The Regeneration Niche of White Spruce Following Fire in the Mixed-wood Boreal Forest

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Early establishment of white spruce (*Picea glauca*) in mixedwood boreal forest stands following fire was examined at several times-since-fire (1-, 2-, 4-, 6-, 14-years). Abiotic and biotic conditions in the stands were assessed at two scales, tree plot ($5 \text{ m} \times 5 \text{ m}$) and microsite ($1 \text{ m} \times 1 \text{ m}$), along with presence, density and height of white spruce seedlings. Germination and survival of seed sown 1- and 4-years post fire were quantified. Survival and growth of nursery-grown seedlings, and mycorrhizal colonization, survival and growth of sterile seedlings, planted 1-year post-fire were assessed. At the tree plot scale, presence of white spruce seedlings 1-year post-fire could be reliably predicted by organic layer depth and distance to and strength of seed source. In contrast, none of the biotic or abiotic factors measured was strongly correlated with occurrence or density of white spruce seedlings 6- and 14- years post-fire. At the microsite scale, seedling recruitment immediately post-fire was limited to a distinct subset of available microsites (greater % cover of downed wood and moss, lower % cover of litter and herbaceous vegetation). Likewise, seedling occurrence in older burns was associated with distinct microsite conditions; although this was more likely an effect of white spruce presence, rather than the cause. Less than 3% of seed sown 1 yr post-fire survived to become 1 yr old germinants, survival was 41% over the next three years. Availability of suitable regeneration microsites declines rapidly with time-since-fire; less than 0.3% of seed sown 4 yrs post-fire survived one year. High rates of mycorrhizal colonization were found on white spruce seedlings planted 1-year post-fire, including early and late stage fungal species. Microsite characteristics were only weakly correlated with mycorrhizal fungal communities. We propose that immediate post-fire recruitment of white spruce is a key process in mixedwood boreal succession.

1   Introduction

Grubb (1977) argued that much of the variation seen in natural forest plant communities reflects regeneration characteristics of the species and the environment at the time of establishment (i.e., the regeneration niche). Recruitment is dependent upon a seed source and availability of 'safe sites' for germination. Subsequent survival and growth will be influenced by abiotic as well as biotic factors, including competition, the presence of symbiotic organisms (e.g., mycorrhizae), and herbivory (Harper 1977, Zasada et al. 1992, Greene et al. 1999). In forests, the initially established tree cohort can be a major determinant of subsequent compositional development and stand productivity (Zoladeski and Maycock 1990, Man and Lieffers 1999).

White spruce (*Picea glauca* (Moench) Voss), a relatively shade-tolerant conifer, is widely distributed in the boreal forests of North America. Frequent (50–100 yr return interval), stand-initiating fires dominate the natural disturbance regime of this region (Heinselman 1981, Johnson 1992). Succession following fire in the boreal is typically characterized as a transition from early dominance by shade intolerant broad-leaf species [(trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.)] to eventual dominance by shade tolerant conifers [(white or black spruce (*Picea mariana* (Mill.) BSP, balsam fir (*Abies balsamea* (L.) Mill.)] (Rowe 1961, Nienstadt and Zasada 1990, Bergeron and Dubuc 1989).

White spruce recruitment may be restricted to a relatively short time-period following fire (Rowe 1961, Dix and Swan 1971) or could be continuous or periodic (Nienstadt and Zasada 1990, DeLong 1991, Kabzems and Lousier 1992, Bergeron and Charron 1994, Kneeshaw and Bergeron 1996, Lieffers et al. 1996). Cone crops of white spruce show high annual variation ('masting') with seeds dispersed in fall and winter, primarily within 100 m of the parent tree (Dobbs 1976, Zasada 1985). They germinate the following spring and have very limited viability in the seedbank (Heinselman 1981). Germination is best on exposed mineral soil (Zasada and Gregory 1969, Zasada 1985) but recruitment has been documented on a variety of other substrates (ash, leaf litter, organic material, downed woody material) (Clautice et al. 1979, Parker et al. 1997, Barras and Kellman 1998, Simard et al. 1998). Cover of competing vegetation, light availability, or development of mycorrhizal relationships may also affect white spruce regeneration (Coates et al. 1994, Lieffers and Stadt 1994, Kneeshaw and Bergeron 1996, Miller et al. 1998).

Many studies have examined the natural regeneration of white spruce following timber harvesting or the populations of saplings in the understory of mature, unmanaged forests (Nienstaedt and Zasada 1990, Zasada et al. 1992, Peterson and Peterson 1994, Lieffers et al. 1996). There is relatively little information, however, on post-fire natural regeneration, especially for the boreal mixedwood forest (for studies in Alaska see Clautice et al. 1979, Densmore 1985, Dyrness et al. 1986). An accurate description of early successional dynamics of the boreal mixedwood following fire is essential for sustainable forest management under the natural disturbance paradigm, for establishing ecologically rational regulations for artificial regeneration following logging, and for development of growth and yield and succession models for these forests (Hunter 1993, Lieffers et al. 1996, Bergeron and Harvey 1997). Our objectives were: 1) to determine the biotic and abiotic correlates of white spruce occurrence at various times-since-fire in the mixedwood boreal forest; 2) to characterize the factors associated with successful establishment of white spruce following fire; and 3) to examine the temporal dynamics of white spruce regeneration in the first few years following fire.

2   Materials and Methods

2.1 Study Location

Fieldwork was carried out in the mixedwood boreal forest region in Alberta, Canada (Fig. 1). This region is characterized by morainal landforms of glacial till underlying Gray Luvisol soils on upland sites. The sub-humid, continental climate has short, cool summers and long, cold winters with an average annual precipitation of 380 mm, falling mostly in summer. Trembling
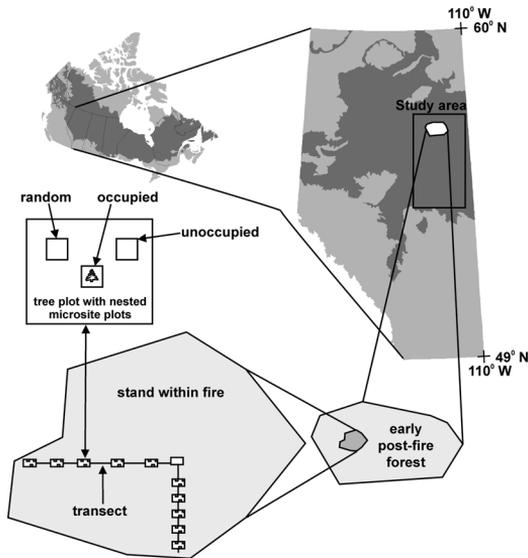
Fig. 1. Map indicating the boreal forest of Canada (top left) and the mixedwood boreal forests of Alberta (top right). The box on the map at the right indicates the general study location. Schematic of sampling design for tree plots ($5\,m \times 5\,m$) and microsite plots ($1\,m \times 1\,m$) within forest stands of different time-since-fire.

aspen is the dominant forest species of mesic sites in this region, occurring in both pure and mixed stands.

