a,e). Leaf chemistry differences across populations were opposite those hypothesized: the MN population had the lowest % leaf nitrogen (Table 3-3c, Fig. 3-2c,g). The TN population had larger seedlings on average than the MN or MO populations, but even among seedlings that were a common size, TN seedlings had higher RGR (Fig. S3-5) and LMF (Fig. S3-6), indicating that population differences in growth and allocation were not solely the consequence of initial seedling size.

Populations differed not only in biomass allocation but also in their growth for a given allocation strategy. In all three populations, seedlings with higher LMF tended to have higher RGR (although less so for the MN population). However, seedlings from the TN population were taller and had greater growth than seedlings from the other populations that had similar biomass investment in leaves (Fig. 3-3). In a RGR model where both initial size and LMF were included as covariates, the effects of population, temperature, and light remained significant, while a population \times light interaction became significant at the $P < .05$ level (Table S3-2).

RESPONSES TO TEMPERATURE

The temperature at which seedlings were grown had a significant effect on growth (Table 3-3a), but contrary to hypotheses, relative growth rate, mass, and height of seedlings grown at 31° C were lower than for those seedlings grown at 25° C (Fig. 3-1). As hypothesized, leaves had a higher percentage of nitrogen for seedlings grown at 25° C (Table 3-3c), and though SLA was not significant, it showed a similar pattern (Fig. 3-2e). There was no significant difference in biomass allocation to leaves across the two growing temperatures, nor were there significant differences in photosynthetic rate, though there was a trend in the hypothesized direction of higher A_{\max} at 31° C for seedlings grown at that temperature (Fig. 3-2h).

In contrast to my hypotheses, the growth response to temperature was generally similar across populations: despite differences in relative growth rate and seedling mass

among populations, there were no significant differences in populations' responsiveness to temperature for either of these variables. Log-transformed seedling height did show population-specific differences in temperature response (population \times temperature interaction, $F_{2,224} = 6.38$, $P = .0020$, Table 3-3a), but in contrast to my hypothesis and expectations that growth response would fall along a climate-of-origin gradient, Missouri seedlings had lower height growth at 31° C than either Minnesota or Tennessee populations (Fig. 3-1d). I also did not find support for my hypothesis that southern populations would increase leaf biomass allocation under warmer growing conditions. Though populations differed in their biomass allocation response to temperature (population \times temperature interaction, $F_{2,201} = 7.58$, $P = .0007$, Table 3-3b), there was no consistent pattern among southern populations: seedlings from Missouri allocated substantially more biomass to leaves when grown at 31° C, while seedlings from Tennessee grown under those same conditions allocated *less* biomass to leaves (Fig. 3-2f). Growing temperature also had marginally significant population-specific effects on leaf morphology (population \times temperature interaction, $F_{2,123} = 2.59$, $P = .0791$, Fig. 3-2e): contrary to hypotheses, the SLA of seedlings grown at 31° C was lower than at 25° C for southern-origin populations and higher than at 25° C for the northern-origin population.

RESPONSES TO LIGHT

Seedlings' response to the light gradient were generally consistent with expectations: relative growth rate, seedling mass, and seedling height all increased under higher light, as hypothesized (Table 3-3a, Fig. S3-7a-c), as did photosynthetic rates (Table 3-3c, Fig. S3-8), and as hypothesized, SLA and percent leaf nitrogen declined as light levels increased (Table 3-3b,c, Fig. 3-4). Leaf mass fraction, however, increased with light (Table 3-3b) rather than decreasing as hypothesized.

Though growth response to temperature was relatively similar across populations, seedlings did exhibit intraspecific variation in growth in response to light. As hypothesized, seedlings from southern (MO and TN) populations increased growth and altered biomass allocation under higher light levels more than those from the Minnesota

population, and this trend was especially true at the cooler growing temperature (Fig. S3-7); three-way interactions between population, temperature, and light were significant for RGR ($F_{2,201} = 3.28$, $P = .0397$), log-transformed seedling mass ($F_{2,203} = 4.50$, $P = .0122$), and log-transformed seedling height ($F_{2,222} = 6.94$, $P = .0012$), and marginally significant for LMF ($F_{2,199} = 2.53$, $P = .0820$), as well as a marginally significant two-way interaction between population and light for RGR ($F_{2,201} = 2.38$, $P = .0948$). Percent leaf nitrogen varied across populations in response to light (population \times light interaction, $F_{2,87} = 12.96$, $P < .0001$, Table 3-3c, Fig. 3-4d), with higher leaf nitrogen levels in the Missouri population at low levels, but the pattern of the effect was consistent neither with my hypotheses nor with a climate-of-origin gradient.

DISCUSSION

Sugar maple populations differed significantly in growth, biomass allocation, leaf chemistry, and leaf morphology, but I found only modest evidence for intraspecific differences in plasticity in response to temperature or light environments. With three populations and variable trait expression along a climate-of-origin gradient, I cannot draw generalized conclusions about the relationship between population origin, seedling growth, and traits. Nevertheless, this study offers insight into the effect these functional traits may have on sugar maple growth and the degree to which these traits vary among sugar maple populations in response to changes in temperature or light.

As has been found in other studies (*e.g.* Odland *et al.* 2003, De Frenne *et al.* 2011, McCarragher *et al.* 2011), the growth response of populations varied along a climate-of-origin gradient: the southernmost (TN) population had the greatest RGR, mass, and seedling height, while the northern (MN) population had the lowest values for each growth variable. The southern populations also had higher SLA and LMF than the northern population, consistent with other studies (*e.g.* Fajardo & Piper 2011, Ran *et al.* 2013), but there was no difference in photosynthetic rates between populations despite higher levels of leaf N in southern populations. Other studies of sugar maple have also found a lack of population differentiation in photosynthetic rates (Ledig & Korbobo

1983, Gunderson *et al.* 2000), and this suggests that SLA and/or LMF play a greater role than A_{\max} in differences among populations in growth rate for this species.

