

Variation in Temperature Responses among Populations of *Betula papyrifera*

Jonathan J. Ruel and Matthew P. Ayres

Ruel, J.R. & Ayres, M.P. 1996. Variation in temperature responses among populations of *Betula papyrifera*. *Silva Fennica* 30(2–3): 145–158.

How will global warming affect southern populations of boreal trees? In paper birch, *Betula papyrifera* (Betulaceae), alpine trees with an evolutionary history of relatively cool summers may be more sensitive to climate warming than valley populations. We evaluated this scenario by growing seedlings from different populations in four temperature treatments (mountain field site, valley field site, and two greenhouse rooms). Populations from low elevations germinated earlier and had higher germination success than populations from high elevations (16.8 vs. 22.0 d; 72 % vs. 11 %). At the valley site, seedlings from native populations grew faster than seedlings from higher elevations (mean \pm SE = 0.25 ± 0.02 vs. 0.09 ± 0.04 mm \cdot cm⁻¹ \cdot d⁻¹) while at the mountain site, all seedlings grew at similar rates. Seedlings grown in cooler environments had higher root : shoot ratios, perhaps to compensate for temperature limitations in nutrient uptake by roots. Leaf area varied among populations but was not affected by environmental differences across the field sites. Net photosynthetic rates at valley temperatures were higher for seedlings grown in the valley than for seedlings grown in the mountains or the warm greenhouse (12.0 vs. 10.3 and 5.8 μ moles \cdot m⁻² \cdot s⁻¹), perhaps due to adaptive phenotypic adjustments. Climatic warming could rapidly produce important phenotypic changes in birch trees (e.g., decreased root : shoot ratio, reduced growth in alpine populations). On a longer time scale, warming could also result in genetic changes as natural selection favors valley genotypes in alpine sites where they are presently rare.

Keywords *Betula*, growth, photosynthesis, temperature, adaptation

Authors' address Department of Biological Sciences, Dartmouth College, Hanover, NH 03755-3576, USA **Fax** +1 603 646 1347 **E-mail** matthew.p.ayres@dartmouth.edu

Accepted June 12, 1996

1 Introduction

Increases in atmospheric carbon dioxide, methane and other greenhouse gases are expected to result in increases of 2–4 °C in global mean temperatures during the next century (Schneider 1993). The cumulative effect of atmospheric changes on plant populations will be a complex combination of the effects of increased carbon dioxide, increased temperature, and changes in cloud cover, precipitation, and nutrient availability (Field et al. 1992). During the last 15 years, there has been extensive research on the direct effects of increased carbon dioxide (e.g., Eamus and Jarvis 1989, Bazzaz 1990, Pettersson and McDonald 1992, Rochefort and Bazzaz 1992), but comparatively little research on plant responses to temperature changes. Our understanding of plant responses to temperature is largely based on studies of graminaceous, herbaceous, and/or crop plants, as opposed to trees (e.g., Scott 1970, Wardlaw 1979, Kemp and Williams 1980, Pollack et al. 1983, Marriot et al. 1988, Patterson 1990, Pollack 1990, Winter and Königler 1991, Ackerly et al. 1992, Coleman and Bazzaz 1992, Kirk and Marshall 1992, Baker and Allen 1993, Bowman and Turner 1993, Mozafar et al. 1993, Wall 1993, Williams and Black 1993, Chen et al. 1994, Krapp et al. 1994, Morse and Bazzaz 1994, Oechel et al. 1994, Wookey et al. 1994; but see Bonan and Sirois 1992, Jones 1993, Lord et al. 1993, Stoneman and Dell 1993, Bassow et al. 1994, Callaway et al. 1994, Clark et al. 1995, Mortensen 1995). We have found few studies that explored genetic variation in tree temperature responses (Sorensen 1983, Drew and Chapman 1992, Wang et al. 1994). Consequently, we have only limited ability to anticipate the consequences of climate change on forests.

How will projected changes in ambient temperature affect tree species and forest communities? One hypothesis is that southern genotypes will tend to extend their distributions northward and supplant cold-adapted genotypes. In mountainous regions, valley populations may extend their distributions into the mountains and supplant cold-adapted alpine populations. Changes could be particularly rapid in mountainous regions because of the potential for rapid dispersal across the geographically compressed climatic

gradients. Our study evaluates the potential for climatically-induced changes in the distribution, morphology, and physiology of birch genotypes within the mountainous regions of the northeastern United States. We selected paper birch, *Betula papyrifera* Marsh. (Betulaceae), as a model species because it is an important component of forest ecosystems throughout northern North America in general and throughout the altitudinal gradients of New England in particular. We tested the following three hypotheses with a combination of field and greenhouse experiments. (1) Paper birch trees originating from populations at different elevations will differ in their growth, morphology, and photosynthesis when grown experimentally under the same conditions. (2) Trees from the same population will differ in their growth, morphology, and photosynthesis when grown at sites with different temperature regimes. (3) Temperature responses will differ among populations, in that trees from high altitude populations will tend to grow relatively better at cool temperatures while trees from low altitude populations will tend to grow relatively better at warm temperatures (i.e., trees are locally adapted to the temperature regimes of their native environments).

2 Methods

2.1 Overview

Seedlings from each of four *B. papyrifera* populations were placed at each of four treatment sites and monitored for one growing season. We measured seed mass, germination date, germination success, relative growth rates, root : shoot allocation, leaf area, and rate of photosynthesis.

2.2 Population Sampling

B. papyrifera seeds were gathered from mature, naturally established trees during October, November and December of 1993. New Hampshire populations were all from a similar latitude (43°40'–44°0' N), but were classed into three groups based on elevation. Eight trees, sampled

from scattered locations within a 15 km radius of Hanover, NH, comprised our Low elevation group (≈ 250 m a.s.l.) The Middle elevation group (350–530 m a.s.l.) was comprised of six trees from the lower slopes of Mt. Moosilauke near Warren, NH and three trees from lower Mt. Kanamagus near Lincoln, NH. Our High elevation group (> 1265 m a.s.l.) consisted of eight trees from upper Mt. Moosilauke. Upper elevation trees were probably *Betula cordifolia* Regel, a closely related species (Brittain and Grant 1965, 1969) or variety (Fernald 1945, Little 1979) that replaces *B. papyrifera* above ≈ 600 m in the White Mountains. Chromosome counts (L.C. Broughton and M.P. Ayres, unpublished data) indicated that our High population was $2n = 28$ (as *B. cordifolia*) while the Low and Middle elevation populations were $2n = 70$ or 84 (as *B. papyrifera*). Our study also included the progeny of fourteen *B. papyrifera* from Midland County, Michigan (43°38' N, 84°10' W, ≈ 200 m a.s.l.). Five to ten seeds from each of the 39 mother trees were individually weighed ($\pm 1 \mu\text{g}$) to test for differences in initial seed mass that might affect seedling growth. Seeds were kept at 5 °C for the winter.

