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THE INTERACTION BETWEEN MASTING AND FIRE IS KEY TO WHITE SPRUCE REGENERATION

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Abstract. We used the mast-seeding tree *Picea glauca* (white spruce) to examine whether the timing of mast years relative to fire had a lasting effect on the density and timing of regeneration. We studied 17 fires that occurred in mast years and in years with low cone production between 1941 and 1994. Trees were carefully aged by crossdating procedures. Over the 59-yr period studied, there was significantly more regeneration after fires that occurred in mast years than after fires that occurred in years of low cone production. Spruce density was significantly lower after fires that occurred 1–3 years before a mast year than after fires during mast years. The cohort of trees that regenerated in the first mast year after a fire was critical to white spruce regeneration for fires that occurred 0–1 year before a mast year, but mast years occurring three or more years after a fire contributed few recruits. Our results suggest that masting is a key process that interacts with fire to shape stand composition in boreal mixedwoods. For species like white spruce, for which establishment is linked to disturbance, masting may have a contingent, historical effect on succession and landscape structure.

Key words: cohorts; crossdating; fire; masting; mixedwood forest; Picea glauca*; regeneration; seedbed; white spruce.*

INTRODUCTION

Masting, the widespread and synchronous production of large seed crops at variable intervals (Silvertown 1980), is a common reproductive phenomenon in North American conifers (Koenig and Knops 1998). Numerous studies have investigated the causes of masting (Shibata et al. 1998, Keely and Bond 1999), but neither the short-term nor long-term consequences of masting on plant community structure and dynamics has received much attention. Despite the frequent inference that mast years are important for recruitment (Sork 1983, Keely and Bond 1999), there is little empirical evidence regarding the influence of mast years on tree regeneration or on long-term age structure and successional development in forests. When regeneration depends upon disturbance, interactions between masting and disturbance could have important effects on succession and landscape structure.

White spruce, *Picea glauca* (Moench) Voss, is an ideal species in which to investigate the long-term ecological implications of an interaction between masting and disturbance because its masting behavior is well-documented and it occurs in the boreal forest, which is characterized by large, high-intensity, stand-replacing fires (Johnson 1992). Masting occurs every two to six years (Coates et al. 1994), at which time synchronous seed production with other *Picea* species occurs over distances of up to 2500 km (Kemp and Keith 1970, Koenig and Knops 1998); these mast years are followed by years of virtual failure of cone production (Nienstaedt and Zasada 1990). From year to year, dispersed seed within a mature white spruce stand can range from 2.5 to 4000 seeds/m^2; density may vary from 1000 to 4000 seeds/m^2 for years of high cone production (Nienstaedt and Zasada 1990). Small mammals, insects, and birds can consume most seeds in years with low to moderate cone crops (Coates et al. 1994, Peters et al. 2003).

Frequently portrayed as a late successional species in boreal mixedwoods, white spruce is commonly found in the understory of forests dominated by broadleaf species such as trembling aspen (*Populus tremuloides* Michx.) and paper birch (*Betula papyrifera* Marsh.) before emerging as a canopy dominant (Youngblood 1995). Seeds are released in the fall and are viable for only one year; thus, dispersal from surviving seed sources is critical for reestablishment in burned areas (Greene and Johnson 2000). Although microsites created by fire (e.g., mineral soil) are important for establishment of white spruce, and seedbed receptivity has been reported to decline rapidly after fire (Zasada and Gregory 1969, Purdy et al. 2002), white spruce is also known to establish for many de-

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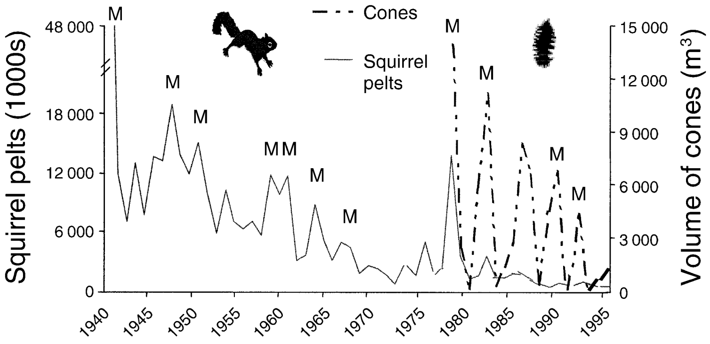

FIG. 1. Masting history of white spruce in Alberta, Canada, from 1941 to 1996. Seed shortages from 1979 to 1996 necessitated cone collections whenever cone crops occurred. Provincial trapping records for red squirrel, 1941–1996, were compiled by the Alberta Trappers Association. Years reported as good or excellent seed years in forestry publications and journal articles are shown for comparison and are indicated by ''M'' (for mast year; Appendix B).

cades after fire (Lieffers et al. 1996). There is currently little information on the influence of interactions between mast years and fire on regeneration of white spruce and subsequent stand development in the boreal mixedwoods.

