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Author(s)	Tsuyuzaki, Shiro; Narita, Kenji; Sawada, Yuki; Kushida, Keiji
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1 **The establishment patterns of tree seedlings are determined**
2 **immediately after wildfire in a black spruce (*Picea mariana*)**
3 **forest**

4 Shiro Tsuyuzaki · Kenji Narita · Yuki Sawada · Keiji Kushida

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7
8 S Tsuyuzaki (✉)

9 Graduate School of Environmental Earth Science, Hokkaido University, Sapporo 060-0810

10 Japan

11 e-mail: tsuyu@ees.hokudai.ac.jp

12
13 K Narita

14 Faculty of Education and Human Studies, Akita University, Akita 010-8502, Japan

15
16 Y Sawada

17 Faculty of Urban Management, Fukuyama City University, Fukuyama, 721-0964, Japan

18
19 K Kushida

20 College of Bioresource Science, Nihon University, Fujisawsa, 252-0880, Japan

21

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Abstract

Fire severity is predicted to increase in boreal regions due to global warming. We hypothesized that these extreme events will alter regeneration patterns of black spruce (*Picea mariana*). To test this hypothesis we monitored seed dispersal and seedling emergence, survival and growth for six years from 2005 to 2010 after the 2004 wildfire on Poker Flat, interior Alaska, using 96 1 m × 1 m plots. A total of 1,300 seedlings of black spruce and three broad-leaved deciduous trees (*Populus tremuloides*, *Betula papyrifera* and *Salix* spp.) were recorded. Black spruce seedlings colonized burned and unburned ground surfaces for the first two years after the wildfire and established on any topographical surface, while the broad-leaved trees emerged less in areas of lower elevation, slope gradient and canopy openness and only on burned surfaces. Vascular plant cover on the ground floor increased the seedling establishment of black spruce and broad-leaved trees, most likely because of seed trap effects. Black spruce grew faster on burned surface than on unburned surfaces. However, broad-leaved trees grew faster than black spruce on burned surfaces. Black spruce regenerates even after severe wildfire when the microtopography restricts the colonization of broad-leaved trees. The regeneration trajectories are determined soon after wildfire by a combination of seed limitation for black spruce and habitat preference for broad-leaved trees.

Keywords Boreal forest · Broad-leaved trees · Burned ground surface · Microtopography · Seed dispersal · Seedling recruitment and survival · Wildfire

1 Introduction

2 Climate projections suggest that extreme events will increase in frequency during this
3 century, and climate effects on arctic ecosystems, specifically, should take into account the
4 impact of extreme climatic events (Flannigan et al. 2000; Anisimov et al. 2007). One
5 outcome is that wildfires in interior Alaska are becoming larger and more severe due to
6 climate change (Kasischke et al. 2010, Turetsky et al. 2010). Black spruce (*Picea mariana*
7 (P. Mill.) B.S.P.) forests are altered to deciduous forests when wildfire is severe (Kasischke
8 et al. 2008, Barret et al. 2011), while severe fires favor less-flammable deciduous forests that
9 may work as a stabilizer of fire regime (Kelly et al. 2013). The changes in fire regime may
10 be an important driver of future ecosystems in the North American boreal region
11 (Kashischke and Turetsky 2006).

12 Black spruce forest is broadly distributed in boreal regions including interior Alaska
13 (Engelmark 1999). This species is a semi-serotinous tree that disperses most of its seeds
14 soon after wildfire (Johnstone et al. 2009). Black spruce seeds utilize remnant *Sphagnum*
15 moss cover for seedling establishment if wildfire incompletely burns the forest floor.
16 *Sphagnum* mosses reduce fuel consumption during wildfire more than feather mosses and
17 lichens by the high water-holding capacity, and remain patchily after wildfire (Shetler et al.
18 2008). Because the regeneration of black spruce forest is dependent on the severity of
19 wildfire (Chapin et al. 2006), severe wildfires, coupled with decreasing unburned ground
20 surfaces, may lead changes in regeneration patterns (Alexander et al. 2012; Hollingsworth et
21 al. 2013).

22 By contrast, long-distance seed-dispersed tree species, such as species in the genera
23 *Betula*, *Populus* and *Salix*, often immigrate soon after disturbances and may establish faster
24 and earlier than black spruce (Greene and Johnson 2000, Tsuyuzaki 2009). Differences in
25 seed dispersal and seedling emergence between species often determine forest regeneration
26 patterns, particularly immediately after disturbance (Norden, et al. 2009). In addition, the
27 durations and timings of seed dispersal determine forest recovery patterns after wildfire

1 (Mendoza et al. 2009), and large-scale disturbances often delay seed immigration,
2 particularly for short-distance seed-dispersed species (Fuller and del Moral 2003).

3 Preferable habitats for seedling survival and growth differ from habitats for seedling
4 emergence between species (Haruki and Tsuyuzaki 2001; Egawa and Tsuyuzaki 2011). On
5 mountainous regions, topographical characteristics, such as elevation, aspect and slope
6 gradient, regulate the pace and pattern of forest regeneration (Kondo and Tsuyuzaki 1999),
7 in particular, after wildfire (Hollingsworth et al. 2013). In this study, the regeneration of
8 black spruce seedlings was examined with respect to the habitat preferences, i.e., the
9 combinations of microtopography and fire severity. It is reported that the regeneration
10 patterns of black spruce should be altered due to competition when trees producing
11 long-distance dispersed seeds, such as birches and poplars, immigrate and colonize the
12 burned surfaces due to competition. Also, pioneer trees often have high allometric
13 plasticity for adapting variable stresses and disturbances (Akasaka and Tsuyuzaki 2005).
14 Therefore we compared the survival, growth and allometry of tree seedlings between burned
15 and unburned ground surfaces after a large-scale wildfire.