On 9 May 1994, seeds were planted in growing medium in germination cell flats in the Murdough Greenhouse, Dartmouth College, Hanover, NH. Twenty cells, with approximately ten seeds per cell, were planted for each mother tree. In order to distribute possible micro-climate effects, we planted seeds from many mothers in each germination flat and periodically rearranged the flats in the greenhouse. The flats were watered twice daily. We conducted daily counts of germinated sprouts until 19 June.

The insect growth regulator Enstar® was applied, according to the manufacturer's directions, on 24 June and 30 June to control a white-fly infestation. On 5–6 July, seedlings were transplanted to individual 15 cm (6 inch) diameter pots with unamended topsoil from a valley site (clay loam) and fertilized with 201 mg of water soluble N-P-K (20-20-20) and 85 mg of trace elements. Fertilization was repeated on 18 August. All seedlings were watered to saturation twice weekly throughout the growing season.

2.3 Treatment Sites

The treatments consisted of two field sites and two greenhouse rooms. The Valley site was in a meadow near Etna, NH (43°43' N, 72°10' W) at approximately 250 meters above sea level. The Mountain site was in a clearing off U.S. Forest Service road FR 190 near Titus Brook in Glencliff, NH (44°3' N, 71°53' W) at 760 meters. The seedlings, in individual pots, were placed side by side in fenced enclosures to exclude vertebrate herbivores. Climate stations equipped with LI-COR Data Loggers (LI-1000) were placed at each site and programmed to record daily precipitation, and hourly means of ambient temperature and photosynthetically active radiation (PAR). Values from a NOAA weather station in Hanover, NH were used for some days when the Valley site climate station failed to record data.

Two greenhouse rooms provided an analogous pair of treatments (Warm Room and Cool Room). Different temperature regimes were produced by adjusting the ventilation settings. The Warm Room and Cool Room were identical with respect to light levels and other environmental conditions. Daily maximum and minimum temperatures were recorded in each room.

On 6 July, seedlings from mother trees in the Low, Middle and Michigan groups were placed in each of the greenhouse treatments. Seedlings were placed at the field sites on 20–21 July. Until then, they were kept in their original greenhouse room at a temperature intermediate between the two greenhouse treatments. Seedlings from the high population were only placed at the field sites (not in the greenhouse rooms) because low germination success resulted in reduced sample size.

2.4 Measuring Growth and Photosynthesis

Above-ground seedling growth was measured three times during the summer (7 July, 25 July, and 8 September). On each occasion, we measured height and number of leaves. The number of leaves per unit height (L_1 / H_1) was calculated as a morphological descriptor at each sampling time. Relative growth rates (RGR) were calculated as:

$$RGR = [\ln(H_t) - \ln(H_i)] / t$$

where \ln = natural logarithm, H_i = initial height, H_t = final height and t = time in days. Relative growth rates were calculated for two periods. RGR_1 describes pre-treatment growth rates, i.e., between the mean germination date (by mother tree) and 7 July. RGR_3 describes growth during the treatment period (25 July to 8 September).

In late October, following leaf senescence but prior to abscission, all leaves were collected from a subsample of Low, Middle and High seedlings at both field sites (1–9 seedlings for each of 3–8 mothers per population at each site). The area of each leaf was measured using computerized video-image capture and the program Optimas©. Fifty-five seedlings were sacrificed for examination of root and shoot allocation. The seedlings, without leaves, were severed at the stem base, oven-dried, and weighed.

On 10–20 September, we measured photosynthesis with a CID infrared CO_2 analyzer (model CI-301PS) with a leaf chamber of 11 cm^2 configured as an open system. A high intensity lamp (General Electric 75 watt 1300 lumen MR16) was attached at 27 cm above the leaf chamber to ensure light saturation (photosynthetically active radiation > 1200 $\mu moles \cdot m^{-2} \cdot s^{-1}$). The analyzer recorded leaf surface temperature, air temperature, evapotranspiration, stomatal conductance, and net photosynthetic rate. On 9 September, we moved seedlings from the Mountain site and the greenhouse to the Valley site so that on subsequent days the photosynthetic rates of trees from all sites could be measured at the same time and under the same environmental conditions.

2.5 Statistics

Statistical comparisons of *Betula* populations were based on the number of mother trees (seedling families) representing each population, and the variance among mother trees. Figures and tables show population means and standard errors calculated from mother-specific means. Pre-treatment relative growth rate (RGR_1), germination date, and seed mass were analyzed with a nested ANOVA model that included population

as a fixed effect and mother trees within populations as a random effect. Percentage germination was analyzed with a one-way ANOVA testing for the effect of population on the percentage of cells with ≥ 1 seedling for each mother.

Analyses of leaf area and relative growth rate during the treatments (RGR_3) were based on individual seedling values (because not all mother trees were represented at all sites so the alternative nested model was intractable). Two sets of RGR_3 data (three populations across the two field sites and four populations across the two greenhouse treatments) and one set of leaf area data (three populations across the two field sites) were analyzed with a two-way ANOVA model that included population and site as fixed effects. Two models were used to test the root and shoot masses and the root : shoot ratios: (1) middle population seedlings were compared across the four sites with a two-way ANOVA model including site as a fixed effect and mother as a random effect; (2) Low, Middle, and Michigan seedlings grown at the Valley site were compared with a nested ANOVA including population as a fixed effect and mothers within population as a random effect. Photosynthetic data were converted to mother-specific means and analyzed as a partial factorial (Milliken and Johnson 1984) for effects of population, growing environment, and measurement day. All variables satisfied assumptions of normality and homoscedasticity. Analyses were conducted with the SAS general linear models procedure (SAS 1990).

