

InfoNorth

Tree-line Dynamics: Adding Fire to Climate Change Prediction

by Carissa D. Brown

INTRODUCTION

FIRE IS THE DOMINANT DISTURBANCE that drives ecosystem structure and function in the boreal forest of North America (Weber and Flannigan, 1997). Fire frequency varies widely across different regions of the boreal forest, but the interval between fires is generally long enough for trees to re-establish and recover to mature stands before the stand burns again (Heinselman, 1981; Payette, 1992). In the western boreal forest of North America, historic fire-return intervals have been estimated as typically 80–120 years between fires (Johnson, 1992). Tree establishment occurs most rapidly in the first years following fire, when the availability of viable seed and nutrients is at its highest (Johnson and Fryer, 1989; Johnstone et al., 2004). In a typical fire cycle of one to two centuries, the individuals that germinate in the first few years following a fire are the same individuals that reach reproductive maturity and are burned in the next fire, continuing the cycle of post-fire self-replacement.

Boreal tree species demonstrate a variety of adaptations to fire, including serotinous cones (that require heat for seed release) maintained in aerial seed banks (*Pinus* spp., *Picea mariana*) and vegetative re-sprouting from roots and stumps following fire (*Betula* spp., *Populus* spp.; Li, 2000). In the latitudinal tree line (or forest-tundra ecotone) of the boreal forest, the growing conditions for trees are suboptimal. Because of the underlying permafrost, the soils of this region are relatively cold and wet and thus have slow nutrient turnover rates. Black spruce (*Picea mariana*), a dominant boreal conifer, exhibits slow growth under these conditions, taking several decades to reach reproductive maturity. However, historical fire cycles allow for black spruce to accumulate enough viable seed for self-replacement after fire.

Many regions of the circumpolar North have undergone an increase in temperature, particularly in the past four decades (Chapin et al., 2005). The northern regions of Yukon and Alaska have experienced a 2°C increase in summer temperatures since the 1960s (Chapin et al., 2005). In the boreal forest, fires are expected to occur more often as the climate warms (Stocks et al., 1998; Flannigan et al., 2005; Soja et al., 2007), and increased fire activity is already being noted in some parts of the region (Gillett et al., 2004; Kasischke and Turetsky, 2006). Because of the long period black spruce require to become reproductively mature, an increase in fire

activity may interrupt the cycle of post-fire self-replacement for this dominant boreal conifer. This interruption could initiate a change in the structure and function of these northern ecosystems that will have important implications for the global carbon cycle because it alters patterns of carbon accumulation and storage (Grace et al., 2002; Bond-Lamberty et al., 2004).

The long-term, landscape-level consequences of altering the fire return interval in the tree-line forest are unknown. On the decadal scale, shifts from coniferous to deciduous dominance after high-severity or frequent fire have been documented in tree-line and interior northern boreal forests (Landhausser and Wein, 1993; Johnstone and Chapin, 2006). The failure of coniferous species following fire is thought to occur because of reduced availability of viable seed (Landhausser and Wein, 1993; Lloyd et al., 2002; Johnstone and Chapin, 2006).

Tree-line forests, by definition, occupy areas on the extremes of species tolerance limits, and thus are likely to be sensitive to direct climate effects. With increased temperatures in northern ecosystems, it is assumed that typically southern species will shift their distributions northwards. In the northwestern boreal forest, however, the bottleneck to forest establishment is recruitment, which is strongly mediated by reproductive output and disturbance effects. Through my PhD research, I am specifically focusing on the indirect pathway of disturbance-mediated recruitment by investigating whether an altered fire return interval will initiate ecosystem change in the tree-line forest of northern Yukon.

