Picea glauca dynamics and spatial pattern of seedlings regeneration along a chronosequence in the mixedwood section of the boreal forest

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Abstract – We studied Picea glauca dynamics in the boreal forest of Saskatchewan, Canada, using 35 stands ranging from < 1 to > 200 y after fire. We determined the spatial pattern and the importance of seedbed conditions to the recruitment of P. glauca. Basal area increased along the chronosequence peaking at 110 y after fire (51.5 m² ha⁻¹). The ratio of softwood to hardwood increased from 0.03 (16 y) to 17.0 (172 y). Picea glauca tree density increased with stand age, highest densities were observed in a 172 y stand (1413 stems ha⁻¹). Picea glauca dominated the canopy between 93 and 172 y after fire. Picea glauca snags appeared about 66 y after fire, and remained relatively low in density until 160 y. Saplings were present at varying densities along the chronosequence. Seedlings established immediately after fire and exhibited bimodality with lowest densities observed between 110 and 125 y. Analysis with Ripley’s K, showed that seedlings were mainly distributed at random in young stands but were clumped at a distances < 12 m in old stands. In young stands, the majority of seedlings regenerated on the organic layer (LFH 73%), while recruitment was almost exclusively on logs in old stands (94%). Picea glauca regeneration depended on propagule availability and seedbed characteristics at early stand age. Logs and the resultant canopy gaps formed, appear to be critical for P. glauca regeneration in mature and old stands.

Picea glauca / boreal forest / stand dynamics / spatial pattern / Ripley’s K

1. INTRODUCTION

White spruce (Picea glauca (Moench) Voss) is one of the most widely distributed conifers in North American boreal forest. White spruce extends from Alaska, where it is the dominant species in the Brooks Range at the northern treeline [14] to Newfoundland in the east and from the treeline south to Montana and the New England States [1]. Fire is the major natural ecological factor controlling structure, function and composition in the western boreal forest of Canada [17]. The change in...
structure of boreal forest along a chronosequence after disturbance has been described by Bergeron and Dansereau [6], Jarvis et al. [23], Rowe [34], Thorpe [36] and Vierreck [39], among others. The speed of tree regeneration following disturbances depends on many factors including seed availability, disturbance type, and seedbed characteristics [17]. In general, on mesic sites in the mixedwood section of the boreal forest, the shade intolerant, fast-growing trembling aspen (Populus tremuloides (Michx.)) and other deciduous hardwoods regenerate readily following disturbance and quickly dominate the canopy [5]. On sites where the organic layer has been removed, white spruce (Picea glauca (Moench) Voss) seedlings may establish if seeds are available [24]. Any established white spruce seedlings are usually overtopped by aspen and remain for decades in subordinate position until canopy gaps are formed [28]. During the this period (around 80 y, [24]), trembling aspen dies back and white spruce is released from the understory, assuming dominance in the stand. Elliot-Fisk [11] lists some of the environmental changes that take place along the chronosequence in the boreal forest in response to canopy closure. These include an increase in thickness of the organic layer or the LFH (Litter, Fermented and Humus layers), and decreases in available nutrients, soil temperature, and soil drainage, resulting in anaerobic conditions and an increase in frost heave and thrust.

The mixedwoods are the most productive and managed sections in the boreal forest ecosystems [8]. In the last two decades, there has been a rapid move to using ecosystem based approaches that mimic natural stand dynamics in forest management and restoration in the boreal forest [19]. To mimic natural stand dynamics, it is essential to understand the ecology and dynamics of boreal species. While there is a rich body of literature on the survival and seedbed characteristics of boreal species like black spruce (Picea mariana) and jack pine (Pinus banksiana) [18], there has been little comparable work done on the recruitment, spatial distribution and seedbed preferences of P. glauca [7], the most widely distributed and economically important conifer in North American boreal forest. In this paper, our objectives are to describe the population dynamics of white spruce through extensive sampling of trees, saplings, seedlings, and snags following fire in the mixedwood section of the boreal forest. Further, we quantitatively characterize the spatial pattern of seedlings and the importance of seedbed conditions to the success of recruitment and survival of white spruce along a 200 year chronosequence.

