

Natural Successional Dynamics of Boreal Forests in Northeastern Ontario

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Abstract

*The dynamics of unmanaged boreal forest stands were examined in northeastern Ontario. The objective was to determine stand compositional development based on time since fire (TSF). We combined repeated field cruises with sequential aerial photographs taken from 1946 to 1990s at intervals of 8-15 years. In field measurements, stand composition and basal area were determined from ten prism stations along a 200 m cruise line in each stand. On the aerial photographs, a 2 ha plot centered on the cruise line was used to estimate stand composition and stocking. Time since fire was determined from fire history maps or estimated from trees when the fire history was unknown. All of the stand cover types showed changes in cover type over time except for white birch (*Betula papyrifera*) and white cedar (*Thuja occidentalis*). Multinomial response models indicated that these changes were significantly related to TSF, and predicted that most stands changed dominance from pioneer species to late successional species over time. More than one pathway was also apparent for all cover types. This may be explained by the variability of species composition within each stand cover type and non-stand-replacing disturbances such as spruce budworm (*Choristoneura fumifera*) outbreaks.*

Introduction

Under the paradigm of emulating natural disturbances and processes through forest management practices, it is crucial to understand the causes of these natural processes so that appropriate practices can be designed (OMNR, 1996). To maintain the composition and structure of forests within the range of natural variability (at landscape level), forest managers need to be able to predict

how forest ecosystems change over time with or without disturbances. These predictions are also essential for estimating timber supply and wildlife habitat (Davis *et al.*, 2000).

Natural succession is defined as the change in forest composition over time without stand-replacing disturbances such as fire (Vasiliauskas *et al.*, 2004). Disturbances such as wind, insects and disease that remove part of the canopy are part of the successional process. In eastern Canada, particularly in Quebec, forest succession studies have advanced our understanding of the dynamics of fire-origin boreal mixedwood ecosystems on mesic sites (e.g., Bergeron, 2000). However, mixedwoods are part of the boreal forest, and a good understanding of the dynamics of other species is necessary for making management decisions (Chen and Popadiouk, 2002). Because of the lack of such understanding, forest managers currently rely on so-called 'expert opinion' models that are based primarily on anecdotal observations (e.g., Vasiliauskas *et al.*, 2004).

The primary objective of this project was to develop natural successional pathways for forest units through adopting a robust sampling approach on naturally established stands in northeastern Ontario. This paper will focus on the pathways and probability of change in species dominance for jack pine (*Pinus banksiana*), poplar (*Populus* spp.), white birch (*Betula papyrifera*), black spruce (*Picea mariana*), balsam fir (*Abies balsamea*) and white cedar (*Thuja occidentalis*) in relation to time since fire (TSF).

Study Area

The study stands were located in Hills' Site Region 3E (Hills, 1959) in northeastern Ontario (47°45' – 49° 30' N, 80° 40' – 85° 00' W; Figure 1). The climate of the area is cool continental with short, warm summers and cold, long winters. Mean annual temperature is 1.3°C and mean annual precipitation 831 cm, of which 313 cm is snow (Canada Climate Normals, 1971-2000). This is a largely forested region, interspersed with lakes, rivers and wetlands and with little topographic relief. Forest soils originated from a variety of modes of glacial deposition and from organic deposits. The area is classified as south-eastern boreal forest (Rowe, 1972). Dominant tree species in order of increasing shade tolerance (Baker, 1949) include jack pine, trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white birch, black spruce, white spruce (*Picea glauca*), balsam fir, and white cedar. Other infrequently occurring species include tamarack (*Larix laricina*), willows (*Salix* spp.), red

pine (*Pinus resinosa*), white pine (*Pinus strobus*), black ash (*Fraxinus nigra*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*) and sugar maple (*Acer saccharum*).

