

## Early life history transitions and recruitment of *Picea mariana* in thawed boreal permafrost peatlands

PHILIP CAMILL,<sup>1,4</sup> LAURA CHIHARA,<sup>2</sup> BRAD ADAMS,<sup>3</sup> CHRISTIAN ANDREASSI,<sup>1</sup> ANN BARRY,<sup>1</sup> SAHIR KALIM,<sup>1</sup> JACOB LIMMER,<sup>1</sup> MIKE MANDELL,<sup>1</sup> AND GREG RAFERT<sup>1</sup>

<sup>1</sup>Carleton College, Department of Biology, One North College Street, Northfield, Minnesota 55057 USA

<sup>2</sup>Carleton College, Department of Mathematics, One North College Street, Northfield, Minnesota 55057 USA

<sup>3</sup>Corporate Executive Board, Washington, D.C. 22209 USA

**Abstract.** Black spruce (*Picea mariana*) is the most abundant tree species in the boreal biome, but little is known about how climate warming may change recruitment in peatlands, especially those affected by permafrost thaw. We used results from a seven-year study in northern Manitoba, Canada, to address the following questions: (1) What is the relative importance of early life history transitions on *P. mariana* recruitment? (2) How are these transitions mediated by biological and environmental factors, including competition, facilitation, disease, herbivory, water table depth, and soil nutrients? (3) Do interactions among these factors create additional recruitment limitations beyond those imposed by environmental factors changing with climate warming, such as hydrology? Seed rain was measured over six years on forested permafrost plateaus and in neighboring collapse scar bogs. Seed germination and seedling survival and growth were measured over 4–5 years in collapse scars and assessed across a three-level water table treatment. Survival and growth experiments examined additional combinations of above- and belowground vascular plant competition and fertilizer addition. Results showed that failure of germination and survival on growing moss surfaces and reduced survival of seedlings in wetter microsites were primary constraints. Seed influx was significantly lower in collapse scars but likely did not limit recruitment. Biological and environmental factors mediating these life history transitions also differed in relative importance, and interactions among them tended to amplify recruitment limitation. Seedling survival was most strongly controlled by fast-growing mosses in wet microsites but also was influenced by apparent drowning in wet plots, herbivory, and loss of foliage caused by a fungal pathogen. Seedling growth was strongly controlled by water table depth, nutrient and competition levels, and fungal pathogens. Multiple, interacting factors will affect *P. mariana* establishment in boreal peatlands during climate warming. Generalizations about recruitment relying on few environmental gradients sensitive to climate change, such as water table, may therefore not fully capture the complexities of establishment.

**Key words:** black spruce; boreal; climate warming; germination; growth; peatland; permafrost; *Picea mariana*; recruitment; Sphagnum; survival.

### INTRODUCTION

Black spruce (*Picea mariana* [Mill.] B.S.P.) is the most abundant tree species in the boreal biome (Payette 1993), especially in peatlands where its capacity to tolerate wet and nutrient-poor conditions make it a dominant tree species. The vast spatial extent of boreal and subarctic peatlands (346 million ha; Gorham 1991) means that changes in *P. mariana* forest cover can have global-scale impacts on the existence of permafrost, plant succession, carbon balance, fire, and energy budgets.

Rapid climate warming in high-latitude ecosystems has altered shrub and forest recruitment in uplands over

the past half century, leading to range shifts (Sturm et al. 2001, Lloyd and Fastie 2003), but less is known about how *P. mariana* cover may change in peatlands, especially those underlain with permafrost, which are experiencing dramatic changes in vegetation structure, composition, and hydrology following thaw (Camill 1999a, Beilman 2001, Camill et al. 2001, Camill 2005). Permafrost plateau bogs are elevated above the regional water table and are dominated by a dense *P. mariana* overstory and an ericaceous shrub–feathermoss understory (Camill 1999a, Beilman 2001). Thaw and subsidence in a permafrost bog landscape creates circular thermokarst features known as collapse scar bogs that are typically large (10–50 m diameter), open, and dominated by a community of *Sphagnum* mosses, *Carex* sedges, and ericaceous shrubs (see Appendix A for a schematic and photo of a permafrost peatland and collapse scar system). Peat accumulation in collapse scars increases peat bulk density over a period of tens to

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<sup>4</sup> Present address: Bowdoin College, Biology and Environmental Studies, 6700 College Station, Brunswick, Maine 04011 USA. E-mail: pcamill@bowdoin.edu

hundreds of years, causing wetter *Sphagnum* communities (e.g., *S. riparium*) to succeed to drier lawn (e.g., *S. angustifolium*) and hummock (e.g., *S. fuscum*) communities suitable for *P. mariana* establishment from seeds dispersed from trees on surrounding permafrost plateaus (Camill 1999b, Beilman 2001, Camill et al. 2001). Permafrost thaw thereby creates new colonization sites analogous to canopy gaps (Shugart 1984, Pickett and White 1985) where seeds can disperse across a natural gradient of water table depths and *Sphagnum* microsites.

Understanding how *P. mariana* establishment will change in thawed peatlands requires a mechanistic analysis of early life history transitions, including seed dispersal, germination, growth, and seedling survival. The literature on *P. mariana* recruitment in peatlands and other lowlands is patchy, with overrepresentation of artificial seeding, germination, and growth studies in commercially drained and fertilized peatlands used for forestry and underrepresentation of studies describing growth and survival in unaltered peatlands. Previous work suggests that germination and survival are poor in wetter microsites where mosses grow comparatively rapidly (Roe 1949, Arnott 1968, Jeglum 1981, Ohlson and Zackrisson 1992, Roy et al. 2000). Saturated soils reduced *P. mariana* growth (Liefvers and Macdonald 1990, Macdonald and Liefvers 1990, Hillman and Roberts 2006) as a result of decreased stomatal conductance and photosynthesis and increased leaf necrosis (Lamhamedi and Bernier 1994, Pepin et al. 2002, Islam and Macdonald 2004, Choi et al. 2007) as well as decreased soil nutrient availability caused by low oxygen diffusion and nutrient mineralization (Prévost et al. 1997, Roy et al. 1999, 2004, Sundström et al. 2000). However, one study showed that dry conditions on hummocks may induce water stress and inhibit growth (Stewart and Bernier 1995), and another study suggests that vascular plant cover may increase transpiration, increase local water table depth, and facilitate *P. mariana* seedling survival (Jutras et al. 2006). Some authors have suggested that sites most favorable for germination may be least favorable for growth (Ohlson and Zackrisson 1992, Groot and Adams 1994, St. Hilaire and Leopold 1995) because moderately moist *Sphagnum* substrates (e.g., hollows or *S. angustifolium* lawns) may inhibit seedling growth, and more rapidly growing mosses in these microhabitats may kill new *P. mariana* germinants. Almost nothing is known about the impacts of natural seed dispersal, herbivory, and pathogens on *P. mariana* recruitment in boreal peatlands.

The challenge in deriving general insights from published studies is that most are not sufficiently comprehensive to assess the relative importance of life history transitions or the biological and environmental factors controlling recruitment across recruitment stages, or the complex interactions among factors affecting recruitment (Clark et al. 1999). Seed dispersal, germination, and survival in boreal peatlands have not been evaluated simultaneously in a single study, which is

essential for assessing the relative importance of these transitions in recruitment. Likewise, the impacts of multiple biological and environmental factors affecting these transitions, including nonvascular and vascular plant competition, facilitation, disease, herbivory by mammals, water table depth, and soil nutrients, have not been evaluated experimentally on a single cohort of seeds or seedlings. The extent to which biological factors increase recruitment limitation beyond the effects of environmental gradients sensitive to climate warming is also not known. Studies of one or a few factors risk mischaracterizing recruitment if they omit other key processes.

