

Enhancing natural regeneration of white spruce (*Picea glauca*) via synchronization
of a mast year with site manipulations in Abitibi, Quebec

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Abstract

Enhancing natural regeneration of white spruce (*Picea glauca*) via synchronization of a mast year with site manipulations in Abitibi, Quebec

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The commercially valuable tree, white spruce (*Picea glauca* (Moench) Voss) has proven difficult to regenerate either naturally or artificially following harvesting. A strongly masting species, its small seeds require mineral soil or thin duff for germination. This study explored the possibility of increasing natural recruitment of white spruce and balsam fir (*Abies balsamea* (L.) Mill) following harvesting by coupling site preparation treatments with a masting episode in the boreal forest of northwest Quebec. Four treatments (on average 4604 m²) were applied to a seed tree retention cut, replicated in three blocks: 1) understory shrub and slash chipping, 2) ground scarification, 3) combination of chipping followed by scarification, and 4) cut with no prescribed site preparation (control). Cumulative seed density in seed traps (area: 1/2 m², made out of wood and mesh; 0.75 m high) located in the treatments was approximately 1000 seeds/m² for spruce and 50 seeds/m² for fir. Quantities of exposed mineral soil differed significantly between treatments, with 25% in the chipped & scarified treatment; however, this was not significantly greater than in the scarified only treatment (12%). There were no significant differences in adjusted germinant densities between mineral soil and decomposed wood in both the scarified and chipped & scarified treatments. The chipped & scarified treatment had the greatest mean recruitment densities for spruce, followed by the scarified treatment ($\approx 3.10/\text{m}^2$). In 2007, both species (lumped) attained full stocking (>60%) in all treatments, including the control. In 2008, full stocking of spruce was maintained in all treatments except the control, while no treatment attained

full stocking of fir. Applying these results within an ecosystem-based and mixedwood management framework would require some degree of flexibility (and operational agility) in forest management planning that would allow adapting appropriate harvesting and site preparation treatments when a mast year occurs.

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Epigraph

The forest is a peculiar organism of unlimited kindness and benevolence that makes no demands for its sustenance and extends generously the products of its life activity; it affords protection to all beings, offering shade even to the axeman who destroys it.

Gautama Buddha

Quoted by E.J. Mullins and T.S. McKnight (eds.)
in "Canadian Woods: Their properties and uses"

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Chapter 1: Literature Review

Introduction

In the last decade, the loss of natural forest as a result of industrial forest harvesting has drawn the attention of environmental and community activists, the scientific community, industrial foresters, government officials and policy makers. In Quebec, public outrage concerning forest practices and policies followed the distribution of the controversial documentary film, “l’Erreur boreale”. Released in 1999, this film asserted that the boreal forest was over-harvested and badly managed as a result of industry-government collusion. In English-speaking Canada, public interest was greatly spurred by a 1992 episode of David Suzuki’s ‘Nature of Things’ that focused on the extensive and, it was argued, debilitating effects of clear cutting natural, diversity-rich forests and replacing them with plantation monocultures. Although many would contest the accuracy of the statements presented in these two documentaries, both were nonetheless instrumental in focusing popular and scientific attention on the relationships between forestry practices and forest health.

Begon et al. (1996) emphasizes that a forest ecosystem is a dynamic network of various communities linked by energy flow. The forest provides many functions and services such as water filtration, flood control, nutrient cycling, wildlife habitat, and sequestration of carbon. As the forest provides a wide range of products and services and is mostly public in Canada, it is normal that the general public feels it has a stake in how forests are managed.