All sampled fires were large, relatively intense, crown fires. Beginning in 1996, we examined white spruce regeneration in several natural fires of different ages: 1-year [Mariana Lake burn of 1995 (56°15´N, 111°45´W)], 6-years [Goodwin Lake burn of 1990 (55°22´N, 111°32´W)], and 14-years [1982 burns near Rock Isle Lake (55°29´N, 113°25´W) and Mariana Lake (56°15´N, 111°45´W)]. The Mariana Lake fire of 1995 (1-year-old stands) covered 1364 km^2, began in late May and was extinguished in early July. The Goodwin Lake fire of 1990 (6-year-old stands) covered 118 km^2, began in late July and burned for approximately 2 months. The two 1982 fires began in mid-June and burned for 14 days (Mariana Lake – 121 km^2) and 22 days (Rock Isle Lake – 14 km^2) respectively. The years immediately following the 6- and 14-year-old fires were characterized by high seed production

whereas during the two years following the 1995 fire white spruce cone crops were very low (V. Peters, M. Dale, and E. Macdonald, unpublished). For this reason we subsequently sampled two 1998 burns (sampled in 1999, 2000); 1998 was a mast year throughout most of Alberta while 1999 had a relatively high cone crop (V. Peters, E. Macdonald, M. Dale, unpublished data). Two stands were sampled from the Virginia Hills Fire (54°40´N, 116°30´W), which burned 1600 km^2 during May and June 1998. A third stand was sampled from the Legal fire (55°31´N, 115°15´W), which burned 170 km^2 during August 1998.

All sampled stands were aspen-dominated mixedwoods (> 100 hectares) pre-fire [trembling aspen with 25 to 50% white spruce, crown height 18–24 metres, crown density 51–70%, 80–130 years of age (based on Alberta Phase III forest inventory and aerial photographs)], were not salvage-logged, and had a relatively uniform pre-fire distribution of white spruce and trembling aspen throughout. Because all burns covered large forest areas and the selected stands were widely separated (minimum 5 km), we considered stands as independent samples.

2.2 Sampling Stands 14-, 6- and 1- (1995 Fire) Years-Since-Fire

In 1996 sampling was conducted in two stands from the 1-year-old and 14-year-old burns, respectively and four stands from the 6-year-old forest. Eight transects were established per stand age. At six sampling locations along each transect (0, 20, 40, 60, 80, and 100 m, Fig. 1) a $5\,m \times 5\,m$ tree plot was established. Density of white spruce seedlings was determined within the tree plots. We did not quantify distance to seed sources or source strength for the 14-, 6- or 1-year old (1995 fire) stands (but see sampling of 1998 fire below).

Three 'microsite' plots ($1\,m \times 1\,m$) were nested within each tree plot (Fig. 1). The three microsite plots were selected from 25 possible $1\,m \times 1\,m$ plots within the tree plot. One microsite plot was randomly chosen, one was chosen which contained a white spruce seedling (occupied), and one was chosen which did not contain a white

spruce seedling (unoccupied). There were only two microsite plots if no seedlings were found (random and unoccupied) or if all plots contained seedlings (random and occupied). Within microsite plots, visual estimates of percent cover were made for each of shrubs, herbs, grass, moss, lichen, litter, downed wood (dwm), and mineral soil. Percent canopy cover was determined at seedling height using a convex spherical densiometer. The type and depth of the surface and subsurface substrates were determined at the plot centre (random and unoccupied plots) or where the seedling was found (occupied plots).

Soil temperature (0, 5, 10 cm depths) was measured twice per growing season using a thermocouple. Soil samples were collected and analysed for pH, and soil moisture (% moisture by weight). Ion exchange resin bags buried at the mineral–organic interface for approximately 60 days were used to assess nutrient availability (nitrate-nitrogen, ammonium-nitrogen and phosphorous). Results were expressed as a concentration based on a standard volume of extract per bag, and corrected by days buried. Soil temperature data for each sampling time were standardized as a difference relative to the average temperature of the 'random' microsite plots along that transect. Decomposition rate was determined as weight loss of cellulose disks enclosed in mesh bags and buried at the mineral–organic interface for 60 days. Height was measured for several seedlings per tree plot. We did not attempt to age the seedlings since destructive sampling and careful cross-dating would be required to ensure accurate ages, especially for the older fires (V. Peters, E. Macdonald, M. Dale, unpublished, see also Desrochers and Gagnon 1997).

2.3 Sampling Stands 1- and 2-Years-Since-Fire (1998 Fire)

Based on analysis of the tree plot data for the 14-, 6- and 1-year old (1995 fire) stands we modified our data collection protocol for sampling the stands from the 1998 fire, 1- and 2-years post-fire. Our objective was to obtain better information on the factors influencing occurrence and density of white spruce recruitment at the tree plot scale (5 m×5 m). Four transects (100 m)

were established in each stand, with six sampling locations (20 m apart) along each transect. At each sampling point a tree plot (5 m×5 m) was established. Slope and aspect were assessed, the number of white spruce seedlings was counted, and canopy cover was estimated using a convex spherical densiometer. The distance to the nearest white spruce seed source was determined and the seed source strength was classified using a three-point scale: 1 = single live reproductive tree of canopy or sub-canopy height, 2 = single live reproductive tree above canopy height, 3 = live patch of reproductive trees (tree height is related to cone production; Zasada et al. 1992). In a 2 m×2 m subplot cover was estimated for each of shrubs, herbs, grasses, moss, lichen, litter, downed wood, and exposed mineral soil; litter layer and organic layer depths were measured at five random points in the subplot and averaged. All plots were sampled 1- and 2-years post-fire (1999, 2000 respectively).

2.4 Experimental Work 1- and 4- Years-Since-Fire (1995 Fire)

Seed germination, seedling growth, and mycorrhizal colonization were examined through experimental studies within each of two stands from the 1995 fire. In August 1996 four 1-year-old white spruce seedlings from a local tree nursery were planted in each of 25 plots established along four 100 m transects in one of the stands (plots = 100, seedlings = 400). For these, the planting microsite was characterized for several abiotic and biotic characters [slope, aspect, soil moisture regime (subjective scale from 1 = dry to 3 = wet), surface and sub-surface substrate (e.g., litter, moss, organic, mineral, etc.), substrate depth, % cover of shrub, herb, grass, moss, litter, downed wood, mineral soil]. Survival and height growth of these seedlings were recorded 1 and 3 years after planting. At the same time three-month-old white spruce seedlings, grown under sterile conditions in the University of Alberta phytotron, were planted into these same 100 plots and another 100 plots along four transects in the second 1-year post-fire stand (in total: stands = 2, plots = 200, seedlings = 800). The planting microsite was characterized as described above. After one full year

of growth (fall 1997) half of these seedlings were removed from the field after recording seedling height and stem diameter, placed in plastic bags and stored at 4 °C for analysis of mycorrhizae. The status of mycorrhizal colonization on the roots of these seedlings was quantified by assessing the % of fine root tips colonized and fungal morphotypes were identified based on morphological features examined under a stereoscope and a compound microscope according to the methods of Hagerman et al. (1999).