16 We present the first six years of monitoring regeneration after a large-scale wildfire; we
17 focused on the life-history stages between seeds and seedlings, because these stages are
18 critical for determining forest regeneration (Glenn-Lewin et al. 1992). We developed three
19 hypotheses. (1) The short duration of seed dispersal determines seedling distribution in
20 semi-serotinous black spruce, whereas seedling recruitment persists in trees producing
21 long-distance dispersed seeds. (2) The distribution of seedlings differs between black
22 spruce and broad-leaved trees because of seed dispersal and habitat preferences, although a
23 few black spruce trees established on un-preferable burned surfaces. (3) Black spruce does
24 not become dominant on completely-burned surfaces, because broad-leaved trees are
25 growing faster by utilizing higher morphological plasticity than black spruce.

26 27 **Materials and methods**

1 **Field research design**

2 Poker Flat, approximately 50 km north of Fairbanks in the interior of Alaska, USA, was
3 selected for monitoring tree regeneration (Tsuyuzaki et al. 2009). Annual precipitation
4 averages 297.4 mm. The maximum monthly mean air temperature was 23.0°C in June,
5 while the minimum was -25.0°C in January at Fairbanks for 30 years during 1971 and 2000
6 (ACRC 2007). There are two major types of upland taiga forests in the region: the forests
7 dominated by black spruce or white spruce (*Picea glauca*) (Van Cleve et al. 1986). Black
8 spruce forest is characterized by a predominance of black spruce on nutrient-poor habitats
9 with permafrost (Bonan and Shugart 1989). The ground surface is often covered with thick
10 moss represented by *Sphagnum* spp. Vegetation on Poker Flat is a typical black spruce
11 forest in the northern part of the Alaskan boreal forest above the boundary between the
12 continuous and discontinuous permafrost zones. Intensive wildfire coded as the Boundary
13 Fire occurred in this region, including Poker Flat, from June to August in 2004, and burned
14 at least 1,847 km² (French et al. 2011).

15 On a northwestern slope at Poker Flat, sixteen 10 m × 10 m plots were established in the
16 spring of 2005. After the fire severities were roughly estimated based on the
17 ground-surface burns and tree damages, these plots were established with various fire
18 severities. Based on vegetation on the unburned surfaces, the dominant species prior to the
19 wildfire were considered to be mosses represented by *Sphagnum* spp. and shrubs, such as
20 *Ledum groenlandicum*, *Vaccinium vitis-idaea*, *Vaccinium uliginosum*, *Betula nana* and
21 *Oxycoccus microcarpus* (Tsuyuzaki et al. 2013). The density of trees of which height was
22 more than 1.3 m before the wildfire was 2512/ha, and black spruce accounted for 97.3% of
23 the densities (Tsuyuzaki et al. 2009). Because the broad-leaved trees did not establish well
24 in the study sites, the seeds were mostly immigrated from the external environments. Two
25 seed traps (52 cm × 26 cm in surface area) were established on the ground surface of each
26 plot in the summer of 2005. The seeds were collected in each summer from 2006 to 2010.
27 Because the seeds of *Betula* consisted of two species, a tall tree, *Betula papyrifera*, and a

1 shrub, *Betula nana*, and could not be distinguished, the birch seeds were not examined.
2 The seeds of willows and poplars were passed through the traps. Therefore, the seeds were
3 counted only for black spruce. The seeds were recovered each summer, and were examined
4 for viability by a germination test in an incubator with a 25°C/15°C (12 hr/12 hr) cycle and
5 discontinuous light (16 hr/8 hr).

6 Within each plot, six 1 m × 1 m quadrats were randomly established. Location, aspect
7 and slope gradient were measured on each quadrat by differential GPS receivers (StarBox
8 SSII-51CPN-19, Amtechs, Tokyo) with an antenna (GPS-701, NovAtel, Calgary) and a laser
9 level meter (Topcon ET-2, Topcon, Tokyo). Subsequent monitoring was conducted
10 annually in summer from 2005 to 2010. The percentage cover of burned area was
11 measured in each quadrat, and the cover of each plant taxa was recorded in the herbaceous
12 layer less than 1.3 m in height. The boundary between burned and unburned surfaces was
13 clear, and unburned surface was defined as areas where no traces of burning remained. The
14 burned surfaces were covered with charred mosses, organic soil with various thicknesses, or
15 exposed mineral soils. Albedo was measured at approximately 1 m above the ground
16 surface with a radiometer (MR-22, Eko Instruments Co. Ltd., Tokyo). Photos toward the
17 canopy were taken each summer in each quadrat at 1.3 m above the ground surface by a
18 fish-eye lens. The photos were used to evaluate canopy openness with the freeware Gap
19 Light Analyzer version 2.0 (Frazer et al. 1999, Hardy et al. 2004).