In order to advance understanding of likely changes in these peatland forests with climate warming, we used results from a seven-year study to address the following specific questions: (1) Following permafrost thaw in peatlands, what is the relative importance of early life history transitions (seed dispersal, germination, and growth and survival) on *P. mariana* recruitment? (2) What are the relative importances of nonvascular and vascular plant competition, facilitation, disease, herbivory by mammals, water table depth, and soil nutrients in regulating these transitions? (3) Do interactions among these factors create additional recruitment limitations beyond those imposed by environmental factors changing with climate warming, such as hydrology?

#### STUDY REGION

Study sites were located in boreal peatlands in northern Manitoba, Canada (Fig. 1). Seed rain was monitored across a regional network of sites (Fig. 1B). We established seed germination, growth, and survival experiments in a large boreal peatland landscape (54°50'01" N, 98°30'01" W) near the town of Wabowden (Fig. 1C).

Geologically, the experimental region is in the Superior Boundary Zone bordering the Thompson Nickel Belt, with bedrock consisting of Archaean gneisses and Paleoproterozoic sequences (Manitoba Energy and Mines 1993). Overlying Quaternary sediments consist of sand and gravel beach ridges at the margin of Lake Agassiz, offshore glaciolacustrine clays and silts deposited in deep water of Lake Agassiz, and sandy outwash fans (Matile and Keller 2006). Peatlands are extensive in this region, and organic histosols 1–5 m thick in lowlands are common (Matile and Keller 2006). Permafrost occurrence is classified as sporadic with medium to high ground ice (Brown et al. 1998; Fig. 1B).

Weather stations are geographically sparse, and climate records between 1998 and 2003 were incomplete in this region. Consequently, we compiled data from several locations (Fig. 1C; Environment Canada 2004). Monthly records available from Wabowden and Jenpeg/Cross Lake stations indicated that growing season (May–October) temperatures ( $11.2^{\circ} \pm 0.4^{\circ}\text{C}$  to  $12.0^{\circ} \pm 0.4^{\circ}\text{C}$ ; mean  $\pm$  SE) and total precipitation ( $310.6 \pm 24.1$  mm to  $347.2 \pm 21.6$  mm; mean  $\pm$  SE) did not differ

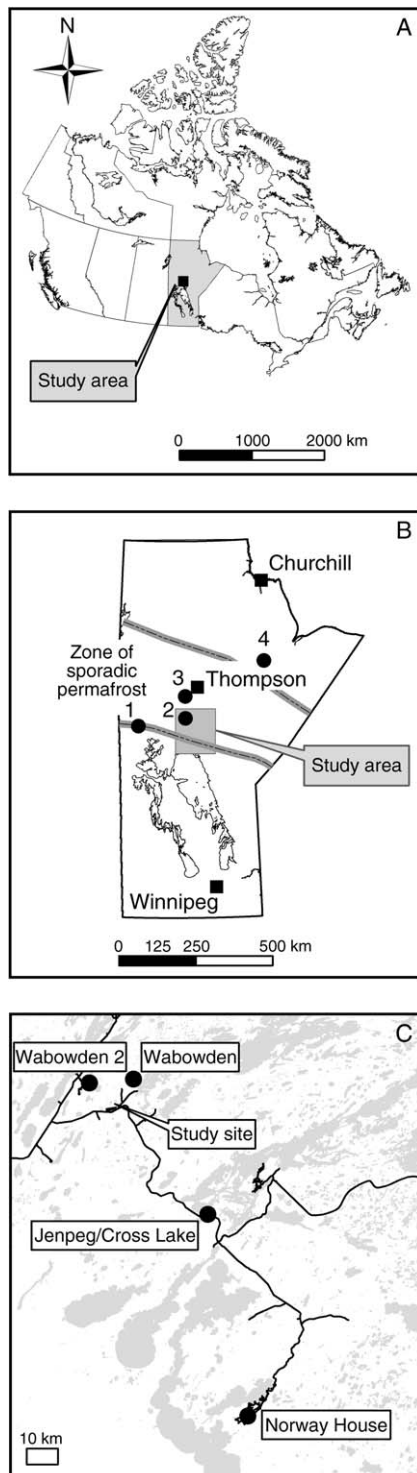


FIG. 1. Location of the study region. (A) Study landscape located in northern Manitoba, Canada. (B) The location of the study region in relation to the zone of sporadic permafrost (after Brown et al. 2001) and the four study zones used for seed rain collection as part of prior analyses of NPP, peat accumulation, and permafrost thaw. (C) The peatland landscape used for germination, growth, and survival experiments was located 11 km southwest of Wabowden, Manitoba.

significantly between years or stations. Annual records from the Norway House A and Jenpeg/Cross Lake stations indicated similarly small variation in annual temperatures ( $0.2^{\circ} \pm 0.4^{\circ}\text{C}$  to  $0.5^{\circ} \pm 0.4^{\circ}\text{C}$  and annual precipitation ( $421.2 \pm 20.3$  mm to  $494.7 \pm 36.2$  mm) (see Appendix B for complete climate data).

## METHODS

### Seed rain and dispersal

Seed rain was measured over six years (1997–2002) using traps located randomly on permafrost plateaus and neighboring collapse scars to quantify *P. mariana* fecundity on plateaus and dispersal into neighboring collapse scars. Stand densities on plateaus ranged from 5000–8000 trees per hectare in this region (Camill 1999a, Camill et al. 2001). Seed traps were  $0.17\text{ m}^2$  polypropylene boxes lined with fiberglass mesh. Traps were placed in three replicate plateau/scar sites (Fig. 1B) in each of four study zones for a total of 12 sites in the seed rain analysis. Each site contained 10 plateau traps and five scar traps for the first two years (1997–1998), but the number of collapse scar traps per site was increased to 15 from 1999 to 2002 for better spatial coverage and sampling intensity. The distance from each trap to the nearest plateau/collapse scar boundary was measured, representing, for collapse scar traps, distance to nearest seed source. The number of seeds collected from each trap was converted to influx (seeds per square meter per year).

### Germination, growth, and survival experiments

Seed germination and seedling survival and growth in thawed collapse scars were measured over 4–5 years following experimental additions of seeds and seedlings in a single peatland landscape (Fig. 1C). We located 15 accessible collapse scar sites separated by distances of 100 m to 5 km. We stratified each site into three water table depth categories, corresponding to the dominance of three *Sphagnum* species: wet ( $\sim 0$ –10 cm, *S. riparium*), medium ( $\sim 15$ –25 cm, *S. angustifolium*), and dry ( $\sim 25$ –50 cm, *S. fuscum*). Thirty plots were located in each of the wet, medium, and dry water table microhabitats for a total of 90 plots in the 15 collapse scar sites. We placed multiple plots in larger collapse scar sites to constrain random variability, but to avoid pseudoreplication, we averaged data from multiple plots per water table treatment to generate a single mean per site, and we handled site, water table categories, and plot treatments as random effects in statistical analysis (see *Methods: Statistical analyses*).

The fraction of *P. mariana* seeds germinating and surviving in collapse scars was assessed by experimental additions of seed collected from sources within 10 km of

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Weather stations at Wabowden, Jenpeg/Cross Lake, and Norway House A are also shown.

the study site (Pineland Nurseries, Hadashville, Manitoba, Canada). Viability tests indicated 96–98% germination for this seed lot. To assess granivory, we randomly established 30 pairs of 0.25-m<sup>2</sup> plots with actively growing moss surfaces in each of three water table categories (wet, medium, dry). Preexisting *P. mariana* seedlings were removed prior to the experiment by clipping at the moss surface to avoid disturbance. One plot in each pair was treated as a control; granivores were excluded from the second by an enclosure (100 cm high  $\times$  50 cm wide  $\times$  50 cm long) constructed from galvanized hardware cloth with 6.35-mm openings. The square base of the enclosure was buried in the peat to a depth of 50 cm for a final aboveground height of 50 cm, maintaining the natural structure of ericaceous shrubs and sedges.