White spruce seed was sown near the centre of the same plots into which the sterile seedlings were planted; 100 seeds per plot were sown in August 1996 (1-year-since-fire) and in new plots along the same transects again in the summer of 1999 (4-years-since-fire). The number of germinants was recorded one and three-years after the 1996 sowing and 1-year after the 1999 sowing. Microsite conditions for the plots sown in 1999 were characterized in the same way as for those sown in 1996 (as per sterile seedling planting plots above).

2.5 Data Analysis

To determine the correlates of white spruce occurrence at the tree plot scale, we used logistic regression with the various abiotic and biotic factors as independent variables. This analysis was conducted for stands 1- (1998 fire), 6- and 14-years-since-fire. Similarly, stepwise multiple linear regression (forward selection) was used to assess the effect of the various independent variables on density of white spruce seedlings at the tree plot scale in these same stands.

To characterize the abiotic and biotic conditions in microsite plots associated with white spruce occurrence, stepwise discriminant function analyses (DFA) (Legendre and Legendre 1998) were performed on the microsite plot data for stands 14-, 6- and 1- (1995 fire) years-since-fire separately. DFAs were first conducted to characterize the microsite conditions of occupied, unoccupied, and random plots. Subsequently, each microsite plot was defined as either containing a white spruce seedling or not. A second DFA was conducted for each age separating between these two plot types to distinguish the microsite

conditions associated with white spruce occurrence or absence. In order to examine further the relationship between substrate and seedling occurrence, frequency distributions for the surface and subsurface substrates for occupied and unoccupied plots were compared to those for the random plots using a goodness of fit test and log-likelihood ratio.

Biotic and abiotic factors influencing survival of seedlings planted 1-year-since-fire (1995 fire) were assessed using stepwise discriminant analysis with the microsite characteristics at the time of planting as the independent variables distinguishing between live and dead seedlings 1- and 3-years after planting. To examine factors influencing growth of surviving seedlings (1- and 3-years after planting) forward selection linear regression was used. Biotic and abiotic factors affecting germination rates for seeds sown 1- and 4- years-since-fire (1995 fire) were identified using forward selection linear regression with microsite characteristics at the time of sowing as the independent variables.

Changes in microsite conditions from 1- to 4-years-since-fire (1995 fire) were assessed using principal components analysis of data from the seed sowing plots. Statistical relationships between the growth of sterile seedlings and their mycorrhizal associations were explored using forward selection linear regression. Detrended correspondence analysis (Jongman et al. 1995) with passive input of site variables was used to explore mycorrhizal associations in white spruce seedlings and relationships to the biotic and abiotic environment of the seedlings.

All statistical analyses (regressions, DFAs) were conducted using SPSS version 10.0 (SPSS 1999). Ordinations were conducted using CANOCO version 4.0 (ter Braak and Šmilauer 1998).

3   Results

There were significant differences between stands of the three different post-fire ages (Appendix 1). Stands in the 1-year-old burn (1995) had lower cover of litter, and higher nitrogen availability and decomposition rate than the older stands. The 6-year-old stands had higher cover of vegeta-
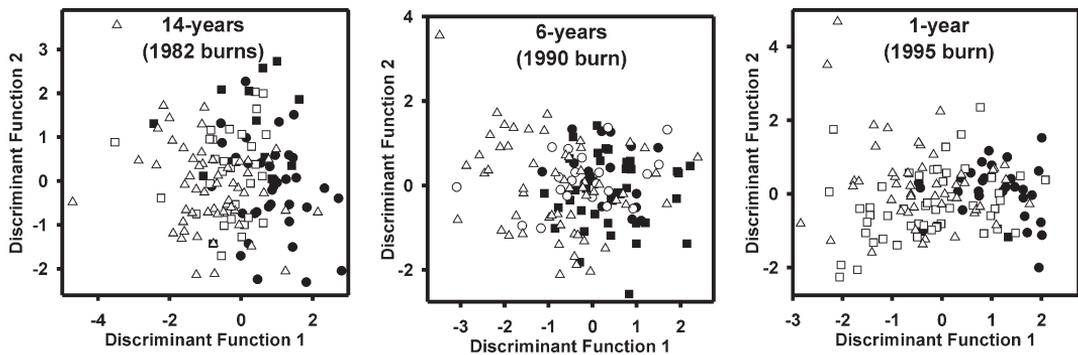
Fig. 2. Discriminant function analysis separating between the three types of microsite plot, random, occupied and unoccupied, 14-, 6- and 1-year-since-fire. Occupied = ●; Random = ■ (with seedling) or □ (without seedling); Unoccupied = △.

tion, downed wood, and mineral soil, but lower ammonium availability and canopy cover than the younger or older stands. The 14-year-old stands had lower moss cover, phosphate availability, soil temperature and deeper surface substrate than either of the younger stands (Appendix 1).

3.1 Correlates of White Spruce Occurrence at the Tree Plot Scale

The highest densities of regenerating white spruce observed were in stands from the 1998 burn, which coincided with a mast cone crop followed by another relatively high cone crop. Densities were 2033/ha 1-year- and 7200/ha 2-years-since-fire in the Legal burn but 0 for stands in the Virginia Hills fire. Seedling densities were similar for stands from the 6- and 14-year-old burns (2000–3000 seedlings/ha) (Appendix 1). Stands in the 1995 burn had the lowest seedling densities (350/ha 1-year-since-fire), presumably as a result of the low cone crops in the immediate post-fire years.

Presence of white spruce seedlings at the tree plot scale 14-years-since-fire was not significantly related to any of the biotic or abiotic variables measured. For stands 6-years-since-fire occurrence of white spruce was negatively related to basal area of dead conifers ([slope] B = –0.70, p = 0.052), although the predictive power was poor (correct classification present: 97%, absent:

10%). In contrast, presence of white spruce seedlings 1-year-since-fire (1998 burn) could be reliably predicted by organic layer depth (B = –0.70), distance to seed source (B = –0.13) and seed source strength (B = 1.9) (logistic regression, p < 0.01; correct classification present: 80%; absent: 96%). Despite abundant, nearby seed sources (mean distance to seed source 42.7 m, source strength 2.4), the two stands in the Virginia Hills 1998 fire had no natural recruitment of white spruce. This was attributed to the deep organic layer in these stands (8.1 cm vs 0.4 cm for the stand in the 1998 Legal burn). Density of white spruce at the tree plot scale 1- (1998 fire), 6- or 14-years-since-fire was not related to any of the independent variables.

