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Natural regeneration of white spruce following natural disturbance in the western boreal forest

SFMN Project: Natural regeneration of white spruce following natural disturbance
in the western boreal forest

by

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EXECUTIVE SUMMARY

In the Mixedwood boreal forest white spruce is typically regarded as a late successional species, which follows early dominance by hardwoods. Previous studies showed conflicting results in terms of the timing of white spruce establishment following fire. We examined establishment of white spruce (*Picea glauca*) in mixedwood boreal forest stands was examined at several times-since-fire (1-, 2-, 4-, 6-, 14-years). Seed source and germination substrate were important drivers of white spruce presence 1- and 2-years post-fire. Seedling recruitment immediately post-fire was limited to a distinct subset of available microsites. Stands changed quickly with time-since-fire such that the availability of regeneration microsites declined dramatically by 4-years post-fire.

We subsequently examined the importance of mast years (periodic years of high cone crops) relative to the time of a burn on density and timing of white spruce establishment. Significantly more recruitment occurred on mast year burns than sites with a two or three year delay before a mast year. Density differences persisted for at least 58 years, despite opportunities for subsequent recruitment from adjacent seed sources. Careful aging of trees with crossdating techniques demonstrated that a majority of trees originated from the first mast year following fire. Ground level ring counts underestimated the true age of trees by as much as 16 years in 38 year-old stands, and thereby inaccurately identified which periods were important for establishment.

These findings help reconcile conflicting results between studies on seedling establishment in recent fires, and studies on stand age structure in older stands. The aging errors we have identified necessitate the use of crossdating procedures in future retrospective studies of white spruce. Aging errors also have profound implications for the softwood industry, because current provincial growth and yield curves may be overly optimistic and white spruce that established under aspen is likely older than previously believed. Mast years play a critical role immediately post-fire in maintaining white spruce presence in mixedwood landscapes. It is important to maintain mature spruce stands throughout the landscape to facilitate natural regeneration following fire. We hypothesize that immediate post-fire recruitment of white spruce is a key process in mixedwood boreal succession.

More detail on this project available in:

Purdy, Brett G., S. Ellen Macdonald and Mark R.T. Dale. The regeneration niche of white spruce following fire in the mixedwood boreal forest. submitted to *Silvae Fennica*.

Peters, Vernon S., S. Ellen Macdonald and Mark R.T. Dale. Aging discrepancies of white spruce affect the interpretation of recruitment processes in the boreal mixedwoods. submitted to *Can. J. For. Res.*

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INTRODUCTION

The disturbance regime of the boreal forest is characterized by frequent, high intensity, stand-replacing fires (Johnson 1992). Post-fire stand regeneration patterns are typically self-replacing, with the same species regenerating in situ immediately following fire from “arboreal seedbanks” via serotinous cones or lateral roots and root sprouts (Rowe 1983). Consequently, secondary succession in boreal forests can generally be characterized by initial floristic composition models (Egler 1954, Connell and Slayter 1977). The reproductive strategy of white spruce is a stark contrast to most boreal tree species because it depends on surviving seed sources to disperse seed into the burned area (Galipeau et al. 1997). Consequently, it is more apt to be recruitment-limited, and local population extinctions are more likely to occur. As a masting species with wind-dispersed seeds that germinate best on mineral seedbeds (Nienstaedt and Zasada 1990), white spruce may colonize most successfully immediately following fire. Immediate post-fire recruitment may be critical to continued white spruce persistence on the boreal landscape because fire cycles average 100 years (Hunter 1993; Johnson 1992) and a high proportion of developing white spruce stands will burn prior to reaching reproductive maturity.

Background

Frequently portrayed as a late succession species, white spruce may regenerate immediately post-fire or over the next 100 years (Lieffers et al. 1996; Youngblood 1995; Galipeau et al. 1997), thereby exhibiting characteristics of both pioneer and late successional species. Initial recruitment has not previously been regarded as critical to spruce stand development because it also establishes over time on decayed logs (Kabzem and Lousier 1992; Galipeau et al. 1997) and studies have suggested that regeneration may be delayed by more than 25 years and then occurs gradually over the next 50 years (Lieffers et al. 1996; Constabel and Lieffers 1996). However, studies on burned substrates show that immediate recruitment occurs at high densities following fires that expose a high percentage of the mineral soil (Zasada 1985; Kabzem and Lousier 1992). Post-fire seedbed receptivity is short-lived, however, because mineral seedbeds convert to an unreceptive humus substrate in less than 6 years (Coates et al. 1994). The contradictory evidence regarding the timing of white spruce regeneration following fire on mixedwood sites require further exploration.

