Age Structure of Eastern White Pine, *Pinus strobus* L., at its Northern Distribution Limit in Québec

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Stand age structures of Eastern White Pine (*Pinus strobus* L.) were analysed on three sites with different fire histories (latest fire 1760, 1825 and 1941, respectively) in Québec to assess whether Eastern White Pine is regenerating or not at its northern limit. Previous paleo-botanical findings suggest that this species once extended ca 100 km further north than the present distribution limit in Québec. All three sites (dry habitats) represented vital populations where the individuals were established after the most recent fire. The results suggest that the relative lack of dry and/or disturbed sites in combination with a more severe fire regime that characterizes the northern lowlands, may explain why white pine expansion is restricted northwards.

Key Words: Eastern White Pine, *Pinus strobus*, fire, boreal forest, tree regeneration, Québec.

Climate is generally considered to be a main factor controlling northern limits of plants (e.g., Woodward 1992; Kullman 1995). However, studies have also reported that other factors such as disturbance, soil conditions, and competition are important for distribution, regeneration and stand dynamics (cf. Currie and Paquin 1987; Bradshaw 1993; Engelmark 1999). Studies on North American pine species, have suggested that fire disturbance is important in controlling the northern distribution, thus indicating that climate per se is not always a limiting factor (Bergeron and Gagnon 1987; Desponts and Payette 1992; Flannigan and Woodward 1994; Meilleur et al. 1997). Jack Pine (*Pinus banksiana*) has serotinous cones, and is regenerating successfully at its northern limit (Desponts and Payette 1992; Johnson and Gutsell 1993). Red Pine (*P. resinosa*) (Bergeron and Brisson 1990, 1994; Engstrom and Mann 1991; Flannigan 1993; Flannigan and Woodward 1994; Flannigan and Bergeron 1998), and Pitch Pine (*P. rigida*) (Meilleur et al. 1997) are also reported to recruit frequently at their respective northern limits (see also Vander Kloet 1973). Studies on Eastern White Pine (*P. strobus*) at its northern limit are however scanty (cf., Holla and Knowles 1988), although its regeneration dynamics further south has been discussed (e.g., Heinselman 1973, 1981; Quinby 1991; Abrams et al. 1995).

We propose that the present Eastern White Pine distribution is not limited directly by climate alone, but possibly also by other environmental factors. To assess whether *Pinus strobus* is regenerating or not at its present northern distribution limit, age structure analyses were performed in three stands with different fire histories at its northern limit in Québec, eastern Canada.

Study area

The study was carried out at the present northern limit of *Pinus strobus*, in the Lake Abitibi-region in NW Québec (Figure 1). The area is located in the southern boreal forest within the Missinaibi/Cabonga forest section (Rowe 1972), where mature forests are dominated by *Abies balsamea* with *Picea mariana*, *P. glauca* and *Betula papyrifera* as co-dominants. Depending on the time since the last disturbance, the type and severity of the disturbance, varying proportions of *Pinus banksiana*, *P. resinosa*, *P. strobus*, *Picea mariana* and *Thuja occidentalis* are found on xeric sites (Bergeron and Dubuc 1989; Bergeron 1991). The area belongs to the Northern Clay belt of Québec and Ontario (Vincent and Hardy 1977). The mean annual temperature and precipitation are 0.6°C and 823 mm, respectively, and the average annual frost-free period is 64 days (Anonymus 1982).

Three stands with elapsed time since the last fire were sampled, viz. fire years were 1760, 1825 and 1941 (hence the stands are named "S17", "S18" and "S19", respectively). These fires were of lethal, crown-destructing character (Clayden and Bouchard 1983; Bergeron 1991). The stands were located on elevated, dry sites with shallow till, and contained a mixture of *Pinus strobus* and *P. banksiana* as dominant trees. The Eastern White Pine individuals were generally vigorous, young individuals with long annual shoots and mature trees with large cone crops (Figure 2).

Field layer dominants in stand S17 and S18 were *Kalmia angustifolia, Vaccinium angustifolium, V.*

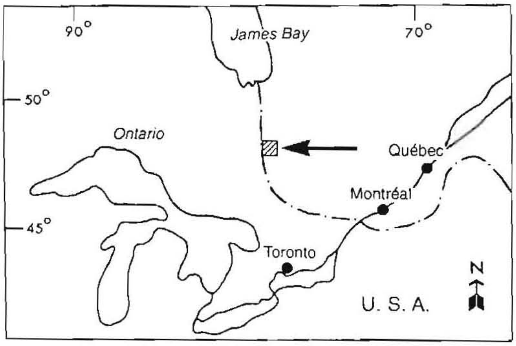

FIGURE 1. Map showing the location of the Lake Abitibi area, which represents the present northern limit of *Pinus strobus* in eastern Canada.

myrtilloides and *Chamaedaphne calyculata*, and *Cladonia* spp. dominated in the bottom layer, while *V. angustifolium, V. myrtilloides* and *Ledum groenlandicum* dominated in S19. Exposed rock was present to about 25% at all sites.

Methods

In July 1994, one sample plot within each stand was selected for data collection. The aim to sample a minimum of 130 pines in each stand resulted in three different plot sizes, viz. S17: 200 × 300 m (n = 176); S18: 70 × 175 m (n = 138); and S19: 70 × 110 m (n = 150). Within the sample plots all *Pinus strobus* individuals with a basal stem diameter <4 cm were age-determined by counting branch nodes. A sample of small trees (n = 25) was cut to verify congruence between number of branch nodes and tree rings ($R^2 = 0.92$). Trees with a basal stem diameter > 4 cm were cored at the root-neck for age determinations. The cores were dried, planed and the annual rings were counted using a stereo-microscope (6–50 ×). The annual rings were easily determined due to high growth rate, and the tree datings could thus be done with high accuracy.

