

Severe forest fire in Alaska and global environmental changes Vegetation recovery for five years after large-scaled wildfire in Alaska

Team Ecology (P4)

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1. INTRODUCTION

Wildfires frequently occurs in *Picea mariana* forests, due mostly to lightning (Engelmark 1999). Crown fire, incompletely burned the ground-surface cover, is ordinal and promotes seedling regeneration (Bonan & Shugart 1989). *P. mariana* develops aerial seedbank, and disperses seeds mostly after the fires. This strategy adapts to establish on wet, nutrient-poor, unburned ground surface (van Cleve et al. 1986). In discontinuous permafrost regions, the scenarios of succession differ between north and south slopes, due mostly to the presence of permafrost on the north slopes, i.e., *P. mariana* forests develop more on the north slopes. Wildfire is likely

to become larger and more intense, i.e., to burn out the ground surface (Dale et al. 2001). To confirm the regeneration patterns, annual monitoring has been conducted on the north slope of Poker Flat, interior Alaska. We have revealed that the vegetation composition on the forest floor is a determinant on seedling emergence of tree species, and thus the vegetation recovery after wildfires should be clarified to predict forest regeneration.

We have researched the followings from 2005 to 2009 after the 2004 wildfire that was large and severe: 1) Detecting plant community recovery patterns with different fire severities, and 2) Characterizing regeneration dynamics after wildfire.

2. STUDY AREA AND METHODS

A typical *P. mariana* forest on the north slope of Poker Flat, ca. 50 km north of Fairbanks, interior Alaska, is selected for monitoring, because of large and severe fire, slope direction, and accessibility. Wildfires (Boundary Fire) stroke this region in the summer of 2004. The field surveys were conducted in May (spring) and July-August (summer) in every year from 2005 to 2007 and summer 2008 and 2009. The total censuses were 8 times.

At the first census, we established 16 10 m × 10 m plots. Based on fire severities, plots were assigned as less-(L), moderately-(M), and heavily-(H) burned. Stem survival and moss cover characterized L. H is burned totally, i.e., all stems were killed and > 80% ground surface was burned out. M was situated between L and H, i.e., most trees were dead but unburned plant cover remained somehow on the ground surface. In each plot, we measured height and diameter at breast height (DBH) for all alive and dead stems ≥ 1.3 m in height. Fallen trees were included on the measurement to reconstruct pre-fire forest structure. Outside the plots, 22 tree cores were sampled by a borer or clippers in summer 2005. The locations, aspects and slope gradients were determined by a portable GPS and lazar compass.

Two seed traps (52 cm × 26 cm in surface area) were set up on each plot in summer 2005. Seeds were collected at every census. Seed germination test was performed in an incubator [15°C/25°C (12

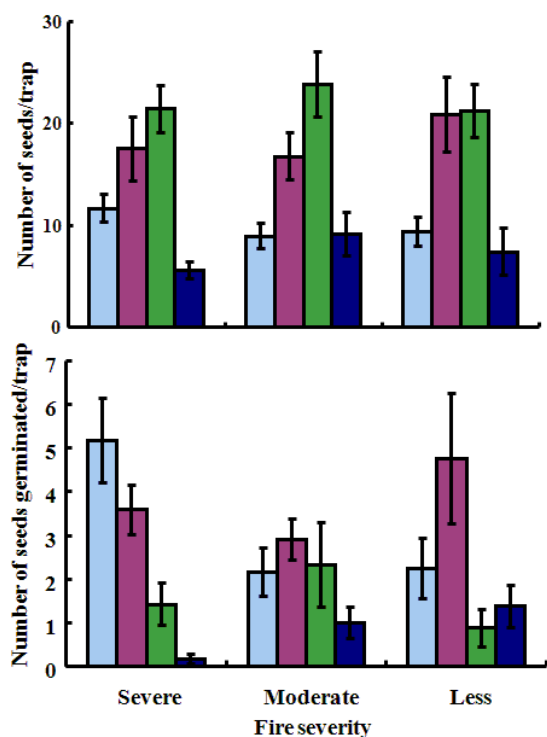


Figure 1. *Picea mariana* seeds captured by seed traps, and germinated in lab-experiment. Mean is shown with SE. Duration: ■ = 2005-2006, ■ = 2006-2007, ■ = 2007-2008, and ■ = 2008-2009. In 2005 and 2006, the data were compiled with spring and summer. Seed density was not different between three fire severities (Tukey's test), and the number of germinated seeds was different between years, and is not significantly different between severities.

