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GEOGRAPHIC VARIATION OF GERMINATION, GROWTH, AND MORTALITY IN SUGAR MAPLE (*Acer saccharum*): COMMON GARDEN AND RECIPROCAL DISPERSAL EXPERIMENTS

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Abstract: If current temperature trends continue and increase as predicted by general circulation models, the persistence and migration of sugar maple (*Acer saccharum*) at its northern limit will become crucial to its continued existence in North America. Specifically, anthropogenic warming may affect germination success and growth of sugar maple. To evaluate this potential limitation, our study addresses two questions. The first involves a growth chamber: Do temperatures at and above (1°, 7°, and 14° C) sugar maple's optimal germination temperature affect its germination? The second involves a common garden: Do sugar maple germination and subsequent growth and mortality rates show evidence of geographic variation under current climatic conditions? While sugar maple germinated successfully at 7° C in the lab, field results suggest that other environmental variables may limit its future establishment as climate changes. Germination of seeds from sugar maple's northern range limit was significantly reduced under warmer conditions, and subsequent seedling mortality rates were significantly increased when grown at a more southerly latitude. Local adaptation was evident with respect to germination, survival, and growth in the field. Ultimately, results from this study further the understanding of how predicted anthropogenic climate change may affect the regeneration of sugar maple in the future. [Key words: *Acer saccharum*, biogeography, common garden experiment, germination, geographic variation, reciprocal dispersal.]

INTRODUCTION

It is estimated that species compositions of one-third of the Earth's current forests could be dramatically altered as a result of projected changes in climate (Iverson and Prasad, 1998, 2001). Given the potential that climate change may alter the regeneration dynamics of plant species, it is essential that biogeographers and ecologists investigate the possible effects of anthropogenic warming on terrestrial ecosystems and on the individual species that comprised them. In general, it is within the earliest stages of development that a plant is most vulnerable to outside disturbances (Silvertown, 1980). Therefore, the seed is of great importance (Bhatnagar and Johri, 1972); after all, it is within the seed that all of the information necessary for germination, development, morphogenesis, and reproduction of the species is stored (Berlyn, 1972) and the survival of the species is based (Bentsink and Koornneff, 2008). As a result, establishment—more specifically, germination and subsequent

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seedling emergence—has been identified as one of the most crucial stages in the life cycle of a plant (Caspersen and Saprunoff, 2005). Ultimately, as forests respond to climate change and biomes shift, new recruits of the migrating species must be able to germinate, mature, and reproduce to further facilitate migration, as species track favorable climatic conditions (Iverson and Prasad, 2001; Goldblum and Rigg, 2005). Variables such as local variations in topography, geomorphology, disturbances, and climate have also been identified as being key drivers in local-scale vegetation models (Iverson and Prasad, 1998; Joyce et al., 2001).

Sugar maple (*Acer saccharum*) is a long-lived, deciduous tree species, recognized as being sensitive to changes in climate (Goldblum and Rigg, 2005; Goldblum et al., 2010) and significant to eastern North America for both ecological and economic reasons (Godman et al., 1990). It makes up about 6% of the hardwood saw timber volume in the United States (Godman et al., 1990) and is frequently used for pulpwood, firewood, high-quality timber, veneer, and the production of maple syrup (Zasada and Strong, 2003). Over large portions of eastern North America sugar maple provides watershed protection, food for seed-eating birds and mammals, substrate for multiple lichens and mosses, browse and cover for a variety of animals, and homes to cavity-nesting birds (Zasada and Strong, 2003). Growing on a total of about 12.4 million ha, sugar maple is the predominant forest tree through much of eastern North America (Fig. 1) (Godman et al., 1990; Kotanen, 2007).

Seed germination can generally be separated into five major stages: (1) imbibition (water absorption through the seed coat of an inactive dry seed), (2) hydration and activation, (3) cell division and cell extension, (4) protrusion (the physical emergence of the embryo from the seed), and (5) completion of non-repetitive morphogenesis (Berlyn, 1972). Viable, intact seeds will not successfully germinate under optimal conditions if they are dormant (Mayer and Poljakoff-Mayber, 1975; Bewley, 1997; Bentsink and Koornneff, 2008). In general, dormancy can occur for a variety of reasons, including: (1) immaturity of embryo, (2) impermeability of seed coat to water or gases, (3) mechanical causes, (4) the presence of substances inhibiting germination, or (5) absence of temperature or light requirements (Mayer and Poljakoff-Mayber, 1975). Dormancy can be a beneficial trait in environments where favorable conditions are often intermixed with unfavorable ones (Kozlowski and Gunn, 1972). Sugar maple seeds, which have morphologically mature, but dormant embryos, require a period of stratification at low temperatures (between 1° and 5° C) accompanied by high soil moisture content in order to break dormancy and germinate (e.g., Jones, 1920; Carl and Yawney, 1966; Yawney, 1968; Webb and Dumbroff, 1969; Carl and Snow, 1971; Webb et al., 1973; Simmonds and Dumbroff, 1974; Webb, 1974; Janerette, 1978, 1979; Carl, 1983; Shih et al., 1985; Godman et al., 1990; Hance and Bevington, 1992; Farmer, 1997). Mayer and Poljakoff-Mayber (1975) found that the temperature range in which a seed can typically germinate is primarily determined by the geographic source of the seeds, the genetic differences found within the species, and the endogenous growth substance levels. To date, however, only a limited number of studies explore sugar maple's germination response to a range of temperatures. Therefore, it is not clear to what extent Canadian Regional Climate Model (Plummer et al., 2006) projections of a 1.5° to 4.5° C average temperature increase by the middle of the 21st century for the region including Upper Michigan,