Seedlings responded similarly to temperature, regardless of population, and were consistently taller and had higher mass and relative growth rate at 25° than at 31° C. This appears to conflict with evidence across species that RGR generally increases with temperature (*e.g.* Stirling *et al.* 1998, Campioli *et al.* 2013), though species may vary in the responsiveness of growth rate to temperature and the temperature at which maximum growth rates occur (Saxe *et al.* 2001), and growth response to temperature may further depend on whether temperature increases occur in a warm or cold growing climate (Reich & Oleksyn 2008). Loveys *et al.* (2002) found growth rates for some species were higher at 18° than 23° C, while Tjoelker *et al.* (1998) found higher RGR at intermediate temperatures (24° to 27° C) than at 18° or 30° C for five boreal species. Consistent with these studies, my results suggest that optimum temperature for sugar maple growth is closer to 25° than to 31° C. Reich *et al.* (2015) found warming enhanced growth of sugar maple seedlings, but the warming treatment (+3.4° C) and ambient temperatures (19 - 21° C) in that study were both cooler than in this experiment, and “warmed” seedlings therefore effectively experienced the “cool” conditions in this experiment.

Seedlings generally responded as expected to light availability: SLA and percent leaf nitrogen decreased with light, and growth and photosynthesis increased. Leaf mass fraction, however, did not decline as expected with increasing light, perhaps because light was still the most limiting resource; even the highest light levels were quite low, and the seedlings, grown in individual pots and regularly watered, had no root competition for soil resources. While plants often display primarily morphological adjustments (such as SLA) rather than shift biomass distribution (such as LMF) in response to changes in light environment (Freschet *et al.* 2015), light levels in this study were an order of magnitude lower, and under such low-light conditions, LMF and photosynthetic rate are more important than SLA and leaf N in affecting plant growth (Seidlova *et al.* 2009). Sugar maple, which is highly shade tolerant (Godman *et al.* 1990), may be able to maintain growth under low-light conditions in part by increasing LMF in response to small changes in light availability.

At high temperatures and under shaded conditions such as characterize this experiment, other studies have found SLA has the strongest effect on RGR, followed by NAR (Loveys *et al.* 2002, Shipley 2006, Medek *et al.* 2007), while LMF tends to explain the least variation in RGR (Tomlinson *et al.* 2014). This leads us to expect that the growth response to temperature would be accompanied by significant changes in SLA and/or A_{\max} , yet SLA had only a weak temperature by population interaction ($P < .1$) and the effect of temperature on A_{\max} was non-significant. Furthermore, in contrast to the observed pattern of lower growth at warmer temperatures, photosynthesis showed a non-significant trend for higher rates at warmer temperatures, a pattern also noted in a similar warming experiment of sugar maple seedlings (Gunderson *et al.* 2000). Leaf mass fraction, in contrast, had a significant temperature by population interaction, and the effect of temperature on LMF was consistent with the direction of the growth response for the TN, though not the MO, population. Population differences in adjustments to LMF in response to temperature could be one reason that RGR and seedling mass were substantially higher for the TN than the MO or MN populations, and suggest that the relative impact of LMF on RGR may differ among populations.

Populations differed not only in traits but also in the direction of trait plasticity: at higher temperatures, the MN population increased SLA and LMF while the TN population reduced SLA and LMF. Though the MN and TN populations occupy opposing positions on a climate-of-origin gradient and differences in trait plasticity could arise from adaptive differentiation in these populations, it could also be the result of genetic variation that is not geographically structured. Few other studies have tried to identify intraspecific variation in trait responses to temperature, and thus far, evidence of such differences has been limited (De Swart *et al.* 2006, Gonzalo-Turpin & Hazard 2009, De Frenne *et al.* 2011, but see van de Weg *et al.* 2012). Further research is needed, and studies that include provenances from range center and range edges would help determine whether population differentiation occurs along a climate gradient or is instead concentrated in peripheral populations, regardless of climate of origin (Giuliani *et al.* 2014).

In some species, intraspecific variation in traits may be associated with climate gradients (Niinemets 2015), and in this study, seedling growth and trait responses to temperature and light appear broadly consistent with populations' climate of origin. While southern populations tend to have higher growth and growth-associated traits than the northern population, however, inconsistencies in this general pattern raise the possibility that variation among populations is not as strongly geographically structured as it appears. Relative growth rate of the MO population, for instance, closely resembled that of the MN population and was not as high as would have been expected based on its climate of origin. There were also rank reversals in SLA and percent leaf nitrogen, with higher values for the MO than TN population. Studies that use additional provenances from the full temperature gradient of the species' range would help determine the extent to which population differentiation in growth and traits is a product of local adaptation to temperature rather than another variable such as soil type and nutrient availability (Ordoñez *et al.* 2009, Maire *et al.* 2015) or the interactive effects of temperature and precipitation (Oke & Wang 2015).

CONCLUSION

Intraspecific variation in trait expression gives us insight into dynamics between traits and growth at several ecological scales: fitness differences at the stand level (*e.g.* Possen *et al.* 2015), trait-based environmental filtering and species assembly at the community level (*e.g.* Jung *et al.* 2010, Messier *et al.* 2010), and patterns of local adaptation to climate at the regional level (*e.g.* Laforest-Lapointe *et al.* 2014). Within-species analyses of functional traits also capture fine-scale patterns of trait and growth response to temperature that may be masked by multi-species analyses across broad environmental gradients (Albert *et al.* 2010a). As global and local climate continues to change, the degree to which populations within a species vary in functional traits and in the plasticity of those traits has implications for species' response to these shifts in temperature (Garzón *et al.* 2011, Oney *et al.* 2013). Trait-temperature relationships may differ widely between and within species (Burns & Beaumont 2009, Seiwa & Kikuzawa

2011), and it is therefore critical that we better understand patterns of intraspecific trait variation.

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TABLES AND FIGURES

TABLE 3-1 Hypothesized response of various traits and growth metrics to growth temperature, temperature of origin (population), and irradiance levels, as well as hypothesized differences in population response to temperature and light. Symbols indicate a positive (+), negative (-), or non-significant (~) hypothesized correlation between response and predictors. In interactions with temperature or light, populations may respond in opposing directions, such as hypothesized growth declining in the northern (N) cold-origin population and increasing in southern (S) warm-origin populations, or one population may display greater plasticity in a positive or negative direction, such as greater positive growth response to light in the southern population.

