

Role of safe sites in black spruce recruitment and growth release
in post-fire *Kalmia* heath

By

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Abstract

The goal of this thesis was to explain black spruce regeneration in post-fire sheep laurel (*Kalmia angustifolia* L., hereafter referred to as *Kalmia*) dominated chronosequence in light of safe site density. The concept of safe site was expanded by including germination as well as seedling establishment and growth phases. Proliferation of *Kalmia*, which dominates heathlands of eastern Newfoundland, has been reported to severely restrict conifer recruitment and growth. As a result, forest regeneration in *Kalmia* heath can be delayed by as much as 60 years. Despite numerous studies, the process by which colonization and establishment of black spruce occurs in *Kalmia* heath is poorly understood.

This problem is addressed in two chapters. In chapter one, it was hypothesized that post-fire black spruce stem density, which represents a relative measure of safe site abundance per plot, is a function of variation in microsite conditions, rather than time since fire. The second hypothesis was that the partially safe sites defined by seedling establishment, but poor seedling growth, overtime, become safe sites allowing a growth release. In chapter two, it was hypothesized that microsites created by scarification and microsite mulching (MSM) enhance black spruce growth by removing the inhibitory effects of *Kalmia* and its organic matter by increased decomposition and soil moisture.

The main findings of the research are (1) black spruce safe site density in post-fire sites is low and diminishes over time; (2) relative safe site density is negatively associated with organic matter thickness; (3) most of the recruited black spruce experience a period of stunted growth; (4) with time, stunted black spruce may overcome the growth check; (5) the likelihood of the growth release has an inverse relationship with OM thickness and positive relationship with OM decomposition; (6) young black spruce seedlings planted in artificially created safe sites show significantly higher growth rates compared to those in undisturbed heath. Based on these results, it was concluded that i) safe sites play a critical role in colonization and growth of black spruce, ii) high OM depth (> 5 cm) makes a microsite unsafe for black spruce regeneration, and iii) safe sites created by scarification and microsite mulching (MSM) can enhance black spruce regeneration in *Kalmia* heath.

By examining the problems of black spruce forest regeneration in *Kalmia* dominated sites, this study advances the current understanding of the safe site concept and its application in forest restoration. From the conceptual point of view, it revealed the need for extending the safe site concept beyond the germination stage to include seedling and adult life stages. This research demonstrates that by removing the growth limiting conditions, it is possible to create safe sites by scarification and MSM which enhance conifer growth in habitats that are otherwise unsuitable for conifer regeneration. For national parks and other conservation areas MSM is preferred to scarification for its minimum soil disturbance.

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General Introduction

The role of the environment in the formation of plant communities has been a central topic of ecology. Seed germination as well as seedling establishment, survival and growth are highly dependent on the adequate supply of resources, including soil moisture (Hebert et al. 2006), soil nutrients (Kachi & Hirose 1983, Paquin et al. 1998), light (Wassink & Stolwijk 1956, Chazdon 1988, Harper 2006) and the absence of dangers such as animal browsing (Wilkinson & Neilsen 1994, Maron & Crone 2006) and potentially harmful chemicals (Wright 1989, Foy 1992). Under natural conditions, the environment is often heterogeneous even at a small microsite scale (Harper 1977). As a result of variation in environmental conditions, some microsites are favourable for seed germination, seedling survival and growth, while others are not.

In plant ecology literature, the terms microsite and microhabitat are unclear and often used interchangeably. Many perceive both microhabitat and microsite as an area characterized by relatively uniform physical, chemical and biotic conditions (Peterson & Pickett 1990, Germino & Smith 2001, Carreira et al. 2008). For the purpose of this study, I considered a microsite as a small area around a seedling with relatively homogeneous environmental conditions controlled only by external factors. On the other hand, I viewed microhabitat as an immediate zone around a seedling/sapling that may have diverse environmental conditions and is affected by possible feedback from the individual plant. A microhabitat can be directly influenced by the plant through resource depletion (Huston & DeAngelis 1994) and indirectly by a variety of secondary mechanisms (Jones 1997). The areas of both microsite and microhabitat are directly proportional to plant size and can increase over time as the seedling/sampling matures.

The distribution of favourable microsites has a strong effect on the distribution of an individual species (Jumpponen et al. 1999, Turnbull et al. 2000, Hegazy & Kabieli 2007) as well as the whole community (Guo 1998). Named "safe sites" by Harper (1961), the favourable microsites provide the necessary conditions for germination, even when the general site conditions are inhospitable (Flores & Jurado 2003). Thus, in harsh habitats, such as deserts or

alpine communities, the recruitment of new individuals is restricted and occurs only in locations of safe sites (Hegazy & Kabieli 2007).

The role of safe sites is not limited to the germination stage, as was stipulated by Harper et al. (1977) in defining the term. Once germinated, the seedlings may face inhospitable conditions leading to higher mortality (Scherff 1994) or slower growth (Burton & Mueller-Dombois 1984). Seedlings that suffer from continuous growth suppression are likely to develop differently from those enjoying optimal growing conditions (Anderson & Treshow 1980).

Many variables may affect growth of seedlings. Inadequate soil moisture can have severe effects on tree growth (Lamhamed et al. 1998, Hebert et al. 2006, Yarie 2008). In forest systems, characterized by a dense canopy, seedling growth is frequently related to levels of available light (Wassink & Stolwijk 1956, Chazdon 1988, Harper 2009). The availability and type of soil nutrients can also affect plant development (Kachi & Hirose 1983, Paquin et al 1998). Aside from these obvious causes, plant growth might be limited by additional factors, such as soil temperature (Myneni et al. 1997, Danby & Hik 2007), animal browsing (Wilkinson & Neilsen 1994, Maron & Crone 2006) and soil toxicity (Wright 1989, Foy 1992). Despite a large body of literature on the growth response of plants to variation in environmental conditions, few authors have investigated the effects of microsite on plant growth from the perspective of safe site concept.

Testing the safe site concept requires a study system where the regenerating species display the clear signs of poor seed germination and seedling growth under varying microsite conditions. A good example is found in post-fire ericaceous heaths of eastern Canada where black spruce (*Picea mariana* L.) regeneration is severely limited in the presence of an ericaceous shrub, sheep laurel (*Kalmia angustifolia* L., hereafter referred to as *Kalmia*). Previous studies have demonstrated that black spruce germination in sites dominated by *Kalmia* is greatly inhibited due to organic matter build up (Mallik et al. 2010). In addition to poor recruitment, black spruce seedlings suffer from poor growth. As a result, the sites, dominated by *Kalmia*, generally form a heath with a few sparse, slow growing black spruce (Fig. 1.1). Poor black spruce regeneration has been attributed to a variety of causes. Some claim that it is caused by direct nutrient competition between black spruce and *Kalmia*

(Bradley et al. 1997), others attribute it to the effects of allelochemicals produced by *Kalmia* (Zhu & Mallik 1994). Regardless of the reason, the combination of poor recruitment and slow growth leads to a considerable delay in forest succession (Bloom & Mallik 2004).

The primary objective of this research was to explain black spruce regeneration in post-fire chronosequence in light of safe site abundance, based on the extended definition of safe site, one that includes seedling establishment and growth phases. The second objective was to determine the effectiveness of scarification and microsite mulching to create safe sites in post-fire *Kalmia* heath by comparing black spruce growth in artificially created safe sites and partially sites.

The first chapter of this thesis concerns black spruce recruitment and growth in eight post-fire *Kalmia* dominated sites from the perspective of safe site concept. The second chapter examined black spruce seedling growth in safe sites, created by scarification and microsite mulching, and partially safe sites in undisturbed *Kalmia* heath.

A



B



C



Figure 1.1. Sites dominated by *Kalmia* 8 years (top photo), 13 years (middle photo) and 33 year (bottom photo) after wildfires.

Chapter I

Safe site availability as a controlling factor in black spruce (*Picea mariana*) forest restoration in *Kalmia* heath

Abstract

The objective of this chapter was to explain black spruce regeneration in post-fire *Kalmia* dominated chronosequence in light of safe site density by expanding the safe site concept to include seedling establishment and growth. Microsite environment and black spruce growth response data were collected in eight 8 – 34 year-old post-fire sites, located in and around Terra Nova National Park, Newfoundland. Black spruce stem density in all sites was considerably lower than 3000 stems/ha required for canopy closure. In addition to low densities, 86.9% of black spruce suffered from stunted growth (less than 0.5 mm/year) for a period of time ranging from 5 to 20 years since germination. With time, many stunted black spruce were able to overcome the growth check. Organic matter depth was identified as a primary factor related to poor recruitment rates. The probability of release in partially safe sites was negatively associated with OM depth and directly with soil decomposition rates. It was concluded that high abundance of microsites with OM depth less than 5 cm and soil respiration greater than 1 g/m²h is necessary for adequate black spruce regeneration.

Introduction

It is well known that environment plays an important role in structuring plant communities. It is also generally accepted that interactions between a plant and its environment occur at a microsite level. Harper et al. (1961) observed varying seed germination in response to substrate type and proposed that recruitment of new individuals in a population depends not only on the presence of seeds, but also on the availability of sites that are suitable for germination. To this effect, Harper (1977) introduced the term “safe site”, defined as an immediate area in which a seed might find itself and that provides 1) appropriate stimuli for breaking the seed dormancy, 2) favourable conditions required for germination, 3) the resources to be used during primary growth and 4) absence of hazards (predation, competition, soil toxicity).

Earlier work on safe sites primarily dealt with morphology-dependent seed response to microsite conditions. Sheldon (1974) reported that the presence of certain structures, such as pappus in fruits of *Compositae* family, allows seeds to be positioned in a most favourable way in microsites with flat, even surfaces. Further research examined the seed germination as a response to microtopography. In a field experiment, Gross & Werner (1982) demonstrated that biennial plants, which can germinate in the presence of other vegetation, on average have larger seeds than species requiring bare soil. By examining germination, mortality and initial growth rates of *Carduus nuatas* in treatments with varying soil micro-topography, Hamrick & Lee (1987) found the highest germination on substrates characterized by cracks, moderately irregular surface and light litter cover.

More recent work on safe sites focused on identifying and characterizing safe sites in a variety of habitats. Jumpponen et al. (1999) studied primary succession after retreating glaciers, and reported that coarse textured, concave surfaces in the vicinity of large rocks were more likely to be colonized than microsites with convex or flat surfaces. Spatial analysis studies on relationship between community composition and variation in microsite conditions concluded that microsite heterogeneity plays an essential part in structuring the plant communities, maintaining species diversity (Guo 1998) and determining spatial distribution of seedlings

(Hegazy & Kabieli 2007).

Some investigators have explored the role of other plants in safe site formation (Cavieres et al. 2002, Castro et al. 2002, Rühl & Schnittler 2011). These studies demonstrated that, in certain habitats, safe site availability is associated with the presence of nurse species, which provide relief from constraining environmental conditions (Tewksbury & Lloyd 2001, Badano et al. 2006). However, the presence of neighbouring plants is not always beneficial and might result in resource competition (Schlag & Erschbamer 2000). In some cases, the benefits of seed aggregation in safe sites outweighs the effects of competition in early life-stages (Fowler 1988).

Several authors have tried to determine the relative importance of seed and safe site availability on germination by counting the number of emerging seedlings in response to varying seed and safe site densities (Turnbull et al. 2000, Zobel et al. 2000). Predictive models have been developed to determine this relationship (Satterthwaite 2007, Duncan et al. 2009). These were supplemented by multiple field experiments in a variety of habitats, some demonstrating seed limitation (Hughes et al. 1988, Peart 1989), while others showing safe site limitation (Crawley & Nachapong 1985, Iacona et al. 2009) as the significant factors in determining the number of new recruits. Based on the existing evidence, Crawley (1990) suggested that generally, safe site availability acts as a limiting factor for plant recruitment, but this may vary depending on the system.

Research concerning safe sites has extensively explored the relationship between safe site availability, distribution and the number of new recruits. Some authors have looked at the effects of microtopography and microsite conditions on plant growth (Christensen & Muller 1975, Franko & Nobel 1988, Danby & Hik 2007). However, to my knowledge, none have offered a conceptual tool that might be helpful for determining the fate of individual plants not only at the germination, but also during seedling and adult stages. In a review on patterns of plant recruitment, Schupp (1995) suggested to view the idea of safe site as a series of sieves applied to a population at different growth stages, inducing mortality of individuals located in less favourable patches. This means that for an individual to have a high chance of reaching reproductive maturity, it needs a safe site throughout all

life stages, and not just at the germination as Harper (1977) originally proposed.

Identifying safe sites based on microsite environmental parameters is problematic. In some cases, requirements for germination and growth might vary (Lamont, et al. 1993, Oswald 1993, Schlag & Erschbamer 2000). Furthermore, microsite conditions might change over time, due to stochastic events, or feedback from the surrounding vegetation (Crain & Bertness 2006). When extending the safe site concept, one needs to acknowledge its potentially dynamic nature and define the safe sites in terms of features that remain relatively stable overtime. Despite these difficulties, is worthwhile to expand the definition of safe site beyond seed germination and seedling establishment phases and include subsequent life-cycle phases from both conceptual and practical points of view. From this perspective, a safe site may be considered a microsite that provides favourable conditions for seed, seedling and of an adult plant, allowing for germination, survival and adequate growth.

Based on this definition, all microsities can be classified into three categories. If the seed germination is unlikely, the microsite can be considered an unsafe site. Microsites with conditions that allow for germination, survival and good growth could be regarded as safe sites. Lastly, if germination is possible, but probability of achieving adequate growth rates is low, such microsities an be considered partially safe sites. Plants that are located in such microsities can be identified by their relatively low growth rates. With time, some plants in partially safe sites may overcome the growth limiting factors and achieve increase in annual growth rates. This phenomenon is called "growth release".

The major problem associated with post-hoc research on safe sites based on seedling/sapling density and growth history is the intrinsic circular argument: the seedlings grow in safe sites and seedling density is safe site density. Applying the safe site concept in a post-hoc study, a researcher may classify all the microsities into distinct categories. It may prohibit exploration of subtle interactions between the environment and the seedling/sapling. However, it is possible to examine the relationship between a single environmental parameter and seedling/sapling response across a

chronosequence and determine relative abundance of safe site types with respect to seedling growth characteristics. The benefit of applying the safe site concept is that it provides an easy tool for determining the fate of the plant population (Jumpponen et al. 1999, Turnbull et al. 2000, Hegazy & Kabieli 2007), assuming a steady and adequate seed supply. The safe site approach might not be valid in habitats defined by smooth environmental gradients where no clear difference between microsites is present. However, it is very useful in systems with distinct micro-topographic (Harper 1977; Hamrick & Lee 1987; Jumpponen et al. 1999) or other habitat features (Cavieres et al. 2002).

Plant response to microsite heterogeneity is especially evident in harsh environments such as deserts (Flores & Jurado 2003) and alpine habitats (Callaway & Walker 1997). In these systems, germination and growth of certain species is restricted to areas that provide a relief from constraining conditions that impede seedling establishment and growth (Franco & Nobel 1988). In order to explore the effects of safe site availability on plant recruitment and growth in a boreal forest, a system with strong negative environmental factors affecting plant community was needed. Good examples of this are conifer-ericaceous communities on both sides of the Atlantic. Removal of canopy cover by non-severe fires, clear cutting and insect defoliation in these communities can lead to the dominance of ericaceous plants such as *Kalmia angustifolia* (Mallik & Roberts 1994, Mallik 1995, Yamasaki et al. 1998; Mallik et al. 2010), *Calluna vulgaris* (Wheatherell 1953, Leyton 1955), *Vaccinium myrtillus* (Mallik & Pellissier 2000), *Rhododendron groenlandicum* (Inderjit & Mallik 1996a) and *Gaultheria shallon* (Messier 1992, Fraser et al. 1995). In other ecosystems seedling growth check is thought to be imposed by low light conditions (Burton & Mueller-Dombois 1984, Ellison & Farnsworth 1993) and insufficient mycorrhizal densities (Plenchette et al. 1983). In habitat dominated by ericaceous shrubs, most of the inhibitory effects on conifer regeneration are attributed to the presence of these shrubs (Mallik 2003). By controlling soil nutrients (Inderjit & Mallik 1999) and having a direct negative effects on germination and growth of conifers (Zhu & Mallik 1994, Mallik et al. 1998), the ericaceous shrubs can prevent heath-to-forest transition (Mallik 2003).