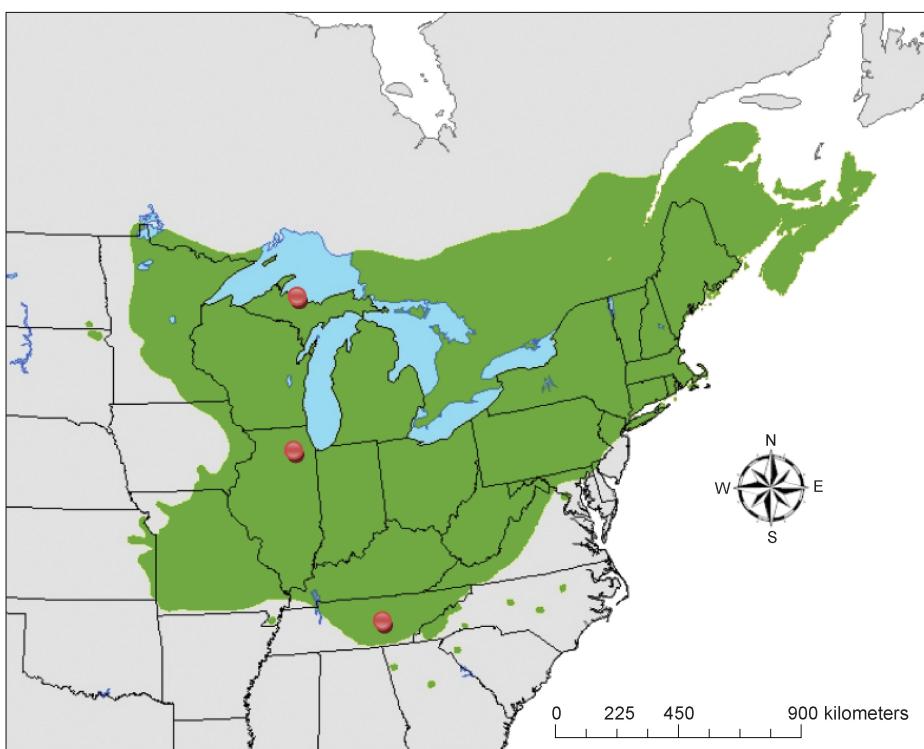


Fig. 1. Map depicting the native range of sugar maple. Dots represent the seed source locations (Big Bay, Michigan; Elburn, Illinois; and Tennessee) with the northern and central dots also representing the two field sites. Native range data obtained through the U.S. Geological Survey (1999).

and a 0° to 3.5° C increase in seasonal average temperature in the Great Lakes region (including Illinois) (Liang et al., 2006; Plummer et al., 2006), will have on sugar maple regeneration, as limited by germination.

The persistence and successful northward migration of sugar maple at its northern range limit will become even more important as the climate continues to change, because many niche-based models show a considerable northern shift in sugar maple's suitable habitat location, potentially as soon as 2100 (Joyce et al., 2001; Prasad et al., 2007–ongoing). Seed dispersal is often cited (e.g., Dyer, 1995; Cain et al., 2000) as a limiting factor in plant migration. For sugar maple, given its specific regeneration requirements, seed germination could ultimately be a significant limiting factor to northward migration (Clark et al., 1999).

Biogeographic studies seeking to isolate the environmental factors that control plant function typically utilize either common garden or reciprocal transplant (dispersal) methods (Hufford and Mazer, 2003; Nuismer and Gandon, 2008). Throughout the years, some controversy has existed over which specific pattern of local populations \times test habitat interactions for fitness should be used when identifying local adaptation (Kawecki and Ebert, 2004). Two criteria have been proposed as ways in which the improved fitness can occur: the local vs. foreign and the home vs. away

(Kawecki and Ebert, 2004). Specifically, the local vs. foreign criterion is met if, within each habitat, local populations show a higher fitness than foreign populations from other habitats. The home vs. away criterion is met if, across habitats, each population has a higher fitness in its own habitat (i.e., home) rather than in other habitats (i.e., away) (Kawecki and Ebert, 2004). While both of these criteria are worth exploring, only the local vs. foreign criterion is directly applicable to divergent natural selection and therefore directly linked to the driving force of local adaptation (Kawecki and Ebert, 2004). The home vs. away criterion adds inherent variations in habitat quality to the mix, which cloud the effects of divergent selection. Therefore, when a pattern only meets the home vs. away criterion, it challenges the theory of local adaptation by implying that some populations always surpass the performances of others in all habitats (Kawecki and Ebert, 2004).

This study sought to evaluate the sensitivity of sugar maple seeds to differences in germination temperature, and potential vulnerability of sugar maple to warmer temperatures. To accomplish this task, we used both the reciprocal transplant (dispersal) and common garden experiments in order to address our two main questions. First, a series of growth chamber experiments addressed how temperature, at and above sugar maple's optimal germination temperature range of 1° to 5° C, affects sugar maple seed germination, and whether geographic variations occur in this response. Second, the field-based reciprocal dispersal experiment dispersed seeds collected from the northern, central, and southern portions of sugar maple's range into forests at the central and northern portions of sugar maple's range to address whether sugar maple seed germination, seedling growth, and mortality rates showed geographic variability, local adaptations, and/or sensitivity to climate. In this study, the patterns that satisfied both the local vs. foreign and the home vs. away criteria, as well as the patterns that satisfied only the local vs. foreign criterion, were interpreted as supporting local adaptation. Overall, the goal of this study was to provide information about the extent to which temperature and geographic variation affect sugar maple's regeneration success.

METHODS

Two field sites were used for this study. The North site is located near Big Bay in the Upper Peninsula of Michigan (46°49'46" N, 87°44'42" W) and the Central site is located in Blackberry Maples Forest Preserve (41°50'10" N, 88°27'17" W) near Elburn, Illinois. Both sites are closed-canopy, sugar maple-dominated forests. Based on conversations with the landowner, sugar maple adults are approximately 80–100 years old at the North site. The sugar maples at the Central site range in size from 5 cm at dbh to 80.9 cm at dbh and have a relative density of 78% within the forest preserve (58.92% relative basal area). Sugar maple reproduction is active at both field sites, as evidenced by the dense sugar maple seedling bank and high seed fall during mast years.

Seed Collection, Storage, and Viability

Using 1 × 1 m seed traps, with a design based on Wiese et al. (1998), we collected sugar maple seeds during a mast year (November 2006) at both the North site and the Central site. The seed counts from the North site seed traps ($n = 16$) ranged between

485 and 1,200 seeds/m², with a mean (\pm std. dev.) of 985 (\pm 206). Our seed counts from the Central site seed traps ($n = 16$) ranged between 1,283 and 2,980 seeds/m², with a mean (\pm std. dev.) of 2411 (\pm 434). We purchased 1.4 kg of sugar maple seed collected in Tennessee (hereafter South site) from horticulturists F. W. Schumacher Co., Inc. (Sandwich, MA). The South site seeds came de-winged, with non-viable seeds likely either removed for commercial purposes or as a consequence of the de-winging process. However, little is known about the collection or handling methods of the South site seeds, because they were collected by independent contractors for F. W. Schumacher. Overall, we purchased 17,233 Tennessee seeds. In total, we collected and purchased 71,574 seeds for this study. To maintain viability, seeds were stored at -10° C until they were used, as per Yawney and Carl (1974).

We used 1000 seeds for a series of viability tests based on the n-pentane (C₅H₁₂) methods described by Carl and Yawney (1969) and Carl (1976). We used the viability percentages calculated from these tests as a baseline for both the field experiments and germination chamber experiments.