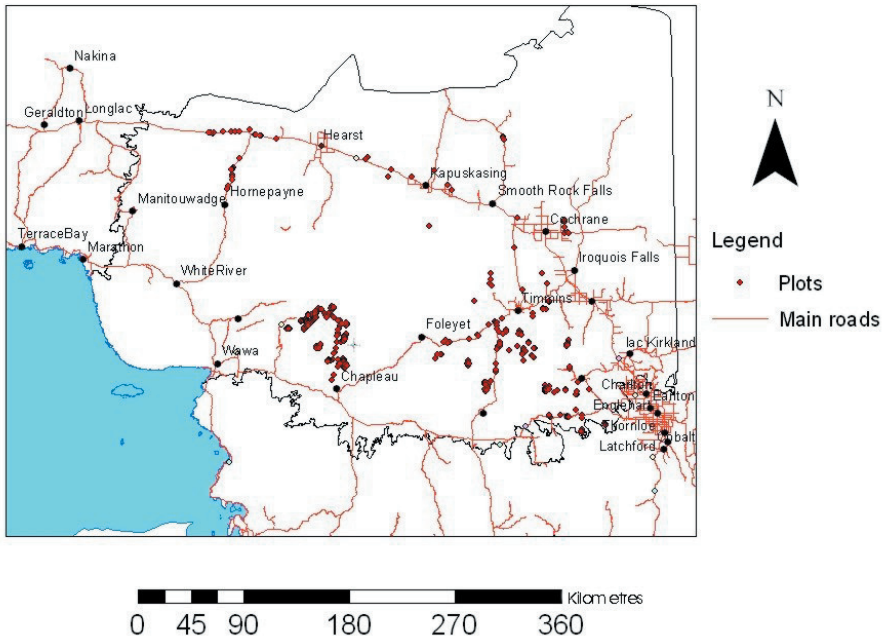


Figure 1. Study region (Site Region 3E) and plot locations in northeastern Ontario.

Fire is the dominant natural disturbance agent with a mean fire interval of 100 to 200 years in the study area (Bergeron, 1991; Perera *et al.*, 1998). Other important natural disturbances include insect outbreaks. Spruce budworm (*Choristoneura fumiferana*) outbreaks defoliate balsam fir and white spruce, making them susceptible to mortality from *Tomentosus* root rot. These outbreaks occur on a 30-year cycle, with the latest infestation in the 1970s (Williams and Liebhold, 2000). Forest tent caterpillar (*Malacosoma disstria*) defoliates trembling aspen and balsam poplar trees, resulting in mortality if the defoliations are repeated over several years. Windstorms can level swaths of forest on an irregular basis. There has been logging in the area since the 1910s. Other anthropological disturbances include small-scale agricultural clearing, urbanization, and mining.

Methods

Two hundred ninety-seven stands were deliberately selected to cover a wide range of stand ages, forest cover types, and site conditions from timber cruise lines marked on *Forest Resource Inventory* (FRI) maps dating between 1961 and 1982 in the study area. Stands with a history of logging were not sampled. Each of the stands had four to six measurements: two from cruising, and two to four from aerial photo interpretation. One of the cruises was done between 1961 and 1982 and the other was in 2000, 2001 or 2003. Less than four aerial photo measurements were for young stands, as stand basal area cannot be estimated for stands less than 20 years old (Zsilinszky, 1963).

Aerial photos at a scale of 1:15,840 are available for the study area from the 1940s to the 1990s at eight to 15 year intervals. Aerial photographs taken since 1986 are at a scale of 1:20,000. The resurveyed cruise lines were relocated from the FRI maps onto these aerial photographs. A 2 ha plot (50 m each side of the 200 m cruise line) was centred on the cruise line and stand composition and stocking were interpreted for this plot according to Zsilinszky (1963).

During the summers of 2000, 2001 and 2003, selected cruise lines were relocated and remeasured using the same methodology as for the original cruise to determine current stand basal area, composition, age, height and site class (Plonski, 1974; OMNR, 1978). On each 200 m cruise line, ten point samples were established 20 m apart, and stems were counted by species using a wedge prism of basal area factor 2 (BAF 2). Stand composition is based on the percent contribution of each species to the total stem count. Stand basal area in m^2ha^{-1} is determined by multiplying the total stem count by two and dividing by ten. Stems had to be at least 10 cm in diameter at 1.3 m above the ground (DBH) to be considered as a part of the tree layer (Hayden *et al.*, 1995). Stand basal areas from aerial photo interpretation were based on the dominant species, site class (from field data), age (corrected from field data to reflect year of photography) and estimated stocking based on canopy cover (Zsilinszky, 1963).