The best example of a successional delay is found in black spruce - *Kalmia* communities of eastern Canada, where the period of ericaceous shrub dominance is much longer compared to the other ecosystems (Mallik 2003).

Apart from *Kalmia's* influence on black spruce germination and seedling growth through the release of allelochemicals (Zhu & Mallik 1994) and resource competition (Bradley et al. 1997), it has the ability to control its microhabitat. *Kalmia* dominated sites are characterized by nutrient poor soils (Inderjit & Mallik 1999), thick organic matter (OM) and low decomposition rates (Walker & Mallik 2007).

Due to the hostile conditions created by *Kalmia*, several types of black spruce growth forms can be observed in post-fire, *Kalmia* dominated sites of Terra Nova National Park, Newfoundland. The first group of seedlings, characterized by high growth rates right from germination, with annual height increments greater than 10 cm, can be called normal. These seedlings are usually tall with a dense and widespread canopy and long, thick needles. In contrast, a second group of seedlings can be characterized by annual height increments of less than 3 cm. These seedlings can remain in the state of suppressed growth (growth check) for as long as 25 years. Stunted black spruce are generally less than 1 m in height, have a relatively sparse canopy and short thin needles. A third group of seedlings exhibit poor growth early in life, which improves over time eventually achieving growth rates similar to that of normal trees. Although released seedlings appear morphologically similar to normal black spruce, they are generally not as tall and have greater branch density near the stem base than the normal seedlings. Previous work in *Kalmia*-black spruce communities identified black spruce safe sites as areas with post-fire residual organic matter depth less than 2 cm (Seigwart-Collier & Mallik 2010). Mallik et al. (2010) demonstrated with a seeding experiment that, even when seeds were abundant, black spruce germination and seedling establishment in post-fire *Kalmia* dominated sites was extremely low and limited only to substrates with exposed mineral soil. These results indicate that *Kalmia* heath is a safe site limiting system, and that the difference in black spruce density is a function of safe site availability, rather than seed abundance. Hence, it may be valid to assume that black spruce germination is only possible in microsites classified as safe and that spruce

density is primarily dependant on microsite conditions rather than seed abundance.

The objective of this chapter was to explain black spruce regeneration in post-fire *Kalmia* dominated chronosequence in light of safe site density by expanding the safe site concept to include seedling establishment and growth phases. It was hypothesized that post-fire black spruce stem density, which represents a relative measure of safe site abundance per plot, is a function of variation in microsite conditions, rather than time since fire. The second hypothesis was that partially safe sites, defined as microsities that allow seedling establishment with stunted growth, can overtime become safe sites allowing a growth release of stunted seedlings.

Methods

Study area

The study was conducted in and near Terra Nova National Park (TNNP), Newfoundland (48°30' N, 50°00' W). The climate in the area is cool and moist with a mean annual precipitation of 1184 mm and a mean growing season temperature of 13 °C (Power 2000). Soils in the region are podzols with pH ranging from 3 to 5 (Damman 1971). Eight post-fire sites (Fig 2.1) were selected on the basis of site age (i.e. time since disturbance). These were Rocky Pond, Triton Brook, Spracklin Road, Thorburn Lake, Blue Hill West, Charlottetown, Terra Nova Road, Terra Nova Dump with respective site ages 8, 12, 14, 20, 24, 28, 33 and 34 years since fire. The sites with the greatest similarities were Triton Brook, Charlottetown and Terra Nova Dump (Table 2.1). These were characterized by moderately vigorous ericaceous shrubs and low conifer densities. The youngest site (Rocky Pond) was the only one with sandy soils and sparse vegetation. Another exception was Terra Nova Road site where relatively shallow organic matter layer was underlined mostly by a soil bedrock. Thorburn Lake and Blue Hill West sites were characterized by very vigorous *Kalmia* and relatively tall black spruce. Most of the sites had a thick organic layer and were dominated by *Kalmia* and other ericaceous plants (Table 2.1).

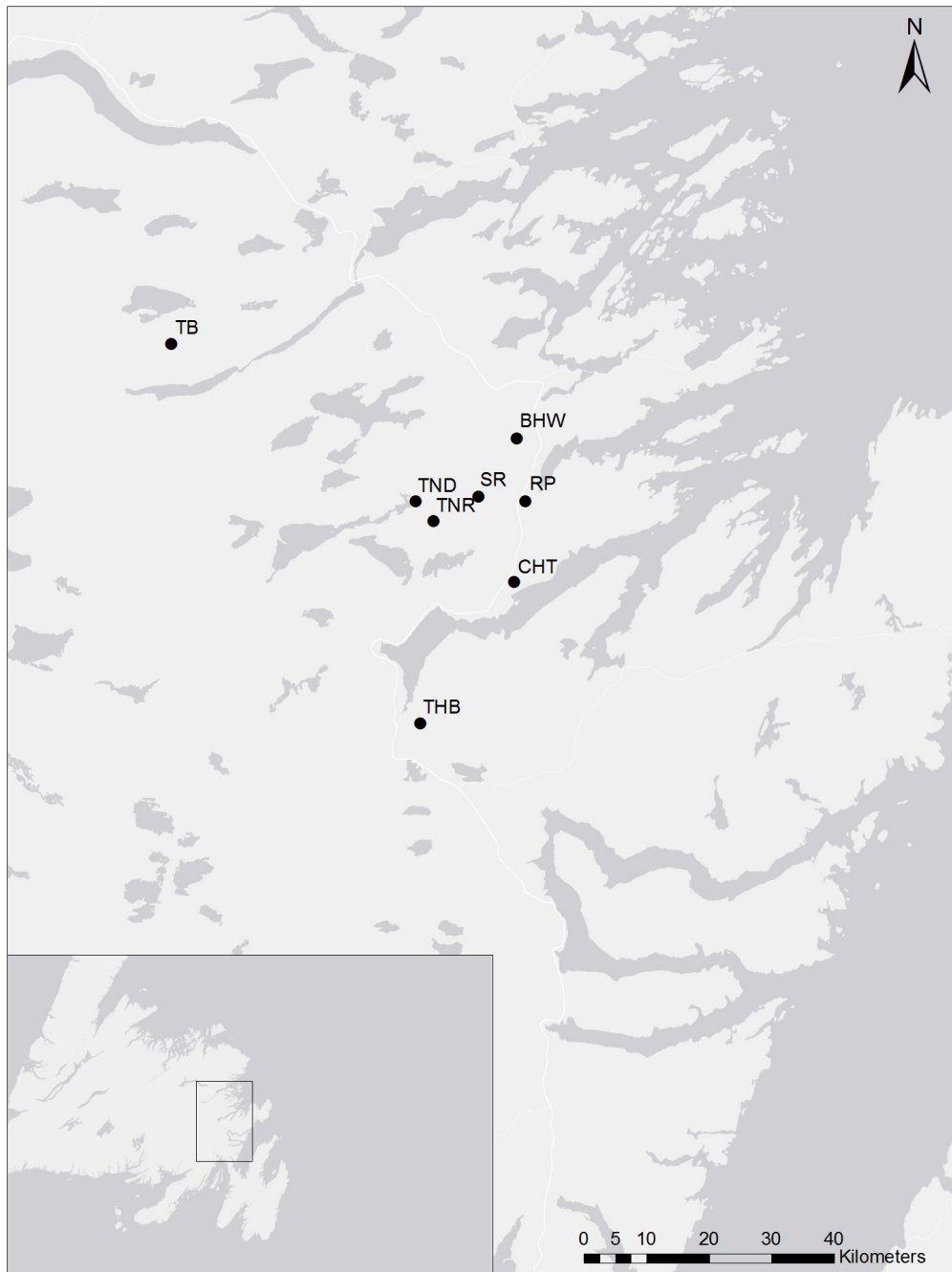


Figure 2.1. Location of eight *Kalmia* dominated study sites (time since fire 8 – 34 years). Site names: Rocky Pond (RP), Triton Brook (TB), Spracklin Road (SR), Thorburn (THB), Blue Hill West (BHW), Charlottetown (CHT) 28, Terra Nova Road (TNR), Terra Nova Dump (TND).

Table 2.1. Location characteristics of eight post-fire study sites in eastern Newfoundland

Site	GPS coordinates	Time since fire (years)	Burned area (ha)	Topography	Dominant vegetation	OM depth mean \pm sd (cm)	OM depth range (cm)	Mineral soil composition
Rocky Pond	N 48° 31' 662" W 53° 58' 967"	8	85	Small hills	<i>Kalmia angustifolia</i> , <i>Vaccinium angustifolium</i>	4.0 \pm 0.5	0 – 20	coarse sand
Triton Brook	N 48° 40' 477" W 54° 29' 334"	12	>500	Large hills with gentle slopes	<i>Kalmia angustifolia</i> , <i>Vaccinium angustifolium</i> , <i>Ledum groenlandicum</i> , <i>Alnus rugosa</i>	16.7 \pm 2.6	5 – 30	sandy clay or partially broken bedrock
Spracklin Road	N 48° 31' 953" W 54° 03' 91"	14	75	Large hill	<i>Kalmia angustifolia</i> , <i>Vaccinium angustifolium</i>	6.1 \pm 0.7	0 – 10	sandy clay
Thornburn Lake	N 48° 18' 73" W 54° 09' 997"	20	67	Large hill	<i>Kalmia angustifolia</i> , <i>Vaccinium angustifolium</i>	5.5 \pm 0.9	0 – 10	silty sand or solid bedrock
Blue Hill West	N 48° 35' 211" W 53° 59' 760"	24	332	Small hills, wetland	<i>Kalmia angustifolia</i> , <i>Vaccinium angustifolium</i>	14.8 \pm 2.7	7 – 31	sandy clay
Charlottetown	N 48° 27' 140" W 53° 59' 923"	28	201	Small hill with gentle slope	<i>Kalmia angustifolia</i> , <i>Vaccinium angustifolium</i> , <i>Ledum groenlandicum</i>	11.7 \pm 1.6	5 – 21	sandy clay
Terra Nova Road	N 48° 30' 487" W 54° 07' 143"	33	313	Wetland with rocky outcrops	<i>Kalmia angustifolia</i> , <i>Vaccinium angustifolium</i> , <i>Ledum groenlandicum</i>	3.9 \pm 0.5	0 – 20	solid bedrock
Terra Nova Dump	N 48° 31' 638" W 54° 09' 082"	34	486	Wetland with rocky outcrops	<i>Kalmia angustifolia</i> , <i>Vaccinium angustifolium</i> , <i>Rhododendron canadense</i>	4.0 \pm 0.6	0 – 20	sandy clay or solid bedrock

Experimental design

Fieldwork was conducted during the summer of 2010. In each study site, five 20 x 20 m plots were placed in random locations. The exception were BHW and TB sites where only three plots were established. Random selection of plot locations was achieved by superimposing a fine grid over the site map with resolution of 1:3351 and using a random number generator to determine the coordinates of each plot location. All the plots were established in areas that had not been altered by human activities since the last wildfire. The plots were restricted to well drained soils with slopes of less than 10°. To avoid edge effects, sampling plots were placed at least 100 m away from the unburned edge. If the selected location did not satisfy these requirements, the plot was moved to the nearest location that conformed to above mentioned conditions.

By the new definition, safe sites are the microsites that provide conditions necessary for germination, establishment and growth. Hence, the easiest way to estimate the density of safe and partially safe sites would be counting the number of seedlings in a plot. However, this method only gives a measure of safe site number with black spruce and does not take into account the possibility of unoccupied safe sites in the plot. Nonetheless, determining the black spruce density in each 20 x 20 m plot provided a relative estimate of safe site abundance, assuming that the proportion of unoccupied safe sites is similar in all plots. Under this rational, relative safe site abundance among the plots was determined as black spruce stem density by counting all black spruce seedlings/saplings in each 20 x 20 m plot.

Microsite conditions under the black spruce canopy were determined by setting up permanent sampling quadrats around five randomly selected black spruce in each 20 x 20 m plot. Each black spruce was assigned a number. The numbers were placed in a hat from which five were picked. In plots where the number of black spruce was less than five, permanent sampling quadrats were established around all of the available black spruce. All selected trees were destructively sampled to obtain tree cookies and cores. The samples were taken near the stem base. The decision on sampling method was based on tree basal diameter. Black spruce with a

basal diameter less than 5 cm were cut down at the stem base with portable saw, whereas trees with basal diameters greater than 5 cm were sampled using a tree core. Upon extraction, the cores were put in plastic straws to prevent breaking. The samples were placed in plastic bags and kept cool during transportation and storage. In the lab, the samples were oven-dried at 105 °C for 24 hours then polished using a belt sander. Tree age and annual growth increments were determined by counting the number and widths of annual growth rings. Stem cookies and cores were scanned on a high-resolution scanner and the images were analyzed using WinDendro software.

Measurements of soil temperature, soil moisture, soil respiration and OM depth were done in each quadrat. These factors were selected based on the previous research which demonstrated the effects of soil temperature (Tryon & Chapin 1983), soil moisture (Bomal & Tremblay 1999; Thiffault et al. 2004), soil respiration (Mallik & Hu 1997; Walker & Mallik 2005; Zeng & Mallik 2006), OM depth (Bradley et al. 1997; Inderjit & Mallik 1999; Seigwart-Collier 2010; Mallik et al. 2010) on black spruce germination and growth in *Kalmia* heath. Soil temperature and moisture were measured using a HH2 moisture meter and WET-2 sensor (Delta-T Devices, Cambridge, UK). The measurements were taken in four cardinal directions at 10 cm distance from a black spruce stem. The information was recorded between 11:00 and 15:00, preceded by at least 48 hours of no precipitation. Soil respiration was determined using EGM-4 meter and SR-1 probe (PP systems, MA, USA) at a 10 cm distance from the stem. Organic matter depth was determined by examining two 5 cm diameter soil cores obtained in each sampling quadrat 10 cm from black spruce stem.

Statistical analysis

All statistical analysis were conducted using R (ver. 2.12.1) software supplemented by additional libraries containing the functions that were unavailable in the base package. Prior to analysis, the data were checked for normality using the Shapiro-Wilks test. Deviations were corrected using log(x) transformation. Black spruce stem density per plot was converted to stems per hectare by multiplying the number of black spruce in each plot by

25 (1 ha/study block area).