Common Garden—Growth Chamber

To evaluate geographic variation in sugar maple response to germination temperature, we ran three growth chamber trials at and above sugar maple's optimal germination temperature range. At the beginning of each trial, seeds were taken from -10° C storage and soaked in de-ionized water for 24 hours at 2° C to break dormancy (Carl and Snow, 1971; Janerette, 1979). After soaking, seeds were subjected to moist stratification on germination paper for 90 days (Carl and Yawney, 1966; Carl and Snow, 1971; Janerette, 1978) at one of three different germination temperatures: 1°, 7°, and 14° C, in a Percival Scientific Inc. (Model LT36VL) plant growth chamber. These temperatures were chosen to match the lower end of the optimal germination temperature range (1° C), test for a worst-case climate change scenario (7° C), and explore whether there is an upper temperature limitation to sugar maple germination (14° C). For each trial, light conditions within the chamber were set to mimic the light intensity in a leafless deciduous forest and a spring, mid-latitude photoperiod. For this study, seeds were considered germinated when the radicle emerged from the seed coat. At the end of each trial, a subset of the ungerminated seeds was opened in order to determine why germination failed (Carl and Snow, 1971).

Reciprocal Dispersal—Field

We established a reciprocal dispersal experiment to assess how seed source affects germination, subsequent growth, and mortality rates under natural conditions. Sixteen plots were established at each of the northern and central sites. Fifteen of the 16 plots at each site were used in the reciprocal dispersal experiments, with one plot at each site used as a control to assess error in the seed collection process. Collected/purchased seeds were manually dispersed beneath the replaced leaf fall, in plots previously covered by the 1 × 1 m seed traps. Five plots at each site received 1000 northern seeds each, five plots received 1000 central seeds each, and the remaining five plots received 500 southern seeds each. The lower dispersal number

was chosen for the southern samaras due to their high viability from our viability analysis. No seeds were manually dispersed within the control plots, allowing us to determine the efficacy of the seed traps.

In both summers of 2007 and 2008, we counted all new germinants and measured heights of new sugar maple germinants within each plot at both field sites. Germinants at the North site were censused in August 2007 and 2008, while the censuses at the central site occurred in September 2007 and 2008. At both sites, all new sugar maple seedlings within the plots were permanently tagged and numbered. Eight seedlings germinated in the North site control plot and five seedlings germinated in the control plot at the Central site.

Statistical Methods

All analyses were performed with either independent sample *t*-tests (assuming unequal variance), one-way ANOVAs using a modified, non-destructive relative growth rate based on Harper (1977) ($(\ln(H_2) - \ln(H_1)) / t_2 - t_1$), where H_1 is seedling height (cm) at time 1 ($t_1 = 2007$) and H_2 is seedling height (cm) at time 2 ($t_2 = 2008$)), Chi-square proportion tests accompanied by Tukey-type multiple comparison testing, or general descriptive statistics. For all statistical tests in this study, $p < 0.05$ was considered statistically significant.

RESULTS

Viability Results

The northern and central seeds had statistically similar mean n-pentane viability percentages, 46.8% and 46.7% respectively, while southern seeds had a significantly ($p < 0.05$) higher average viability percentage, 82.7%. After visual inspection of the seeds (confirming the n-pentane results) the actual viability for the northern and central samaras decreased slightly to 43.5% and 45.0%, respectively, while the southern samaras viability increased to 83.5%. All results presented herein were adjusted based on the actual viability rates, meaning that all germination proportions and seed counts in this study are calculated based on the predicted number of viable seeds rather than the total number of dispersed seeds in order to gain an accurate representation of what would occur in nature.

Common Garden—Growth Chamber Results

A cumulative germination proportion was calculated throughout each trial to track emergence patterns based on seed source. At the conclusion of the 1° C temperature trial, 838 seeds had germinated. In the 1° C trial, the southern seeds germinated at a significantly ($p < 0.01$) lower proportion than both the northern and central seeds, which were statistically similar (Fig. 2). At the conclusion of the 7° C temperature trial, a total of 978 seeds had germinated. The three seed source germination proportions were significantly ($p < 0.01$) different, with the northern seeds having the highest germination proportion, the southern seeds having the lowest,

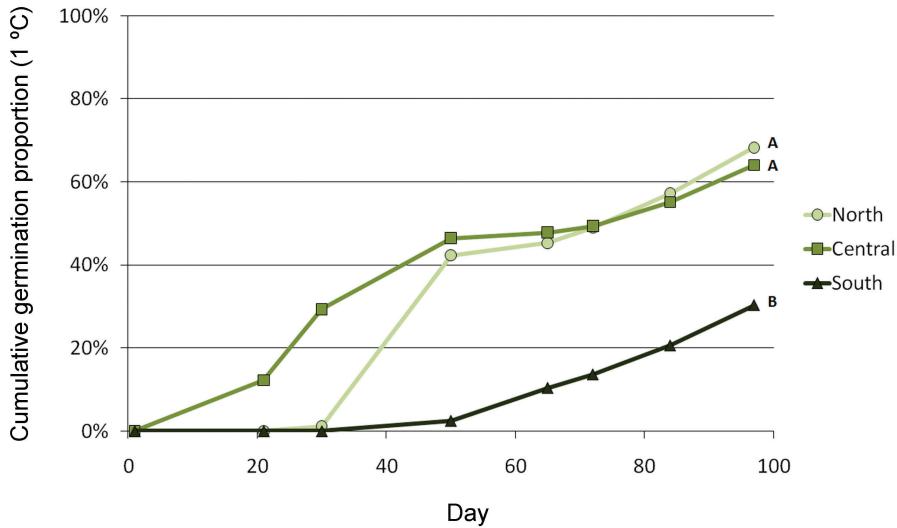


Fig. 2. Cumulative germination proportions during the 1°C trial. Symbols on the lines indicate each time a germination count was recorded. Based on proportion tests, significant ($p < 0.01$) differences were found between seed sources, as denoted by the letters.

