

Red hot maples: *Acer rubrum* first-year phenology and growth responses to soil warming

J.A. Wheeler, N.M. Gonzalez, and K.A. Stinson

Abstract: Microhabitat environmental conditions are an important filter for seedling establishment, controlling the availability of optimal recruitment sites. Understanding how tree seedlings respond to warming soil temperature is critical for predicting population recruitment in the future hardwood forests of northeastern North America, particularly as environmental conditions and thus optimal microhabitat availabilities change. We examined the effect of soil warming of 5 °C during the first growing season on germination, survival, phenology, growth, and stem and root biomass allocation in *Acer rubrum* L. (red maple) seedlings. While there was no effect of soil warming on germination or survival, seedlings growing in warmer soils demonstrated significantly accelerated leaf expansion, delayed autumn leaf senescence, and an extended leaf production period. Further, seedlings growing in warmer soils showed larger leaf area and stem and root structures at the end of the first growing season, with no evidence of biomass allocation trade-offs. Results suggest that *A. rubrum* seedlings can capitalize on soil warming by adjusting leaf phenology and leaf production, resulting in a longer period of carbon uptake and leading to higher overall biomass. The absence of growth allocation trade-offs suggests that *A. rubrum* will respond positively to increasing soil temperatures in northeastern forests, at least in the early life stages.

Key words: *Acer rubrum*, soil temperature, leaf phenology, leaf production, biomass allocation.

Résumé : Les conditions environnementales des microhabitats ont une influence déterminante sur l'établissement des semis en contrôlant la disponibilité des emplacements de recrutement optimaux. Il est essentiel de comprendre comment les semis d'arbres réagissent au réchauffement du sol pour prévoir le recrutement de la population des futures forêts feuillues du nord-est de l'Amérique du Nord, particulièrement en ce qui a trait aux changements des conditions environnementales et, par conséquent, à la disponibilité des microhabitats optimaux. Nous avons étudié l'effet d'un réchauffement du sol de 5 °C sur la germination, la survie, la phénologie, la croissance et l'allocation de la biomasse à la tige et aux racines de semis d'*Acer rubrum* L. (érable rouge) pendant la première saison de croissance. Bien que le réchauffement du sol n'ait pas eu d'effet sur la germination ou la survie, les semis croissant dans des sols plus chauds ont eu une expansion foliaire significativement plus rapide, une sénescence automnale des feuilles plus tardive et une période de production foliaire plus longue. De plus, les semis croissant dans des sols plus chauds ont augmenté les dimensions de leur surface foliaire, de leur tige et de leurs structures racinaires à la fin de la première saison de croissance sans qu'il y ait de signe de compromis dans l'allocation de la biomasse. Ces résultats indiquent que les semis d'*A. rubrum* peuvent tirer profit du réchauffement du sol en ajustant la phénologie et la production foliaires, ce qui allonge la période d'absorption du carbone et accroît la biomasse globale. L'absence de compromis dans l'allocation de la croissance indique qu'*A. rubrum* réagira positivement à l'augmentation de la température du sol dans les forêts du nord-est, au moins pendant les premiers stades de développement. [Traduit par la Rédaction]

Mots-clés : *Acer rubrum*, température du sol, phénologie foliaire, production foliaire, allocation de la biomasse.

Introduction

The regeneration and future distribution of forest tree species depend largely on conditions within the microhabitat at early stages of recruitment, because local environmental conditions act as a filter for germination, emergence, and survival of individual seedlings (Harper 1977). Soil temperature in the seedling microhabitat is known to influence survival and recruitment of woody plants across a range of taxa and community types, from Mediterranean communities to deciduous forest to alpine tundra (Caldeira et al. 2014; Castro et al. 2011; Utsugi et al. 2006). Fine-scaled soil temperature and related effects on seedling performance may be driven in part by microtopography (Schmidt et al. 1998), but changes in broader climate conditions are also known to increase local soil temperatures (Qian et al. 2011). Therefore,

ongoing anthropogenic changes in climate that affect local soil temperature can have important consequences for tree recruitment via effects on seedling emergence (Thompson and Naem 1996) and growth (Rogiers et al. 2014).