We dispersed 100 seeds evenly across the moss surfaces in each of the 180 plots. Based on results of a 1998 pilot study assessing germination for spring and fall plantings, all plantings from 1999 to 2002 took place in June. Seedlings were censused in June and late August to monitor germination and survival. We replicated the entire experiment for four years by establishing 90 new control plots each June from 1999 to 2002. The granivore enclosure plot was not replicated each year because of the logistical difficulty of moving and reburying the enclosure without damage. Instead, we maintained the original location of each cage and added 100 seeds to the enclosure plots each June from 1999 to 2002. The cumulative fractions of seeds germinating and surviving in the enclosure plots were calculated by summing the number of surviving seedlings at each census and dividing by the cumulative number of seeds added to each enclosure by that date.

By June 2001, it became evident that the growing *Sphagnum* moss surface was burying and killing newly germinated *P. mariana* seedlings. To confirm this effect, we imposed a third treatment, establishing 30 sheared plots each in the medium and dry water depth treatments (this treatment was not repeated in wet sites because of extremely poor germination in general). In June 2001 and 2002, we removed the growing meristems ( $\sim$ 2 cm) of the *Sphagnum* mosses in sheared plots to prevent vertical moss growth. We sowed 100 seeds each into these sheared plots and monitored germination and survival through June 2003.

We also measured *P. mariana* seedling survival and growth over a five-year period by transplanting 2160 one-year-old, containerized nursery seedlings grown from seed collected within 80 km from the study site (Tolko Industries, The Pas, Manitoba and Pineland Nurseries, Hadashville, Manitoba, Canada). A randomized 3  $\times$  2  $\times$  2 split-split plot design was established by first stratifying plots across three levels of water table depth, then subdividing each plot into four subplots randomly assigned to all combinations of a two-level nutrient amendment treatment (fertilized/unfertilized) and a two-level above- and belowground vascular plant competition experiment (competition removed/competi-

tion present). Plots were 1.3  $\times$  1.3 m, allowing a 0.3-m buffer between 0.5  $\times$  0.5 m subplots. In all plots and subplots, the surface consisted of growing *Sphagnum* mosses. Plots were fertilized with slow-release 19-6-12 (NPK) pellets (Scotts Osmocote, Marysville, Ohio, USA) delivered to the rooting zone of each tree  $\sim$ 3–5 cm below the moss surface, providing 3.8 g N·m<sup>-2</sup>·yr<sup>-1</sup>, 1.2 g P·m<sup>-2</sup>·yr<sup>-1</sup>, and 2.4 g K·m<sup>-2</sup>·yr<sup>-1</sup>, which was similar to other studies using high-nutrient fertilizer treatments in Swedish bogs (Aerts et al. 1992) and Alaskan tundra (Chapin et al. 1995). Aboveground and belowground vascular plant competition was removed semiannually (June and August) by weeding and trenching to a depth of 50 cm. Relatively high bulk density of the peat allowed trenching with a serrated knife without disturbing the peat profile. Six sub-replicate trees were planted on uniform spacing in each subplot over a one-week period in early June 1998, and each tree was supplemented once with 0.5 L of distilled water to minimize transplant shock. Permanent wells for measuring water table depth were established by coring peat at points adjacent to each of the four subplots. We censused trees and measured water table depths for each subplot semiannually in mid-June and late August from June 1998–June 2003.

At each census we recorded mortality, cause of death (when possible), tree height (centimeters) from the moss surface to the highest living terminal bud, stem diameter (millimeters) at the moss surface, fraction of needles lost (10–50%, >50%), presence/absence of pathogens (spruce needle rust, *Chrysomyxa ledicola*), and the presence/absence of herbivory by snowshoe hares (*Lepus americanus*) or moose (*Alces alces andersoni*). Seedlings experienced an outbreak of *C. ledicola* midway through the experiment in years 3–4 (2000–2001). This pathogen has a dual-host life cycle (the other host is the common ericaceous shrub Labrador tea, *Rhododendron groenlandicum*) and causes chlorosis, necrosis, and shedding of *P. mariana* foliage (see Plate 1). At the end of the study, one tree in each subplot was harvested for the measurement of aboveground biomass (foliage + stem biomass), for a total of 30 trees from the 15 sites for each water table/fertilizer/competition treatment combination.

The use of containerized seedlings can affect experimental results and interpretation. Nitrogen was applied to all nursery seedlings at a conventional rate of 8–10 mg N·seedling<sup>-1</sup>·yr<sup>-1</sup> (Pineland Nurseries, Hadashville, Manitoba, Canada), so it is likely that seedlings experienced enhanced growth in the first year from nutrient retranslocation. For this reason, we omitted growth in year 1 from our statistical analyses, and the five-year duration of this study was sufficient to accommodate initial conditions and transplantation effects. The high-fertilizer treatment seedlings in this study received annual additions  $\sim$ 4 $\times$  this initial N loading, which proved sufficient to induce significant differences across fertilizer and competition combinations. One-year-old container-



ized seedlings were also larger than similar-aged seedlings germinating naturally in peatlands. We therefore interpreted transplanted seedling mortality based on treatment effects in the context of seedling size rather than age. For comparison, the germination experiment described provided a complimentary assessment of survival in *P. mariana* seedlings germinated from seed.

#### Statistical analyses

Seed influx data were analyzed by (1) testing for differences in mean influx between individual plateau and collapse scar traps and (2) determining the spatial location of seed rain limitation. For the first test, we assumed that seed dispersal limitation exists if unforest-ed collapse scars had significantly fewer seeds than forested permafrost plateaus. To determine if mean seed influx differed between plateaus (p) and collapse scars (s), we used a resampling procedure in S-Plus (Tibco Software, Palo Alto, California, USA) with 10 000 resamples to bootstrap confidence intervals on  $\mu_p - \mu_s$  and test  $H_0: \mu_p - \mu_s = 0$ ,  $H_a: \mu_p - \mu_s > 0$ . A significant difference was identified by a 95% confidence interval not bounding zero. For the second test, mean seed rain influx was plotted as a function of distance to the plateau-scar boundary, and the seed rain shadow was fitted as a second-order polynomial. We resampled plateau data 10 000 times to bootstrap 95% confidence intervals on the mean plateau seed rain influx and used distance from collapse scar boundary where the fitted influx curve fell below the lower confidence interval to determine areas with significantly fewer seeds than permafrost plateau traps. Bootstrap modeling approaches were used because seed trap data were spatially autocorrelated, violating assumptions of data independence for parametric approaches.

For analyses of germination and survival from seed, we used a mixed-effects model incorporating water table depth categories as fixed effects and site, water table depth categories, and plots as random effects. The random effects take into account the correlation of outcomes within sites, the variability of water table depths within moisture levels, and the correlation between plots chosen within the same site/moisture combinations. Mixed-effects models were fit using lme (from the nlme3 library in S-PLUS) and lmer (from the nlme4 package in R, available online).<sup>5</sup> For germination, the outcome of interest was the proportion of seeds that had germinated in each plot. Because there was no germination in the wet microsites 12 months after planting, analyses used only data from plots in the dry and medium water levels. We also used a logistic mixed-effects model, with time (months) and water table depth categories as fixed effects and site, water table depth categories, and plots as random effects, to estimate the probability of a plot having at least one seed germinate. The distributions of

the fraction of seeds germinating and surviving for the unmanipulated controls were strongly right-skewed, indicating that the median was a more appropriate measure of center. Thus, to determine the effects of moisture on the untreated plots, we first log-transformed (base 10) the proportions before using a linear mixed-effects model. We interpreted the results with respect to both the mean and median of the fraction of seeds germinating and surviving. We used Kolmogorov-Smirnoff tests to compare the distributions of the fraction of seeds germinating and surviving between the unmanipulated control and experimentally sheared plots.