3 Results

3.1 Germination

Middle, High, and Michigan populations had similar seed masses, but seeds from the Low populations weighed less than half as much (Table 1, $F_{3,35} = 71.33$, $p < 0.001$). Seed mass also varied significantly among mothers within populations ($F_{35,185} = 4.84$, $p < 0.001$). Germination success (% of germination cells with at least one seedling) varied from 11 % in the High population group to 90 % in the Michigan population group (Fig. 1a, $F_{3,35} = 23.17$, $p < 0.001$).

Table 1. Seed mass of four *Betula* populations ($n = 8$ –14 mothers per population, with 5–10 seeds per mother).

Tree population	Seed mass (mg)		
	Mean	SE	n
Low elevation	0.121	0.019	8
Middle elevation	0.269	0.019	9
High elevation	0.285	0.009	8
Michigan	0.258	0.017	14

Among the New Hampshire populations, seeds from lower elevations had higher germination. Of cells with some germination, date of first germination (mean number of days after planting) varied across populations, with seeds from higher elevations germinating later (Fig. 1b, $F_{3,35} = 15.81$, $p < 0.001$). Date of first germination also varied among mothers within populations ($F_{35,433} = 3.10$, $p < 0.001$).

3.2 Treatment Sites

The mean daily temperature at the Valley site averaged 2.1 °C greater than that at the Mountain site (from 20 June to 20 September, Fig. 2a). This was primarily due to differences in day-time temperatures; night-time temperatures were similar (Fig. 2b). The greenhouse Warm Room site had daily temperature maxima that averaged 13.6 °C warmer and minima that averaged 2.4 °C warmer than those of the Cool Room treatment (from 1 June to 1 October, Fig. 3). The Warm Room was the warmest treatment overall; the Mountain site was the coolest, and the Valley and Cool Room treatments had similar temperature regimes.

Potted seedlings at the two field sites were exposed to natural precipitation in addition to the twice-weekly waterings. The Mountain site had 17 more days with measurable precipitation resulting in a cumulative growing season sum of 368 mm, which was slightly higher than the Valley's sum of 312 mm (Fig. 4). This difference was less than the equivalent of two water-

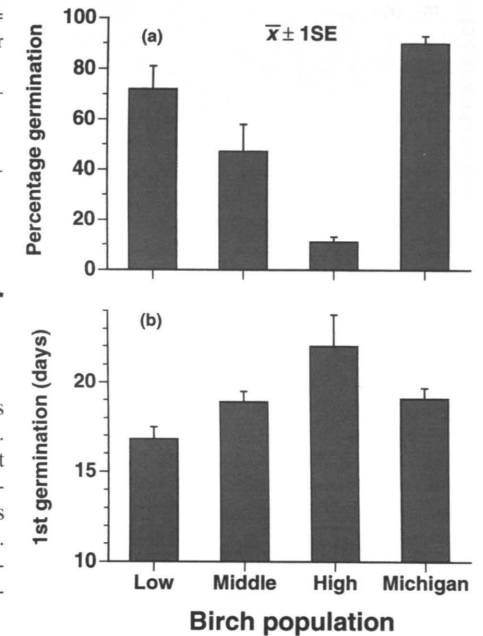


Fig. 1. (a) Germination success of four *Betula* populations ($n = 20$ germination cells per mother and 8–14 mothers per population). (b) Time from planting until germination in four *Betula* populations ($n = 1$ –20 germinated cells per mother and 7–14 mothers per population).

ings, so was very small in terms of total water received during the season. A comparison of light data at the two field sites for the periods 21 June–12 July and 3 September–19 September indicated very similar patterns of photosynthetically active radiation. (A failure of the data logger prevented comparisons of radiation during other times.)

3.3 Growth and Photosynthesis

In seedlings grown at the field sites, population of origin had a large effect on tree relative growth rate (RGR_3 ; $F_{3,52} = 7.92$, $p < 0.001$). Seedlings from the Low elevation population grew faster

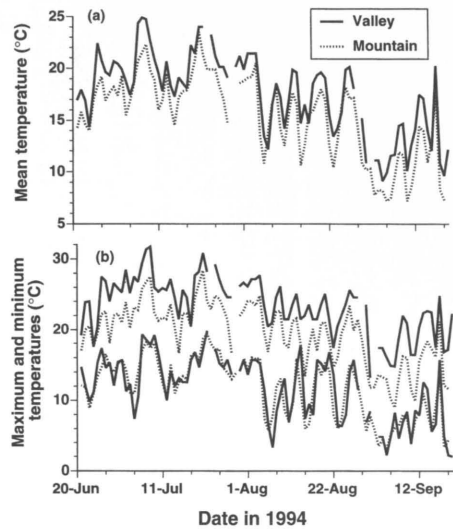


Fig. 2. (a) Daily mean temperature at valley and mountain field sites during the 1994 growing season. (b) Daily maxima and minima of hourly temperatures at the two field sites.

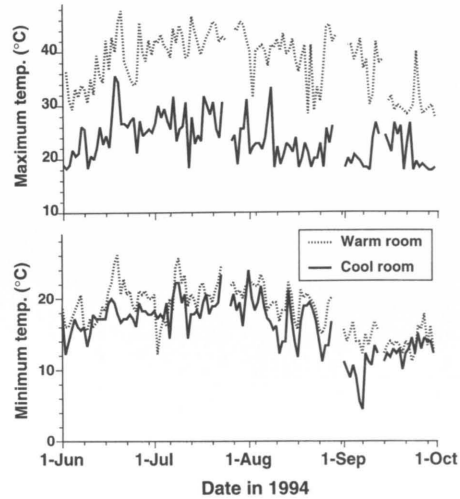


Fig. 3. Daily maximum temperatures (upper) and daily minimum temperatures (lower) in the two greenhouse rooms during the 1994 growing season.