Table 1. Yearly changes in cover on dominant plant taxa from 2005 to 2008. On each life form, the first three leading species, except for shrubs that showed five because of high frequencies, are shown, when the number of species is more than five. Each numeral shows mean with standard deviation. +: less than 0.1%. Occurrence frequency (%) is shown in parentheses.

Species	2005	2006	2007	2008	2009	Total mean
Herbs and ferns (13 taxa)						
<i>Carex bigelowii</i>	1.7 (49)	1.8 (49)	2.5 (50)	2.9 (51)	3.0 (51)	2.4 (50)
<i>Calamagrostis canadensis</i>	0.9 (41)	1.4 (39)	6.2 (48)	7.2 (48)	7.7 (50)	4.7 (45)
<i>Epilobium angustifolium</i>	1.9 (30)	3.0 (33)	2.6 (38)	2.7 (38)	1.9 (39)	2.4 (36)
Shrubs (12 taxa)						
<i>Ledum groenlandicum</i>	4.3 (91)	5.7 (89)	8.1 (89)	9.4 (90)	11.3 (90)	7.8 (90)
<i>Vaccinium vitis-idaea</i>	1.6 (72)	2.2 (70)	4.4 (71)	5.0 (74)	5.5 (75)	3.8 (72)
<i>Vaccinium uliginosum</i>	2.4 (70)	3.0 (70)	3.8 (71)	4.3 (70)	4.8 (69)	3.6 (70)
<i>Betula nana</i>	1.6 (51)	2.5 (54)	4.7 (54)	6.1 (55)	7.0 (56)	4.4 (54)
<i>Oxycoccus microcarpus</i>	0.3 (51)	0.4 (50)	0.8 (51)	0.8 (51)	0.9(51)	0.6 (51)
Trees (4 taxa)						
<i>Picea mariana</i>	0.6 (64)	0.6 (70)	0.7 (68)	0.9 (65)	0.9 (65)	0.7 (66)
<i>Betula neoalaskana</i>	+ (12)	0.1 (20)	0.2 (19)	0.5 (22)	0.7 (21)	0.3 (19)
<i>Populus tremuloides</i>	+ (8)	0.6 (16)	0.5 (19)	0.8 (19)	1.0 (19)	0.6 (16)
Mosses/lichens (13 taxa)						
<i>Polystichum formosum</i>	0.9 (56)	1.0 (46)	3.2 (65)	4.7 (65)	6.1 (69)	3.2 (60)
<i>Sphagnum subsecundum</i>	29.3 (62)	29.0 (62)	26.3 (55)	21.9 (48)	21.1 (48)	25.5 (55)
<i>Ceratodon purpureus</i>	1.9 (30)	5.2 (42)	13.4 (71)	15.3 (75)	14.7(80)	10.1 (60)
Total number of species	39	40	40	41	40	42
Plot cover (%)	47.6	56.4	75.4	80.3	82.8	68.5
Species richness	9.8	10.1	10.9	11.1	11.3	10.7
Species diversity	1.24	1.35	1.47	1.56	1.61	1.44
Evenness	0.56	0.60	0.63	0.66	0.68	0.63

hr/12 hr)] with continuous or 12-hr light.

In each plot, 6 1 m × 1 m quadrats were randomly set up. Vegetation was annually monitored in all the quadrats. The environments were monitored in five of six quadrats, as needed. For examples, canopy openness was estimated in summer 2005 and 2008 (Frazer et al. 1999), albedo was annually measured (Tsuyuzaki et al. 2009), and duff thickness was estimated by a steel stake. The cover of each species was recorded on burned (hereafter, i.e., BS) and unburned (US) ground surfaces, separately, at summer census. When a tree seedling was observed in the quadrats, the seedling was marked by a numbered flag, and was recorded on height, crown area and location. In summer 2007, > 20 seedlings for *P. mariana*, *Populus tremuloides* and *Betula neoalaskana* were excavated to investigate allometry on stem height and biomass. In summer 2008, twenty litterbags that contained dead *Sphagnum* was established on the slope to estimate litter decomposition rates.