Survival of transplanted seedlings was analyzed using a parametric, accelerated time model (Klein and Moeschberger 1997). Following Beckage and Clark (2003), we developed models of the following form:

$$f(\text{seedling lifetime}) = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{w} + \sigma\epsilon$$

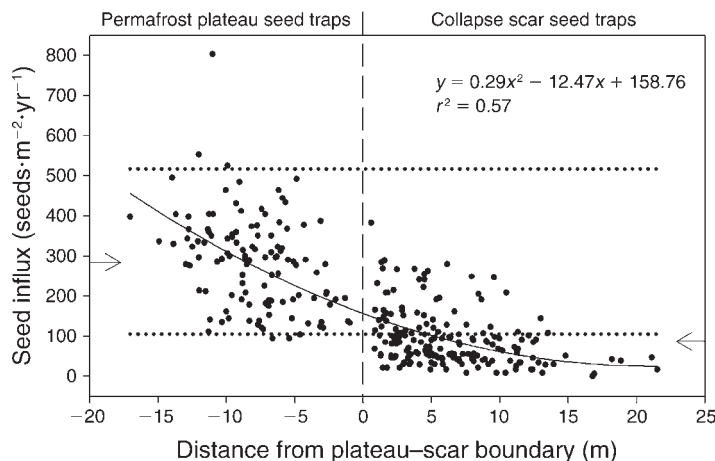
where  $f(\cdot)$  is a model-dependent identity or log link,  $\mathbf{X}$  is the matrix of fixed effects,  $\boldsymbol{\beta}$  is a vector of fixed-effects coefficients,  $\mathbf{Z}$  is the matrix for random effects,  $\mathbf{w}$  is the vector of random effects coefficients,  $\sigma$  is the scale parameter, and  $\epsilon$  is the model-dependent error distribution. Data were interval and right-censored because some seedlings died between censuses and others lived beyond the five-year duration of the study. Based on Akaike's Information Criterion (AIC), we chose a best-fit model with water table depth categories, competition, and fertilizer as fixed effects; site as a random effect with coefficient  $\mathbf{w}$  modeled with Gaussian error; and  $\epsilon$  modeled with Weibull errors and natural log link. We chose accelerated time models over nonparametric survival analyses, such as the Kaplan-Meier estimator, because they allow statistical inferences about fixed-effect treatments (Beckage and Clark 2003).

We analyzed growth of transplanted seedlings in a particular year using, for the seedlings still alive at that year, the change in height from the initial year. We ran a linear mixed-effects model with water table depth categories, competition, and fertilizer as the fixed effects and site, water table depth categories, and plots as random effects. To analyze the overall growth trend over the period of the study, we used only those trees that remained alive through the fifth year of the experiment. Because only 4% (31 out of 720) of seedlings in the wet microsites survived all five years (compared to 95.3% and 90.3% for the dry and medium sites, respectively), we analyzed them separately. We restricted our attention to growth trends for the years 2–5 to eliminate possible effects in year 1 caused by transplant shock or possible carryover effects on containerized seedlings.

To test for differences in aboveground biomass (foliage + stem) for the sample of seedlings harvested in year 5, we used linear mixed-effects model with water table depth categories, competition, and fertilizer as the fixed effects and site, water table depth categories, and plot as random effects.

<sup>5</sup> <http://www.r-project.org>

FIG. 2. Mean seed influx for traps located on permafrost plateaus and collapse scars as a function of distance from the plateau-collapse scar boundary. Each point represents the mean influx for one trap from 1997 to 2002. The vertical dashed line denotes the boundary between forested plateau and unforested collapse scar bog. Overall mean seed influx for plateaus and collapse scars is denoted by the arrows. The horizontal dotted lines represent the 95% confidence intervals on mean plateau seed influx. The overall relationship is fitted with a second-order polynomial.



## RESULTS

### Environmental covariates

Microsite water table depths differed among our three water table categories ( $P < 0.0001$ ), indicating that assignments based on the dominant species of *Sphagnum* moss were robust. Water table depths from 1998 to 2002 were  $7.1 \pm 0.6$  cm (mean  $\pm$  SE) for wet *S. riparium* plots,  $18.7 \pm 1.0$  cm for medium *S. angustifolium* lawns, and  $34.9 \pm 1.7$  cm for dry *S. fuscum* hummocks. For all water table categories, we observed an unanticipated trend of deeper water tables in subplots with vascular plant competition, which was significant for all years in medium plots ( $P = 0.005$ ) and for all years except 1998 in the dry plots ( $P = 0.02$  in 1999,  $P = 0.001$  for 2000–2002; see Appendix C).

### Seed rain

Collapse scar bogs had significantly lower mean seed influx ( $93.1 \text{ seeds} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ) than permafrost plateaus ( $284.5 \text{ seeds} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ), suggesting possible dispersal limitation (Fig. 2). Of 178 collapse scar traps, 123 (69%) had seed influx rates less than the lower 95% confidence interval for mean plateau seed influx (Fig. 2). The best-fit, second-order polynomial indicated that seed influx in collapse scars was significantly lower at distances  $> 5$  m from the plateau-collapse scar boundary (Fig. 2) for all six years ( $P < 0.007$ ) for all tests (see Appendix D for mean site seed influx by year and all test results).

### Germination and survival from seed

Two months following seeding in unmanipulated plots, mean (median) germination and survival were 19.6% (17%), 13.4% (8.5%), and 0.4% (0%) in dry, medium, and wet microsites (Fig. 3A). All pairwise differences between medians were significant ( $P < 0.001$ ). Beyond two months, 100% of germinants in wet microsites were dead. The fractions of seeds germinating and surviving in the dry and median plots were significantly different (Kolmogorov-Smirnov:  $P <$

0.001), with survival from 0 to 24 months higher in dry plots but becoming slightly greater in medium microsites from months 26 to 48 (relative to month 26 in the medium microsites) (Fig. 3A). The survival of germinants in unmanipulated sites was  $< 0.2\%$  across all water table levels after 48 months. Dead seedlings were typically found buried by mosses, suggesting that mortality was due to overtopping of seedlings by vertical growth of the moss surface, especially in the wet microsites. Mean annual *Sphagnum* growth rates in the

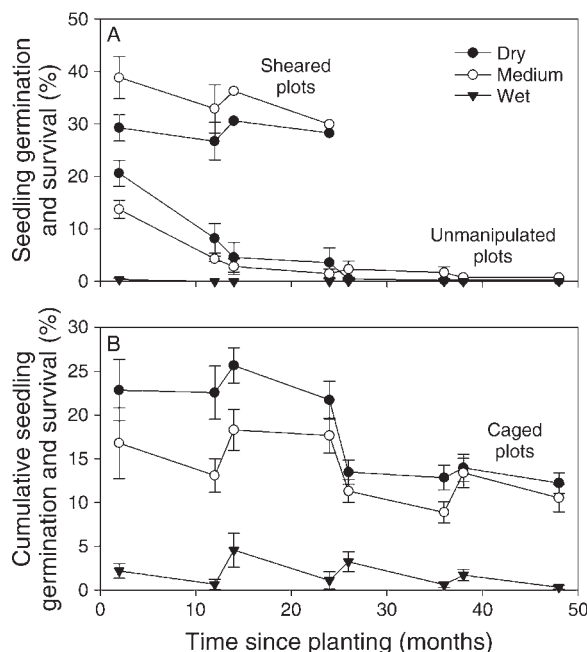


FIG. 3. Seed germination and survival as a function of water and moss growth. (A) Seedling germination and survival (mean  $\pm$  SE) over 48 months in unmanipulated control plots and plots where the growing meristems were removed (sheared plots). Data are reported for each level of the water table treatment. (B) Cumulative seedling germination and survival (number of seedlings per total number of seeds added) in granivore exclusion cages (mean  $\pm$  SE).

