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The establishment patterns of tree seedlings are determined immediately after wildfire in a black spruce (*Picea mariana*) forest

Shiro Tsuyuzaki · Kenji Narita · Yuki Sawada · Keiji Kushida

S Tsuyuzaki (✉)
Graduate School of Environmental Earth Science, Hokkaido University, Sapporo 060-0810 Japan
e-mail: tsuyu@ees.hokudai.ac.jp

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

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

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

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

Introduction

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

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

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

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

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

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

Materials and methods

Field research design

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

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

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

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

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

Statistical analysis

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

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

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

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

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

Results

Seed dispersal

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

Vegetation and environments

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

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

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

Seedling emergence

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

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

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

Seedling survival

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

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

Seedling growth

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

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

	Picea mariana		Broad-leaved tree species	
Explanatory variable	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				
Betula papyrifera	-	-	-2.712*	+0.782*
Salix spp	-	-	-3.205*	+0.140

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

Explanatory variable	All	*Picea mariana*	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 (^{o})	+0.100	-0.007	+0.093
Slope gradient (^{o})	-0.079	-0.030	+0.155
Moss cover (%)	+0.147 *	+0.021 *	+0.128 *
Vascular plant cover (%)	-0.034 *	-0.002	+0.005
Species			
Populus tremuloides	+2.868 *	-	+3.857 *
Betula papyrifera	+13.078 *	-	+14.088 *
Salix spp	+4.756 *	-	+5.607 *
Stem age	+2.061 *	+0.745 *	+4.103 *

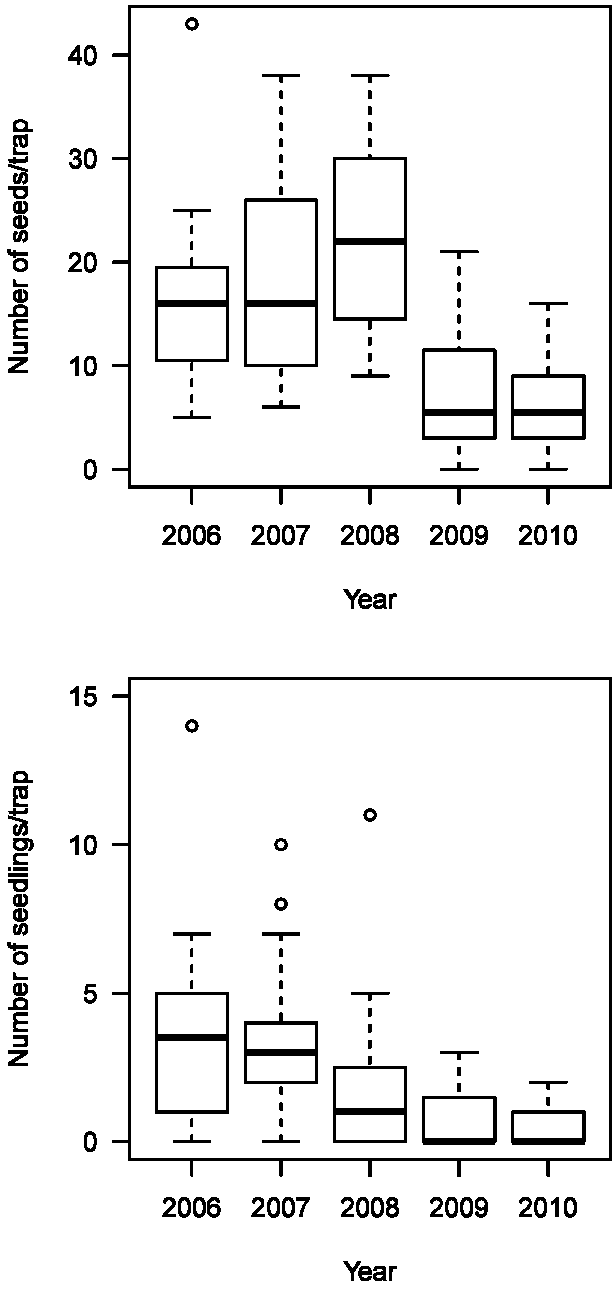

Fig. 1 The numbers of *Picea mariana* seeds captured by 32 52 cm × 26 cm seed traps (4.33 m^2 in total area) and the number of seedlings germinated in an incubator, shown by box-whisker plots. Lower and upper edges of boxes: 25% and 75% quartiles, respectively. Whiskers: range of maximum and minimum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