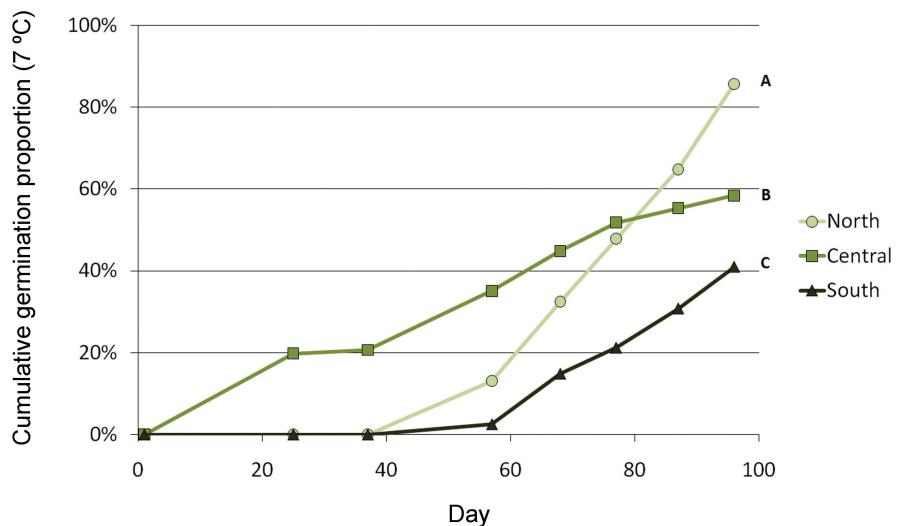


Fig. 3. Cumulative germination proportions during the 7°C trial. Symbols on the lines indicate each time a germination count was recorded. Based on proportion tests, significant ($p < 0.01$) differences were found between seed sources, as denoted by the letters.

and the central seeds having the intermediate germination proportion (Fig. 3). At the conclusion of the 14°C temperature trial, 978 seeds had germinated. Similar to the 7°C temperature trial, all three seed source germination proportions were

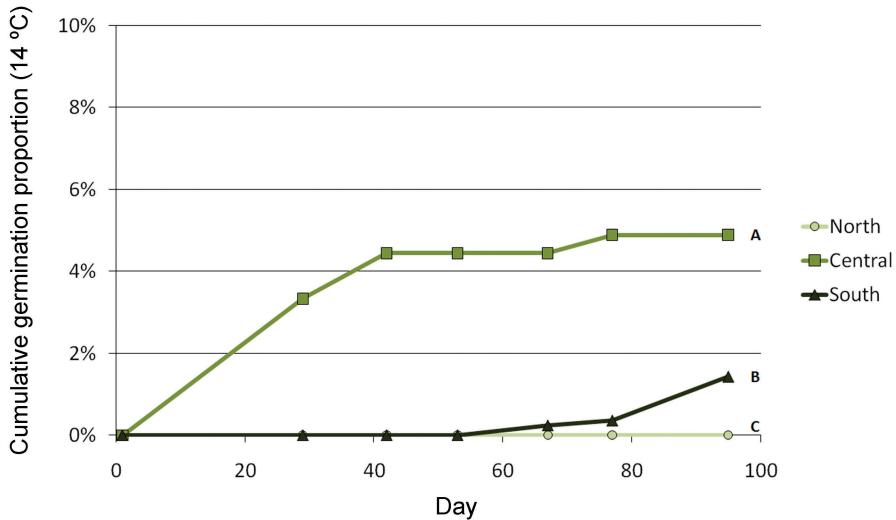


Fig. 4. Cumulative germination proportions during the 14° C trial. Symbols on the lines indicate each time a germination count was recorded. Based on proportion tests, significant ($p < 0.01$) differences were found between seed sources, as denoted by the letters.

significantly ($p < 0.01$) different from each other; however, the central seeds had the highest germination proportion, while only a small proportion of the southern seeds germinated and the northern seeds failed to germinate (Fig. 4).

The final germination proportions of the northern seeds from all three temperature trials were found to be significantly ($p < 0.01$) different from one another, with the highest germination rate occurring at 7° C and the lowest occurring at 14° C (Fig. 5). Phenologically, the northern seeds at 1° C were the first to begin germinating, at day 30. Northern seeds that germinated in the 7° C trial emerged after day 37, but none germinated in the 14° C trial. The 1° and 7° C final germination proportions for the seeds from the central source were statistically similar, while the final proportion of central seeds germinating at 14° C was significantly ($p < 0.01$) lower (Fig. 6). No matter the germination temperature, central seeds began germinating shortly after being placed in the germination chamber (within the first 20 days). The number of germinants in the 1° and 7° C trials steadily increased during the trials, while germinations at 14° C remained relatively low and stable through the trial. The final germination proportions of the seeds from the southern source, on the other hand, differed significantly ($p < 0.01$) from one another (Fig. 7). More specifically, the southern seeds germinated significantly better at 7° C than at 1° C and had the lowest germination rate at 14° C. Germination of Southern seeds was considerably more delayed than that of seeds from the other two seed sources, but was consistent across the different temperature trials. In general, the southern seeds germinating at 1° C were the first to germinate after day 30, with those germinating at 7° C emerging shortly thereafter, at day 40, while the seeds germinating at 14° C began germinating long after this, around day 65.

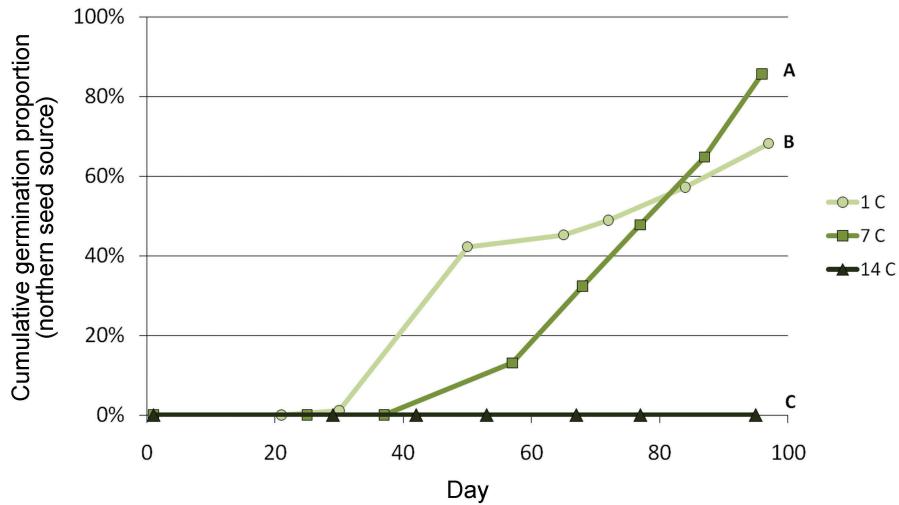


Fig. 5. Cumulative germination proportions of all northern seeds from the three temperature trials. Symbols on the lines indicate each time a germination count was recorded. Based on proportion tests, significant ($p < 0.01$) differences were found between temperature trials, as denoted by the letters.