We investigated the importance of the timing of mast years relative to fire over a 59-yr period of white spruce regeneration in boreal mixedwood forest in Alberta, Canada. Our objective was to determine whether the timing of mast years relative to fire affects the density and timing of white spruce regeneration and the extent to which any such effects remain evident over time. We hypothesized that more regeneration occurs after mast-year fires than after non-mast-year fires because when a fire and mast year coincide, more seed is available when seedbeds are most receptive (the mast-year effect). We also hypothesized that an initial mast cohort persists as the dominant cohort over time after mast-year fires, but that this initial cohort is less important if there is a time lag between the fire and the next mast event.

METHODS

Study area and experimental design

The study took place in a 60 000-km^2 area of boreal mixedwood forest in east-central Alberta (Appendix A). We sampled fire-origin stands dominated by trembling aspen, balsam poplar (*Populus balsamifera* L.), and white spruce, although paper birch, jack pine (*Pinus banksiana* Lamb.), and black spruce (*Picea mariana* (Mill) BSP) were also present.

We identified years between 1959 and 1996 as mast or non-mast years within Alberta, primarily on the basis of provincial cone collection records (Alberta Tree Improvement and Seed Center, *personal communication*) and cone survey data (Kemp and Keith 1970). These results were corroborated by red squirrel trapping records (Todd and Giesbrecht 1979; Fred Neumann, Alberta Trappers Association, *personal communication*), which were then used to identify mast and non-mast years from 1941 to 1958 (Fig. 1; Appendix B). The number of red squirrels trapped in Alberta for a given year is correlated with provincial cone crops in that year ($r^2 = 0.911$, $P < 0.01$; Kemp and Keith 1970); populations peak in mast years and are much lower in non-mast years (Rusch and Reeder 1978). Peaks in cone or squirrel numbers were identified as mast years; we then chose the lowest year in the adjacent intermast period as a non-mast year. For field sampling we chose 1941, 1961, 1979, and 1991 as mast years, and 1942, 1958, 1980, 1981, 1982, 1992, and 1994 as non-mast years because accessible fires occurred in these years (Fig. 1). One fire was selected for most of the recent years and two fires were selected for 1941, 1942, 1961, and 1981. In cases where we only refer to the year, data from all fires of that year have been combined. We tested the influence of the length of delay between fire and the next mast year on white spruce density and age structure, using data from one fire that burned in a mast year (1979; 0-yr delay) and fires of similar age for which there was a 1-, 2-, or 3-yr delay after the fire until the next mast year (1982, 1981, and 1980, respectively). We identified 1983 as a mast year that could have contributed to regeneration in the sampled non-mast-year fires from 1980 to 1982, but no fires from 1983 could be sampled. All fires selected were larger than 200 ha and burned primarily between 1 June and 15 August (Appendix C).

Sampling design

Within each fire, we sampled a minimum of seven burned stands that were separated by 300 m to 15 km. These stands were randomly selected from a set of 20–30 stands that had pre-fire mixtures of primarily aspen and white spruce, canopy kill exceeding 95%, and a seed source within 100 m. Seed sources contained trees that were producing seed at the time of fire (i.e., ≥80 years old according to forest vegetation inventories), and in the canopy at the time of the fire according to historical air photos.

Sampling was conducted during the summers of 1998–2000. In each stand, three 5-m^2 plots were established in the burned area at both 20 and 100 m from the seed source; plots at each distance were randomly located between 8 and 20 m apart. In each plot, the density and height of all established spruce (≥1 yr old) were recorded. Spruce densities were also recorded within a 3-m radius of each plot center (28.3-m^2 plot).

In a minimum of three stands per fire, we collected for aging up to five live established spruce trees that were located nearest to the plot center.

