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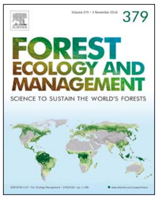

Recruitment and ontogenic patterns of stunting and growth release of black spruce (*Picea mariana*) in post-fire *Kalmia* heaths

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ABSTRACT

Recruitment of seed regenerating plants after disturbance depends on adequate seed supply and favourable microsites that allow germination and seedling establishment (safe sites). Forest disturbance in nutrient stressed conifer-ericaceous communities in boreal and temperate forests become quickly dominated by ericaceous shrubs and restrict tree recruitment. Habitat filter due to limitation of safe sites has been attributed to inadequate seedling regeneration. Furthermore, large proportions of the regenerating seedlings exhibit stunted growth but some over time exhibit growth release. Despite wide occurrence of poor natural regeneration of conifers in ericaceous shrubs, the ontogenic patterns of stunting and growth release of conifer seedlings received little attention. We used post-fire black spruce- *Kalmia* ecosystems to study this. We hypothesized that (i) post-fire residual OM thickness controls seedling recruitment by limiting safe sites even in presence of sufficient seed supply, (ii) black spruce density of a site depends on its OM depth, which controls safe sites, and (iii) partially safe sites, which permit germination and seedling establishment with stunted growth, can become safe sites overtime allowing growth release. We experimentally tested black spruce seed regeneration on seedbeds with variable OM thickness and studied the ontogenic patterns of seedling/sapling growth in eight post-fire *Kalmia* heaths along an 8–34 year chronosequence. We found that despite ample seed supply OM depth controls seedling recruitment. In the chronosequence study we found only 17.8% of burnt area accounts for occupied safe sites, recruiting only 317 seedlings/ha and only 13% of them exhibit normal growth, others remain stunted for 5–20 yrs. With time, successive cohorts of stunted seedlings overcome growth check. Black spruce density was negatively associated with OM depth and *Kalmia* cover. The probability of growth release was associated negatively with OM depth and positively with soil respiration. We conclude that poor black spruce regeneration in *Kalmia* heath is largely due to safe site limitation controlled by OM depth, which also controls seedling stunting and growth release. The novelty of this work is the discovery of ontogenic patterns of conifer seedlings in nutrient stressed habitats. Our findings have implications for tree regeneration in other environmentally and nutritionally stressed ecosystems such as treelines.

1. Introduction

Poor conifer recruitment and slow seedling growth in nutrient stressed habitats dominated by ericaceous plants following forest harvesting and fire is widely reported from Western Europe (Wheatherell, 1953; Gimingham, 1972; Read and Jalal, 1980, Read, 1982; Taylor and Tabbush, 1990), Scandinavia (Nilsson and Zackrisson, 1992; Jaderlund et al., 1997) and across North America (Fraser et al., 1995; Mallik and Prescott, 2001; Inderjit and Mallik, 1996; Mallik 2001, 2003; Thiffault et al., 2004). The per-disturbance communities in all these ecosystems have several things in common, (i) top canopy consisting of conifer trees, (ii) ericaceous shrubs as the main understory, and (iii) ground vegetation of pleurocarpous moss over thick forest-floor humus. After canopy removing disturbance the sites quickly become dominated by ericaceous shrubs causing delay in forest succession. The best example of successional delays can be found in black spruce - *Kalmia angustifolia* (hereafter referred to as *Kalmia*) communities in nutrient-poor, coarse textured soils of eastern Canada, where the periods of ericaceous dominance can last for decades and in worst cases the forests transform into heaths (Mallik, 2003; Payette and Delwaide, 2003). How does this happen and more specifically what is the role of post-fire OM on ontogenic growth pattern of naturally regenerating conifers in ericaceous heath?.