20 On each seedling in the 96 quadrats, stem height and the lengths of long and short axes
21 of the crown were measured annually with a ruler. Canopy area was calculated from the
22 two lengths with the assumption of an oval shape. Although *Salix* spp. are short trees or
23 shrubs, these species often develop the seral stages of succession after wildfire in black
24 spruce forests (Chapin et al. 2006). Therefore, the seedlings of *Salix* spp. were also
25 censused as tree.

26 27 **Statistical analysis**

1 The relationship between burned area and topographical characteristics was investigated by a
2 generalized linear mixed-effects model (GLMM). The response variable was burned area
3 in each quadrat, and the explanatory variables were elevation, aspect and gradient. The plot
4 code was used as the random effect. The number of seeds captured by seed traps and the
5 number of seedlings that emerged in the laboratory experiment were analyzed with a GLMM
6 assuming a Poisson distribution. The eight explanatory variables were years after wildfire,
7 burned area, elevation, gradient, aspect, canopy openness, vascular plant cover, and moss
8 cover, with the random effect of plot code.

9 The determinants of seedling emergence were examined by a Hurdle model because of
10 excess zeros in the quadrats. The Hurdle model is constructed by combining two models:
11 the count and zero-Hurdle models. The zero-Hurdle model investigates the binomial
12 distribution of the presence and absence of seedlings in the quadrats, and the count model
13 estimates the number of seedlings after correcting for overdispersion of zero seedlings.
14 Two characteristics of seedling emergence were examined. First, the seedling emergence
15 of black spruce on burned and unburned surfaces was compared. Second, the seedling
16 emergence was compared between black spruce and broad-leaved tree taxa on burned
17 surfaces. The response variable was the number of emerged seedlings in each quadrat, and
18 the nine explanatory variables were tree taxa plus the eight variables used in the seed-trap
19 analysis, as described above. The best models were selected by Akaike's information
20 criterion (AIC) (Burnham and Anderson 2002).

21 Seedling survival was compared by GLMM with the assumption of binomial
22 distribution. Survivors were assigned a value of 0, and the dead seedlings were assigned a
23 value of 1. The explanatory variables were tree height plus the nine variables used for
24 seedling emergence analysis. The plot code was used for the random effect. Like
25 seedling emergence, seedling survival was compared for black spruce on burned and
26 unburned surface, and between tree taxa on burned surfaces. The explanatory variables of
27 environmental factors were the same as those in the seedling emergence analysis. The

1 determinants of stem height were also examined by GLMM under the assumption of gamma
2 distribution with the random effect of plot code. The explanatory variables were the same
3 as in the survival analysis. The stem height in the previous year was used for the offset
4 term after log-transformation ($\log(H_p + 1)$), where H_p indicates the stem height in the
5 previous year.

6 The allometry between stem height and canopy area was compared between burned and
7 unburned surfaces for black spruce and between species on burned surfaces. The slopes
8 and intercepts of the allometric relationships were compared using standardized major axis
9 estimation (SMA) (Warton et al. 2012). All statistical analyses were performed with the
10 statistical program R (version 2.12.2) (R Core Team, 2012).

11 12 **Results**

13 Seed dispersal

14 The number of black spruce seeds captured in the traps decreased with time (GLMM, $P <$
15 0.01) (Fig. 1). In addition, the viable seeds decreased annually during the surveyed period
16 ($P < 0.01$) (Fig. 1). The number of seeds captured in the traps was positively related to the
17 overstory vascular plant cover ($P < 0.01$), suggesting that the overstory plants was an
18 obstacle to disperse seeds and accumulated the seed on the ground surface.

19 20 Vegetation and environments

21 The burned area of the 96 quadrats averaged 66%, ranging from 0% to 100%. The total
22 cover of vascular plants ranged from 1% to 67% in 2005 and increased annually up to 115%
23 in 2010. Hurdle model indicated that the effects of herb cover on tree seedling
24 establishment increased with increasing time (Table 1). The species composition of mosses
25 was completely different between burned and unburned surfaces; the common mosses were
26 *Sphagnum subsecundum* Nees and *Hylocomium splendens* (Hedw.) B.S.G. on unburned
27 surfaces and *Ceratodon purpureus* (Hedw.) Brid. and *Polytrichum commune* Hedw. on

1 burned surfaces. The total cover of moss did not differ for the six years, i.e., a mean value
2 of 58% in 2005 and 59% in 2010, because the *Sphagnum* moss annually decreased in cover
3 on unburned surfaces due mostly by death but the non-*Sphagnum* moss on burned surfaces
4 increased.

5 The elevation ranged from 244 to 437 m on the 96 quadrats. The gradient and aspect
6 ranged between 3.4° and 29.8° and between 43.5° and 71.0° from north to west, respectively.
7 Therefore, a wide range of variation for each environmental variable was captured. The
8 canopy openness ranged from 57% to 94%, and did not differ greatly during the surveyed
9 periods except when the openness was increased by gaps created by fallen logs. The
10 burned area was not explained by any examined microtopographical variables, elevation,
11 aspect and gradient (GLMM, $P > 0.1$), showing that the burned area was not dependent on
12 the microtopography.