2. METHODS

2.1. Study area

The study area was located in the mixedwood section of the southwestern boreal forest of Saskatchewan, Canada. The area falls between 53° 38’ and 54° 41’ N latitude, and 105° 00’ and 106° 20’ W longitude. The climate is cool continental, characterized by long cold winters and short warm summers. Monthly average temperatures vary from −20 °C in January to 17 °C in July and the annual average precipitation is around 450 mm [4] with approximately 70% falling as rain from June through August [20]. Soils are mainly orthic gray luvisols and brunisolic gray luvisols; a more detailed description of soil characteristics is provided by Thrasher-Haug [37]. The vegetation on mesic sites is dominated by white spruce (Picea glauca (Moench) Voss), balsam poplar (Populus balsamifera L.) and paper birch (Betula papyrifera Marsh.). Important understory species are bunchberry (Cornus Canadensis L.), twin flower (Linnea borealis L.), sarsaparilla (Aralia nudicaulis L.), bishop’s cap (Mitella nuda L.) and dewberry (Rubus pubescens Raf.) [4, 37].

With the use of forest inventory and topographic maps, 35 stands were selected in and around the Prince Albert Model Forest (PAMF), a member of the Canada Model Forest Network. PAMF encompasses 315,000 ha in the mixedwood section of the boreal forest. PAMF includes land situated within a National park, a reserve land, and a Crown land. The selected stands spanned a chronosequence ranging from less than one year to 201 y after fire. Stand selection was based on topography, soil characteristics, time since fire, and species composition. Time since fire was estimated by measuring ages of the largest overstory white spruce and aspen and/or taken directly from forestry records (for more details see Thrasher-Haug [37]).

2.2. Picea glauca population dynamics

In each stand, a 40 m × 20 m plot was established and further divided into 32 quadrats of 5 m × 5 m. Tree density (height > 4 m) and diameter at breast height (dbh, cm) of the dominant tree species (Picea glauca, Populus tremuloides and Abies balsamea) were recorded, and basal area was calculated. White spruce (P. glauca) tree height was measured with an Abney hand level [22]. Picea glauca sapling (height 0.5–4 m), seedling (height < 0.5 m), and snag (standing dead; height > 4 m) densities were also recorded.

2.3. Spatial analysis and seedbed characteristics

Using the quantitative results from the 35 stands, regression analysis were performed and nine representative plots of the average species composition for a specific stand age were chosen for the detailed sampling of P. glauca seedling pattern: younger (5, 16, 43 y) (the 43 y old plot did not have any seedlings and therefore was not included in the spatial analysis), mature (76, 77, 93 y) and older (157, 172, 201 y) stands. The locations of all seedlings were mapped, and substrate characteristics next to each seedling were recorded; specifically, whether the seedling was found on the LFH (Litter, Fermented, Humus layers), on decomposing logs, or on mineral soil. At each plot, the LFH thickness was measured at the center of each 5 × 5 m quadrat (32 readings per plot).

Ripley’s K function second-order analysis was used to characterize the spatial patterns of the mapped seedlings. Ripley’s K function [32, 38] tallies the number of occurrences within a given distance (t) across a range of distances available within the sampling area. For a spatially random Poisson process, \( K(t) = \pi t^2 \). K can be estimated (\( \hat{K} \)) by this function that includes edge correction [9]:

\[
\hat{K}(t) = a / n^2 \sum_{i} \sum_{j} w_{ij} I(i,j)
\]

(1)

where a is the area of the sample plot; \( w_{ij} \) is a weighing factor used for edge effect correction (\( w_{ij} = 1 \) when the circle centered on \( i \) with a radius t lies totally within \( a \), otherwise it is inversely proportional to the circle circumference that lies within the plot); \( I(i,j) \) is a counter and is equal to 1 when the distance between \( i \) and \( j \) is less than \( t \) and 0 otherwise; and \( n \) is the number of occurrences in \( a \). A variance-stabilizing transform of \( \hat{K} \) makes it easier to evaluate deviations from Poisson randomness:

\[
L(t) = \sqrt{\hat{K}(t) / \pi}.
\]