Preliminary analysis was conducted to compare the growth rates of normally grown and stunted seedlings, as well as to confirm growth release of stunted black spruce. To do this, annual radial increments (ARI), obtained from tree ring data, were plotted over-time to produce growth history for every sampled black spruce. The initial observations indicated that that annual radius increments were different for the trees considered as normal ($ARI > 1.3$ mm/year) and stunted ($ARI < 0.5$ mm/year). Both types were identified in the field according to annual height increments (normal > 10 cm/year, stunted < 3 cm/year) and number of morphological features, such as branch density, needle thickness and length. The tree ring data suggested that many black spruce experienced a period of stunted growth, lasting 5 – 20 years, followed by a rapid increase in growth rates. This pattern fit well with the expected growth history features of a tree undergone a release from growth check. Hence, the black spruce that exhibited the described growth history were classified as released. Their tree ring data were combined to produce a mean growth curve. This information was utilized for determining the ARI values that marked the release from stunted condition and reaching the upper growth limit. The age, when release started and ended, was determined by calculating the inflection points (R functions: `smooth.spline`, `diff`; library: `stats`). This method identifies the points on the graph where the line changes its curvature. The inflection point is often used as an indication of a threshold. In this case, the lower threshold value of 0.49 mm/year closely corresponded to estimated maximum growth rates of stunted (0.5 mm/year) trees. The upper threshold value 1.37 mm/year was similar to estimated minimum growth rates of normal (1.3 mm/year) black spruce. Therefore, 0.5 mm/year and 1.3 mm/year growth rate were considered as cut off points for defining stunted and released trees respectively.

Lack of environmental data at the time of germination prohibited us from determining the environmental thresholds that could describe the black spruce safe sites during the germination stage. However, it was possible to identify the environmental factors that affected spruce germination by running a regression analysis on black spruce density per plot, which corresponds to relative abundance of safe and partially safe sites as well as mean

environmental conditions in each plot.

Prior to analysis, the environmental data were screened for correlation. All of the examined parameters were well within the set range ($0.70 > \text{Pearson correlation coefficient} > -0.70$) and were included in the model. The data were analyzed using step-wise multiple regression (R functions: `lm`, `step`; library: `stats`) with $\log(\text{OM depth})$, soil moisture, temperature, respiration and years since fire as independent variables and \log transformed black spruce density as the response variable.

To demonstrate the changes in recruitment of normal, released and stunted black spruce over time, a descriptive model was constructed using the combined tree ring data and stem density (per plot) from eight study sites. Tree ring data was used to determine how many of the sampled trees have germinated and were alive at any given year starting from 0 years (disturbance event) to 25 years. The obtained values were scaled up according to corresponding stem density per plot. The seedlings were divided into three categories according to their growth rates at 5 year intervals: 1) $\text{ARI} < 0.5 \text{ mm/year}$; 2) ARI between 0.5 and 1.3 mm/year and 3) $\text{ARI} > 1.3 \text{ mm/year}$. The continuous black spruce density, expressed as lines, were calculated as a sum of all the seedlings in each class (normal, released, stunted) germinated and alive in each year after forest fire.

Identification of environmental parameters, that could be used as primary characteristics of black spruce safe sites during adult stages, was conducted through multiple step-wise regression (R functions: `lm`, `step`; library: `stats`). The age at which black spruce seedlings exceeded the lower growth threshold ($\text{ARI} 0.5 \text{ mm/year}$) was used as the response, while OM depth, soil respiration, soil temperature, soil moisture, measured in each quadrat, were independent variables. The factors that had a significant relationship with age of release were used in logistic regression model (R functions: `glm`; library: `stats`) to determine the environmental thresholds defining the black spruce safe sites during adult growth stage. The resulting model was used to produce a series of predicted values (R functions: `predict`; library: `stats`) for three age groups (0 – 10, 10 – 20, 20 – 30 years after germination).

Results

Black spruce germination

Black spruce stem density, in all the study sites, was well below the prescribed silvicultural value of 3000 stems/ha (Newton & Weetman 1993) required for desired forest regeneration. There was no relationship between black spruce density and time since fire (Fig 2.2). The mean stem density was 314 stems/ha and ranged from 100 stems/ha in Triton Brook to 665 stems/ha in Terra Nova Dump. Relatively low spruce density (< 200 stems/ha) was observed in both younger (8 – 12 years) and older sites (28 – 33 years). Higher stem density (400 stems/ha) was found in sites of intermediate age (14 – 24 years) and some old sites (34 years).

Analysis of the relationship between black spruce density, representing a relative abundance of safe and partially safe sites, and measured environmental parameters revealed that a combination of OM depth and *Kalmia* cover explained 19% variation in stem density (Table 2.2). Greater black spruce density was associated with shallow (< 5 cm) OM depth (Fig 2.3) and high *Kalmia* cover. The highest black spruce densities were found in plots with mean OM depth less than 5 cm. Based on the standardized regression coefficients (Table 2.2), OM depth was determined to be the primary factor associated with black spruce germination.

Black spruce growth

In addition to poor recruitment rates, many black spruce seedlings suffered from stunted growth early in life. By examining the mean annual radius increments of normal, released and stunted seedlings/saplings, the minimum growth rate of black spruce in safe sites was estimated to be 1.3 mm/year. Similarly, the maximum growth rate of stunted trees was estimated at 0.5 mm/year. By plotting annual radius increments (ARI) over time, it was determined that only 13.1% of all black spruce had high growth rate starting at germination (Fig. 2.4). About 87.8% of all seedlings showed very little growth (ARI < 0.5 mm/year) in the first five years. With time, some of these were released from stunted condition, eventually reaching the growth rates comparable to black spruce in safe sites. However, many seedlings (54.9%) remained stunted for prolonged period of time followed by growth release.

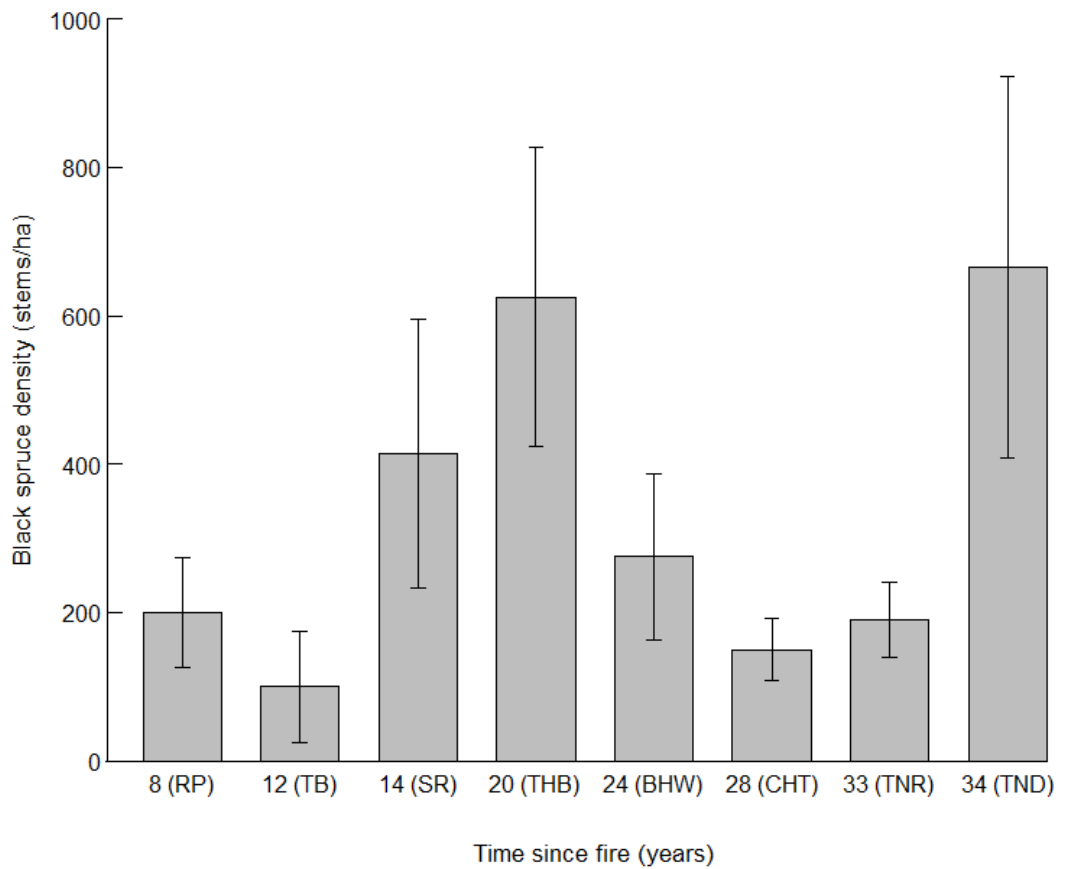


Figure 2.2. Black spruce stem density (mean \pm SE) in post-fire *Kalmia* dominated sites of varying age. The sites were arranged according to time since fire: Rocky Pond (RP), Triton Brook (TB), Spracklin Road (SR), Thorburn (THB), Blue Hill West (BHW), Charlottetown (CHT), Terra Nova Road (TNR), Terra Nova Dump (TND).

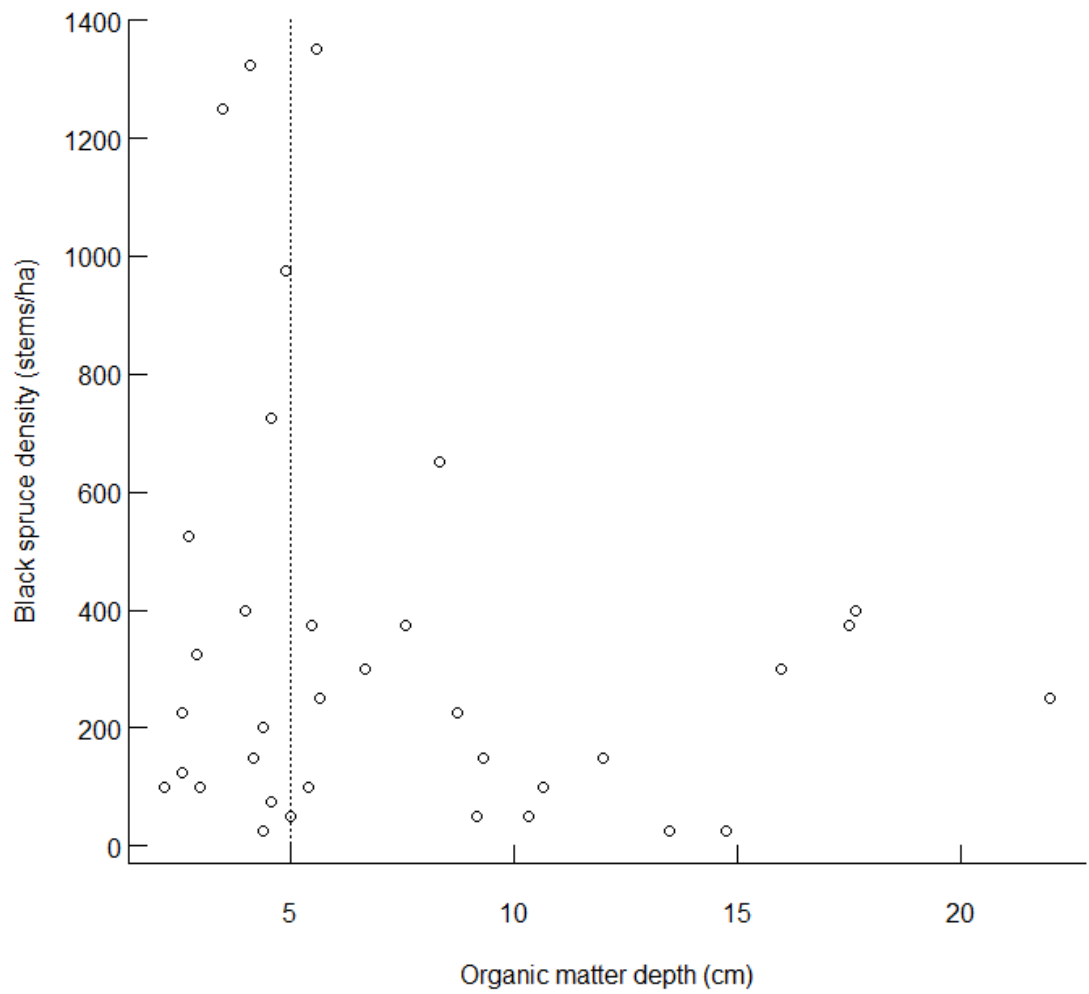


Figure 2.3. Relationship between black spruce density per ha and organic matter depth in *Kalmia* dominated sites. The vertical line shows that the highest black spruce stem density was observed in plots with 0 – 5 cm organic matter depth.

Table 2.2. Results of multiple step-wise regression analysis on black spruce stem density and mean environmental conditions in each study plot.

Independent variables	Intercept	Partial regression coefficients		β	Sig.T
		<i>b</i>	SE <i>b</i>		
Organic matter depth	310	-42.06	16.17	-0.58	0.01
<i>Kalmia</i> cover	310	14.79	6.07	0.54	0.02
Overall model fit	$r^2 = 18.9$	$F = 2.60$	$DF = 2, 32$	$p = 0.03$	

Most black spruce recruitment was limited to the first 15 years after fire, with little recruitment occurring at latter ages (Fig. 2.5). Furthermore, recruitment of normal seedlings was even more restricted. According to the data, all black spruce occupying the safe sites were recruited in first ten years following the disturbance. Recruitment of seedlings in partially safe sites continued up to 15 years since fire with relatively few black spruce germinating 15 – 25 years since fire.

Despite the absence of new safe site recruits at site age greater than ten, the proportion of seedlings/saplings with ARI > 1.3 mm/year increased steadily over time. The model predicted that as a result of growth release, by 25 years after fire almost half of the black spruce may reach ARI greater than 1.3 mm/year.

Out of all environmental parameters, organic matter depth and soil respiration had a significant relationship with age of release in partially safe sites (Table 2.3). The logistic regression analysis revealed that both OM depth and soil respiration had a significant relationship with probability of black spruce being released from stunted condition (Table 2.4). Although standardized regression coefficients indicated that soil respiration had a stronger relationship with release probability, the limit imposed by deep OM was more severe (Fig. 2.6).

According to the model, in microsites with OM depth less than 5 cm and soil respiration of 0.6 g/m²h, the probability of black spruce overcoming the growth check was 48% (age: 0 – 10 years), 61% (age: 10 – 20 years) and 77% (age: 20 – 30 years). As the OM depth increased, the probability dropped sharply, with only 7% mean chance for black spruce having high growth in microsites with 40 cm OM thickness.

On the other hand, the rate of decomposition, represented by soil respiration, had a positive relationship with the probability of release. In microsites with soil respiration greater than 1 g/m²h and OM depth of 5.7 cm, the probability of black spruce overcoming growth check was 63% (age: 0 – 10 years), 77% (age: 10 – 20) and 87% (age: 20 – 30 years). The lower limit (34% chance of growth release) imposed by low decomposition (soil respiration: 0.1 g/m²h), was considerably higher compared to the effects of OM.