Additional biotic and abiotic variables were measured within one 5-m^2 plot at each distance per stand (see Appendix D: Table D1). Percentage cover of vegetation and potential regeneration substrates were visually estimated. For each tree species, the number of live and dead individuals (post-fire regeneration) was recorded in the 28.3-m^2 plot, and percentage canopy cover for each species was estimated with a convex spherical densiometer. For the plots located 20 m from the seed source, we recorded the number of seed trees that occurred in unburned patches within 30 m, 60 m, and 100 m of the plot center. The direction of the sample plots from the seed source was also recorded.

To determine the timing of regeneration and address the greater error associated with aging older white spruce, the procedures in Peters et al. (2002) were used as follows: (1) trees from 1991, 1992, and 1994 fires were aged by counting rings at the root collar; (2) trees from 1979 to 1982 fires were aged by crossdating below ground with skeleton plots; and (3) trees from 1941 to 1961 fires were aged by crossdating below ground and above ground according to a master chronology (Appendix E: Fig. E1). These procedures were used to age ~15 trees per distance from a minimum of two stands per fire. The stands that were aged were randomly selected from all stands sampled in each fire.

Data analysis

To test whether stands originating from mast-year fires had more white spruce regeneration than stands originating from fires in years of low cone crop, all fires from mast years and years with very low cone crops between 1941 and 1994 (excluding 1980 and 1982, which had non-mast-year fires with moderate seed crops) were analyzed in a generalized linear model (GLM). Because the error distribution was over dispersed (McCullagh and Nelder 1983), counts of all white spruce from the 5-m^2 plots were modeled by quasi-likelihood estimation. Stands (rather than fires) were treated as the sampling unit because ''replicate'' fires were not available for many years and because fire intensity between stands is highly variable. The analyses were performed at the stand and the plot level. Variables (e.g., time since fire, mast vs. non-mast year, distance, direction and strength of seed source, dead wood, vegetation cover and composition; see Appendix D) were added to the model by a stepwise procedure until additional variables did not yield a significantly better model ($P < 0.05$ accepted as significant in ANOVA comparisons of models). All variables were tested for nonlinear effects using generalized additive models and a smoothing spline. Variables with significant nonlinear effects were modeled with a third-order polynomial function.

Model I ANOVAs (Sokal and Rohlf 1981) were used to compare white spruce density from the 28.3-m^2 plots in two ways: (1) between mast-year and non-mast-year fires paired by similar age (i.e., with planned comparisons of 1941 vs. 1942, 1961 vs. 1958, 1979 vs. 1981, and 1991 vs. 1992 and 1994); and (2) between fires with a 0-, 1-, 2-, or 3-yr delay after fire until the next mast year (fires in 1979, 1982, 1981, and 1980, respectively). Replicate stands (random effect) were nested within the fixed effect (e.g., mast vs. non-mast fire, and delay length) for each analysis. The Type IV sums of squares method was used for the ANOVA and the Tamhane's test was used for post-hoc comparisons (Sokal and Rohlf 1981). To determine which variables were the best predictors of white spruce density, a GLM analysis was performed on delay-length fires (0-, 1-, 2-, and 3-yr delay) using a step-wise procedure to test delay length, pre-fire composition, and other variables as described in Appendix D. The appropriate transformations were used to normalize data for all ANOVAs (Sokal and Rohlf 1981).

A one-tailed ANOVA was used to determine whether the proportion of regeneration originating from the first mast year after fire differed between fires with a 0–3-yr delay before a mast year. Tukey's test was used for post-hoc tests. A two-sided Kolmogorov-Smirnov test was used to test whether the timing of regeneration differed between stands within fires and between fires from 1979 through 1982. Bonferroni corrections were applied in all the pairwise Kolmogorov-Smirnov tests to maintain $\alpha = 0.05$. See Peters (2003) for detailed age structure comparisons for the 1941–1961 fires. S-Plus 2000 Professional Release, Version 2.1 (Mathsoft, Seattle, Washington, USA) was used for GLM analyses while SPSS Version 11.5 (SPSS, Chicago, Illinois, USA) was used for all other statistical tests.