Growth or Trait Response Variable	Temperature	Temp. of origin (Population)	Pop. x Temp.	Light	Pop. x Light
RGR, Mass, Height	+	+	N – S +	+	S ++
Specific Leaf Area	+	+	N – S +	–	S – –
Photosynthesis	+	–	~	+	S ++
Percent Leaf N	–	–	~	–	S – –
Leaf Mass Fraction	+	+	N – S +	–	S – –

TABLE 3-2 Climate-of-origin data for the three populations in this experiment, based on 30-year climate normals (1981-2010) obtained from the PRISM Climate Group of Oregon State University. Moisture availability index (PPT/PET) and heat index were calculated using equations from Thornthwaite (1948). Seedlings were purchased from three nurseries whose seed sources were sugar maple populations in Mille Lacs County, MN, Lincoln Co., MO, and Warren Co., TN, and were grown in growth chambers under two temperature treatments that approximated the growing conditions in the northern (MN population) and southern (MO and TN populations) portions of the range. Those in the cool temperature treatment had a maximum temperature of 25° C (average daily temperature of 19.5°, summer heat index of 23.55), while those in the warm temperature treatment had a maximum temperature of 31° C (average daily temperature of 25.5°, summer heat index of 35.35).

Pop.	Latitude	Elev. (m)	Annual				Summer (June/July/August)			
			Temp _{mean} (° C)	Heat Index	PPT _{total} (mm)	Moist. Avail.	Temp _{mean} (° C)	Heat Index	PPT _{total} (mm)	Moist. Avail.
MN	45.90453	368	5.3	35.28	780.9	1.34	19.3	23.15	321.6	0.88
MO	39.02523	179	12.6	60.08	1031.1	1.36	24.3	32.81	290.64	0.67
TN	35.68671	300	14.6	67.54	1334.9	1.68	24.2	32.74	324.95	0.78

TABLE 3-3 The effects of population (MN, MO, and TN), temperature treatment (25° or 31° C), and log-transformed light (maximum light measured for each seedling) on relative growth rate (RGR), log-transformed seedling mass, and log-transformed seedling height (a), specific leaf area (SLA) and leaf mass fraction (LMF) (b), and percent leaf nitrogen (% leaf N) and photosynthesis (A_{max})(c), with model outcomes summarized and compared to hypotheses. In these linear mixed-effects models, chamber light and temperature treatments (nested within chamber) were entered as random effects to account for chamber-specific variation in seedling performance. Log-transformed initial diameter was used as an initial size covariate for all models but final height, percent leaf nitrogen, and photosynthesis, where the log-transformed initial height was used instead. Significance levels: $p < .0001$ (****), $p < .001$ (***), $p < .01$ (**), $p < .05$ (*), $p < .1$ (+)

a) Fixed Effect	RGR R ² = 0.59 N = 217	Seedling Mass R ² = 0.85 N = 218	Final Height R ² = 0.74 N = 240	Hypotheses supported?
Population	****	****	****	Yes: TN > MO > MN
Temperature	**	*	*	No: RGR, mass, height > @ 25°
Pop*Temp	-	-	**	No: Ht. diff. btwn. 25°, 31° > for MO pop
LogLight	****	****	****	Yes: increases with light
Pop*Light	+	-	-	Yes: TN, MO RGR ↑ with light
Temp*Light	-	-	-	ns
Pop*Temp*Light	*	*	**	↑ light: MN > @ 31°, TN > @ 25°
Initial size cov.	****	****	****	

b) Fixed Effect	SLA R ² = 0.65 N = 140	SLA hypotheses supported?	LMF R ² = 0.49 N = 216	LMF hypotheses supported?
Population	****	Partial: MO > TN > MN	****	Yes: TN > MO > MN
Temperature	-	ns	-	ns
Pop*Temp	+	No: TN > @25°, MN > @31°	***	No: TN LMF @ 25° > 31°
LogLight†	****	Yes: SLA ↓ with ↑ light	*	No: increases with light
Pop*Light	-	ns	-	ns
Temp*Light	-	ns	-	ns
Pop*Temp*Light	-	ns	+	↑ light: MN > @31°, TN > @25°
Initial size cov.	-		-	

c) Fixed Effect	% Leaf N R ² = 0.60 N = 102	Percent Leaf N hypotheses supported?	A_{max} R ² = 0.29 N = 116	Photosynthesis hypotheses supported?
Population	****	No: MO > TN > MN	-	ns
Temperature	*	Yes: % N > @ 25°	-	ns
Pop*Temp	-	ns	-	ns
LogLight†	***	Yes: % N ↓ with ↑ light	*	Yes: increases with light
Pop*Light	****	No: MO % N > TN, MN @ ↓ light	-	ns
Temp*Light	-	ns	-	ns
Pop*Temp*Light	-	ns	-	ns
Initial size cov.	-		-	

† In SLA, % leaf N, and photosynthesis models, log-transformed leaf-level light measurements used instead