Climate warming by up to 5 °C is predicted to affect temperate deciduous forests in northeastern North America in the next century (Intergovernmental Panel on Climate Change (IPCC) 2013), and a number of ecological studies use experimental soil warming to understand how concomitant forest floor surface temperature changes can alter ecosystem processes (Frey et al. 2013). Soil warming improves microhabitat conditions for seedlings of some hardwood species (Rogiers et al. 2014) but has a detrimental effect on others (Danyagri and Dang 2014). Further, soil warming can increase growth in belowground structures while having less impact on aboveground structures such as leaves (Štraus et al. 2015)

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and lead to changes in patterns of biomass allocation. Compared with atmospheric warming (Norby et al. 2003; Wertin et al. 2011; Searle et al. 2012), the effect of microhabitat soil warming on early responses in many hardwood species is relatively understudied (but see Rogiers et al. (2014) and Štraus et al. (2015)). Soil temperature may be particularly important at this stage, as tree seedlings in their early life stage have very low growth forms; plants with low growth forms may be more decoupled from atmospheric temperatures and more closely linked to ground-level microclimates (Körner 2003). Information on individual seedling performance in warmer soils is thus needed to understand how predicted changes to soil microsite conditions can affect the early life history stages of different hardwood tree species.

Acer rubrum L. (red maple) is a common canopy tree in the hardwood forests of the northeastern United States and Canada. This species can successfully germinate and grow under a broad range of microhabitat conditions: it occupies a wide germination niche, is relatively shade-tolerant, and can exploit a variety of recruitment site conditions, particularly in disturbed litter and large canopy gaps (Rinkes and McCarthy 2007; Poznanovic et al. 2013). *Acer rubrum* seedlings are also strongly responsive to air temperature: spring seedling phenology accelerates with air warming (Kaye and Wagner 2014), and seedlings can also rapidly acclimate photosynthetic and respiration rates to air temperature changes (Lee et al. 2005; Sendall et al. 2015). This species has one of the widest distributions and broadest ecological amplitudes of any eastern deciduous forest species (Chapman and Bolen 2015) and is further becoming a dominant subcanopy species in many forests in response to long-term fire suppression, land use changes, and curbing of competitors by deer browsing, defoliating insects, and pathogens (Abrams 1998). Understanding how fine-scaled changes in soil temperature can affect growth and performance in first-year *A. rubrum* seedlings is critical to understanding how this common tree species will respond to changing patterns of microhabitat conditions during its early life stages. Further, it will help predict future patterns of microhabitats with optimal temperatures for *A. rubrum* seedlings.

The objectives of this study were thus to determine the impacts of warmer soil temperatures on the germination, leafing phenology, survival, growth, biomass accumulation, and biomass allocation in first-year *A. rubrum* seedlings. Our study quantifies the effects of soil temperature on the early life stages of *A. rubrum* and determines whether *A. rubrum* seedlings growing in warmer soils demonstrate any trade-offs in key performance traits.

Methods

Site description

We set up our experiment in a lath house situated on a cleared meadow abutting mixed hardwood stands at the Harvard Forest in Petersham, Massachusetts, USA. A lath house is a wooden structure composed of a series of narrow strips (laths) meant to protect young seedlings from desiccation and herbivory. The lath house at Harvard Forest is 4.5 m tall and provides 50% shade. Concerning climate, the yearly average air temperature at the Fisher Meteorological Station near the site (since 2001) is 8.1 °C, with summer air temperatures averaging 17.4 °C (mean May–September). Total annual precipitation, including water equivalent of snow, averages 1100 mm (Contosta et al. 2011).

Experimental setup

In June 2015, we filled eighty 15.25 cm (6 in.) diameter pots with local soil sourced from the edge of the forest (<20 m from our experimental site, an area occupied by mature *A. rubrum*). We placed pots in dark plastic trays to standardize surface colour and drainage. There were two levels of soil temperature treatment in this experiment: unheated (ambient temperature) control pots, which we placed on bare dark gravel groundcover, and soil-

warming pots (+5 °C above ambient), which we placed on electric hydroponic heating mats (Root Radiance, China). We randomly assigned pots to one of the two treatments. The pots were slightly shaded under a 3 m tall wooden lathe structure but were situated close together (in a 2 × 4 m area) to minimize variation in light and other microscale environmental conditions. In addition, we randomized pot position halfway through the growing season to minimize any effect of light variation.

In the first week of June, we collected mature *A. rubrum* seeds in a single batch from a series of local *A. rubrum* trees (within 1 km of the experiment site). *Acer rubrum* germinates immediately after maturation (Walters and Yawney 1990), so we planted seeds one day after sampling. We planted six seeds in each pot (40 pots per treatment; total seed $N = 480$) and marked the planted seeds with toothpicks to minimize the probability of counting an *A. rubrum* seed already present in the soil or from an outside seedfall. Four weeks after planting, we thinned germinants to one seedling per pot ($N = 80$ seedlings) to eliminate the effects of intraspecific competition on experimental seedling growth. We monitored pots daily or every other day through the growing season, weeded as necessary to remove interspecific competitors, and watered to saturation when needed.

