Experimental Warming: How Temperature Affects Germination and Survival of
Minnesota Tree Species

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Acknowledgements

Dedication

This thesis is dedicated to my fellow "Dream Team" members.

Abstract

Seed germination and survival were assessed for ten Minnesota tree species and *Rhamnus cathartica*, a Minnesota invasive, grown under three temperature treatments (ambient, +1.8 °C, +3.6 °C) and two canopy types (open, understory) at two study sites near the ecotonal boundary between southern boreal and northern temperate forest biomes. Initial germinant establishment, overall establishment, and survivorship were analyzed in response to temperature and canopy type. When it had an effect, elevated temperature negatively influenced all three life-history phases, but the effects were more prevalent for overall establishment and survivorship. *Abies balsamea, P. glauca, P. banksiana, B. papyrifera*, and *A. rubrum* all showed considerable negative effects to heating, while *P. strobus* and *P. tremuloides* showed moderately negative effects. Meanwhile, both *Quercus* species and *R. cathartica* appear relatively unaffected by heating. Thus, even moderate climate warming will likely influence the germination and survival of Minnesota boreal and temperate tree species.

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INTRODUCTION

Physiological responses to temperature and water availability influence species-specific range distributions (Woodward 1987, Peñuelas and Boada 2003). Under current projections temperatures are expected to increase 1.4–5.8 °C globally and 2.5–6.9 °C in the Midwestern United States by 2100 (IPCC 2007, Wuebbles and Hayhoe 2004). As such, it is predicted that the abundance and distribution of boreal and temperate species, especially at range boundaries, will change during the next century as temperatures warm (Jump and Peñuelas 2005, Matala et al. 2006, Scholze et al. 2006).

In the absence of temperature-induced drought stress, it is predicted that northern-hemisphere species will shift poleward in latitude and upward in elevation as climate warms (Barber et al. 2000, Rehfeldt et al. 2004, Wilmking et al. 2004). Populations at the leading edge of species ranges are expected to expand as warmer temperatures ameliorate geographical limits caused by climate, poor reproduction, and low survival rates (Jump and Peñuelas 2005). Meanwhile, heightened competition is expected to result in range contractions at southern and low altitude range boundaries (Conolly & Dahl 1970, Pigott & Pigott 1993).

Numerous recent studies have attempted to document these predicted range shifts. For example, studies in Northern Europe (Kullman 2001), New Zealand (Wardle and Coleman 1992), and Alaska (Danby and Hik 2007) have all documented upward treeline movement of species in response to warmer temperatures. Less is known, however, regarding latitudinal shifts brought about by climate change. Although studies have attempted to track latitudinal migrations (Kennedy 1995, Strum et al. 2001), such reports

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remain rare (Parmesan 2006, Jump et al. 2009), and those that do exist, often fail to

attribute distributional changes to climate (Aerts et al. 2006). It is surprising that

relatively little is known regarding how climate will affect boreal and temperate forest

latitudinal-range distributions, especially given that cold biome species are particularly

sensitive to warming (Wookey et al. 1995, Parsons et al. 1994, Aerts et al. 2006,

Parmesan 2006).

     As boreal and temperate species track anthropomorphic-climate change, seed and

seedbed ecology is likely to become an increasingly important factor in the natural

regeneration of these tree species (Wang et al. 1994). Two important factors influencing

the ability of plants to track climate along latitudinal gradients are migration potential and

the resilience of resident populations to change (Higgins et al. 2003). Migration ability

depends on seed establishment, since seeds are often the only means of long-distance

dispersal (Eriksson 1993). Similarly, the resilience of local populations is at least partially

dependent upon the capacity of sexual reproduction, especially in a changing

environment, since this will determine genetic variation in the population (Ellstrant and

Roose 1987). Thus, understanding the impacts of warming on the regeneration of boreal

and temperate species from seed is paramount to our understanding of how plant-

population dynamics will change as the climate warms (Jeltsch et al. 2008).

     It has long been understood that the seed and seedling growth stages represent a

critical bottleneck in forest compositional change (Bewley 1997, Körner 2003, Peñuelas

and Boada 2003, Clark et al. 2006, Graae et al. 2009, Shevtsova et al. 2009, Walck et al.

2010). Numerous studies have examined the relationship between temperature and

seedling establishment for arctic plant species. Several studies conclude that germination and/or seedling survival benefited from warming (Chambers 1995, Wookey et al. 1995, Diemer 2002, Cooper et al. 2004), while others report that germination may increase but seedling survival will decrease with warming (Hobbie and Chapin 1998). Yet other studies demonstrate that both natural and experimental temperature increases may reduce seedling emergence and establishment (Molau 1997, Germino et al. 2002, Graae et al. 2009, Shevtsova et al. 2009). Relatively little is known, however, regarding how the germination and subsequent survivorship of boreal and temperate species will be affected by climate warming (Thompson and Naeem 1996). What is clear though is that if boreal and temperate species fail to track climate and germinate in new habitats, it is far less likely that they will become a major component of the regenerating forest (Greene et al. 1999, Kembell et al. 2010).

It is well understood that temperature affects the germination of boreal and temperate species (Thompson et al. 1977, Adkins et al. 1983). The relationship between seed maturation and thermal climate has been studied for numerous boreal species, including norway spruce (*Picea abies*), scots pine (*Pinus sylvestris*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), red pine (*Pinus resinosa*), fraser fir (*Abies fraseri*), and paper birch (*Betula papyrifera*) (Adkins et al. 1984, Henttonen et al. 1986, Zasada et al. 1992, Flannigan and Woodward 1993, Johnson et al. 1995, Selas et al. 2002, Meunier et al. 2007, Grenier and Sirois 2009). These studies have largely focused on attempts to link thermal period (i.e., temperature) and germination in greenhouse settings or along altitudinal and latitudinal gradients in common-garden experiments. Little,

however, is understood as to how climate change will affect seed germination in natural habitats (Lieffers et al. 1993, Zasada et al. 1997). To address this gap, my research assessed how temperature affects the germination and subsequent survival of boreal and temperate seeds using an *in situ* experiment that incorporates other biotic factors (e.g., competition from vascular and non-vascular plants, facilitation, or chemical effects from established vegetation, etc.).

The present study, split into two research strands, examined how temperature affects the early developmental phases of boreal and temperate tree species. The overarching experiment implemented above- and belowground warming (+1.8 °C and +3.6 °C) and documented seedling growth, phenology, physiology, and survival of boreal and temperate tree seedlings. Meanwhile, my experiment, a subset of the overarching project, examined how these temperature treatments affected seed germination and subsequent survival of the same Minnesota tree species. Although temperature is thought to be an important environmental variable that influences the timing of germination (Probert 2000), other microclimate factors, such as light availability and soil moisture, can influence seed germination and subsequent survival. As such, the effect of two different canopy types (open and understory) was also examined in concert with the heating treatments.

Therefore, I tested the following hypotheses: (i) whether warming will more negatively influence boreal species germination and subsequent survival in comparison to similar warming of temperate species; and (ii) whether warming will enhance germination and subsequent survival of temperate species at the cold (northern) edge of

their range, but reduce germination and survival of boreal species at the warm (southern) edge of their range.