Post-fire recruitment of seed regenerating plants (most conifers are seed regenerating) depends on adequate seed supply and availability of favorable microsites also called “safe sites” (*sensu* Harper et al., 1977),

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which control their distribution (Duncan, et al. 2009; Turnbull et al., 2000; Taylor and Tabbush, 1990; Hegazy and Kabiel, 2007) and sets the template for the development of entire plant community (Guo, 1998; Fraije et al., 2015). Harper et al. (1977) defined safe site as an immediate area surrounding a seed that provides, (i) appropriate stimuli for breaking seed dormancy, (ii) favourable conditions required for germination, (iii) the resources to be used during primary growth and (iv) absence of hazards (predation, competition, soil toxicity). After germination, seedlings may face inhospitable site conditions and succumb to mortality (Lamont et al., 1993) or slow growth (Burton and Mueller-Dombois 1984). Seedlings suffering from growth suppression (growth check) develop differently from those enjoying optimal growth (Anderson and Treshow, 1980). Schupp (1995) suggested viewing the idea of safe site as a series of sieves or filters applied to a population at different growth stages. A site may be safe for seeds (germination) but may not be safe for seedlings (growth). This means that for an individual to reach reproductive maturity it needs safe site throughout all life stages, not just the germination and primary growth stages as defined by Harper et al. (1977).

For successful conifer recruitment and growth in post-harvest and post-fire sites with high ericaceous cover and thick humus (common in boreal and coastal oceanic climate), seeds and seedlings must pass through several ecological filters. In this context we can view the first filter controlling seedling recruitment and the second filter controlling their growth. Previous studies have shown that fire-severity by modulating residual organic matter (ROM) thickness can control seedling recruitment (Zasada et al., 1983; Turner, et al., 1999; Lecomte et al., 2006; Hollingsworth et al., 2013; but see Perrault-Hébert et al. 2017, who argued that although thin ROM resulting from high fire-severity helps seedling establishment high fire-severity also limits seedling regeneration by destroying canopy seedbank). After recruitment, the seedlings must to pass thorough further abiotic (Yarie, 2008; Harper et al., 2009; Wright, 1989; Foy, 1992; Zhu and Mallik, 1994; Kayes, 2015) and biotic filters (Wilkinson and Neilsen, 1994; Maron and Crone, 2006).

After initial establishment, the regenerating conifers may experience stunted growth due to intense above and belowground competition from the ericaceous plants (Mallik, 1994; Mallik et al., 2016) and priority effects Kalmia immediately after disturbance due to their rapid vegetative growth from near ground and belowground organs (Mallik and Gimingham, 1985; Mallik, 1993). By contrast the seeds of conifers must land on the limited ‘safe sites’ with thin or no OM for germination and adequate growth. Growth of conifer seedling is substantially slower than the vegetatively growing ericaceous shrubs. Furthermore, the ericaceous plants are equipped with ericoid mycorrhizae that can access nitrogen bound in protein-lignin/phenol complexes in ericaceous litter (Bending and Read, 1996a,1996b; Joanisse et al., 2009). Conifer seedlings in ericaceous habitats often suffer from insufficient ectomycorrhizal colonization making them unable to absorb the limited soil nitrogen and phosphorous and remain stunted (Yamasaki et al., 2002). These abiotic and biotic filters together paly a strong role in their stunted growth. However, over time some stunted conifers have been found to achieve improved growth by ‘growth release’ attributed to changed microsite conditions (Gimingham 1972; St. Martin and Mallik, 2016). The abiotic and biotic variables are spatially and temporally dynamic. This follows that a microsite at one time may be safe for germination, but may not be safe for seedling establishment and growth. In other words, a site may be partially safe allowing germination and seedling survival with stunted growth but with time a partially safe site can become safe allowing normal growth of stunted seedlings through growth release.