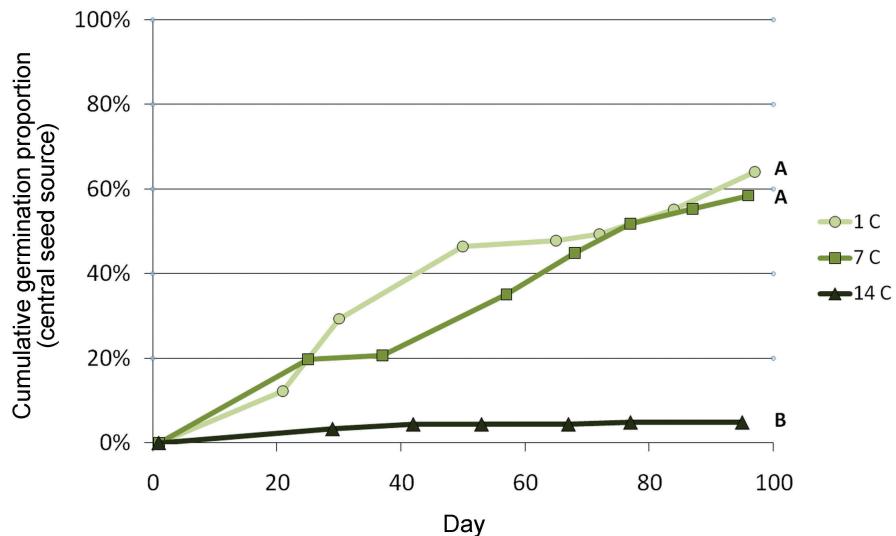


Fig. 6. Cumulative germination proportions of all central seeds from the three temperature trials. Symbols on the lines indicate each time a germination count was recorded. Based on proportion tests, significant ($p < 0.01$) differences were found between temperature trials, as denoted by the letters.

Reciprocal Dispersal—Field Results

After the first growing season, a total of 1702 sugar maple seedlings were growing at the North site. More specifically, within the North site, the northern seeds

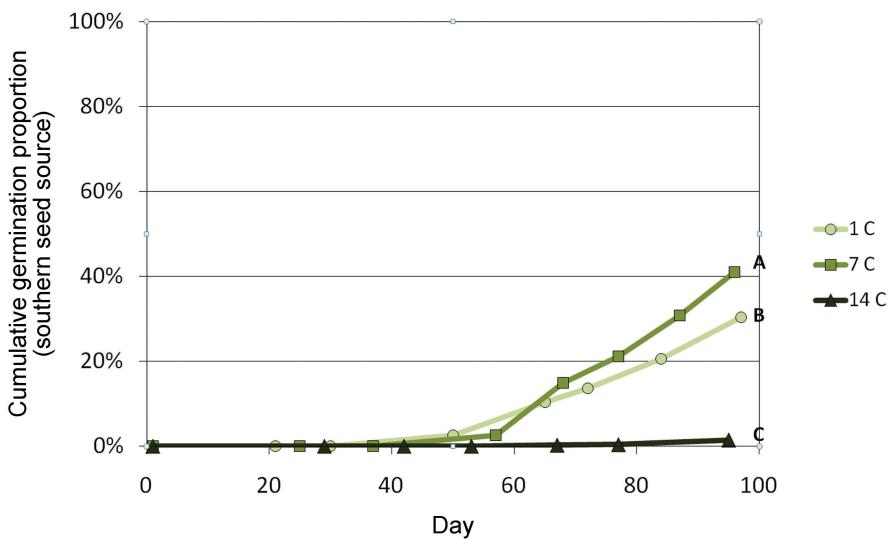


Fig. 7. Cumulative germination proportions of all southern seeds from the three temperature trials. Symbols on the lines indicate each time a germination count was recorded. Based on proportion tests, significant ($p < 0.01$) differences were found between temperature trials, as denoted by the letters.

germinated at a significantly ($p < 0.05$) higher proportion (36.9%) than either the central or southern seeds, with the central seeds germinating at the lowest proportion (15.6%) and the southern seeds falling between the two (26.3%). At the Central site, the germination proportion of southern seeds (9.7%) was significantly ($p < 0.05$) larger than that of the central seeds (6.8%) or northern seeds (6.5%).

Comparing germination patterns between the North and Central sites, germination at the North site, regardless of seed source, was significantly ($p < 0.05$) higher than germination proportion at the Central site. Additionally, between the North and Central sites, we compared final germination proportions (Fig. 8A), average relative growth rates (Harper, 1977) (Fig. 8B), and juvenile survival rates (Fig. 8C) for all three seed sources. The northern seeds had a germination proportion of 37% within the North site and a germination proportion of 6.8% within the Central site. The central seeds on the other hand, had germination proportions of 16% and 6.5% within the North and Central sites, respectively. The average relative growth rate for the northern seeds within the North site was 0.18, compared to 0.19 within the Central site. The average relative growth rate for central seeds within the North site was 0.19, in contrast to 0.34 at the Central site. With regard to juvenile survivorship, 50.6% of the northern first-year seedlings survived within the North site, while only 34.5% survived within the Central site. Within the North site, 48.3% of the central first-year seedlings survived, while 59.9% survived within the Central site.

Based on field measurements in the second field season, we calculated mortality and growth rates for both field sites. At the North site, seedlings that germinated from northern and central seeds had statistically similar mortality rates, while the mortality rate for the southern seedlings was found to be significantly ($p < 0.001$) lower

