

Decadal observations of tree regeneration following fire in boreal forests¹

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Abstract: This paper presents data on early postfire tree regeneration. The data were obtained from repeated observations of recently burned forest stands along the Yukon – British Columbia border and in interior Alaska. Postfire measurements of tree density were made periodically for 20–30 years, providing direct observations of early establishment patterns in boreal forest. Recruitment rates of the dominant tree species in both study areas were highest in the first 5 years after fire, and additional net establishment was not observed after 10 years. The postfire population of spruce (*Picea mariana* (Mill.) BSP and *Picea glauca* (Moench) Voss s.l.) remained constant after the first decade in the two study areas. Populations of aspen (*Populus tremuloides* Michx.) and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) both declined after 10 years in mixed-species stands along the Yukon – British Columbia border. Mortality rates of aspen and pine were positively correlated with their initial densities, indicating that thinning occurred as a density-dependent process. At all sites, measurements of stand density and composition made early were highly correlated with those made late in the monitoring period, indicating that patterns of stand structure initiated within a few years after fire are maintained through subsequent decades of stand development.

Résumé : Cet article présente des données sur la régénération établie peu de temps après feu, obtenues à partir d'observations répétées dans des peuplements forestiers récemment brûlés, situés le long de la frontière entre le Yukon et la Colombie-Britannique et à l'intérieur de l'Alaska. Des mesures de la densité des arbres ont été effectuées périodiquement au cours des 20 à 30 premières années après feu, fournissant ainsi des observations directes des patrons d'établissement de la régénération dans la forêt boréale. Le taux de recrutement des espèces forestières dominantes dans les deux aires d'étude était à son niveau le plus élevé lors des cinq premières années après feu. Aucun nouvel établissement net n'a été observé après 10 ans. Après la première décennie, la dimension des populations d'épinettes (*Picea mariana* (Mill.) BSP et *Picea glauca* (Moench) Voss s.l.) établies après feu est demeurée constante dans les deux aires d'étude. Dans les peuplements mélangés situés le long de la frontière du Yukon, les populations de peuplier faux-tremble (*Populus tremuloides* Michx.) et de pin tordu latifolié (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) ont toutes deux décliné après 10 ans. Les taux de mortalité du peuplier et du pin étaient positivement corrélés avec leur densité initiale, ce qui indique que l'éclaircie suit un processus dépendant de la densité. Dans toutes les stations, il y a eu de fortes corrélations entre les mesures de la densité et de la composition des peuplements effectuées tôt dans la période de suivi et celles effectuées tard. Cela indique que les patrons de la structure du peuplement initiés quelques années après feu se maintiennent tout au long des décennies subséquentes du développement du peuplement.

[Traduit par la Rédaction]

Introduction

Fire disturbance is a major factor driving patterns of vegetation structure and composition in boreal forest landscapes. Much of the boreal forest in North America is subject to short fire-return intervals of 50–150 years, and most forests in this region are at some stage of recovery following fire (Payette 1992). An understanding of variations in boreal vegetation composition therefore requires knowledge of patterns of postfire succession. To date, most information on

boreal succession comes from chronosequence studies comparing communities of different ages (e.g., Carleton and Maycock 1978; Yarie 1983; Cogbill 1985; Foster 1985; Zoladeski and Maycock 1990) or stand reconstructions inferring past growth and establishment patterns from the current stand-age structure (Johnson and Fryer 1989; Sirois and Payette 1989; Bergeron and Charron 1994; Johnson et al. 1994; Galipeau et al. 1997; Gutsell and Johnson 2002). Although these methods have provided important information on successional patterns, their utility relies on assumptions

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Table 1. Description of study sites.