RESULTS

Regeneration density relative to fire and mast years

Over the 59-yr period studied, current spruce densities were significantly (2.5 times) higher following mast-year fires (1941, 1961, 1979, and 1991) than following fires in years of low cone production (1942, 1958, 1981, 1992, and 1994; Fig. 2A; $P < 0.001$; Appendix D: Table D2). Spruce densities were significantly higher for mast-year fires than for non-mast-year fires of similar age for fires as old as 20 years (1991 vs. 1992 and 1994, $F_{1,24} = 11.8$, $P = 0.002$; and 1979 vs. 1981, $F_{1,23} = 17.8$, $P < 0.001$), and the difference was nearly significant for fires as old as 41 years (1961 vs. 1958; $F_{1,18} = 4.1$; $P = 0.057$); densities did not differ significantly at nearly 60 years after fire (1941 vs. 1942; $F_{1,28} = 0.154$; $P = 0.697$; Fig. 2A). The best predictors of white spruce density in stand-level models were related to seedbed deterioration (mast-year vs. non-mast-year fires), seed rain density (direction and distance from seed source, and the number of seed

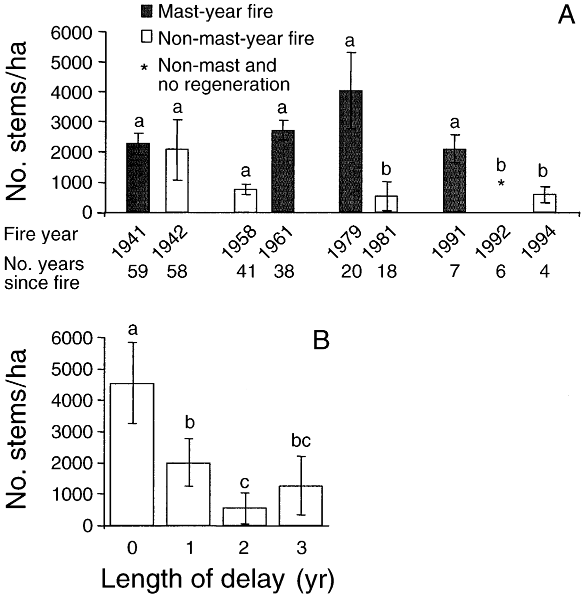

FIG. 2. White spruce densities (mean ± SE) for fires relative to the timing of mast years. (A) Densities in stands that burned in non-mast years (years of low cone crop) vs. mast years (fire occurred in year with large cone crop) over time. Data were obtained from two fires for the years of 1941, 1942, 1961, and 1981, and from one fire for 1958, 1979, 1991, 1992, and 1994 ($n \geq 7$ stands/fire). "Years since fire" is relative to the date of sampling. Significant differences between mast-year fires and non-mast-year fires of similar age are denoted by different letters. (B) Densities (mean ± SE) relative to the length of delay after fire before the 1983 mast year. Fires with a 1-, 2-, or 3-yr delay occurred in 1982, 1981, and 1980, respectively ($n = 2$ fires/yr). Densities for a 1979 mast-year burn (0-yr delay) are shown for comparison. Different letters above bars denote fires with significant differences ($P < 0.05$).

trees), and black spruce regeneration (Appendix D: Table D2). Plot-level models verified the importance of all significant predictor variables in the stand-level analysis (Appendix D: Table D2). Percentage cover of herbs, shrubs, tree species, and ground cover (mosses, litter) did not improve either the stand-level or the plot-level model.

The density of white spruce differed significantly among fires with different delay lengths before a mast year ($F_{3,51} = 4.4$, $P = 0.008$) and between stands with the same delay length ($F_{50\ 245} = 8.6$, $P = 0.008$). The fire coinciding with the 1979 mast year had significantly higher white spruce density than fires with a 1-, 2-, or 3-yr delay before the 1983 mast year (1982, 1981, and 1980, respectively; $P < 0.02$ in all cases; Fig. 2B). However, spruce density did not decline consistently with increasing delay length before a mast year. Ratios of regeneration density to seed tree abundance were much greater for the 1991, 1979, and 1961 mast-year fires than the 1–3-yr delay fires (82, 166, and 133 vs. 41, 27, and 38, respectively). In both the stand-level and plot-level analyses of fires with a 0-, 1-, 2-, and 3-yr delay before a mast year, the best predictors of white spruce density were delay length, number of seed trees, and distance and direction from seed source (Appendix D: Table D3). The percentage cover of grass, herbs, shrubs, and tree species did not improve the model.

