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Lichen mated seedbeds inhibit while moss dominated seedbeds facilitate black spruce (*Picea mariana*) seedling regeneration in post-fire boreal forest

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ABSTRACT

The subject of conifer regeneration failure after canopy removing disturbance leading to expansion of ericaceous heaths in boreal forests received considerable attention. However, despite seedbed quality being a key factor in tree regeneration, our understanding of the role of lichen and moss dominated seedbeds on tree seedling regeneration after forest fires remains unclear. Objective of this study was to investigate the effect of time since fire and post-fire cryptogamic (lichen and moss) seedbeds with variable organic matter thickness on black spruce regeneration. We conducted black spruce seeding experiment in black spruce – *Kalmia* forests burned 11, 17 and 37 years ago. In each site we applied three seedbed manipulation treatments (mat-intact, mat-mixed and mat-removed) to test if seedbed manipulation improves spruce regeneration. This experiment was extended to three moss-dominated seedbeds to compare seedbed moisture and temperature effects on spruce regeneration. We also tested potential allelopathic effect of two common lichen and moss species in laboratory bioassay. Seed regeneration was low in all seedbeds. Black spruce germination and seedling growth was lowest in presence of *Cladonia cristatella* followed by *C. stellaris*, *Polytrichum juniperinnum* and *Pleurozium schriberi*. HPLC analysis of *C. cristatella* indicated the presence of usnic acid, a common germination inhibiting allelochemical. Moss seedbeds were relatively favourable for spruce regeneration. We conclude that (i) lichen seedbeds inhibit seedling regeneration due to adverse biophysical and chemical (allelopathic) effects, (ii) moss seedbeds facilitate black spruce regeneration by maintaining favourable moisture and temperature, and (iii) seedbed manipulation treatments produce mixed results depending on the dominant cryptogam, organic matter thickness and seedbed moisture and temperature.

1. Introduction

The subject of conifer regeneration failure after canopy removing disturbance such as wildfire and insect infestation leading to expansion of lichen woodlands in the boreal forest received considerable attention (Payette et al., 2000; Payette and Delwaide, 2003; Girard et al., 2008, 2009; Veilleux-Nolin and Payette, 2012). Wildfires modify abiotic and biotic conditions of post-fire seedbeds (Mallik, 2003; Mallik et al., 2010) leaving an ash/charcoal layer and unburned/partially burned organic matter (hereafter called OM) depending on fire severity. Seedling recruitment in severely burned sites is higher than those in low severity burns (Charron and Greene, 2002; Girard et al., 2009). In the absence of high severity natural fires due to aggressive fire suppression, understory ericaceous shrubs, mosses and lichens become dominant in post-fire habitats and interfere conifer regeneration by creating unfavourable seedbeds (Brown and Mikola, 1974; Sedia and Ehrenfeld, 2005, 2006; Fauria et al., 2008; Veilleux-Nolin and Payette, 2012; Thiffault et al., 2013). This may delay forest succession and in some cases convert conifer forests in to ericaceous heaths (Mallik, 1995, 2003; Nilsson and Wardle, 2005; Hyppönen et al., 2013).

Despite seedbed quality being a key factor in seedling regeneration (Siegwart Collier and Mallik, 2010) the role of common boreal seedbeds (lichen and moss-dominated) on conifer regeneration in post fires sites remains unclear (but see Steijlen et al., 1995; Wheeler et al., 2011). Cryptogamic species (lichens and mosses) form a carpet or mat-like structure on top of post-fire seedbeds, which by affecting their physical and chemical properties influence conifer seedling regeneration (Belnap et al., 2001; Steijlen et al., 1995; Sedia and Ehrenfeld, 2003). Mosses can both facilitate and inhibit vascular plant establishment through a variety of mechanisms (Michel et al., 2011; Zackrisson et al., 1997). Moss mats increase soil moisture (Zackrisson et al., 1997), intercept and sequester nutrients from throughfall and litter decomposition (Chapin III et al., 1987), and supply nutrients from senescing tissues to ectomycorrhizal hyphae (Carleton and Read, 1991). Wheeler

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et al. (2011) showed that feather-moss (*Pleurozium screberi* (Brid.) Mitt.) seedbeds facilitate black spruce seedling regeneration in forest-tundra ecotone. They argued that seedbed composition may influence micro-habitat physical and nutrient condition, and seedling predation. The structure of *P. schreberi* likely protects young seedlings from temperature extremes (Steijlen et al., 1995). Similar results are reported from Swedish boreal forests where feather-mosses add nitrogen to soil in old growth forests (Zackrisson et al., 2004; Lagerström et al., 2007). In contrast, Zackrisson et al. (1997) found that aboveground removal of feather-moss from the seedbed enhances Scots pine (*Pinus sylvestris* L.) germination and growth.

Lichens can also have both positive and negative effects on tree seedling regeneration (During and van Tooren, 1990). Approximately 500 secondary compounds have been reported from lichens, many of which can inhibit conifer regeneration (Mallik, 1987; During and van Tooren, 1990; Steijlen et al., 1995; Zackrisson et al., 1997; Sedia and Ehrenfeld, 2003; Hawkes and Menges, 2003). Both allelopathic effect of lichens and drought or nutrient limitation could suppress germination (Hawkes and Menges, 2003). Growth of planted conifer seedlings can also be inhibited in lichen woodland due to both physical and chemical effects of lichens (Brown and Mikola, 1974). It is critical to understand the causes and consequence of conifer regeneration failure in lichen woodlands, which is rapidly expanding in changing climate (Girard et al., 2008, 2009; Splawinski et al., 2018).