13 14 Seedling emergence

15 The seedlings consisted of four tree taxa, *Picea mariana*, *Populus tremuloides* Michx.
16 (trembling aspen), *Betula papyrifera* Marsh (paper birch) and *Salix* spp. (willows). During
17 the six surveyed years on the 96 quadrats, a total of 727 seedlings emerged on unburned
18 surfaces and 573 emerged on burned surfaces (Fig. 2). Seedling density on unburned
19 surfaces was an average of 2.5 times higher than that on burned surfaces. Seedling
20 emergence was high for all taxa in the first two years, 2005 and 2006, and then decreased
21 annually. Most of the seedlings on the unburned surfaces were black spruce, and only three
22 paper birch seedlings were established. Trembling aspen established all on burned surface
23 followed by black spruce and willows. The most of these seedlings did not emerge on thick
24 organic soil on burned surfaces, although the microhabitats were not recorded.

25 The seedling emergence of black spruce was higher on burned surfaces (Fig. 2), and
26 was synchronized with seed dispersal, i.e., the numbers decreased over the years (Fig. 1),
27 suggesting that the seedling emergence was restricted by both seed dispersal patterns and

1 habitat. Black spruce emerged more seedlings in areas where the vascular plant cover was
2 high. The other examined factors were not significantly related to the seedling emergence.
3 The seedling recruitments of broad-leaved trees on burned surfaces increased with canopy
4 openness, elevation, aspect, gradient, moss cover and vascular plant cover (Table 1),
5 showing that microtopography was related to the seedling emergence of broad-leaved trees
6 more than that of black spruce.

7 8 Seedling survival

9 Because seedling emergence began in 2005, i.e., one year after the wildfire that occurred in
10 the summer of 2004, survival and mortality were recorded annually from 2005 to 2010 (Fig.
11 2). When the survival of black spruce was compared between burned and unburned
12 surfaces, no factors, including stem height and years after fire, were related to survival
13 (GLMM, $P > 0.05$). The vascular plant cover remained in the model, although vascular
14 plant cover was not significantly related to survival. These results indicated that the
15 survival of black spruce was constant between years independent of microtopography.

16 Paper birch displayed greater survival than black spruce (GLMM, $P < 0.01$) and
17 Trembling aspen and willows did not differ in survival from black spruce. Canopy
18 openness increased survival ($P < 0.01$). The other examined factors were not related to
19 survival, although year, elevation, gradient, and moss cover remained in the model. Taller
20 trees exhibited lower mortalities ($P < 0.01$). The topographical factors, i.e., elevation, slope
21 gradient and aspect, were related to broad-leaved trees more than to black spruce, because
22 black spruce survived on unburned surfaces independent of any topographical factors.

23 24 Seedling growth

25 Height growth differed between black spruce and broad-leaved trees and between unburned
26 and burned surfaces (Fig. 3). Growth decreased with increasing elevation, slope gradient
27 and moss cover (GLMM, $P < 0.01$) (Table 2). The growth was significantly faster on

1 burned surfaces than on unburned surfaces ($P < 0.01$). However, broad-leaved trees
2 displayed much more rapid height growth than black spruce on burned surfaces ($P < 0.01$).

3 The allometric relationships between stem height and canopy area for black spruce
4 indicated that black spruce allocated more to canopy-area growth on burned surfaces than on
5 unburned surfaces (SMA, $P < 0.01$) (Fig. 4). The slopes of the allometric relationships for
6 burned surfaces did not differ between the four taxa ($P > 0.05$), while the intercepts differed
7 ($P < 0.01$), demonstrating that the allocation to canopy area on burned surfaces did not differ
8 between the taxa. In total, therefore, the stem forms, evaluated by allometry, of black
9 spruce differed between burned and unburned surfaces and the allocation patterns were
10 constant between the four tree taxa on burned surfaces.

11 12 **Discussion**

13 The seed dispersal and seedling emergence of black spruce decreased with time, and the
14 seedling emergence of broad-leaved trees decreased. Black spruce provides viable seeds
15 for several years after wildfire, by producing semi-serotinous cones (Bonan and Shugart
16 1989). Between Yukon and British Columbia, seedling recruitment of black spruce is
17 highest in the first 5 years after wildfires, while additional establishment is not observed
18 after 10 years (Johnstone et al. 2004). These results indicate that the seedling establishment
19 of black spruce is determined immediately after wildfire. In this sense, short-term seed
20 dispersal determined the regeneration. The available seeds of black spruce are reduced by
21 severe wildfire and separation from unburned seed sources (Johnstone et al. 2009). When
22 the seed dispersal is reduced by large and severe wildfire, therefore, regeneration should be
23 slowed or altered.

24 The seedling establishment of black spruce occurred on both burned and unburned
25 surfaces independent of microtopography, suggesting that safe sites for black spruce seedling
26 establishment were provided on both burned and unburned surfaces. We did not measure
27 the thickness of organic layer. However, burned organic soils of which depth is more than

1 2.5 cm decrease sharply conifer establishment (Johnstone and Chapin 2006), and the
2 thickness is positively and negatively related to the seedling densities of black spruce and of
3 broad-leaved trees, respectively (Johnstone and Kasischke 2005). Interactions among
4 disturbance regime and plant-soil-microbial feedbacks regulate soil organic layer thickness
5 (Johnstone et al. 2010a). The categorization of ground surfaces was likely to hide the
6 effects of thickness in this study.