Timing of regeneration

For fires up to 20 years old, the cohort from the first mast year after the fire was the most important (largest) in the two mast-year fires (Fig. 3A, B), in one fire with a 1-yr delay (Fig. 3C), and in one fire with a 2-yr delay (Fig. 3F). For fires with a 3-yr delay, the cohort from the first post-fire mast year was smaller than cohorts from several non-mast years preceding it (Fig. 3G, H). These age structures were based on belowground crossdating, which increased the estimated age by 1–10 yr per tree compared with ground-level ring counts (Appendix F). The proportion of regeneration originating from the first mast year declined significantly from 0.60 for mast-year fires to 0.38 for 1-yr delay fires, 0.20 for 2-yr delay fires, and 0.14 for 3-yr delay fires (one-tailed ANOVA, $F_{3,19} = 15.4$, $P < 0.05$ for all post-hoc comparisons). Mast years occurring four or more years after fire (e.g., 1987, 1991) did not contribute a large cohort for any of the 1979–1982 fires, and very little regeneration occurred 7–20 yr after fire (Fig. 3A, C–H).

For the 1979–1983 fires, we observed significant differences in age structure between fires with different delay lengths, but not between fires with the same delay length (Fig. 3). The age structure for the mast-year fire differed significantly from that of some 1- and 2-yr delay fires, both of which had limited regeneration before the cohort arising from the 1983 mast year (Fig. 3). Surprisingly, age structures were similar between the mast-year and 3-yr delay fires; this appeared attributable to the 1981 cohort that dominated the age structure for 3-yr delay (1980) fires, although this was a non-mast year (Fig. 3). There were no significant differences in the age structure between stands within 1-yr delay fires and within the 1980 Winefred Lake fire (3-yr delay). In contrast, we found significant variation between stands in both the 2-yr (1981 B fire) and the 3-yr delay fires (1980 Conklin Trail fire; Appendix G).

Overall, an initial mast cohort was less apparent for older fires, and initial regeneration periods appeared considerably longer in fires from 1941–1961 than for fires from 1979–1982 (Fig. 3 and Appendix E: Fig. E2, respectively). Crossdating helped to show the timing of regeneration better than ground-level ring counts; age underestimation increased from a mean of 2.7 years for 1979–1982 fires, to 6.0 years for 1941 and 1942 fires (Appendix F).

DISCUSSION

Our results suggest that the interaction between disturbance by fire and masting is key to white spruce regeneration and subsequent stand dynamics in the bo-