Results

All three sites presented vital and continuously recruiting white pine populations. The 464 sampled pines were established between 1790 and 1993 (Figure 3). The separate stand age structures exhibit postfire regeneration, although not until the study year (1994) was the surviving regeneration cohort discernible after the 1760-fire in stand S17. This may be related to the fact that old Eastern White Pines (> 200 yr) often suffer from fungal stem rot and are prone to blow down (Holla and Knowles 1988; Webb 1989; Abrams et al. 1995). For S18, an Eastern White Pine cohort was recorded after the 1825-fire. Stand S19 shows a significant regeneration increase after the fire in 1941.

FIGURE 2. A view from S19 showing *Pinus strobus* individuals, about 40-yr-old.

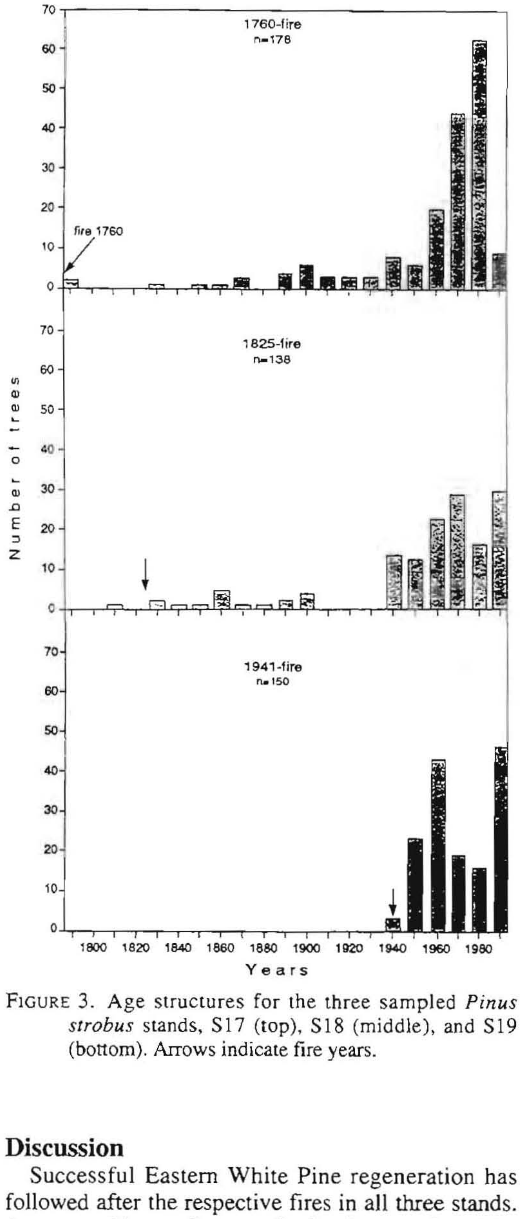

FIGURE 3. Age structures for the three sampled *Pinus strobus* stands, S17 (top), S18 (middle), and S19 (bottom). Arrows indicate fire years.

Discussion

Successful Eastern White Pine regeneration has followed after the respective fires in all three stands. A comparable postfire age-distribution was found for Red Pine also at its northern limit in the same area (Bergeron and Gagnon 1987), a pattern which is indicative of broadly stable populations at the landscape level (Parker 1986; Engelmark et al. 1994). The pattern of postfire recruitment is also reported for Jack Pine (Desponts and Payette 1992) and Pitch Pine (Meilleur et al. 1997) at their northern limits. This supports our idea that climate is not solely controlling the northern distribution limits of these pines.

Further, the multi-aged Eastern White Pine distribution found in this study is congruent with results presented by Holla and Knowles (1988) at the Eastern White Pine limit in Ontario, corroborating that a continual recruitment is possible even without recent fire disturbance (> 230 yr in this study), provided that small-scale gaps suitable for regeneration (e.g., wind-throws or open xeric outcrops) are available in the landscape (Quinby 1991). Germination is regarded to be most successful on bare soil or thin organic layers. In addition, many seed trees form the uppermost canopy and as Eastern White Pine has a relatively large seed production (Fowells 1965), seeds disseminate easily. Accordingly, in this study regeneration was successful within existing stands. But maybe the relative lack of dry habitats suitable for regeneration (e.g., rock outcrops) in the landscape of the Northern Clay Belt (cf. Clayden and Bouchard 1983), is partly limiting further Eastern White Pine expansion under present climate and disturbance regimes. This is, in part, contradicted by the greater northward expansion of Eastern White Pine in this area during the Holocene warming up to about 3000 yr BP, indicating that dry, suitable sites then were available (cf., Terasmae and Anderson 1970; Liu 1980).

Thus, under the presently low to moderately intense fire regimes, Eastern White Pine recruits well on dry habitats at its northern limit. With regard to the actual, continously occurring regeneration, we suggest that further expansion is prevented by the prevailing high-intensity fire-regime north of the present Eastern White Pine distribution. This lethal fire-regime, characteristic to the north, instead favours conifers with serotinous cones, as Jack Pine (Desponts and Payette 1992). We hypothesize therefore that in parallel to Jack, Red and Pitch pine, the northern limit of Eastern White Pine is fire-controlled, rather then climatically-controlled, and, finally, that these pine species respond specifically to different fire regimes.

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