(2)

Plotting \( L(t) \) against distance \( t \) produces a straight line with a slope 1 when the point distribution is random. Deviations from such a line can be described as clumped, random or even, for any distance \( t \) up to approximately half the length of the shortest plot side [9, 30]. Significance
of $L(t)$ is determined using simulations of the randomized data sets [38]. Using S-Plus, empirical confidence interval envelopes were established as the maximum and minimum values of $L(t)$ from $10^3$ simulations. $L(t)$ values exceeding the envelopes are considered non-random: slopes larger than the confidence interval indicate clumped distribution and slopes smaller than the confidence interval indicate a more even distribution.

3. RESULTS

3.1. Basal area

Basal area along the chronosequence increased in the first 50 y after fire, and showed little directional change between 50 and 165 y, peaking at 110 y after fire (51.5 m$^2$ ha$^{-1}$), before started to decline in old stands (24.4 m$^2$ ha$^{-1}$ in a 201 y stand) (Fig. 1). During the period between 50 and 165 y, stands shifted from being deciduous to coniferous dominated. The ratio of softwood to hardwood basal area increased from 0.03 in a 16 y stand to 17.0 in a 172 y stand. *Populus tremuloides* constituted 96% of the total basal area in a 16 y stand and remained the dominant tree species until 93 y. *Picea glauca* dominated the tree canopy between 93 and 172 y coinciding with increasing *P. tremuloides* mortality. *Abies balsamea* trees were mainly found in older (>125 y) stands (Fig. 1).

3.2. Picea glauca dynamics

*Picea glauca* tree density and height increased gradually along the chronosequence after fire (Figs. 2 and 3). Trees (> 4 m) were first observed in two 16 y plots after fire (444 stems ha$^{-1}$). Maximum density of *P. glauca* (1413 stems ha$^{-1}$) was in a stand aged 172 y, although the oldest stands averaged about 600 stems ha$^{-1}$. The average tree height increased with age after fire to peak between 110 and 127 y (Fig. 3). The largest trees averaged 26 m tall with a dbh of 69 cm. During the period of white spruce dominance (93 to 172 y), the average tree height was 20 m and dbh was 17 cm.

*Picea glauca* snag density along the chronosequence was made up of two cohorts: residual snags originating from the pre-burn stands and new snags originating within the current stand (Fig. 2). Residual snags density averaged 419 stems ha$^{-1}$ immediately after fire, and declined as they fell to the ground by 5 to 16 y after fire. The new *P. glauca* cohort of snags appeared at about 66 y after fire, but remained relatively low until 160 y after fire.

Saplings (0.5–4 m), even though were present at varying densities (Fig. 2) seemed to gradually increase along the chronosequence with high densities observed at 16, 135 and 172 y after fire (2300, 1400 and 1200 stems ha$^{-1}$, respectively). Seedlings (< 0.5 m height) established immediately after fire during the initial phase of succession, behaving as a pioneer species (Fig. 2). Recruitment continued at varying densities, peaking 50 y after fire (1250 stems ha$^{-1}$). During the following decades,
recruitment decreased to reach its lowest levels between 110 and 125 y. A second wave of recruitment started at 127 y and peaked at 172 y (1537 stems ha$^{-1}$). Large variability in saplings and seedlings densities was reported, this was attributed to variability in site conditions such as the presence of mature producing trees, soil moisture, organic layer thickness, dead woody debris, microclimate and predation.