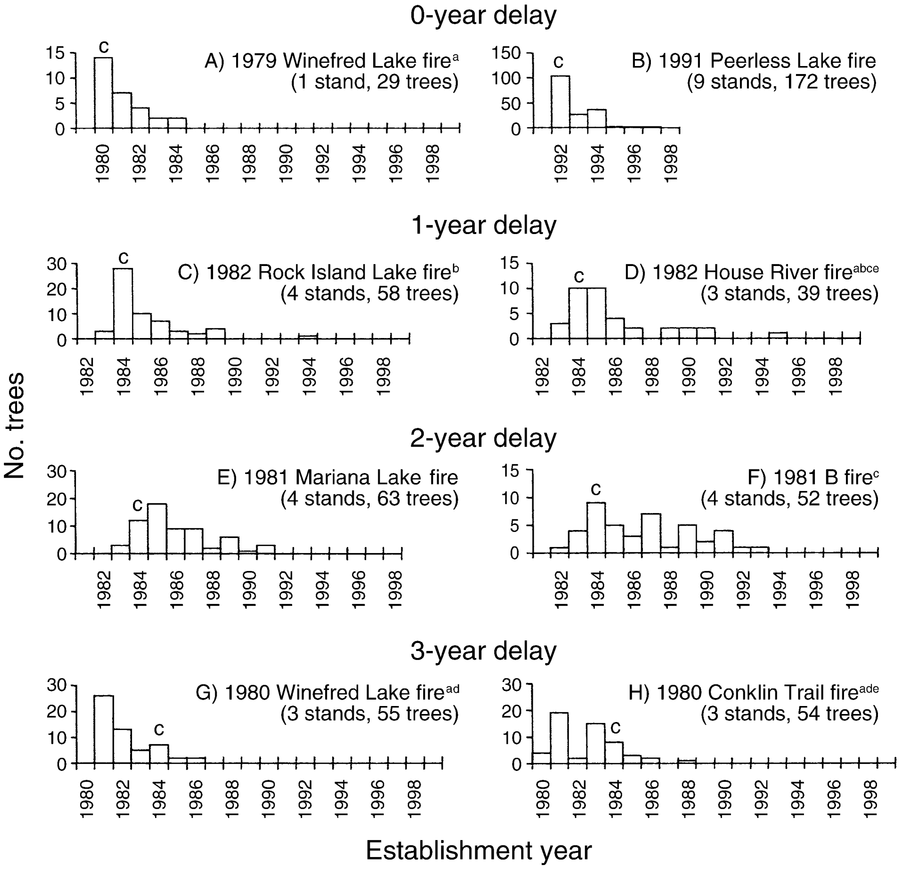

FIG. 3. White spruce regeneration timing relative to the length of delay before a mast year, for eight fires; sample sizes are given. Note the different *y*-axis scales. The first mast cohort is shown in all figures, one year after the mast year. All trees were crossdated below ground with skeleton plots, except trees from the 1981 Mariana Lake fire (graph E), which were aged at ground level. The 1979 and 1991 data (graphs A and B) were published in Peters et al. (2002). Age distributions of trees differ significantly between fires that do not have any of the same superscript letters (two-sided Kolmogorov-Smirnov tests were used; *P* is Bonferroni-corrected).

real mixedwood forest. We found significantly higher densities of white spruce in stands originating from fires that coincided with mast years than from fires coinciding with years of low cone crops (mast-year effect). Although a few studies have demonstrated that higher recruitment does occur in individual mast years (Taylor and Aarssen 1989, Sato 2000, Wurtz and Zasada 2001), the importance of masting at a regional scale (60 000 km^2 in our case) and for longer term stand dynamics has not previously been thoroughly explored. We discuss how the interaction between two factors, post-fire seedbed deterioration and masting synchrony, is essential to the occurrence of a widespread and long-lasting mast-year effect in white spruce.

A key factor in the importance of the fire × mast year interaction is the rapid deterioration of the seedbed after fire. Previous studies have reported that white spruce regeneration is restricted to a 3–5-yr window after fire because of seedbed deterioration (Zasada and Gregory 1969, Purdy et al. 2002). Our results provide three lines of evidence in support of a rapid and important decline in seedbed receptivity after fire. First, the significantly lower density of white spruce after non-mast-year vs. mast-year fires (1941–1994) suggests that for non-mast-year fires, seedbed receptivity had declined considerably by the time the next mast year occurred. Second, our analysis of regeneration density relative to delay length (1979–1982 fires) suggested there was a substantial decline in seedbed receptivity even within 1 yr after fire. This result should be interpreted cautiously, as it is based on only one series of recent fires and we had to use different mast years for the 0-yr delay fire than for the 1–3-yr delay fires. Thus, variation in seed rain between mast years may have contributed to this result (Nienstaedt and Zasada 1990). Nonetheless, 1–3-yr-delay fires all had much lower ratios of regeneration to seed tree abundance than 1991, 1979, and 1961 mast-year fires. Finally, the proportional contribution of the first mast cohort to total spruce regeneration declined rapidly with increasing delay length between a fire and the next mast year, further supporting rapid seedbed deterioration after fire. Confounding effects on absolute density include (1) differences in seed rain between mast years, (2) the effect of drought on seedling survival, and (3) fire intensity.

Our results further demonstrate that seed limitation, in addition to seedbed deterioration, affects age structure in white spruce. If substrate deterioration was the main factor controlling age structure, we would expect all age structures to be dominated by the cohort regenerating in the first year(s) after fire. Instead, many stands (53%) exhibited no regeneration in the immediate post-fire non-mast years, although this is when seedbeds are most receptive (Appendix G). Differences in timing of regeneration between the 1979 mast-year fire and similarly aged fires with 1- and 2-yr delays (1982 and 1981) also showed that seed availability has an important influence on age structure. Variation among stands within fires in the timing of initial establishment could suggest different rates of seedbed deterioration. Several factors relating to substrate deterioration and seed availability were also important predictors of white spruce regeneration density. Rapid seedbed deterioration likely augments the mast-year effect for white spruce as compared to species that are not as dependent on short-lived, disturbance-created regeneration microsites. Other masting species have less specific microsite requirements, permitting frequent recruitment (Taylor and Aarssen 1989, Sato 2000) and reduced reliance on a single mast cohort for successful regeneration.