Perspectives on the commercial forest

Forests were long regarded as an unlimited resource, and few restrictions were imposed on cutting up until the early 20th century when wood shortages in eastern Canada lead to initial measures of regulation (Messier et al. 2003). However, seriously constraining regulations were not legislated until the 1978 Reed Report showed that all the provinces were fast approaching their annual allowable cut (AAC); that is that the level of harvesting was exceeding the forest's capacity to regenerate and grow (Lortie 1983). That report recommended the broad implementation of plantations of genetically-improved nursery stock on large clearcuts – essentially an agricultural model applied to forestry -which would become the norm in Canada, particularly in the boreal forest. It was believed that this agricultural approach, which university-trained foresters had been advocating for decades, would finally permit the wood supply to be managed on a sustainable basis as a result of plantation silviculture. However, while the classic forestry principle of sustainability was narrowly focussed on wood supply, ecologists and conservationists were becoming increasingly concerned about the sustainability of ecosystem functions and the species diversity that was a manifestation of those functions. (Spear 1997).

Environmental concerns increased in the early 1980s as the mean size of trees harvested declined; average forest age was becoming younger and industry in many regions increasingly had to extend harvesting operations further north to less productive forests. As a result of industries' higher mean annual harvest rates, compared to natural disturbance, certain changes in landscape composition have occurred in some boreal

regions, notably an increase in forest cover of shade intolerant hardwoods to the detriment of conifers, became evident. Other environmental problems that have been associated with forestry activities include soil erosion and compaction, and the deterioration of water quality (Messier et al. 2003). By the late 1980s, the annual allowable cut had already been attained in parts of several provinces in Canada and wood shortages were anticipated in the next 25 years (Messier et al. 2003). In fact, based on concerns raised regarding the reliability of data, modeling techniques and assumptions used in provincial annual allowable cut calculations, the Québec government followed the recommendations of the 2004 Coulombe Commission and imposed a 20% reduction in the provincial softwood AAC, pending improved calculations (NAFA 2006).

In Québec, forest companies are required to ensure adequate stocking and growth of regeneration following harvesting, which may be accomplished by natural regeneration (for shade tolerant species such as balsam fir, which is commonly advance regeneration that has been protected during harvesting) or through artificial regeneration. Very little artificial seeding is done in Québec; most artificial regeneration is accomplished through planting. Both natural and artificial regeneration may be tended to “free to grow” status (i.e. not overtopped by non-commercial, competing species) through spacing, brush clearing and fill-planting. Provincial regulations require that cutovers be regenerated to a hardwood and softwood stocking level similar to or greater than the pre-harvest levels (Bergeron & Harvey 1997). Clear-cutting, including variants to protect advance regeneration and soils (CPRS), is the most economical and most frequently applied harvesting system in the Canadian boreal forest. However, a great deal of research has shown that clear-cutting can have a number of detrimental effects on the

environment and on habitat including soil erosion, nutrient loss, loss and fragmentation of habitat, decreases in biodiversity, and species composition changes (Hayes et al. 2005). Can we expect forest ecosystems to maintain their natural productivity, composition and functions in the long term if our interpretation of sustainability is simply limited to wood supply? Largely because of public disapproval of clearcutting, this type of harvesting was replaced in the early 1990s by Cutting with Protection of Regeneration and Soils (or CPRS, '*Coupe avec protection de la regeneration et des sols*'). CPRS restricts harvesting machinery movement to parallel trails that cannot exceed a total of 25% of the cutover area (Harvey & Brais 2002). While variable retention harvesting has been used for several years in most western provinces and Ontario, as well as in Sweden and Finland (Work et al. 2003), it has only recently been applied on an experimental basis in Quebec and recent changes in forest legislation indicate that more retention will be applied in the future.

Since the Rapport Coulombe (Coulombe et al. 2004), there has been growing pressure to: 1) establish more protected areas, 2) ensure protection of a representative proportion of old-growth forests, and 3) practice ecosystem management. Although definitions of forest ecosystem management (FEM) vary somewhat, the underlying premise is that a better understanding and integration of natural ecosystem dynamics into forest management practices is probably the best way to assure maintenance of natural (indigenous) biodiversity, ecosystem processes, and forest productivity. The natural disturbance regime therefore provides a natural reference or framework for designing forest-level strategies for reducing the differences between landscape patterns and ecological processes driven by natural disturbances and those issued from management

practices. The approach essentially identifies differences between the natural and the managed disturbance regimes and proposes forest- and stand-level measures for reducing these differences (Grumbine 1994). Despite the fact that the entire Canadian forestry sector is currently going through one of its worst economic crises in recent history, the “natural disturbance paradigm” is orienting forest policies and practices in much of the country and it is within this context that this Masters project is situated.