Study area	Fires	Location	Area burned (ha)	Sites monitored (n)	Plot layout	Dates of measurement (years postfire)
Southeastern Yukon	Tom Creek	60°13'N, 128°55'W	8 000	11	Single 100-m ² plots	1–3, 5, 10, 19
	Fireside	59°40'N, 127°09'W	182 000	20		
	Lower Post	59°58'N, 128°00'W	1 200	5		
Interior Alaska	Wickersham 1971 wildfire	65°10'N, 147°54'W	6 313	5	Grid of twenty 4-m ² plots	1–10, 15, 31
Interior Alaska	Wickersham 1978 experimental burns	65°11'N, 147°52'W	2 (per burn)	7	Grid of twenty 4-m ² plots	1–3, 24

that are difficult to validate and often violated. Chrono-sequence studies, for example, assume that variations in initial conditions have little effect on observed patterns, which is unlikely when establishment is sensitive to initial seed availability or substrate quality (Zasada et al. 1992) or when variations in species composition influence other ecosystem processes (Fastie 1995). Likewise, stand reconstructions depend on assumptions that ages of individual trees can be correctly determined and that age-dependent variations in survivorship are adequately detected and accounted for in the analysis. Using standard coring procedures to determine the ages of boreal trees can introduce large biases (DesRochers and Gagnon 1997; Parent et al. 2000; Wong and Lertzman 2001; Gutsell and Johnson 2002), and improved accounting of mortality may alter the interpretation of age structures (Johnson and Fryer 1989; Johnson et al. 1994). Alternative approaches using different methodologies are therefore valuable in interpreting the general body of research on postfire succession. This study presents data gathered from long-term observations of in situ postfire succession measured in boreal forest stands for two to three decades after fire. We use these data to test predictions of the timing of tree recruitment and mortality derived from stand reconstructions and to evaluate the importance of early establishment patterns to subsequent stand development.

Materials and methods

This study uses data from two long-term monitoring programs, one along the Yukon – British Columbia border near southeastern Yukon (here referred to as SE Yukon) and another in interior Alaska, near Fairbanks. Both studies were initiated to monitor long-term changes in vegetation following fire and currently encompass 20–30 years of repeated observations in permanent plots.

Southeastern Yukon study area

Long-term monitoring plots were established in 1983 following three large fires near Watson Lake, Yukon, in 1982 (Oswald and Brown 1990). Each of the fires occurred in the summer of 1982 and burned a cumulative area of about 190 000 ha along the Yukon – British Columbia border (Table 1). The forest types included in the study were dominated by black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss s.l.), lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), and trembling aspen (*Populus tremuloides* Michx.). Paper birch (*Betula papyrifera* Marsh.), balsam poplar (*Populus balsami-*

fera L. subsp. *balsamifera*), and Alaskan larch (*Larix laricina* (Du Roi) K. Koch) were occasionally present in the prefire forest. Soils in the study area primarily consisted of Regosols and Brunisols, with occasional Gleysol types in wetter areas (Agriculture Canada 1987; Oswald and Brown 1990).

Vegetation measurements were made in 1983, 1984, 1985, 1987, 1992, and 2000–2001 (1, 2, 3, 5, 10, and 19 years postfire) in 36 permanent plots established by Forestry Canada the year following fire. Sites were selectively located to include a variety of soil types, topography, and prefire vegetation within each burn. The plots were established along road corridors and were originally located at least 50 m from a road right-of-way. These distances have changed for some of the plots, as a result of subsequent rerouting of the Alaska Highway.

At each site, measurements were made within a single 10 m × 10 m plot, which was divided into 5 m × 5 m sub-plots. Measurements during the first 5 years after fire were taken by researchers at Forestry Canada and are detailed in an earlier report (Oswald and Brown 1990). Vegetation observations in each year consisted of counting and measuring the heights of all tree seedlings within a plot and visually estimating percent cover of vegetation. Observations were made separately in each 5 m × 5 m subsection of the main plot and then summed or averaged to obtain an estimate for the whole plot. Seedlings of black and white spruce were pooled into a generic spruce category because of the difficulty in distinguishing between young black and white spruce seedlings. Seedling counts were based on the number of individual stems coming out of the soil, and main stems that branched above the soil surface were counted as a single individual. Tree height for each stem was set as the distance from the ground to the apical bud, measured with a metre stick or telescoping tree-height pole. An eight-class, semi-logarithmic cover scale (Mueller-Dombois and Ellenberg 1974) was used for visually estimating vegetation cover for groupings of vegetation growth forms (trees, shrubs, herbs).