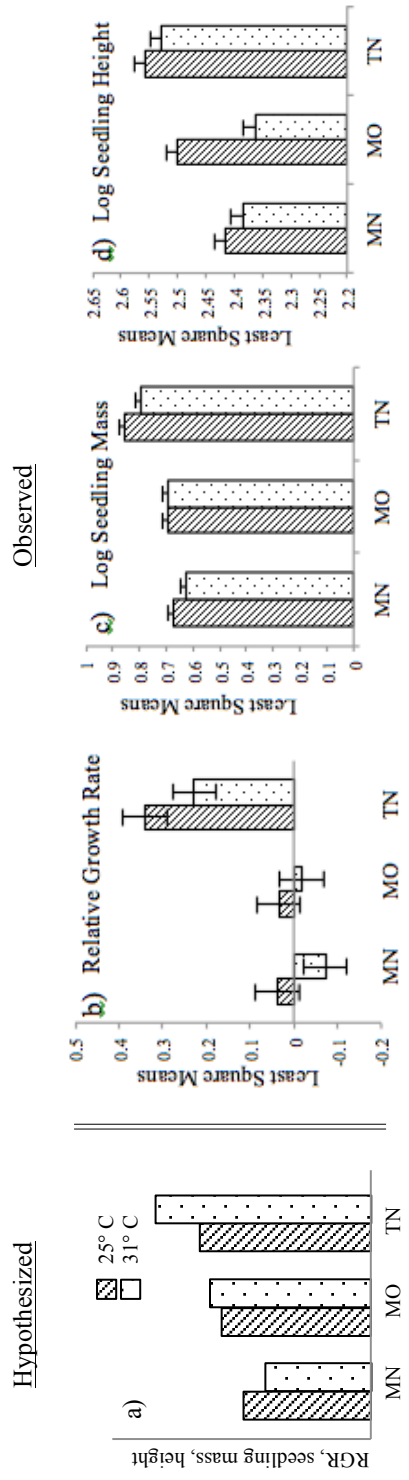


FIGURE 3-1 Hypothesized seedling RGR, mass, and height growth (a) of the three populations under two growing temperatures, and observed population differences for seedling growth (b-d). The relative performance of the populations in RGR was consistent with hypotheses (b), but in contrast to our hypothesis, all populations had a lower growth rate at 31° C. The southernmost (TN) population had highest seedling mass (c) and height (d), contrary to our hypothesis, and all populations had either equivalent or higher mass and height growth under cooler (25° C) growing conditions.

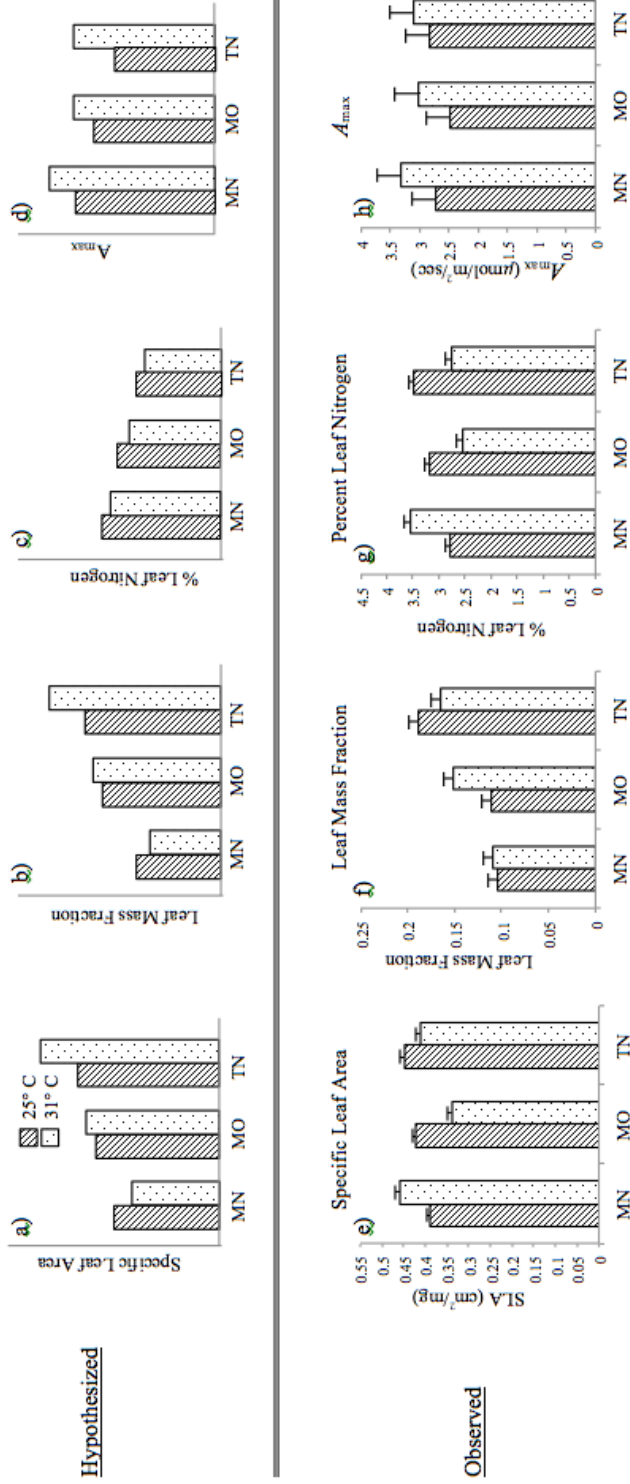


FIGURE 3-2 Hypothesized specific leaf area (a), percent leaf nitrogen (b), leaf mass fraction (c), and photosynthetic rate (d) of seedlings from the three populations grown under two temperature regimes, and observed differences in least square means between populations for each of these response variables (e-h). Our hypotheses concerning SLA and percent leaf nitrogen were not supported: the MN population had higher SLA (e) and percent leaf nitrogen (g) at 31°C, rather than 25°C as hypothesized, and under 25°C growing conditions, it was the TN population, rather than the MN population, that had highest SLA and percent leaf nitrogen. Allocation to leaves was highest in the southernmost (TN) population and lowest in the northernmost (MN) population (f), as hypothesized, but in contrast to hypotheses, the TN population had greater allocation to leaves under 25°C growing conditions. There were no significant differences among the populations in A_{max} , though all populations showed a trend towards higher photosynthetic rates for those individuals grown (and measured) at 31°C (h).

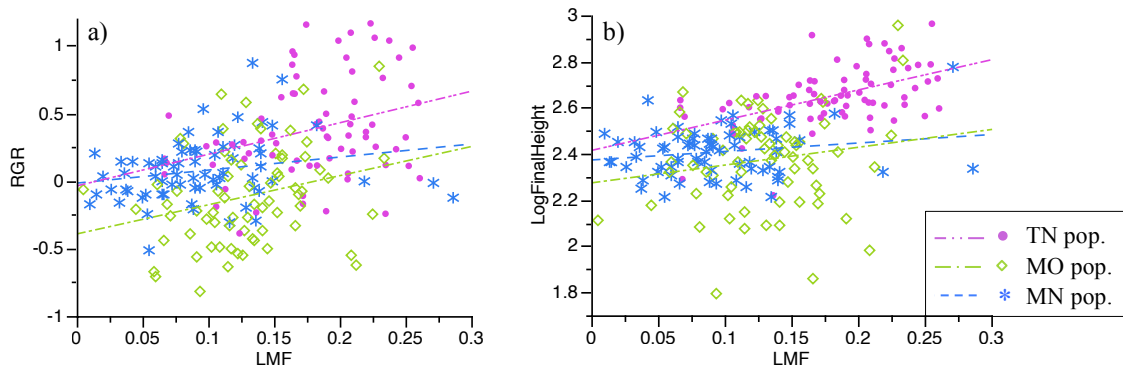


FIGURE 3-3 Population-level differences in RGR (a) and log-transformed final height (b) for seedlings that vary in biomass allocation to leaves. Seedlings from the TN population have higher growth rate and are taller than seedlings from other populations with similar allocation to leaves.