3.2 Characterization of Microsite Plots Containing White Spruce

Discriminant function analysis separating occupied, unoccupied, and random microsite plots for each age of burn [1- (1995 fire), 6-, 14-years-since-fire] illustrated that white spruce seedlings occurred in a subset of available microsites (Fig. 2). For each age, DF 1 separated occupied from unoccupied plots while random plots were indistinguishable from either. The subsequent DFAs successfully separated plots with vs without white spruce for each of the times-since-fire. Microsite plots without seedlings were correctly

Table 1. Mean and standard error (in parentheses) of independent variables used in the discriminant function analysis separating microsite plots with vs without white spruce seedlings 1-year-since-fire (1995 burn). Variables are listed in the order they were entered. The correlations between discriminating variables and the standardized discriminant function are also presented. The eigenvalue for the discriminant function was 0.590.

Plot variable	Discriminant function 1	Seedling	No seedling
% canopy cover	0.46	44 (5)	68 (3)
Relative soil (0 cm) temperature	–0.33	1.3 (0.6)	–0.3 (0.3)
Organic substrate 2	0.22	55 (9)	73 (4)
Moss substrate 1	–0.20	77 (8)	61 (5)
Depth substrate 1 (cm)	0.19	1.1 (0.3)	2.0 (0.3)
% cover mineral soil	0.10	0 (0)	0.1 (0.1)
% cover downed woody material	–0.28	16 (2)	10 (1)
% cover moss	–0.42	42 (4)	25 (2)
% cover lichen	0.11	0 (0)	0.1 (0.1)
% cover litter [a]	0.27	7 (1)	18 (2)
Litter substrate 1 [a]	0.26	0 (0)	14 (3)
Relative soil (5 cm) temperature [a]	–0.25	0.5 (0.3)	–0.1 (0.1)
% cover grass [a]	0.21	5 (2)	8 (2)
Slope (degrees) [a]	–0.16	4.7 (0.7)	3.5 (0.4)
% cover shrub [a]	0.16	9 (3)	17 (2)
PO_4 ppm [a]	0.15	6.0 (1.1)	10.6 (1.9)
% cover mineral soil [a]	0.12	0 (0)	0.1 (0.1)
Miner. soil substrate 2 [a]	–0.09	32 (9)	23 (4)
% cover herb [a]	0.09	24 (4)	34 (3)
NO_3 ppm [a]	0.08	0.6 (0.2)	1.2 (0.2)
pH [a]	–0.05	5.2 (0.1)	5.0 (0.1)
NH_4 ppm [a]	0.04	3.1 (0.3)	3.5 (0.3)
Decomposition rate (mg/day) [a]	–0.02	3.0 (0.2)	2.7 (0.1)
Organic substrate 1 [a]	0.02	23 (8)	21 (4)

[a] Variables not selected for entry in the discriminant function analysis (stepwise method).

Table 2. Mean and standard error (in parentheses) of independent variables used in the discriminant function analysis separating microsite plots with vs without white spruce seedlings 6-years-since-fire. Variables are listed in the order they were entered. The correlations between discriminating variables and the standardized discriminant function are also presented. The eigenvalue for the discriminant function was 0.354.

Plot variable	Discriminant function 1	Seedling	No seedling
% cover lichen	0.39	17 (4)	5 (2)
% cover downed woody material	–0.33	38 (5)	52 (5)
pH	0.36	5.2 (0.1)	4.9 (0.1)
% canopy cover	0.37	56 (3)	48 (3)
% cover herb	0.23	56 (5)	46 (5)
% cover moss	–0.02	53 (4)	54 (4)
Litter substrate 1 [a]	0.16	69 (6)	66 (6)
Depth substrate 1 (cm) [a]	0.15	1.4 (0.1)	1.4 (0.1)
Lichen substrate 1 [a]	0.15	4 (2)	2 (2)
% cover shrub [a]	–0.14	42 (5)	39 (5)
NH_4 ppm [a]	–0.12	0.6 (0.1)	1.0 (0.2)
PO_4 ppm [a]	–0.10	7.9 (0.7)	9.3 (0.8)
Slope (degrees) [a]	–0.28	3 (1)	5 (1)
Relative soil (0 cm) temperature [a]	–0.04	–0.3 (0.6)	0.6 (0.6)
Relative soil (5 cm) temperature [a]	–0.01	–0.3 (0.3)	0.3 (0.3)
% cover litter [a]	–0.04	73 (3)	75 (3)
% cover grass [a]	–0.05	11 (4)	16 (5)
% cover mineral soil [a]	–0.08	5 (3)	6 (3)
Moss substrate 1 [a]	–0.20	25 (5)	32 (7)
Organic substrate 2 [a]	–0.09	47 (7)	56 (7)
Miner. soil substrate 2 [a]	0.01	18 (5)	14 (5)
NO_3 ppm [a]	0.09	0.2 (0.0)	0.2 (0.0)
Decomposition rate (mg/day) [a]	0.02	1.8 (0.2)	2.0 (0.2)

[a] Variables not selected for entry in the discriminant function analysis (stepwise method).

classified more often than plots with seedlings, for all stand ages [correct classification for absent/present: 82/71%, 76/71%, 82/77% for 1-, 6- and 14-years-since-fire, respectively].

In stands 1-year-since-fire, seedlings were found in microsites with lower canopy cover, warmer soil temperature, that were more likely to have moss as the surface substrate and less likely to have an organic second substrate than plots without seedlings. Plots with seedlings also had higher % cover of downed wood and moss (Table 1). For stands 6-years-since-fire, plots with seedlings had higher lichen, canopy and herb cover, higher pH and lower cover of downed wood (Table 2). In 14-year-old stands, microsites with white spruce saplings were much more likely to have moss as the surface substrate and mineral soil as the second substrate, lower pH, and higher shrub, litter and herb cover, shallower surface substrate and lower ammonium availabil-

Table 3. Mean and standard error (in parentheses) of independent variables used in the discriminant function analysis separating microsite plots with vs without white spruce seedlings 14-years-since-fire. Variables are listed in the order they were entered. The correlations between discriminating variables and the standardized discriminant function are also presented. The eigenvalue for the discriminant function was 0.686.