Interior Alaska study area

The Alaskan monitoring plots were located along the ridge and in the valley of Wickersham Dome, a small mountain adjacent to the Eliot Highway and about 50 km north of Fairbanks, Alaska. The vegetation in the area was strongly dominated by black spruce, with occasional trembling aspen or birch trees. Most of the area was underlain by permafrost, and in mature stands the mineral soil was covered with a thick moss mat (Viereck and Dyrness 1979). Two sets of

sites are included in the study, one set that was burned by a natural wildfire in 1971 and a second set that was burned by a series of experimental burns in 1978 (Table 1).

The 1971 wildfire burned the hillslopes and valley of Washington Creek, adjacent to Wickersham Dome (elevation 325–400 m above sea level (a.s.l.)). Five sites were established for monitoring vegetation recovery following fire: two in a lightly burned area that had live trees that survived the fire and three in more severely burned areas where all the trees had been killed (Viereck and Dyrness 1979). The prefire stands were composed almost entirely of black spruce. The experimental burns in 1978 were located along the southwest slopes of Wickersham Dome, near the ridgetop (elevation 490–550 m a.s.l.). Seven experimental burns, about 2 ha each, were ignited on different days in July and August 1978 and differed in level of severity (Dyrness and Norum 1983). Prefire vegetation in these plots was largely black spruce, but some sites had a small component of trembling aspen or paper birch.

Postfire vegetation changes at the Wickersham sites were monitored in a grid of 20 sample points laid out at 10-m intervals along four or five parallel transects at each site (Table 1). Seedling counts at each sample point were made in circular, 4-m² (114-cm radius) plots, marked with a metal stake at the centrepoint. Measurements in the 1971 wildfire were made yearly for the first 10 years after fire and then made again at 15 (1986) and 31 (2002) years after fire. The vegetation plots in the seven 1978 experimental burns were measured annually for the first 3 years after fire and then not measured again until 2002, at 24 years after fire. Measurements of the Wickersham plots before 2002 were conducted by the Institute of Northern Forestry at the University of Alaska.

Statistical analysis

Only summary data tables were available for the first 3 years of observations in the SE Yukon plots, so we did not perform any statistical analyses on data collected during that period. The SE Yukon data set was also missing data for year 10 in four plots at the Fireside burn site. These plots were excluded from any time-series or pairwise analyses that included data from year 10. We confined our analyses of establishment patterns to plots reaching more than four stems of a given species on at least one sample date. Total stem counts or mean cover values across the four subplots were used for analyses of the SE Yukon data. Means from the twenty 4-m² plots within a site were used for analyses of the Wickersham Dome data.

The distributions of stem-count data for each species tended to be highly skewed with large outliers, and we were frequently unable to transform these data to meet the assumptions of parametric statistics. In addition, some of our data sets had small sample sizes, making it difficult to assess departures from normality or homoscedasticity. We therefore used nonparametric tests for our statistical analyses (Potvin and Roff 1993; Conover 1999). Data presented in the figures represent the original data, which were then rank-transformed for statistical tests. We used Wilcoxon signed-ranks tests (equivalent to paired *t* tests) to test for significant positive or negative changes in species density between measurement years 10 and 19. Thinning was estimated as the ab-

solute change in stem counts between years 10 and 19. We used Spearman's rank correlation coefficients to test for correlations between data series. To compare patterns of net establishment or mortality across species and plots, we standardized tree-seedling counts at each measurement date by dividing the observed value by the maximum count observed in that plot over the entire record. In this study, net establishment refers to the period or amount of population growth occurring between the disturbance event and the point of maximum population density, whereas net mortality indicates a period or amount of population decline following the point of maximum density.