METHODS

Study Sites

The two field sites were located at Cloquet Forestry Center (CFC), Cloquet, MN (46°31' N, 92°30' W, 386 m a.s.l.; 4.5 °C MAT) and Hubacheck Wilderness Research Center (HWRC), Winton, MN (47°55' N, 92°30' W, 453 m a.s.l.; 3.0 °C MAT). The CFC site is 30–50 km north of the ecotonal boundary between southern boreal and northern
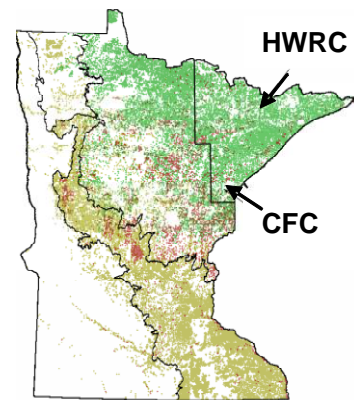
temperate forest biomes, and the HWRC site is another 120 km further north (Fig. 1). At both sites, the warming experiments were located in (≈40-60 year old)

Figure 1. Pre-settlement distribution of all spruce, maple, and oak in MN (Friedman and Reich 2005). Location of the CFC and HWRC study sites are indicated.

mixed aspen-birch-fir stands (with scattered pine, spruce, and other species) and in both understory (≈5-10% of full light) and relatively open (≈40-60% of full light) conditions, representative of typical light levels in these habitats (Machado and Reich 1999, Lusk and Reich 2000, Reich et al. 2001a). These sites were chosen because of their close proximity to the boreal forest-temperate forest ecotone and for other logistical reasons.

MAT in the region has risen ≈1.5 °C since 1940 (Fig. 2) and is expected to increase an additional 3-5 °C (winter) and 4-9 °C (summer) by the year 2095 (Kling et al. 2003). In comparison, precipitation appears to be unchanged over the past 60 years (Fig. 2), and regional projections suggest little future change in average precipitation.

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Study Design

Treatments

The experimental design is a 2 (site) x 2 (habitat) x 4 (treatment) factorial, with six replicates of each for a total of 96 plots (Table 1). The treatments include three levels of simultaneous air and soil warming—ambient, + 1.8 °C, +3.6 °C. Treatments mirror the predicted anticipated warming during the next 75–100 years (IPCC 2007, Kling et al. 2003, Wuebbles and Hayhoe 2004). Warming, implemented throughout the growing season, was a synchronized above- and belowground open air system that combined aboveground infrared heat lamps with soil heating cables under an integrated microprocessor-based feedback control in order to maintain warmed vegetation and soil temperatures in a concurrent-realistic fashion. The overarching experiment included research strands to examine how temperature affects the plant growth, phenology, physiology, and survival of Minnesota boreal and temperate tree
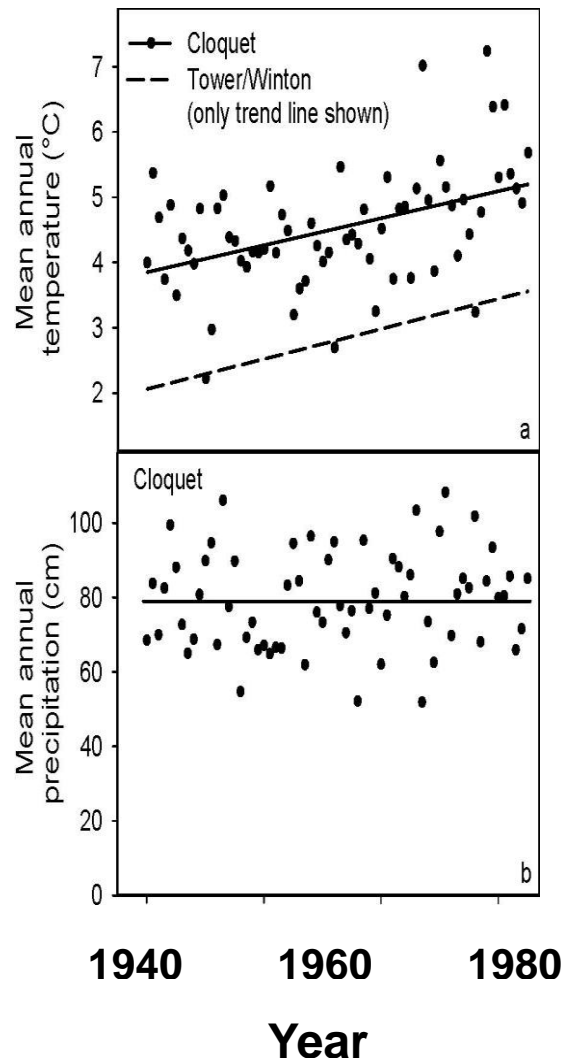

Figure 2. MAT trends for Cloquet, MN and Tower/Winton, MN. For both data sets, increase in MAT with time is significant (P<0.05). There is no trend in mean annual precipitation at either site (only Cloquet shown). Data from Midwestern Regional Climate.

species. My thesis, however, focused on how temperate affects the germination and

subsequent survival of these same Minnesota tree species, a subset of the overall project.

The experimental heating treatments were located in both understory and open

plots because regeneration in both habitat types is important in determining boreal forest

canopy composition (Heinselman 1973, Grigal and Ohmann 1975, Frelich and Reich

1995).

Table 1. Summary of the experimental design, which consists of six replicates of each of sixteen factorial treatment combinations (96 plots in all).

Treatments	Sites	Habitats	Warming Treatments
(2 x 2 x 4 = 16)	CFC, HWRC	Open, Understory	Ambient (no soil cable), Ambient (with cable), +1.8 °C, +3.6 °C

Aboveground heating followed methods developed by Kimball (2005) and

Kimball et al. (2008). Ceramic infrared lamps (Model FTE-1000, 240V, 245 mm x 60

mm; Mor Electric Heating Assoc., Inc.) were operated under a proportional–integrative–

derivative control system where wattage output was increased in sufficient amounts to

maintain temperature treatments of +1.8 °C and +3.6 °C above ambient control plots. Six

1000 W lamps for the 1.8 °C treatment and eight 1000 W lamps for the +3.6 °C treatment

were placed around the perimeter of 3-m diameter plots to face the plot interior at a 45°

angle from horizontal at a height of 1.5 m above the soil. Thermal imaging of this lamp

configuration showed uniform distribution of radiation over the entire plot. Analysis of

the heating data indicates that that the +1.8 °C and +3.6 °C heating treatment goal was

achieved relatively well (Fig. 3).
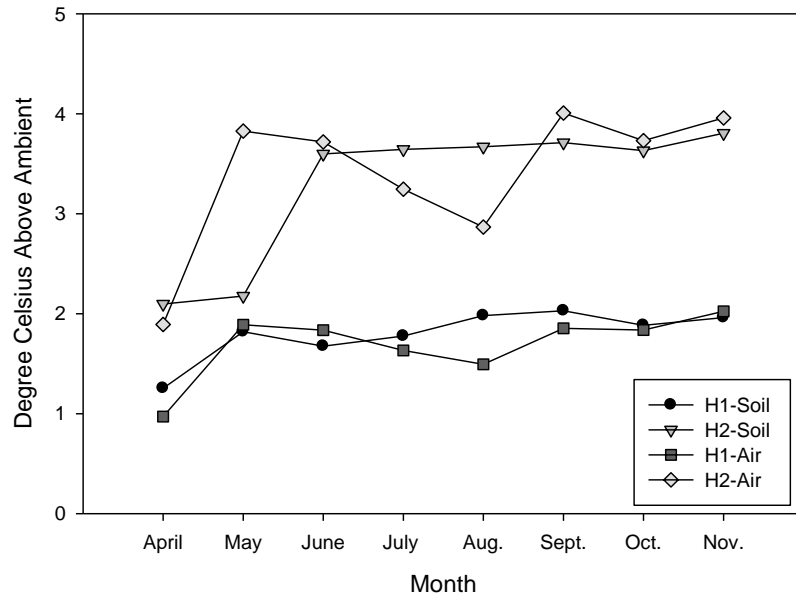
Figure 3. Δ° Celsius above ambient for both the H1 and H2 treatment during the 2009 growing season. Temperature data was calculated as an hourly average. Data for HWRC and CFC is combined.

Soil warming was accomplished through a buried heating cable system (Peterjohn et al. 1993, Bergh and Linder 1999). Heating cables (GX, Devi A/B, Denmark) were installed via slit trench at a depth of 10 cm and spaced 20 cm apart. Soil temperature (1.8 °C or 3.6 °C above ambient) had a feedback control on an individual plot basis. In-ground thermocouples at various depths in the 0-30 cm zone in the soil horizon, connected via multiplexer to a Campbell Scientific CR-1000 controller, regulated a relay that turned on and off the electronic cables.