Plot variable	Discriminant function 1	Seedling	No seedling
Moss substrate 1	0.37	40 (7)	14 (4)
% cover shrub	0.26	22 (3)	14 (2)
pH	–0.24	4.9 (0.1)	5.2 (0.1)
Mineral soil substrate 2	0.19	4 (3)	0 (0)
% cover litter	0.15	70 (4)	63 (4)
NH_4 ppm	–0.20	3.0 (0.5)	4.5 (0.6)
Relative soil temperature (5 cm)	–0.14	–0.3 (0.3)	0.1 (0.2)
Relative soil temperature (0 cm)	0.14	0.2 (0.3)	–0.2 (0.2)
% cover lichen	0.12	2 (1)	1 (0)
Depth substrate 1 (cm)	–0.22	2.4 (0.3)	3.3 (0.3)
Downed woody material substrate 2	0.04	10 (4)	8 (3)
% cover herb	0.17	25 (3)	20 (2)
Litter substrate 1 [a]	–0.29	58 (7)	80 (5)
Organic substrate 2 [a]	–0.25	73 (7)	89 (4)
Organic substrate 1 [a]	0.22	55 (9)	73 (4)
% cover grass [a]	–0.19	6 (1)	10 (2)
% cover moss [a]	0.16	24 (5)	13 (3)
% cover downed woody material [a]	–0.15	15 (2)	24 (3)
Decomposition rate (mg/day) [a]	0.14	2.0 (0.2)	1.9 (0.1)
Slope (degrees) [a]	0.09	7 (1)	5 (1)
% cover mineral soil [a]	0.06	0 (0)	0 (0)
% canopy cover [a]	–0.05	67 (4)	66 (3)
Lichen substrate 1 [a]	0.04	0 (0)	1 (1)
PO_4 ppm [a]	0.03	6.0 (0.8)	6.2 (0.7)
NO_3 ppm [a]	–0.01	0.1 (0.0)	0.2 (0.0)

[a] Variables not selected for entry in the discriminant function analysis (stepwise method).

ity than microsites without seedlings (Table 3).

The analysis of the frequency distribution of surface substrates confirmed that, in stands 1-year-since-fire, seedlings occurred more frequently than expected on microsites with a moss surface substrate and less frequently than expected on microsites with litter, downed wood or organic surface substrates (log-likelihood ratio

goodness of fit test G = 17.6, ν = 3, p < 0.01). Seedlings were most often found on a shallow moss surface substrate (mean depth = 0.6 cm depth) over mineral soil. Likewise, in stands 14-years-since-fire the results of the DFA were supported; seedlings occurred more frequently than expected on microsites with a moss surface substrate and less frequently on microsites with a litter surface substrate (G = 22.8, ν = 3, p < 0.01).

3.3 Survival and Growth of White Spruce Seedlings Regenerating after Fire

Of the 400 one-year-old seedlings planted 1-year-since-fire (1995 fire), 94% survived for one year after planting and 84% were still alive after three growing seasons. Therefore our ability to detect factors associated with seedling survival was severely hampered. Still, survival for one year after planting was negatively related to litter cover and higher soil temperature, and positively affected by shrub cover, whereas survival over three years was positively affected by a shallow organic surface substrate (DFA, results not shown). Posterior classification of survival in the first year post-planting was better for dead (79%) than live (69%) seedlings but vice versa for survival over three years (dead: 46% correct; alive: 73%). Forward selection linear regression showed that height growth in the first year after planting was positively affected by % cover of downed wood and negatively influenced by increasing soil moisture, soil temperature, and by downed wood as the seedlings' surface substrate (Table 4). Height growth over three growing seasons was negatively related to increasing soil moisture and the % cover of grass and herbs (Table 4).

On average, 2.3% of the seeds sown in plots 1-year-since-fire germinated and survived the first year (Fig. 3). For seeds sown in similar plots 4-years-since-fire, only 0.2% germinated and survived for one year (Fig. 3). Very little of the variation in survival for one year after sowing was explained by the microsite plot characteristics (stepwise multiple regression 1-year-since-fire: R^2 = 0.107, p < 0.05; 4-years-since-fire: R^2 = 0.09, p < 0.05).

There were significant differences in germination rates between the two stands 1-year-since-

Table 4. Results of forward selection multiple linear regression analysis of height growth over one and three growing seasons of seedlings planted 1-year post-fire to microsite conditions. Slope (B) and its standard error are given along with significance (p) for the various independent variables and the R^2 for the whole model. The growth rate for the first year was 7.9 cm/year (SE=0.22) and over three growing seasons the growth rate averaged 6.5 cm/yr (SE=0.15). Downed woody material=dwm.

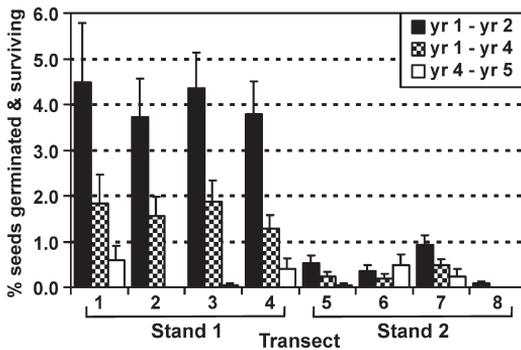|	Model	B	SE	p
Height growth 1996–1997	(Constant)	23.67	3.77	< 0.01
	Soil moisture	–2.62	0.54	< 0.01
	% cover dwm	0.05	0.02	< 0.01
	Soil temperature (10 cm)	–0.77	0.28	0.01
R^2=0.144	Seedling substrate (dwm)	–4.75	2.28	0.04
Height growth 1996–1999	(Constant)	31.99	2.41	< 0.01
	Soil moisture	–4.72	1.14	< 0.01
	% cover grass	–0.08	0.03	< 0.01
R^2=0.092	% cover herb	–0.05	0.02	0.01

Fig. 3. The percent of seeds germinating and surviving for one growing season when sown 1-year and 4-years-since-fire. Survival over three growing seasons for seed sown 1-year-since-fire.

fire (Fig. 3, p < 0.01) but not at 4-years-since-fire (p=0.57). Of those seeds that germinated and survived the first growing season after fire, 41% (0.94% of original number of seeds) were still alive four years later (Fig. 3). There was no difference in first to fourth year survivorship of seedlings between the two stands (p=0.32). Microsite conditions changed dramatically from 1- to 4-years-since-fire (1995 burn). Grass cover increased from 10% to 30–40% and downed wood increased from 10% to 20% while there were declines in cover of moss (from 50% to 10%) and herbs (40% to 30%) (Fig. 4).