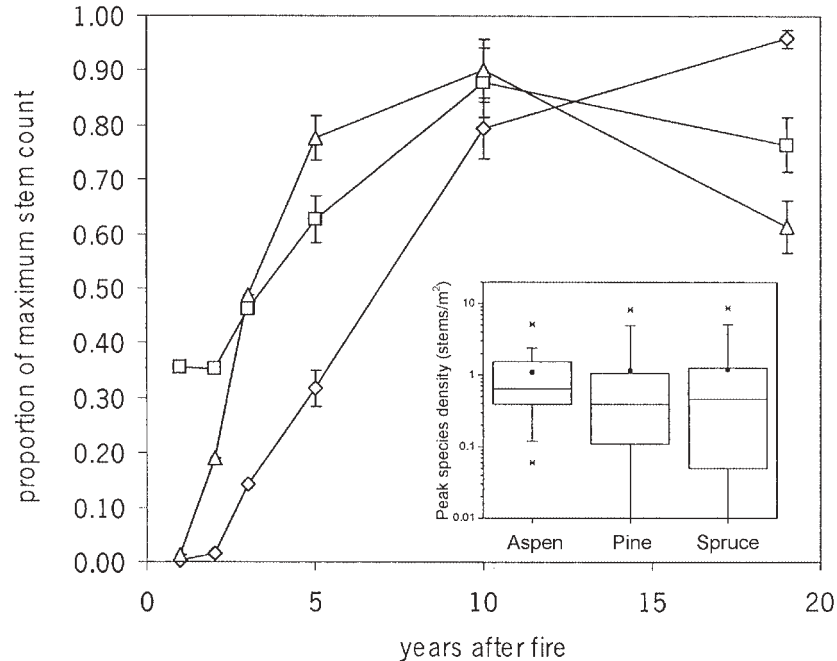
Results

In the SE Yukon, maximum stem densities of aspen, pine, and spruce measured within the 20-year observation period spanned three orders of magnitude (Fig. 1). Pine and spruce densities in individual plots exceeded 8 stems/m², and aspen densities reached 5 stems/m². More commonly, densities of 0.5–0.6 stems/m² were observed for the three species. In SE Yukon, stands with high densities of pine also tended to have high densities of spruce (Spearman's $r_s = 0.54$, $p = 0.0014$, $n = 32$), but variations in aspen density were uncorrelated with conifer densities. Mean heights (\pm SE) of the three species measured 19 years after fire were 204 ± 26 , 224 ± 30 , and 52 ± 5 cm for aspen, pine, and spruce, respectively. Ranges of mean heights across the plots were 20–650 cm for aspen, 16–686 cm for pine, and 18–126 cm for spruce. Variations in species heights were not correlated with variations in either total tree density or individual species density ($p > 0.1$).

Seedling establishment of pine and aspen in SE Yukon peaked within 10 years after burning and reached 50% of the maximum stem counts for those species within 3 years after fire (Fig. 1). Spruce counts in these plots did not reach 50% of maximum counts until 5–10 years after fire. Between years 10 and 19 of the observation period, densities of pine and aspen declined significantly (Wilcoxon's $S = -103$ and -218.5 , $p < 0.0001$, $n = 25$ and 32 , respectively), indicating the onset of net mortality for these species. In contrast, spruce densities did not change significantly between years 10 and 19 ($S = 64.5$, $p = 0.08$, $n = 26$). By year 19, aspen stem densities had thinned to a level below that observed in year 5 ($S = -144.5$, $p = 0.003$, $n = 32$), whereas pine densities in year 19 did not significantly differ from year 5 densities ($S = 58.5$, $p = 0.095$, $n = 25$; Fig. 1). Thinning rates of pine and aspen in the second decade after fire were significantly correlated with stem densities of the same species in year 10 ($r_s = 0.81$ and 0.78 , $p < 0.001$, $n = 25$ and 32 for pine and aspen, respectively), such that the highest mortality rates occurred in plots with the greatest initial densities of that species. Thinning rates of pine and aspen were not correlated with percent cover of trees, shrubs, or total vegetation or with stem densities of other species ($p > 0.1$).