TABLE 1. Rank-ordered causes of *Picea mariana* seedling mortality by water table level in boreal peatlands in northern Manitoba, Canada.

Wet plots		Medium plots		Dry plots	
Factor	No. seedlings	Factor	No. seedlings	Factor	No. seedlings
Burial by <i>Sphagnum</i> mosses	411	dead foliage	50	loss of foliage	19
Drowning	147	loss of foliage	12	herbivory	8
Herbivory	57	herbivory	5	dead foliage	3
Herbivory followed by <i>Sphagnum</i> moss burial	30	unknown	3	unknown	2
Overtopped by <i>Carex</i> spp.	21	buried by <i>Sphagnum</i> mosses	1	moose trampling	1
Loss of foliage	18				
Fallen branch	2				
Total dead	686	total dead	71	total dead	33
5-yr survival (%)	4.7	5-yr survival (%)	90.1	5-yr survival (%)	95.4

study area averaged 6.55 cm (*S. riparium*), 3.46 cm (*S. angustifolium*), and 1.7 cm (*S. fuscum*) (Camill et al. 2001) compared to 1–2 cm for a subsample of killed seedlings.

The sheared moss treatment provided corroborating evidence for the strong effect of moss growth on the survival of *P. mariana* germinants (Fig. 3A). Seeds sown into sheared plots showed two-year germination and survival rates between 26.6% and 30.5% for dry microsites and 29.9% and 38.8% for medium microsites (Fig. 3A). Seed germination and survival in dry and medium sheared plots were significantly higher than in the dry and medium unmanipulated control plots for all months (Kolmogorov-Smirnov tests,  $P < 0.0001$ ).

The fraction of seeds germinating and surviving in the granivore enclosure plots over the full 48 months averaged 12.2–22.8% for dry microsites, 8.9–18.2% for medium microsites, and 0.3–4.5% for wet microsites (Fig. 3B). Survival percentages in dry and medium microsites were significantly different ( $P < 0.01$ ) for five of the eight periods. Survival was always lower in wet microsites ( $P < 0.0001$ ). As for sheared plots, the distributions of the fraction of seeds germinating and surviving in the enclosures was significantly greater in dry and medium microsites relative to unmanipulated control plots (Kolmogorov-Smirnov:  $P < 0.0001$ ).

#### *Survival of transplanted seedlings*

The rank-ordered causes of mortality differed among the three microhabitats (Table 1). In wet microsites, the majority of seedlings were killed by being overgrown by fast-growing *S. riparium* mosses or by intolerance to wet conditions (apparent drowning). Herbivory by snowshoe hares (*Lepus americanus*) in wet microsites contributed to 13% of the mortality. Death caused by *Carex* shading, loss of foliage, and fallen tree stems from adjacent permafrost plateaus were less common causes of mortality in wet microsites. The major cause of death in medium and dry microsites (67–87%) was loss of foliage caused by the spruce needle rust outbreak (and possibly additional unknown factors).

Water table depth had a significant effect on mortality over the five-year experiment, with trees grown in dry and medium microsites showing five-year survival rates of 95.4% and 90.1% compared to 4.7% for wet microsites (Fig. 4). By year 5, the difference between dry and medium microsites was not significant, but the difference between these microsites and wet microsites was highly significant ( $P < 0.0001$ ; see Appendix E for the survival model parameter estimates). The accelerated time model indicated that the time to death for seedlings grown in medium and wet microsites was significantly shorter than for seedlings in dry microsites ( $P < 0.0001$ ; see Appendix F for details).

Overall effects of competition and fertilizer on time to death were also significant, with the unpredicted result that competition increased survival and fertilizer reduced survival (Fig. 4,  $P < 0.0001$ ,  $P = 0.002$ , respectively; Appendix F). Competition and fertilizer treatment combinations showed water table-specific effects on survival. In dry microsites, survival time was greater for unfertilized seedlings, with those experiencing competition and no fertilizer surviving significantly longer than seedlings in either of the fertilizer treatments. In medium microsites, there was no significant difference between any of the competition/fertilizer combinations, although seedlings growing in the presence of competition had a higher survival time. In wet microsites, seedlings experiencing competition and no fertilizer survived significantly longer than seedlings with no competition.

#### *Growth of transplanted seedlings*

Seedling growth responded strongly to all combinations of water table depth, competition, and fertilization (Fig. 5). Height growth was greater in dry and medium water table plots compared to wet plots ( $P < 0.001$ ), while, after year 1, height growth in the medium microsites was greater than growth in the dry microsites ( $P = 0.01$ ). In dry and medium microsites, height growth differed between all competition/fertilizer combinations with treatments ranked (highest to lowest growth): (1)

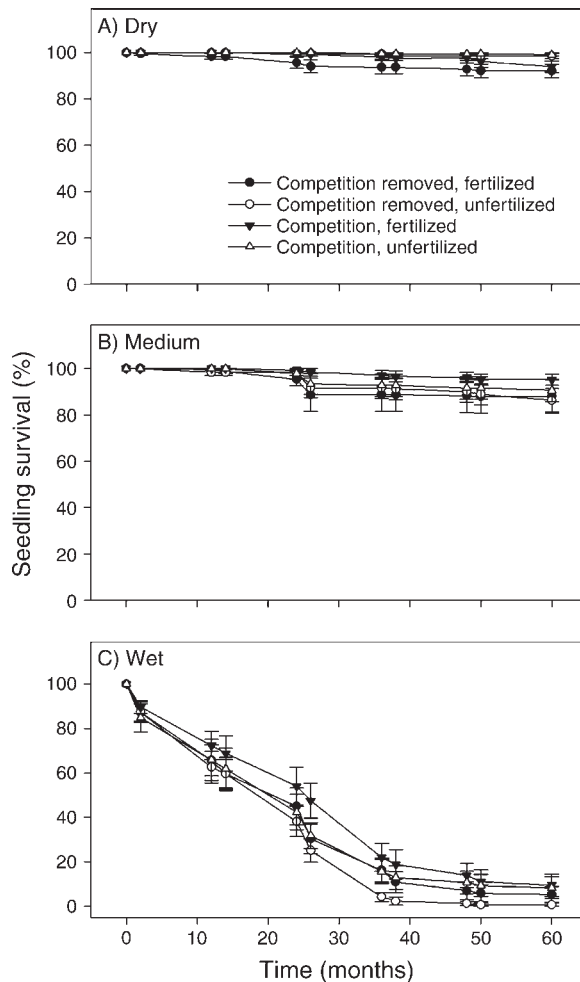


FIG. 4. Transplanted seedling survival (mean  $\pm$  SE) as a function of water table and competition-fertilizer treatments over 60 months: (A) dry microsites dominated by *Sphagnum fuscum* mosses; (B) medium microsites dominated by *S. angustifolium* mosses; (C) wet microsites dominated by *S. riparium* mosses.

fertilized/no competition, (2) fertilized/competition, (3) unfertilized/no competition, (4) unfertilized/competition (Fig. 5A, B;  $P < 0.0001$ ). Fertilized seedlings grew significantly faster than unfertilized seedlings, regardless of competition, suggesting nutrient limitation and the importance of belowground competition for nutrients (Fig. 5). However, aboveground competition for light was likely also important in dry and medium microsites, where ericaceous shrub density was greatest (Camill 1999a), because the removal of competition in fertilized plots made seedlings grow even faster (Fig. 5). Seedlings in unfertilized dry plots with competition showed decreased height growth over time as moss growth outpaced seedling growth (Fig. 5A). In wet microsites, seedling growth in unfertilized plots where competition was removed was negative in years 1–3, indicating that moss growth outpaced tree growth (Fig. 5C). For the 31 trees that survived all five years in the wet microsites, we

found no relationship between competition and fertilizer treatments and growth ( $P = 0.19$  and  $P = 0.51$ , respectively). Seedling diameter growth patterns were similar to height growth (*data not shown*).