OBJECTIVES AND APPROACH

My first objective is to identify how fire stimulates tree recruitment in the latitudinal tree line. For the northern boreal forest to maintain its current structure, or for the forest to expand into the tundra, there must be a source of viable seed. While at the patch scale individual trees may spread through clonal growth, reproduction via seed is necessary for landscape-scale advance of the tree line (Holtmeier and Broll, 2007). Adverse environmental conditions at the northern margin of the boreal forest may limit its expansion into tundra through one or more of the following filters: (a) the availability and dispersal of viable seed, (b) the germination and establishment of seedlings, or recruitment, and (c) their growth and survival (Fig. 1). Each step is

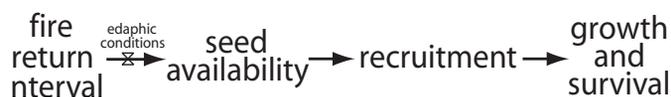


FIG. 1. Filters that may limit black spruce establishment after fire.

necessary for the successful establishment of a black spruce tree in the tree line. Using field surveys of existing forest patches along a latitudinal transect, I aim to quantify the reproductive potential of black spruce across the tree-line transition and identify past patterns in tree establishment.

We collected cones from individual black spruce in northern Yukon in 2007, 2008, and 2009 and conducted germination tests on their seed, with the intention of quantifying seed production and viability across the tree line. We also measured environmental gradients along the tree-line transect in an effort to identify catalysts of change in the past and potential constraints on forest expansion. Preliminary analyses indicate that in comparison to closed canopy forest, treed tundra had both fewer trees to bear cones and fewer cones per tree, and thus a lower reproductive potential. The low availability of viable seed at the tree line may slow or limit the expansion of boreal forest northward into tundra communities. Environmental gradients across the forest-tundra transition were not as easily identified, probably because of the complex plant-environment interactions in northern ecosystems. The factors limiting tree establishment are not as straightforward as simple temperature and nutrient gradients (Holtmeier and Broll, 2005; Danby and Hik, 2007), in part because of the complex indirect effects of temperature on plant response (Chapin and Shaver, 1996; Shaver et al., 2000).

Along the same latitudinal tree-line transect, we conducted surveys to quantify stand age structure and density in an attempt to determine the past pattern of tree establishment along the transition. In adjacent regions of northern North America, past establishment of tree-line forests has been either episodic, coinciding with historic disturbance or favourable climate (Szeicz and Macdonald, 1995), or gradual (Lloyd et al., 2002). Preliminary results suggest that past tree establishment in our study area was episodic, and that this pattern may have been due to a mosaic of historic fires on the landscape (C. Brown and J. Johnstone, unpubl. data).

My second objective is to investigate the response of tree-line forest to a change in fire return interval. Post-fire species composition depends on 1) the availability of seed or a means of vegetative reproduction and 2) the quality of the seedbed (or forest floor). The majority of black spruce in our northern Yukon study region are killed during a fire and cannot reproduce asexually. Post-fire seed availability is dependent on the reproductive maturity of the individual black spruce before the fire. Seedbed quality is affected by fire-induced changes to the structure, composition, and physical environment of the forest floor. Typically, the forest floor is partially consumed during a fire. This can alter the seedbed's physical structure (e.g., the bulk density of the

soil organic horizons) and influence soil moisture and temperature, as the charred surface of the seedbed can absorb more solar energy than the pre-fire moss cover. Fire can also alter the composition and interactions of the understory plant community. Some individuals may be killed in the fire, while others survive via underground stems, changing the competitive interactions of the forest floor. These factors related to seed availability and seedbed quality contribute to the success of black spruce post-fire self replacement.

I hypothesized that burned areas with a short interval between fires would have more dramatic changes to seedbed condition than those with a long interval because of the increased consumption of organic matter. In short-interval burned areas, the shorter time between fires meant that stands would not have recovered to unburned condition prior to the most recent fire. Therefore, soil organic horizon biomass that was not consumed during the initial fire was partially or completely consumed during the second. I also hypothesized that natural recruitment of black spruce would be absent or severely reduced in short-interval burned areas, as the aerial seed bank would have been consumed in the most recent fire.