The heat treatments were operational only briefly during the 2008 growing season. At CFC the heating treatments were turned on from August 27 to September 24 (n=28 days) and at HWRC from September 4 to September 11 (n=7 days). During the 2009 growing season, the heating treatments were operational beginning March 22 and

March 30 at CFC and HWRC, respectively. The heating treatments at both sites were

turned off on November 22 (CFC: n=246 days; HWRC: n=238 days).
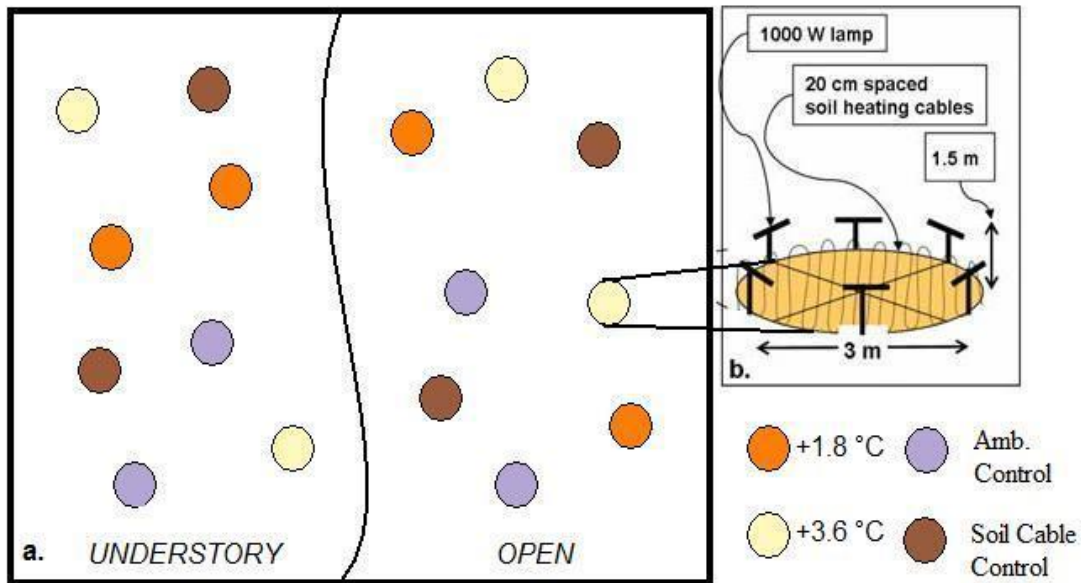
Figure 4. Experimental design including: a) individual block design of each treatment in open and understory habitat (replicated three times at each site), and b) side view of an individual 3-m radius plot.

Study Species

The study species include five true boreal species that vary widely in shade

tolerance (*Abies balsamea> Picea glauca >> Betula papyrifera> Populous tremuloides≈*

Pinus banksiana) and five temperate species that also vary widely in shade tolerance

(*Acer saccharum > Acer rubrum > Quercus macrocarpa ≈ Pinus strobus > Quercus*

macrocarpa). In addition, there was one invasive species, *Rhamnus cathartica*, which is

shade tolerant. Both boreal and temperate groups include evergreen conifers and

deciduous hardwoods. These study species were chosen due to their historical-range

distributions that overlap in northern Minnesota (Fig. 5).
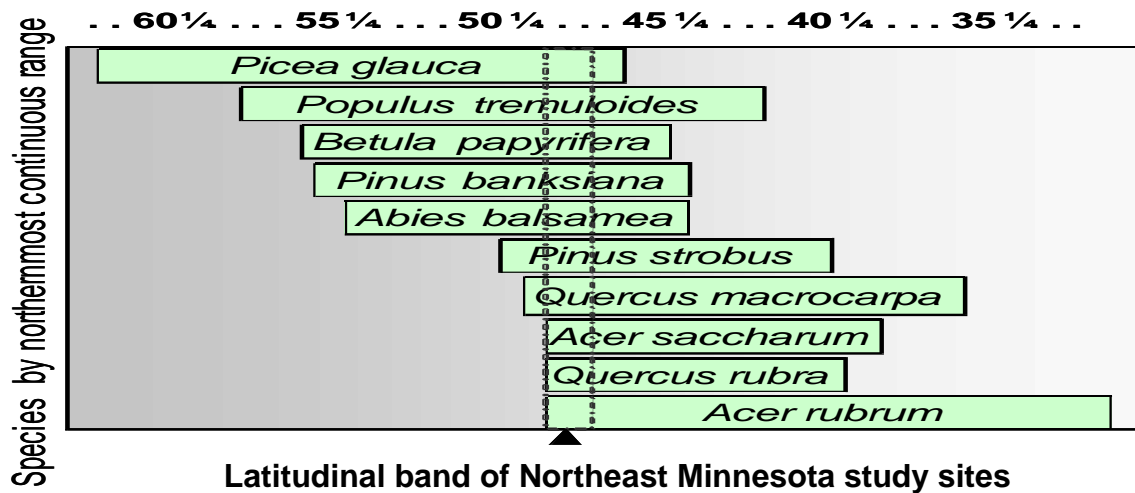
Figure 5. Latitudinal range of target species in the central part of North America in relation to the location of the study sites.

All seeds used in this experiment originated from latitudinal ranges intermediate to the CFC and HWRC study sites. All trees chosen for seed collection were without any visible disease or mechanical damage, and were collected from healthy forest sites outside city limits. Seed collection occurred in the fall prior to planting (except for red maple, which was collected in the spring), and all seeds were stored in cold stratification over the winter months.

Planting Sample Population

Each 3-meter plot was divided into subplots. In a majority (n = 121) of the subplots, one-year old, bare-root seedlings were planted as part of the overarching experiment. In a minority of the subplots (n = 12), I planted seeds of all eleven target species in a 20cm x 40cm seed bed to assess germination and initial establishment success (Fig. 6; n = 96 study plots*12 seed beds/plot*(9 species with 5 seeds/seed bed+2 species with 3 seeds/seed bed = 58,752 seeds). With the exception of the *Quercus*

species, five seeds of each species were planted per seed bed. Due to seed bed space

constraints, only three *Q. rubra* and *Q. macrocarpa* were planted in each seed bed.

Less than ten days prior to planting, seeds were removed from cold stratification

and placed into seed-bed specific sealable plastic bags (except for *Quercus*). For each

growing season, seeds were planted in less than a seven-day time span. Initially, seeds

were to be planted in concert with the peak fruiting of each species, but due to logistical

constraints, seeds were placed in the field in late May for those planted in 2008 (C1) and

in late June for those planted in 2009 (C2).
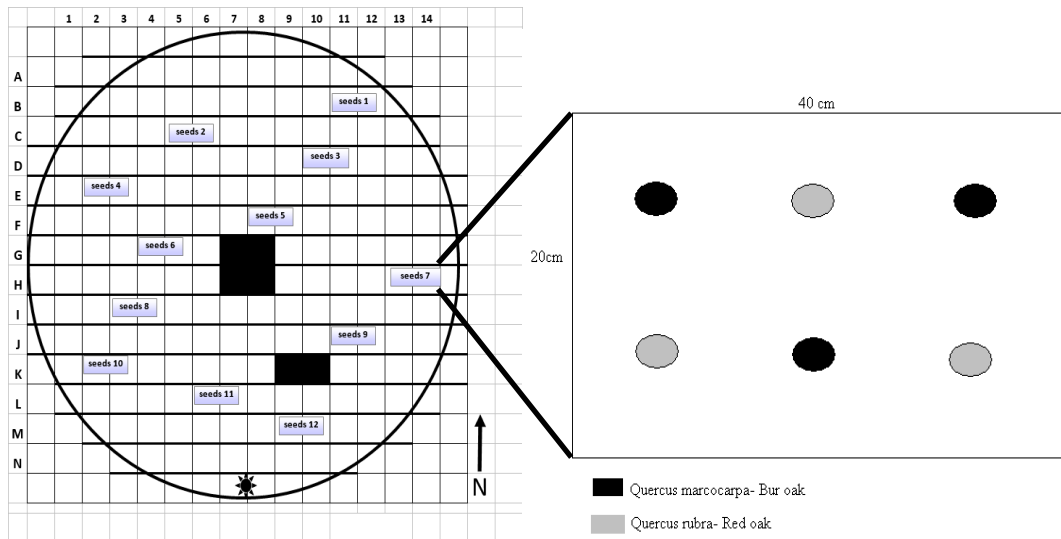
Figure 6. Overhead view of typical plot and location of *Quercus* species in each seed bed. All seed beds are 20cm x 40cm.