Field data collection

After planting, we recorded day of onset of germination for each seed, in addition to total germination per pot (of six planted seeds). After germination, we recorded germinant survival over the first four weeks and day of first true leaf expansion. Once per week until mid-August, we measured stem height, counted leaf number, and measured the largest leaf area (leaf length × width) using calipers to determine the maximum number of leaves and the largest leaf size produced during the growing season. Because *A. rubrum* produces lobed leaves, our leaf measurements represent an approximation of individual leaf area. At the end of the growing season (early October), we measured total seedling height and stem diameter just above the root collar for each seedling using calipers. In early October, we also recorded leaf senescence on each seedling; a seedling was defined as senescent if no green leaf tissue remained. In early November, we removed seedlings from pots and washed the roots to remove soil. We counted the number of branches from the main root and measured the lengths of both the primary root and the longest secondary root using calipers. Root and stem tissues were then dried at 60 °C for 72 h. We removed any senescent leaf tissue and then weighed stem tissue and root tissue separately using an analytic balance. We calculated root–stem ratios as root dry mass divided by stem dry mass.

We collected soil temperature data using a standard handheld soil probe at a depth of 5 cm in each pot containing an experimental seedling. We measured temperatures in a random sample of 10 pots per treatment during each collection period. We collected temperature data daily during July to mid-August and then every 2–3 days until late September. To verify that soil-warming treatments were also effective at night and across soil depths within the pots, we measured soil temperatures at depths of 7.5, 5, and 2.5 cm below soil surface at midday and midnight within six pots containing no seedlings over a three-day period.

Statistical analyses

We used linear and general linear models using soil-warming treatment as the explanatory variable to determine the effects of soil warming on phenology, survival, final size, and biomass allocation. When needed, we transformed response variables and used residual diagnostic plots when appropriate to confirm good model fit and normal residual distribution. To examine growth responses over the course of the growing season, we used linear and general linear mixed models, in which treatment and number of days after sowing were treated as fixed effects and plant identity was used as a random factor to address any issues of

Table 1. Germination, phenology, size, and biomass allocation in *Acer rubrum* (red maple; $N = 80$) seedling under a 5 °C soil-warming treatment during the 2015 growing season at the Harvard Forest in Petersham, Massachusetts, USA.

| Response | Model error structure | Effect of soil warming |
|--------------------------------------|-----------------------|--------------------------|
| Germination proportion | Binomial | $z = -1.47, p = 0.14$ |
| Germinant survival proportion | Binomial | $z = -0.009, p = 0.99$ |
| Onset of germination | Gamma | $t = 0.28, p = 0.78$ |
| Onset of leaf expansion | Gamma | $t = 3.09, p = 0.0028^*$ |
| Leaf senescence in October | Binomial | $z = -4.98, p < 0.001^*$ |
| Final seedling height (mm) | Gaussian | $t = 5.30, p < 0.001^*$ |
| Final stem diameter (mm) | Gaussian | $t = 9.72, p < 0.001^*$ |
| Maximum leaf number produced | Poisson | $z = 13.65, p < 0.001^*$ |
| Largest leaf area (mm ²) | Gaussian | $t = 6.03, p < 0.001^*$ |
| Final stem dry mass (mg) | Gaussian | $t = 6.02, p < 0.001^*$ |
| No. of main root branches | Poisson | $z = 1.53, p = 0.13$ |
| Main root length (mm) | Gaussian | $t = 2.72, p = 0.0074^*$ |
| Secondary root length (mm) | Gaussian | $t = 8.76, p < 0.001^*$ |
| Root dry mass (mg) | Gaussian | $t = 8.86, p < 0.001^*$ |
| Root-stem ratio | Gaussian | $t = 7.87, p < 0.001^*$ |

Note: The data are from linear and general linear models. Error structure used for each model is listed, as are t or z values and p values (asterisks shown when significant at $p < 0.05$).

temporal pseudoreplication. We report model error structures in Table 1. We performed all analyses using R statistical software v. 3.1.2 (R Core Team 2014).