3.3. Spatial pattern of seedlings and seedbed characteristics

_Picea glauca_ seedlings were present in all stands selected for intensive study, except for a 43 y stand. Recruitment pattern of _P. glauca_ seedlings changed along the chronosequence. $L(t)$ analysis (Fig. 4) showed that the spatial distribution of _P. glauca_ seedlings was mainly random in 5, 16, 76, 77 y stands. In a 16 y stand, seedlings were clumped at distances of 2.5–3 m. Spatial distribution was significantly clumped at scales of 1–8 m, 1–12 m, 1–6 m and 1 m in mature 93 y, and old 157, 172 and 201 y stands, respectively. In addition, seedlings were evenly distributed at 15–20 m in 93 y stand.

Over all sites, around 60% of _P. glauca_ seedlings were established on logs and 40% on the forest floor (LFH) (Tab. I). Seedlings in the younger age class (0 to 43 y) occurred mainly on LFH (73%) rather than on logs (27%). In older plots (> 157 y), the recruitment occurred almost exclusively on logs (94%). In mature stands (76 to 93 y), 45% of seedlings recruitment was found on logs and 55% on LFH. The thickness of LFH increased along the chronosequence from an average of 6.4 cm in the 5 y stand to 13 cm in the 172 y stand (Fig. 5A). This increase in LFH was accompanied by a significant decline in seedling recruitment on this layer (Fig. 5B).

4. DISCUSSION

Total basal area increased in the first few decades and, despite the little directional change between 50 y and 165 y, stands shifted from being dominated by _P. tremuloides_ to being dominated by _P. glauca_. This shift resulted in part from the mortality of _P. tremuloides_. Kazbens et al. [24] suggested that around 80 y, _P. tremuloides_ started to senesce in Saskatchewan boreal forest, releasing _P. glauca_ from the understory. At a stand age 175 y, _P. glauca_ density declined, releasing _A. balsamea_ from competition and forming an uneven aged stand (201 y), dominated by _A. balsamea_, _P. glauca_ and some scattered _P. tremuloides_.

![Figure 3. Mean tree height (m) of _Picea glauca_ along a chronosequence after fire (35 stands), in the mixedwood section of Saskatchewan boreal forest.](image)

![Figure 4. $L(t)$ values of spatial distribution of _Picea glauca_ seedlings in 5, 16, 76, 77, 93, 157, 172 and 201 y stands in the mixedwood section of Saskatchewan boreal forest. The solid line shows the $L(t)$ values, while the dotted line shows the confidence envelope and the average of 1000 simulations. When the solid line is above (or below) the confidence envelope, the spatial pattern at that distance is significantly more clumped (or more even) than random expectation.](image)

<p>| Table I. <em>Picea glauca</em> seedling density (ha$^{-1}$), substrate preference and log volume (dbh &gt; 10 cm) in nine stands along the chronosequence after fire in the mixedwood section of Saskatchewan boreal forest. |
|---------------------------------|-----------------|-----------------|-----------------|
| <strong>Stand age</strong> | <strong>Seedling density (ha$^{-1}$)</strong> | <strong>Substrate preference (% seedlings)</strong> | <strong>Log volume (m$^3$ ha$^{-1}$)</strong> |</p>
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Picea glauca tree density increased gradually along the chronosequence. These trees were generally overtopped at least 2 m by P. tremuloides. The height difference further increased (by around 7 m) until 77 y after fire before P. glauca began to catch up [35]. Similar findings were reported for Manitoba’s mixedwood boreal forest [10] and the southern Canadian boreal forest of Quebec [6]. As stands aged, and in the absence of major disturbances, P. glauca tree density commenced to decline and snag density to increase as it became incapable of successfully reproducing [29].