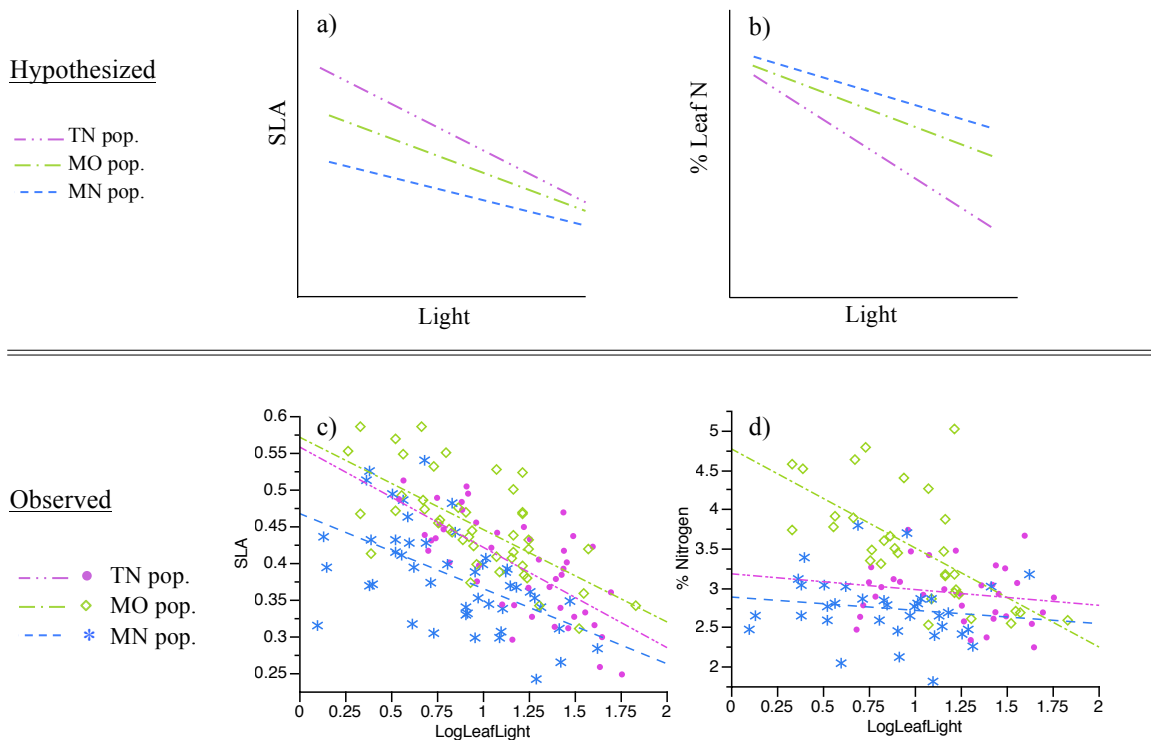


FIGURE 3-4 Hypothesized (a, b) and observed (c, d) population differences in specific leaf area (SLA) and percent leaf nitrogen across light levels. Specific leaf area declined with increasing light for all populations (c), as hypothesized, but in contrast to our hypothesis, the MN population had the lowest SLA and the MO population had highest SLA. As hypothesized, percent leaf nitrogen declined with increasing light (d), but in contrast to our hypothesis, the MN population had the lowest percent leaf nitrogen, and the southernmost and northernmost populations (TN and MN) had similar and relatively constant percent leaf nitrogen across light levels while the MO population had higher leaf nitrogen at low light level.

SUPPLEMENTAL INFORMATION

TABLE S3-1 Distribution of light values for seedlings in “low-light” versus “higher-light” growth chambers (measured in micromols/m²/sec using an AccuPAR LP-80). Quantiles show some overlap between the two light gradients but also substantial differences in light availability.

Quantiles	Light (micromols/m ² /sec)	
	“Low-light” chambers	“Higher-light” chambers
90%	13.4	36.1
75% quartile	8.4	24.5
Median	5.2	15.7
25% quartile	3.1	10.3
10%	2.0	5.0

TABLE S3-2 A full-factorial model evaluating the effects of population, temperature, and light on RGR, accounting for differences in initial diameter and leaf mass fraction ($R^2 = .611$, $N = 215$). In this mixed-effects model, temperature and chamber light (nested within chamber) were entered as random effects to account for chamber-specific variation in seedling performance.

Fixed effect	df	<i>F</i>	<i>P</i>
Population	2, 200	11.0	<.0001
Temperature	1, 6	6.4	.0442
Light	1, 20	81.8	<.0001
Population x Temperature	2, 196	0.0	.9936
Population x Light	2, 198	3.7	.0274
Temperature x Light	1, 19	1.3	.2608
Population x Temp. x Light	2, 198	2.9	.0587
Leaf mass fraction	1, 195	6.8	.0010
LogInitialDiam	1, 201	27.5	<.0001

TABLE S3-3 A full-factorial model evaluating the effects of population, temperature, and light on RGR, accounting for differences in initial diameter and leaf area ratio ($R^2 = .702$, $N = 133$). In this mixed-effects model, temperature and chamber light (nested within chamber) were entered as random effects to account for chamber-specific variation in seedling performance.