Results

Temperature on ambient vs. soil-warming treatments

The heating mats significantly raised the daily mean soil temperature of the soil-warming treatment at a depth of 5 cm below the soil surface, with a daytime mean soil temperature of 24.7 °C compared with 19.3 °C in control pots, for an average difference of 5.3 °C between treatments during the growing season ($t = 46.11, p < 0.001$; Supplemental Fig. 1¹). Temperature measurements taken at midnight over a three-day period showed that night soil warming was consistent with average daytime warming, with night mean soil temperatures of 19.4 °C at a depth of 5 cm in the soil-warming treatment compared with 14.4 °C in control pots, for an average night temperature difference of 5.0 °C (Supplemental Fig. 2¹). The warming mats significantly raised soil temperatures by 2.97, 4.49, and 6.1 °C relative to the control pots at the surface, middle, and deepest soil layers, respectively ($t = 5.77, p < 0.001$; $t = 8.79, p < 0.001$; $t = 12.81, p < 0.001$). Supplemental Figure 3¹ shows temperatures at soil surface and at depths of 5 cm and 7.5 cm below soil surface measured at midday and midnight over a three-day period.

Germination and germinant and seedling survival

Overall germination was relatively high, with a minimum of one seed germinating in all pots, and 63% of all seeds germinating. Seed germination was similar between control and soil-warming treatments, with no significant effect of warming (Table 1). Survival after germination was very high; 98% of seedlings survived to the thinning stage. Soil warming also had no significant effect on germinant survival in the first four weeks (prior to thinning; Table 1). Seedling survival after thinning was uniformly high and unaffected by soil-warming treatment, with 97% of seedlings in control treatments and 95% of seedlings in soil-warming treatments surviving during the first growing season.

Phenology

Onset of germination occurred 9 days after sowing for both treatments, with the last new germination occurring 21 days after sowing. Germination onset was similar in controls and soil-warming treatments (control mean germination onset = 12.5 days after sowing, SE = 0.36; soil-warming mean germination onset = 12.4 days after sowing, SE = 0.44; Table 1). Onset of leaf expansion began 13 days after sowing and occurred significantly earlier under soil-warming treatments relative to controls (control mean leaf expansion onset = 15.5 days after sowing; soil-warming mean leaf expansion onset = 14.4 days after sowing; Table 1). The day of peak leaf production (post-sowing day after which seedlings did not produce significantly more leaves) occurred later under soil-warming treatments (control mean peak leaf production = 55 days after sowing; soil-warming peak leaf production = 93 days after sowing; Fig. 1A). By early October (118 days after sowing), leaf senescence was more likely to have occurred for seedlings in control treatments relative to seedlings in soil-warming treatments (Table 1). By early October, 74% of control seedlings were fully senescent compared with 11% in the soil-warming treatment.

Growth responses

Soil warming had a significant and positive effect on above-ground structure size. At the end of the growing season (early October, 118 days after sowing), seedlings were significantly taller under soil-warming treatment (mean height = 83.1 mm) relative to controls (mean height = 61.1 mm; Table 1; Fig. 2A). Final stem diameter just above the root collar was larger for seedlings in the soil-warming treatment (mean stem diameter = 2.74 mm) relative to controls (mean stem diameter = 1.82 mm; Table 1; Fig. 2B). Final stem dry mass was significantly higher under soil-warming treatment (mean dry wood mass = 99.95 mg) relative to controls (mean dry wood mass = 39.73 mg; Table 1; Fig. 2C). At peak leaf production, maximum leaf number was significantly higher under soil-warming treatment (mean leaf $N = 11.8$) relative to controls (mean leaf $N = 5.8$; Table 1; Fig. 2D). Similarly, mean largest leaf area was higher under soil-warming treatment (mean leaf area = 985 mm²) relative to controls (mean leaf area = 462 mm²; Table 1; Fig. 2E).

Stem height, leaf number, and leaf area also significantly varied as a function of soil-warming treatment, time after sowing, and the interaction between both factors (Table 2). Leaf number was the first growth trait to respond to soil warming, followed by stem height and lastly by leaf area. Leaf number was similar between treatments, although somewhat higher in soil-warming treatments, until 55 days after sowing (late July), after which seedlings in soil-warming treatments consistently demonstrated significantly higher leaf numbers (Fig. 1A). After 55 days after sowing, control seedlings no longer produced new leaves (leaf number did not significantly increase), while seedlings in soil-warming treatments continued to produce new leaves until the last leaf count at 93 days after sowing, an increase in new leaf production of 38 days (Fig. 1A). Stem height was similar between treatments until 69 days after sowing (mid-August), after which seedlings in soil-warming treatments demonstrated significantly taller stems (Fig. 1B). After 62 days after sowing, control seedling stem height did not significantly increase, whereas seedlings in soil-warming treatments continued to grow until 93 days after sowing, an increase in stem elongation time of 24 days (Fig. 1B). Mean largest leaf area was similar between treatments until the last leaf measurement period 93 days after sowing (early September), at which point seedlings in soil-warming treatments showed significantly larger leaves (Fig. 1C). Model results for differences in leaf number, mean largest leaf area, and stem height between treatments for each measurement period are reported in Supplemental Table 1¹.