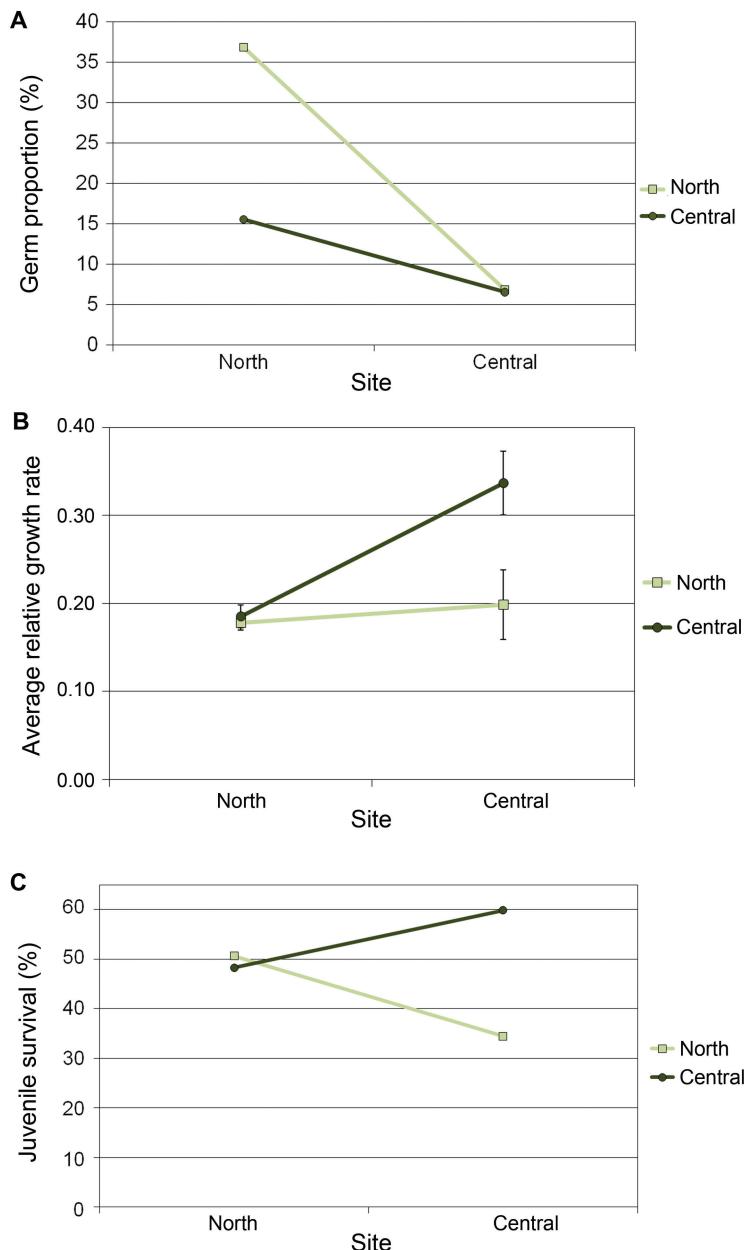


Fig. 8. Patterns of local populations (from northern and central seed source) \times habitat interaction (between the North and Central sites) for three levels of fitness: (A) establishment based on germination proportions, (B) average relative growth rates, and (C) juvenile survival based on seedling survivorship proportions. Squares represent the local population originating from the North site, while circles represent the local population originating from the Central site. When applicable, error bars depict the 95% confidence level.

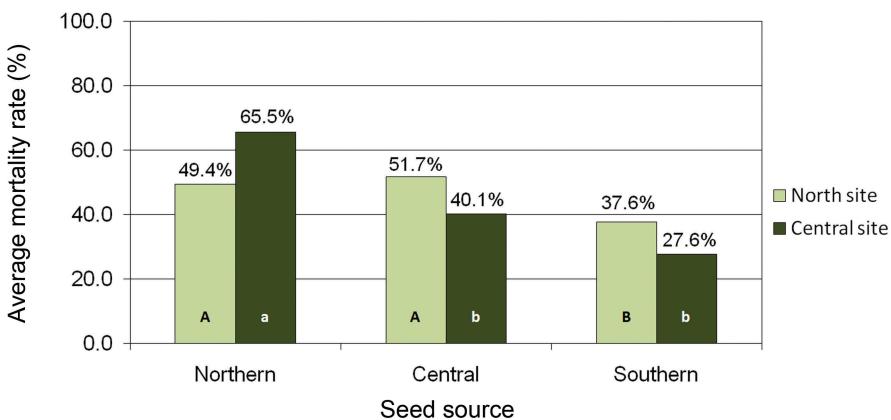


Fig. 9. Average percent mortality rates based on second-year survivorship for all seed sources at both the North and Central sites. Based on two-sample difference of proportion tests, significant ($p < 0.01$) differences were found within both the North and Central sites between the seed sources, as denoted by the letters, which are site specific.

than the others (Fig. 9). At the Central site, seedlings that germinated from central and southern seeds had statistically similar mortality rates, while the mortality rate for the northern seedlings was found to be significantly ($p < 0.01$) higher than the others (Fig. 9). Comparing mortality rates between sites, only seedlings from the northern source were found to differ significantly ($p < 0.01$), with the highest mortality rate occurring at the Central site (Fig. 9).

At the North site, the relative growth rates of the southern seedlings were significantly ($p < 0.001$) higher than the statistically similar northern and central seedling relative growth rates (Fig. 10). At the Central site, the relative growth rates of the northern seedlings were significantly ($p < 0.001$) lower than those of both the central and southern seedling relative growth rates, which were statistically similar (Fig. 10). When relative growth rates were analyzed between sites, both the central and southern seedlings were found to grow at different rates at the two field sites. In both cases, the Central site had significantly ($p < 0.001$) higher relative mean (\pm std. dev.) growth rates (central seeds in Central site = 0.34 ± 0.17 , southern seeds in Central site = 0.33 ± 0.13) than the North site (central seeds in North site = 0.19 ± 0.08 , southern seeds in North site = 0.22 ± 0.10) (Fig. 10).

DISCUSSION

Given that future climate change may alter plant communities (Williams and Jackson, 2007), our study suggests that significant genetic variability exists within the population of sugar maple with respect to its regeneration, potentially affecting its response to future climate change. The capability of sugar maple and other plant species to continually track optimal climatic envelopes into the future will involve successful establishment and survival, as well as growth to maturity.

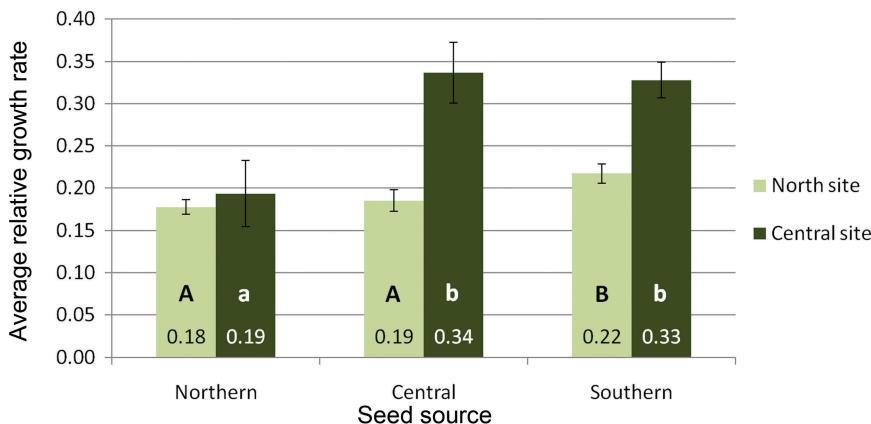


Fig. 10. Relative growth rates (yr^{-1}) for all seed sources germinated within both the North and Central sites. Based on ANOVA tests, significant ($p < 0.001$) differences were found between seed sources within both the North and Central sites, as denoted by the letters, which are site specific. Error bars depict the 95% confidence level.