Time since fire (TSF) was determined from fire history maps when stands were located within documented fires since 1920 (Donnelly and Harrington, 1978). For other stands, we used tree ages to estimate the date of the last fire (Bergeron, 1991). A minimum of three canopy stems were used to determine TSF. The same trees used to determine site class were also used to determine TSF if they were from even-aged stands dominated by jack pine, aspen, white

birch, tamarack and/or black spruce. Trees with fire scars were not sampled and were very rarely encountered. In stands that were uneven-aged and with more than one cohort(s), additional stems were selected that would better determine TSF. Trees from an earlier cohort were selected, and are identifiable by their larger size, larger branching or top dieback. Jack pine was the preferred species, as they rarely regenerate without fire. If jack pine was absent, poplar, white birch, white pine, red pine and black spruce were preferentially selected for dating the last major disturbance (Bergeron, 1991). In stands dominated by shade tolerant species such as black spruce, white spruce, balsam fir, or white cedar, the least shade-tolerant species was chosen. If the more shade-tolerant trees were older than the less shade-tolerant trees, we used the former to determine TSF. Cores were taken to the pith at breast-height and stored in labeled plastic straws for age determination in the laboratory using a binocular microscope. Tree ages were corrected to TSF using the model developed by Vasiliauskas and Chen (2002). TSF for previous measurements was derived by subtracting the TSF for the latest survey with the difference in sample years.

Data Analysis

We classified stand cover type by tree species dominance (He and Mladenoff, 1999; Yemshanov and Perera, 2002), based on percentage of basal area of each species in the stand. Stands dominated equally by two or more species were classified into the least shade tolerant species. Baker's (1949) shade tolerance classification was used with increasing shade tolerance: jack pine < *Populus* < white birch < *Picea* < balsam fir < white cedar. *Populus* includes stands dominated by trembling aspen and balsam poplar and are referred to as poplar in the paper. Most of the stands were dominated by trembling aspen. *Picea* includes stands dominated by black spruce or white spruce, and most of these were black spruce dominated. These groupings were made because it can be difficult to separate these species on aerial photographs (Zsilinszky, 1963).

For each stand, stand cover type was determined for each of the four to six repeated measurements through field cruising or aerial photo interpretation. Stands were then grouped according to the initial cover type. For each initial group of cover type, we tested if stand cover type change (π_j) was significantly related to TSF.

The probability of stand cover type change was modeled using the following multinomial logit model (Agresti, 1990):

$$\pi_j = \frac{\exp(\alpha_j + \beta_j x)}{\sum_h \exp(\alpha_h + \beta_h x)}, \quad J = 1, \dots, J-1$$

where $\sum_h \pi_j = 1$, α and β are regression parameters to be estimated, and x is time since fire. We used the logit regression analysis procedure in SYSTAT 10 (SPSS Inc. 2000).

Results

Stands that were initially dominated by shade-intolerant species shifted significantly toward shade-tolerant cover types with TSF (Figure 2). Shade tolerant species either maintained their dominance, or in some cases shifted toward less shade-tolerant dominance. Jack pine dominated stands shifted towards-dominance by poplar, balsam fir or black spruce with TSF (Figure 2a). Poplar stands shifted significantly towards dominance by balsam fir, white birch, white cedar, and the change to domination by spruce was independent of TSF (Figure 2b). White birch stands shifted significantly toward dominance by balsam fir or white cedar with a shift toward spruce or poplar independent of TSF (Figure 2c). Spruce stands maintained their dominance and started to show a significant shift toward dominance by white cedar after 200 years of TSF. Shifts in dominance for spruce stands toward white birch, balsam fir or poplar were not related to TSF (Figure 2d). Balsam fir-dominated stands showed a significant shift toward dominance by black spruce or white cedar. The shift toward dominance by white birch or poplar was independent of TSF (Figure 2e). Cedar stands showed the most stability as dominance of white cedar did not change significantly towards any other cover type including black spruce (Figure 2f).