Forest policy inevitably involves compromises of certain forest values for others and trade-offs between economic needs and the requirements of conservation (Burton et al. 2003). The Canadian Council of Forestry Ministers (CCFM) established the Criteria and Indicators (C&I) framework for sustainable forest management in order to establish national Sustainable Forest Management standards and allow monitoring of forest management practices in Canada (CCFM 2003). The CCMF proposes four biophysical criteria, all of which may be affected by forest practices such as harvesting: 1) biological conservation, 2) maintenance and improvement of the conditions and productivity of forest ecosystems, 3) conservation of water and soil resources, and 4) contributions of forest ecosystems to the “Global Ecology”. These criteria represent a broad set of forest values to which, ostensibly, the public strongly adheres.

Forest Ecosystem Management

It is worth discussing the recent evolution of provincial policies on harvesting and regeneration as this has a direct bearing on my thesis. I explore alternatives to conventional clear-cutting followed by monoculture plantations precisely because there

appears to exist to as yet few well-explored alternatives: CPRS is perhaps an exception but it often favours less desirable species such as balsam fir.

Within CCFM's six criteria of sustainable forest management, forest ecosystem management (FEM) constitutes a contemporary approach to maintenance of the four biophysical criteria. The basic premise of FEM is that the manager must maintain the structure, composition, and dynamics of a natural forest; i.e. manage the forest as an ecosystem (Grumbine 1994; MacDonald 1995). This approach requires an understanding of regional natural dynamics (disturbance regime and stand-level dynamics) and an evaluation of the landscape- and stand-level differences generated by these natural processes as well as by past and current forest management regimes. Socially acceptable and economical feasible management strategies should then be developed to reduce these differences. It has been emphasized by a number of authors (*cf* Gauthier et al. 2008) that varying harvesting practices would better reflect the heterogeneity of severity, size, configuration of (and intervals between) natural disturbances such as wildfires and insect outbreaks, giving way to the coarse filter approach to maintaining biodiversity. The coarse filter approach posits that because it is impossible to manage forests specifically for the innumerable species that inhabit a region, it makes more sense to preserve as much as possible the natural ecological processes and representative habitats in a certain area as possible (Bergeron et al. 2002). Since the main killers of trees are, by definition, the natural disturbances, and since (virtually) all species in the ecosystem have been able to persist over the millennia under natural disturbance regimes, it follows that reducing differences between forest management regimes and natural disturbance regimes would favour maintenance of indigenous biodiversity.

Within the framework of FEM, some of our current management practices have been altered (Work et al. 2003). In the southern boreal mixedwood forests of Quebec, a combination of clearcutting and selection or partial cutting is being increasingly practiced or proposed, as it most resembles the mix of disturbance agents that constitute the natural disturbance regime (fire, insects, ice storms, wind storms) common in this region (Bergeron & Harvey 1997).

As forests age in the absence of catastrophic disturbance or major secondary disturbances, gap dynamics shape stand structure and composition (White & Pickett 1985; Attiwill 1994; Bergeron & Harvey 1997). Insects, windthrow, ice storms, etc invariably spare some fraction of the trees so that subsequent recruitment by seed is not as constrained by limited dispersal as it might otherwise be following a large disturbance. Furthermore, with the exception of severe wind events, the understory and duff are barely affected by disturbances other than fire. Thus, these disturbances tend to benefit shade-tolerant species via their “seedling or sapling bank” and those with large seeds (necessary for root penetration of thick duff) (Greene et al. 1999). By contrast, fire generally leads to large distances between residuals (except for aerial seedbank species) and thus seed dispersal can be a major constraint for post-disturbance colonization (Greene & Johnson 2000). Further, fire routinely removes about 40% of the duff, and survivorship of small germinants can be quite high on the patchy areas where mineral soil has been exposed (Greene et al. 2007). Thus, fires tend to foster a dominance of shade-intolerant, smaller-seeded species, often with an aerial seedbank. Black spruce (*Picea mariana*) is something of an exception in that it is a shade-tolerant species which maintains an aerial seedbank and thus possesses traits of both pioneer and late-successional species. Also,