The spruce needle rust (*C. ledicola*) outbreak in 2000–2001 infected between 86% and 99% of the seedlings in the dry and medium microsites (few seedlings survived in wet microsites by this date) (Fig. 6A). Infection rates did not differ among the four treatment combinations or the dry and medium microsites (Fig. 6A;  $P > 0.05$ ). Infections caused chlorosis and eventual shedding of foliage. Fertilized treatments showed recovery of needles (less needle loss and greater needle regrowth) by year 5 (Fig. 6B;  $P < 0.0001$ ).

Rankings of treatment combinations by foliage and stem biomass at year 5 (Fig. 6C, D) followed the same significant trend observed in height growth and resili-

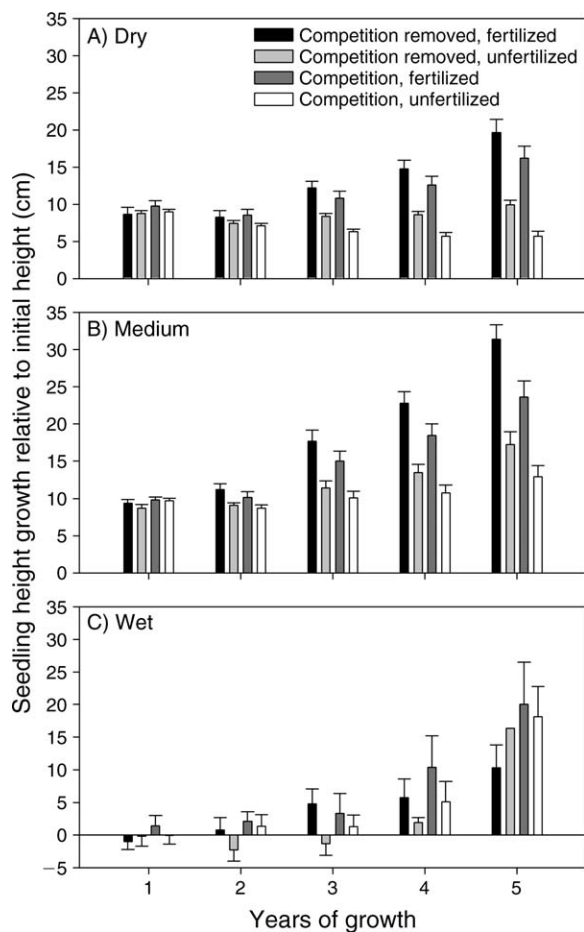


FIG. 5. Growth (mean  $\pm$  SE) of transplanted seedlings over 60 months. Growth represents the increase in seedling height relative to the initial height for each census period. Results are shown as a function of water table and competition-fertilizer treatments for (A) dry microsites dominated by *Sphagnum fuscum* mosses, (B) medium microsites dominated by *S. angustifolium* mosses, and (C) wet microsites dominated by *S. riparium* mosses.



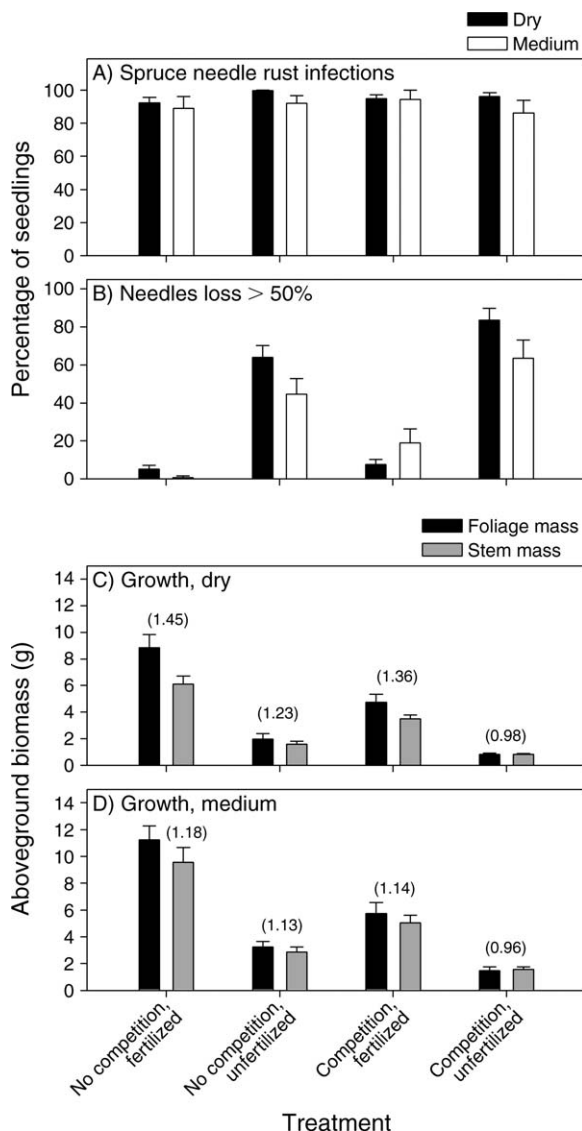


FIG. 6. Seedling infections by spruce needle rust (*Chrysomyxa ledicola*) and attendant responses in biomass as a function of water table and competition-fertilizer treatments. (A) Percentage of seedlings infected in each treatment combination during years 3–4 of the experiment (2000–2001). (B) Percentage of seedlings losing >50% of their needles by the fifth year of the experiment (2002). (C, D) Aboveground biomass (foliage and stem) for seedlings collected at the end of the five-year experiment for (C) dry and (D) medium microsites. In all panels, data are means  $\pm$  SE.

ience to needle loss (highest to lowest biomass): (1) fertilized/no competition, (2) fertilized/competition, (3) unfertilized/no competition, (4) unfertilized/competition (Fig. 5A, B;  $P < 0.0001$ ). The ratio of foliage-to-stem biomass was greatest in fertilized treatments, especially in dry microsites (Fig. 6C). Unfertilized seedlings with competition were the only ones to show final stem biomass greater than foliage biomass, indicating a larger fraction of lost foliage.

## DISCUSSION

Results from this study reveal several insights for understanding potential changes in *P. mariana* recruitment in boreal peatlands during climate warming. Comparison of early life history transitions indicates that failure of germination and survival on growing moss surfaces (across all water table depths) and reduced survival of seedlings in wetter microsites were primary constraints (Figs. 3 and 4). Factors controlling bryophyte mortality, which are poorly understood, likely play a significant role in *P. mariana* establishment. The unmanipulated germination plots were open to natural seed influx, which likely explained a random, slight increase in seedling germination and survival at 26 months in medium microsites (Fig. 3A). Although seed influx was significantly reduced in collapse scars (Fig. 2), two lines of evidence suggest that it was probably not limiting recruitment. First, seed influx in wet microhabitats within 5 m of the permafrost plateau margin was not significantly different than the permafrost plateau seed influx (Fig. 2), yet *P. mariana* recruitment was extremely poor in wet microsites (Figs. 3–5), suggesting that the combination of shallow water table and moss growth (Table 1) were stronger constraints than seed influx. Second, although seed influx was reduced significantly in drier collapse scar interiors, an average of 25 seeds  $\text{m}^{-2} \cdot \text{yr}^{-1}$  were able to disperse there (Fig. 2), suggesting the potential for germination and survival without the pressure of growing moss surfaces.