Fixed effect	df	<i>F</i>	<i>P</i>
Population	2, 118	12.5	<.0001
Temperature	1, 6	4.2	.0829
Light	1, 38	112.8	<.0001
Population x Temperature	2, 119	0.8	.4583
Population x Light	2, 117	5.2	.0068
Temperature x Light	1, 34	5.1	.0306
Population x Temp. x Light	2, 115	6.4	.0022
Leaf area ratio	1, 117	0.0	.9607
LogInitialDiam	1, 103	30.9	<.0001

TEMPERATURE / TRAIT HYPOTHESES

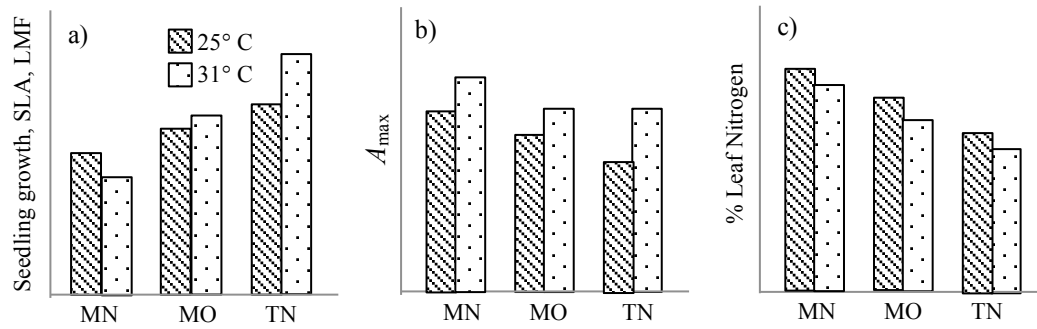


FIGURE S3-1 Hypothesized populations differences in temperature response for growth (RGR, seedling height, seedling mass), SLA, and LMF (a) as well as A_{max} (b) and percent leaf nitrogen (c). The northern (MN) population is expected to have greater growth, SLA, and LMF at 25° C, while southern (MO and TN) populations are expected to have higher growth, SLA, and LMF at 31° C (a). We do not expect populations to differ in the degree or direction of their temperature response for photosynthetic rates and percent leaf nitrogen, however; higher A_{max} and lower percent leaf nitrogen at 31° than 25° C is hypothesized for all populations (b,c).

LIGHT / TRAIT HYPOTHESES

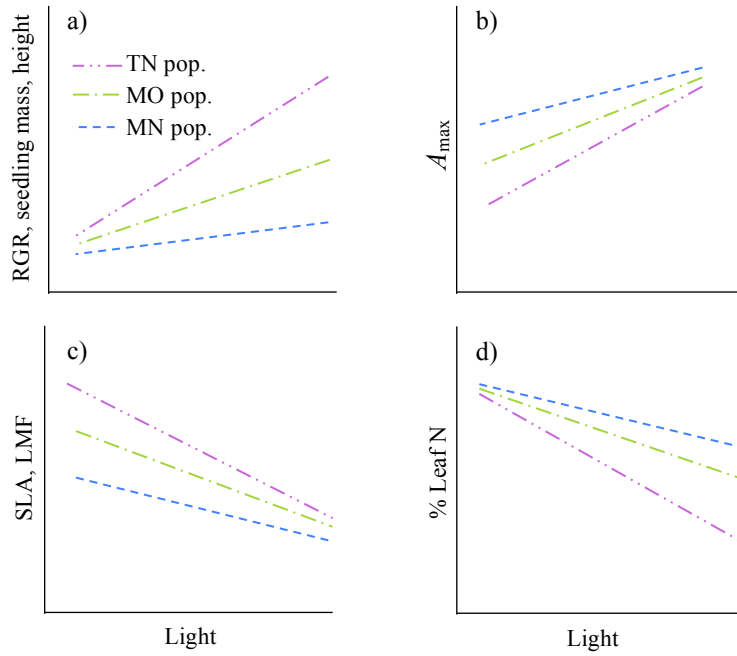


FIGURE S3-2 Hypothesized differences between populations in light response (a-d). The southernmost (TN) population is also expected to be most responsive to changing light availability, increasing growth and A_{max} and decreasing SLA, % N, and LMF to a greater extent than the other populations.

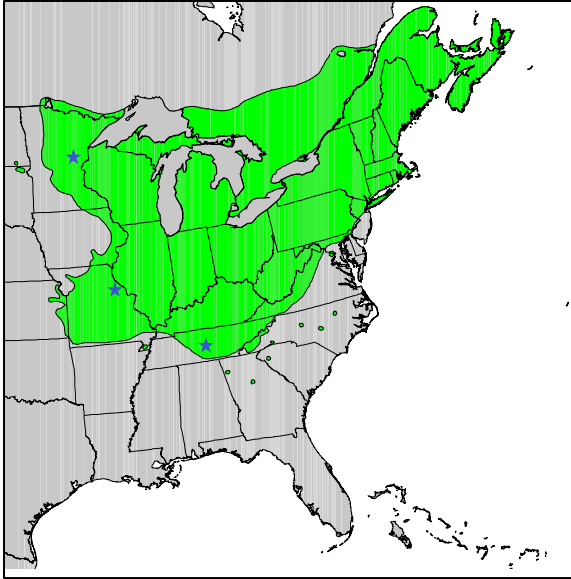


FIGURE S3-3 Range of sugar maple (*Acer saccharum*), adapted from Little (1971). In the western portion of its range, sugar maple can be found from southern Missouri and central Tennessee to the Minnesota/Ontario border. Stars indicate counties of seed origin: from north to south, Mille Lacs Co., MN, Lincoln Co., MO, and Warren Co., TN.

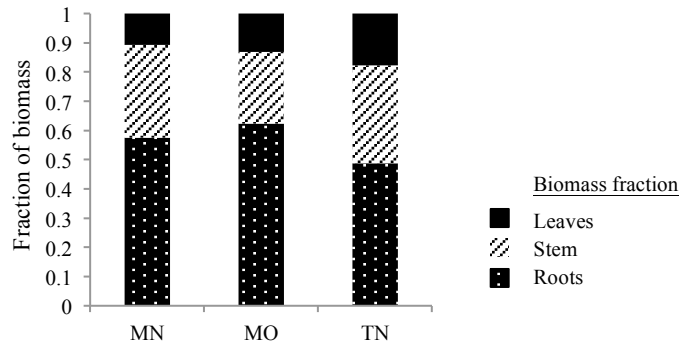


FIGURE S3-4 Relative distribution of biomass between roots, shoots, and leaves in the three populations. The MO population showed intermediate patterns of biomass distribution: MN and MO populations had more roots than the TN population, but the TN and MO population had more leaves than the MN population.