Of 96 quadrats, 80 quadrats were used for investigating relationships between forest-floor vegetation and the environmental factors, by non-metric multi-dimensional scaling (NMDS). Based on vegetation and environmental factors (burned area, canopy openness, elevation, slope gradient, aspect, and years after wildfire), NMDS extracted significant environmental factors and revegetation patterns.

3. RESULTS

3.1 Fire severities

The altitude ranged from 244 m to 437 m, and the slopes faced 7.0°-43.5° from N to W with 4.8°-19.0° slope angles. By the 2004 wildfire 81% of stems were burned and dead. The maximum tree height was 13.0 m. The age of tree cores was less than 175.

The canopy openness ranged from 57% to 95% in 2005 and from 45% to 82% in 2008. The plant cover on the forest floor ranged from 0% to 100%, indicating that the floor was patchily burned with various scales and thus was suitable for this study. Albedo is positively correlated with total plant cover in quadrats (refer to Kodama's report and Tsuyuzaki et al. 2009). Plant cover on the forest floor decreased down to 40% by the fire even on L. Duff thickness ranged from 3 cm to 73 cm.

3.2 Seed dispersal and germination

In summer 2007, cones were counted for 12 *P. mariana* snags, and confirmed that the seeds were still available on the snags. The number of seeds were estimated by:

$$y = -26700 + 32200 \cdot \ln x \quad (r^2 = 0.715, n = 8),$$

where y is estimated number of seeds, and x is stem height.

P. mariana seeds were captured by seed traps until summer 2008 (Fig. 1). Therefore, even after severe wildfire, seed immigration from the snags was not limited for a few years after the wildfire. However, the seeds captured by seed traps decreased abruptly in 2009 from everywhere. In addition, the germination of *P. mariana* annually decreased, in particular, on H.

If this trend was true, the regeneration success of *P. mariana* was mostly determined for a few years after wildfires. This fate should be confirmed in this summer. *B. neolaskana* was second dominant in the traps (data not shown).

3.3 Plant communities in forest floor

Although the unburned surface was mostly covered with *Sphagnum* spp. soon after the 2004 wildfire (Table 1), the cover declined gradually due probably to desiccation and fire damage. The cover increased least in most plots, with a few exceptions. In contrast, *Ceratodon purpureus* increased frequency and now established in 80% of quadrats. *Polystichum formosum* followed *C. purpureus*, i.e., showed 45-70% in frequency, and increased annually in cover.

Of herbs and ferns, *Carex bigelowii* and *Calamagrostis canadensis* were most common and had the highest cover of herbs (Table 1). These two species are monocotyledons. *Epilobium angustifolium* became dominant in 2006, but thereafter decreased in cover.

Shrubs, represented by *Ledum groenlandicum*, *Vaccinium vitis-idaea*, and *V. uliginosum*, came from legacies through the last fire (Table 1). Since there were few seedlings on shrubs, vegetative reproduction was most important for shrub regeneration. Shrubs annually increased the cover. The most of these plants survived through the wildfire, and reproduced vegetatively.

Although *P. mariana* slightly increased the cover

(Table 1), the cover increase was mostly derived from survived saplings that showed 0.6% in 2005. the cover of broad-leaved trees was less than 0.1% in 2005, showing that most broad-leaved trees regenerated from seedlings. In addition, the cover of broad-leaved trees exceeded the cover of *P. mariana* in 2008.

3.4 Forest-floor vegetation patterns

NMDS indicated that burned area was the most significant determinant on forest-floor vegetation structures (Fig. 2). The scores of quadrats aggregated in the right side of figure 2 meant the quadrats on less-burned surface, and *vice versa*. The scores of less-burned quadrats fluctuated less, indicating that the vegetation structures changed little. The scores of burned quadrats shown on left-side in the figure fluctuated greatly along axis II, showing that the vegetation structures annually changed but did not go towards the scores of less-burned quadrat. In total, the vegetation structures changed annually on burned surface, but did not recover to the pre-burned vegetation structures.