I aim to identify links between fire history, seedbed condition, and the germination, survivorship, and growth of potential colonizing tree species. An unusually short fire return interval has occurred in some areas of the western boreal forest, where recent fires have overlapped. Two fires burned in the black spruce transitional forest of the Eagle Plains Ecoregion of northern Yukon in the early 1990s (1990: 33 500 ha and 1991: 4800 ha). In 2005, a 69 000 hectare fire burned in the region, partially overlapping both the 1990 and 1991 burns. This combination of fire history allowed us to sample unburned, long-interval burned, and short-interval burned sites immediately adjacent to one another. Sites in three stages of post-fire forest recovery were selected for study: 1) mature long-interval burned forest (previous fire > 100 years ago), 2) early successional stands following a long-interval burn (fire in 2005 following > 100 fire-free years), and 3) early successional stands following a short-interval burn (fire in both 1990–91 and 2005) (Fig. 2).

I initiated a natural field experiment in 2007, incorporating seed traps, seeded plots, and planted tree seedlings in a two-factor design. Eight 30 m × 30 m sites were selectively placed within each fire history class (mature long-interval, early successional long-interval, and early successional short-interval). Each site contained seven east-west transects composed of seeded and planted plots, seed traps, or destructive sampling plots (for soil sampling and active-layer measurement). In each of the eight sites, 10 plots were planted with tree seedlings and 10 plots were seeded with tree seed. Five seeded and five planted plots were located on earth hummocks, a natural feature on the landscape created by cryoturbation, and five were positioned in hollows.

I used five tree species native to the northern Yukon in the field experiment: black spruce from two separate Yukon populations, white spruce (*Picea glauca*), balsam poplar (*Populus balsamifera*, used in seeded plots), trembling