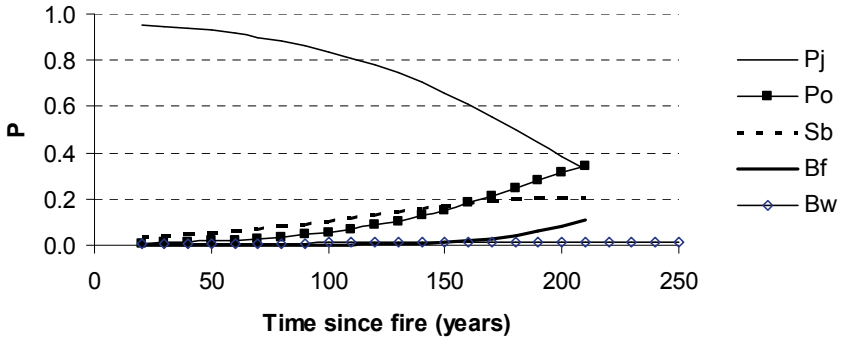


Figure 2a. Probability (P) of change in species dominance for stands initially dominated by jack pine (Pj) in relation to time since fire (TSF).

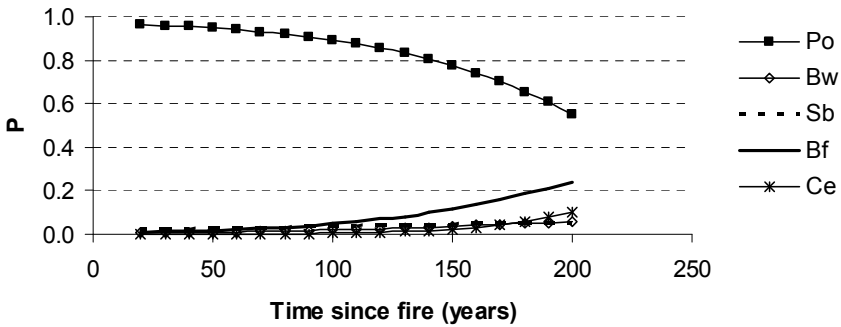


Figure 2b. Probability (P) of change in species dominance for stands initially dominated by poplar (Po) in relation to time since fire (TSF).

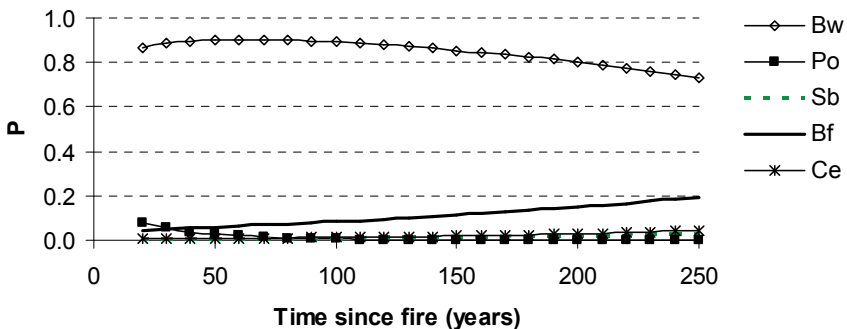


Figure 2c. Probability (P) of change in species dominance for stands initially dominated by white birch (Bw) in relation to time since fire (TSF).

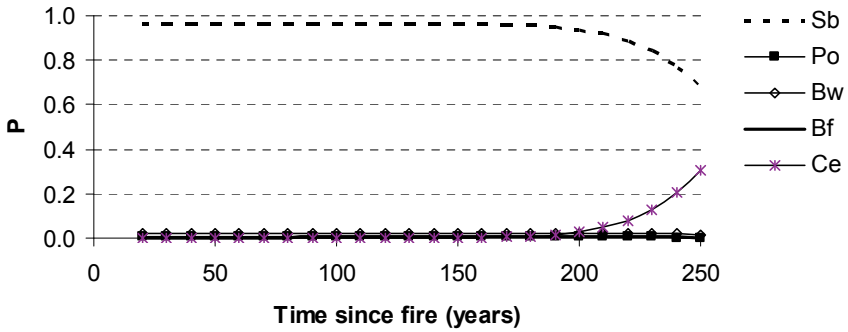


Figure 2d. Probability (P) of change in species dominance for stands initially dominated by black spruce (Sb) in relation to time since fire (TSF).