The viability results from this study support the observation of Carl and Yawney (1969) and Carl (1976) that n-pentane is a reliable method for separating filled and unfilled samaras, unless the coats of the seeds are heavily damaged. Damage creates a large discrepancy between those that sink because they are filled with a seed versus those that sink because of physical damage. Carl and Yawney (1969) found n-pentane 96.5% efficient, while we found it to be about 93% efficient. According to Clark et al. (1998), sugar maple seed viability has been observed to range from 5 to 70%. Carl and Yawney (1966) found sugar maple seed viability to range anywhere from 20 to 74%. Seed viability rates for the North (43.5%) and Central (45.0%) sites fell about midway within previously reported ranges for sugar maple. The southern seed viability rate (82.7%), however, fell outside of the normal ranges. This above-average viability is primarily due to pre-sorting by the commercial seed supplier in order to select for filled samaras.

In the lab, sugar maple showed signs of spatial and temporal variation in their germination responses to temperature. Both the northern and southern seeds germinated best at 7° C, despite the fact that 7° C lies outside the previously-reported optimal germination temperature range of between 1° and 5° C (e.g., Jones, 1920; Tubbs, 1965; Carl and Yawney, 1966, 1969; Webb and Dumbroff, 1969; Carl and Snow, 1971; Webb et al., 1973; Carl, 1976; Janerette, 1978, 1979; Shih et al., 1985; Walker et al., 1985). Specifically, the northern seeds had higher germination rates than the other two seed sources at 7° C, and the central seeds had the highest germination rates of the three seed sources at 14° C. These findings suggest that no single optimum germination temperature can be assigned to sugar maple across its entire range and that there is genotypic variation throughout the range. The central seeds, however, did not demonstrate a difference between 1° and 7° C, but did germinate significantly less at 14° C, implying that within the central part of its range, sugar maple might have a wider germination temperature tolerance.

Within the lab, phenological variations in germination response were evident. According to other studies (Carl and Yawney, 1966; Carl and Snow, 1971; Janerette, 1978; Shih et al., 1985) germination typically begins within the first 30 to 40 days of a 90-day stratification period. We found that the time within which sugar maple seeds begin germinating may differ by seed origin. More specifically, the seeds from the central source were consistently the first to germinate (within the first 25 days) during all three temperature trials. Shih et al. (1985) observed the maturation of phloem to occur within sugar maple seeds on about the 17th day of stratification (about 21 days before germination was observed). In our study, the germination of the central seeds was closely followed by the germination of seeds from the northern source, taking place on average after about the 30th day. Shih et al., (1985) further observed that mature xylem cells were identifiable by the 37th day of stratification, with germination first occurring on the 38th day. Given that the central and northern seeds germinated earlier, all essential stages of development must also have occurred rapidly. Throughout all three temperature trials, the southern seeds were the last to begin germinating, sometime after the 50th day. While 50 days falls outside the typical range within which germination begins, it is by no means the longest observed period, since germination occurred after day 60 in a study conducted by Walker et al. (1985). Potentially, these differences in emergence timing could be due to slight variations in the seed covering structure's permeability to water throughout sugar maple's range, thereby allowing imbibition, and, ultimately, the breaking of dormancy, to occur at different rates. Or perhaps differences might arise due to slight genetic variations in the nature of the metabolic block that is known to accompany the testa's restriction of imbibition (Carl, 1983).

Overall, all mean lab germination proportions from this study's 1° and 7° C germination trials are similar to those in a study by Webb and Dumbroff (1969), in which they conducted five germination trials at five different temperatures: 5°, 10°, 15°, 20°, and 25° C (after moist stratifying all seeds for 41 days at 5° C). Webb and Dumbroff (1969) found the highest germination proportions to occur at 5° C. Our results suggest that 5° C may not be the optimal germination temperature for sugar maple, as we found an even higher germination proportion (61%) at 7° C than the ~57% in Webb and Dumbroff's (1969) 5° C trial. Additionally, there is a large discrepancy between our 14° C total germination proportions (2%) and those of Webb and Dumbroff (1969) 15° C trials (~28%). We found that 14° C exceeds the maximum germination temperature for the northern seeds, inasmuch as no germination occurred; however, more research is needed to evaluate germination behavior between 7° C and 14° C to more accurately identify whether 14° C is in fact the maximum germination temperature. The maximum germination temperature for the central and southern seeds, however, has yet to be identified since germination was only greatly suppressed and not prevented entirely at 14° C. As was the case for germination phenology, our study suggests that maximum germination temperature limits may vary geographically.

For most species, establishment limitations are the strongest barriers to recruitment (Clark et al., 1998; Caspersen and Saprunoff, 2005). In the field, we found seedling establishment for all seed sources was significantly higher in the northern, cooler field site than in the central field site. It is worth noting that, even though the

average precipitation during the first growing season was similar at both sites, the central site received approximately 11 cm of rain within a five-day period in August 2007. Moreover, there was about a 5° C temperature difference between the North and Central sites throughout the first growing season, with the northern site being the cooler of the two. This abundance of rain within a short period of time, combined with the warmer temperatures may account for the lower germination percentages, as this combination could have contributed to additional water stress within the seedlings at the central site.

When the northern and central seed germination proportions from the North and Central sites were used as traits to measure fitness, only the northern population showed signs of local adaptation by meeting both the local vs. foreign and the home vs. away criteria (*sensu* Kawecki and Ebert, 2004). Caspersen and Saprunoff (2005) observed that lack of suitable substrate caused the highest rate of recruitment failure for sugar maple in a study at Haliburton Forest and Wildlife Reserve in central Ontario. For the most part, all germination occurred on undisturbed forest soil in the present study with little shrub cover. Therefore, neither substrate nor understory vegetation cover would have been a contributing factor to the geographic variations in establishment in this study. Recruitment failure for sugar maple has also been attributed to both dispersal limitations and light availability (Caspersen and Saprunoff, 2005), although both were identified as minor limitations because sugar maple is a fairly well dispersed, shade-tolerant species (Clark et al., 1998).

Temperature of the seed bed and moisture availability have also been identified as dominant factors in the initial establishment of sugar maple (Hett and Loucks, 1971). Tubbs (1965) found that April temperatures were extremely important to the germination of sugar maple seedlings in Upper Michigan, such that temperatures near freezing would result in double the number of germinants compared to temperatures above 5° C. Hett and Loucks (1971), however, found that in southern Wisconsin April temperatures had no effect on sugar maple seedling establishment. Given that the study by Hett and Loucks (1971) in southern Wisconsin was much further south than Upper Michigan, it may, in fact, be March temperatures that are important to seedling establishment, rather than April temperatures.