¹Supplemental material is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2016-0288>.

Fig. 1. *Acer rubrum* (red maple; $N = 80$): (A) mean leaf number, (B) stem height, and (C) largest leaf area under ambient (open circles) and 5 °C soil-warming (grey circles) treatments during the first growing season after sowing. Note different scales on the y axes. Error bars are used to denote standard error (SE).

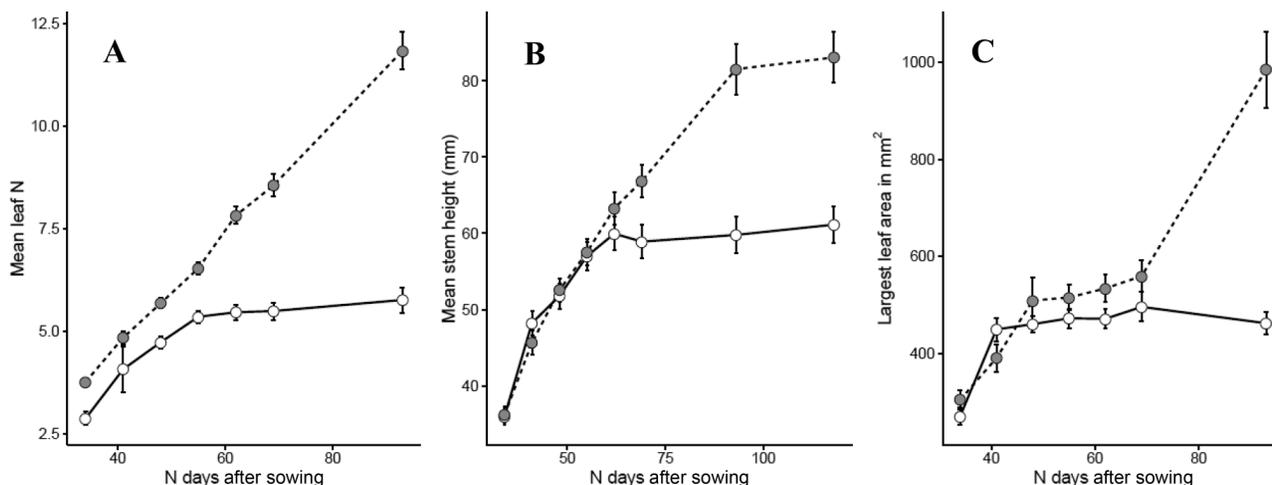


Fig. 2. *Acer rubrum* (red maple; $N = 80$): (A) seedling height at the end of the growing season, (B) stem diameter at base at the end of the growing season, (C) stem dry mass at the end of the growing season, (D) maximum leaf number produced, and (E) largest leaf area under ambient (open bars) and 5 °C soil-warming (grey bars) treatments during the 2015 growing season at the Harvard Forest in Petersham, Massachusetts, USA. Note different scales on the y axes. Error bars are used to denote standard error (SE).