Saplings were present in 25 of the 35 sampled plots. Highest sapling densities were observed 16 y after fire, indicating the potential importance of P. glauca on sites where high initial regeneration occurs immediately after fire in shaping the composition and structure of the forest. There was a large variation in both sapling densities along the chronosequence, and saplings heights and ages within stands reflecting more or less continuous regeneration. Ages varied between 5 and 34 y and heights between 1 and 4 m in some sampled stands [2]. Seedling density exhibited bimodality with peaks at both 50 y and 172 y. Regeneration was lowest between 110 and 125 y after fire. Galipeau et al. [13] found that white spruce recruitment after fire was characterized by two peaks: one shortly after fire (5–20 y) and a second smaller peak at around 50 y. The large variability in seedling density suggests that white spruce recruitment after fire was site specific and seemed to be associated with available seedbed and seed trees, since the white spruce seed bank is severely depleted by fire [27]. In older stands, the decline of white spruce establishment (110–125 y) was in part associated with canopy closure by coniferous species. Light intensities were reduced to around 10% between 110–125 y, which limits white spruce growth [3]. In contrast, 35% of full sunlight was transmitted in a 38 y stand dominated with P. tremuloides, yielding sufficient insolation to support P. glauca establishment and growth [2]. The second peak in seedlings recruitment (172 y) may have resulted from higher density of seed trees, increased light intensity due to gap formation, and increased availability of microsites especially logs. Some older stands (150, 170 and 201 y) showed few white spruce and these stands were dominated by a thick organic and moss layers and a medium to dense cover of balsam fir seedlings and saplings [37]. The continuous advanced regeneration reported in this study has been mostly overlooked in forest management, but has the potential of replacing the overstory following natural disturbances or harvesting.

Population distributions can occur in spatial arrangements that range from uniform to random to clumped. Observed spatial patterns can reflect the reproduction properties of a species, microsite variability, interaction of species with its environment and other organisms, in addition to the spatial and temporal characteristics of the observing process [21, 40]. Analysis with Ripley’s K showed that the pattern of seedlings recruitment changed along the chronosequence. Picea glauca seedlings were mainly distributed at random in the younger and the mature stands but they were clumped at distances < 12 m in older stands. No seedlings were found on mineral soils (despite mineral soil exposure immediately after fire). Charron and Greene [7] reported that mineral soils were a more favorable seedbed for white spruce in a sowing experiment than litter or organic layer. In our study, the majority of seedlings regenerated at random on LFH in younger stands. Seedlings in older plots, were found almost exclusively on decaying logs (logs that were either partially degraded with bark partially or entirely sloughed, or logs starting to be integrated into the soils). In some cases, several individuals were established on the same log leading to a tightly clumped linear pattern. This clumpy pattern in older stands indicates that logs provided a more suitable microsite for P. glauca recruitment than LFH. Gray and Spies [16] reported that substrate characteristics were more important for the establishment of Tsuga heterophylla than gap size in Oregon. In closed canopied forests, establishment of T. heterophylla on logs was significantly greater than establishment on the litter layer, due to the higher moisture content of wood compared to litter in summer [16] and the burial of seedlings by litter during snow melt in the spring [15]. Our results have shown that regeneration on logs increased from 63% of total seedlings in 93 y stand to 100% in 172 and 201 y stands. The important role of logs for seedling establishment is well known in several forest types [25, 27, 33]. Logs provide moisture during the summer; reduce the barrier to seedling establishment posed by the mosses and litter; and provide an elevated environment for better light competition. In contrast, the thick layer of undecomposed litter, the lower soil temperatures, and light intensities in older stands limit P. glauca regeneration. Seedlings established on LFH of less than 8 cm, but LFH greater than 12 cm seemed to significantly impair P. glauca recruitment [12]. Knapp and Smith [26] reported that Picea engelmannii were mostly located in areas with thin (2 cm) LFH. Place [31] found that 5 cm of undecomposed litter (L layer) inhibited the establishment of P. glauca while 7 cm was needed to inhibit the establishment of A. balsamea.
Our results show that *Picea glauca* regeneration depends on the presence of propagules and seedbed characteristics at early stand age and, in older stands, on the presence of suitable microsites. Initial recruitment of *P. glauca* was also shown to be essential for the success of this species, especially for providing the basal area and the recruitment of the second wave of seedlings or advanced regeneration associated with the opening of the canopy. Logs created by the death of *P. tremuloides* and the resultant canopy gaps formed, appear to be critical for *P. glauca* regeneration in mature and old stands. Natural regeneration may be enhanced by taking advantage of the advanced regeneration during harvesting operations.

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**REFERENCES**