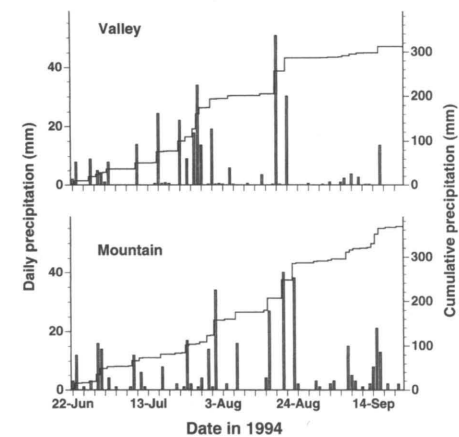


Fig. 4. Daily precipitation (columns) and cumulative sum of precipitation (line) at valley and mountain field sites during the 1994 growing season.

than seedlings from the Middle elevation population, which grew faster than High elevation population seedlings (Fig. 5; least square means \pm SE = 0.23 ± 0.012 , 0.19 ± 0.012 , 0.13 ± 0.017 $\text{mm} \cdot \text{cm}^{-1} \cdot \text{d}^{-1}$, respectively). Michigan seedlings grew at rates similar to Low and Middle seedlings (mean \pm SE = 0.21 ± 0.010 $\text{mm} \cdot \text{cm}^{-1} \cdot \text{d}^{-1}$). There was a significant population \times growing site interaction because High seedlings grew faster at the Mountain site than at the Valley site, while Low and Middle seedlings tended to grow faster at the Valley site (Fig. 5, $F_{3,52} = 3.30$, $p < 0.03$). In the greenhouse, Middle population seedlings grew slower than the Low and Michigan seedlings (mean \pm SE = 0.22 ± 0.01 vs. 0.25 ± 0.01 and 0.26 ± 0.01 $\text{mm} \cdot \text{cm}^{-1} \cdot \text{d}^{-1}$, respectively; $F_{2,42} = 4.12$, $p < 0.03$), but there was no site \times population interaction ($F_{2,42} = 1.37$, $p > 0.26$). Relative growth rates during the pre-treatment period (RGR_1) did not differ across populations (grand mean \pm SE = 0.78 ± 0.04 $\text{mm} \cdot \text{cm}^{-1} \cdot \text{d}^{-1}$;

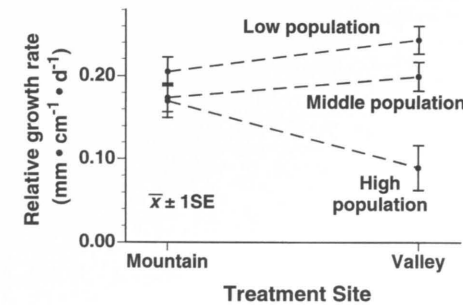


Fig. 5. Relative growth rates from 25 July through 8 September for seedlings from three New Hampshire birch populations grown at the mountain and valley sites ($n = 3\text{--}10$ mothers per population and 1–10 seedlings per mother).

$F_{3,28} = 1.87$, $p > 0.13$), but did differ among mothers within populations ($F_{28,505} = 3.84$, $p < 0.001$).

Neither root mass nor shoot mass of Middle seedlings varied significantly across sites (Fig.

6a, root: $F_{3,22} = 0.51$, $p > 0.5$; shoot: $F_{3,22} = 1.03$, $p > 0.3$) or among mothers ($F_{7,22} = 1.19$, $p > 0.3$; $F_{7,22} = 0.92$, $p > 0.5$). However, seedlings grown at cooler treatment sites had markedly higher root : shoot ratios (Fig. 6c, $F_{3,22} = 6.16$, $p < 0.003$). There were no significant differences in root mass, shoot mass, or root : shoot ratios across Low, Middle, and Michigan seedlings grown at the Valley site (Fig. 6b, d; all F -statistics < 2.2 , $p > 0.11$).

At the end of the growing season, the number of leaves per centimeter of height, a description of growth form, was highly dependent on seedling height (Fig. 7). Mean height at the end of the growing season ranged from the 4.4 ± 0.3 cm ($\bar{x} \pm \text{SE}$) in the High elevation trees at the Valley site to the 22.5 ± 1.1 cm in the Low elevation trees in the Cool Room (Fig. 8).

Among trees grown at the field sites, seedlings from higher elevation populations had smaller leaves (mean \pm SE = 6.23 ± 1.32 , 8.97 ± 0.85 , 10.56 ± 0.80 cm^2 for High, Middle and Low populations; $F_{2,18} = 4.27$, $p < 0.05$). There were no significant effects of site ($F_{1,117} = 2.99$, $p >$

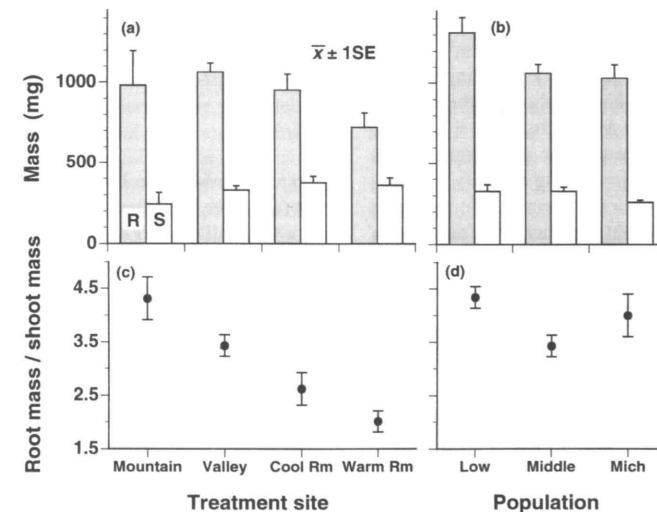


Fig. 6. Root masses (R), shoot masses (S), and root : shoot ratios of *B. papyrifera* ($n = 3\text{--}15$ seedlings per treatment combination). Figures on left (a and c) show data from the Middle elevation population grown at four sites. Figures on right (b and d) show data from three populations grown at the valley site.

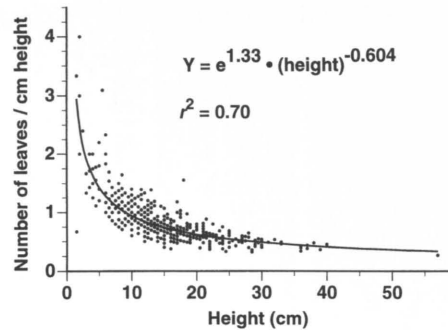


Fig. 7. The number of leaves per unit height as a function of height. Each point represents an individual seedling at the end of the growing season. All populations tended to fall on the same function.

0.08) or site \times population interaction ($F_{2,117} = 0.56$, $p > 0.55$) on leaf size.