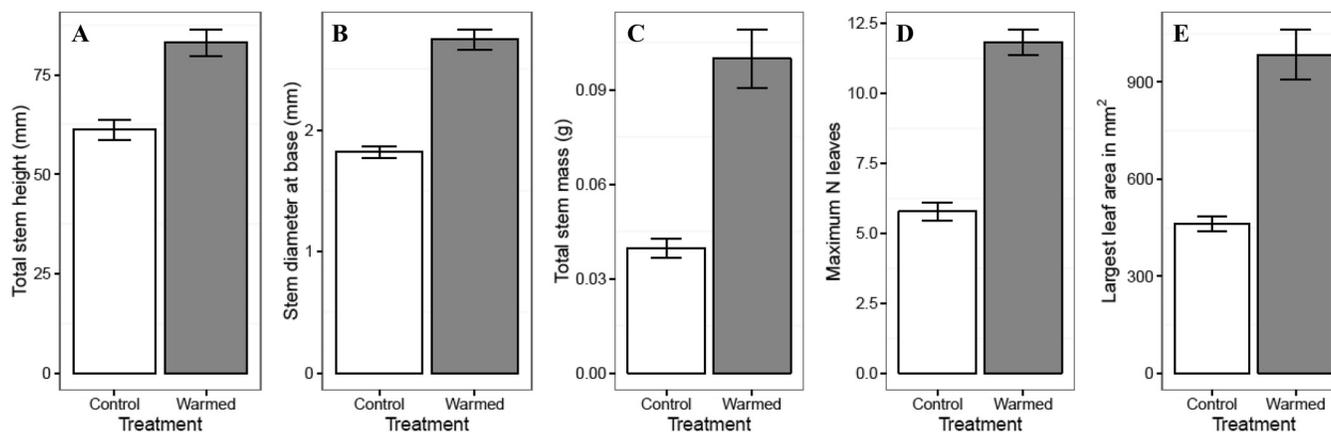


Table 2. *Acer rubrum* (red maple; $N = 80$) growth responses to soil warming (5 °C) over time during the 2015 growing season at the Harvard Forest in Petersham, Massachusetts, USA.

| Response | Model error structure | Soil warming | No. of days after sowing (time) | Soil warming × time |
|------------------------|-----------------------|------------------------------|---------------------------------|------------------------------|
| Seedling height (mm) | Gaussian | $t = 2.62$ $p = 0.011^*$ | $t = 11.43$ $p < 0.001^*$ | $t = 11.93$ $p < 0.001^*$ |
| Mean largest leaf area | Gaussian | $t = 4.98$ $p < 0.001^*$ | $t = 4.09$ $p < 0.001^*$ | $t = 10.37$ $p < 0.001^*$ |
| Leaf number | Poisson | $z = 10.90$ $p < 0.001^*$ | $z = 5.99$ $p < 0.001^*$ | $z = 4.93$ $p < 0.001^*$ |

Note: The data are from linear and general linear models. Error structure used for each model is listed, as are t or z values and p values (asterisks shown when significant at $p < 0.05$).

Root size and root-stem ratios

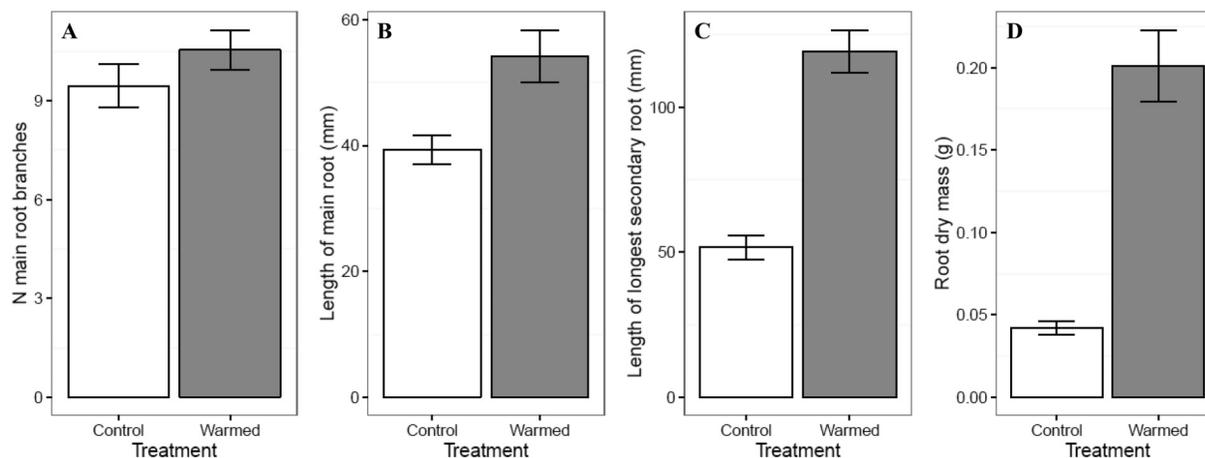
Soil warming also had a strongly significant positive effect on belowground biomass. While the number of main root branches was similar in both treatments (control mean N branches = 9.3, soil-warming mean N branches = 10.4; Table 1; Fig. 3A), soil warming significantly influenced root lengths and dry mass. Soil warming had a weakly significant positive effect on the length of the

main root (control mean length = 39.3 mm, soil-warming mean length = 53.0; Table 1; Fig. 3B). Soil warming had a stronger positive effect on secondary root length (control mean length = 51.6 mm, soil-warming mean length = 118.6 mm; Table 1; Fig. 3C). Root dry mass was significantly higher in the soil-warming treatment (mean dry root mass = 198.40 mg) relative to controls (mean dry root mass = 41.56 mg; Table 1; Fig. 3D). Soil warming also significantly influenced biomass allocation. Seedlings grown in the soil-warming treatment demonstrated significantly higher allocation to root biomass over stem biomass (mean root-stem ratio = 2.057) relative to controls (mean root-stem ratio = 1.024; Table 1).