In the boreal forest low-severity fires leave patches of unburned/partially burned OM that may amplify seedbed temperature and moisture fluctuations during summer. The residual OM may contain moss and lichen fragments that allow their rapid recovery after fire (Racine, 1981). Soon after fire, the pioneer crustose lichens and acrocarpous mosses colonize the unburned/partially burned OM followed by foliose and fruticose lichens and pleurocarpous mosses in the later part of succession (Bloom and Mallik, 2004, 2006). Mosses and lichens create unique seedbeds by altering their biophysical and chemical properties. The potential role of lichens and mosses in seedling regeneration may vary depending on residual OM thickness, time since fire and cryptogamic species composition. The mechanism of spruce regeneration failure in post-fire seedbeds is likely multi-faceted involving physical, chemical (allelopathy) and microclimatic conditions of seedbeds. Successful conifer regeneration in lichen-spruce woodlands requires a better understanding of seedbed properties and innovative approach in creating safe sites for tree seedling regeneration (Mallik and Kravchenko, 2018).

Our objective was to investigate the role of lichen and moss dominated seedbeds on black spruce seedling regeneration in post-fire sites by addressing three questions, (i) how does time since fire and seedbed type (lichen vs. moss) and OM thickness affect black spruce regeneration? (ii) does mechanical mixing of cryptogamic mats with OM and removal of lichen or moss mat help black spruce regeneration? and (iii) what role the seedbed physical (moisture and temperature) and chemical (allelopathy) properties play in black spruce seed regeneration? We hypothesised that, (i) seedbed properties will vary depending on time since fire and because cryptogamic mats pose physical barrier for primary roots reaching moist soil, mat-mixing and mat removal would result better spruce regeneration than mat-intact seedbeds, (ii) moss seedbeds will support higher seedling regeneration than lichen seedbeds by retaining higher soil moisture and lower surface temperature, and (iii) higher phenolic concentration of lichens would lower black spruce germination and seedling growth than mosses.

2. Materials and methods

2.1. Study area

We conducted this study in the greater Terra Nova National Park (TNNP) ecosystem, located in the east-central and north shore eco-regions of Newfoundland, Canada (48° 33′ N latitude, 53° 58′ W longitude). Climatic conditions are both continental and maritime, due to prevailing westerly winds and close proximity to the Atlantic Ocean. Summers are brief and cool with regional mean summer temperature averaging 12.5 °C and mean annual precipitation ranging from 1000 to 1300 mm (Power, 2000, 2005). TNNP is nearly 80% forested and stands are similar to those of the mainland boreal forests of Canada. Forests are dominated by black spruce and balsam fir (*Abies balsamea* (L.) Mill.) mixed with white birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.) and, to a lesser extent, larch (*Larix laricina* (du Roi) Koch) and red maple (*Acer rubrum* L.). Black spruce communities are among the most common in the Terra Nova region, occupying 52% of total forest cover. The dominant sub-canopy species associated with black spruce forests and barrens is *Kalmia* and black spruce-*Kalmia* associations occupy nearly 50% of the land base in TNNP (Siegwart Collier and Mallik, 2010). Other ericaceous shrubs such as Labrador tea (*Rhododendron groenlandicum* (Oeder) K.A. Kron and W.S. Judd), Rhododendron (*R. canadense* (L.) Torr.) and low-bush blueberry (*Vaccinium angustifolium* Aiton) are also associated with these forest types (Power, 2000). Pre-fire forest floor is composed of lichens (mainly *Cladonia* and *Cladina* spp.), mosses (mainly Acrocarpous and Pleurocarpous), accumulated leaf litter and organic matter (Power, 2000, 2005). High-severity fire has historically facilitated black spruce recovery, producing even-aged stands throughout the region (Power, 2000; Bloom and Mallik, 2006). Effective fire suppression since 1970s decreased stand replacing fires resulting poor conifer regeneration and increased ericaceous heaths (Power, 2000).

2.2. Site selection

We selected three post-fire sites, Rocky Pond (RP), Spracklin Road (SR) and Terra Nova Road (TNR), burned respectively 11, 17 and 37 years ago, to cover varying time since fire, OM thickness and seedbed types (only in SR) to conduct seeding experiments (Table 1). In the early and late post-fire sites, two dominant lichen and moss species were respectively *Cladonia cristatella*, *C. stellaris* and *Polytrichum juniperinnum* and *Pleurozium schreberi* (Brid.) Mitt. (Bloom and Mallik, 2006).

Table 1
Location and characteristics of post-fire sites in Rocky Pond (RP), Spracklin Road (SR) and Terra Nova Road (TNR) used for the *in situ* seedbed manipulation experiment in Terra Nova National Park (TNNP), Newfoundland (modified from Mallik and Kravchenko (2016)).

Site	Location	GPS coordinates	Time since fire (yrs)	Burn area (ha)	OM depth (cm) ± se	OM depth range
1	Rocky Pond (RP)	N48°31′ 662″ W53°58′ 967″	11	85	4.0 ± 0.5	0–20
2	Spracklin Road (SR)	N48°31′ 953″ W54°03′ 091″	17	75	6.1 ± 0.7	0–10
3	Terra Nova Road (TNR)	N48°30′ 487″ W54°07′ 143″	37	313	3.9 ± 0.5	0–20