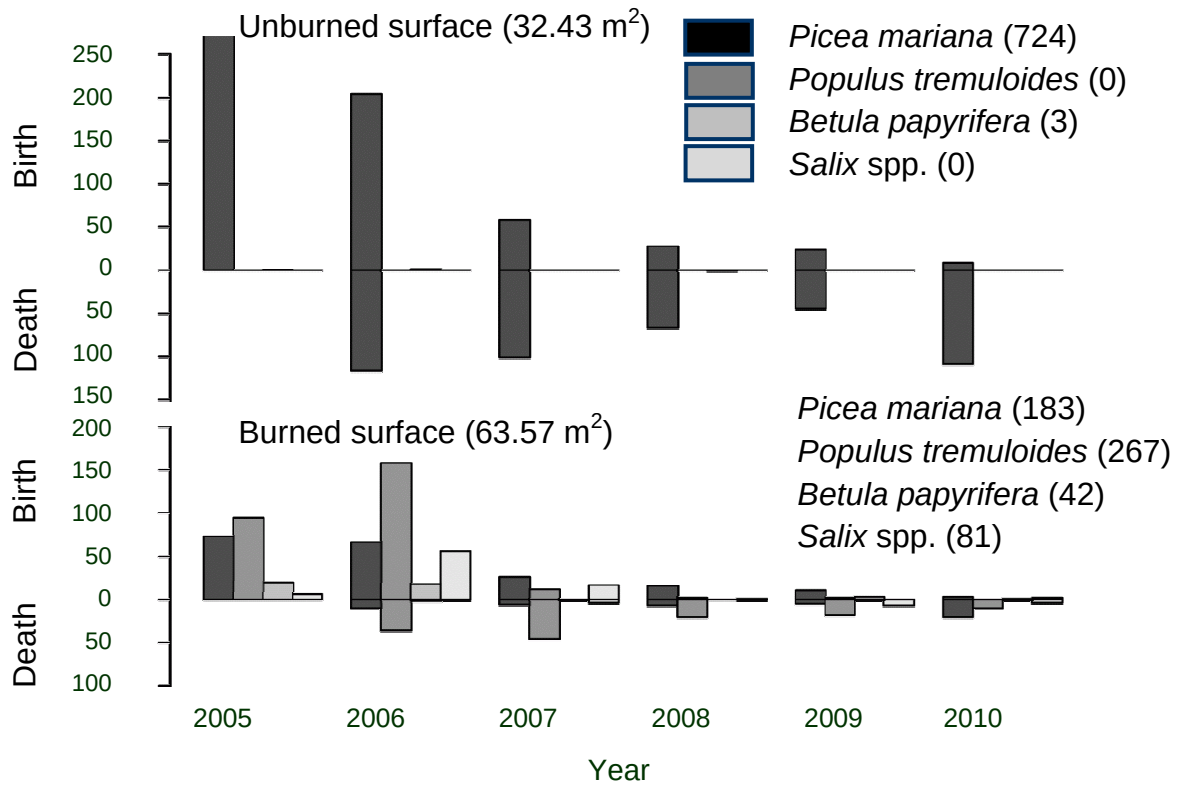

Fig. 2 The numbers of births (recruitment) and deaths (mortality) of seedlings from 2005 to 2010. No deaths occurred in 2005 because the seedlings began to emerge in 2005 after the wildfire in the summer of 2004. Total number of unburned and burned areas is indicated in parentheses to the right of the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