We studied the phenomenon of poor black spruce recruitment and variable growth in post-fire *Kalmia* heaths of eastern Canada. Our previous studies showed that black spruce germination in sites dominated by *Kalmia* is greatly inhibited due to thick organic matter (OM) that makes very poor seedbed (Mallik et al., 2010). During field visits we observed, not only black spruce seedling recruitment being poor in post-fire sites with high *Kalmia* cover, but many of the sparsely distributed black spruce seedlings remain stunted and chlorotic. Recently St. Martin and Mallik (2016) showed from two post-burn sites in Newfoundland that most of the naturally regenerating seedlings remained stunted, some exhibit growth release, and very few show normal growth. In Canada stunted growth of planted black spruce in post-fire and post-harvest sites with *Kalmia* and other ericaceous plants such as *Vaccinium angustifolium* and *Rhododendron groenlandicum* has been reported from Newfoundland (Yamasaki et al., 1998; Mallik, 2001), Quebec (Thiffault et al., 2004) and Ontario (Inderjit and Mallik, 1996). The poor black spruce recruitment and growth has been attributed to a variety of factors including allelopathy (Mallik, 1987; Zhu and Mallik, 1994; Wallstedt et al., 2002), poor ectomycorrhizal association (Yamasaki et al., 1998) and direct nutrient competition between black spruce and *Kalmia* (Thiffault et al., 2004, Bradley et al., 1997). Regardless of reasons, poor recruitment and slow conifer growth leads to considerable delays in forest succession (Bloom and Mallik, 2004) affecting forest productivity. Despite the widespread occurrence in variability of growth (i.e. stunting and growth release) of naturally regenerating conifers in the presence of ericaceous shrubs little is known about what proportion of seedlings enjoys normal growth from the start, what proportion remains stunted and for how long and how many achieve growth release i.e. their ontogenic growth patterns and what role OM of the sites plays in such patterns?. This critical knowledge gap is directly related to the widely observed phenomenon of inadequate natural regeneration of black spruce in post-fire sites with ericaceous dominance. Our aim was to fill this knowledge gap by determining the temporal variation in density of naturally regenerating black spruce seedlings/saplings and their ontogenic growth patterns in relation to OM thickness using a post-fire *Kalmia* heath chronosequence as a model system (Foster and Tilman 2000; Walker et al., 2010). Since previous research demonstrated that thickness of post-fire ROM is associated with black spruce seedling regeneration (Johnstone and Chapin, 2006; Siegwart Collier and Mallik, 2010) and conifer growth is generally linked to the amount of recalcitrant forest floor organic matter (Prescott et al., 2000; Lecomte, et al., 2006; Brown et al., 2015; Perrault-Hébert et al., 2017) it is reasonable to assume that black spruce growth stunting and growth release (i.e., their ontogenic patterns) might be related to site OM thickness.

Generally speaking, time since disturbance (in this case time since fire, TSF) is a good predictor of the rate of forest succession (Foster and Tilman 2000; Walker et al. 2010). This is true in case of progressive succession in boreal forests where wildfires reset succession by reducing/eliminating forest floor OM, removing allelochemicals, eliminating competition, releasing available nutrients and creating initial conditions that allow colonization of both seed and vegetatively regenerating plants. Over time tree species out compete other plants eventually leading into pre-disturbance forest structure and composition. However, in conifer forests with ericaceous understory site to site variability in fire severity results variability in post-fire residual OM thickness, which determines if the succession will be progressive or retrogressive. Partially burned thick OM creates poor seedbed for seed regenerating conifers while protects the belowground vegetative organs of the ericaceous plants, which regenerate rapidly after fire and dominate the post-fire habitat leading to retrogressive succession; high severity fires on the otherhand by creating favourable seedbeds for conifers and eliminating ericaceous plants support progressive succession (Mallik et al., 2010; Siegwart-Collier and Mallik, 2010). We assume that it is the variability of post-fire OM thickness that determines if a site is safe (little or no OM), unsafe (thick OM) or partially safe (intermediate OM thickness plus time) for conifer regeneration. We predict that given sufficient seed supply, if a post-fire site has few microsites with little or no OM (unsafe) then black spruce density will be low compared to a site with many microsites with thin or no OM, which will have high density of safe sites and hence high density of black spruce. In this case the