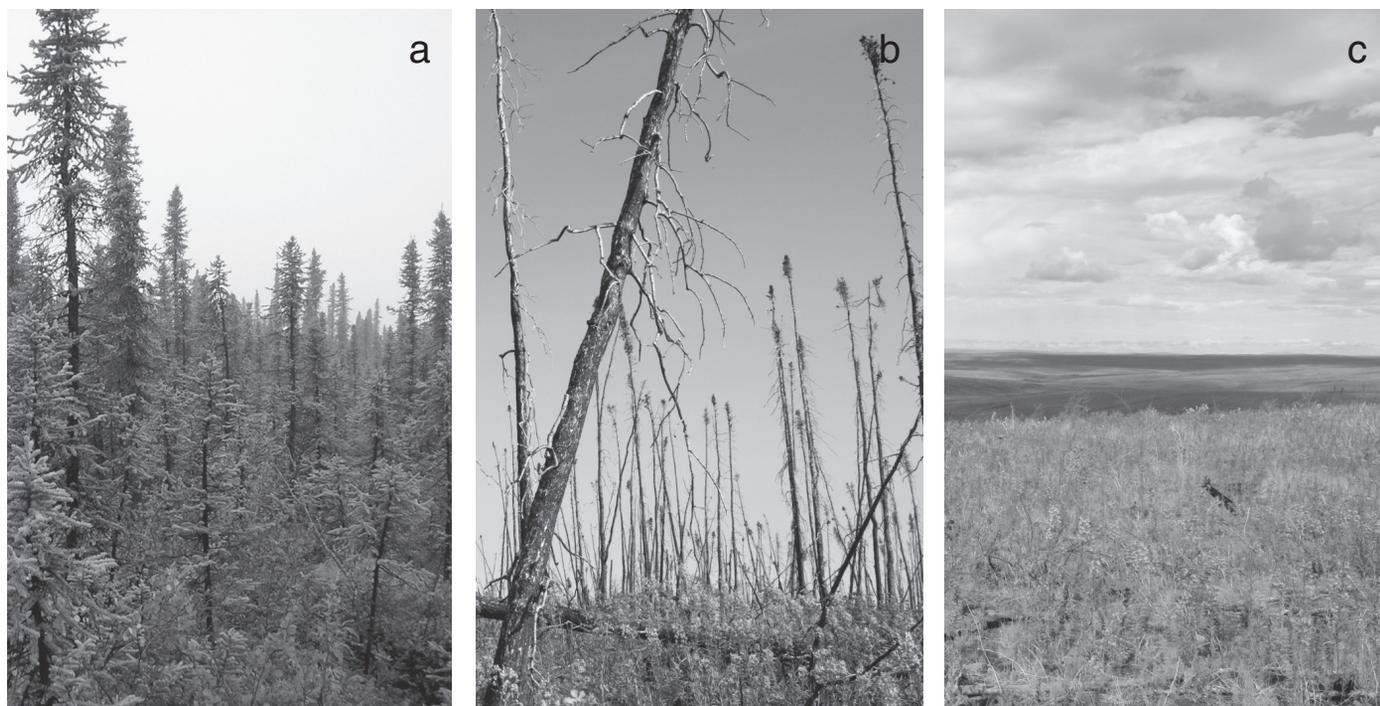


FIG. 2. (a) Mature long-interval, (b) early successional long-interval, and (c) early successional short-interval black spruce forests in the northern Yukon study area (Photos: Carissa Brown).

aspen (*Populus tremuloides*, used in planted plots), and birch (*Betula neoalaskana*). In 2008, 2009, and 2010, we measured seedling emergence (Figs. 3 and 4); seedling height, diameter, and health; and seed trap contents on a monthly basis. In addition, we measured black spruce stem biomass and density (fire-killed stems in burned stands and living stems in mature stands), soil organic horizon thickness, soil moisture and temperature, active layer thickness, and understory vegetation cover in each experimental site. In July 2010, we conducted the final survey of the natural field experiment and removed the planted seedlings for measurement of aboveground biomass.

Preliminary results suggest that increases in fire activity may lead to a degradation of tree-line forests in some areas, rather than the increased tree density and forest extent predicted with climate warming. Black spruce recruitment was drastically reduced following two closely timed fires. However, when seed was added to short-interval burned sites, germination increased, suggesting that black spruce recruitment is limited by seed availability, not by substrate conditions (C. Brown and J. Johnstone, unpubl. data). The absence of natural seedling establishment following a short-interval burn may result in stands' shifting from black spruce forest to deciduous woodlands or graminoid-dominated tundra in this tree-line region.

SIGNIFICANCE

There are several possible repercussions of an ecosystem shift from coniferous tree-line forest to deciduous

woodlands or graminoid-dominated tundra. The boreal forest stores more than one-third of the world's terrestrial carbon (Smith et al., 1993). The permafrost underlying the northern boreal forest holds even more. Permafrost soils remain frozen, in part because of the insulating layers of moss that make up the boreal forest understory. During a fire, some of those moss layers are consumed. As the forest regenerates after fire, the moss understory thickens and once again insulates the permafrost from solar heat. If black spruce fails to self-replace after fire, there will likely be a change in the carbon storage capacity of the region. Permafrost degradation due to the removal of the insulating moss layer will cause changes of an even larger magnitude.

This research tests explicit hypotheses regarding the dynamics of vegetation in an ecologically sensitive biome in Canada. It will increase our understanding of relations between environmental variations and forest structure across an unburned latitudinal tree line and relations between environmental variations and the fire return interval, as well as allowing comparisons of environmental and fire return interval effects on species recruitment, survivorship, and growth. Understanding the ability of native species to survive under rapidly changing conditions is vital for predicting the future landscape of northern regions. The expansion or contraction of the boreal forest will influence habitat for animal and plant species important to northern communities, such as moose, caribou, blueberries, and cranberries. The species that will succeed under predicted climatic conditions will dictate the composition of the northern forest landscape, which will affect species dependent on tree-line habitat. Presenting scenarios of probable



FIG. 3. Carissa Brown counting black spruce seedlings in an early successional long-interval burned stand in northern Yukon (Photo: Jayme Viglas).

forest composition will aid in making informed decisions on current and future forest conservation.