3.4 The Role of Mycorrhizae

Sterile seedlings planted 1-year-since-fire showed 75% survival over the first year. Almost all live seedlings (99%) and live root tips (99%) examined formed a mycorrhizal association within 1 year (Table 5). Most seedlings (53%) had formed mycorrhizal associations with only one species, though two (31%), three and four (15%) or more (0.7%) mycorrhizal species were sometimes detected on individual seedlings (Table 5). Thirteen distinct ectomycorrhizal types were observed on white spruce seedling root tips in the first to second year post-fire. E-strain fungi were the most abundant, comprising 59% of all colonized root tips and occurring on 68% of the mycorrhizal seedlings (Table 5). For E-strain, *Thelophora terrestris*, *Tomentella* spp., *Amphinema byssoides* and *Lactarius rufus* the % of seedlings colonized was similar to the % of total mycorrhizal root tips with that species (Table 5). In contrast, *Cenococcum geophilum* colonized root tips of 22% of the mycorrhizal seedlings but was infrequent when it occurred, comprising only 4% of all mycorrhizal root tips.

Seedling growth was positively related to

Table 5. First-year colonization by mycorrhizal fungi of sterile white spruce seedlings (n = 275) planted 1-year post-fire and collected for analysis after one growing season.

Mycorrhizal species	% of total mycorrhizal root tips with species	% of seedlings with mycorrhizal species	% seedlings having only that species
E-strain	58.9	68.0	26.4
Cenococcum geophilum	4.3	22.1	1.1
Thelophora terrestris	12.2	19.9	5.5
Tomentella spp.	9.5	16.5	2.2
Amphinema byssoides	6.9	15.1	1.9
Lactarius rufus	3.5	9.2	1.4
Cortinarius spp.	0.5	2.9	0.0
Dermocybe spp.	2.1	2.9	0.8
Mycelium radicus atrovirens	0.2	2.2	0.0
Hebeloma spp.	0.8	2.2	0.5
Tuber spp.	0.8	1.1	0.3
Piloderma spp.	0.2	1.1	0.3
Russula spp.	0.0	0.4	0.0

Table 6. Results of forward selection multiple linear regression of mycorrhizal colonization of white spruce root tips for sterile seedlings planted 1-year post-fire and collected for analysis after one growing season. Slope (B) and its standard error are given along with significance (p) for the various independent variables and the R^2 for the whole model.

	Model	B	SE	p
Seedling growth 1996–1997	(constant)	2.22	0.181	< 0.001
	% mycorrhizal root tips	2.39	0.318	< 0.001
	Lactarius rufus	–2.38	0.865	0.006
$R^2 = 0.163$	E-strain	–0.70	0.318	0.028

% mycorrhizal root tips (multiple linear regression partial $R^2 = 0.14$, B = 1.9, p < 0.001) but presence of *Lactarius rufus* and E-strain fungi was negatively associated with seedling growth ($R^2 = 0.163$, Table 6). Community analysis of mycorrhizae (DCA) showed separation of E-strain from all other types along the first axis, and *Tomentella* spp. and *Russula* spp. from most other types along the second axis (Fig. 5). The % mycorrhizal root tips had a positive loading on the first axis. Soil moisture, remaining germinants (from sown seed), and % cover of moss, grass, and herbs loaded to the left on the first axis, associating these factors with occurrence of E-strain mycorrhizae. Seed germination in the first post-

fire year, along with % cover of shrubs, litter, and downed wood were associated with the other mycorrhizal types to the right of the first axis (Fig. 5).

4 Discussion

4.1 Presence and Density of White Spruce

White spruce occurrence immediately following fire could be explained by seedbed conditions (organic layer depth) and the existence of a nearby seed source but none of the measured
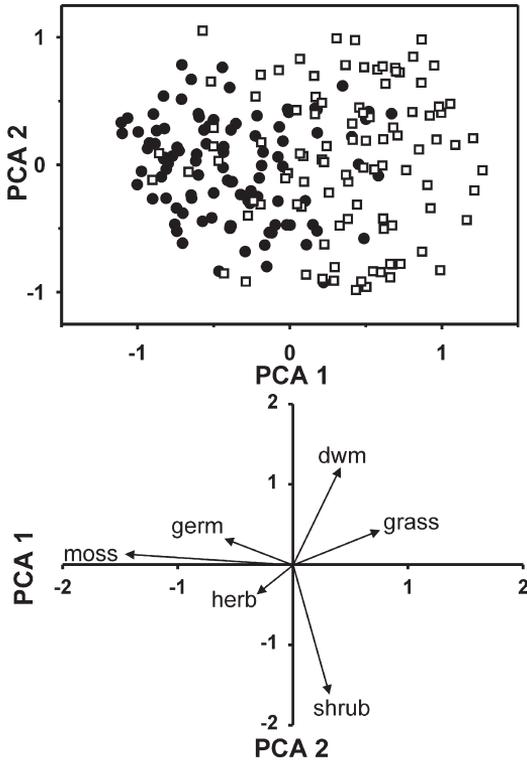
Fig. 4. Results from a principal component analysis of vegetation characteristics 1-year (●) and 4-years (□) since-fire. Eigenvalues for the first two axes were 0.35 and 0.23 respectively. Sample values for the germination rate were entered into the analysis passively.

biotic and abiotic factors explained occurrence in older stands. These results support what has been found for other tree species; i.e. seed source and seedbed conditions at the microsite scale in the immediate post-disturbance period are major drivers of recruitment (Zasada et al. 1992, LePage et al. 2000). They also suggest that abiotic and biotic conditions following initial establishment have little influence on regeneration. A thick organic layer at the two stands within the Virginia Hills (1998) fire likely explains the complete lack of white spruce recruitment, despite abundant nearby seed supply. While fire often exposes mineral soil, creating an excellent seedbed, remaining ash and residual organic matter can severely inhibit germination (Coates et al. 1994, Zasada

1985). The stand in the Legal (1998) fire had a much thinner organic layer, and consequently high seedling recruitment, variability in which was related to distance to and strength of seed source. The low density of seedlings in the 1995 fire (350/ha), compared to the other fires (3000+/ha) also highlights the importance of seed source for recruitment, since the 1995 fire was followed by two years of poor cone crops. The 1995 burn appeared to have abundant suitable microsites, many of which did not have seedlings (Fig. 2). Other studies have found a strong effect of seed source strength on recruitment (Densmore 1985, Kneeshaw and Bergeron 1996, V. Peters, E. Macdonald, M. Dale unpublished).

4.2 Microsite Conditions Associated with White Spruce Occurrence

Even within the confines of a relatively intense burn, white spruce recruitment was restricted to a distinct subset of available microsites. Previous work has suggested that mineral soil is the best seedbed for white spruce germination (Zasada and Gregory 1969, Walker et al. 1986, Nienstadt and Zasada 1990, Zasada et al. 1992). In Alaska, white spruce was found to establish on decomposed organic matter or a shallow humus layer over mineral soil. We found that white spruce seedlings occurred most often on mineral soil (~30% of seedlings) and thin organic (~55% of seedlings) substrates suggesting these are most favourable for establishment. A thick organic substrate appears to be very unsuitable, as indicated by the complete lack of recruitment in the Virginia Hills (1998 fire) stands. Rapid establishment of ground mosses in association with white spruce establishment was observed for both the 1995 and 1998 burns. *Polytrichum* spp. (hair cap) mosses are known to be associated with recruitment of conifers, reportedly because of positive effects of the moss on microsite moisture conditions and inhibition of competing vascular plants (Parker et al. 1997).