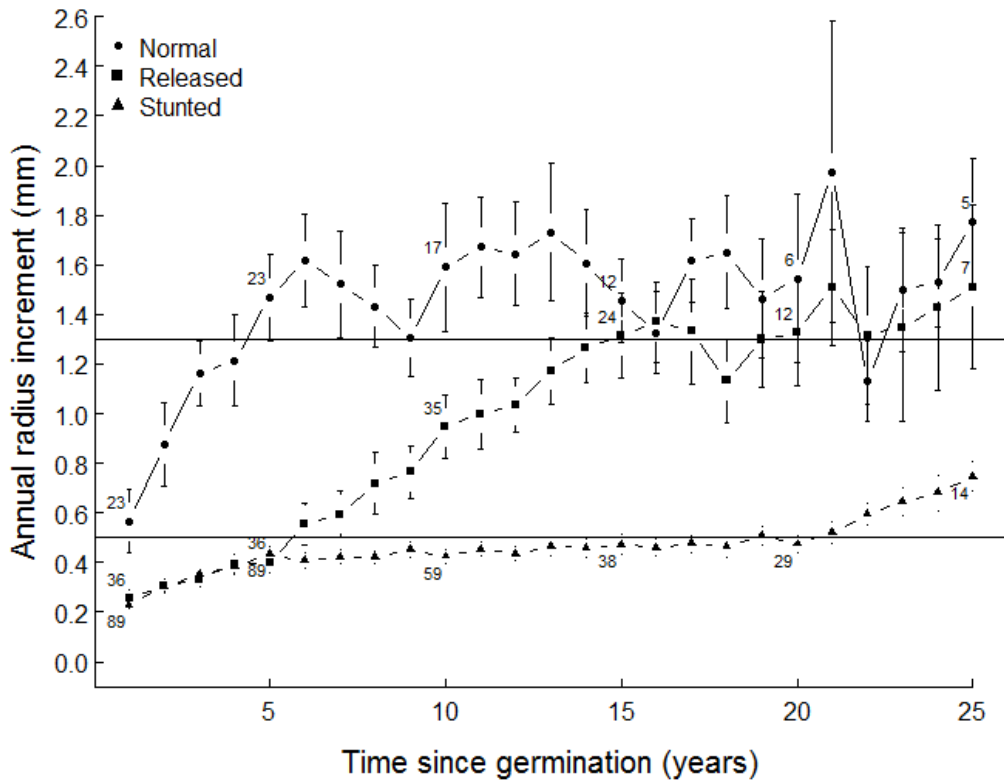


Figure 2.4. Mean (± 1 S.E.) annual radius increments of normal, released, and stunted black spruce over time. The mean values for annual radius increments were calculated using the combined data from all study sites. Horizontal lines correspond to estimated maximum growth rates of stunted (ARI = 0.5 mm/year) and minimum growth rates of normal trees (ARI = 1.3 mm/year). Numbers along the growth curves represent sample size used to calculate the mean ARI.

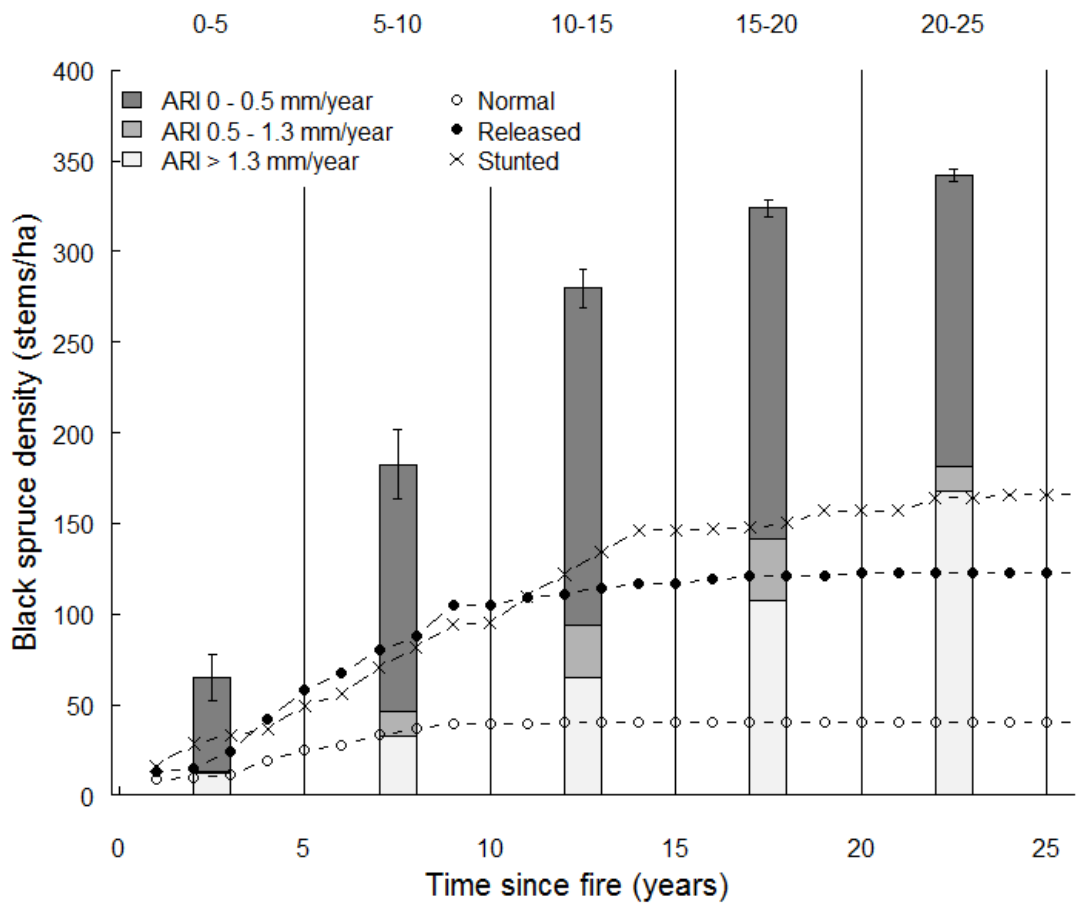


Figure 2.5. Black spruce recruitment model showing changes in stem density over time. The model was constructed using annual radius increments data and black spruce stem density per plot, obtained from all sites. Bars correspond to mean (± 1 S.E.) density and mean proportion of trees with annual radius increments of (i) 0 – 0.5, (ii) 0.5 – 1.3 and (iii) 1.3 mm/year, at 5 year intervals. Lines represent stem density per ha of normal, released and stunted trees as a function of time since fire.

Table 2.3. Results of multiple step-wise regression analysis on years of stunted growth and environmental conditions in corresponding quadrats.

Independent variables	Intercept	Partial regression coefficients		β	Sig.T
		<i>b</i>	SE <i>b</i>		
Organic matter depth	10.8	0.24	0.12	0.24	0.04
Soil respiration	10.8	-3.02	1.55	-0.22	0.05
Soil moisture	10.8	-0.14	0.12	-0.16	0.14
Overall model fit	$r^2 = 0.08$	$F = 2.70$	$DF = 3, 84$	$p = 0.05$	

Table 2.4. Results of logistic regression analysis on probability of black spruce overcoming stunted growth in partially safe sites and environmental conditions in corresponding quadrats.

Independent variables	Intercept	Partial regression coefficients		β	Sig.Z
		<i>b</i>	SE <i>b</i>		
Organic matter depth	-1.1	-0.08	0.04	-0.95	0.02
Soil respiration	-1.1	2.10	0.66	1.66	0.002
Age group 2 (10 – 20 years)	-1.1	0.72	0.45	1.14	0.11
Age group 3 (20 – 30 years)	-1.1	1.37	0.50	1.08	0.01
Overall model fit	Log Lik. = -84.0 DF = 4,137				

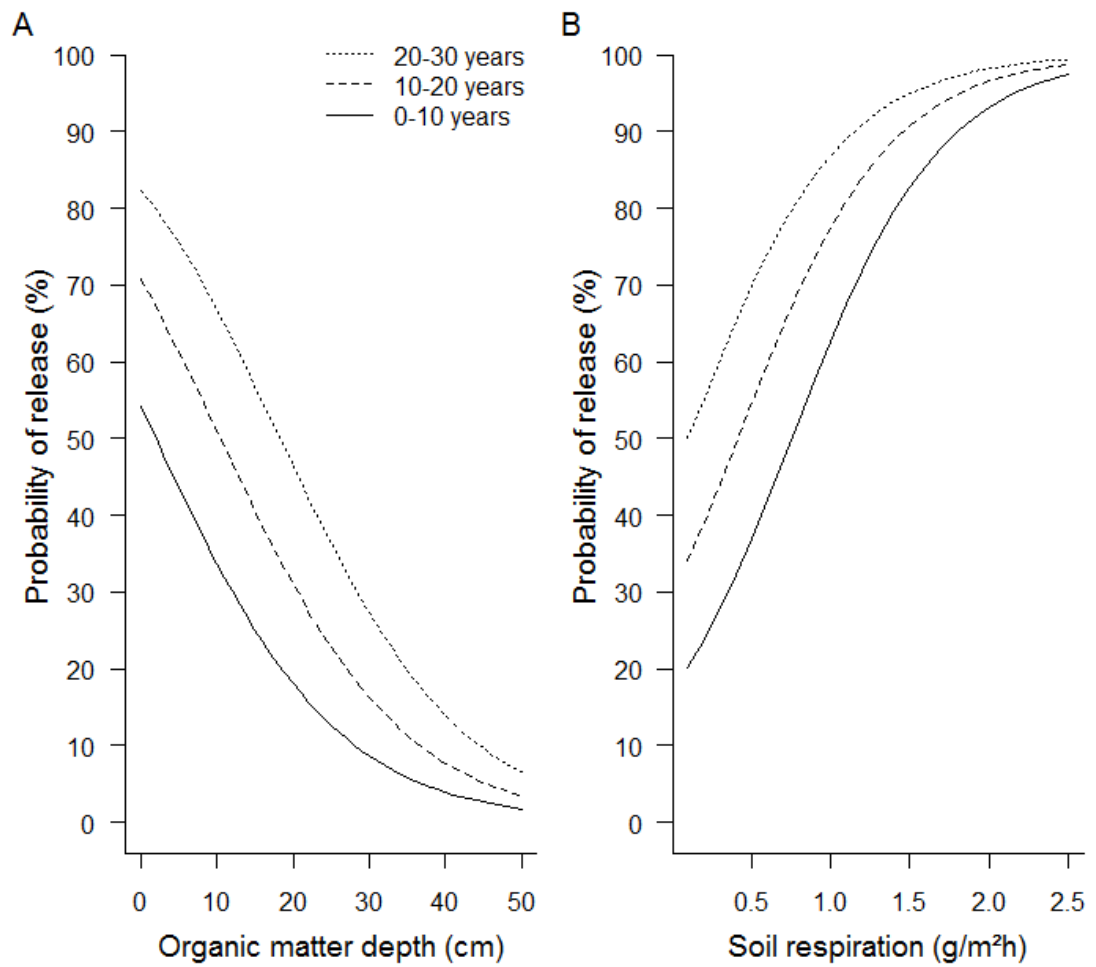


Figure 2.6. Probability model of black spruce having an annual radius increments greater than 0.5 mm/year as a function of (A) organic matter and (B) soil respiration. The predicted values were calculated for three age groups (0 – 10, 10 – 20, 20 – 30 years after germination), each represented by a line.

These results indicated that not only OM depth and decomposition have a significant relationship with growth release in partially safe sites, the older trees generally had a higher chance of overcoming growth check, compared to younger seedlings under the same conditions.

Discussion

The objective of this chapter was to explain black spruce regeneration in a post-fire *Kalmia* dominated chronosequence in light of safe site density by expanding the safe site concept to include seedling establishment and growth. By surveying the black spruce populations in post-fire sites of varying site age, it was confirmed that black spruce density in *Kalmia* heath was much lower than the prescribed silvicultural value of 3000 stems/ha (Newton & Weetman 1993). It was also concluded that variation in microsite conditions, produced by disturbance severity and site topography, was likely a cause for differences in spruce stem density. These conclusions were made based on the following results. Black spruce stem density among the post-fire sites varied independently of site age (i.e. Time since fire). The study plots with relatively high number of safe sites were characterized by thin OM matter (< 5 cm). Black spruce recruitment was mostly limited to initial 15 years following the fire event.

It was also concluded that black spruce located in partially safe sites, overtime, had an increasingly higher chance to overcome the growth check. The results that confirm this hypothesis show an increasing proportion of trees with ARI > 1.3 mm/year overtime, despite lack of black spruce recruitment in safe sites. Some black spruce, after being stunted for 5 – 20 years, exhibited rapid increase in growth rates, eventually reaching ARI values comparable to normal trees providing support for the second hypothesis. The data demonstrated that probability of the release was the highest in seedling/sapling age group 20 – 30 years since germination and was associated with variation in OM thickness and decomposition rates.

Field research in plant ecology provides many challenges. In the current study, the main problem was to identify and quantify safe and partially safe sites. Estimating safe site abundance was achieved by counting seedling/sapling, which precluded determining the number of unoccupied

safe sites. This approach does not provide the exact number of safe and partially safe sites. Nonetheless, it allowed an estimate of relative safe sites abundance across the chronosequence. The basis for using this method was the knowledge that black spruce recruitment in *Kalmia* heath is primarily limited by the lack of favourable seedbed substrates (i.e. favourable microsites or safe sites), rather than seed availability. In a field experiment, where black spruce seeds were planted in seven different seedbed types, Mallik et al. (2010) found that seed germination and establishment was only possible on mineral soil seedbed and mineral soil with thin OM. Based on these results, it was assumed that the effects of variation in seed availability on black spruce density was negligible compared to favourable microsite (safe site) availability.

Another limitation was the lack of environmental data for each black spruce throughout its life. As a post-hoc study, it was only possible to obtain a snapshot picture of microsite conditions, resulting in data where some of the interactions between black spruce and its environment were masked.

One of the main results produced by the study was the information on black spruce recruitment across the post-fire chronosequence. The black spruce density, across all study sites, was markedly lower than the recommended value of 3000 stems/ha (Newton & Weetman 1993) needed for canopy closure. One can argue this to be a matter of safe site limitation (Harper 1977). Presuming that some safe sites were unoccupied by black spruce at the time of sampling, stem density did not represent an exact number of safe sites in each plots. However, information on number of black spruce per plot allowed a relative comparison of safe site abundance among the sites. With this in mind, a comparison of mean stem density among eight post-fire sites (Fig. 2.2) suggested that safe site number was not a function of site age (time since disturbance), but was primarily associated with site to site variation in environmental conditions. A difference in fire severity is known to have a direct impact on OM depth, and thereby plant community composition (Lecomte et al. 2006). Post-fire sites with high OM thickness remaining after disturbance events (greater than 2 cm) have been observed to have a considerably lower black spruce stem density (Seigwart-Collier 2010). The current study demonstrated that variation in OM depth was a

primary factor associated with variation in stem density. Analysis indicated that stem density was the highest in plots with mean OM depth less 5 cm. These results support the previous work showing a direct negative effect of OM on black spruce germination (Mallik et al. 2010).

Further support for the idea of safe site density being largely dependent on initial site conditions comes from the limitation of black spruce recruitment to the initial few years after the disturbance event. Most of the black spruce seedlings were recruited in the first 15 years after fire (Figure 2.5). Furthermore, recruitment of black spruce, with initially high growth rates (ARI > 1.3 mm/year), was limited to 0 – 10 years since fire. As seen in literature, the total density of safe and partially safe sites remains constant or decrease overtime, due to OM build up (Lavoie et al. 2007, Mallik et al. 2010). The current study observed the number of unoccupied safe and partially safe sites declining over time. The difference in recruitment among trees, in safe and partially safe sites, confirmed the assumption that *Kalmia* heath is a safe site limited system. If that was not the case, the results in figure 2.5 would show proportional increase in density of normal black spruce relative to total density value.

In addition to low recruitment rates, only 13.1% of trees were able to enjoy normal growth (ARI > 1.3 mm/year) starting from germination. Most seedlings (86.9%) experienced a growth check (ARI < 0.5 mm/year) lasting 5 to 20 years. With time, many of the stunted seedlings started to show growth improvement (Fig 2.4). For some (31.9%) it took 5 years to overcome stunted growth, while others (54.9%) remained stunted for more than 20 years. It is likely that given enough time many of these trees can overcome the growth limitations.

The analysis indicated that the probability of overcoming a growth check in partially safe sites had a direct relationship with tree age and was also associated with variation in OM thickness and decomposition rates. The probability of black spruce being released from growth check was the highest in microsites with shallow OM depth and high decomposition, represented by soil respiration. According to the predicted values, the probability of black spruce release from stunted condition in soil with deep OM (greater than 40 cm) was only 7%. On the other hand, in microsites characterized by low soil

respiration ($0.1 \text{ g/m}^2\text{h}$) the probability of release was 34%. Standardized regression coefficients indicated that soil respiration had a stronger relationship with release probability compared to OM depth. However, the likelihood of a release in deep OM was much lower compared to the effects of low decomposition (Fig. 2.6). Hence, it was concluded that both factors play equally important role in the process of growth release.