The biological and environmental factors mediating these life history transitions also differed in relative importance. In addition to the primary constraints of water table depth and growing moss surfaces (Figs. 3–5, Table 1), other significant, but less-important, factors controlling growth and survival included herbivory by snowshoe hares (*L. americanus*), nutrients and competition, and loss and death of foliage likely caused by the fungal pathogen (Figs. 4–6, Table 1). The least important factors were facilitation of survival by competing vegetation, herbivory and trampling by moose (*Alces alces andersoni*), overgrowth by *Carex*, and damage by falling trees at the thawing margin (Table 1). Results from the granivory treatment were inconclusive. We believe elevated survival in the granivore enclosures was not caused by decreased seed herbivory, of which we saw no evidence throughout the entire experiment. Rather, an unintended effect of drying out the moss surfaces occurred within the dry and medium enclosures (due to desiccation caused by the cage creating an air gap between the moss inside and outside the enclosure), which slowed the vertical growth of the *Sphagnum*.

Interactions among these factors tended to amplify more than relieve recruitment limitation:

1) In recently thawed plots near the plateau margin, high rates of herbivory by snowshoe hares (*L. americanus*) increased mortality beyond that caused by apparent drowning, in part because dramatic seedling height

reduction put them at a severe disadvantage relative to fast-growing *S. riparium* (Table 1; Appendix A).

2) Although vascular plant competition lowered nutrient availability and negatively impacted *P. mariana* growth directly (Fig. 5), reduced nutrient availability also diminished regrowth of foliage lost to fungal pathogens, thereby amplifying the decline in growth rate (Figs. 5 and 6). This could be why competition/fertilizer treatment differences in height growth became especially pronounced and significant beginning in year 3 (2000) following the pathogen outbreak (Fig. 5). Repeated outbreaks by *C. ledicola* in unfertilized peatlands have the potential to cause significant foliage loss and diminished growth over the life span of seedlings and mature trees.

3) Survival was greater in plots with vascular plant competition (Fig. 4; Appendix F). It is possible that this pattern represents facilitation, but potential mechanisms differ across microsites. In wet microsites, this effect could have arisen as from the higher density of vascular plants increasing transpiration and lowering the local water table (Appendix C; Jutras et al. 2006). In medium and dry microsites, survival was enhanced because the presence of competing shrubs decreased herbivory by snowshoe hares (11/13 seedlings killed by herbivory were in plots with vascular plant competition removed), possibly by making seedlings more difficult to find or access. This effect was not observed in wet microsites, where the number of seedlings killed by herbivory was roughly equal between plots with no competition (45) and competition (41), because ericaceous shrubs occur in low abundance in wet microsites (Camill 1999a).

Our work indicates the importance of considering a wider range of water table depths than previously considered when generalizing about microsite-specific differences in germination, growth, and survival. Results from this study indicated that initial germination and long-term growth and survival were all greatest in medium and dry microsites (Figs. 3 and 5). Previous work suggesting that sites most favorable for germination may be least favorable for growth (Ohlson and Zackrisson 1992, Groot and Adams 1994, St. Hilaire and Leopold 1995) did not examine sufficiently wet *Sphagnum* microhabitats to show that the overall inverse relationship between germination and survival becomes positive.

Because of the logistical constraints of our experimental approach, we chose to exclude factors known to be important to *P. mariana* establishment in boreal forests, such as fire and vegetative reproduction (Sirois and Payette 1991, Frelich and Reich 1995, Greene et al. 1999). Little is known about how fire frequency and severity relates to community changes through time and across space in boreal peatlands (Kuhry 1994, Turetsky et al. 2004). Paleoecological data from another peatland site in northern Manitoba indicate that fire is more severe in drier forested bogs than in wetter fens (P. Camill, unpublished data). However, at the scale of individual collapse scars, it is unknown whether differences in water



PLATE 1. A transplanted *Picea mariana* seedling showing chlorotic needles (light color) and loss of foliage on lower branches and the main stem caused by the fungal pathogen *Chrysomyxa ledicola*. Photo credit: P. Camill.

table depth are sufficient to cause differences in fire frequency or severity. Also, early life history transitions occur over periods of years to decades, periods much shorter than mean fire return intervals in peatlands similar to those in this study (624–2930 years; P. Camill, unpublished data), suggesting the need to consider recruitment in the absence of fire. Because the focus of our study was to understand recruitment in thawed peatlands, where reproduction by seed is the major mode of establishment, we also chose to omit vegetative reproduction by layering, which occurs primarily on permafrost plateaus and mature peatland forests.

We conclude that multiple, interacting factors will simultaneously promote and hinder *P. mariana* establishment in boreal peatlands during climate warming. Overall, the factors that inhibit *P. mariana* recruitment appear to be stronger than those facilitating establishment. Environmental gradients, including water table and attendant differences in moss growth, will clearly cause reduced *P. mariana* recruitment following permafrost thaw. However, biological factors operating at higher trophic levels, including herbivory and fungal pathogens, cause growth and survival to be significantly

reduced beyond that caused solely by environmental gradients. Vascular plant competition reduced *P. mariana* growth but increased survival. Generalizations about *P. mariana* recruitment that rely on few environmental gradients sensitive to climate change, such as water table, may therefore not fully capture the complexities of establishment during climate warming.