Species scores supported these facts (Fig. 2). Broad-leaved trees established more on burned quadrats, while shrubs established more on unburned quadrats. The establishment of mosses had a contrast between *Sphagnum* and the others. The establishment of *Sphagnum* was completely dependent on unburned surfaces. In contrast, *C. purpureus* and *P. formosum* established more on burned surfaces. These facts indicated that moss

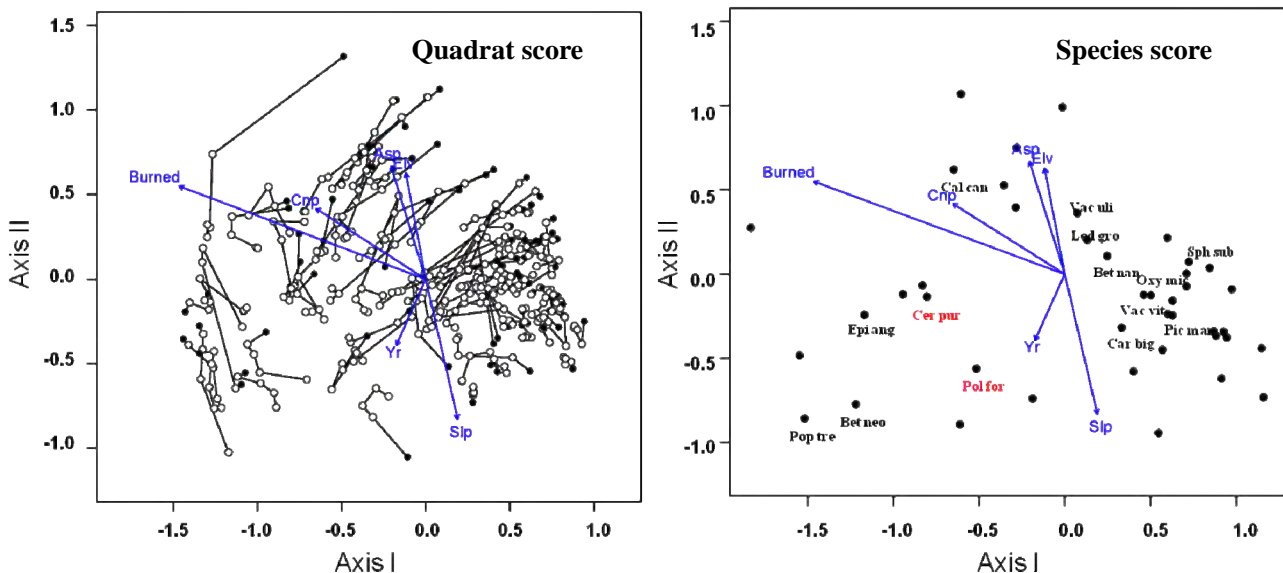


Figure 2. NMDS ordination diagram. (Quadrat scores) The connected lines show the same quadrats surveyed from 2005 to 2009. NMDS scores at the first survey, i.e., in 2005, are shown by solid circles, and the others are by open circles. Environmental factors: Yr = years after wildfire, Brn: burned area (%), Cnp = canopy openness (%), Elv = elevation (m), Slp = slope gradient ($^{\circ}$), and Asp = aspect ($^{\circ}$). (Species score) Car big = *Carex bigelowii*, Cal can = *Calamagrostis canadensis*, Epi ang = *Epilobium angustifolium*, Led gro = *Ledum groenlandicum*, Vac vit = *Vaccinium vitis-idaea*, Vac uli = *Vaccinium uliginosum*, Bet nan = *Betula nana*, Oxy mic = *Oxycoccus microcarpus*, Pic mar = *Picea mariana*, Bet neo = *Betula neolaskana*, Pop tre = *Populus tremuloides*, Pol for = *Polystichum formosum*, Sph sub = *Sphagnum subsecundum*, and Cer pur = *Ceratodon purpureus*.