In Alaska, maximum stem densities of black spruce at the Wickersham 1971 burn ranged from 1 to 9 stems/m² (Fig. 2). Black spruce constituted 98% of the postfire tree seedlings that established at these sites. The highest densities among the 1971 plots occurred in the two low-severity areas containing mature trees that survived the fire. The site

Fig. 1. Patterns of seedling establishment after fire in the southeastern Yukon plots. The main graph shows the mean (± 1 SE) proportion of aspen (triangles), pine (squares), or black and white spruce (diamonds) stems established at a given time, standardized relative to the maximum observed density in each plot. Boxplots (insert) show the distribution of maximum observed densities of aspen, pine, and spruce from the 36 permanent plots. Note the logarithmic y-axis scale. Within the boxes, the sample median is designated as a horizontal line; the mean is shown as a black dot. Bars extending from the box encompass 95% of the observations, and additional ticks show extreme observations.



with the lowest observed densities (H3) had no surviving trees and was at a higher elevation on the valley sides than the other four sites, potentially reducing seed rain at H3 compared with the other sites. Average establishment patterns in the Wickersham 1971 burn sites showed that 50% of the net spruce establishment occurred within 3 years after fire (Fig. 2). Many of the sites experienced a sharp decrease in stem counts in year 4, followed by a period of continued net establishment until about 10 years after fire. After 10 years, spruce densities remained nearly constant for the following two decades. Mean spruce heights measured 31 years after fire in the 1971 burn were 60 ± 4 cm (range in plot means, 30–106 cm). In the 1978 burn, mean heights measured 24 years after fire were 56 ± 5 cm (range, 34–116 cm) for spruce, 182 ± 19 cm (128–270 cm) for birch, and 82 ± 18 cm (29–154 cm) for aspen. Stem counts in the Wickersham 1978 burns were made too infrequently for estimating the temporal pattern of seedling establishment at those sites.