Widespread masting synchrony leads to regional-scale effects of the fire × masting interaction on white spruce regeneration. The fact that a large initial mast cohort was seen in all recent mast-year and 1-yr delay fires (1991–1961), even though fires occurred up to 215 km apart, supports the assumption of mast year synchrony across large areas (Kemp and Keith 1970, Koenig and Knops 1998). In our study region cone crops of white spruce exhibited great variation in seed production between years (1998–2001) and showed less variation between locations in a mast year than in non-mast years (Peters 2003). Masting synchrony has been detected at large spatial scales among six conifer genera in North America (Koenig and Knops 1998). Our results suggest that, for those species for which regeneration is linked to disturbance, masting could have contingent historical effects on landscape structure and succession at regional scales.

Mast-year effects on the density of white spruce were long lasting. Forty years after fire, mast-year fires still had 2.5 times more spruce regeneration than non-mast-year fires, and crossdating verified that the first post-fire mast year created the largest cohort in mast-year fires. Wurtz and Zasada (2001) also observed a dominant mast cohort of spruce in a 27-yr-old shelterwood cut. The persistence of the mast-year effect suggests that when mast years occur in, or soon after, a burn year, the initial mast cohort is more important than regeneration in all subsequent mast and non-mast years.

Unavoidable aging inaccuracies no doubt interfered with our ability to detect the true strength of the mast-year cohort. For example, the first mast cohort after the 1981 Mariana Lake fire (a 2-yr delay) may have been larger than depicted; crossdating with skeleton plots would no doubt have resulted in higher age estimates, moving more trees into the mast-year cohort. If all trees in older stands could be aged accurately, age distributions would be shifted to higher abundance in older classes, and it is likely that a larger mast cohort would have thus been recognized in the 1941 and 1961 mast-year fires (Peters et al. 2002).

Although our results demonstrate the importance of the interaction between mast year and fire for white spruce, delayed regeneration is likely more important in stands lacking a mature seed source at the time of the fire (Lieffers et al. 1996). Regeneration on decayed logs permits later ingress; however, such trees may fail to reach reproductive maturity before the next stand-replacing fire (Peters 2003). Sites with little white spruce regeneration immediately after fire may have too few seed trees in the long term to maintain the white spruce population. Thus, the coincidence of fire and mast years may be critical in maintaining white spruce populations in the boreal mixedwood forest of Alberta. Relationships between fire and masting history could contribute to temporal stochasticity in forest composition over several fire cycles, creating a shifting mosaic in forest composition. Similar interactions may be observed for other masting species for which regeneration is linked to disturbance. In systems where the regeneration of masting species affects plant community dynamics and habitat suitability for wildlife, the disturbance × regeneration interaction may be a key to biodiversity.

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APPENDIX A

A diagram of the study area in northeastern Alberta showing the dates and locations of study fires is available in ESA's Electronic Data Archive: *Ecological Archives* E086-093-A1.

APPENDIX B

A description of white spruce cone crops that were rated in Alberta-based forestry publications, as well as supplemental information on interpreting squirrel harvest records, is available in ESA's Electronic Data Archive: *Ecological Archives* E086-093-A2.

APPENDIX C

Characteristics and locations of study fires, based on provincial fire inventories, are available in ESA's Electronic Data Archive: *Ecological Archives* E086-093-A3.

APPENDIX D

Variables tested in generalized linear models predicting white spruce regeneration, as well as tables showing the results of analyses, are available in ESA's Electronic Data Archive: *Ecological Archives* E086-093-A4.

APPENDIX E

Figures showing age structures for trees in 1961, 1942, and 1941 fires, and one of the master chronologies used for crossdating, are available in ESA's Electronic Data Archive: *Ecological Archives* E086-093-A5.

APPENDIX F

A table presenting age underestimation in white spruce between ground-level ring counts and crossdating at the root collar is available in ESA's Electronic Data Archive: *Ecological Archives* E086-093-A6.

APPENDIX G

A figure showing the variability in timing of white spruce regeneration between stands within fires is available in ESA's Electronic Data Archive: *Ecological Archives* E086-093-A7.