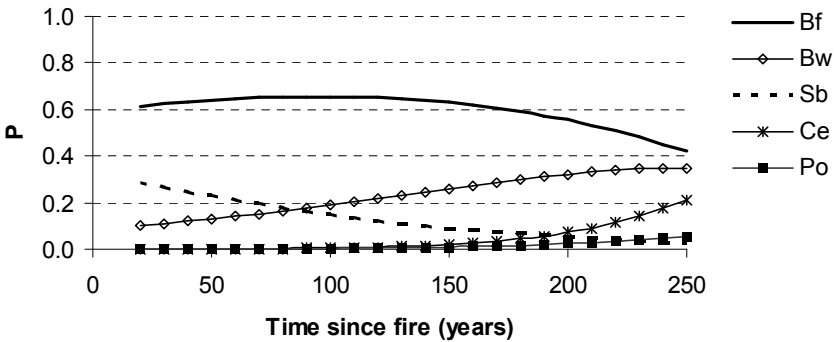


Figure 2e. Probability (P) of change in species dominance for stands initially dominated by balsam fir (Bf) in relation to time since fire (TSF).

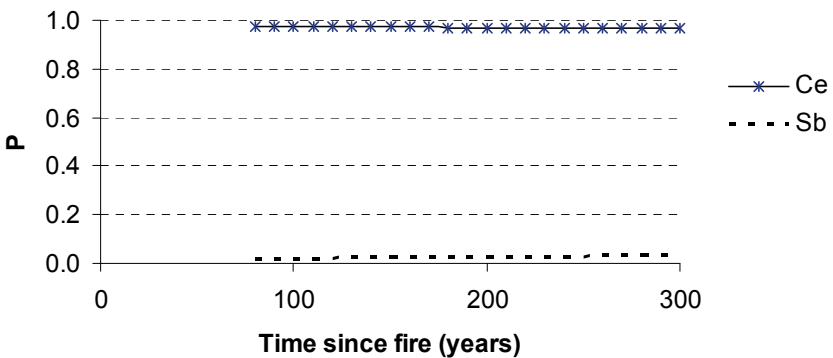


Figure 2f. Probability (P) of change in species dominance for stands initially dominated by white cedar (Ce) in relation to time since fire (TSF).

Discussion

Our work confirmed the trend of stand dominance shifting from shade-intolerant to shade-tolerant species (Bergeron, 2000; Chen and Popadiouk, 2002). Shade tolerant species maintained their dominance over time, with the probability of shifting towards other species not affected by TSF (Bergeron, 2000). We also found multiple pathways for the boreal species studied (Cattelino *et al.*, 1979; Frelich and Reich, 1995; Chen and Popadiouk, 2002).

We found evidence to support four of the five directional models proposed by Frelich and Reich (1995) from the literature. These are the 1) convergent, 2) divergent, 3) parallel and 4) individualistic models. We found partial evidence for the cyclic model in the form of species A succeeding to species B. We did not find evidence for stands with species B returning to species A after disturbance, as this study did not investigate stand-replacing disturbances that would reset the successional trend.

Both white birch and balsam fir followed similar patterns in changes in dominance. Unlike jack pine and poplar which showed decreased dominance with age, white birch and balsam fir showed an initial increase in dominance followed by a gradual decrease. This suggests that white birch and balsam fir can maintain their dominance on a site with time and that changes in dominance are influenced by other factors in addition to TSF. Most likely this is due to spruce budworm. Balsam fir regenerates in the understories of stands and assumes dominance as the canopy breaks up (Frank, 1990). A budworm outbreak would remove some or all of the fir in the canopy (Baskerville, 1960; MacLean, 1984), and dominance would shift towards birch or another species (Frank, 1990), either through gap regeneration or through survival of canopy stems (depending on the time since the last outbreak). The longevity of birch relative to other boreal species and its dominance on the landscape has been previously noted (Bergeron and Dubuc, 1989; Bergeron, 2000).

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