7 The seedling emergence of broad-leaved trees is unlikely to be restricted by seed
8 limitation, because these species disperse seeds over long distances by wind and usually
9 produce enormous numbers of seeds (Boucher 2003, Tsuyuzaki 2009). The seedling
10 emergence of broad-leaved trees occurred only on burned surfaces and was further restricted
11 by microtopography. The unburned surfaces were covered with moss represented by
12 *Sphagnum* spp., which often restrict the establishment of broad-leaved trees due to low
13 nutrients, desiccation and/or reducing available water (Rydin 1985; Fritz et al. 2012).
14 Although the seedbeds of black spruce are limited by biotic filter on post-fire black spruce
15 forests in eastern Canada (Mallik et al. 2010), black spruce normally establishes on unburned
16 surfaces (Van Cleve et al. 1986; Bonan and Shugart 1989) and the forest expansion is related
17 to the dominance of *Sphagnum* spp. (Fenton et al. 2007).

18 Vascular plant cover increased seed capture and the resultant seedling emergence. The
19 long-distance seed dispersal patterns are determined by topography at large scale (Kondo
20 and Tsuyuzaki 1999), and wind-dispersed seeds are captured more by rough ground surfaces
21 and variation in microtopography at small scale (Egawa and Tsuyuzaki 2011). Therefore,
22 the removal of plant cover by severe wildfire slows the regeneration of black spruce through
23 the limitation of seed supply.

24 The mortalities of black spruce seedlings were constant during the surveyed period,
25 independent of stem height, habitat and year, while the mortality of broad-leaved tree
26 seedlings was decreased with increasing canopy openness and stem height. The mortality
27 of shade-tolerant trees, including *P. mariana*, does not vary with size in boreal forests while

1 the survival of shade-intolerant, sun trees increases with size (Luo and Chen 2011).
2 Mortality was probably reduced by the fast growth derived from canopy openness,
3 particularly for broad-leaved trees that are shade-intolerant pioneer species.

4 Broad-leaved trees grew faster than black spruce on burned surfaces, as expressed by
5 stem height and crown area. When trembling aspen and black spruce establish on remnant
6 organic layer after wildfire, the stem density and biomass are negatively and positively
7 related to the depth of organic layer, respectively (Shenoy et al. 2011). These results
8 suggest that habitat preferences greatly differ between black spruce and broad-leaved trees.
9 Area-based inorganic-nitrogen uptakes are higher on severely burned than lightly burned
10 sites for both black spruce and trembling aspen, but are much lower for black spruce than for
11 trembling aspen on the burned sites (Shenoy et al. 2013). The growth of black spruce
12 seedlings should be faster on burned surfaces but was slower than that of broad-leaved tree
13 species.

14 The allometry indicated that black spruce altered its stem forms between burned and
15 unburned surfaces. When open space is provided through disturbances, trees often allocate
16 more to canopy-area growth to obtain solar energy (Akasaka and Tsuyuzaki 2005; Egawa
17 and Tsuyuzaki 2011). Black spruce appeared to apply this strategy, although growth was
18 slower than that of broad-leaved trees, even on burned surfaces. After clearcutting or
19 wildfire in northern Ontario, broad-leaved trees, represented by trembling aspen, increased
20 their relative dominance, while needle-leaved trees, including black spruce, decreased
21 (Ilisson and Chen 2009). The stem forms on burned surfaces did not differ between species,
22 suggesting that their stem forms were optimized for establishment on burned surfaces.
23 However, deciduous trees outcompete with conifers on mineral soils after wildfires
24 (Johnstone and Chapin 2006). Competition and growth difference should be evident on
25 burned surfaces during the next stage of seedling development, i.e., saplings.

26 In conclusion, broad-leaved trees immigrate more when wildfire removes moss layer
27 completely. Since the establishment of black spruce seedlings is more in moist sites with

1 high density of prefire spruce, the regeneration of black spruce after wildfire takes place only
2 in moist sites with low fire severity (Johnstone et al. 2010b). The establishment sites for
3 broad-leaved trees are restricted by microtopographical characteristics. Thus, broad-leaved
4 trees do not always regenerate after severe wildfire, even though the cover of deciduous trees
5 increases at the regional scale (Alexander et al. 2012). Under similar edaphic conditions, a
6 single gradient related to time since disturbance is insufficient to account for the full
7 spectrum of ecosystem dynamics that occur in black spruce, highlighting the importance of
8 considering soil burn severity (Lecomte et al. 2006; Hollingsworth et al. 2013). The
9 establishment patterns of broad-leaved trees will be critical for predicting the regeneration
10 patterns after severe wildfire because black spruce regenerates everywhere when seeds are
11 supplied sufficiently.

12
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1 **Table 1** Seedling recruitment patterns analyzed by Hurdle models. The explanatory
 2 variables selected by stepwise AIC are shown. The differences between the broad-leaved
 3 trees were compared between *Populus tremuloides* and the other two tree taxa (*Betula*
 4 *papyrifera* and *Salix* spp.). *: significant at $P < 0.01$. -: not examined in the model, because
 5 of the low number of broad-leaved trees on burned surfaces.