Net photosynthetic rates of seedlings grown in the Warm Room were dramatically lower than those of seedlings grown at either the Mountain or Valley sites (mean \pm SE = 5.8 ± 0.88 vs. 10.3 ± 0.50 and 12.0 ± 0.55 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, respectively; $F_{2,103} = 7.21$, $p < 0.01$). Seedlings grown in the Valley had higher photosynthetic rates than seedlings at the Mountain site ($t = 2.35$, $p = 0.02$, $df = 80$). There were no significant effects of population ($F_{2,103} = 1.51$, $p > 0.20$) or measurement day ($F_{3,103} = 0.89$, $p > 0.44$); nor were there any significant interactions (population \times date $F_{3,103} = 0.02$, $p > 0.97$; site \times date $F_{1,103} = 0.20$, $p > 0.65$; population \times site $F_{2,103} = 0.96$, $p > 0.38$). There were no significant effects on stomatal conductance (all F-statistics < 1.42 , $p > 0.24$).

4 Discussion

Germination, relative growth rate and leaf area were strongly influenced by population of origin (Hypothesis 1 in introduction). This suggests genetic differences among paper birch populations. Given our experimental protocol, such differ-

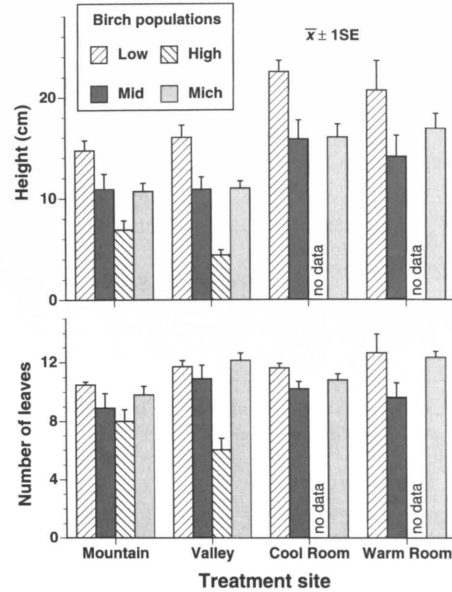


Fig. 8. Mean seedling height and total number of leaves at the end of the growing season for four *Betula* populations grown at four different sites ($n = 1-10$ seedlings per mother and 3–10 mothers per population).

ences could also have been due to maternal effects (e.g., due to differences in seed mass), but this seems unlikely because the populations with the most rapid seedling growth were those with the smallest seeds (Table 1, Fig. 5). Differences among treatment sites had strong effects on root : shoot ratio and net photosynthesis, which indicates that some parameters of growth and photosynthesis are highly dependent on environment (Hypothesis 2). Therefore, phenotypic variation among birch populations inhabiting different environments appears to have both genetic and environmental components. Variation in seedling growth across field sites (Figs. 5, 8) partially supported the hypothesis that populations differ in their temperature responses in ways that reflect evolutionary adaptation to environmental conditions (Hypothesis 3).

4.1 Germination

Low elevation seeds were much smaller than those from Middle and High elevations, but showed earlier germination and greater overall germination success (Table 1, Fig. 1). This runs counter to some data indicating that larger seeds germinate earlier and have greater germination success (Stanton 1984, Wang et al. 1994), although Wang et al. also showed that genetic differences often outweigh effects of seed mass. It is possible that the observed late germination in the High elevation population was a statistical artifact of the lower germination success, but this seems unlikely because we estimated germination time based on first germination within cells and the frequency distributions of germination time are strongly skewed to the right. Presumably, germination success in mountain populations is not so low every year, but years of low germination success could be more frequent because of overlap between frost-risk and seed maturation. Further studies are needed to fully characterize inter-annual and geographic variation in seed size and viability.

Relatively later germination in seeds from higher elevations (Fig. 1b) could represent an adaptation to minimize the risk of mortality from late spring frosts in the mountains. In the absence of freezing risk, we would have expected selection to favor early germination in the mountains because of the shorter growing season. In fact, greenhouse comparisons of birch from Alaska and Michigan (D.A. Herms, unpublished data), indicate that the more northerly populations germinate sooner (with fewer degree days) than their southern counterparts. The timing of germination may be an attribute where the analogy between altitudinal and latitudinal patterns in physiological adaptation breaks down. Nonetheless, all data are consistent in indicating high genetic variation in the thermal sum required for germination. Thus, observed differences in the timing of germination in the wild are due to a combination of environmental and genetic factors. In some scenarios of climate warming, low elevation seeds dispersed into the mountains would benefit from earlier germination.

4.2 Seedling Growth Rate

The relative growth rates of seedlings grown in the field suggest that natural selection has led to variation among populations in the responses of growth to temperature (Fig. 5). Differences in growth rate across the sites indicate relatively high phenotypic plasticity in high elevation populations. Reduced growth of the high elevation seedlings in the valley site could have resulted from an inability of high elevation seedlings to acclimatize to the warmer valley environment. Low and middle elevation seedlings did not show phenotypic plasticity in above-ground growth (i.e., they maintained similar relative growth rates across the sites; Fig. 5). Apparently, 1994 temperatures in the mountains were within the range suitable for growth of valley seedlings, while valley temperatures were too warm for optimal growth of mountain seedlings. Obviously, these results could be sensitive to year-to-year variation in climatic patterns. Temperatures during this field study happened to be rather typical of long-term patterns: at Concord, NH (65–90 km from our field sites) the mean August temperature in 1994 was only 0.5 °C different (cooler) than the long term average (NOAA 1994).

Emery et al. (1994) compared alpine and valley populations of *Stellaria longipes* (Caryophyllaceae) using a similar reciprocal transplant. Results were similar to those for *Betula* in that valley populations of *Stellaria* tended to grow faster than mountain populations at the valley site, while all *Stellaria* populations had similar growth rates at the mountain site. However, *Stellaria* differed from *Betula* in that the valley population showed higher phenotypic plasticity than the mountain population (i.e., valley populations grew slower in the mountains than the valley, while alpine populations showed no effect of site). Some interspecific comparisons have indicated that valley species (like valley populations of *Stellaria*) tend to be more affected by environmental variation than their alpine counterparts (Woodward 1975, 1979, Graves and Taylor 1988). Studies with *Stellaria* and *Betula* support the expectation that valley genotypes are the best competitors in their native environment, but pose a paradox by suggesting that mountain genotypes may not be superior competitors in

any environment.