White spruce regeneration is ultimately dependent on a seed source; therefore, regeneration density may be controlled by the proximity of seed sources and annual variation in seed production (Nienstaedt and Zasada 1990; Kabzems and Louisier 1992). Seed dispersal declines rapidly downwind of a seed source; consequently, few trees may regenerate beyond 100 meters in average seed rain years (Zasada and Lovig 1983; Nienstaedt and Zasada 1990; Dobbs 1976). The additive effects of small mammal herbivory (Dobbs 1976; Alden 1985), high microsite specificity (Lieffers and Stadt 1994; Delong et al. 1997), and high first year mortality (Coates et al. 1994) further limit recruitment. Mast years are widely synchronized throughout Alberta (Kemp and Keith 1970). Good mast years are always followed by poor mast years (Nienstaedt and Zasada 1990) with more than 40 fold differences in seed production between

consecutive years (Nienstaedt and Zasada 1990). Based on annual cone collection records and forestry publications, mast frequency in Alberta has ranged between 2-6 years over the last 50 years (Palamarek pers. com.; Peters 2001, thesis in prep). Solid evidence for the importance of initial recruitment from mast years to long term spruce recruitment dynamics is not available.

Studies of long-term tree recruitment dynamics require retrospective approaches due to the long lifespan of trees (Coates et al. 1994). Chronosequence approaches looking at progressively older stands are helpful in determining stand dynamics. Such an approach is necessary in understanding spruce recruitment dynamics because of conflicting results between seedling recruitment studies and studies in older stands. Studies which address long-term mixedwood recruitment dynamics have taken a “snap-shot” look at only one age class of stands (60-80 years) (Lieffers et al. 1996; Galipeau et al. 1997), (120 -160 years) (Youngblood 1995). Explanations for observed patterns in these stands are limited because historical seed source proximity, source strength, and burn intensity are not readily apparent. Furthermore, successional processes may not be accurately inferred from static age structures if assumptions about aging methodology are inaccurate (ie. ground level equals root collar, and ring count equals age) (Desrochers and Gagnon 1997; Gutsell and Johnson 1999). Ground level ring counts were used in the previous studies; however, this method missed up to 20 years in black spruce growing on upland sites (Desrochers and Gagnon 1997).

Our objectives in this work were: 1) to characterize the abiotic and biotic conditions associated with successful establishment of white spruce following fire in the mixedwood boreal forest; and 2) to determine how these change in the first few years following fire; 3) determine the influence of timing of fire in relation to mast years on the density and timing of white spruce recruitment; and 4) to determine whether ring count at ground level provides an accurate age of white spruce. An accurate picture 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).

METHODS

The regeneration niche of white spruce following fire

We examined white spruce regeneration in several burns of different ages: 1-year, 6-years, and 14-years. All sampled fires were large relatively intense crown fires in conifer-dominated and mixedwood forests. All sampled stands were aspen-dominated mixedwoods (>100 hectares) pre-fire, were not salvage-logged, and had a relatively uniform distribution of white spruce and trembling aspen throughout.

Sampling of burns

Live tree and snag density, basal area, white spruce seedling density, slope, aspect, and % canopy cover were determined in 5x5m plots. Biotic and abiotic conditions were quantified in three 'focus' plots (1x1m) nested within each tree plot: one randomly chosen, one which contained a white spruce seedling (occupied), and one which did not contain a white spruce seedling (unoccupied).

Experimental work in 1995 burn

In August 1996 four 1-year-old seedlings were planted in plots at the 1995 burn and the planting microsite was characterized based on several abiotic and biotic characters. Survival and height growth of these seedlings were recorded after 1 and 3 years in the field. White spruce seed was sown into plots in August 1996 (1-year post-fire) and in new plots in the 1999 (4-year post-fire); % germination was recorded one year after sowing.

