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Persistence at the Tree Line: Old Trees as Opportunists

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ABSTRACT. While old trees have long been of interest, their significant role in responding to climate change at northern tree lines has been overlooked. Long-lived black spruces at the tree line in Labrador show a radial growth response that is synchronous with recent climate warming. The ability of individuals to persist with suppressed radial growth rates during adverse growing conditions may have significant implications for the rate at which these trees are able to respond when conditions become favourable.

Key words: persistence, krummholz, dendrochronology, tree line, forest-tundra ecotone, Mealy Mountains, Labrador, climate change, black spruce, *Picea mariana*

RÉSUMÉ. Même si les vieux arbres revêtent de l'intérêt depuis longtemps, on a négligé de considérer le rôle important qu'ils jouent en matière de réaction au changement climatique à la hauteur des limites forestières boréales. Au Labrador, les épinettes noires de longue date se trouvant à la limite forestière affichent une croissance radiale qui est synchrone avec le récent réchauffement climatique. L'aptitude des individus à persister malgré des taux de croissance radiale opprimés lorsque les conditions de croissance sont déficitaires peut avoir des incidences importantes sur le taux de réaction de ces arbres lorsque les conditions deviennent favorables.

Mots clés : persistance, krummholz, dendrochronologie, limite forestière, écotone de toundra forestière, montagnes Mealy, Labrador, changement climatique, épinette noire, *Picea mariana*

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Despite the recent attention given to tree-line advance resulting from climate warming (e.g., Harsch et al., 2009), the significance of old trees as the "front line" of this advance has not been adequately explored. While the persistence of long-lived trees has been reported from other climatically harsh environments (e.g., Larson et al., 2000), northern tree lines (e.g., Vallée and Payette, 2004; Asselin and Payette, 2006), and some altitudinal tree lines (LaMarche and Mooney, 1972), the importance of a persistence-mediated response to climate change deserves more attention. Long-lived clonal patches at the tree line have been used to reconstruct post-glacial migration patterns (e.g., Kullman, 2006), but the importance of ramets has been little discussed. In North America, the widely distributed black spruce (*Picea mariana*) is the dominant species forming these clonal patches (Pereg and Payette, 1998), making these trees ideal for exploring ideas of persistence.

On 19 July 2007, a cone-bearing, shrub-like krummholz black spruce in the Mealy Mountains, Labrador (53˚36′N, 58˚51′W; Fig. 1A) was sampled at ground level, using an increment borer. The sampling of this black spruce, found at 748 m elevation (~130 m above the forest limit; sensu Scott, 1995), was part of a larger survey effort exploring patterns of age structure and reproductive potential at the alpine tree-line ecotone (for details see ppsarctic.nina.no). Using a Velmex® micrometer (precision 0.005 mm) under a binocular microscope at 40× to count annual rings, we determined that the individual's oldest living stem was at least 370 years old. A literature review and the CanDendro database (www.mta.ca/candendro) indicate that this tree is the oldest known living black spruce in Atlantic Canada and at alpine tree line across Canada. The black spruce krummholz measured 4.8 m by 3.1 m, with an average stem height of 0.7 m. The tallest of the 14 clonal stems was 1.85 m high, with a diameter of less than 3 cm at breast height and no evidence of older dead stems. Three stems produced mature pollen and seed cones in the 2007 and 2008 growing seasons, and although viability was not tested for this individual, viable black spruce pollen and seeds were documented within 585 m from its site (R.G. Jameson, unpubl. data).

The mechanisms by which tree lines are able to respond to climate warming may depend on how long individual trees can persist, often in suboptimal conditions, once established. Climatic conditions directly affect all stages of sexual reproduction in boreal tree species (Zasada et al., 1992; Farmer, 1996) and can limit viable seed production and the successful recruitment of new individuals, particularly toward the edge of a species' range (e.g., Elliott, 1979; Henttonen et al., 1986; Sirois, 2000). Vegetative