Explanatory variable	<i>Picea mariana</i>		Broad-leaved tree species	
	Binomial	Poisson	Binomial	Poisson
Intercept	-1.850	-4.213	-1.878*	-4.928*
Factor examined				
Years after fire	-0.514*	-1.025	-0.636*	-0.742*
Burned surface	+0.017	+0.042	-	-
Canopy openness			-0.002	+0.028*
Elevation			+0.007*	+0.006*
Aspect			+0.004	+0.025*
Slope gradient	-0.085	+0.098	+0.095*	+0.128*
Moss cover			+0.002	+0.009*
Vascular plant cover	-0.005	+0.038*	+0.009	+0.008*
Species				
<i>Betula papyrifera</i>	-	-	-2.712*	+0.782*
<i>Salix</i> spp	-	-	-3.205*	+0.140

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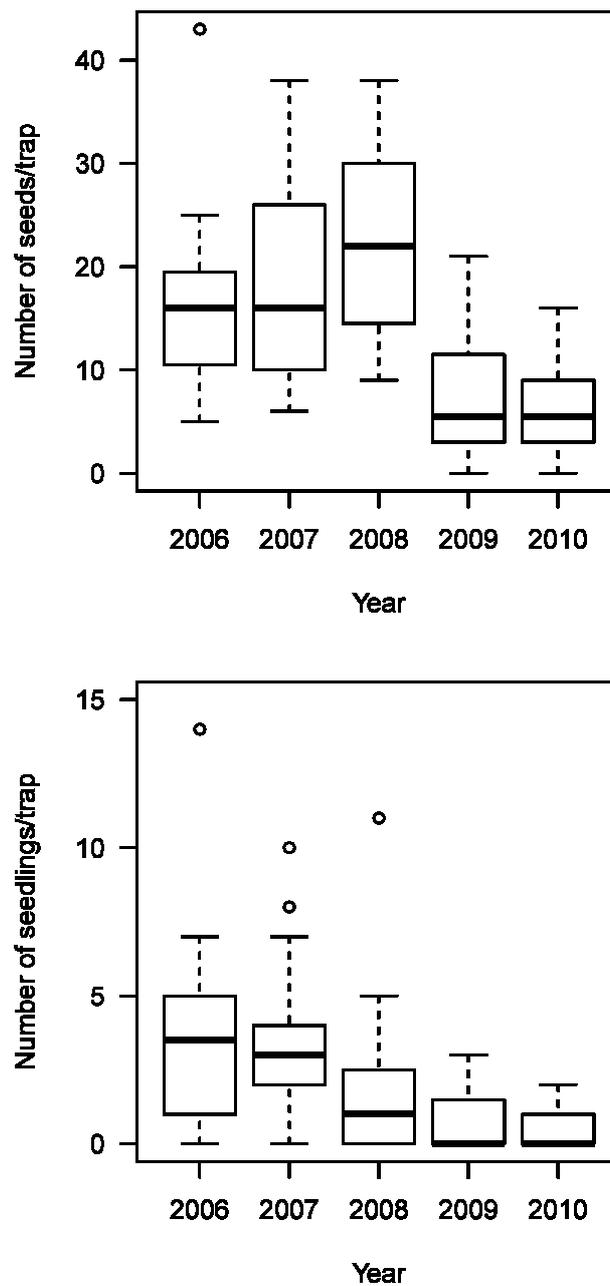
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1 **Table 2** Determinants of stem height, as examined by GLMM with the random effect of
 2 plot identification. *: significantly different from *P. mariana* to the other species, or burned
 3 to unburned surfaces, at $P < 0.01$. -: not examined.

Explanatory variable	All	<i>Picea mariana</i>	Burned surface
Intercept	-16.736	-1.473	-26.975
Years after wildfire	+0.198	-0.019	-0.730
Environmental factor			
Ground surface	+0.572	+0.004	-
Burned area (%)	+0.142 *	+0.035 *	+0.139 *
Canopy openness (%)	+0.006	-0.004	+0.055
Elevation (m)	-0.002	-0.002	-0.019
Aspect (°)	+0.100	-0.007	+0.093
Slope gradient (°)	-0.079	-0.030	+0.155
Moss cover (%)	+0.147 *	+0.021 *	+0.128 *
Vascular plant cover (%)	-0.034 *	-0.002	+0.005
Species			
<i>Populus tremuloides</i>	+2.868 *	-	+3.857 *
<i>Betula papyrifera</i>	+13.078 *	-	+14.088 *
<i>Salix</i> spp	+4.756 *	-	+5.607 *
Stem age	+2.061 *	+0.745 *	+4.103 *