All study species establish well in bare mineral soil (Burns and Honkala 1990ab).

As such, during the planting process each seed bed was temporarily cleared to expose

bare mineral soil and seeds were haphazardly scattered throughout the seed bed. The

exception to this protocol was for the *Quercus* species that were buried 1–3cm below the

soil surface due to rodent predation concerns (Fig. 6). After all species were planted, the

litter layer was gently redistributed throughout the seed bed so as to minimize any effects on the soil-nutrient cycling studies.

Census Sampling

The presence/absence of all germinants was sampled on a biannual schedule. The first census of C1 was in October 2008, roughly five months after initial planting. All seedlings were marked with colored toothpicks and their identity was recorded on field-sheets and in PDAs. In June 2009 seed beds were recensused to examine overwinter germination and mortality. At this same time, all seeds were added for C2. Plots were sub-sampled (half of all seed beds examined) one additional time during the 2009 growing season. At the end of the 2009 growing season (October), a comprehensive census of both C1 and C2 was undertaken. *Acer saccharum* germination was less than 0.5% for C1, and thus its germination and subsequent survival results have been excluded from this analysis.

Statistical Analysis

Statistical Approach

This thesis examines two life-history stages and a comparison between these life-history stages. The first measurement is termed "initial germinant establishment" and is a measurement of germinant presence at either the October 2008 or the June 2009 census for C1 and at the October 2009 census for C2. This sampling technique allowed for an examination of over-winter mortality for C1, while still accounting for germination that occurred prior to the first census in 2009. It may seem peculiar to include the June 2009 census in the calculation for C1, but it is not uncommon for some species to emerge

during the following spring, especially since temperatures obtained in the present study may have exceeded optimum germination temperatures (Graae et al. 2009).

The second life-history measurement is termed "overall establishment" and is an examination of germinant presence/absence at the end of the 2009 growing season for C1. The final analysis is termed "survivorship," and it compares those germinants that were observed at either germinant survey to those still present in October 2009. Overall establishment and survivorship results are not available for C2.

All full-study analyses were calculated using a generalized linear fit model, a technique for analyzing count data such as germination (Nicholls 1989). This model uses an assumption of Poisson errors and a logarithmic link function. It also uses a maximum likelihood to fit model parameters. Species-specific comparisons and tests for significance were made using a Tukey-Kramer HSD analysis. All statistical analysis was performed using JMP 8.0 (SAS Institute 2008).

Controls

Two controls were present in this experiment. In the first control, no heating effect was present and the soil was undisturbed. For shorthand, this control is termed "AC." The second control also lacked a heating effect, it did, however, have non-functional heating coils buried in the soil. These control plots, termed "DS," were implemented to examine whether disturbing the soil to bury the heating cable had any effect on initial germinant establishment, overall establishment, or survival. The germination rates for all species at both CFC and HWRC were not significantly different between AC and DS treatments in 2008 (Apdx. 1). This trend continued into 2009 (Apdx.

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2). As such, AC and DS were lumped into one control group—termed "ambient"—for purposes of this analysis.

RESULTS

Overall, heating appears to decrease initial germinant establishment, overall establishment, and survivorship. The negative effects of heating were more pronounced for overall establishment and survivorship.

Initial Germinant Establishment

C1: Seeds planted in 2008

Initial germinant establishment is a measure of the germination that occurred during the first growing season, or in spring of the following year (i.e., from planting in 2008 through first census in 2009). As the heat treatments were only on briefly in 2008, but for different lengths of time, for this year only I examine the two sites separately. The overall effect on germinant establishment of the fall heating in 2008 was not significant at HWRC (P=0.1088) (Table 2). Surprisingly, given the short length of heating, the species by heating interaction was significant (P<0.0001) (Table 2). *Abies balsamea*, *P. glauca*, and *A. rubrum* all had lower, albeit only slightly at 1-4%, initial germinant establishment in the H2 treatment than in the ambient treatment (Table 3). Conversely, initial germinant establishment for *Q. rubra* was roughly 8% higher in the H2 treatment than the ambient treatment (Table 3).

At CFC, the brief heating did not have a significant overall effect on initial germinant establishment (P=0.7155), and the species by heating interaction was not significant (P=0.4543) (Table 2). Although not a significant trend, all species except *B.*

papyrifera, *Q. macrocarpa*, and *Q. rubra* had lower initial germinant establishment in the H2 treatment when compared to the ambient treatment (Table 3).

The overall effect of canopy type on germinant establishment was significant at HWRC and CFC ($P<0.0001$) (Table 2). The species by canopy interaction was also significant at both sites ($P<0.0001$), while the canopy by heat treatment interaction did not lead to significantly different initial germinant establishment (HWRC: $P=0.1830$; CFC: $P=0.4017$) (Table 2). At HWRC, *A. balsamea*, *A. rubrum*, and *R. cathartica* all had significantly higher initial germinant establishment in the understory sites (Table 4). At CFC, only *A. balsamea* had a significantly higher initial germinant establishment rate in the understory site (Table 4).

Table 2. Summary of effects test for initial germinant establishment for C1 in 2008 and C2 in 2009 (Generalized Linear Model, $P=0.05$).

	C1		C2
P value Comparison Table	Establishment-HWRC	Establishment-CFC	Combined Sites
Species	**0.0000**	**<0.0001**	**<0.0001**
Site	-	-	**<0.0001**
Canopy	**<0.0001**	**<0.0001**	0.7924
Heat Treatment	0.1088	0.7155	**0.0333**
Species * Site	-	-	**<0.0001**
Species * Canopy	**<0.0001**	**<0.0001**	**<0.0001**
Species * Heat Treatment	**<0.0001**	0.4543	0.4561
Site * Canopy	-	-	0.0579
Site * Heat Treatment	-	-	0.3271
Canopy * Heat Treatment	0.1830	0.4017	0.5888

C2: Seeds planted in 2009

The heat treatments were fully functional in 2009. As such, examination of the two sites is combined for analysis of C2 initial germinant establishment. The overall

effect of heating on germinant establishment in 2009 was negative (P=0.0333). The

species by heat treatment interaction was not significantly different (P=0.4561) (Table 2).

Only *A. balsamea* and *R. cathartica* had significantly lower initial germinant

establishment in heated plots. That said, all species except *P. banksiana* and *A. rubrum*

had lower initial germinant establishment in the H2 treatment when compared to the

ambient treatment (Table 3). These differences, however, were slight and averaged less

than a full percentage point.

The effect of canopy on germinant establishment was not significant in 2009

(P=0.7924) (Table 2). And while the species by canopy interaction was significant

(P<0.0001), the canopy by heat treatment interaction was not significant (P=0.5888)

(Table 2). The largest difference in initial germinant establishment between canopy types,

at just over 3%, was for *A. balsamea* (Table 4).

Table 3. Mean initial germinant establishment (%) for C1 and C2 among heating treatments. Significantly different initial establishment rates are highlighted in bold text (Tukey-Kramer, *P*=0.05). For purposes of this figure, Ambient is H0.