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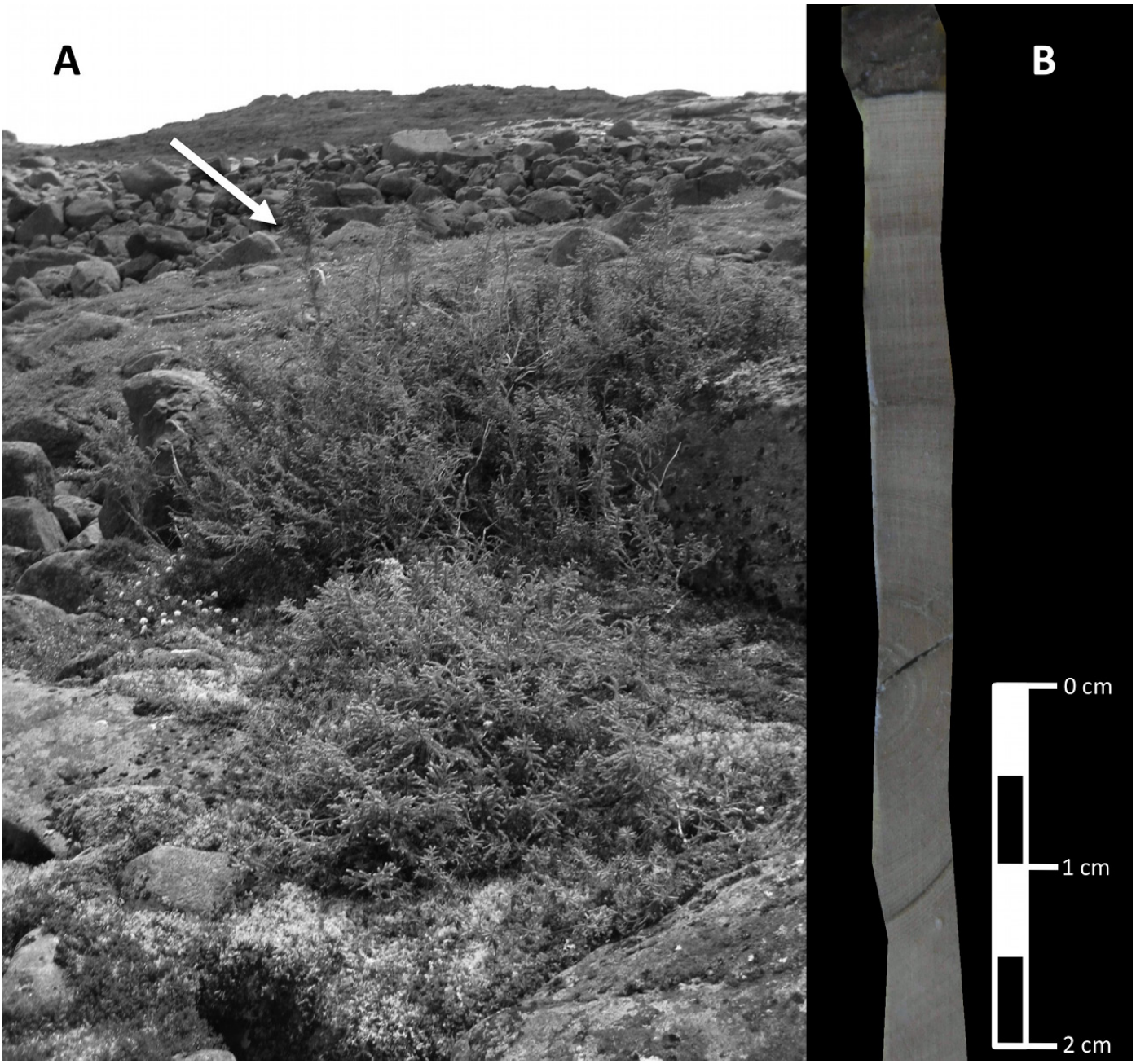

FIG. 1. Black spruce krummholz at 748 m elevation, near the species limit in the proposed Mealy Mountains National Park, Labrador, with A) arrow indicating tallest leader of krummholz and B) basal increment core used for age determination.

growth requires fewer growing degree-days than reproductive growth, which suggests that reproductive growth does not occur when radial growth is suppressed (Woodward, 1987). In the long term, the ability of black spruce to grow and regenerate vegetatively allows long-lived individuals to endure unfavourable climates and resume sexual reproduction when conditions improve.

Krummholz is the dominant tree form at many tree lines. These low-lying trees, the result of winter wind desiccation and ice-crystal abrasion, rarely grow higher than the average snow depth (Scott, 1995). Nurse effects of deciduous shrubs, microtopography, and glacial erratics may play a significant role in the establishment and persistence of krummholz in otherwise inhospitable environments by protecting them from increased snow drifting and sheltering them in snow-free periods (see Fig. 1; Cranston, 2009; Daley, 2009). Since growing conditions at these higher elevations are often suboptimal, krummholz put down much less radial annual wood than forest trees of the same species; in our study area, mean ring size for krummholz is 0.17 mm, compared to 0.45 mm for forest trees.

Despite its old age and harsh growing conditions, the basal sample shows that the black spruce reported here has experienced a dramatic increase in annual radial growth (Fig. 2A) that matches the pattern of temperature increase observed in recent climate records (Bell et al., 2008). For