According to the extended definition, a safe site is a microsite that provides soil resources and environmental conditions for germination, seedling survival and growth. In regard to black spruce regeneration in *Kalmia* dominated sites, the current study concluded that low black spruce density across the chronosequence was associated primarily with a lack of microsites characterized by shallow OM (less than 5 cm). The variation in microsite conditions was likely a function of initial site conditions produced by a combination of fire severity and site topography. Although, the majority of trees suffer from growth suppression, many are able to overcome the limitations. The safe sites that provide the conditions for germination and good growth are characterized by shallow OM (less than 5 cm) and high soil respiration (greater than $1 \text{ g/m}^2\text{h}$).

Management implications

The results of this study demonstrate that black spruce forest regeneration in *Kalmia* heath is poor. If left unattended, this situation might result in lengthy successional delay (Mallik et al. 2010). Due to a thick organic layer which inhibits both germination and growth, simply seedling, or planting the area with conifers is likely to result in low black spruce stem density and poor growth. In order enhance forest restoration, it might be necessary to alter site conditions creating microsites with shallow OM and high soil decomposition.

Chapter II

Artificially created safe sites to restore *Picea mariana* forest in *Kalmia* heath

Abstract

The relationship between safe site availability and plant germination is fairly well studied. However, the role of safe and partially safe sites during early seedling stage remains unexplored. The objective of this chapter was to determine the effectiveness of scarification and microsite mulching to create safe sites by comparing black spruce growth in artificially created safe sites and partially safe sites. Safe sites were prepared by exposing mineral soil using scarification and microsite mulching. Following the site preparation, black spruce seedlings were planted in scarified, MSM and undisturbed microsites (control). Seedling growth and environmental conditions were monitored over four years. Seedling survival was above 90% in all the three microsite types. However, more than 20% of the black spruce, in microsites considered safe, suffered from damage by herbivores and frost heaving. On the other hand, seedlings in partially safe sites remained mostly undamaged. Black spruce in scarification and MSM treatments had higher growth rates compared to the control, with differences amplified in each consecutive year since planting. In year two, the highest black spruce growth was observed in microsites characterized by moist, cool soils. In year three, seedling growth was primarily associated with organic matter thickness. Nutrient data, from year one, showed that scarification, MSM and control microsites were distinctly different in soil nutrient conditions. Scarified microsites had the highest Fe concentration in mineral soil. Microsites with mulched soil had the highest P and K, while the control soil had high concentrations of Mg, Ca, and Zn. Despite the clear differences in nutrient conditions among the treatment types, soil nutrients had little or no effect on black spruce growth in year one. It was concluded that high seedling growth in artificially created safe sites was due to higher soil moisture, lower organic matter depth and lower temperature. It was also confirmed that microsites created by scarification and MSM can be considered safe for black spruce seedlings.

Introduction

Post-disturbance forest regeneration has been a topic of interest for ecologists, conservation biologists and land-use managers alike. In a conifer-ericaceous shrub community, canopy removal by wildfires, clear-cutting and insect infestation may lead to the dominance of ericaceous plants such as *Kalmia angustifolia* (Mallik 1993, Mallik & Roberts 1994, Mallik 1995, Yamasaki et al. 1998), *Calluna vulgaris* (Wheatherell 1953, Leyton 1955), *Vaccinium myrtillus* (Mallik & Pellissier 2000), *Rhododendron groenlandicum* (Inderjit & Mallik 1997), and *Gaultheria shallon* (Messier 1992, Fraser et al. 1995). By achieving site dominance, ericaceous plants may inhibit conifer germination and growth, delaying heath-to-forest transition (Mallik 2003). The best example of successional delay is found in black spruce (*Picea mariana*)-*Kalmia* dominated communities of eastern Canada, where *Kalmia* dominance may last for up to 60 years (Bloom & Mallik 2006).

Once *Kalmia* occupies the area, it can modify the soil conditions through accumulation of poor quality litter and the release of allelochemicals (Inderjit & Mallik 1999). This leads to an increase in soil acidity and inhibition of bacterial activity reducing organic matter (OM) decomposition and nutrient availability (Mallik 1994; Bradley et al. 1997). *Kalmia* has also been reported to interfere with mycorrhizal infection (Yamasaki et al. 1998), black spruce seed germination and seedling root growth (Zhu & Mallik 1994, Mallik et al. 1998). As a result, black spruce recruitment and growth in *Kalmia* dominated sites is extremely poor (Mallik 2003). Even when seeds are abundant, black spruce germination and seedling establishment are limited to areas with thin organic matter (Mallik et al. 2010). Under these circumstances, black spruce regeneration is greatly dependent on the presence of safe sites that provide favourable conditions for seed germination (Harper 1977), seedling establishment and growth. As discussed in the previous chapter, black spruce safe site density in *Kalmia* heath is low, and declines overtime, presumably due to rapid organic matter accumulation (Mallik et al. 2010). In addition to poor germination, most black spruce seedlings suffer from stunted growth, which further inhibits forest recovery. An increase in the number of safe sites may help reduce the successional delay and promote forest restoration in *Kalmia* heath.

Previous research has shown that if one avoids the seed germination stage by planting young black spruce, the planted seedlings may suffer from stunted growth (Thiffault & Jobidon 2006). Removal of *Kalmia* with herbicides provides little benefit to seedling growth (Mallik & Inderjit 2001), because of the humus residual effects of *Kalmia* that remain in the soil (Wallstedt et al. 2002). Prescribed burning has the potential to change the soil conditions, but the temperature required is high (Mallik & Roberts 1994) and can only be reached by a severe fire. Application of high severity prescribed burning is not only expensive and logistically challenging, but also potentially dangerous. Attempts to enhance black spruce growth by fertilizer application showed that the benefits are short lived (LeBel et al. 2008) and have a potential to increase *Kalmia* growth (Mallik 1996). Mycorrhizal inoculation produced little positive effect on seedling growth, at least within two years after out-planting (Walker & Mallik 2009).

To date a common forest management practice to deal with poor conifer regeneration in *Kalmia* heath has been scarification. This mechanical site preparation technique exposes mineral soil providing substrate favourable for black spruce seed germination (Thiffault et al. 2004). Scarification, planting and spot fertilization has been reported to produce increased black spruce growth compared to unscarified treatments (Thiffault & Jobidon 2006). An alternative method, suggested by Mallik (1991) and Walker & Mallik (2009), involves mixing organic matter with part of the mineral soil. This mulching technique prevents *Kalmia* regeneration, by killing its below-ground rhizomes, and improves soil respiration, by enhancing decomposition (Walker & Mallik 2009).

Although beneficial, scarification (Thiffault et al. 2004) and large-scale soil mulching (Walker & Mallik 2009) result high levels of soil disturbance leading to increased erosion, fluctuations of soil moisture and temperature (Thiffault et al. 2004). Large-scale soil mulching is also expensive and thereby cannot be used as a routine site preparation method. However, if soil mulching is done at a microsite level (hereafter referred to as microsite soil mulching or MSM), it might alleviate some of the problems associated with large-scale site preparation by scarification and mulching, while retaining their positive effects.

The objective of this chapter was to determine the effectiveness of scarification and microsite mulching to create safe sites in post-fire *Kalmia* heath by comparing black spruce growth in artificially created safe sites and partially sites. It was hypothesized that microsites created by scarification and microsite mulching (MSM) enhance black spruce growth by removing the inhibitory effects of *Kalmia* and its organic matter as well as by increasing decomposition and soil moisture.

Methods

Site description

The study was conducted in a 12 year-old post-fire site (Triton Brook) in eastern Newfoundland (48°30' N, 50°00' W). Climate in the region is cool and moist with a mean annual precipitation of 1184 mm and a growing season temperature of 13 °C (Power 2000). The site was located in an area of large hills with gentle slopes and several small streams. The soil in the region could be described as well drained podzols. The surface of the soil formed a dark coloured crust. Organic matter depth at the site ranged from 6 to 34 cm. Mineral soils were composed of large rocks embedded in silty sand. Micro-topography was uneven with *Kalmia* hummocks rising as much as 40 cm. Vegetation was dominated by *Kalmia*, *Vaccinium angustifolium* and *Rhododendron groenlandicum* with scattered black spruce and *Alnus rugosa*.

Experimental design

Three 100 x 100 m blocks were established in random locations within the study site. Each block was divided into four 25 x 100 m plots (Fig. 3.1). Each plot was randomly assigned one of the following treatments: 1) unplanted *Kalmia* heath, 2) black spruce planted (control), 3) black spruce planted after MSM and 4) black spruce planted after disk scarification. The site preparation treatments (scarification and MSM) were applied in the summer of 2008 and were immediately followed by planting half of each

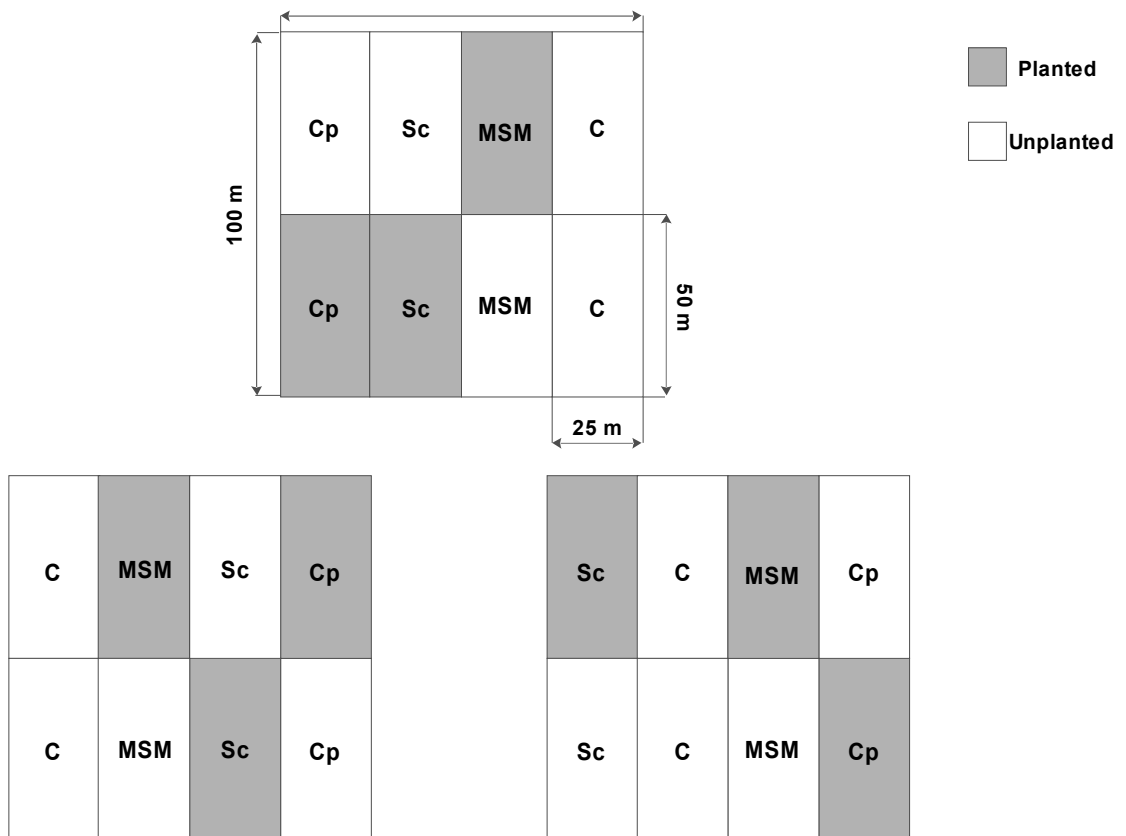


Figure 3.1. Experimental design showing application of scarification, MSM and control treatments in three study blocks. The letters within the rectangles correspond to treatment type: control (C), control planted (Cp), scarified (Sc), microsite soil mixing (MSM). Shaded parts represent areas planted with black spruce. Clear portions represent the parts left unplanted.

plot with 150 commercially grown containerized black spruce seedlings. The other half of the plot was left unplanted for use in a different project. An unplanted control treatment was used to assess black spruce regeneration in *Kalmia* heath under natural conditions.

The scarification treatment was applied using a disc scarifier attached to a skidder. This machine works by cutting the organic layer and flipping it aside. The treatment resulted in long parallel trenches of exposed mineral soil of about 60 cm wide positioned 2 m apart. During planting, black spruce seedlings were placed every 3 m, following a protocol similar to that of commercial tree planting. Application of MSM treatment was done by removing vegetation in 1 m radius circular area using a brush saw. This was followed by mixing organic and mineral soil horizons with a portable rototiller. The result was a relatively undisturbed area with 1 m diameter mulched microsites positioned in a grid, with 3 m intervals between neighbouring spruce seedlings. The MSM treated microsites were characterized by an absence of vegetation with soil composed of organic and mineral soil mixture. During planting, one black spruce seedling was placed at the centre of each mulched microsite. In planted control, black spruce were placed in undisturbed heath. The seedlings were planted along a grid with 3 m distance between the neighbouring seedlings.

In each 25 x 50 m sub-plot, 5 permanent sampling quadrats were established around randomly selected seedlings. Black spruce response was determined as the difference in height and basal diameter of seedlings between early June and mid-August in 2009, 2010, 2011 field seasons. In each of the sampling quadrats, measurements of soil moisture, soil temperature, soil respiration and organic matter depth were taken at 10 cm from a black spruce stem between early June – late August of 2010 (year 2) and 2011 (year 3).

Soil temperature and moisture (HH2 Moisture meter and WET-2 sensor, Delta-T Devices, Cambridge, UK) were measured from 11:00 to 15:00, preceded by at least 48 hours of no precipitation. Soil microbial activity, which is related to the amount of available soil nutrients (Vogel *et al.* 2005), was measured by determining soil respiration (EGM-4 meter and SR-1 probe, PP systems, MA, USA). Organic layer depth was determined by

examining two 5 cm diameter soil cores taken in each microsite 10 cm from black spruce stems. Herbivore and heaving damage of seedlings was assessed visually by inspecting all the planted seedlings assigning a value of 0 (no damage) or 1 (damaged).

Soil nutrients were measured by using plant root simulator (PRS™) probes (Western Ag Innovations Inc., Saskatoon, SK, Canada). In each study plot, eight set of probes, forming two samples, were installed for two weeks in randomly selected quadrats. The PRS probes work by binding positively and negatively charged ions to an ion exchange resin membrane. The resulting data is expressed as amount of nutrients absorbed by 10 cm² membrane over a period of time (µg /10 cm² 14 days). The PRS probes were placed in soil vertically keeping the upper side of 5 cm long membrane just below the surface. Each set of PRS consisted of two probes, which were installed next to each other. Immediately after extraction, the PRS™ probes were washed with distilled water, then put in plastic bags for transportation. In the laboratory the probes were cleaned of any residual soil, placed in clean plastic bags, and kept cool, until sent for analysis to Western Ag Innovations Inc., Saskatoon, SK, Canada. For chemical analysis the four set of probes were combined forming one sample. The ions bound to the membranes were extracted and their concentration determined.

Statistical analysis

Prior to analysis all the data were checked for normality using the Shapiro-Wilks test. Deviations were corrected using log(x) transformation. Growth of black spruce seedlings in scarified, MSM and undisturbed control treatments were compared according to a nested design and with elements of a repeated measures approach. For this study, the treatment sub-plots were considered nested within the blocks. By doing so, it was possible to account for variation in data associated with differences among the blocks, and increase the precision of the analyses. A repeated measures element was introduced to account for multiple measurements of black spruce height, basal diameter and microsite conditions taken in the same quadrats over a course of few years.