Importance of mast seed years

A chronosequence approach was used to test whether timing of fire relative to the first mast year following fire is critical to eventual spruce stand development. Historical mast years within the province were identified between 1941-1996 from provincial cone collection records, Alberta based forestry publications, and red squirrel trapping records, which are statistically significant correlates of cone crop (Kemp and Keith 1970). One fire from each of three mast years (1991, 1979, 1961) and four non-mast years (1994, 1992, 1981, and 1940) was selected. Fires were located within a 60,000-km² area of boreal mixedwood in east central Alberta, North of Lac la Biche (54°46'N 111°8'W), and Athabasca (54°43'N 113°17'W). Fires larger than 200 ha, that occurred between June 1st - Aug -15th were selected from provincial fire databases.

A minimum of seven burned aspen-white spruce stands, adjacent to spruce seed sources with seed producing individuals at the time of fire, was sampled per fire. Quadrat sampling was conducted at 20 and 100 meters into the fire from seed sources. The variables measured included: 1) spruce density and rooting substrate, 2) pre-fire and post-fire tree species density, 3) percent cover of bryophyte, herb, graminoid, and shrub strata, and 4) site variables including slope, aspect, duff thickness, and soil texture. Plotless methods were used in unburned seed sources to determine stand composition, basal area, and number of seed producing trees within 30, 60, and 100 m of the regenerating stand. Multiple regression analysis with forward selection procedures was used to determine significant predictors of spruce density.

Timing of recruitment was determined by aging a minimum of two stands per fire (30 trees per stand). Trees were cut at ground level, and the entire below ground portion of the tree was removed. Below ground portions of trees were crossdated with skeleton plots to identify missing rings. In trees older than 20 years, we measured ring widths, and used a master chronology to visually crossdate trees. The computer crossdating program "Cofecha", was used to help locate missing rings. We evaluated burned stands with a one, two, or three-year delay before the 1983 mast year, using the same sampling procedures outlined above.

Results

The regeneration niche of white spruce following fire

Stand structure varied significantly with time-since-fire at the scale of the tree plot and at the microsite scale. Stands in the 1-year-old burn had lower cover of litter, and higher nitrate and ammonium availability and decomposition rate than the older stands. The 6-year-old stands had higher % cover of shrubs, herbs, grass, lichen, moss, 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.

Presence of seedlings one year following fire was related to a shallow organic layer depth and a strong seed source nearby. Seedlings occurred in a subset of available microsites. In 1-year-old stands, seedlings were present in microsites with higher % cover of downed wood and moss, lower % cover of litter, lichen, mineral soil, shrub and grass, lower % canopy cover, warmer soil temperature, and shallower surface substrate. For the 6-year-old stands seedlings occurred in plots with higher canopy, lichen and herb cover, lower cover of downed wood and lower ammonium and phosphate availability than plots without seedlings. In 14-year-old stands white spruce seedlings/saplings were present in microsites with greater shrub, litter, herb and moss cover but lower cover of grass and downed wood, shallower surface substrate and lower ammonium availability and pH than microsites without seedlings.

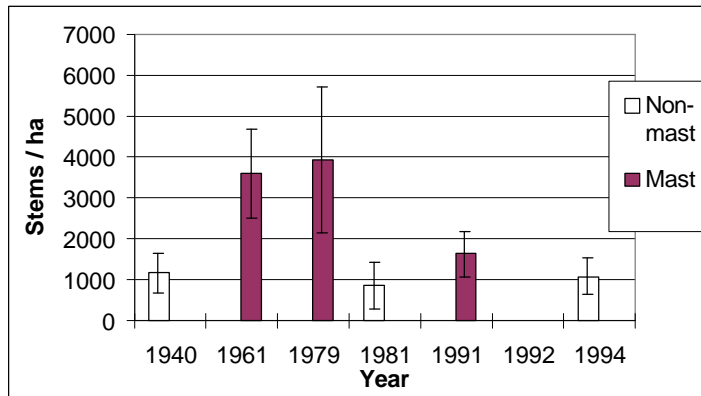
Survival of planted seedlings from one to four years post-fire was 84%. Height growth of planted seedlings was positively affected by cover of downed wood and negatively influenced by increasing soil moisture, soil temperature, and by downed wood as the seedlings' surface substrate. Only 2.3 % of the seed sown in plots 1-year post-fire germinated and survived the first year. For seed sown 4-years post-fire, only 0.22% of the seeds germinated and survived for one year. Site conditions changed dramatically between 1- and 4-years post-fire. Grass cover increased while moss and herb cover declined.