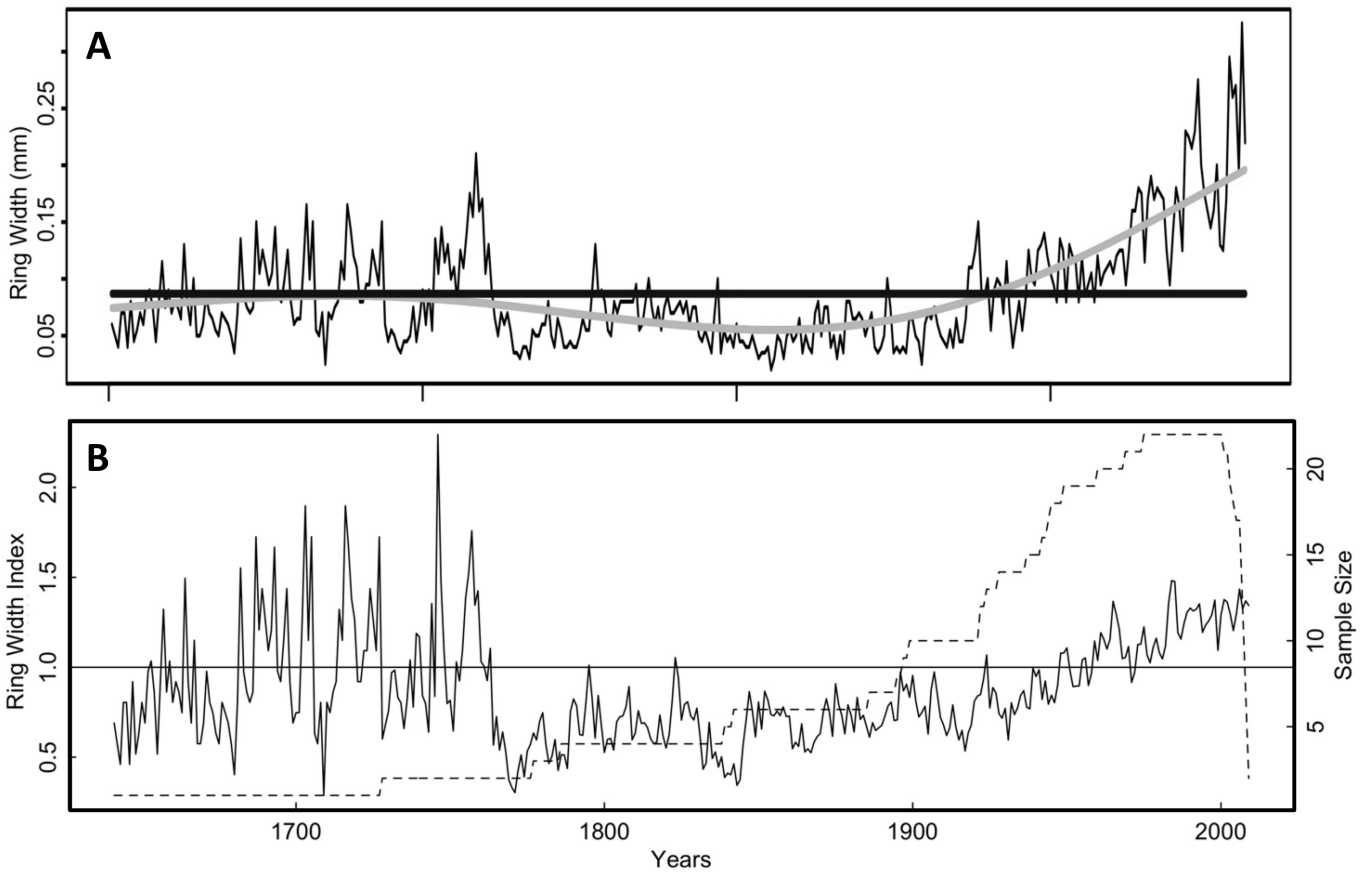

FIG. 2. Ring widths of black spruce krummholz. A) Raw ring widths for the old black spruce krummholz individual. The black line represents the overall mean, and the grey line is the running mean, with a 50-year window. B) Standardized Ring Width Index chronology of black spruce krummholz for the Mealy Mountains, Labrador. The straight black line shows the average Ring Width Index of 1, and the broken line represents sample size.

the greater part of the 20th century, ring width values were larger than the series mean, and these values have continued to increase from Little Ice Age minima around 1770 and 1850 (Fig. 2) to the present day. For the running mean (Fig. 2A: grey line), we used a 50-year window between points, excluding some of the interannual variation, in order to show this long-term trend. On a larger scale, a chronology for 22 radii from 20 stems of black spruce krummholz in the Mealy Mountains shows a similar pattern (Fig. 2B), with significant suppression of radial growth for the majority of the available record and dramatic recent increases that correspond to increases in growing-season temperature (Bell et al., 2008). This chronology was detrended using a modified negative exponential model that removes biological growth trends thus presenting standardized ring width indices.

These old krummholz may persist for centuries until conditions become more favourable, at which time they may increase radial growth rates and initiate sexual reproduction. Older trees are likely to have greater belowground biomass and access to resources essential to these processes. Once viable seeds are produced, expansion of the tree line could occur rapidly as strong winds disperse seeds from the "front line" of old tree islands. Light black spruce seeds, disseminated from semi-serotinous cones throughout the year, have the potential to travel great distances atop hard snow and ice layers during the winter. In slow-growing environments such as the tree line, the advantage may be given to those individuals who have been waiting.

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