OUTREACH: TELLING THE STORY OF THE NORTHERN BOREAL FOREST

Tree-line dynamics are a complex story, and it is important to keep the public informed of our current knowledge of this changing ecosystem. I have had several opportunities to present my research to Northerners in the Yukon. Two instances stand out as particularly valuable experiences: speaking at Tombstone Territorial Park, and discussing boreal forest dynamics with Yukon College's Renewable Resources class. I have participated in two of Tombstone Territorial Park's annual Botany Days; both times introducing my study to individuals who have traveled, lived, and worked on the Dempster Highway and have an interest in plant research. During the International Polar Year, I was fortunate to have the Renewable Resources class visit my study area. While standing in the very plant communities we were discussing, I spoke about boreal forest processes and my natural field experiment. In both cases, I learned that context-specific talks in the North have the added characteristic of an audience that is invested in the outcome of the research in a practical sense. This investment creates interactions that are quite different from those at presentations I



FIG. 4. Three-year-old black spruce seedling in an early successional long-interval burned stand in northern Yukon (Photo: Carissa Brown).

have given in southern Canada. They have provided me with a valuable perspective of my research, which keeps me conscious that northern science is important not only to the academic community, but also to the communities surrounding the ecosystems being studied.

ACKNOWLEDGEMENTS

I am honoured to be the recipient of the Arctic Institute of North America's Jennifer Robinson Memorial Scholarship. Funding for my research has also been provided by the Government of Canada Program for International Polar Year as part of the project PPS Arctic Canada, the Natural Sciences and Engineering Research Council of Canada, the Association of Canadian Universities for Northern Studies Canadian Northern Studies Trust (W. Garfield Weston Foundation), the International Association of Wildland Fire, the University of Saskatchewan, Indian and Northern Affairs Canada (Northern Scientific Training Program), and the Northern Research Institute (Yukon College) Research Fellowship Program. I am grateful to the Yukon Territorial Government (Department of Environment and Yukon Parks), Northern Forestry Centre (Canadian Forest Service), and Friends of Dempster Country for logistical and analytical support, and to the Vuntut Gwitchin First Nation for permission to carry out research within their traditional territory.

My research successes thus far have been due in large part to the invaluable support and encouragement provided by my supervisor, Dr. Jill Johnstone, and the members of the Northern Plant Ecology Lab at the University of Saskatchewan. I am also indebted to the many people who have assisted me in the field and laboratory during the four summers I conducted fieldwork in northern Yukon.