Importance of mast seed years

Stand recruitment densities were greater on mast year burns (MYB) than non-mast year burns (NMYB) at 20 m (nearly 3 times) and 100 m (four times) from seed sources (Fig. 1). Deterioration in seedbed receptivity for initial recruitment with time since fire is the most likely explanation for this result (see above and next section). Variation in spruce recruitment was explained by burn timing relative to mast years (best predictor), the number of initial seed trees within 30 m, proportion of aspen regeneration, and direction and distance from seed source (partial r^2 values = 0.156, 0.064, 0.065, 0.033, and 0.030 respectively; $p < 0.001$, $df = 297$). The distribution of seed trees within the unburned forest was important for predicting recruitment densities; seed trees adjacent to the edge provided stronger predictive relationships than trees at

distances into the unburned forest. Recruitment was greatest in burned stands situated downwind of seed sources in the direction of prevailing Northwesterly winds.

a)



b)

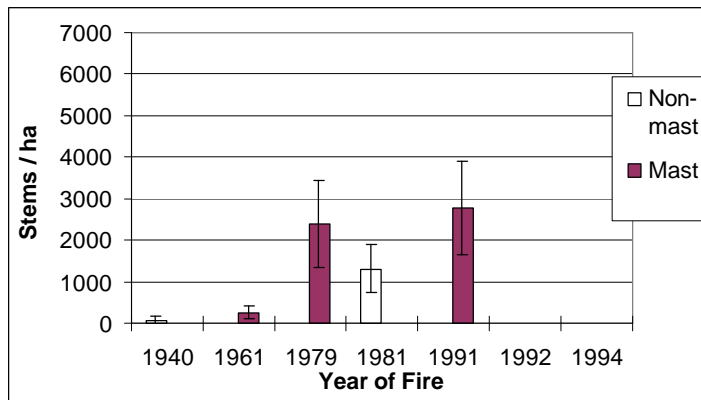
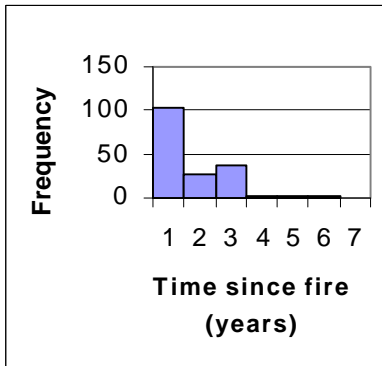


Figure 1: Average white spruce densities at 20 m (a) and 100m (b) from seed sources in burned stands burned in the mast year and stands burned one or more years prior to a mast year (non-mast years). 1992 was a non-mast burn that had no spruce recruitment at either distance, while 1994 was a non-mast burn with no recruitment at 100 m.

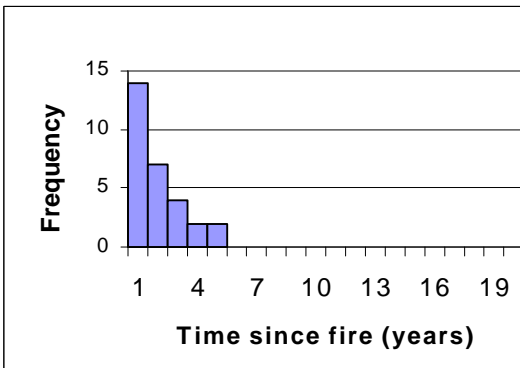
Recruitment did not occur continuously over time in 4-20 year old stands. Most recruitment occurred in the first mast year following fire in stands up to 20 years old (Figures 2a and 2b). Age structures in 20 year-old stands indicated that no recruitment occurred between 7-20 years after fire. Recruitment patterns showed little variation between stands or fires. Initial recruitment periods appeared considerably longer in stands 38 years-old (Fig. 2c) and older, indicating that despite crossdating, the true age of many trees could not be obtained.