root-suckering species such as poplars and basal sprouting species such as white birch (*Betula papyrifera* Marsh.) and red maple (*Acer rubrum*) are favoured by fire. Where there is a mix of disturbance types such as in the southern boreal mixedwood boreal forest of Quebec, the three-cohort model of variable harvesting intensities (mimicking fire, insect damage and gap dynamics), has been proposed (Bergeron et al. 1999; Harvey et al. 2002).

Conventional boreal forestry is characterised by relatively short rotations and an even-aged, clear-cut (or careful logging) harvesting regime. These two aspects tend to reduce structural complexity at the stand and landscape levels (Harvey et al. 2002; Messier et al. 2003). Some old silvicultural systems (for example, seed tree retention or shelterwoods) are now seen as alternative treatments to clear-cutting because they retain some structure, although generally only temporarily, and promote allelic diversity within the regeneration layer.

Québec's new forest law includes provisions for implementing FEM in public forests. While forest ecosystem management is a relatively new approach, different elements of the approach have been at least partly implemented in most provinces in Canada. The reasons for the limited adoption of FEM practices are manifold: coarse filter measures to conserve biodiversity are likely to have repercussions on wood supply and are therefore contentious; diversifying silvicultural practices (including increased use of partial cutting) may increase short-term costs for wood fibre; and the flexibility required for implementing FEM practices is difficult to employ in the rigid regulatory framework that characterizes most provincial forest policies in Canada today. As well, some of the baseline knowledge concerning ecosystem dynamics and functioning that

should form the foundation of FEM is lacking in many parts of the country. However, gradual implementation of FEM practices is largely due to the novelty of the approach (and the importance placed on maintaining various ecosystem functions besides industrial wood supply) rather than a question of insufficient knowledge about ecosystem dynamics.

White spruce autoecology

White spruce (*Picea glauca* (Moench) Voss) is widespread across Canada and is one of the most important commercial species in the mixedwood portion of the western and eastern boreal forest (Rowe 1972). In the Abitibi lowlands, mixed stands can contain black (*Picea mariana* (Mill) B.S.P), white spruce, balsam fir (*Abies balsamea* (L.) Mill.), jack pine (*Pinus banksiana* Lamb.), eastern white cedar (*Thuja occidentalis*), eastern larch (*Larix occidentalis*), trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh.).

More than any other commercial tree species, white spruce is difficult to regenerate after harvesting (Lees 1964; Steill 1976; Greene et al. 1999; Stewart et al. 2000). Unlike some other boreal tree species (e.g. black spruce, jack pine and aspen), white spruce has no capacity (e.g. by cone serotiny or root suckering) for in situ regeneration after fires (Greene et al. 1999). The problem for foresters is made worse by the fact that naturally regenerating white spruce tends to grow slowly at first—much slower than competitors such as paper birch, aspen and jack pine.

Sexual reproduction of white spruce

The number of cones produced by an individual white spruce is proportional to the tree basal area and to the ambient light environment around the crown (Greene et al. 2002). The minimum size for reproduction is about 4 cm diameter at the stem base in full light but much greater in shaded conditions; indeed, in the understory far from any forest edge or canopy opening, sub dominant white spruce essentially produces no cones no matter how tall it might be (Greene et al. 2002).

Many plant species, both gymnosperms and angiosperms, and in both the tropics and temperate forests, are known to have marked temporal variation in annual seed production, a trait referred to as masting. In addition, masting is also characterized by the synchronous production of seeds by conspecifics at a regional scale (Kelly & Sork 2002).