Discussion

Our findings suggest that warmer soils positively affect the performance and potential recruitment of first-year red maple seedlings, as evidenced by taller, thicker *A. rubrum* seedlings with larger root systems in our +5 °C soil-warming treatment. Our phenological and growth data suggest that the mechanism driving this response is an increase in the duration of the active growth period. Earlier leaf expansion and later leaf retention led to a longer active leaf production period, larger leaves, and a longer stem elongation period, leading to increased final height, stem

Fig. 3. *Acer rubrum* (red maple; $N = 80$) root structure: (A) number of branches on the main root, (B) length of main root, (C) longest secondary root length, and (D) root dry mass at the end of the growing season under ambient (open bars) and 5 °C soil-warming (grey bars) treatments at the Harvard Forest in Petersham, Massachusetts, USA. Note different scales on the y axes. Error bars are used to denote standard error (SE).



thickness, and stem and root biomass accumulation. Biomass allocation to roots was also higher under soil-warming treatment, although this did not indicate an allocation trade-off, as stem biomass accumulation also significantly increased under soil warming. In the text that follows, we discuss these findings in more detail, along with implications for future recruitment of *A. rubrum*.

Extended leaf retention and production period

Leaf expansion and leaf senescence are two key factors controlling carbon acquisition in deciduous trees, as they control the initiation and end of the photosynthetically active growing season. Our results show that soil warming led to slightly earlier leaf expansion and later leaf retention in fall. These results are similar to those of other studies examining atmospheric warming and *A. rubrum* seedling phenology; Norby et al. (2003) showed that warmer air temperature accelerated budbreak and delayed leaf abscission, and Kaye and Wagner (2014) found earlier leaf expansion with air warming. We found that soil temperature did not influence germination timing, likely because *A. rubrum* has no environmental requirements for germination and predominantly germinates rapidly after seed maturation (Abbott 1974). Interestingly, soil warming significantly extends the active leaf production periods for *A. rubrum* seedlings later in the growing season, as control seedlings set buds and stopped producing new leaves in late July, whereas seedlings grown in the soil-warming treatment continued to produce new leaves until early September. This is likely one factor accounting for the differences in size and biomass accumulation between treatments. Soolanayakanahally et al. (2013) demonstrated that earlier bud set was associated with reduced height in *Populus balsamifera* L. and that there was a strong correlation between longer leaf retention and stem growth in *Populus trichocarpa* Torr. & A. Gray (Dunlap and Stettler 1998). We suggest that soil warming most strongly affects *A. rubrum* seedlings later in the growing season, through the extended leaf production period and later leaf retention, and the effect of soil warming on leaf phenology and production period directly affects growth and biomass accumulation patterns.

Positive growth and biomass allocation responses to soil warming

We observed positive effects of soil warming on growth both above and below the ground for *A. rubrum* seedlings, a result that contrasts with other studies examining soil or air warming, which generally demonstrated either neutral, negative, or mixed effects of warming on growth in *Acer* seedlings and saplings. Farnsworth

et al. (1995) found no effect of soil warming on leaf size in *A. rubrum* saplings, while Rogiers et al. (2014) found that root-zone soil warming increased leaf biomass and root size but not height in *Acer negundo* L. seedlings. Carón et al. (2015) found that soil warming reduced both above- and below-ground biomass in *Acer platanoides* L. and *Acer pseudoplatanus* L. seedlings, and Norby and Luo (2004) showed smaller aboveground woody dry mass accumulation after four years of air-warming treatments in *A. rubrum* and *Acer saccharum* Marsh. saplings. Most studies that found no or negative effects of soil or air warming on *A. rubrum* examined older saplings; however, similarly to our results, Butler et al. (2012) showed that soil warming increased relative growth rate in older, larger *A. rubrum* (>5 cm diameter at breast height). Our results contribute further evidence that growth responses to air and soil warming may be highly species-dependent in *Acer* species. Further, growth responses to warming may be contingent on life stage. Other environmental conditions may interact with warming to affect seedling performance. For example, in Norby and Luo (2004), relative growth rates in *A. rubrum* were only depressed by air warming in one of the four years in that study, highlighting the role of stochastic events such as spring frost altering normal phenology and severe heat waves causing heat stress. We watered our experimental pots to saturation as needed, so the seedlings were not water-limited, and the soil temperature record shows no extreme cold events during the course of the experiment. Thus, our results suggest that in the absence of extreme drought or frost events, *A. rubrum* responds positively to soil warming on its own and that seedlings in microsites with warmer soils will have greater biomass accumulation both above and below the ground, at least in the first year of growth.