Crossdating indicated that ground level ring counts underestimated age by 2.1 years in 20 year old stands (range 1-6) and 6.7 years in 38 year-old stands (range 1-16). There were significant increases in missing rings, buried stem length, and adventitious root development with increasing stand age. Crossdated age structures in 20 and 38 year-old stands differed significantly from ground level ring counts. A few trees did establish after 20 years in 38 year-old stands. Prior to crossdating, it was impossible to distinguish these recruits from initial

recruits on stands 38 years old or older. The importance of later recruits (more than 20 years after fire) to stand development will be tested in 58 and 59 year old stands.



a) 7 year-old stands trees)



b) 20 year-old stand

c) 38 year-old stand

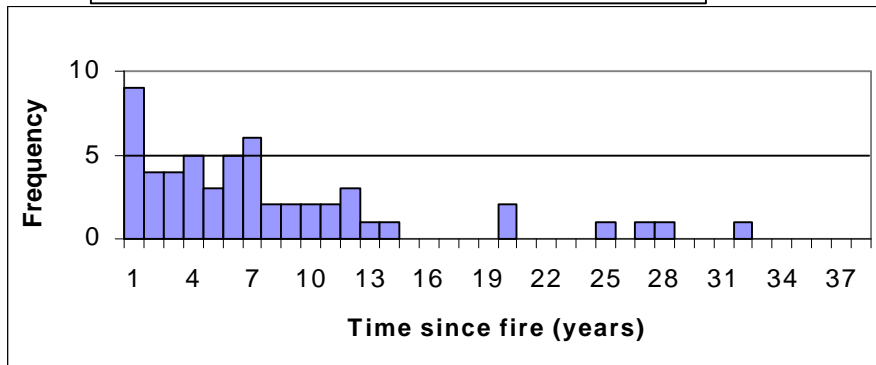


Figure 2: White spruce recruitment timing in a) nine 7 YOS, b) one 20 YOS, c) two 38 YOS. Trees in 20 and 38 YOS were crossdated, while trees age estimates in 7 YOS were based solely on ring counts at ground level. All fires shown were mast year burns.

Recruitment versus delay length before a mast year

The importance of the first mast year following fire for recruitment varied with how many years had passed since fire. Fires with a one-year delay before the next mast year did not differ from a mast year burn, however, fires with 2 and 3-year delays had substantially less recruitment (Fig. 3). These results suggest that seedbed receptivity declines rapidly in the first 3 years following fire. Stand age structures show that the most recruits established from the 1983 mast year on fires with a one or two year delay (1982 and 1981 fires respectively), however the fire with the three year delay virtually lacked a mast year cohort (Figures 4a and 4b). Mast years occurring four or more years after fire did not contribute a large cohort on any fires. No recruitment (1981 and 1982 fires) to very little recruitment (1980) was observed in years prior to the first mast year (Figures 4a and 4b). These results suggest that mast years must occur within 2 years of fire in order for high recruitment densities to occur.