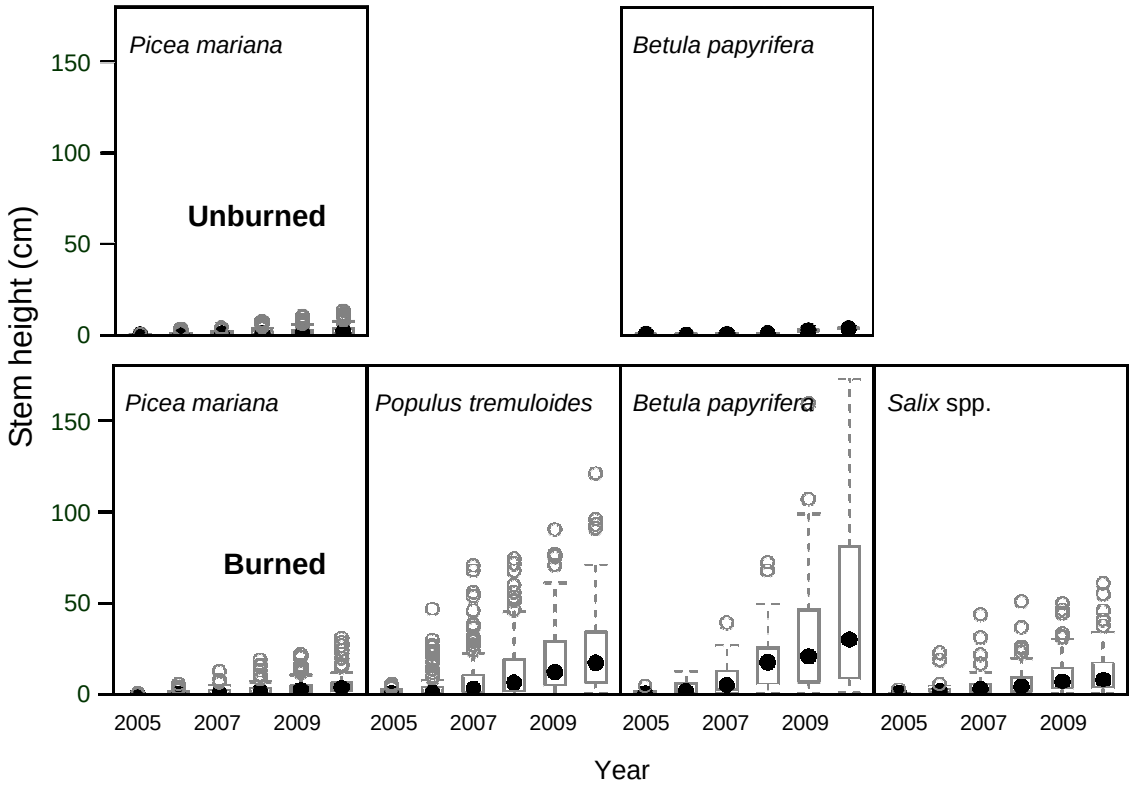

Fig. 3 Stem heights of the four tree species on unburned and burned surfaces. Whiskers: range of maximum and minimum values (length of whiskers is 1.5 times the interquartile range). Circles: outliers.

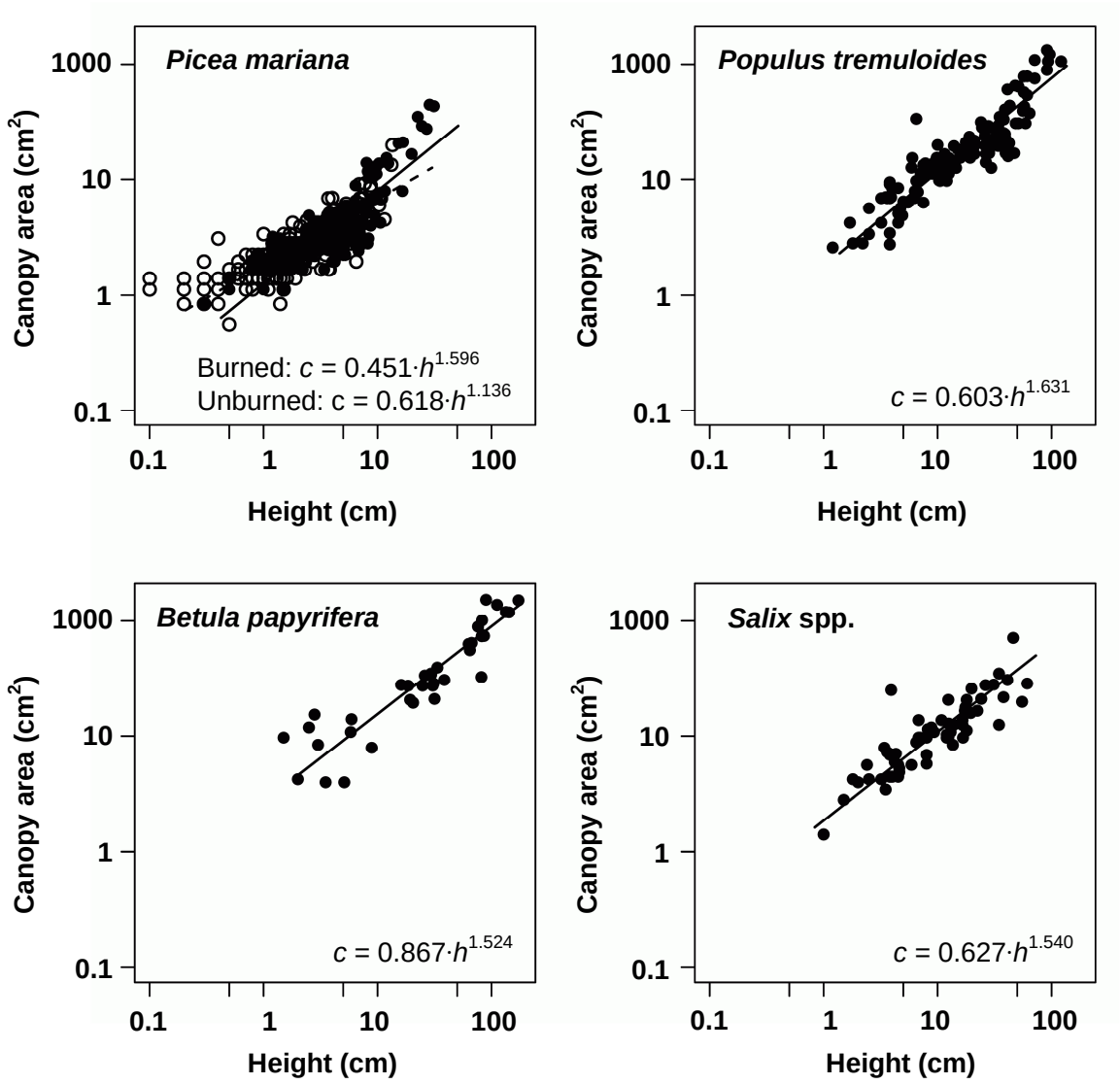

Fig. 4 Allometry between height and canopy area for the four tree species established on Poker Flat six years after the wildfire. Closed and open circles for *Picea mariana* indicate trees established on burned and unburned surfaces, respectively. Solid and interrupted lines indicate the allometric regression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

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