Within a study area, patterns of relative tree density and composition that were established within a few years after fire remained stable for the duration of the observation periods. In SE Yukon, rankings of stands based on total tree densities were highly consistent between observations made 5 years after fire and those made 19 years after fire ($r_s = 0.86$, $p < 0.0001$, $n = 32$; Fig. 3). This pattern was also true at the species level. Spruce densities measured in year 3 (Wickersham 1978 burns) or year 5 (SE Yukon and Wickersham 1971 burns) were strongly correlated with densities measured 24, 19, or 31 years after fire, respectively ($r_s = 0.89$, 0.92 , and 0.81 ; $p = 0.007$, 0.0001 , and 0.10 ; $n = 7$, 32 , and 5 ; Fig. 3). This correlation was only apparent for

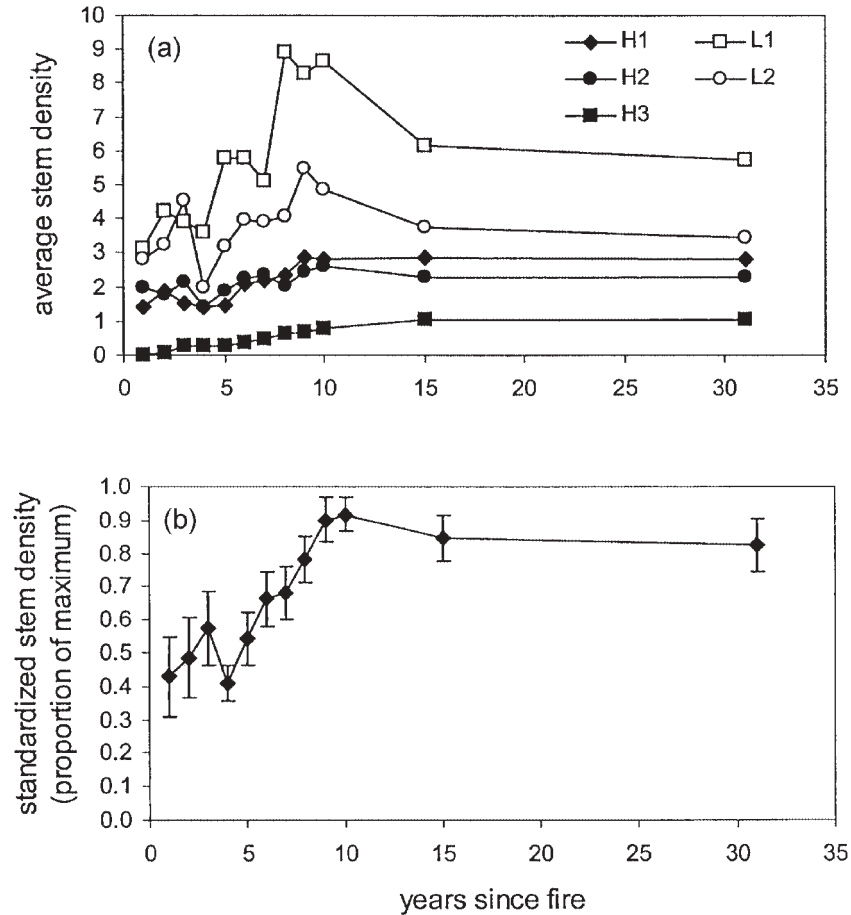
stands within a study area, as the relative changes in stem densities (equivalent to the slope of the regression line) varied for different sites. The nonsignificant correlation observed for the Wickersham 1971 burn appears to be more a function of the low sample size ($n = 5$) than of a weak relationship (Fig. 3). Patterns of relative species composition observed shortly after fire were also highly consistent with composition patterns observed later in succession (Fig. 4). For example, the proportion of deciduous individuals within a stand was significantly correlated between years 5 and 19 in SE Yukon ($r_s = 0.95$, $p < 0.0001$, $n = 32$) and between years 3 and 24 in the Wickersham 1978 burns ($r_s = 0.82$, $p = 0.02$, $n = 7$). The relative proportions of conifers that were pine and spruce were also significantly correlated between years 5 and 19 in SE Yukon ($r_s = 0.75$, $p < 0.0001$, $n = 29$).