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#### LITERATURE CITED

- Aerts, R., B. Wallen, and N. Malmer. 1992. Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. *Journal of Ecology* 80: 131–140.
- Arnott, J. T. 1968. Germination and survival of black spruce on certain moss seedbeds. Canada Department of Forestry and Rural Development, Forestry Branch, Forest Research Laboratory, Quebec Region, Information Report Q-X-4.
- Beckage, B., and J. S. Clark. 2003. Seedling survival and growth of three forest tree species: the role of spatial heterogeneity. *Ecology* 84:1849–1861.
- Beilman, D. W. 2001. Plant community and diversity change due to localized permafrost dynamics in bogs of western Canada. *Canadian Journal of Botany* 79:983–993.
- Brown, J., O. J. Ferrians, Jr., J. A. Heginbottom, and E. S. Melnikov. 1998. Circum-Arctic map of permafrost and ground-ice conditions. Revised February 2001. National Snow and Ice Data Center/World Data Center for Glaciology. Digital media. Boulder, Colorado, USA.
- Camill, P. 1999a. Patterns of boreal permafrost peatland vegetation across environmental gradients sensitive to climate warming. *Canadian Journal of Botany* 77:721–733.
- Camill, P. 1999b. Peat accumulation and succession following permafrost thaw in the boreal peatlands of Manitoba, Canada. *Ecoscience* 6:592–602.
- Camill, P. 2005. Permafrost thaw accelerates in boreal peatlands during late-20th century climate warming. *Climatic Change* 68:135–152.
- Camill, P., J. A. Lynch, J. S. Clark, J. B. Adams, and B. Jordan. 2001. Changes in biomass, aboveground NPP, and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Canada. *Ecosystems* 4:461–478.
- Chapin, F. S., III, G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre. 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76:694–711.
- Choi, W. J., S. X. Chang, and J. S. Bhatti. 2007. Drainage affects tree growth and C and N dynamics in a minerotrophic peatland. *Ecology* 88:443–453.
- Clark, J. S., B. Beckage, P. Camill, B. Cleveland, J. Hille-RisLambers, J. Lichter, J. McLachlan, J. Mohan, and P. Wyckoff. 1999. Interpreting recruitment limitation in forests. *American Journal of Botany* 86:1–16.
- Environment Canada. 2004. National Climate Data and Information archive. ([http://climate.weatheroffice.ec.gc.ca/advanceSearch/searchHistoricDataStations\\_e.html](http://climate.weatheroffice.ec.gc.ca/advanceSearch/searchHistoricDataStations_e.html))
- Frelich, L. E., and P. B. Reich. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecological Monographs* 65:325–346.
- Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications* 1:182–195.
- Greene, D. F., J. C. Zasada, L. Sirois, D. Kneeshaw, H. Morin, I. Charron, and M. J. Simard. 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research* 29:824–839.
- Groot, A., and M. J. Adams. 1994. Direct seeding black spruce on peatlands: fifth year results. *Forestry Chronicle* 70:585–592.
- Hillman, G. R., and J. R. Roberts. 2006. Tamarack and black spruce growth on a boreal fen in central Alberta 9 years after drainage. *New Forests* 31:225–243.
- Islam, M. A., and S. E. Macdonald. 2004. Ecophysiological adaptations of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) seedlings to flooding. *Trees* 18:35–42.
- Jeglum, J. K. 1981. Black spruce seedling growth and nutrition on *Sphagnum* and feathermoss peats from a northern Ontario peatland. Canadian Forestry Service, Information Report O-X-326. Great Lakes Forest Research Centre, Sault Ste. Marie, Ontario, Canada.
- Jutras, S., H. Hökkä, J. Bégin, and A. P. Plamondon. 2006. Beneficial influence of plant neighbours on tree growth in drained forested peatlands: a case study. *Canadian Journal of Forest Research* 36:2341–2350.
- Klein, J. P., and M. L. Moeschberger. 1997. Survival analysis: techniques for censored and truncated data. Springer-Verlag, New York, New York, USA.
- Kuhry, P. 1994. The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada. *Journal of Ecology* 82:899–910.
- Lamhamedi, M. S., and P. Y. Bernier. 1994. Ecophysiology and field performance of black spruce (*Picea mariana*): a review. *Annales des Sciences Forestières* 51:529–551.
- Lieffers, V. J., and S. E. Macdonald. 1990. Growth and foliar nutrient status of black spruce and tamarack in relation to depth of water table in some Alberta peatlands. *Canadian Journal of Forest Research* 20:805–809.
- Lloyd, A. H., and C. L. Fastie. 2003. Recent changes in treeline forest distribution and structure in interior Alaska. *Ecoscience* 10:176–185.
- Macdonald, S. E., and V. J. Lieffers. 1990. Photosynthesis, water relations, and foliar nitrogen of *Picea mariana* and *Larix laricina* from drained and undrained peatlands. *Canadian Journal of Forest Research* 20:995–1000.
- Manitoba Energy and Mines. 1993. Bedrock geology compilation map of the Wekosko lake map sheet (NTS 63J), Manitoba. Surficial Geology Compilation Map Series, MAP CA2 MEM MRD bgcms NTS 63J, scale 1:250,000. Manitoba Science, Technology, Energy and Mines, Manitoba Geological Survey, Canada.
- Matile, G. L. D., and G. R. Keller. 2006. Surficial geology of the Wekosko lake map sheet (NTS 63J), Manitoba. Surficial Geology Compilation Map Series, SG-63J, scale 1:250,000. Manitoba Science, Technology, Energy and Mines, Manitoba Geological Survey, Canada.
- Ohlson, M., and O. Zackrisson. 1992. Tree establishment and microhabitat relationships in north Swedish peatlands. *Canadian Journal of Forest Research* 22:1869–1877.
- Payette, S. 1993. The range limit of boreal tree species in Québec-Labrador: an ecological and paleoecological interpretation. *Review of Palaeobotany and Palynology* 79:7–30.
- Pepin, S., A. P. Plamondon, and A. Britel. 2002. Water relations of black spruce trees on a peatland during wet and dry years. *Wetlands* 22:225–233.
- Pickett, S. T. A., and P. S. White, editors. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida, USA.

- Prévost, M., P. Belleau, and A. Plamondon. 1997. Substrate conditions in a treed peatland: responses to drainage. *Ecoscience* 4:543–554.
- Roe, E. 1949. *Sphagnum* moss retards black spruce regeneration. U.S. Department of Agriculture Forest Service Technical Note 321. Lake States Forest Experiment Station, St. Paul, Minnesota, USA.
- Roy, V., P. Y. Bernier, A. P. Plamondon, and J. C. Ruel. 1999. Effect of drainage and microtopography in forested wetlands on the microenvironment and growth of planted black spruce seedlings. *Canadian Journal of Forest Research* 29:563–574.
- Roy, V., A. P. Plamondon, and Y. P. Bernier. 2004. Persistence of early growth of planted *Picea mariana* seedlings following clear-cutting and drainage in Quebec wetlands. *Canadian Journal of Forest Research* 34:1157–1160.
- Roy, V., J. C. Ruel, and A. P. Plamondon. 2000. Establishment, growth and survival of natural regeneration after clearcutting and drainage on forested wetlands. *Forest Ecology and Management* 129:253–267.
- Shugart, H. H. 1984. *A theory of forest dynamics*. Springer-Verlag, New York, New York, USA.
- Sirois, L., and S. Payette. 1991. Reduced postfire tree regeneration along a boreal forest–forest-tundra transect in northern Quebec. *Ecology* 72:619–627.
- Stewart, J. D., and P. Y. Bernier. 1995. Gas exchange and water relations of 3 sizes of containerized *Picea mariana* seedlings subjected to atmospheric and edaphic water stress under controlled conditions. *Annales des Sciences Forestières* 52:1–9.
- St. Hilaire, L. R., and D. J. Leopold. 1995. Conifer seedling distribution in relation to microsite conditions in a central New York forested minerotrophic peatland. *Canadian Journal of Forest Research* 25:261–269.
- Sturm, M., C. Racine, and K. Tape. 2001. Increasing shrub abundance in the Arctic. *Nature* 411:546–547.
- Sundström, E., T. Magnusson, and B. Hånell. 2000. Nutrient conditions in drained peatlands along a north–south climatic gradient in Sweden. *Forest Ecology and Management* 126:149–161.
- Turetsky, M. R., B. D. Amiro, E. Bosch, and J. S. Bhatti. 2004. Historical burn area in western Canadian peatlands and its relationship to fire weather indices. *Global Biogeochemical Cycles* 18(4):GB4014.

#### APPENDIX A

The interface between frozen and unfrozen peat landforms in a boreal permafrost peatland landscape (*Ecological Archives* E091-034-A1).

#### APPENDIX B

Climate data for weather stations shown in Fig. 1C (*Ecological Archives* E091-034-A2).

#### APPENDIX C

Mean annual water table depths from 1998 to 2002 used as a treatment in the seedling growth and seedling survival experiments (*Ecological Archives* E091-034-A3).

#### APPENDIX D

Seed rain influx on permafrost plateaus and in collapse scars by year (*Ecological Archives* E091-034-A4).

#### APPENDIX E

Parameter estimates for the parametric seedling survival model (*Ecological Archives* E091-034-A5).

#### APPENDIX F

Treatment combinations for the parametric seedling survival functions rank ordered by the median time to death (months) (*Ecological Archives* E091-034-A6).