	C1-HWRC			C1-CFC			C2-Combined Sites		
	H0	H1	H2	H0	H1	H2	H0	H1	H2
A. balsamea	9.7	10.3	6.8	15.3	15.3	14.6	**5.6**	**4.4**	**3.5**
B. papyrifera	2.0	3.5	2.8	3.2	5.00	3.5	0.5	0.3	0.3
P. banksiana	9.5	11.9	9.0	5.3	5.6	4.0	0.7	0.8	0.9
P. glauca	2.6	2.5	1.4	4.0	4.4	3.8	1.4	1.0	0.6
P. tremuloides	3.2	5.1	3.6	3.1	3.2	2.5	0.1	0.1	0.1
P. strobus	4.0	2.2	4.4	5.6	4.3	5.0	0.8	1.0	0.7
A. rubrum	**11.0**	**5.8**	**6.5**	7.6	6.7	6.8	0.7	0.6	0.7
A. saccharum	–	–	–	–	–	–	0.6	0.2	0.4
Q. macrocarpa	45.2	47.7	45.1	6.1	6.0	7.2	4.2	4.3	3.7
Q. rubra	**52.3**	**57.6**	**60.5**	2.6	1.9	3.7	3.6	3.8	3.1
R. cathartica	1.2	2.1	1.3	2.2	1.0	1.5	**2.7**	**1.6**	**1.2**

Table 4. Mean initial germinant establishment (%) for C1 and C2 between canopy types. Significantly different initial establishment rates are highlighted in bold text (Tukey-Kramer, *P*=0.05).

|	C1-HWRC		C1-CFC		C2-Combined Sites	
	Understory	Open	Understory	Open	Understory	Open
A. balsamea	**13.7**	**4.6**	**17.6**	**12.6**	**3.1**	**6.4**
B. papyrifera	**1.0**	**4.1**	**1.7**	**5.7**	0.5	0.3
P. banksiana	**1.9**	**18.1**	**4.0**	**6.0**	**0.2**	**1.4**
P. glauca	**1.1**	**3.4**	3.5	4.5	**0.7**	**1.5**
P. tremuloides	**2.0**	**5.6**	**0.3**	**5.7**	0.1	0.1
P. strobus	**1.0**	**6.3**	**4.0**	**6.2**	**0.5**	**1.2**
A. rubrum	**10.6**	**6.5**	7.3	7.0	0.7	0.6
A. saccharum	–	–	–	–	0.5	0.4
Q. macrocarpa	**25.7**	**65.9**	**4.2**	**8.6**	**5.2**	**3.1**
Q. rubra	**43.6**	**67.9**	**1.2**	**4.2**	**4.8**	**2.3**
R. cathartica	**2.3**	**0.6**	1.4	2.0	**2.8**	**1.3**

Overall establishment

Total numbers of seedlings alive in October 2009 reflects both initial germinant establishment and subsequent survival. The effect of heating on overall establishment

was significantly negative by October 2009 (*P*<0.0001) (Table 5). The species by heating interaction was also significant (*P*<0.0001) (Table 5). Although *P. tremuloides*, *R. cathartica*, and *Q. macrocarpa* had similar overall establishment among heating treatments, all other species had lower overall establishment in warmed plots. This response was significantly negative for *A. balsamea*, *A. rubrum*, and *P. glauca* (Fig. 7).

The response to heating was not identical at both study sites. At CFC the overall establishment of *P. banksiana* and *P. glauca* was significantly lower in heated plots, but a detrimental response to heating was absent for these species at HWRC. At HWRC, *Q. rubra* survival significantly increased with heating. This response to heating was not present at CFC.

The overall effect of canopy on overall establishment was significant in 2009 (*P*<0.0001) (Table 5). The species by canopy interaction was also significant (*P*<0.0001), as was the canopy by heat treatment interaction (*P*<0.0030) (Table 5). *Abies balsamea*, *A. rubrum*, and *R. cathartica* all had lower overall establishment in understory plots (4.4%, 2.6%, 0.7%, respectively). In comparison, both *Quercus* species had nearly 15% higher overall establishment in the open sites (Table 6).
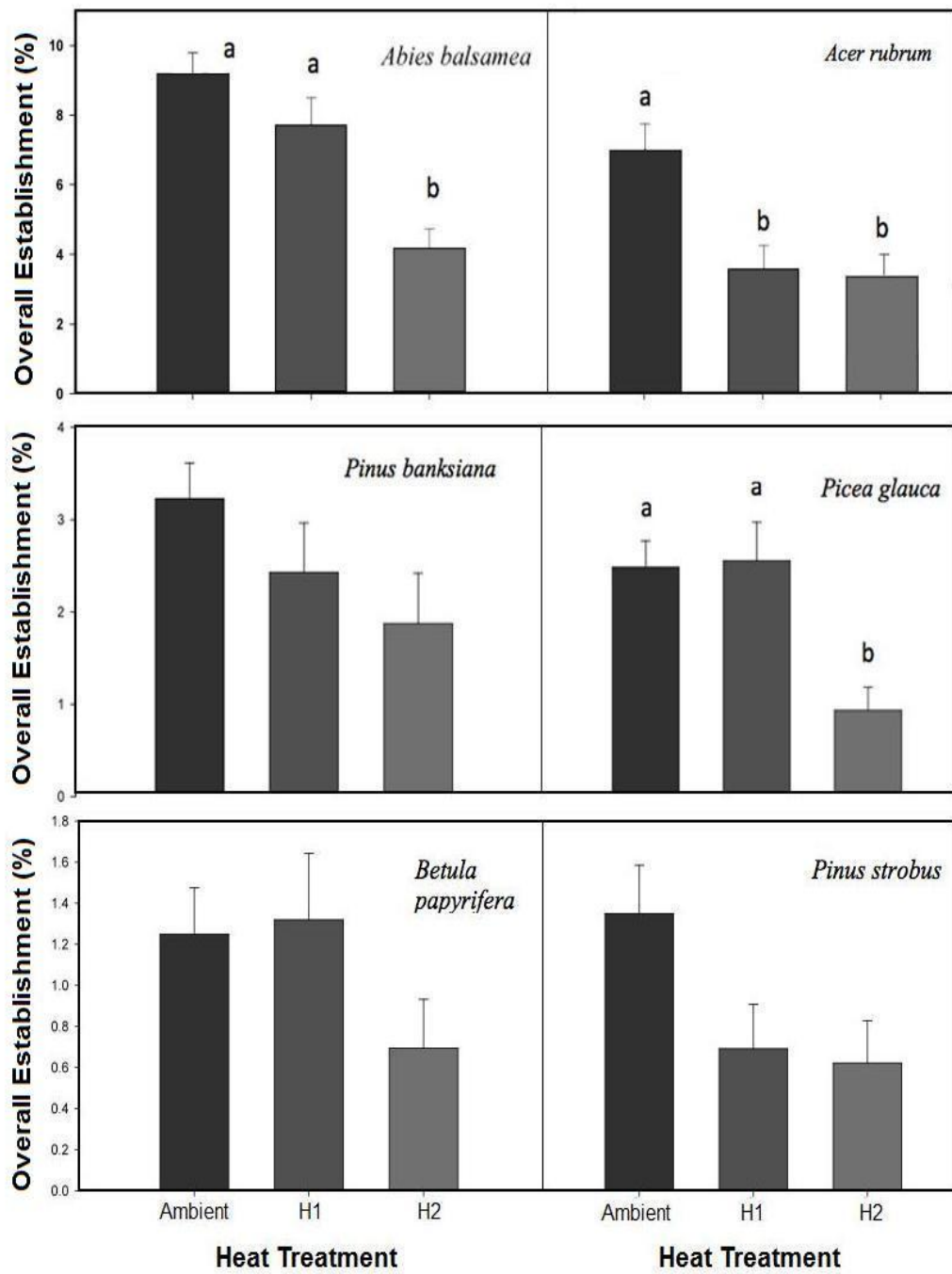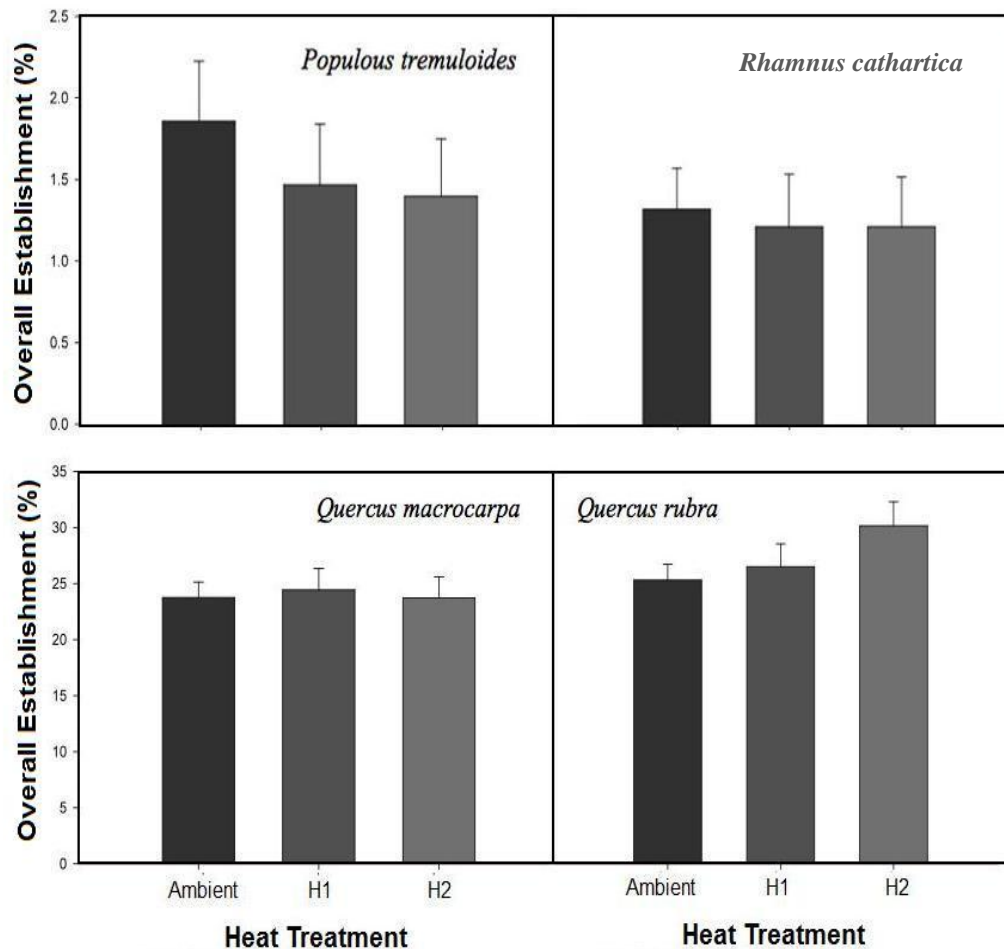
Figure 7. Overall establishment rates (%) among heating treatments for ten species in October 2009. Means with dissimilar lowercase letters are significantly different (Tukey-Kramer, P=0.05). *Acer saccharum* overall establishment was not graphed because germination was less than 0.5%.