How do these individuals ‘know’ when to mast with their conspecifics? There are three methods by which plants are known to ‘communicate’: chemical signalling, reproductively (i.e. pollen coupling) and as a response to environmental (weather) variables (Koenig & Knops 2000). Chemical signalling, through airborne means or plant root systems, and reproductive “cues” may be discounted as an explanation for masting synchronicity because the effective distances over which chemical cues (and pollen) can operate are much smaller than the wider geographical range affected by a masting episode (or year). Synchronicity has been detected within genera across areas as great as 196,000 km² and within families across areas up to 785 000 km²; moreover, many individuals exist in fragmented populations (Koenig & Knops 1998). Based on a few studies, some sort of weather cue sensed by all individuals in the populations of a region

offers the best explanation for triggering a particular synchronized seed production episode. Warm and dry weather experienced at the time of bud differentiation has been cited as the cue in several conifer species (Norton and Kelly 1988; Sakai et al. 1999; Koenig & Knops 2000; Shibata et al. 2002; Selas et al. 2000; Kon et al. 2005). Moreover, mast years tend to lead to large seedling cohorts (Sork 1983; Keely & Bond 1999; Peters et al. 2005). In the boreal forest, all species mast except for the aerial seedbank species (jack pine and black spruce) whose temporal variation in crop size is much more subdued (Greene & Johnson 2004).

Two other boreal tree species that exhibit mass seeding are trembling aspen and balsam poplar. Their very small seeds mature promptly in late spring and are released in early summer. Seeds from other mixedwood species (i.e. white birch, white spruce, cedar, and balsam fir) mature by early August, begin dispersing in late August, and have released about 90% of the crop by the late autumn (Greene et al. 1999).

Seed abscission and dispersal

Seeds of all boreal tree species are both released and dispersed by the wind (Greene et al. 1999). A decrease in moisture at the maturing abscission zone of the vascular bundle coupled with windy conditions promotes abscission. For conifers other than firs, low relative humidity differentially affects the two bands of fibres making up an ovulate scale and this leads to a flexing opening of the scales; thus exposing the winged seed to the wind (Dawson et al. 1997). Most white spruce seed abscission occurs from late August to mid-November although a small fraction continues to abscise in the winter

and spring (Greene et al. 1999). Thus some secondary dispersal of seeds occurs on snow rather than making direct contact with the forest floor.

Seed density on the ground in white spruce monocultures can vary temporally from year to year (2.5 - 4000 seeds/m²) and within a mast year (1000 - 4000 seeds/m²) (Nienstaedt & Zasada 1990). Stewart et al. (1998) suggested that in an intact aspen stand in Alberta, 500 or more white spruce seedlings will become established within about 80-100 m downwind and about 10 m upwind of the edge of a stand of white spruce. Greene and Johnson (1996) showed that by 200 m into a clearing (fire; clearcut; pasture) from the edge of a white spruce stand, the seedling or deposited seed density was only about 5% of what was found at the forest edge. This has led to recommendations that either clearcuts should be relatively small or that patches of seed trees should be left within cutover blocks (Greene & Johnson 2000).

There is presently no reliable basis on which to predict mast year occurrence. As mentioned earlier, we know only that a weather cue (dry, warm spring) in the previous spring prior to the year of seed abscission, should trigger a mast year in conifers (Koenig & Knops 2000). But it is not clear which specific period is important, and this would perhaps vary altitudinally and latitudinally for phenological (heat-sum) reasons. Although it would be possible to examine initiated buds in the late summer one year before a mast crop on a sample of felled trees, no one has ever taken advantage of this for predictive purposes. More typically, mast years are first noticed the year in which they occur. The most obvious first sign is the clusters of male cones in the middle third of the crown in late spring. Good correlation between male and female reproductive effort for both conifers and hardwoods in long-term Finnish studies (Koski & Tallquist 1978) may be