It could still be that high elevation *Betula* trees are actually better adapted to the mountains than valley trees, but if so, it is because of parameters or time scales that were not included in this study. Long-term treatment effects (i.e., over many years) could differ from the short-term effects reported here. Inter-annual climatic variation could also be important. For example, mountain populations may be better able to survive unusually short, cool summers; increased allocation to storage (Sawada et al. 1994) instead of growth might benefit survival in cool summers but subtract from growth during favorable summers. It is also possible that mountain populations have adapted to herbivory and pathogen pressures present in their native environment with increased allocation towards chemical defenses (and therefore reduced growth; Herms and Mattson 1992). Our study was also unable to test for differences in winter cold-hardiness, which can be important for some tree species in the region (Marchand and Chabot 1978, Kincaid and Lyons 1981, Marchand et al. 1986, Doulis et al. 1993).

Relative growth of valley and mountain populations may differ with different soils. We were only able to use one soil type in this study (and it was drawn from the valley), so it is possible that our experimental soil favored the valley populations. We are planning factorial experiments that will compare mountain and valley populations grown in naturally occurring soils from the mountains and valley to test for local adaptation to soils.

4.3 Root : Shoot Allocation

The root : shoot ratios indicate high phenotypic plasticity in relative allocation to above-ground and below-ground organs. Cooler temperatures resulted in markedly increased allocation to roots relative to shoot tissue (Fig. 6c). Similar trends have been reported in an herbaceous perennial (*Scrophularia marilandica*, Cline 1966), a sedge (*Carex aquatilis*, Chapin and Chapin 1981), Douglas fir (*Pseudotsuga menziesii*, Sorensen 1983), and a number of other plant species (Graves and Taylor 1986, Clarkson et al. 1988,

Patterson 1990, Winter and Königer 1991, Jones 1993, Clark et al. 1995). Increased relative allocation to roots at lower temperatures could be adaptive if nutrient uptake (per gram of root) is more limited by low temperature than photosynthetic rate (per gram of leaf). This seems likely because mineralization rates and root uptake kinetics are strongly temperature sensitive (Chapin 1974, Bravo-F and Uribe 1981, Clarkson et al. 1986, MacDuff et al. 1987), while photosynthetic rates can be relatively insensitive across a broad range of temperatures (Berry and Björkman 1980, Hällgren et al. 1982, Sveinbjörnsson 1983). If this is true for *Betula*, increased root : shoot ratios might be required to maintain a favorable carbon : nutrient balance in cool environments.

4.4 Photosynthesis

When compared in a common environment (the valley site), seedlings grown at the valley site showed higher rates of carbon assimilation per unit leaf area than seedlings grown at the mountain site or in the Warm Room. This pattern might reflect adaptive phenotypic plasticity (i.e., seedling response to the treatment sites altered optimal photosynthetic temperatures to match treatment temperature regimes), but the experiments would have been strengthened if we had measured photosynthetic rates under a range of temperatures spanning that of the mountain and greenhouse treatments. Seedlings grown in the warm greenhouse treatment, versus those grown in the field, may have had lower photosynthetic rates per unit leaf area due to differences in leaf structure. Although we were unable to obtain measurements, greenhouse trees appeared to have much larger leaves than trees grown in the field which suggests that photosynthetic rates on a per leaf basis might have been similar.

4.5 Conclusions

This study suggests that climatic warming could rapidly produce important phenotypic changes in birch trees (e.g., decreased root : shoot ratio, reduced growth in alpine populations). On a long-

er time scale, warming could also result in genetic changes (e.g., as natural selection favors valley genotypes in alpine sites where they are presently rare). In combination, such phenotypic and genetic changes could have broad implications for forest productivity, community interactions, and ecosystem processes in boreal forests.

Acknowledgements

This project benefited from the contributions of Laura Broughton, Mark Erelli, Brendan Everett, Fritz Gerhardt, Dan Liptzin, Alice Shumate and Andrew Swanson. Jayn Bier and Lisa Palmer facilitated work in the greenhouse. Daniel Herms collected seeds from the Michigan populations. Greg Eaton, Richard Holmes, Ross Virginia, and two anonymous reviewers commented on the manuscript. Research was made possible by the cooperation of The White Mountain National Forest. Financial support was provided by grants from the Andrew W. Mellon Foundation and the Richter Memorial Trust.

References

- Ackerly, D.D., Coleman, J.S., Morse, S.R. & Bazzaz, F.A. 1992. CO₂ and temperature effects on leaf area production in two annual plant species. *Ecology* 73: 1260–1269.
- Baker, J.T. & Allen, L.H., Jr. 1993. Contrasting crop species responses to CO₂ and temperature: rice, soybean and citrus. *Vegetatio* 104: 239–260.
- Bassow, S.L., McConnaughay, K.D. M. & Bazzaz, F.A. 1994. The response of temperate tree seedlings grown in elevated CO₂ to extreme temperature events. *Ecological Applications* 4: 593–603.
- Bazzaz, F.A. 1990. The response of natural ecosystems to the rising global CO₂ levels. *Annual Review of Ecology and Systematics* 21: 167–196.
- Berry, J. & Björkman, O. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology* 31: 491–543.
- Bonan, G.B. & Sirois, L. 1992. Air temperature, tree growth, and the northern and southern range lim-

its to *Picea mariana*. *Journal of Vegetation Science* 3: 495–506.