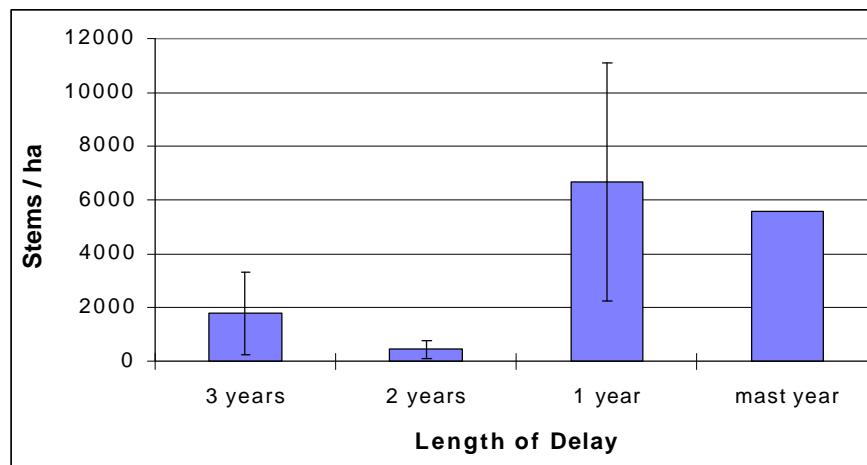
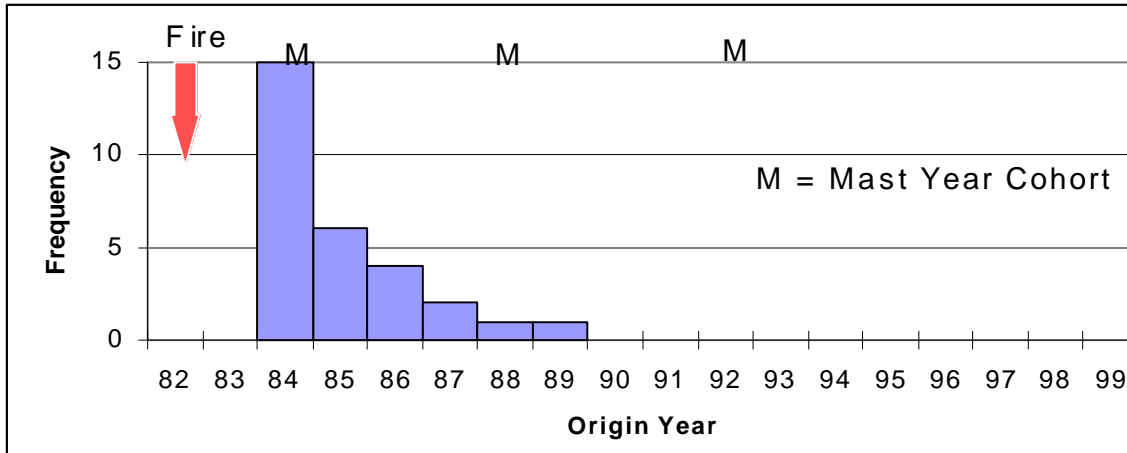


Figure 3: Density relative to length of delay period following fire, before a 1983 mast year at 20 m from a seed source (+/- 1 std. error). Fires with a 1, 2, and 3 year delay were 1982, 1981, and 1980 respectively (n = 2 fires per year), while the mast year was 1979.

a)



b)

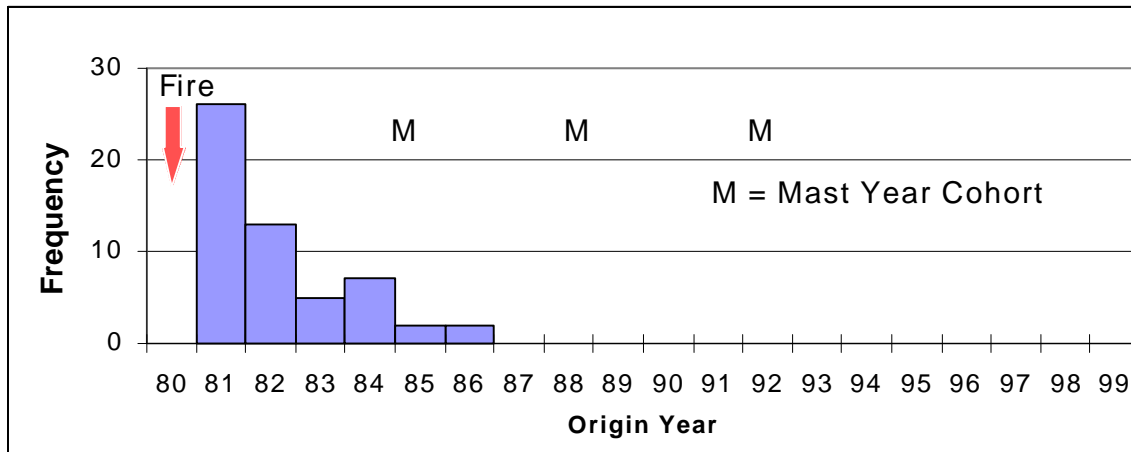


Figure 4: White spruce recruitment timing relative to delay period before mast years for a 1982 (a) and 1980 (b) fire.