assumed to hold true for white spruce. There is a need for better predictability of mast years if foresters are to take advantage of the heavy seed fall by scheduling interventions such as seed tree retention, understory scarification or other site preparation treatments that could favour natural recruitment of white spruce. There are two principal factors governing the mortality of deposited seed and subsequent germinants: 1) granivory, and 2) abiotic factors (seedbed and/or establishment site qualities) (Greene & Johnson 1998). Pre-abscission granivores in the boreal include insects, rodents (squirrels, mice, voles, etc) and birds (especially the blackbird and finch families). Greene & Johnson 1998 reported pre-abscission losses of initially viable seeds for conifers average around 50%, but with immense variation from year to year. In Alberta, Peters et al. (2004) observed on control trees in forests adjacent to cutblocks on average about ~50% removal of white spruce cones by squirrels when the cone crops were largest, and ~58% removal when crops were at their smallest.

Germination requirements

Despite the potential of a good mast year to produce and disseminate large quantities of seed, this alone will not ensure adequate white spruce stocking if the right seedbed conditions are absent or if there is heavy competition from fast-growing vegetation. That is, in addition to a good seed supply, acceptable natural regeneration of white spruce requires a receptive seedbed, a suitable microclimate, and minimal competition from other vegetation (Lees 1972).

Usually some kind of ground disturbance is required to ensure proper soil conditions over a large area. Natural substrate disturbances may be caused by duff combustion as a result of fire, windthrow of trees during extreme wind events, animal digging, etc., all of which can potentially remove or reduce the duff layer, increase soil temperature, moisture and aeration, and remove competing vegetation (Sutton 1993).

These forest-floor disturbances occur episodically in the boreal forest (Greene et al. 2007). Especially important are large, high-intensity, stand replacing fires. Although highly variable, fire removes on average about 40% of the organic surface layer (Greene et al. 2007) and competing vegetation (although much of that can return quickly via suckering or sprouting from roots, stumps or rhizomes). Organic matter removal by fire is generally patchy: mineral soil is typically exposed near the bases of boles, but there is often only minor thinning (a few cm) of the duff in the inter-bole matrix (Greene et al. 2007). Thus, the post-fire forest floor of mixed boreal stands consists of small patches of well-combusted duff and a much thicker charred mat.

The best seedbeds for white spruce recruitment are mineral soil, very thin duff (a few cm thick), and decomposed wood because: (1) they are relatively free of competing vegetation and leaf litter, and more importantly, (2) are low-porosity substrates that can readily deliver water to the first few cm of the organic layer via capillarity (Harvey et al. 1978; Greene et al. 1999; Rowe 1955; Delong et al. 1997). Water availability in the upper 2 or 3 cm of the substrate is crucial to the subsequent survival of these small germinants. Stewart et al. (2001) found that white spruce was 10 times more likely to establish on exposed mineral soil or rotten logs than on undisturbed forest floor. Similar results have been found by Greene and Johnson (1998), Simard et al. (2003) and Delong

et al. (1997). Likewise, Wang and Kemball (2005) showed that exposed mineral soil was 19 times more receptive than undisturbed forest floor. They also showed that mineral soil provided the most stable soil moisture environment compared to any other seedbed type. Drier seedbeds are more deleterious for spruce than for balsam fir (Place 1995; in Wang & Kemball 2005). The larger size of balsam fir seeds may explain this species' higher threshold to germinant desiccation compared to spruce. Well-decomposed wood (fallen logs; stumps) can improve establishment of slower growing species such as white spruce by providing seedlings with an elevated position above competitive species (Harmon and Franklin 1989; in Stewart et al. 2001).

The quality of post-fire exposed mineral soil seedbeds diminishes steadily after fire (Purdy et al. 2002). Studies have found that following a fire, a good seedbed will offer a 3-5 year window for best recruitment of white spruce after which seedling establishment drops considerably (Purdy et al. 2002; Peters et al. 2005; but see Charron & Greene 2002).