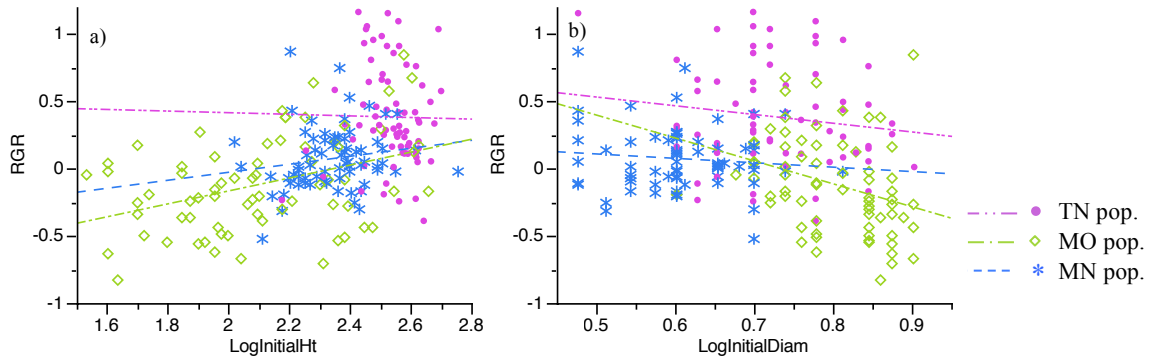


FIGURE S3-5 Population-level differences in RGR across seedlings differing in log-transformed initial seedling height (a) and diameter (b). Seedlings from the TN population were larger on average than those from the other two populations, but had higher growth rate even at a common height or diameter.

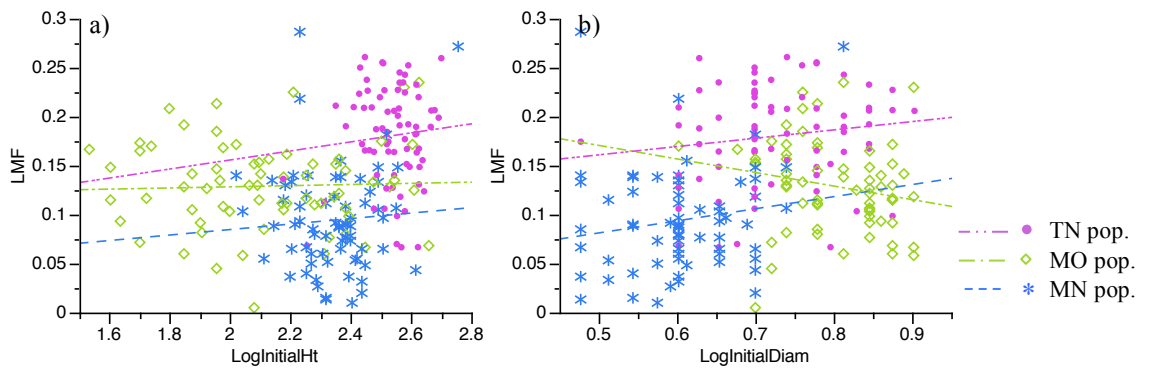


FIGURE S3-6 Population-level differences in LMF across seedlings differing in log-transformed initial seedling height (a) and diameter (b). As with RGR, seedlings from the TN population tended to have higher biomass allocation to leaves than MO or MN seedlings of a similar size.

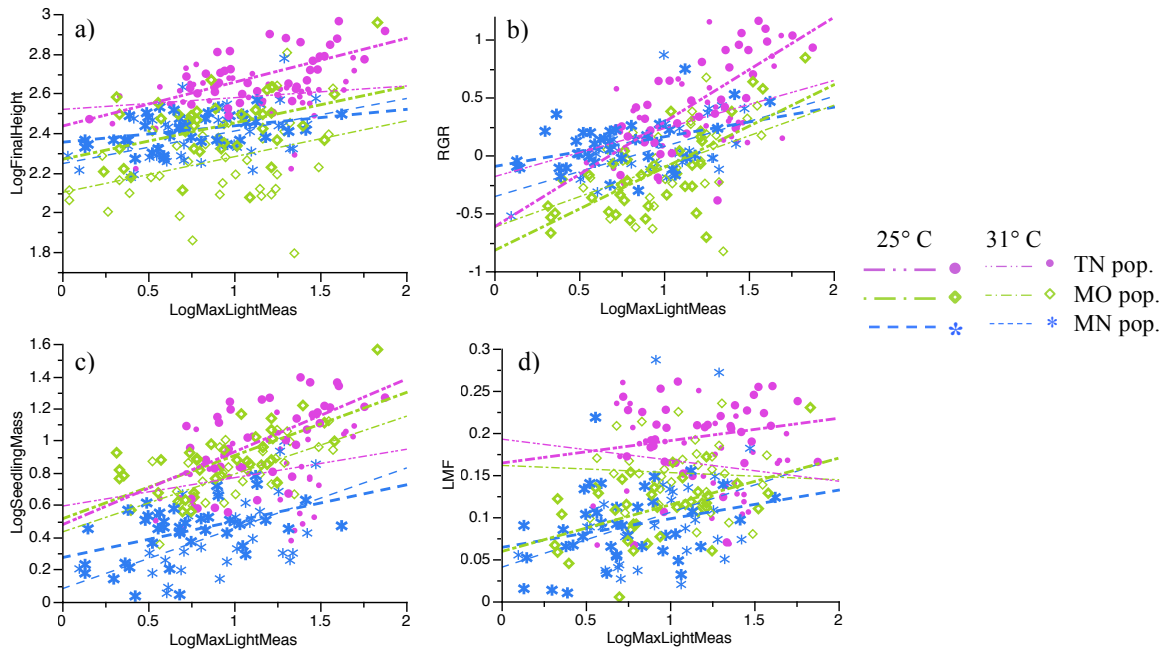


FIGURE S3-7 Seedling height (log-transformed) (a), relative growth rate (b), seedling mass (log-transformed) (c), and leaf mass fraction (d) as a function of light and temperature. Seedlings from the southernmost (TN) population were taller and had higher mass, RGR, and LMF than MO or MN populations, and except for RGR, where the MN population had higher growth rates at the lowest light levels, this held true across light levels. There were significant three-way interactions between light, temperature, and population for seedling height ($P = .0012$), RGR ($P = .0267$), and seedling mass ($P = .0122$): at high light, MN population seedlings were taller and had higher RGR and mass at 31° than 25°, while the TN population showed the opposite pattern. The TN population was also more responsive to light than the MN population. A three-way interaction between light, temperature, and population for LMF was significant at the .1 level ($P = .0820$). While the populations' LMF all responded similarly to increasing light, the TN population had lower LMF at 31°, especially at high light, while the MN population had higher LMF at high light when grown at 31°.