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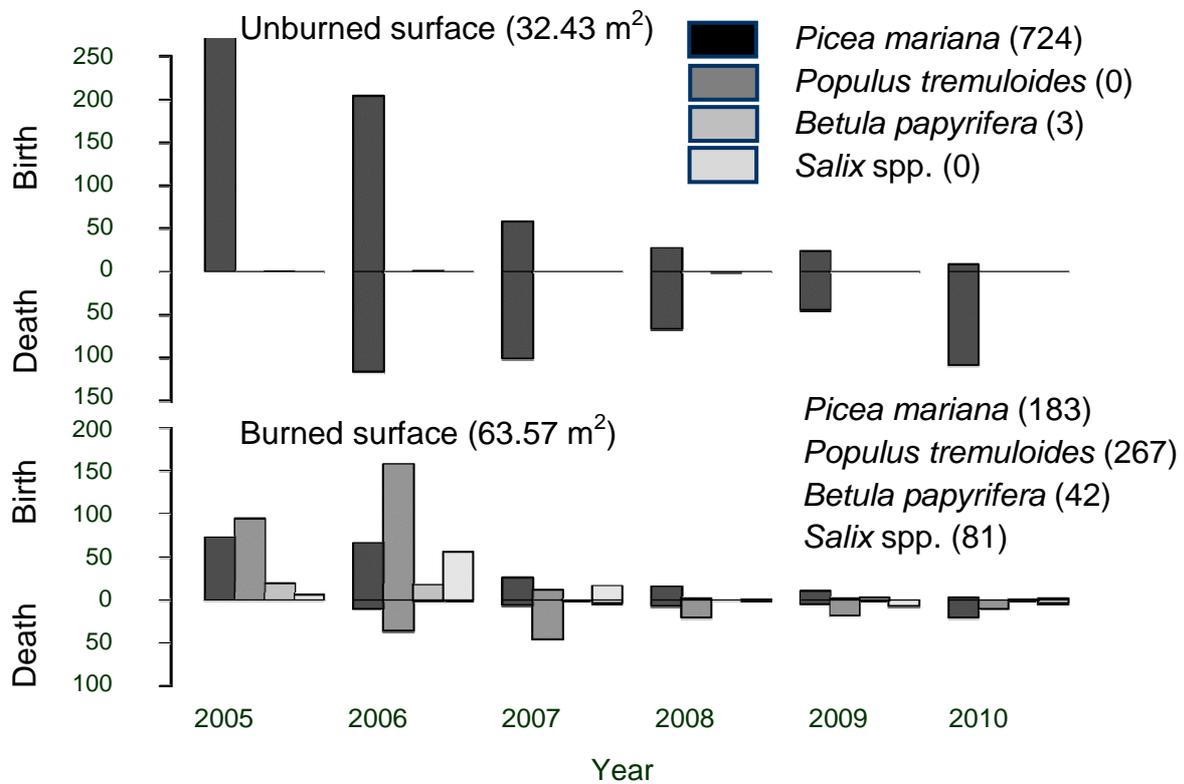
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2 **Fig. 1** The numbers of *Picea mariana* seeds captured by 32 52 cm × 26 cm seed traps (4.33
3 m² in total area) and the number of seedlings germinated in an incubator, shown by
4 box-whisker plots. Lower and upper edges of boxes: 25% and 75% quartiles, respectively.
5 Whiskers: range of maximum and minimum values (length of whiskers is 1.5 times the
6 interquartile range). Circles: outliers

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Fig. 2 The numbers of births (recruitment) and deaths (mortality) of seedlings from 2005 to 2010. No deaths occurred in 2005 because the seedlings began to emerge in 2005 after the wildfire in the summer of 2004. Total number of unburned and burned areas is indicated in parentheses to the right of the habitat names, respectively. The total number of seedlings is shown in parentheses to the right of the species names.