Microsites occupied by white spruce 1-year following fire had warm soil with low cover of competing vegetation and higher amounts of downed wood. Others have found that understory recruitment of white spruce into mixedwoods is
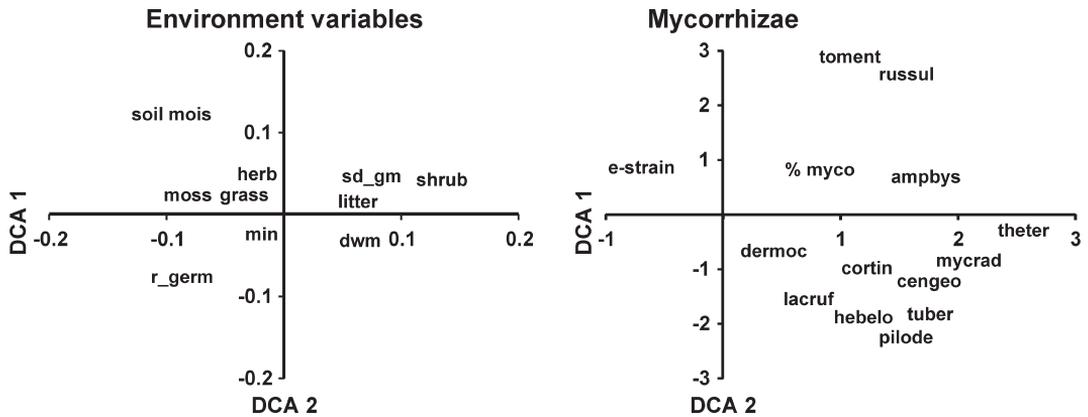
Fig. 5. Results of Detrended Correspondence Analysis of mycorrhizal colonization (% of root tips) of sterile planted white spruce seedlings. Abbreviations for species are: *Amphinema byssoides* (ampbys), *Cenococcum geophilum* (cengeo), *Cortinarius* spp. (cortin), *Dermocybe* spp. (dermoc), *E-strain* (e-strain), *Hebeloma* spp. (hebelo), *Lactarius rufus* (lacruf), *Mycelium radicus atrovirens* (mycrad), *Piloderma* spp. (pilode), *Russula* spp. (russul), *Thelophora terrestris* (theter), *Tomentella* spp. (toment), *Tuber* spp. (tuber). Abbreviations for environmental data are: coarse woody material (cwm), % grass cover (grass), % herb cover (herb), % litter cover (litter), % mineral soil cover (min), % moss cover (moss), remaining germinants 96-00 (r_germ), seed germination in 96-97 (sd_gm), % shrub cover (shrub), soil moisture (soil mois). Eigenvalues for the first two axes are 0.372 and 0.170, respectively.

impeded by low soil temperature and competing vegetation (DeLong et al. 1997). The positive effects of downed wood on seedling recruitment may be due to the fact that fires burned deeper near downed wood better exposing mineral soil (personal observation). In addition, downed wood appeared to shelter establishing seedlings; high densities were found right beside or just under downed logs. No seedlings were found on downed wood, however, and litter or deep organic substrates also appeared unfavourable for establishment.

In older stands, as well, microsites containing white spruce seedlings or saplings were distinguishable from those without. In stands 6-years-since-fire, plots occupied by white spruce (*vs* unoccupied) had greater lichen cover and lower nutrient availability. Some of the differences between plots with vs without seedlings in the older fires could be the effect, rather than the cause, of white spruce recruitment. For example, shade and low levels of litterfall under spruce (compared to broad-leaf trees) would favour lichen and moss establishment and influence nutrient cycling (Dix and Swan 1971). This sug-

gests that the early establishment of white spruce on mixedwood sites could have a significant impact on subsequent ecosystem function as well as successional development (Paré and Bergeron 1996, Bergeron and Harvey 1997, Man and Lieffers 1999). Plots occupied (vs unoccupied) by white spruce 14-years-since-fire had higher shrub cover. Shade from shrubs may initially have a positive impact on spruce seedling establishment, but there is ample evidence that competition can negatively affect white spruce survival and growth (Rowe 1955, Coates et al. 1994, Kabzems and Lousier 1992). The negative relationship between white spruce occurrence and downed wood in the older fires (vs a positive relationship for 1-year-since-fire) could be due to the fact that falling snags damage or kill seedlings/saplings.

4.3 Early Establishment, Growth and Survival of White Spruce

Our results for first year survival of seed sown 1-year-since-fire was a bit lower than found by

others [2.3% vs 3–20% (Nienstadt and Zasada 1990); 10% (DeLong et al. 1997)]. Germination rates for seed sown 4-years-since-fire were dramatically lower and similar to rates reported for litter or organic seedbeds (0.1 to 0.5%) (Zasada 1971, Zasada et al. 1978). Our results suggest that microsite suitability declines rapidly following fire. Even excellent mineral seedbeds, created by mechanical site preparation, are known to decline rapidly over 2 or 3 years as a result of increasing litter, plant and moss cover (Zasada et al. 1978). From 1- to 4-years-since-fire there was a dramatic increase in grass cover and a decline in moss cover. Forest floor moss and litter substrates have been associated with seed pathogens, which may partially explain lower germination rates on these substrates (Zhong and van der Kamp 1999).

Stand structure and composition changed rapidly with time-since-fire such that opportunities for white spruce recruitment would likely continue to be limited for at least 14 years after fire. Standing snags provided cover in stands 1-year-since-fire but had fallen by 6-years-since-fire, resulting in lower canopy cover; canopy cover was higher, again, 14-years-since-fire as a result of rapid growth of aspen from suckers. Canopy and understory cover, amount of downed wood and substrate depth increased with time-since-fire while moss cover, soil temperature, nutrient availability and decomposition declined. We found no new seedlings establishing in the older burns (6- and 14-years-since-fire) and these stands did not have many, or any, microsites matching those in which white spruce was found to establish immediately post-fire. Although stands in the 6-year-old fire had higher % cover of mineral soil (perhaps due to soil disturbance resulting from blowdown of snags), on-going white spruce recruitment would be inhibited due to higher vegetation and litter cover along with increased surface substrate depth. Other studies have also provided evidence that mineral seedbeds deteriorate rapidly with time since disturbance and that regeneration of white spruce in intact forest is poor (Zasada et al. 1978, Nienstadt and Zasada 1990, Simard et al. 1998). Further, dispersal of white spruce seed may be lower in intact stands than in open areas (Stewart et al. 1998). Recruitment onto decayed logs is likely restricted to intact forests, where moisture and relative humid-ity are sufficient (Zasada 1971, Coates et al. 1994).