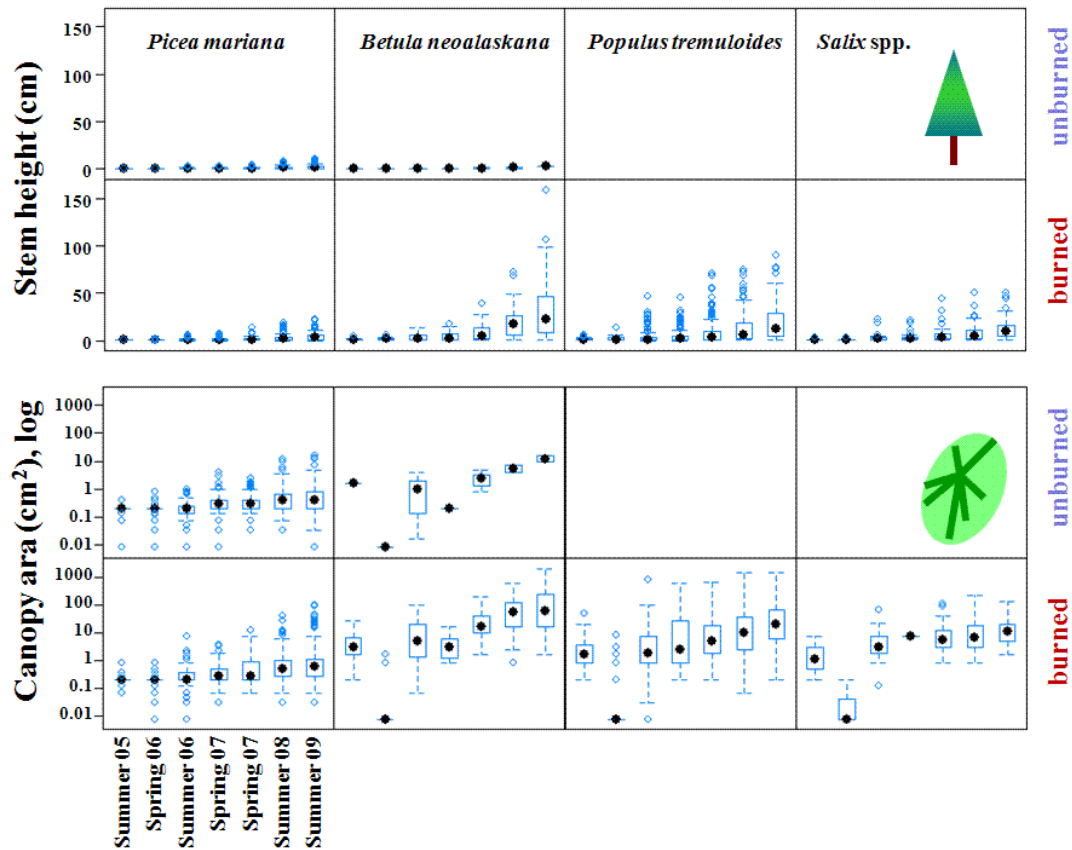


Figure 3. Changes in stem height and crown area on tree seedlings for five years surveyed. Height and crown area are significantly different for *P. mariana* between BS and US at $P < 0.01$ (repeated measures ANOVA), and are different between *P. mariana* and broad-leaved trees at $P < 0.01$.

communities were differentiated by severity.

3.5 Tree seedling growth

In total, 1246 tree seedlings were marked for the five years. *P. mariana* was most abundant, i.e., 860 seedlings in the quadrats, and germinated more on unburned surface. Three broad-leaved tree taxa, *P. tremuloides*, *B. neoalaskana* and *Salix* spp., totaled 386 seedlings. All of these broad-leaved tree seedlings established on burned surface with a few exceptions. Stems \geq DBH on broad-leaved tree species were least in the surveyed plots, showing that the seeds of broad-leaved trees immigrated from the external environments.

On *P. mariana* seedlings emerged in 2005, seedling survival did not differ greatly between burned and unburned surfaces. On broad-leaved trees on burned surface, the survival was more than 63% by 2009. The survivals of *P. mariana* were 79% on burned surface and 47% on unburned surface. In total, the survival of *P. mariana* was higher on burned surface than unburned surface, and was higher than broad-leaved trees on burned surface. However, total number of seedlings was more for broad-leaved trees. Therefore, the density of survived seedlings on burned surface was higher on broad-leaved trees

than on *P. mariana*.