- Bowman, W.D. & Turner, L. 1993. Photosynthetic sensitivity to temperature in populations of two C4 *Bouteloua* (Poaceae) species native to different altitudes. *American Journal of Botany* 80: 369–374.
- Bravo-F, P. & Uribe, E.G. 1981. Temperature dependence on concentration kinetics of absorption of phosphate and potassium in corn roots. *Plant Physiology* 67: 815–819.
- Brittain, W.H. & Grant, W.F. 1965. Observations on Canadian birch (*Betula*) collections at the Morgan Arboretum. II. *B. papyrifera* var. *cordifolia*. *Canadian Field Naturalist* 79: 253–257.
- & Grant, W.F. 1969. Observations on Canadian birch (*Betula*) collections at the Morgan Arboretum. VIII. *Betula* from Grand Manan Island, New Brunswick. *Canadian Field Naturalist* 83: 361–383.
- Callaway, R.M., Delucia, E.H., Thomas, E.M. & Schlesinger, W.H. 1994. Compensatory responses of CO₂ exchange and biomass allocation and their effects on the relative growth rate of ponderosa pine in different CO₂ and temperature regimes. *Oecologia* 98: 159–166.
- Chapin, F.S., III. 1974. Morphological and physiological mechanisms of temperature compensation in phosphate absorption along a latitudinal gradient. *Ecology* 55: 1180–1198.
- & Chapin, M.C. 1981. Ecotypic differentiation of growth processes in *Carex aquatilis* along latitudinal and local gradients. *Ecology* 62: 1000–1009.
- Chen, D., Coughenour, M.B., Eberts, D. & Thullen, J.S. 1994. Interactive effects of CO₂ enrichment and temperature on the growth of dioecious *Hydrilla verticillata*. *Environmental and Experimental Botany* 34: 345–354.
- Clark, H., Newton, P.C.D., Bell, C.C. & Glasgow, E.M. 1995. The influence of elevated CO₂ and simulated seasonal changes in temperature on tissue turnover in pasture turves dominated by perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*). *Journal of Applied Ecology* 32: 128–136.
- Clarkson, D.T., Earnshaw, M.J., White, P.J. & Cooper, H.D. 1988. Temperature dependent factors influencing root uptake: an analysis of responses at different levels of organization. *Symposia of the Society for Experimental Biology* 42: 288–309.