REFERENCES

- Bond-Lamberty, B., Wang, C., and Gower, S.T. 2004. Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. *Global Change Biology* 10:473–487, doi:10.1111/j.1529-8817.2003.0742.x.
- Chapin, F.S., III, and Shaver, G.R. 1996. Physiological and growth responses of Arctic plants to a field experiment simulating climatic change. *Ecology* 77(3):822–840, doi:10.2307/2265504.
- Chapin, F.S., III, Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H., McGuire, A.D., et al. 2005. Role of land-surface changes in Arctic summer warming. *Science* 310:657–660, doi:10.1126/science.1117368.
- Danby, R.K., and Hik, D.S. 2007. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *Journal of Ecology* 95:352–363, doi:10.1111/j.1365-2745.2006.01200.x.
- Flannigan, M.D., Logan, K.A., Amiro, B.D., Skinner, W.R., and Stocks, B.J. 2005. Future area burned in Canada. *Climatic Change* 72:1–16, doi:10.1007/s10584-005-5935-y.
- Gillett, N.P., Weaver, A.J., Zwiers, F.W., and Flannigan, M.D. 2004. Detecting the effect of climate change on Canadian forest fires. *Geophysical Research Letters* 31, L18211, doi:10.1029/2004GL020876.
- Grace, J., Berninger, F., and Nagy, L. 2002. Impacts of climate change on the tree line. *Annals of Botany* 90(4):537–544, doi:10.1093/aob/mcf222.
- Heinselman, M.L. 1981. Fire and succession in the conifer forests of northern North America. In: West, D.C., Shugart, H.H., and Botkin, D.A., eds. *Forest succession: Concepts and application*. New York: Springer-Verlag. 374–405.
- Holtmeier, F.-K., and Broll, G. 2005. Sensitivity and response of Northern Hemisphere altitudinal and polar tree lines to environmental change at landscape and local scales. *Global Ecology and Biogeography* 14:395–410, doi:10.1111/j.1466-822X.2005.00168.x.
- . 2007. Treeline advance – driving processes and adverse factors. *Landscape Online* 1:1–33, doi:10.3097/LO.200701.
- Johnson, E.A. 1992. *Fire and vegetation dynamics: Studies from the North American boreal forest*. Cambridge: Cambridge University Press.
- Johnson, E.A., and Fryer, G.I. 1989. Population dynamics in lodgepole pine–Engelmann spruce forests. *Ecology* 70(5):1335–1345, doi:10.2307/1938193.
- Johnstone, J.F., and Chapin, F.S., III. 2006. Fire interval effects on successional trajectory in boreal forests of Northwest Canada. *Ecosystems* 9:268–277. doi:10.1007/s10021-005-0061-2.
- Johnstone, J.F., Chapin, F.S., III, Foote, J., Kemmett, S., Price, K., and Viereck, L. 2004. Decadal observations of tree regeneration following fire in boreal forests. *Canadian Journal of Forest Research* 34:267–273.
- Kasischke, E.S., and Turetsky, M.R. 2006. Recent changes in the fire regime across the North American boreal region—Spatial and temporal patterns of burning across Canada and Alaska. *Geophysical Research Letters* 33, L09703, doi:10.1029/2006GL025677.
- Landhäuser, S.M., and Wein, R.W. 1993. Postfire vegetation recovery and tree establishment at the Arctic treeline: Climate-change–vegetation-response hypothesis. *Journal of Ecology* 81:665–672.
- Li, C. 2000. Fire regimes and their simulation in reference to Ontario. In: Perera, A.H., Euler, D.L., and Thompson, I.D., eds. *Ecology of a managed terrestrial landscape: Patterns and processes of forest landscapes in Ontario*. Vancouver: UBC Press. 115–140.
- Lloyd, A.H., Rupp, T.S., Fastie, C.L., and Starfield, A.M. 2002. Patterns and dynamics of treeline advance on the Seward Peninsula, Alaska. *Journal of Geophysical Research* 107, 8161, doi:10.1029/2001JD000852.
- Payette, S. 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R., and Bonan, G.B., eds. *A systems analysis of the global boreal forest*. Cambridge: Cambridge University Press. 144–169.
- Shaver, G.R., Canadell, J., Chapin, F.S., III, Gurevitch, J., Harte, J., Henry, G., Ineson, P., et al. 2000. Global warming and terrestrial ecosystems: A conceptual framework for analysis. *BioScience* 50:871–882.
- Smith, T.M., Cramer, W.P., Dixon, R.K., Leemans, R., Neilson, R.P., and Solomon, A.M. 1993. The global terrestrial carbon cycle. *Water, Air, and Soil Pollution* 70:19–37, doi:10.1007/BF01104986.
- Soja, A.J., Tchepakova, N.M., French, N.H.F., Flannigan, M.D., Shugart, H.H., Stocks, B.J., Sukhinin, A.I., Parfenova, E.I., Chapin, F.S., III, and Stackhouse, P.W., Jr. 2007. Climate-induced boreal forest change: Predictions versus current observations. *Global and Planetary Change* 56:274–296, doi:10.1016/j.gloplacha.2006.07.028.
- Stocks, B.J., Fosberg, M.A., Lynham, T.J., Mearns, L., Wotton, B.M., Yang, Q., Jin, J.-Z., et al. 1998. Climate change and forest fire potential in Russian and Canadian boreal forests. *Climatic Change* 38:1–13, doi:10.1023/A:1005306001055.
- Szeicz, J.M., and Macdonald, G.M. 1995. Recent white spruce dynamics at the subarctic alpine treeline of north-western Canada. *Journal of Ecology* 83:873–885.
- Weber, M.G., and Flannigan, M.D. 1997. Canadian boreal forest ecosystem structure and function in a changing climate: Impact on fire regimes. *Environmental Reviews* 5:145–166, doi:10.1139/er-5-3-4-145.

Carissa Brown, a doctoral student in plant ecology in the Department of Biology, University of Saskatchewan, is the 2010 recipient of the Jennifer Robinson Memorial Scholarship. carissa.brown@usask.ca