Stem growth, measured by height and crown area, was significantly higher on the three broad-leaved trees than on *P. mariana* on burned surface (Fig. 3). In addition, on *P. mariana*, stem growth was significantly slower on unburned surface than on burned surface.

For estimating carbon fixation by tree seedlings, the following allometric equations were obtained. Aboveground biomass (mg) (y) is predicted by stem height (cm) (x) and aboveground biomass (y)

Picea mariana

$$\text{On US: } y = +0.508x - 0.326$$

$$\text{On BS: } y = +0.465x - 0.090$$

Populus tremuloides on BS: $y = +0.593x - 0.428$

Betula neoalaskana on BS: $y = +0.532x - 0.330$

The differences were significant between burned and unburned surfaces for *P. mariana*, and between species on burned surface (ANCOVA, $P < 0.05$). The significant differences in the slopes of allometry indicated that resource allocation differed between *P. mariana* and broad-leaved tree species. Broad-leaved trees allocated more to belowground than to aboveground, and to stem than to leaf. Broad-leaved trees allocated aboveground biomass more to height growth than *P. mariana*, indicating

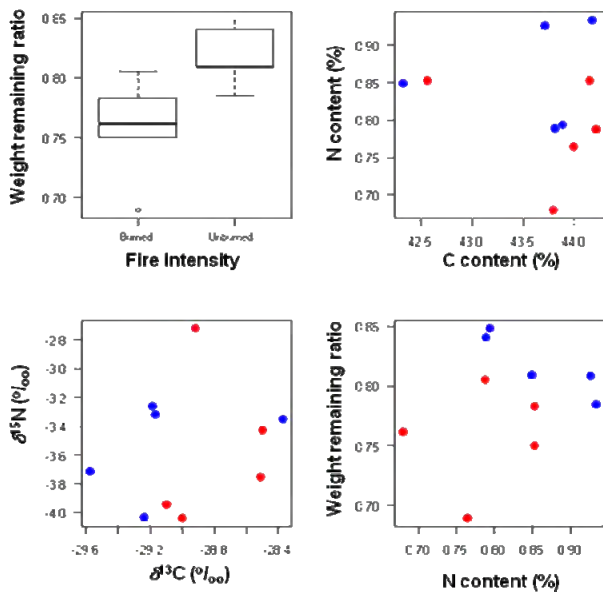


Figure 4. *Sphagnum*-litter decomposition rates expressed by weight remaining, N content, and $\delta^{15}\text{N}$. Red and blue circles indicate litterbags established on burned and unburned surfaces, respectively. The relationship between N content and weight remaining is also shown.

that broad-leaved trees obtained light energy more effectively than *P. mariana*, and did not allocate more to aboveground. We measured the carbon and nitrogen content in these trees, and will evaluate the C and N fixation.

3.6 Litter decomposition

Litter decomposition was faster on burned surface than unburned surface (Fig. 4), suggesting that burned surface accelerated litter decomposition. In addition, N content in litter seemed to become lower on burned surface. This monitoring will be made again in 2010.

4. DISCUSSION

4.1 Seed immigration and seedling establishment

P. mariana seeds were captured fluently by seed traps by 2008 and germinated. However, the numbers of dispersed and germinated seeds decreased in 2009. Also, number of germinated seeds gradually decreased in severely-burned sites. *P. mariana* provides viable seeds for a few years, by producing semi-serotinous cones (Bonan & Shugart 1989). Seed production estimated by tree height supports this. The seed immigration was unlikely to be limited for *P. mariana* regeneration immediately after wildfire. However, viable seeds decreased annually, and were lowest in 2009. The decline in viable seeds suggested that more seeds came from the aerial seedbank on the canopy. Between Yukon and British Columbia, seedling recruitment on *P. mariana* is highest in the first 5 years after fires, while

additional establishment is not observed after 10 years (Johnstone et al. 2004). Number of seedling recruits declined annually on Poker Flat, indicating that tree regeneration patterns on *P. mariana* was determined for the first several years after fire.