Table 5. Summary of effects test for overall establishment and survivorship in 2009 (Generalized Linear Model, P=0.05).

P value Comparison Table	Overall establishment	Survivorship
Species	**<0.0001**	**<0.0001**
Site	**<0.0001**	**<0.0001**
Canopy	**<0.0001**	0.5720
Heat Treatment	**<0.0001**	**<0.0001**
Species * Site	**<0.0001**	**0.0028**
Species * Canopy	**<0.0001**	**<0.0001**
Species * Heat Treatment	**<0.0001**	**0.0005**
Site * Canopy	0.2015	**0.0004**
Site * Heat Treatment	0.1251	**0.0078**
Canopy * Heat Treatment	**0.0030**	0.1495

Table 6. Mean overall establishment (%) and survivorship (%) for C1 in 2009. Significantly different rates among canopy types are highlighted in bold text (Tukey-Kramer, P=0.05).

	Overall establishment		Survival	
	Understory	Open	Understory	Open
A. balsamea	**9.9**	**5.3**	64.2	60.5
B. papyrifera	**0.4**	**1.9**	23.9	40.5
P. banksiana	**0.6**	**4.8**	**18.2**	**38.6**
P. glauca	**1.7**	**2.7**	75.0	72.7
P. tremuloides	**0.7**	**2.6**	59.4	43.5
P. strobus	**0.6**	**1.4**	23.9	22.7
A. rubrum	**6.5**	**4.0**	**71.1**	**55.6**
Q. macrocarpa	**13.4**	**34.4**	90.1	91.5
Q. rubra	**20.0**	**33.7**	90.1	93.0
R. cathartica	**1.6**	**0.9**	**85.7**	**63.3**