The overall comparison of black spruce growth and size was

accomplished by mixed linear model (R function: lme; library: nlme). This method is an extension of linear regression. The benefit of this technique is that it allows the analysis of data with few levels of hierarchy and accounts for random sources variation, such as location of the study blocks. The mean values of basal diameter and height as well as basal diameter and height increments in each sub-plot were used as the response variables. Treatment type (scarification, MSM, control) was considered as a fixed parameter, block as random intercept and year as random slope.

The analyses of seedling size and growth differences among the scarification, MSM and control in individual years, were carried out by constructing separate mixed linear models. In the models, mean values per sub-plot of seedling height, basal diameter, height increments or basal diameter increments were used as the response variables. Treatment type (scarification, MSM, control) was considered as a fixed parameter and block as random intercept.

In order to determine the relationship between black spruce growth and microsite conditions, further analyses were conducted using growth and environmental data for individual quadrats. The effects of herbivore damage and frost heaving on seedling survival in year one were estimated using multiple regression. For this analysis, survival of all seedlings in year one was used as a response variable, while presence/absence of herbivore and heaving damage as independent factors. Environmental factors associated with higher growth were identified using step-wise multiple regression (R functions: lm, step; library: stats). The data were checked for correlations. All of the examined parameters were well within the set range ($0.70 > \text{Pearson correlation coefficient} > -0.70$) and were included in the preliminary model. Basal diameter increments for each sampled seedling were used as response, while environmental measurements in each plot as independent variables.

To account for growth differences among black spruce in the three treatments, bio-physical and nutrient soil conditions were plotted using non-metric multidimensional scaling (NMDS) ordination (R function: metaMDS; library: vegan). The points were plotted based on environmental or nutrient data in corresponding quadrats. The relationship between seedling growth

and microsite conditions was determined as a correlation between basal diameter increments in each quadrat and corresponding microsite conditions (function : envfit; library: vegan). The results were plotted on NMDS plot. The relationship between seedling basal diameter increments and microsite coordinates in ordination space were expressed as an arrow. The direction of an arrow indicated a position in ordination diagram where black spruce growth was the highest among the microsities. The length of an arrow corresponded to the magnitude of variation in seedling growth relative to position of the points.

Results

Black spruce response

Survival of planted black spruce seedlings in all three treatments was above 90% (Fig. 3.2). There was no significant difference (Table 3.1) in seedling survival rates among scarification, MSM and control treatments. The proportion of live seedlings in scarified, MSM and control microsities was 91.7, 94.0 and 91.5% respectively.

Planted black spruce seedlings in MSM microsities experienced a higher degree of herbivore damage (likely from snowshoe hair) compared to control, with as many as 22.2% seedlings showing signs of browsing. Seedlings in the scarified treatment were less browsed (11.3%) than those in MSM treatment. However black spruce in scarification were susceptible to frost heaving (10.2%), which resulted in large portion of the root system pushed out of the soil. Black spruce seedlings, in undisturbed microsities, experienced very little browsing (3.5%) and no heaving damage. Neither browsing ($\beta = 0.01$, Sig.T = 0.65) nor heaving ($\beta = -0.04$, Sig.T = 0.105) had a significant effect ($r^2 = 0.0021$, $F_{2, 1349} = 1.43$, $p = 0.24$) on the survival of black spruce seedlings two years after planting.

Seedling size was the highest in scarified, lowest in control and intermediate in MSM microsities (Fig. 3.3 A,B). Overall, black spruce basal diameter was significantly greater in scarification and MSM compared to control treatment (Table 3.2). The analysis also revealed a significant difference in black spruce height between scarification and control as well as MSM and control.

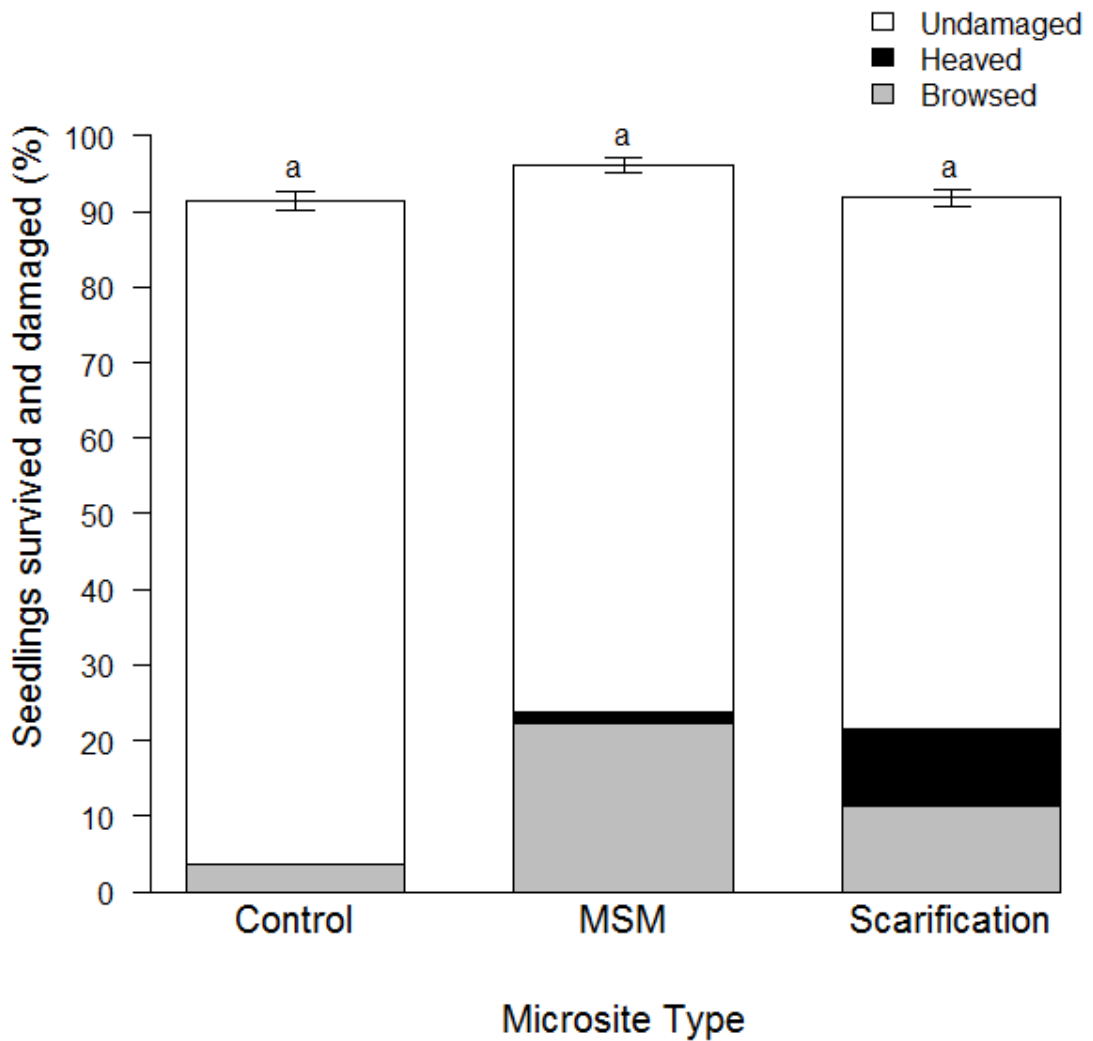


Figure 3.2. Black spruce seedling survival as well as proportion damaged by browsing and heaving in scarification, MSM and control during year one. Total column height represent percent of seedlings survival in each treatment. Shaded areas are percent of seedlings damaged by herbivores or frost heaving. Same letter indicates no significant difference ($p = 0.05$).

Table 3.1. Results of mixed linear regression analysis on seedling survival in scarification, MSM and control treatments during the first year. Values for $p < 0.05$ represent significant difference from control treatment.

Model	Comparison	β	SE β	p
Seedling survival in year 1	Scarification Control	0.001	0.052	0.98
	MSM Control	0.02	0.052	0.67
	Scarification MSM	0.02	0.052	0.69
Log Lik = 6.34			DF = 4	

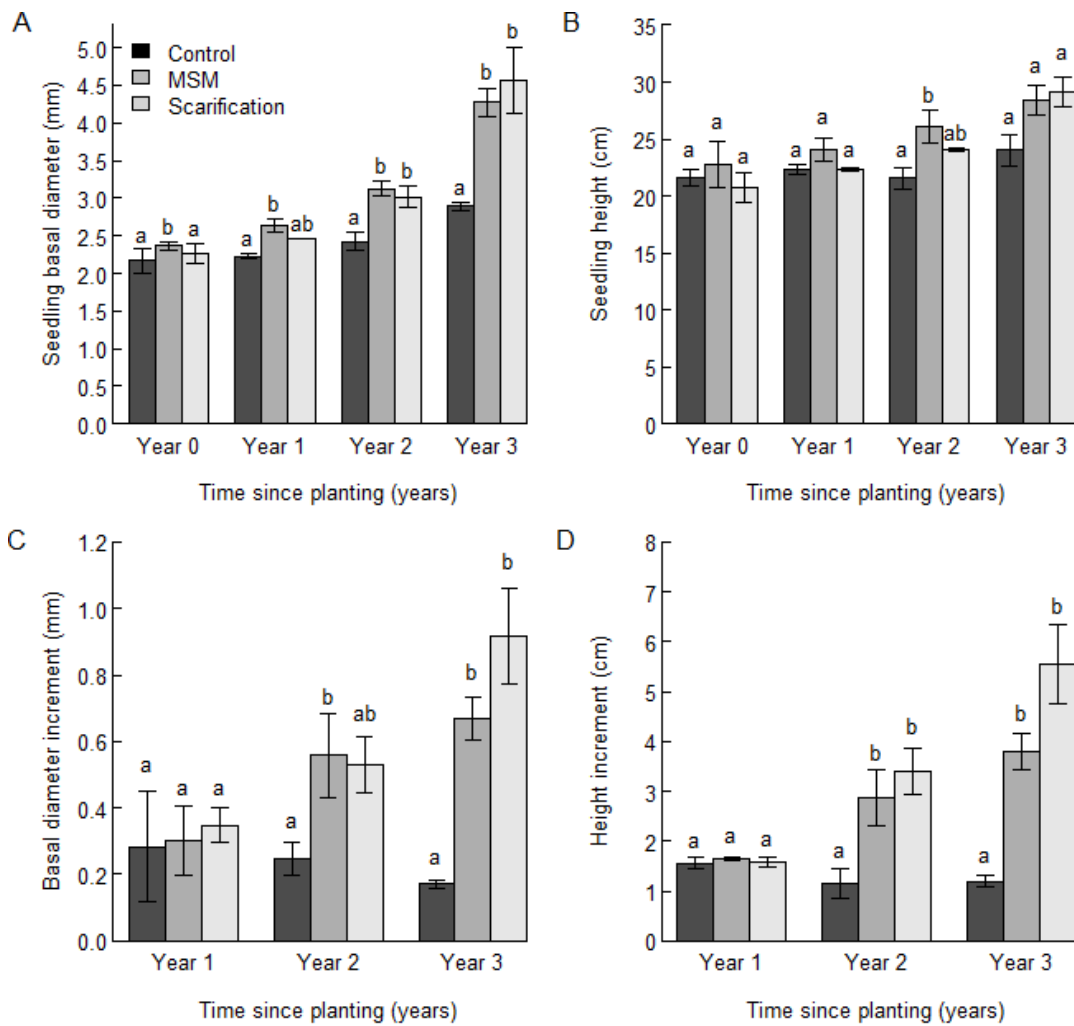


Figure 3.3. Variation in mean (A) basal diameter, (B) height, (C) basal diameter increments (early June – late August) and (D) height increments (early June – late August) of seedlings in three microsite types over four year interval. Unlike characters represent significant difference among the columns with in the same year.

Table 3.2. Results of multiple mixed linear regression analyses of basal diameter and height of black spruce seedlings in scarification, MSM and control treatments. Values for $p < 0.05$ represent significant difference from control treatment.

Model	Comparison	Basal diameter			Height		
		β	SE β	p	β	SE β	p
Years 0 – 3 combined	Scarification Control	0.76	0.17	< 0.001	2.26	1.01	0.002
	MSM Control	0.83	0.17	< 0.001	3.54	1.01	0.04
	Scarification MSM	0.07	0.17	0.68	1.28	1.01	0.22
Log Lik = -0.04 DF = 15				log Lik = 1.68 DF = 15			
Year 0	Scarification Control	0.1	0.13	0.50	-0.94	1.73	0.60
	MSM Control	0.2	0.13	0.20	1.12	1.73	0.50
	Scarification MSM	-0.1	0.13	0.47	-2.06	1.73	0.29
Log Lik = -0.34 DF = 4				Log Lik = -15.46 DF = 4			
Year 1	Scarification Control	0.23	0.06	0.02	-0.03	0.72	0.90
	MSM Control	0.41	0.06	0.002	1.68	0.72	0.08
	Scarification MSM	-0.18	0.06	0.04	-1.71	0.72	0.07
Log Lik = 4.66 DF = 4				Log Lik = -10.35 DF = 4			
Year 2	Scarification Control	0.59	0.09	0.002	2.49	1.44	0.16
	MSM Control	0.7	0.09	0.001	4.57	1.44	0.03
	Scarification MSM	-0.11	0.09	0.26	-2.07	1.44	0.22
Log Lik = 1.07 DF = 4				Log Lik = -13.57 DF = 4			
Year 3	Scarification Control	1.7	0.23	0.01	5.12	2.08	0.09
	MSM Control	1.38	0.23	0.01	4.36	2.08	0.10
	Scarification MSM	0.32	0.23	0.24	0.76	2.08	0.74
Log Lik = -2.66 DF = 4				Log Lik = 2.28 DF = 4			

Table 3.3. Results of multiple mixed linear regression analyses on basal diameter increments and height increments of black spruce seedlings in scarification, MSM and control treatments. Values for $p < 0.05$ represent significant difference from control treatment.

Model	Comparison	Basal diameter increments			Height increments		
		β	SE β	p	β	SE β	p
Years 1 – 3 combined	Scarification Control	0.36	0.09	0.001	2.21	0.53	< 0.001
	MSM Control	0.28	0.09	0.01	1.47	0.53	0.01
	Scarification MSM	0.09	0.09	0.35	0.74	0.53	0.17
Log Lik = -1.49 DF = 15				Log Lik = -42.77 DF = 15			
Year 1	Scarification Control	0.06	0.12	0.6	0.02	0.11	0.9
	MSM Control	0.02	0.12	0.9	0.08	0.11	0.5
	Scarification MSM	0.04	0.12	0.72	-0.06	0.11	0.61
Log Lik = -0.03 DF = 4				Log Lik = 1.68 DF = 4			
Year 2	Scarification Control	0.28	0.11	0.06	2.25	0.61	0.02
	MSM Control	0.31	0.11	0.05	1.72	0.61	0.05
	Scarification MSM	-0.03	0.11	0.81	0.52	0.61	0.43
Log Lik = 1.02 DF = 4				Log Lik = -8.69 DF = 4			
Year 3	Scarification Control	0.75	0.10	0.001	4.364	0.73	0.004
	MSM Control	0.5	0.10	0.01	2.6	0.73	0.02
	Scarification MSM	0.25	0.10	0.06	1.76	0.73	0.07
Log Lik = 1.42 DF = 4				Log Lik = -9.46 DF = 4			

At the time of planting, seedlings size did not vary significantly (Table 3.2) among the treatments, with exception of slightly higher basal diameter in MSM treatment. In years 1 – 3, black spruce basal diameter and height became noticeably greater in scarification and MSM compared to control (Fig. 3.3 A,B).