All broad-leaved trees observed in Poker Flat produce long-distance wind-dispersed seeds. The seeds of these broad-leaved trees immigrated from the external environments, since the mature stems were least in the surveyed area. Therefore, seed supply will persist for broad-leaved trees. Furthermore, the intensive forest fire, that removes duff layer, promotes the seedling establishment of those broad-leaved trees.

4.2 Environmental changes and litter deposits

If moss mat, mostly consisting of *Sphagnum*, remains on the ground surface after wildfire, soil temperature keeps low. However, the complete removal of *Sphagnum* moss mat promotes soil temperature increase and melting permafrost (Yoshikawa et al. 2002). Albedo also declines by fire, and is mostly determined by plant cover on the ground surface in Poker Flat (Tsuyuzaki et al. 2009). Fire severity, in particular, on the forest floor, must be mentioned to predict the regeneration. Surface temperature increases after wildfire in a *P. mariana* forest, due to increase in canopy openness and decrease in albedo (Chambers et al. 2005). In addition, *Sphagnum* cover influences permafrost distribution (see Sawada's report). Therefore, a trigger on environmental changes is considered to be in *Sphagnum* layer. The dominance of *Sphagnum* spp. is related to *P. mariana* forest expansion (Fenton et al. 2007).

4.3 Regeneration patterns

Although the seedling survival on burned surface was higher on *P. mariana* than on broad-leaved trees, the growth rates were significantly higher on broad-leaved trees. After disturbances, including wildfire, in northern Ontario, broad-leaved trees, represented by *Populus tremuloides*, trees increased the relative dominance, and needle-leaved trees, including *P. mariana*, decreased it (Ilisson & Chen 2009). Mean annual biomass increment is higher in dry sites than in wet sites along a chronosequence on *P. mariana* forests in Manitoba, Canada, but carbon pools in bryophyte, understory and forest floor are less for the dry sites (Wang et al. 2003). The allometric relationships indicated that *P. mariana* has low allocation plasticity, and the growth is reduced on the burned ground surface.

On Poker Flat, plant cover removal from the ground surface determines seedling colonization and vegetation recovery. Canopy openness influences the distribution pattern and productivity of

herbaceous plants on the forest floor (Whigham 2004). However, initial tree composition after fire had little effects on understory composition in the coniferous forests of eastern Canada, while soil burn severity affected temporal changes in understory species (Lecomte et al. 2005). Those suggest that forest regeneration after large-scaled fire differs from weak fire, including crown fire. Fire severity may change successional sere on *P. mariana* forests towards mixed conifer and/or broad-leaved forests.

4.4 Conclusions, perspectives and future plans

By monitoring for five years, four findings were summarized. (1) Seedling regeneration patterns of *P. mariana* might be determined soon after wildfires, because of seed immigration. (2) *P. mariana* established more on unburned and burned surfaces, and broad-leaved trees were restricted to establish on burned surface. (3) Broad-leaved trees grew up significantly faster than *P. mariana*. (4) The regeneration of *P. mariana* forests is limited by the dominance of burned surface.

To clarify plant community-climate interactions with micro-and macro-spatiotemporal changes, we need further observations on: 1) changes in plant community structures for longer term, and 2) seedling survival and growth related to the determinants on *Sphagnum* recovery. To predict carbon balance as well as regeneration pattern, we have to mention *Sphagnum* layer more details. The keystone and umbrella species on the north slopes of interior Alaska must be *Sphagnum* spp.

In summer 2010, the monitoring should be continued to ensure the findings. However, the recovery stages of trees are shifted from seedling to sapling, and became too large to monitor the growth that exceeds to monitor them by using the 1 m × 1 m quadrat. Therefore, we have to change the survey design. Since the vegetation changes slowed, it may be better that the monitoring interval is extended. Also, if we have a chance, we will make a plan to compare regeneration patterns after the other wildfire(s) that recently burned out the ground surfaces. Another idea is that we assist the other projects, by collecting vegetation data. Anyway, we have to clean up the slope to maintain the plots for monitoring conveniently.