Germinant Survival

Germinant survival examines whether germinants observed at the initial germinant establishment life-history stage survived to a later date. The overall effect of heating on seedling survival for C1 was significantly negative ($P<0.0001$) (Table 4). The species by heating interaction was also negative ($P=0.0005$) (Table 4). Five species, four of which are boreal species, showed a significant decrease in survivorship when heated (Fig. 8). Of those, *A. balsamea* and *P. glauca* had the largest difference, at nearly 35% for each species. Similarly, *B. papyrifera*, *P. banksiana*, and *A. rubrum* survival decreased by 26%, 19%, and 18%, respectively. Both *Quercus* species and *R. cathartica* had similar survivorship among heating treatments, while the other species exhibited slight (<15%) decreases in survival when heated.
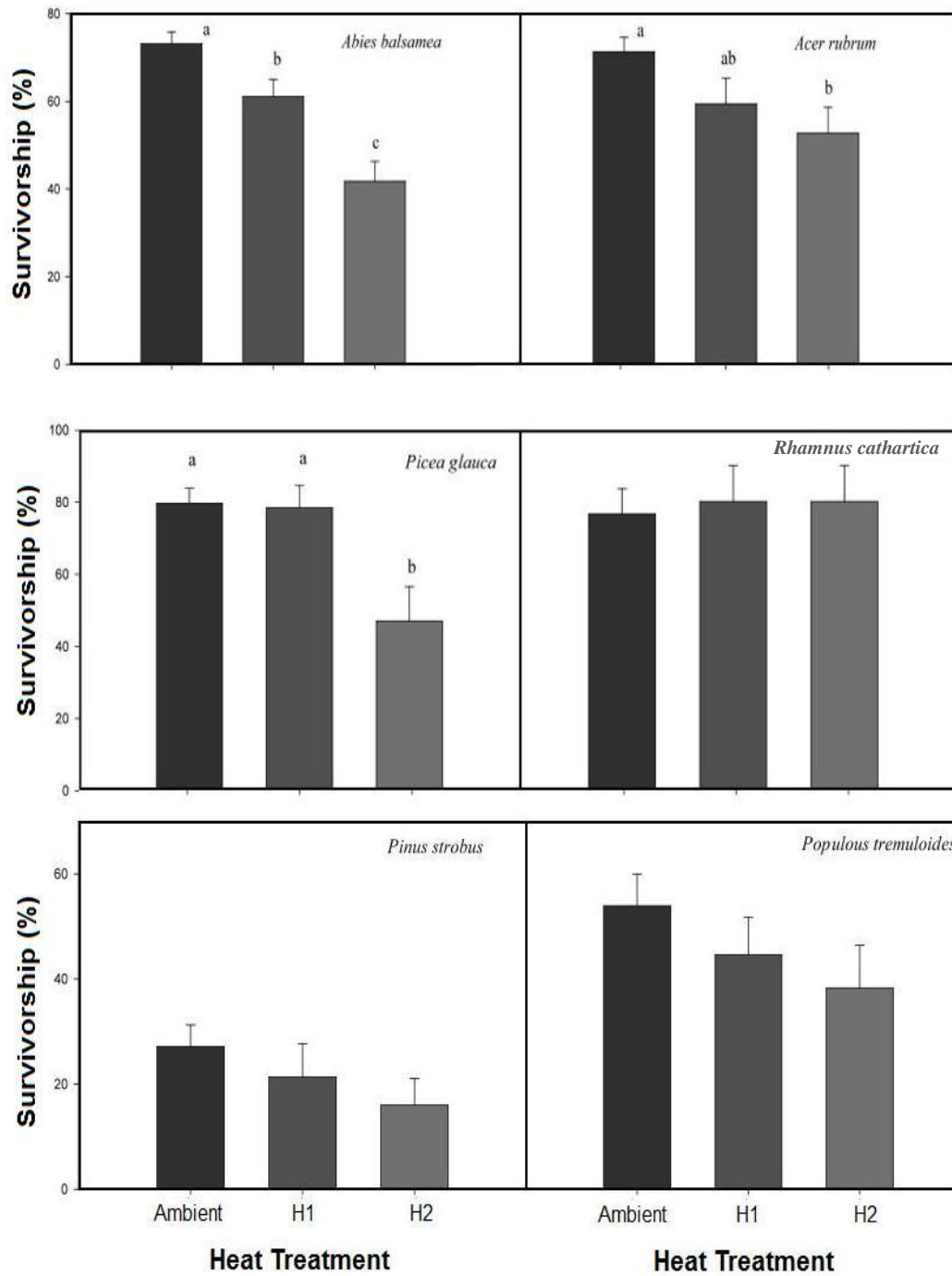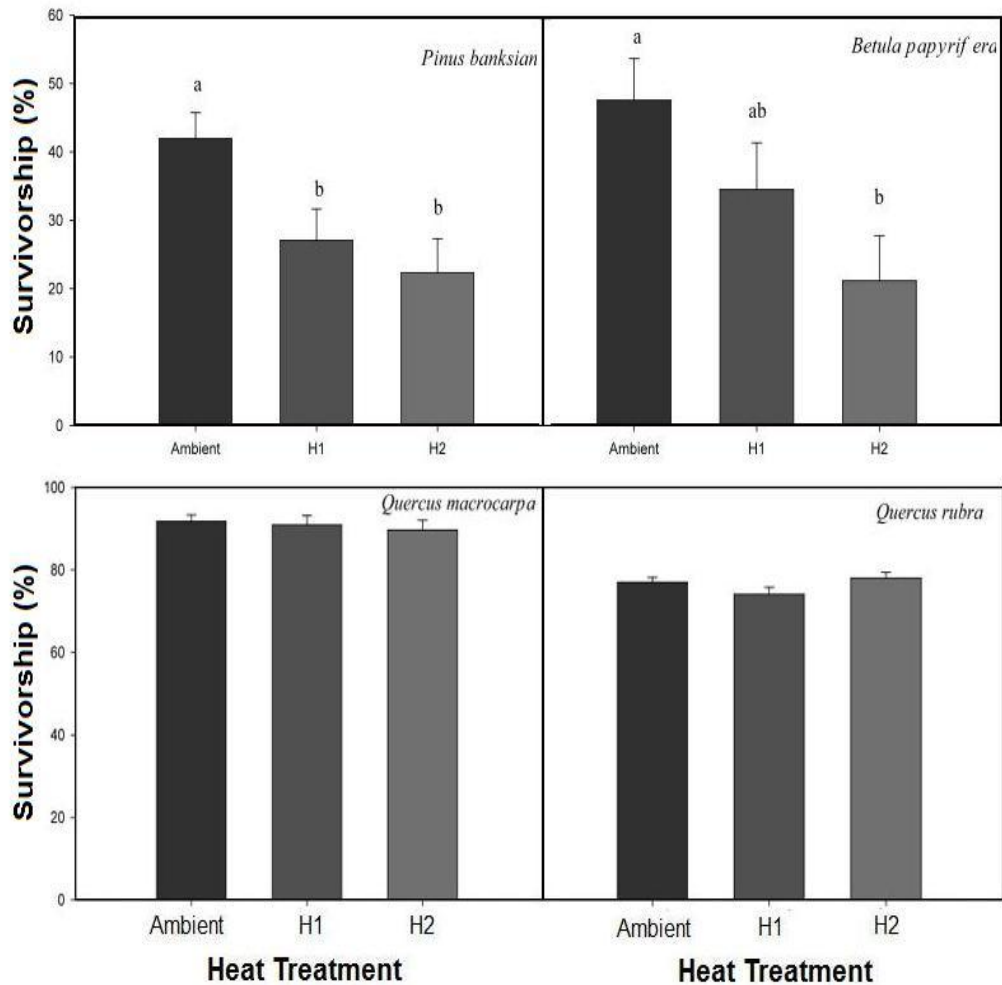
Figure 8. Survivorship rates (%) among heat treatments for ten species in October 2009. Means with dissimilar lowercase letters are significantly different (Tukey-Kramer, *P*=0.05). *Acer saccharum* survivorship was not graphed, because germination was less than 0.5% .

The response to heating was different between the two study sites. At CFC, *A. rubrum* and *P. glauca* had significantly lower survivorship in the heated plots. A detrimental survivorship response was not present for these species at HWRC. At CFC *Q. rubra* did not exhibit significantly different survivorship among heating treatments, but at HWRC the heating significantly affected survivorship. Survivorship in the H1 treatment was significantly lower in comparison to the ambient and H2 treatment for *Q. rubra*.

Canopy type did not significantly affect survivorship ($P=0.0572$) (Table 4). The species by canopy interaction was significant ($P<0.0001$), but the canopy by heat treatment interaction was not significantly different ($P=0.1495$) (Table 4). Six of the ten species had higher survivorship in the understory sites (*A. balsamea*, *A. rubrum*, *P. glauca*, *P. strobus*, *P. tremuloides*, and *R. cathartica*) (Table 6).

DISCUSSION

As global temperatures rise, it is expected that the abundance and distribution of boreal and temperate species will change, especially at range boundaries (Jump and Peñuelas 2005, Matala et al. 2006, Scholze et al. 2006). Therefore, the aim of this study was to assess how temperature affects tree species near the ecotonal boundary between southern boreal and northern temperate forest biomes in Northern Minnesota. Specifically, the results from this experiment assess (i) how temperature affects seed germination and subsequent survival of boreal and temperate species, (ii) whether the effects of temperature on seed germination and subsequent survival of boreal and temperate species are magnified at range boundaries; and (iii) whether canopy type influences the effect that heating has on seed germination and subsequent survival of boreal and temperate species.

In general, the heat treatment, when it had an effect, decreased initial germinant establishment, overall establishment, and survivorship. The only significantly positive response to heating was for a single species, at a single study site, in a single cohort, and for a single life-history stage. The negative effects of heating were more pronounced for overall germination and survivorship. This is somewhat converse to the canopy

treatment, which had nearly no effect on survivorship. Further, species differed in their response to heating. *Abies balsamea, P. glauca, P. banksiana, B. papyrifera*, and *A. rubrum* all showed considerable negative effects to heating, while *P. strobus* and *P. tremuloides* showed moderately negative effects. Meanwhile, both *Quercus* species and *R. cathartica* appear relatively unaffected by heating.

Initial Germinant Establishment

The heat treatment had a minimal effect on initial germinant establishment. Except for the species by heating interaction at HWRC, neither site exhibited significant responses to heating for C1. This is not surprising given that the heat treatment was operational for only a short period of time at the end of the growing season. The August heating may have been too late in the growing season to influence initial germinant establishment, especially since the breaking of seed dormancy is a physiological process that is independent of seedling establishment and requires the correct temperature and moisture combination (Baskin and Baskin 1998, Fenner and Thompson 2005, Walck et al. 2011). Surprisingly, a similar trend was also present for C2— where the heating treatment was operational for the entire growing season. This is not the first study, however, to find that small temperature differences only marginally affect initial germinant establishment (Suzuki & Kudo 2005).