The northern seedlings had the lowest mortality rate and therefore the highest success within their original habitat (North site), while both the central and southern seedlings had statistically similar success rates between the two field sites. Juvenile survival is considered an important component of plant fitness; therefore, survivorship rates between the northern and central seedlings within and between each habitat were used in this study to explore local adaptation. In the North site, the local vs. foreign criterion was not met since the northern and central seedlings had statistically similar survivorship rates. On the other hand, the local vs. foreign criterion was met in the Central site, because the central seedlings had a significantly higher average survival rate than the northern seedlings. The fact that the central seedlings did not also meet the home vs. away criteria did not matter, since alone, the local vs. foreign pattern was adequate for detecting local adaptation according to Kawecki and Ebert (2004). In contrast, the fact that the northern seedlings only met the home vs. away criterion was not sufficient evidence to imply local adaptation (Kawecki and Ebert, 2004).

We found that the highest survival rates, those of the southern seedlings, were statistically similar between both the North and Central sites. In contrast, a similar study by Hett and Loucks (1971) in Wisconsin found a gradient of germination success from south to north that largely mimicked our findings, given that their northernmost field site provided the best conditions for the initial survival of sugar maple. In the current study, the mean first-year survival percentages from the North and Central sites (ranging between 34.5% and 72.4%) were comparable to sugar maple first-year survival percentages found in a study conducted by Hett and Loucks (1971), which ranged between 27.8% and 64.9%. Additionally, Marks and Gardescu (1998) observed a 63% first-year survival rate for new sugar maple seedlings in central New York. Ultimately, a variety of abiotic and biotic factors contribute to the health and, therefore, survival of sugar maple (Horsley et al., 2002). More so than any environmental stress, Hett and Loucks (1971) suggested that the survival of sugar maple seedlings may actually be related to overstory stresses, which ultimately reduce essential elements, such as throughfall precipitation and light availability.

Ultimately, the southern sugar maple seedlings in our study had the highest relative growth rates in the North site, while the northern seedlings had the lowest relative growth rates in the Central site. Sensitivity to frost may play a role in this relationship, inasmuch as similar geographic differences in growth have been observed in Douglas fir (*Pseudotsuga menziesii*) saplings with varying degrees of vulnerability to frost damage, from different provenances in California (Haddock, 1967; Kellman, 1975). There was a tradeoff between frost tolerance and long-term growth in Douglas fir, because the seedlings that were highly susceptible to frost damage had, in the long-run, higher growth rates when compared to the seedlings that had a tolerance to frost damage. The fact that the northern sugar maple seedlings in the current study had a lower relative growth rate than the southern sugar maple seedlings, at both field sites, suggests a biological tradeoff. However, the mortality rates in the current study do not provide support for this yet, because the northern seedlings would have been expected to have a lower mortality rate if they were tolerant to frost damage, but were actually found to have a higher mortality rate in the North site than the southern seedlings at that site. However, our period of observation is likely too short to draw any definitive conclusions concerning this tradeoff.

Because growth can be considered a measure of performance, it in turn is also a measure of fitness and can be used to recognize local adaptations. The growth pattern of the central seedlings met both the local vs. foreign and the home vs. away criteria, thereby implying that local adaptation has occurred within this population. The growth pattern of the northern seedlings, on the other hand, met neither of the criteria for local adaptation, implying that this population has not undergone local adaptation. Angert and Schemske (2005) observed that a locally adapted population should also show decreased growth with increasing distance from the population's origin. The central population certainly does, but the northern population does not. Ultimately, this may explain why the central seedlings grew significantly better within their own habitat, while the northern seedlings grew statistically similar between both habitats. Soil chemistry may also be an important factor. A study by Ouimet et al. (2008) in Quebec, Canada, found that sugar maple growth was negatively associated with soil acidification. Furthermore, Finzi (2009) noted that high

concentrations of exchangeable aluminum and low base cation activity in soils, as well as low soil pH levels are associated with slow growth rates and canopy dieback in sugar maple. Finzi (2009) also found growth rates to correlate with soil phosphorus availability.

CONCLUSION

This study has implications for how sugar maple might respond to climate change. The persistence and successful migration of sugar maple at its northern range will become more important as climate continues to change. Our study provides evidence that 7° C promotes germination better than 1° C, suggesting that the original optimum germination temperature range for sugar maple, thought to lie between 1° and 5° C, may need to be expanded and explored in more depth and that optimal germination temperatures may vary geographically. The finding that sugar maple germinates successfully at 7° C ultimately suggests that temperature may not be the limiting factor to future initial establishment of the species as climate changes. This may at least be true in the locations at which this study was conducted, given that the seasonal average temperature is projected to increase by between 1.5° and 2.5° C during March, April, and May in the northern region of the sugar maple range by the middle of the 21st century (Plummer et al., 2006). Therefore, at the northern limit of the current range of sugar maple, the mean temperature in April, the month whose temperatures were identified by Tubbs (1965) as important to the germination of sugar maple in the northern portion of its range, could increase to anywhere between 4.4° and 5.4° C, which is still a few degrees below the potentially new high (7° C) end of the optimal germination range. Likewise, if (1) March temperatures are found to be important to the germination of sugar maple in the central portions of its range, and (2) mean temperature for March in the central regions of the current range of sugar maple shifts between 2° and 3.5° C, as projected by the middle of the 21st century (Plummer et al., 2006), then the current mean could increase to between 4.9° and 6.4° C, which also does not exceed 7° C. In fact, an increase in March temperatures could actually be positive for adult sugar maple growth in the long run (Goldblum and Rigg, 2005).

Furthermore, this study identified that the maximum germination temperature for sugar maple seeds from the northern portion of its range lies somewhere between 7° and 14° C, while sugar maple seeds from the central and southern portions of the range have a maximum germination temperature somewhere beyond 14° C, even though germination percentages were greatly reduced at the higher temperature. Ultimately, the success of the northern seedlings in the current study, within the slightly warmer central habitat, are *in situ* analogs of what might occur as the climate warms near the higher latitudes. Contrary to the lab results, our field results suggest the prospects for sugar maple at its northern limit are questionable given that the initial establishment of northern seeds was significantly reduced and the subsequent seedling mortality rates were significantly increased in the slightly warmer central habitat. Some vegetation models have projected that climatically suitable habitats to the north of the current sugar maple range will not become fully occupied in the future (Morin et al., 2008); moreover, they suggest that the presence of an unknown

limiting factor, most likely biotic in nature, may restrict the northern migration of sugar maple. Finally, it is worth speculating on what our findings imply for the southern range limit of sugar maple. While southern range limits are likely caused, in part, by competition exclusion (Loehle, 1998), sugar maple may also become constrained at its southern limit by high air temperatures at time of germination, which exceed its ecological tolerance. In the end, therefore, sugar maple may continue to persist at its southern range only at higher elevations as temperatures increase in the future.

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