- , Hopper, M.J. & Jones, J.H.P. 1986. The effect of root temperature on the uptake of nitrogen and the relative size of the root system in *Lolium perenne* L. Solutions containing both NH_4 and NO_3 . *Plant, Cell, and Environment* 9: 535–543.
- Cline, M.G. 1966. Effects of temperature and light intensity on the growth of *Scrophularia marilandica*. *Ecology* 47: 782–795.
- Coleman, J.S. & Bazzaz, F.A. 1992. Effects of CO_2 and temperature on growth and resource use of co-occurring C3 and C4 annuals. *Ecology* 73: 1244–1259.
- Doulis, A.G., Hausladen, A., Mondy, B., Alschler, R.G., Chevone, B.I., Hess, J.L. & Weiser, R.L. 1993. Antioxidant response and winter hardiness in red spruce (*Picea rubens* Sarg.). *New Phytologist* 123: 365–374.
- Drew, A.P. & Chapman, J.A. 1992. Inheritance of temperature adaptation in intra- and inter-specific *Populus* crosses. *Canadian Journal of Forest Research* 22: 62–67.
- Eamus, D. & Jarvis, P.G. 1989. The direct effects of increase in the global atmospheric CO_2 concentration on natural and commercial temperate trees and forests. *Advances in Ecological Research* 19: 1–44.
- Emery, R.J.N., Chinnappa, C.C. & Chmielewski, J.G. 1994. Specialization, plant strategies, and phenotypic plasticity in populations of *Stellaria longipes* along an elevational gradient. *International Journal of Plant Sciences* 155: 203–219.
- Fernald, M.L. 1945. Some North American *Corylaceae* (*Betulaceae*)-I. Notes on *Betula* in eastern North America. *Rhodora* 47: 303–329.
- Field, C.B., Chapin, F.S., Matson, P.A. & Mooney, H.A. 1992. Responses of terrestrial ecosystems to the changing atmosphere – a resource-based approach. *Annual Review of Ecology and Systematics* 23: 201–235.
- Graves, J.D. & Taylor, K. 1986. A comparative study of *Geum rivale* L. and *G. urbanum* L. to determine those factors controlling their altitudinal distribution. I. Growth in controlled and natural environments. *New Phytologist* 104: 681–691.
- & Taylor, K. 1988. A comparative study of *Geum rivale* L. and *G. urbanum* L. to determine those factors controlling their altitudinal distribution. II. Photosynthesis and respiration. *New Phytologist* 108: 297–304.
- Hällgren, J.E., Sundbom, E. & Strand, M. 1982. Photosynthetic responses to low temperature in *Betula pubescens* and *Betula tortuosa*. *Physiological Plantarum* 54: 275–282.
- Herms, D.A. & Mattson, W.J. 1992. The dilemma of plants: to grow or defend. *Quarterly Review of Biology* 67: 283–335.
- Jones, R.H. 1993. Influence of soil temperature on root competition in seedlings of *Acer rubrum*, *Liquidambar styraciflua* and *Sapium sebiferum*. *American Midland Naturalist* 130: 116–126.
- Kemp, P.R. & Williams, G.J., III. 1980. A physiological basis for niche separation between *Agropyron smithii* (C3) and *Bouteloua gracilis* (C4). *Ecology* 61: 846–858.
- Kincaid, D.T. & Lyons, E.E. 1981. Winter water relations of red spruce on Mount Monadnock, New Hampshire. *Ecology* 62: 1155–1161.
- Kirk, W.W. & Marshall, B. 1992. The influence of temperature on leaf development and growth in potatoes in controlled environments. *Annals of Applied Biology* 120: 511–525.
- Krapp, A., Chaves, M.M., David, M.M., Rodrigues, M.L., Pereira, J.S. & Stitt, M. 1994. Decreased ribulose-1,5-bisphosphate carboxylase/oxygenase in transgenic tobacco transformed with 'antisense' rbcS. VIII. Impact on photosynthesis and growth in tobacco growing under extreme high irradiance and high temperature. *Plant, Cell and Environment* 17: 945–953.
- Little, E.L., Jr. 1979. Checklist of United States trees (native and naturalized). *Agricultural Handbook* No. 541. U.S.D.A. Forest Service, Washington, D.C.
- Lord, D., Morissette, S. & Allaire, J. 1993. Influence of light intensity, nocturnal air temperature and carbon dioxide levels on greenhouse black spruce seedlings (*Picea mariana*). *Canadian Journal of Forest Research* 23: 101–110.
- MacDuff, J.H., Hopper, M.J., Wild, A. & Trim, F.E. 1987. Comparison of the effects of root temperature on nitrate and ammonium nutrition of oil seed rape (*Brassica napus* L.) in flowing solution culture. I. Growth and uptake of nitrogen. *Journal of Experimental Botany* 38: 1104–1120.
- Marchand, P.J. & Chabot, B.F. 1978. Winter water relations of treeline plant species on Mt. Washington, New Hampshire. *Arctic and Alpine Research* 10: 105–116.
- , Goulet, F.L. & Harrington, T.C. 1986. Death by attrition: a hypothesis for wave mortality of subalpine *Abies balsamea*. *Canadian Journal of Forest Research* 16: 591–596.
- Marriott, C.A., Thomas, R.J., Smith, M.A., Logan, K.A.B., Baird, M.A. & Ironside, A.D. 1988. The effect of temperature and nitrogen interactions on growth and nitrogen assimilation of white clover. *Plant and Soil* 111: 43–51.
- Milliken, G.A. & Johnson, D.E. 1984. Analysis of messy data volume I: designed experiments. Van Nostrand Reinhold Company, New York. 473 p.
- Morse, S.R. & Bazzaz, F.A. 1994. Elevated CO_2 and temperature alter recruitment and size hierarchies in C-3 and C-4 annuals. *Ecology* 75: 966–975.
- Mortensen, L.M. 1995. Effect of carbon dioxide concentration on biomass production and partitioning in *Betula pubescens* Ehrh. seedlings at different ozone and temperature regimes. *Environmental Pollution* 87: 337–343.
- Mozafar, A., Schreiber, P. & Oertli, J.J. 1993. Photoperiod and root-zone temperature: interacting effects on growth and mineral nutrients of maize. *Plant and Soil* 153: 71–78.
- National Oceanic and Atmospheric Administration (NOAA). 1994. Local climatological data, monthly summaries.
- Oechel, W.C., Cowles, S., Grulke, N., Hastings, S.J., Lawrence, B., Prudhomme, T., Riechers, G., Strain, B., Tissue, D. & Vourlitis, G. 1994. Transient nature of CO_2 fertilization in Arctic tundra. *Nature* 371: 500–503.
- Patterson, D.T. 1990. Effects of day and night temperature on vegetative growth of Texas panicum (*Panicum texanum*). *Weed Science* 38: 365–373.
- Pettersson, R. & McDonald, A.J.S. 1992. Effects of elevated carbon dioxide concentration on photosynthesis and growth of small birch plants (*Betula pendula* Roth.) at optimal nutrition. *Plant Cell and Environment* 15: 911–919.
- Pollack, C.J. 1990. The response of plants to temperature. *Journal of Agricultural Science* 115: 1–5.
- , Lloyd, E.J., Stoddart, J.L. & Thomas, H. 1983. Growth, photosynthesis, and assimilate partitioning in *Lolium temulentum* exposed to chilling temperatures. *Physiological Plantarum* 59: 257–262.
- Rocheftort, L. & Bazzaz, F.A. 1992. Growth response to elevated CO_2 in seedlings of 4 co-occurring birch species. *Canadian Journal of Forest Research* 22: 1583–1587.
- SAS. 1990. SAS/Stat User's Guide: Version 6, Fourth Edition. SAS Institute Inc., Cary, North Carolina. 1686 p.
- Sawada, S., Nakajima, Y., Tsukuda, M., Sasaki, K., Hazama, Y., Futatsuya, M. & Watanabe, A. 1994. Ecotypic differentiation of dry matter production processes in relation to survivorship and reproductive potential in *Plantago asiatica* populations along climatic gradients. *Functional Ecology* 8: 400–409.
- Schneider, S.H. 1993. Scenarios of global warming. In: Kareiva, P. M., Kingsolver, J. G. & Huey, R. B. (eds). Biotic interactions and global change. Sinauer Associates, Sunderland, MA. p. 9–23.
- Scott, D. 1970. Relative growth rates under controlled temperatures of some New Zealand indigenous and introduced grasses. *New Zealand Journal of Botany* 8: 76–81.
- Sorensen, F.C. 1983. Geographic variation in seedling Douglas-fir (*Pseudotsuga menziesii*) from the western Siskiyou Mountains of Oregon. *Ecology* 64: 696–702.
- Stanton, M.L. 1984. Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. *Ecology* 65: 1105–1112.
- Stoneman, G.L. & Dell, B. 1993. Growth of *Eucalyptus marginata* (Jarrah) seedlings in a greenhouse in response to shade and soil temperature. *Tree Physiology* 13: 239–252.
- Sveinbjörnsson, B. 1983. Bioclimate and its effect on the carbon dioxide flux of mountain birch (*Betula pubescens* Ehrh.) at its altitudinal tree-line in the Tornetrask area, northern Sweden. *Nordica* 47: 111–122.
- Wall, D.A. 1993. Comparison of green foxtail (*Setaria viridis*) and wild oat (*Avena fatua*) growth, development, and competitiveness under three temperature regimes. *Weed Science* 41: 369–378.
- Wang, Z.M., Lechowicz, M.J. & Potvin, C. 1994. Early selection of black spruce seedlings and global change: Which genotypes should we favor? *Ecological Applications* 4: 604–616.
- Wardlaw, P. 1979. The physiological effects of temperature on plant growth. *Proceedings of the Agronomical Society of New Zealand* 9: 39–48.
- Williams, D.G. & Black, R.A. 1993. Phenotypic variation in contrasting temperature environments: Growth and photosynthesis in *Pennisetum setaceum* from different altitudes on Hawaii. *Functional Ecology* 7: 623–633.
- Winter, K. & Königer, M. 1991. Dry matter produc-

- tion and photosynthetic capacity in *Gossypium hirsutum* L. under conditions of slightly suboptimum leaf temperatures and high levels of irradiance. *Oecologia* 87: 190–197.
- Woodward, F.I. 1975. The climatic control of the altitudinal distribution of *Sedum rosea* L. Scop. and *S. telephium* L. II. The analysis of plant growth in controlled environments. *New Phytologist* 74: 335–348.
- 1979. The differential temperature responses of the growth of certain plant species from different altitudes. I. Growth analysis of *Phleum alpinum* L., *P. bertolonii* D.C., *Sesleria albicans* Kit. and *Dactylis glomerata* L. *New Phytologist* 82: 385–395.
- Wookey, P.A., Welker, J.M., Parsons, A.N., Press, M.C., Callaghan, T.V. & Lee, J.A. 1994. Differential growth, allocation and photosynthetic responses of *Polygonum viviparum* to simulated environmental change at a high arctic polar semi-desert. *Oikos* 70: 131–139.

Total of 67 references