Discussion

The patterns of recruitment we observed are consistent with data from stand reconstructions showing a large pulse of postfire tree recruitment followed by several decades of low or no recruitment (Johnson and Fryer 1989; Sirois and Payette 1989; Johnson et al. 1994; DesRochers and Gagnon 1997; Galipeau et al. 1997; Lavoie and Sirois 1998; Gutsell and Johnson 2002). Our data support studies indicating that the majority of tree establishment occurs within 3–7 years after fire (Johnson and Fryer 1989; St-Pierre et al. 1992; Johnson et al. 1994; Turner et al. 1997; Lavoie and Sirois 1998; Charron and Greene 2002; Gutsell and Johnson 2002).

The time-series data of species density in this study indicate that aspen and pine experience the onset of thinning within the second decade of stand development. Stand re-

Fig. 2. Black spruce seedling establishment over time following the 1971 Wickersham fire. (a) Seedling counts for individual plots. Plots H1–H3 are high-severity plots, with complete stand mortality; and L1–L2 are low-severity plots, with some surviving trees. (b) Mean (± 1 SE) seedling counts standardized to the maximum density observed in each plot.

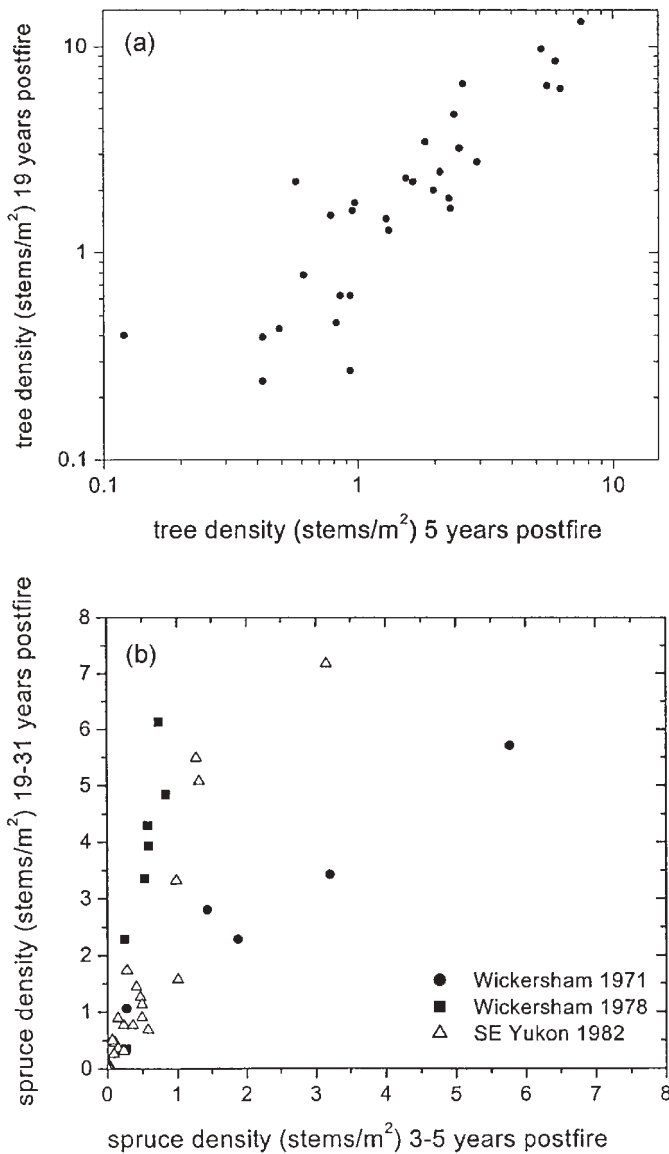


constructions of lodgepole pine in the Canadian Rockies show a similar onset of thinning in the second or third decade after fire (Johnson and Fryer 1989). In contrast, our observations of initiation of aspen thinning more than 10 years postfire conflict slightly with other studies that show aspen net mortality occurring almost immediately after establishment (Zasada et al. 1992; Greene and Johnson 1999). This difference in the timing of mortality may derive from a higher proportion of aspen established from seed (with a slower initial rate of growth) in our plots, compared with the predominantly asexually regenerating stands described in the literature (Zasada et al. 1992; Greene and Johnson 1999). In many of our plots, there were no detectable aspen present in prefire stands or surroundings (Oswald and Brown 1990), suggesting that aspen establishment in these plots came from seed. The smaller initial size of seed-originating aspen may allow for a longer growth period before density-dependent thinning starts. However, our mean estimate of aspen density (0.6 ± 0.1 stems/m²) after 19 years in SE Yukon is close to the predicted density of 0.9 stems/m² obtained from the thinning curve presented by Greene and Johnson (1999) for asexually produced aspen stems. This similarity suggests that thinning trajectories converge for seed- and sprout-originating stems.

We found that rates of mortality were density dependent for both aspen and pine, suggesting that self-thinning had