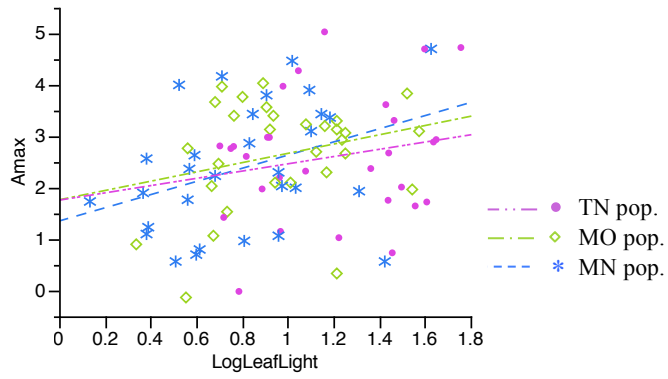


FIGURE S3-8 Relationship between maximum photosynthetic rate (A_{\max}) and leaf-level irradiance (log-transformed) in three populations representing a climate-of-origin gradient. A_{\max} was measured at the daytime maximum growing temperature (either 25° or 31° C) and at light saturation (500 PAR); light and photosynthesis were measured on the same leaves.

CONCLUSION

This research examines how sugar maple survival, growth, and traits vary across a climate gradient and with light and neighbor density environments, and whether populations from a climate-of-origin gradient differ in response to temperature or neighbors. I find population-specific responses to temperature in both field and growth chamber settings. Survival and net growth increase with temperature across a latitudinal transect for all populations, but the northern population has high survival and low net growth overall while the southern population has higher net growth across sites but low survival and a higher proportion of biomass in roots at cold northern sites. The southern population also has higher growth in the growth chambers, but in that experiment, relative growth rate, mass, and height are lower in the warmer temperature treatment, perhaps due to contrasting responses of photosynthesis and respiration to field versus controlled growing conditions influencing carbon balance. Burton and Pregitzer (2003) measure increases in sugar maple root respiration (R_{amb}) with temperature; growth reductions at the higher temperature in the growth chamber might therefore be due to increased respiration costs. In the field, increasing respiratory costs at warmer sites may be reduced by lower soil water availability (Rodríguez-Calcerrada *et al.* 2009) and offset by higher photosynthesis in forest-grown seedlings, which are less light-limited than those in the growth chamber.

Populations vary in trait expression as well as growth, and northern population seedlings seem to have more conservative trait values. The two southern populations do not show geographically consistent trait variation, however, and growth chamber comparisons of trait response to temperature among populations suggest that intraspecific variation in traits, while important, may not reflect climate-of-origin gradients. Further research is needed to examine intraspecific trait variation among multiple populations representing a more complete climate-of-origin gradient, with a particular focus on range margins. This study emphasizes the importance of measuring intraspecific variation in trait values rather than relying on species means for range limit studies, as nearly every trait measured differs significantly among populations and trait differences in turn affect patterns of survival and growth.

A central goal of this research is to identify some of the potential mechanisms that might be limiting the distribution of sugar maple at northern and southern range margins. Over the three-year span of the field experiment, I do not find evidence of either climate or competition as range-limiting constraints for locally adapted populations. This study does not exclude either possibility, however, as one or both might be limiting at a different life stage, and limitation could also occur over a longer time frame than was experimentally observed. Though reducing neighbors beyond the southern range margin has little effect on seedling survival and growth, competitive exclusion at later growth stages could play a role in limiting sugar maple distribution if other shade-tolerant species have higher growth rates and success in filling canopy gaps (Yetter and Runkle 1986). Observed patterns in this study of high survival and growth in seedlings experimentally planted at and beyond the southern range margin is consistent with 20 years of demographic data on sugar maple in the region that indicate the species' southern distribution has neither expanded nor contracted in that time (Hart *et al.* 2014), despite model predictions that the southern margin of sugar maple's range will shift northward with climate warming (Prasad *et al.* 2007). It may be that climate warming has not yet regularly exceeded certain critical thresholds that would affect minimum chilling periods required for germination (Godman *et al.* 1990) and reproduction (Morin *et al.* 2007); alternatively, it is possible that such effects are already occurring but have not yet been detected in the smallest-diameter demographic cohort due to slow growth of sugar maple.

Intraspecific differences among the populations in survival and growth suggest local adaptation and are consistent with a cold-hardiness and growth rate trade-off. At and beyond northern range margins, survival of the northern population is much higher than that of the other populations, an indication that temperature may broadly constrain the species' northward distribution. Consistent with this, recent northward distributional shifts in sugar maple have been noted that coincide with climate warming (Boisvert-Marsh *et al.* 2014). As climate warms and is potentially less limiting at northern range margins, however, locally adapted cold-hardy sugar maple populations might be at a

competitive disadvantage if other co-existing species have a greater capacity to increase relative growth rates at warmer temperatures.

At both range margins, patterns of reproduction and dispersal could influence range limits and are an important topic for further research, though beyond the scope of this study. Further research is also needed on climate-driven changes in reproductive phenology at and beyond range margins (Morin *et al.* 2007), though this presents a considerable challenge in long-lived species. Finally, this research emphasizes the importance of further attention and experimental work to identify the degree of intraspecific variation in growth and trait response to environmental gradients across species.

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