Root mass differences under soil warming were likely a factor driving the observed differences in growth and seedling size. Root biomass in tree seedlings generally increases with soil and air warming to species optima (Pregitzer et al. 2000; Yuan and Chen 2010). For *A. rubrum* specifically, Wan et al. (2004) showed that air warming increased fine root production and turnover in seedlings in the short term. The larger root systems in the soil-warming treatment likely absorbed more nutrients and water from the soil, stimulating aboveground growth. The increase in leaf number, leaf size, and active leaf production period in seedlings grown in warmer soils likely also increased carbon acquisition, although we did not measure nonstructural carbohydrates. The larger sizes and masses of seedlings grown under soil warming are also likely driven by the rapid response of metabolic processes in *A. rubrum* to changes in temperature. Lee et al. (2005) demonstrated that young

(3-year old) *A. rubrum* can rapidly acclimate leaf respiration rates to warmer air temperatures, and Sendall et al. (2015) demonstrated that *A. rubrum* seedlings also rapidly acclimate photosynthetic responses to warmer air temperatures. Although we did not measure metabolic rates, our results suggest that these patterns of respiration and photosynthetic responses may too be characteristic of first-year *A. rubrum* under soil-warming conditions, contributing to the observed differences in growth and biomass accumulation.

Implications of soil warming for *Acer rubrum* recruitment

The availability and suitability of small-scale microhabitats can strongly control seedling recruitment, particularly when seedfall is not limited. For some species, conditions affecting recruitment can change rapidly with increasing variability in climate conditions between years (Pérez-Ramos et al. 2013), and in the long-term, climate change could alter the pattern of suitable microhabitat at the landscape scale. As *A. rubrum* is generally considered a relatively fecund species (Beckage and Clark 2003), suitable microhabitat availability and changes in microhabitat conditions may become increasingly important for future recruitment. With atmospheric warming under climate change, soil temperatures are increasing across a range of ecosystem types (Qian et al. 2011; Ooi et al. 2012). Further, increases in other landscape-level disturbances such as treefalls (Peterson et al. 1990), canopy gaps (Zhang et al. 2006), and edge effects (Redding et al. 2003) can increase the availability of warm soil microsites in forests and thereby benefit seedling performance and subsequent recruitment of *A. rubrum*.

Although our study examined the effects of soil warming in the first season, our results suggest that short-term as well as sustained periods of warmer soils can have implications for long-term *A. rubrum* survival and recruitment. Canham et al. (1999) showed that roots functioned as the main carbon storage sink in *A. rubrum* seedlings and that seedlings with higher carbon reserves demonstrated higher overwinter survival. Low growth rates over multiple seasons are strongly linked to mortality in *A. rubrum* (Wyckoff and Clark 2002), whereas larger, sturdier seedlings are likely more resistant to mechanical damage from animal trampling (Newman and Powell 1997). Larger stem and root sizes could further confer competitive advantages in the following growing seasons, particularly as *A. rubrum* is a relatively weak competitor with other tree seedlings (Beckage and Clark 2003). Thus, the positive effects of warmer soils in the first year could extend to recruitment success in the first few years of the seedling life stage.

The limitations of this study include that this is a potted-plant experiment, with soil warming initiated from below, as opposed to soil warming driven by higher atmospheric warming. Further, we could not reasonably measure a multitude of possible interactions with the biotic and abiotic environments. For example, photosynthesis is stimulated up to a threshold beyond which heat stress and drought can reduce carbon sequestration (Ciais et al. 2005). Other factors such as early frosts could also negatively impact *A. rubrum* when the growing season is prolonged under soil-warming conditions (Norby et al. 2003). Soil warming may also affect arbuscular mycorrhizal fungi colonization (Rillig et al. 2002) and potential interactions with competitors and natural enemies (Landhäusser and Lieffers 1998; Dukes et al. 2009). However, even if we conservatively estimate that soil warming augments biomass accumulation and growing period only in the first summer, our results suggest that *A. rubrum* will perform better as microsites with warmer soils become increasingly abundant through the production of larger, sturdier structures in the first season, with no evident trade-offs in biomass allocation above and below the ground.

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