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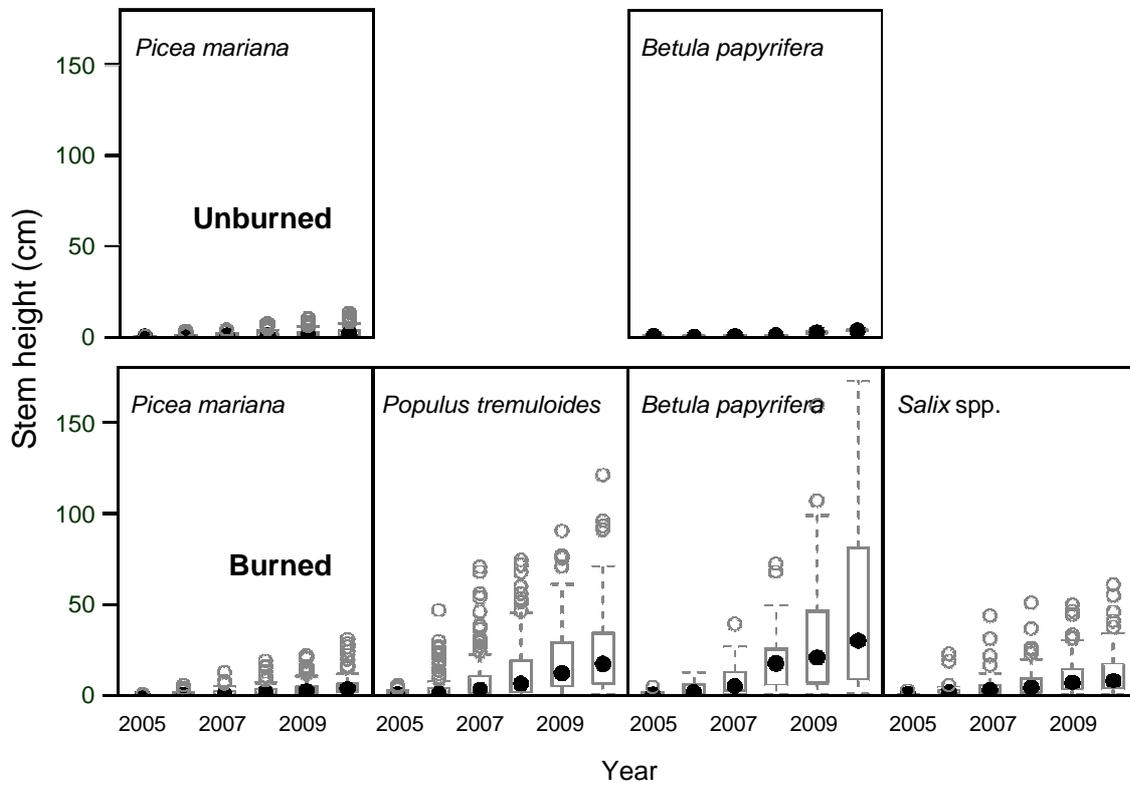
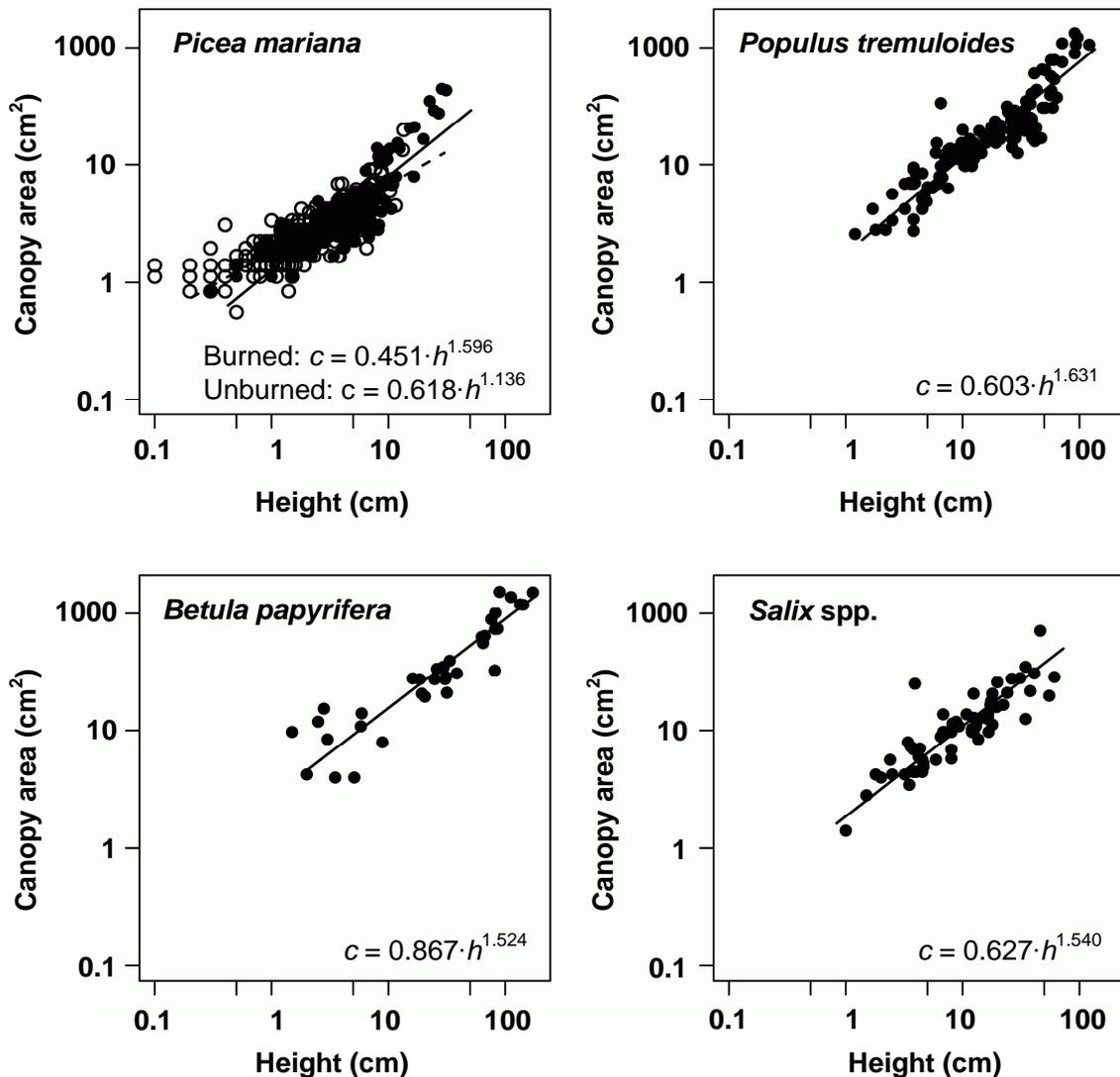


Fig. 3 Stem heights of the four tree species on unburned and burned surfaces. Whiskers: range of maximum and minimum values (length of whiskers is 1.5 times the interquartile range). Circles: outliers.

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5 **Fig. 4** Allometry between height and canopy area for the four tree species established on
 6 Poker Flat six years after the wildfire. Closed and open circles for *Picea mariana* indicate
 7 trees established on burned and unburned surfaces, respectively. Solid and interrupted lines
 8 indicate the allometric regression lines on burned and unburned surfaces (only for *P.*
 9 *mariana*), respectively. Allometric equations are also shown as follows: $c = a \cdot H^b$ (c :
 10 canopy area and h : stem height)

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