Our results agree with others in that first year survival seemed to be most critical for seedling establishment (Zasada et al. 1978, Zasada and Wurtz 1990); survival increased to 40% for the subsequent three years. The planted seedlings, which were obviously larger with a well-developed root system, had very high survival (94%); although their growth was negatively affected by excessive moisture, cover of competing vegetation (grasses and herbs), warm soil temperatures, and planting into decayed wood. White spruce seedlings on rotting logs may not grow as well as on mineral soil (Rowe 1955), although not all studies support this (Lieffers et al. 1996).

Overall, our results suggest that initial germination and first year survival is the key limiting step for white spruce regeneration following fire. Probability of germination declines rapidly with time since fire; in addition, later-recruiting seedlings could have a significant disadvantage in terms of survival and growth, compared to seedlings establishing immediately after fire (Zasada et al. 1978, Zasada et al. 1992, Lieffers et al. 1996).

4.4 The Role of Ectomycorrhizae

Ectomycorrhizae have several ecophysiological functions of importance to vascular plants (Kropp and Langlois 1990) and influence vascular plant succession and community composition following disturbance (Perry et al. 1989). Mycorrhizal colonization during the first growing season may be an important process affecting conifer seedling survival (Miller et al. 1998). Previous studies have shown that in early post-fire communities, all *Pinus contorta* var. *latifolia* seedlings (Miller et al. 1998) and most *Pinus halapensis* seedlings (Torres and Honrubia 1997) were mycorrhizal one year following fire. We had similar results in white spruce (~99% of seedlings; >99% of root tips), although we found higher overall mycorrhizal diversity. Both common and rare mycorrhizal species occurred across the transects and stands we sampled and species occurrence was only weakly related to microsite conditions (% cover of local vegetation, surface substrate type,

soil moisture). Mycorrhizae were seen to affect white spruce seedling height growth in our study both positively and negatively.

The succession of ectomycorrhizal communities following disturbance generally follows a sequence from early-stage, through multi-stage to late-stage fungi as the forest matures (Visser 1995). Early successional mycorrhizae such as E-strain, *Thelophora terrestris* and *Cenococcum geophilum* are often more abundant following fire (Miller et al. 1998, Torres and Honrubia 1997, Visser 1995) and clearcut logging (Hagerman et al. 1999, Durall et al. 1999). We also found these groups predominated. We also, however, found low abundances of typical late-stage ectomycorrhizae (*Russula* spp., *Cortinarius* spp., *Lactarius* spp.) on our seedlings only 2-years-since-fire. Other recent studies on young forests following fire (Visser 1995) and clearcut logging (Bradbury et al. 1998, Hagerman et al. 1999) have also found occurrence of these so-called late-stage ectomycorrhizae.

In some forest systems, early-stage mycorrhizal fungi can colonize seedlings by spores whereas late-stage fungi cannot (Fox 1983). Live residual trees within a disturbed area help maintain a diverse mycorrhizal community (Kranabetter 1999), increasing the opportunity for late-stage mycorrhizal fungi to colonise seedlings in young forests. There were no residual live white spruce near the plots used for our mycorrhizal studies but trembling aspen was abundant, regenerating rapidly by means of suckering. Two of the species and five of the genera of ectomycorrhizal fungi we found on white spruce seedlings can form mycorrhizal associations with trembling aspen (Godbout and Fortin 1985, Cripps and Miller 1993). Multi-host ectomycorrhizae may constitute up to 60% of the mycorrhizal community among conifer seedlings (Kranabetter et al. 1999), and mycorrhizal linkages have been demonstrated between angiosperms and gymnosperms (Simard et al. 1997). Trembling aspen may, therefore, play an important role in maintaining mycorrhizal diversity in post-fire mixedwood forests and facilitate mycorrhizal colonization of white spruce seedlings.

4.5 Conclusions and Implications for Mixedwood Succession

Our results suggest that white spruce recruitment on mixedwood sites depends upon both seed availability and suitable microsite conditions in the immediate post-fire period. Further, it seems that opportunities for white spruce recruitment are poor beyond the first three or four years post-fire. If white spruce fails to establish a significant presence on a mixedwood site, an aspen-dominated stand could possibly remain as such for long periods of time, even in the absence of disturbance (Cumming et al. 2000). We propose that immediate establishment of white spruce following fire may be a 'keystone' process in boreal mixedwood succession; having a major influence on stand productivity (Man and Lieffers 1999) and future development, including the likelihood that the stand will ever succeed to pure spruce.

Acknowledgements

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Appendix 1. Characteristics of early post-fire mixedwood forests in Alberta based on data from 5 m×5 m tree plots (seedling density) and random 1 m×1 m microsite plots. Standard errors are in parentheses.

Plot variable	Stand age		
	14-years	6-years	1-year (1995)
% shrub cover	17(2) [a]	41(4) [b]	16(2) [a]
% herb cover	22(2) [a]	51(3) [c]	32(2) [b]
% grass cover	8(1)	13(3)	7(1)
% moss cover	17(2) [a]	53(3) [c]	29(2) [b]
% lichen cover	1(0) [a]	11(3) [b]	0(0) [a]
% litter cover	65(3) [b]	74(2) [c]	15(2) [a]
% dwm cover	20(2) [b]	44(4) [c]	11(1) [a]
% cover mineral soil	0(0) [a]	6(2) [b]	0(0) [a]
% canopy cover	66(2) [b]	52(2) [a]	62(3) [b]
Surface substrate (cm)	3.0(0.2) [b]	1.4(0.1) [a]	1.7(0.2) [a]
Soil temperature (0 cm)	18.4(0.4)	18.6(0.6)	18.6(0.3)
Soil temperature (5 cm)	12.5(0.3)	12.9(0.3)	14.3(0.2)
Soil temperature (10 cm)	10.4(0.3)	11.3(0.3)	13.4(0.1)
NH_4 (ppm)	3.44(0.43)	0.79(0.13)	3.39(0.26)
NO_3 (ppm)	0.12(0.02)	0.16(0.03)	1.05(0.20)
PO_4 (ppm)	5.93(0.54)	8.48(0.52)	9.04(1.51)
Decomposition (mg/day)	0.11(0.01)	0.12(0.01)	0.17(0.01)
Density (seedlings/ha)	2950(411) [b]	2908(419) [b]	350(49) [a]

[a,b,c] Significant differences among ages based on ANOVA and Student-Neuman-Keuls testing ($p < 0.05$).