Both basal diameter increments and height increments were generally significantly greater (Table 3.4) in scarification and MSM than in control treatment (Fig. 3.3 C,D). During year one seedling growth did not vary significantly among the three treatments (Table 3.4). However, in years 2 – 3 basal diameter increments and height increments were considerably greater in scarification and MSM, compared to control treatments.

Microsite conditions

In year two, black spruce seedling growth had a significant relationship with soil moisture and temperature (Table 3.4). Step-wise multiple regression explained 38% of the variance in black spruce basal diameter increments ($r^2 = 0.41$, $r^2_{\text{adj}} = 0.38$). The analysis revealed a direct positive relationship of black spruce basal diameter increments with soil moisture and inverse relationship with soil temperature.

In year three, 34% of variation in black spruce basal diameter increments ($r^2 = 0.37$, $r^2_{\text{adj}} = 0.34$) was explained by combined effects of OM depth and soil respiration (Table 3.4). Unlike the previous year, OM depth played a greater role in black spruce growth with a significant negative effect. When taken individually, soil respiration did not have a significant relationships with black spruce growth.

Non-metric multidimensional scaling (NMDS) ordination using microsite environmental data for year two, gave two dimensional solution accounting for 99% (stress = 8.6) of cumulative variance of environmental parameters measured in each quadrat. The first NMDS axis presented a gradient of microsites with high to low OM depth (Fig. 3.4). The distribution of points along axis one corresponded to treatment type. The majority of scarified quadrats were clearly segregated from MSM and control, and were distributed along the right edge of the diagram. The separation between MSM and control microsites was not as evident; the two types of microsites

formed closely located clusters in ordination space.

The underlying factor behind the variation along the second NMDS axis was not as clear. Variation in microsite conditions along axis two was associated with increasing soil moisture and decreasing soil temperature.

Variation in seedling basal diameter increments was associated with both axis one and two. The highest growth rates were observed in quadrats located in top right corner of ordination space, which were characterized by relatively high soil moisture, low soil temperature and shallow OM depth.

Ordination analysis of year three environmental data also produced a two dimensional solution accounting for 98% (stress = 14.0) of cumulative variance of environmental parameters measured in each quadrat. As in year two, OM gradient was associated with axis one, with higher values towards the negative end of the axis (Fig. 3.5). Distribution of points along the first axis corresponded to treatment type. Scarification, MSM and control microsites formed three closely located clusters in ordination space. The scarification microsites were concentrated towards bottom-right corner. Most of the control quadrats were in top-left portion of the ordination plot, while MSM microsites were concentrated around the centre.

Similar to year two, the highest seedling growth rates were observed in scarification quadrats. However, unlike previous year, high seedling growth was primarily associated with lower in OM depth, and had little relation with other environmental factors.

Year one nutrient data showed that scarification, MSM and control microsites were characterized by three distinct sets of nutrient conditions (Fig. 3.6). NMDS ordination produced a two dimensional solution explaining 99% (stress = 10.4) of cumulative variance in available nutrients. Although the plots from three treatments did not produce distinct clusters, their distribution was limited to certain areas on the ordination plot. Control quadrats were aggregated at bottom-left and were associated with higher content of metals such as Mn, Ca, Zn, Mg. Distribution of MSM microsites was mostly limited to the top-left portion of the diagram. These quadrats were characterized by higher amounts of available phosphorus. Most of the scarification microsites were located in the right portion of the ordination space, and were associated with high amounts of available Fe.

Table 3.4. Results of step-wise multiple regression analyses on seedlings basal diameter increments as a function of microsite conditions in years two and three.

Model	Independent variables	Intercept	Partial regression coefficients			Sig.T
			<i>b</i>	SE <i>b</i>	β	
Year 2	Soil moisture	0.17	0.002	0.001	0.35	0.02
	Soil temperature	0.17	-0.01	0.002	-0.39	0.01
	Overall model fit	$r^2 = 0.41$	$F = 14.48$	$DF = 2, 42$	$p < 0.001$	
Year 3	Independent variables	Intercept	<i>b</i>	SE <i>b</i>	β	Sig.T
	OM depth	0.98	-0.03	0.01	-0.46	0.002
	Soil respiration	0.98	-1.22	0.63	-0.26	0.056
	Overall model fit	$r^2 = 0.37$	$F = 12.52$	$DF = 2, 42$	$p < 0.001$	

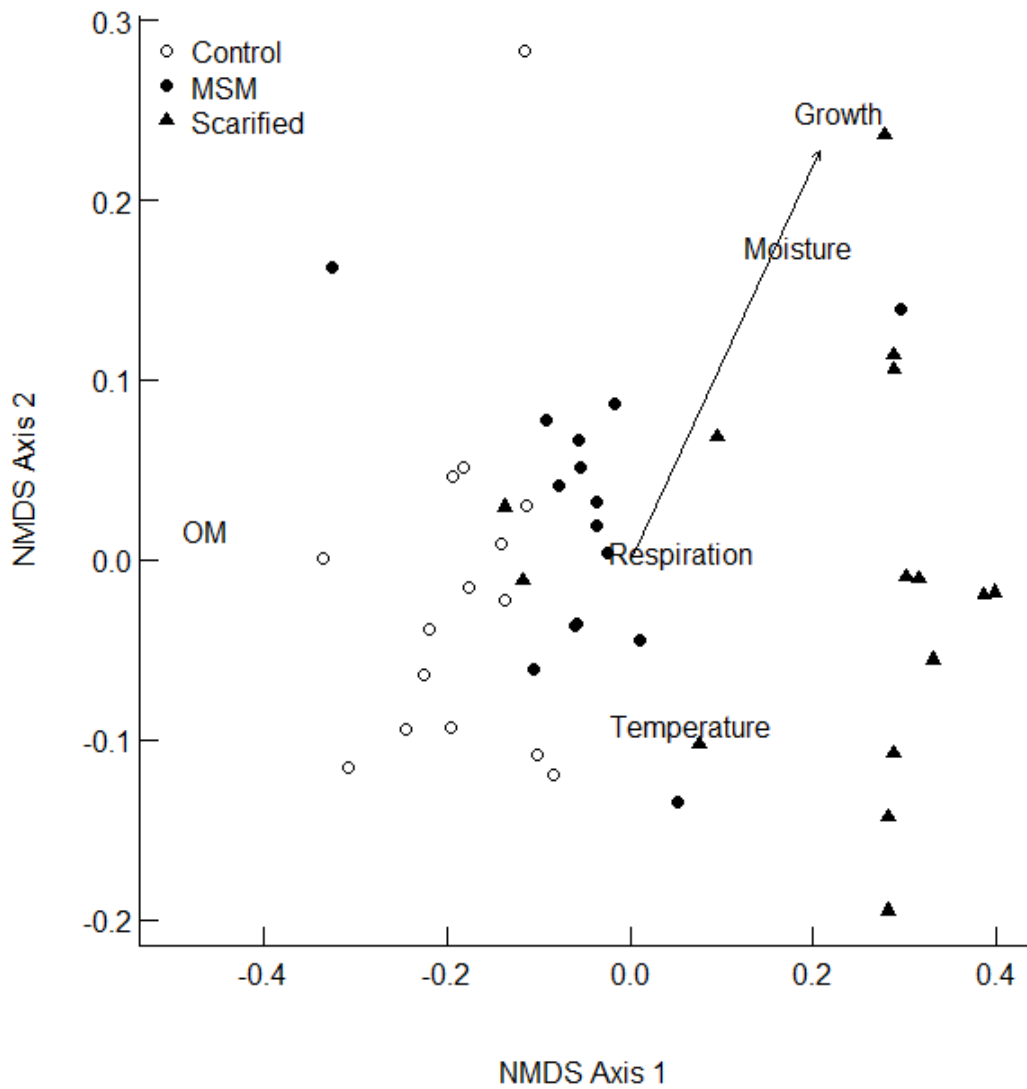


Figure 3.4. NMDS ordination demonstrating the difference in microsite conditions among scarification MSM and control treatments during year two. Points represent individual sampling quadrats in three treatments. The point coordinates were determined based on microsite environmental conditions in year two. Text indicates distribution of individual environmental parameters along the axis. Arrow corresponds to variation in seedlings basal diameter increments in relationship to position of points in ordination space ($r = 0.64$).

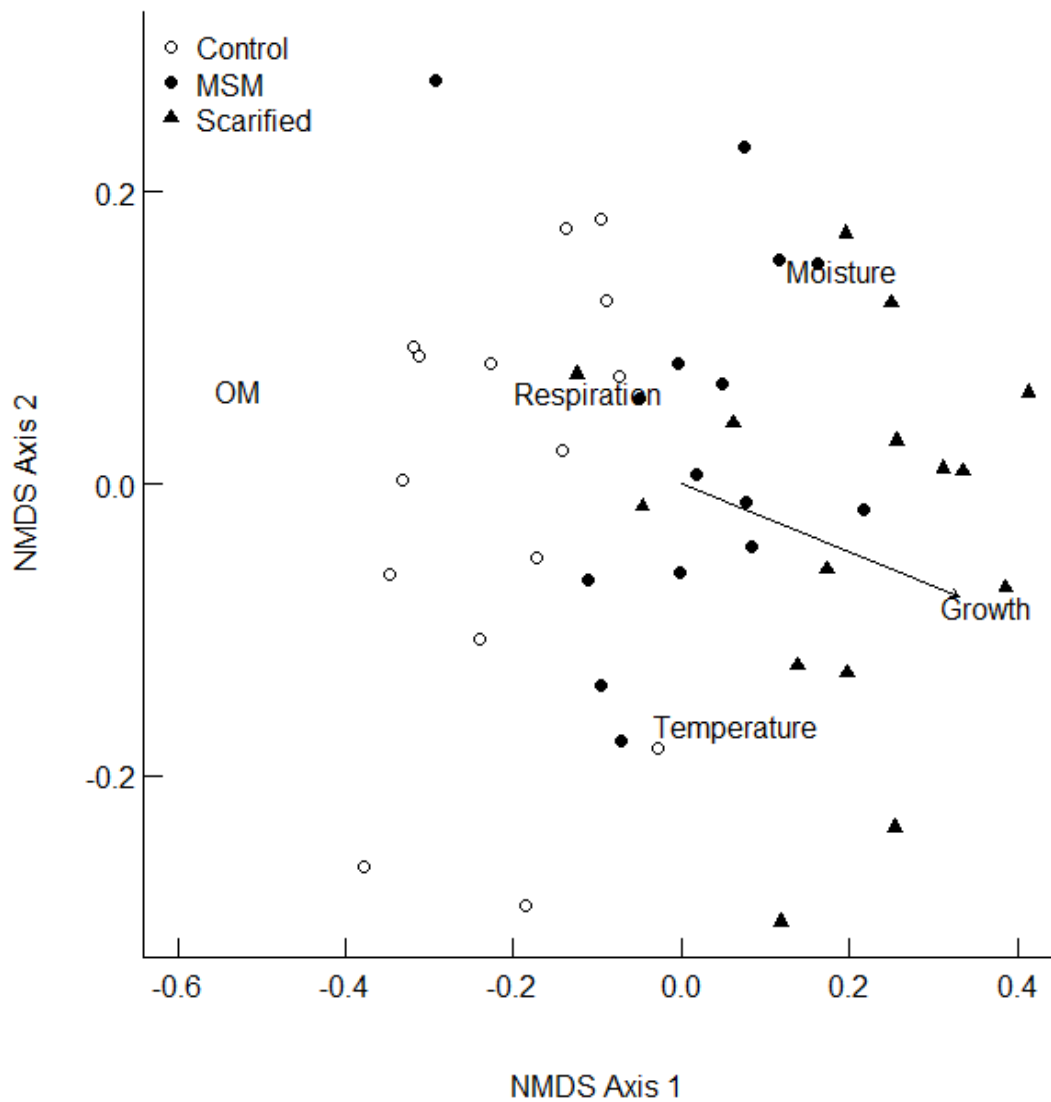


Figure 3.5. NMDS ordination demonstrating the difference in microsite conditions among scarification, MSM and control treatments during year three. Points represent individual sampling quadrats in three treatments. The point coordinates were determined based on microsite environmental conditions in year three. Text indicates distribution of individual environmental parameters along the axis. Arrow corresponds to variation in seedlings basal diameter increments in relation to position of points in ordination space ($r = -0.57$).

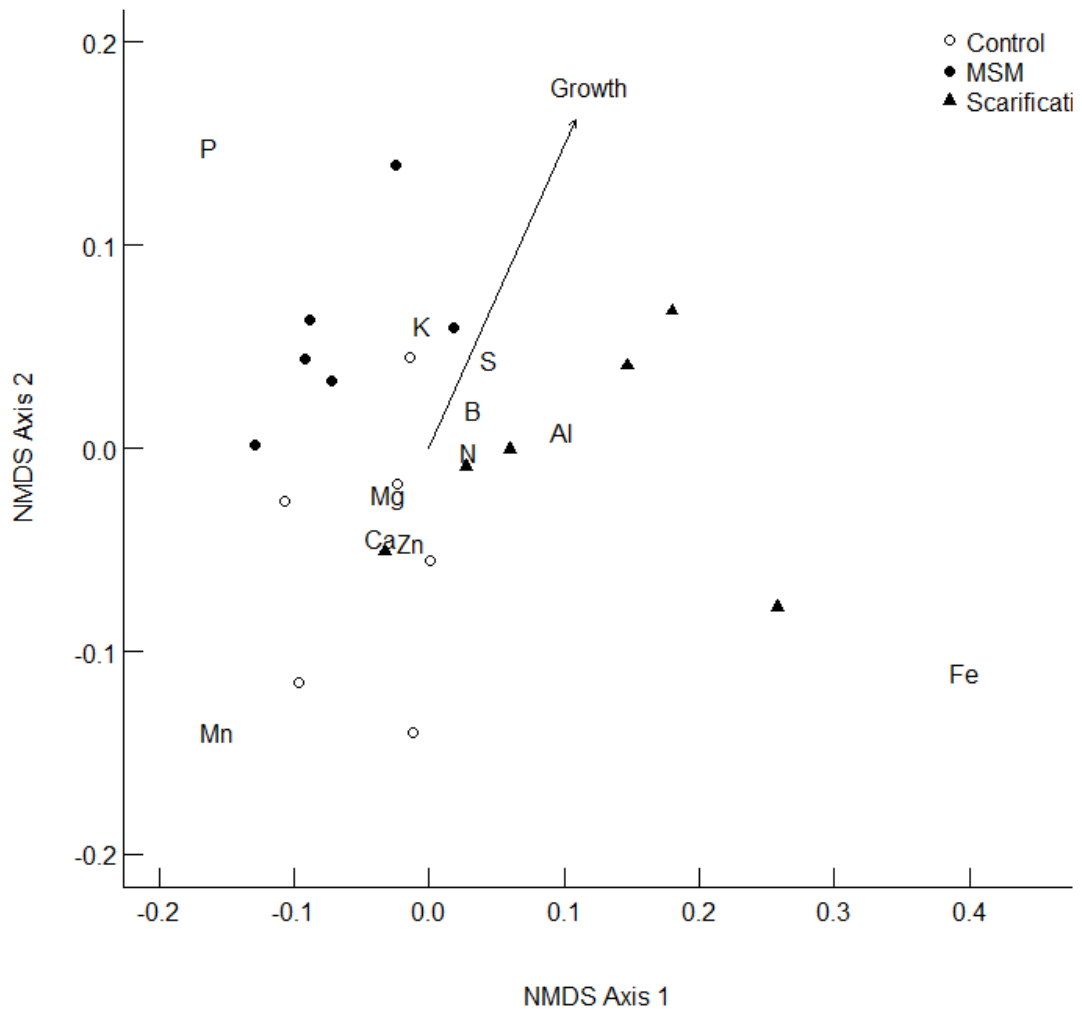


Figure 3.6. NMDS ordination demonstrating the difference in nutrient conditions among the microsites in scarification MSM and control treatments. The position along the axes determined using year one nutrient data. Points represent samples in each of three treatments. Text indicates distribution of individual nutrients along the axis. Arrow corresponds to variation in seedlings basal diameter increments in relation to position of points in ordination space ($r = 0.34$).