REFERENCES

Bonan GB, Shugart HH. 1989. Environmental factors and ecological processes in boreal forests. *Ann. Rev. Ecol. Syst.* **20**, 1-28
 Chambers SD, Beringer J, Randerson JT, Chapin III FS. 2005. Fire effects on net radiation and energy partitioning: contrasting responses of tundra and boreal forest ecosystems. *J. Geophys. Res.* **110**, doi: 10.1029/2004JD005299
 Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP,

Flannigan MD, Hanson PJ, Irland LC, Lugo AE, Peterson CJ, Simberloff D, Swanson FJ, Stocks BJ, Wotton BM. 2001. Climate change and forest disturbances. *BioScience* **51**, 723-734
 Engelmark O. 1999. Boreal forest disturbances. In: Walker LR (ed.). Ecosystems of the world 16: Ecosystems of disturbed ground. Elsevier, Amsterdam, pp. 161-186
 Fenton, N.J., Beland, C., de Blois, S., Bergeron, Y. 2007. *Sphagnum* establishment and expansion in black spruce (*Picea mariana*) boreal forests. *Can. J. Bot.* **85**: 43-50.
 Frazer GW, Canham CD, Lertzman KP. 1999. Gap Light Analyzer (GLA), ver. 2.0. Simon Fraser Univ, Burnaby, BC/Inst Ecosyst Studies, Millbrook, NY
 Ilisson T, Chen HYH. 2009. Response of six boreal tree species to stand replacing fire and clearcutting. *Ecosystems* **12**, 820-829
 Johnstone JF, Chapin III FS, Foote J, Kemmett S, Price K, Viereck L. 2004. Decadal observations of tree regeneration following fire in boreal forest. *Can.J.For.Res.* **34**, 267-273
 Lecomte N, Simard M, Bergeron Y, Larouche A, Asnong H, Richard PJH. 2005. Effects of fire severity and initial tree composition on understory vegetation dynamics in a boreal landscape inferred from chronosequence and paleoecological data. *J. Veg. Sci.* **16**, 665-674
 Tsuyuzaki S., Kushida K., Kodama Y. 2009. Recovery of surface albedo and plant cover after wildfire in a *Picea mariana* forest in interior Alaska. *Climatic Change* **93**, 517-525
 van Cleve K, Chapin III FS, Flanagan PW, Viereck LA, Dyrness CT. 1986. Forest ecosystems in the Alaskan taiga. Springer-Verlag, NY
 Wang C, Bond-Lamberty B, Gower ST. 2003. Carbon distribution of a well-and poorly-drained black spruce fire chronosequence. *Global Change Biol.* **9**, 1066-1079
 Whigham DF. 2004. Ecology of woodland herbs in temperate deciduous forests. *Ann. Rev. Ecol. Evol. Syst.* **35**, 583-621
 Yoshikawa K, Bolton WR, Romanovsky VE, Fukuda M, Hinzman LD. 2002. Impacts of wildfire on the permafrost in the boreal forests of Interior Alaska. *J. Geophys. Res.* **107**, 8148, doi:10.1029/2001JD 000438

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Activities (2008-2010)

Publications

Kushida K., Kim Y., Tsuyuzaki S., Fukuda M. 2009. Spectral vegetation indices for estimating shrub cover, green phytomass and leaf turnover in a sedge-shrub tundra. *Int. J. Remote Sensing* **30**, 1651-1658
 Tsuyuzaki S., Kushida K., Kodama Y. 2009. Recovery of surface albedo and plant cover after wildfire in a *Picea mariana* forest in interior Alaska. *Climatic Change* **93**, 517-525
 Tsuyuzaki S, Sawada Y, Kushida K, Fukuda, M. 2008. A preliminary report on the vegetation zonation of palsas in the Arctic National Wildlife Refuge, northern Alaska, USA. *Ecol. Res.* **23**, 787-793
 Tsuyuzaki S, Sento N, Fukuda M. (in press) Baidzharakhs (relic mounds) increase plant community diversity by interrupting zonal vegetation distribution along the Arctic Sea, northern Siberia. *Polar Biol.* DOI: 10.1007/s00300-009-0727-x