When the heat treatment did have an effect, most species exhibited a negative response. For C1 at HWRC, *A. rubrum* had significantly lower germination in the heated plots. For C2, *A. balsamea* and *R. cathartica* initial germinant establishment was significantly lower in heated plots. Conversely, *Q. rubra* initial germinant establishment

improved with heating at HWRC for C1. This was the only positive response to heating present in the entire two-year study. These results marginally support Shevtsova et al. (2009), which found that species-specific responses to warming vary considerably by functional type.

The species-specific trends that emerged during the initial germinant establishment life-history stage continued into overall establishment and survivorship for both *A. rubrum* and *Q. rubra* (although not in a statistically significant fashion for the latter), tending to support the conclusion that initial germinant establishment is a bottleneck for future success (Greene et al. 1999, Kembell et al. 2010). Unfortunately, overall establishment and survivorship results for C2 are unavailable, so it is difficult to gauge the relative strength of this conclusion.

Unlike temperature, canopy had a marked effect on initial germinant establishment. For both cohorts, almost all species were significantly influenced by canopy type. These observations may suggest that canopy, as opposed to temperature, has a greater influence on initial germinant establishment. This observation, however, is somewhat puzzling since numerous studies across multiple functional groups have shown that light availability rarely limits seedling emergence (Grime et al. 1981, Bell et al. 1993, Holl 1999, Araki and Washitani 2000, Forcella et al. 2000, Kondo et al. 2011). Most species are able to germinate after exposure to light for only fractions of a second (Forcella et al. 2000) and many species-specific emergence rates are identical in fully lit and light-absent environments (Grime et al. 1981). Although our results link canopy type and initial germinant establishment, the more important factor is likely soil moisture.

Germination is highly dependent upon available soil moisture (Kos and Poschlod 2008, Walck et al. 2011), and soil moisture levels were significantly lower in open canopy plots. These results may better explain initial germinant establishment than does canopy type and should be examined in subsequent studies.

Overall establishment

The results tend to indicate that for the year subsequent to planting, temperature may be a more important factor to overall establishment, than it was for initial germinant establishment. Alternatively, similar results at the initial germinant establishment stage may have occurred if the heating treatment was operational for the entire 2008 growing season.

Abies balsamea and *P. glauca* exhibited significantly lower overall establishment rates for the H2 treatment in comparison to the ambient treatment. For *A. rubrum*, overall establishment rates in the H1 and H2 treatment were both significantly lower than for the ambient treatment. Although not significant, *P. banksiana*, *P. glauca*, *B. papyrifera*, *P. strobus*, and to a lesser extent, *P. tremuloides* exhibited lower overall establishment in the H2 treatment when compared to the ambient treatment. All five boreal study species exhibited some form of a negative response to heating, two of which were statistically significant. In comparison, only two of the four temperate species were negatively influenced by heating. These results tend to support the hypothesis that the negative effect of heating will be more pronounced for boreal species.

Site-specific responses were also observed. At CFC, *P. banksiana* and *P. glauca* overall establishment was significantly lower in heated plots. Neither trend was present at

HWRC for the same species. Additionally, *Q. rubra* overall establishment at HWRC was significantly higher in heated plots. This trend, however, was not present at CFC. The site-specific responses match predictions that warming will enhance germination and the subsequent survival of temperate species at the cold (northern) edge of their range, but reduce germination and survival of boreal species at the warm (southern) edge of their range (Jump & Peñuelas 2005, Higgins & Harts 2006, Ibanez et al. 2006).

Survivorship

Survivorship appears greatly influenced by temperature. All five boreal species exhibited lower survivorship rates in the heated plots. All responses, except for *P. tremuloides*, were statistically significant. As for temperate species, *A. rubrum* and *P. strobus* were negatively affected by heating, but only the trend for *A. rubrum* was significant. Both *Quercus* species and *R. cathartica* survivorship appears unaffected by the temperature treatment.

Canopy type, on the other hand, appears to have had a much lesser impact on survivorship than did temperature. Canopy did not significantly affect survivorship, but just barely at *P*=0.0572. Unlike the initial germinant establishment and overall establishment, where canopy type significantly influenced species-specific responses, canopy type had a significant effect on survivorship for only three species. These results tend to indicate that the effect of canopy on survivorship is minimal in comparison to the effect of heating.

Implications

It seems reasonable to interpret these results as suggesting that the predicted warming will likely influence the germination and survival of Minnesota boreal and temperate species, with responses varying markedly by species and by proximity to range boundaries. As the climate warms, northern hemisphere tree species are expected to move their southern and northern range boundaries (Iverson and Prasad 1998, Soja et al. 2007), and this study appears to support such a prediction given the poor performance of these Minnesota tree species, especially boreal species, when planted in heated plots.

Somewhat surprising was that a positive heating effect was not observed for temperate species at their northern-range boundary. A positive response to heating was present for only a single species, at a single study site, in a single cohort, and for a single life-history stage. It is predicted, however, that competitive exclusion will drive species replacement at southern-range boundaries (Woodward 1987). Given this and because the present study examined seedling establishment and only one year of subsequent survival, without an examination of physiological responses to heating, it is too early to predict whether warming will encourage a northern-range expansion for temperate species.

Species migration, however, depends on both physical dispersal and the successful establishment of seeds in new populations (Jump and Peñuelas 2005). This study examined only the latter, and in order to assess how the range boundaries of boreal and temperate species will change as climate warms, future studies should examine the migration potential of these species. Overall, these results suggest that modest warming

will have negative consequences on the natural germination and survival of Minnesota

tree species, especially for boreal species at their southern-most range boundary.

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Appendix 1. Initial establishment (%) of non-heating controls at CFC and HWRC for C1 in 2008. No germination rates are significantly different (Tukey-Kramer, *P*=0.05).

Establishment HWRC-2008	AC	DS	*P* value
A. balsamea	4.3	4.6	0.9966
A. rubrum	7.8	6.5	0.8418
B. papyrifera	1.5	1.7	0.999
P. banksiana	9.9	6.7	0.3863
P. glauca	1.8	2.2	0.948
P. strobus	3.5	3.1	0.6344
P. tremuloides	1.5	2.9	0.4489
Q. macrocarpa	41.0	45.7	0.6804
Q. rubra	50.1	51.2	0.9938
R. cathartica	0.7	1.7	0.4118

Establishment CFC-2008	AC	DS	*P* value
A. balsamea	11.8	13.6	0.8064
A. rubrum	3.9	5.8	0.5474
B. papyrifera	1.8	3.6	0.4145
P. banksiana	5.0	4.0	0.8576
P. glauca	2.9	3.5	0.9627
P. strobus	4.6	5.3	0.9423
P. tremuloides	1.4	3.1	0.3640
Q. macrocarpa	6.5	4.4	0.5953
Q. rubra	3.0	2.1	0.8602
R. cathartica	2.6	1.4	0.3357

Appendix 2. Initial establishment (%) of non-heating controls for C2 in 2009. No germination rates are significantly different (Generalized Linear Model, *P*=0.05).

Establishment - 2009	AC	DS	*P* value
A. balsamea	9.6	9.0	0.9459
A. rubrum	6.6	7.3	0.9085
B. papyrifera	0.9	1.6	0.3618
P. banksiana	3.6	2.9	0.7468
P. glauca	2.1	3.1	0.2876
P. strobus	1.4	1.3	0.9981
P. tremuloides	1.5	2.2	0.7469
Q. macrocarpa	22.9	24.6	0.9269
Q. rubra	25.4	25.2	0.9997
R. cathartica	1.3	1.3	0.9988