Table 3.5. Available soil nutrients (mean \pm SE) expressed as $\mu\text{g} / 10 \text{ cm}^2 \times 14$ days (see methods for details) in scarified, MSM and control microsites, one year after planting.

Nutrient type	Treatments		
	Control	MSM	Scarification
N (NO_3N & NH_4N)	18.4 \pm 2.1	17.5 \pm 1.5	18.9 \pm 1.9
P	1.6 \pm 0.43	3.5 \pm 1.47	0.6 \pm 0.12
Ca	181.9 \pm 25.5	117.8 \pm 14.8	110.2 \pm 16.7
Mg	82.3 \pm 18.3	64.4 \pm 7.2	61.0 \pm 12.0
K	63.4 \pm 7.2	142.4 \pm 24.5	100.1 \pm 7.36
Fe	2.1 \pm 1.1	1.5 \pm 0.19	13.7 \pm 10.1
Mn	8.9 \pm 2.3	5.7 \pm 1.64	2.7 \pm 0.88
Zn	0.73 \pm 0.08	0.6 \pm 0.1	0.5 \pm 0.11
B	1.03 \pm 0.16	0.93 \pm 0.16	0.8 \pm 0.15
S	41.4 \pm 2.5	44.6 \pm 3.26	53.2 \pm 3.72
Al	12.1 \pm 1.46	11.2 \pm 0.88	17.1 \pm 3.22

Total available N did not vary much among the three treatments (Table 3.1). Available P was the highest in MSM treatment with values 5.5 times greater compared to scarified and 2 times greater than in control. Total K was highest in MSM (142.4 $\mu\text{g}/10 \text{ cm}^2 \times 14 \text{ days}$), lowest in control (63.4 $\mu\text{g}/10 \text{ cm}^2 \times 14 \text{ days}$) and intermediate in scarified plots (100.1 $\mu\text{g}/10 \text{ cm}^2 \times 14 \text{ days}$). Total available Ca on the other hand was highest in control (Table 3.1).

Seedling basal diameter increments fitted to the ordination plot (Fig 3.6) indicated that the growth rates were higher in scarification and MSM microsites compared to control. However, a relatively low correlation coefficient ($r = 0.34$) suggested that difference in seedling growth rates was not directly associated with variation in nutrient conditions.

Discussion

The aim of this chapter was to determine the effectiveness of scarification and microsite mulching (MSM) to create safe sites. It was hypothesized that scarification and microsite mulching (MSM) enhance black spruce growth by removing the inhibitory effects of *Kalmia* and organic matter as well as increasing decomposition and soil moisture. The results indicate that all three microsite types were suitable for establishment and survival of black spruce seedlings. The growth rates however, were noticeably higher in safe sites created by scarification and MSM, compared to partially safe sites in undisturbed heath.

Seedling survival in scarification, MSM and control was above 90% with no significant difference among the treatments. Therefore, microsites created by any of the treatments were suitable for seedling survival. According to the extended safe site definition, microsites should provide suitable conditions not only for the seedling establishment, but also the growth. Black spruce seedlings in both scarified and MSM treatments were more susceptible to damage from herbivores and frost heaving compared to control. On the other hand, height and basal diameter increments in scarified and MSM treated microsites were much greater than control. Thiffault et al. (2004) and Thiffault & Jobidon (2006) reported positive effects of scarification on black spruce growth. The present study showed that microsites created by scarification and MSM produced higher basal diameter and height

increments compared to control. Walker & Mallik (2009) reported increased black spruce seedling growth and higher available soil nutrients in mulched soils (prepared by mechanically mixing *Kalmia* humus with mineral soil) compared to control (unmulched) in 4.5 x 4 m plots. In the current experiment, a similar increase in black spruce growth was obtained by MSM treatment which created significantly less ground disturbance compared to that of Walker & Mallik (2009). The attraction of MSM is its minimal ground disturbance which would make its use appropriate for ecologically sensitive areas such as national parks, ecological reserves and other conservation areas.

To determine which treatment creates seedling safe sites, it is necessary to consider three factors, i) establishment and survival, ii) risk of being damaged and iii) good growth. Establishment and survival rates were similar in all three treatments. Seedlings in control microsites were less likely to be damaged, but exhibited slower growth. In *Kalmia* heath, black spruce seedlings may remain stunted for decades (Chapter 1) causing a delay in forest succession after wild fires (Mallik et al. 2010). On the other hand, seedlings in scarified and MSM microsites were more likely to suffer from animal browsing and frost heaving, but were able to recover grow at much higher rates. Considering the overall effect, it can be concluded that both scarification and MSM create safe sites for black spruce seedlings.

Investigation into environmental drivers that might characterize black spruce safe sites in *Kalmia* heath revealed that in year two 38% of variation in seedlings growth was explained by the combined effects of soil moisture and soil temperature. Organic matter (OM) depth and soil respiration did not have any significant effect on black spruce basal diameter or height increments in year two. Soil temperature was inversely associated with seedling growth. In a study by Tryon & Chapin (1983) on root elongation of six boreal species in response to soil temperature, the authors noted higher root growth of black spruce located in cold and wet sites. This situation closely corresponds with our findings which show greater black spruce basal diameter and height increments in microsites with higher moisture and lower temperatures. The best growth conditions were observed in a small number of scarified microsites (Fig. 3.4). Earlier research by Thiffault et. al. (2004)

demonstrated that scarification could result in higher soil moisture compared to undisturbed control. However, the same workers have also reported higher soil temperature fluctuation in a scarification treatment, with generally higher values during the summer. Ordination results demonstrate that even though scarification did produce the best growth conditions, a majority of scarified microsites did not provide the optimal conditions due to lack of moisture and higher soil temperature. On the other hand, MSM treatment resulted in consistently better growth conditions compared to undisturbed heath. As a result mean seedling growth was similar in microsites altered by scarification and MSM.

In year three 34% of variance in black spruce basal diameter increments was explained by the combined effects of OM depth and soil respiration. Contrary to results from year two, soil temperature and soil moisture were found to have little or no effect on seedling's growth. Unlike the previous year, OM depth appeared to be a predominant factor affecting black spruce growth, with greater basal diameter increments in microsites characterized by shallow OM. A number of studies have demonstrated that *Kalmia* litter which makes up a large portion of the organic layer in heath can have a negative impact on black spruce growth (Mallik 1994, Bradley et al. 1997, Inderjit & Mallik 1999). Higher decomposition rates associated with greater soil respiration is thought to alleviate negative effects of *Kalmia* through degradation of allelochemicals (Zeng & Mallik 2006) and release of locked up soil nutrients (Staaf & Berg 1981). It was also demonstrated that soil mulching can enhance decomposition (Walker & Mallik 2009) and is associated with higher soil respiration (Mallik & Hu 1997). Thus, it was expected that soil respiration would have a positive relationship with black spruce growth. However, data in year three (Fig. 3.5) revealed an inverse relationship between soil respiration and black spruce basal diameter increments. This result is likely caused by relatively low respiration rates in scarification microsites (Mallik & Hu 1997) which are characterized by substrate composed of mineral soil. It is also likely that a snapshot of environmental data collected at a selected time did not reflect the overall near-ground environmental conditions of the microsites in the three treatments. Therefore, one must acknowledge this limitation in interpreting

the environmental data with respect to black spruce seeding growth and soil nutrients.

Previous studies suggested that one of the main mechanisms by which *Kalmia* inhibits conifer growth is by controlling soil nutrients (Bradley et al. 1997, Mallik & Inderjit 1999, Yamasaki et al. 2002). Loose clusters observed in NMDS ordination (Fig. 3.6) suggest that application of scarification and MSM produces microsites with distinctly different sets of conditions. The distribution of points in ordination space did not follow a single gradient, which could have been interpreted as decreasing proportion of organic/mineral soil components. It was concluded that axis one was directly related to the presence of a mineral soil component. The supporting evidence comes from a high concentrations of iron (Fe) on the right portion of ordination plot (Fig. 3.6). Along with other effects on the environment, *Kalmia* has been noted to induce iron pan formation (Damman 1971). During this process, Fe ions contained in the humus travel downwards with rain water and are deposited in mineral layer. Scarification exposed mineral soil creating substrate with high iron content. Axis two was strongly associated with available phosphorous. Phosphorous concentrations were the highest in the MSM treatment, intermediate in the control and lowest in the scarification (Table 3.5). This trend closely corresponded with soil respiration values observed in three microsite types. It was previously shown that *Kalmia* has a strong capacity to affect availability of soil nutrients (Bloom & Mallik 2006). In particular, it was demonstrated that *Kalmia* cover has an inverse relation with total N and P concentrations. It is known that organic matter decomposition results in release of locked up P and N (Staaf & Berg 1981). Hence, it would be logical to suggest that removal of *Kalmia* and enhancing decomposition through soil mixing would lead to higher P concentrations. By the same logic we would expect to see a similar trend for nitrogen. However, total available N varied only slightly among the treatments. It is possible, that in this system the rate at which N is released is slower compared to P. As such, the effects of higher decomposition, due to soil mixing, would not be detected one year after treatment application.

While ordination results indicate that black spruce seedlings performed better in microsites altered by scarification and MSM, the growth rates were

not associated with any particular nutrient. This situation is likely due to low availability of total N which acts as a limiting factor in this system (Bloom & Mallik 2006). Although three types of microsites did vary in nutrient conditions, the mechanism by which they affect black spruce growth does not seem to be based on nutrient availability, at least in one year after treatment application.

As initially predicted, scarification and MSM produced microsites favourable for growth. Despite differences between scarification and MSM, their effects on black spruce were similar. Even though seedling survival in three microsites types was high, the growth response indicates that only scarification and MSM treatments created safe sites for black spruce. In year two, both scarification and MSM enhanced black spruce growth by providing conditions necessary for root elongation (Tryon & Chapin 1983). In year three, seedling growth was primarily influenced by organic matter thickness. Although soil nutrient content varied among scarified, MSM and control microsites, it was not directly involved in the mechanism responsible for higher seedling growth, at least one year after planting. Furthermore, the differences in environmental factors associated with seedling growth between year two and three confirmed the temporally dynamic and complex nature of safe sites. The results also indicate the need to identify safe sites in terms of features that remain relatively constant with passage of time.

Management implications

From the forest management perspective it is important to consider not only the ecological effects, but also logistical problems and public opinion associated with site preparation treatments. In some areas, it is acceptable to use commercially available methods, such as scarification, associated with high level of ground disturbance. However, in protected areas, such as national parks and ecological reserves, this may not be a desirable option. With strong pressures from the public to conserve the natural environment and opposition to the use of large scale disturbance methods, such as scarification, the park managers are left with very few options.

The current study demonstrates that MSM can enhance black spruce growth similar to scarification, but with minimum soil disturbance. If black

spruce seedlings are to be planted at a density required for canopy closure (2600 stems/ha), the disturbed area resulting from MSM (estimated $1313 \pm 159 \text{ m}^2/\text{ha}$) would be much smaller compared to scarification (estimated $4456 \pm 1000 \text{ m}^2/\text{ha}$). As such, MSM appears to be a better choice of site preparation method in environmentally and socially sensitive area where large scale disturbance is not desirable.

General Discussion

The primary objective of this research was to explain black spruce regeneration in post-fire chronosequence in light of safe site abundance, based on the extended definition of safe site, one that includes establishment and growth. The second objective was to determine the effectiveness of scarification and microsite mulching to create safe sites in post-fire *Kalmia* heath by comparing black spruce growth in artificially created safe sites and partially safe sites. In the first part of this study, it was discovered that black spruce safe sites are characterized by shallow OM (less than 5 cm) and high respiration rates (1 g/m²h). In chapter two, it was determined that removal of OM through scarification or MSM creates safe sites for spruce seedlings, allowing for significantly higher growth rates compared to undisturbed heath.

Previous work by Mallik et al. (2010) suggested that organic matter thickness is a major factor controlling black spruce seed germination in *Kalmia* dominated sites. Another study by Segwart-Colier & Mallik (2010) demonstrated that substrates with residual OM less than 2 cm were favourable for black spruce germination, while soils with deep OM were likely to be colonized by *Kalmia*. An inverse relationship between OM thickness and black spruce stem density, observed in the current study, confirmed the importance of OM for black spruce recruitment. A model, based on tree ring data (Fig. 2.5), demonstrated that the recruitment of new individuals declined over time with little germination occurring 15 years after fire. Such dynamics can be explained by gradual saturation of microsites favourable for black spruce seed germination. Mallik et al. (2010) have demonstrated that the area of substrates favourable for germination declines with time due to OM build up. Combination of previous knowledge and current results suggest that microsites suitable for germination are not only rare, but their number declines, potentially leaving only small number of partially safe sites available 20 years after the fire event.

In addition to poor recruitment, a large proportion of black spruce (87%) suffered from stunted growth (ARI < 0.5 mm/year). Some authors suggested that growth check of black spruce in *Kalmia* heath is caused by

direct competition for resources between *Kalmia* and black spruce (Yamasaki et al. 2002, LeBel et al. 2008). Others claimed that poor conifer growth is a result of chemical interference caused by *Kalmia* allelochemicals (Zhu & Mallik 1994, Mallik et al. 1998). There is also evidence suggesting that *Kalmia* acts as environmental engineer leading to accumulation of OM (Inderjit & Mallik 1999), that interferes with soil nutrient cycling (Bradley et al. 1997) and inhibits microbial activity (Bradley et al. 2000).

Some of the observed stunted black spruce were able to overcome stunted condition and achieved relatively high growth rates (ARI > 1.3 mm/year). The probability for release was inversely associated with OM thickness and directly with soil decomposition. Many black spruce, in microsites characterized by deep OM and low soil respiration, remained stunted for more than 20 years, which fit well with our definition of partially safe site. Organic matter depth had a significant relationship with both black spruce density and release probability. Hence, it can be concluded that OM is the primary characteristic of black spruce safe sites in *Kalmia* dominated heath.

The problem of slow growth and low germination rates can be resolved by removal of constraining conditions leading to the creation of safe sites. The idea was tested using two site treatment methods. Both scarification, which exposes mineral soil, and MSM, which promotes soil decomposition (Walker & Mallik 2009), were effective at increasing seedling growth rates compared to undisturbed heath. These results, in addition to previous findings (Mallik et al. 1998, Inderjit & Mallik 1999, Bradley et al. 2000, Yamasaki et al. 2002, LeBel et al. 2008), validate the argument that seedlings and adult plants require a safe site in order achieve high growth rates.

While the phenomenon of growth check (stunted growth) of conifers in ericaceous heath has been reported previously (Leyton 1955, Messier 1992, Zhu & Mallik 1994, Bradley et al. 1997) this study, for the first time, elucidates the degree of growth stunting and release. By examining the relation between black spruce growth and microsite conditions, I confirmed that stunted growth may indeed be associated with absence of safe sites during adult stage. Although safe site concept might not be applicable in all of the

systems, it may be a useful tool for determining the future of individual plants as well as whole population in harsh habitats, where microsite differences are clearly distinguishable.

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