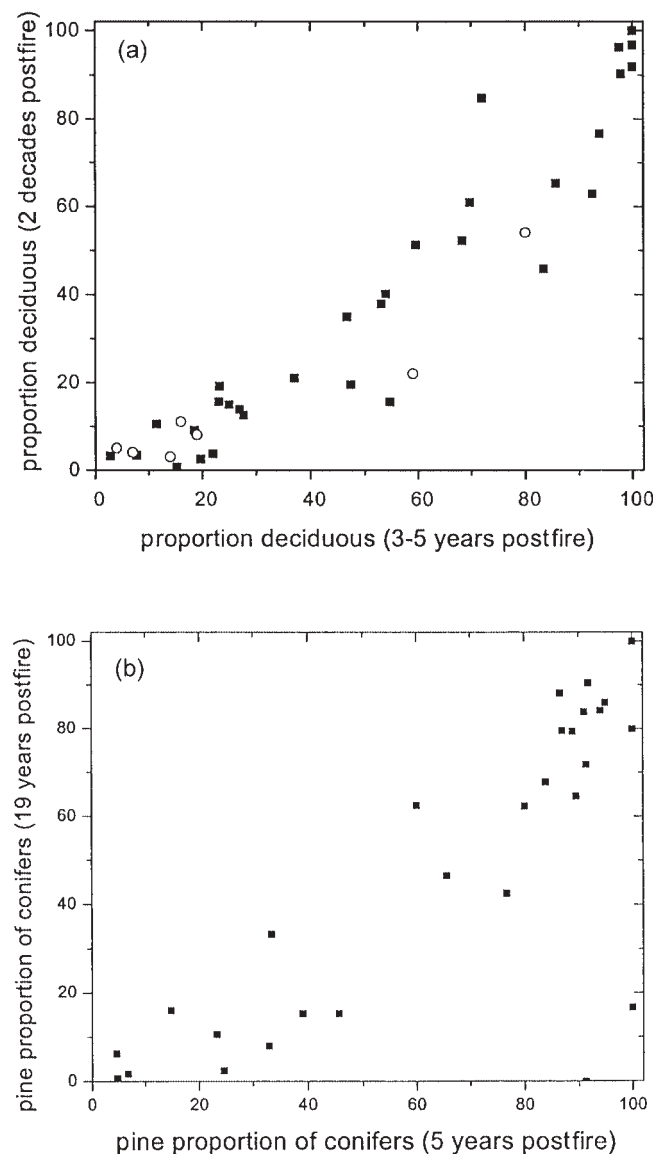
begun for these species. Thinning rates were positively correlated with initial densities within a species, but not with density or percent cover of trees or shrubs. This pattern indicates that the density dependence is operating at an intra-specific level, even when other species are present in the canopy. Dead pines at several of our sites showed evidence of infection by the western gall rust (*Peridermium harknessii* J.P. Moore), suggesting that pathogen infection contributed to the density-dependent pine mortality. The strong correlations we observed between species densities measured a few years after fire and those measured two or three decades after fire support the hypothesis that early patterns of tree establishment are a strong driver of stand structure (Sirois and Payette 1989). Although we observed periods of both net population growth and decline in our measurements, relative patterns of species density or composition within a study area were maintained over time, suggesting that future stand composition could be predicted from observations made early in succession. Stand reconstructions have shown that continued low levels of tree establishment may occur as a stand ages (Carleton 1982; Johnson and Fryer 1989; Sirois and Payette 1989; Johnson et al. 1994; Gutsell and Johnson 2002), but these later cohorts also experience high rates of mortality (Johnson and Fryer 1989; Johnson et al. 1994). As a result, the early postfire cohorts usually dominate the canopies of mature

Fig. 3. Relationships between early and late postfire measurements of tree densities. (a) Total stem density measured in the southeastern Yukon burns (years 5 and 19 postfire). Note the logarithmic axes. (b) Spruce (black and white pooled) stem density measured in the southeastern Yukon 1982 burns (years 5 and 19 postfire), the Wickersham 1971 burn (years 5 and 31 postfire), and the Wickersham 1978 burns (years 3 and 24 postfire).



stands (Johnson and Fryer 1989; Johnson et al. 1994; DesRochers and Gagnon 1997; Lavoie and Sirois 1998; Gutsell and Johnson 2002). Successional changes in canopy composition thus appear to arise as a result of species differences in growth rates and mortality, rather than differences in the timing of establishment (Gutsell and Johnson 2002; however, see Galipeau et al. 1997 and Bergeron 2000 for exceptions in the case of balsam fir (*Abies balsamifera* (L.) Mill.)). Given these successional dynamics, factors that affect postdisturbance recruitment should play a central role in driving landscape patterns of boreal forest vegetation. As a result, monitoring and manipulation of early seedling estab-

Fig. 4. Relationships between early and late postfire measurements of tree composition. (a) Deciduous stems as a proportion of total trees in the southeastern Yukon 1982 burns (solid squares; years 5 and 19 postfire) and Wickersham 1978 burns (open circles, years 3 and 24 postfire). (b) Pine stems as a proportion of total conifers in the southeastern Yukon burns (years 5 and 19 postfire).



lishment patterns may provide powerful tools for applied management of boreal forest stands.

In conclusion, this study provides additional independent support for the generalization that the majority of boreal tree recruitment occurs within a short (3–10 year) period after fire. Repeated seedling counts have shown that density-dependent thinning of the fast-growing species may be initiated within the second decade after fire. Despite the early onset of mortality, patterns of stand density and composition observed within 5 years after fire strongly predict patterns observed two or three decades after fire. This suggests that landscape variations in forest composition will be strongly

influenced by factors that affect postfire recruitment and that observations of early establishment patterns are likely to provide powerful insights into future stand development.

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