CONCLUSIONS

Previous studies have suggested that white spruce recruitment on aspen-dominated mixedwoods may occur immediately following a burn, after a delay of 20+ years (Kabzems and Lousier 1992), may be more or less continuous post-disturbance (DeLong 1991, Bergeron and Charron 1994, Kneeshaw and Bergeron 1996, Lieffers et al. 1996), or might occur in waves (Galipeau et al. 1997). In the time frame we examined post-fire, our data suggests that a good seed source and distinct microsite conditions are required for post-fire establishment of white spruce and that opportunities for white spruce recruitment are poor beyond the first three or four years post-fire. Natural regeneration of white spruce is heavily dependent on recently burned

mineral seedbeds. The most important period for successful white spruce recruitment in the 38 years following fire is the first five to seven years.

Because there is such a narrow window of opportunity for white spruce recruitment following fire annual variability in seed production is a critical determinant of white spruce recruitment. The first mast year following fire contributes the majority of recruits and the timing of when this year occurs greatly determines the density of recruitment. A two-year delay was sufficient to greatly reduce recruitment. Non-mast years frequently do not contribute to recruitment despite moderate seed production, but in cases where they do, it is at substantially lower densities than mast years. Recruitment densities were greatly influenced by seed source strength, direction, and distance.

On recent fires (38 years old and younger), recruitment patterns showed little variation between stands or fires, and we conclude that considerable aging errors on suppressed trees have inaccurately depicted continuous recruitment patterns during early stand development stages. Crossdating limitations on suppressed trees prevent age structures from showing the short recruitment duration that is apparent in younger stands. These results present a different picture of spruce succession in mixedwood forests and have important implications for forest management.

Several authors have suggested that if white spruce is to attain importance on a site, recruitment must be within a few years following disturbance (Bergeron and Dubuc 1989, Zasada et al. 1992). 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). Thus, initial establishment of white spruce following fire may be a key process determining development of a mixedwood (vs a pure hardwood) forest. We hypothesize 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.

MANAGEMENT APPLICATIONS

Our results suggest that provincial growth and yield curves based on fire-origin stands (Alberta Forestry Lands and Wildlife 1985) may need to be adjusted in order to reflect juvenile development periods that are considerably longer and more variable than currently assumed. An accurate picture of stand development time is critical to establishing cut rotation length, predicting yield, and defining “natural” silvicultural systems in mixedwoods. Any future studies on recruitment dynamics or growth of white spruce need to use detailed crossdating procedures in order to accurately estimate age. By quantifying the error associated with ground level ring counts, our results help to explain discrepancies between previous studies on the timing of white spruce succession.

While not wanting to suggest that burned seedbeds are analogous to post-logging seedbeds, many of our findings are relevant to silviculture. Cutblocks left to naturally regenerate of white spruce need site preparation that is appropriately timed with mast years, since recruitment in non-mast years is poor to nonexistent. Seed trees exert a short influence, and ingress after the first mast year cannot be relied on. We also suggest that salvage logging activities should be mindful of masting cycles. Harvesting should be restricted to after seed dispersal in mast years, and maintenance of any surviving trees is critical for at least four years after fire. Special provision should be made to maintain suitable seedbeds for this time period after salvage logging.

Our results indicate that mast years play a critical role in maintaining white spruce presence in mixedwood landscapes. In light of harvesting pressures that will shift forest age distributions towards younger age classes, it is important to maintain a sizeable component old spruce or mixedwood stands in the landscape to facilitate natural regeneration following fire. This is particularly important because current estimates of spruce growth are over-optimistic, and reliance of fire origin stands to reach merchantable size classes will take considerably longer than projected. Given the large number of stands that will burn prior to white spruce reaching reproductive age, existing mature stands are essential as a landscape level seed pool. Artificial regeneration of white spruce in burned stands is a costly alternative to natural ecosystem processes.

Mixed spruce aspen whites spruce stands appear to be an artifact of fire intensity, timing in relation to masting, seed source strength, and dispersal limitations, consequently softwood versus hardwood land base designations in mixedwoods must be regarded as temporally variable. A shifting mosaic of forest composition in this system appears to occur. Recognition of this shifting mosaic provides an ecological basis for “Mixedwood management”.

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