Some studies have shown that overstory cover lowers surface soil desiccation and summer frost damage compared to open conditions (Von Sydow & Orlander 1994; Man & Lieffers 1999), implying that although white spruce might benefit from some extra light, too much opening of the canopy might be detrimental to juvenile survivorship. Certainly, white spruce densities on mineral soil in clear cuts are notoriously low (e.g. Lepage et al. 2000), presumably due to the lack of shading. Interestingly, Youngblood et al. (1991) found that seeds that land directly on mineral soil, in partially shaded microsites (e.g. next to a fallen branch, cone or bole) have the greatest probability of establishment and survival versus seeds deposited in open microsites.

Light is not a particular requirement in the germinant stage, as initial growth relies largely on seed reserves. Lieffers and Stadt (1994) state that light becomes a limiting factor affecting white spruce regeneration only at the subsequent seedling stage.

Within intact forest, the better seedbeds (exposed mineral soil, exposed humus, and well-rotted wood) are quite rare: typically 5% or less, with rotted wood accounting for the bulk of that coverage (Greene & Johnson 1998). Broadleaf litter is especially problematic as it not only dries out quickly but also can constitute a mechanical barrier for epicotyl elongation from below or radical penetration from above (Greene & Johnson 1998). Feathermosses on upland sites also dry out readily several days after the last rain.

Mineral soil exposed by disturbance from clear cut harvesting, and/or other mechanical techniques, has been shown to dramatically increase the number of naturally regenerated white spruce seedlings and to improve the survivorship of planted trees (Karlsson & Nilsson 2005). Silvicultural techniques used to create these seedbeds or microsites include disc trenching and mounding but, as mentioned, the enhanced quality of the seedbeds in clearcuts appears to be more than offset by the drying of the substrate due to the lack of even partial shade.

In natural conditions, snowfall pushes downward on the litter, crushing tiny germinants and seedlings of white spruce, and balsam fir (Gregory 1966; Waldron 1966; Delong et al. 1997, McLaren & Janke 1996). Wang and Kembell (2005) showed that when broadleaf litter is removed, overwinter mortality was reduced for both white spruce and balsam fir on undisturbed forest floor. Given that deep broadleaf litter is by far the major seedbed type within mature trembling aspen stands (>90%; Greene et al. 2007), it

is clear that removal of litter before and after the spruce cohort is established can contribute significantly to increasing the natural regeneration success of spruce.

Natural versus silvicultural disturbances

In the mixedwood region of Northwestern Québec, natural disturbances such as fire and insect outbreaks (particularly of spruce budworm (*Choristoneura fumiferana* (Clemens) and eastern tent caterpillar (*Malacosoma americanum* (Fabricius))), play an important role in shaping the forest landscape dynamics and mosaic. If aspen is present in a forest prior to a stand-replacing fire, root suckers will quickly exploit favourable light conditions, growing 1-2 m in the first few years, and tower over any tiny white spruce germinants and seedlings that might establish. Similarly, after forest harvesting, faster-growing shrubs (e.g. *Acer spicatum*, *Alder* spp., and *Rubus idaeus* L.) and tree species (e.g. *Papyrus tremuloides* and *Populus balsamifera*) often propagate over large areas. As a result, re-establishment of white spruce from natural regeneration alone is generally difficult after harvesting (Lees 1964; Steill 1976; Greene et al. 1999; Stewart et al. 2000). Planting white spruce after forest harvesting has proved to be fairly effective, particularly where herbicides are used against competitive species; but this is costly (Greene et al. 2002), and herbicide use in public forests of Québec has been banned since 2001. As a result, and true to the FEM principles, foresters are increasingly interested in developing new silvicultural and management approaches based on an improved understanding of natural ecosystem dynamics and processes, including regeneration processes.

Scarification

Scarification following even-aged forest harvesting creates, at least partially, conditions similar to those generated by disturbances, particularly by increasing exposure of the mineral soil seedbed. Therefore, improved recruitment is expected to result from scarification during a mast year. Mechanical scarification is usually done with heavy machinery, and includes mounding, disking, trenching and inverting, all of which have been associated with improved regeneration (Sutton et al. 1993; Lieffers & Beck 1994; Orlander et al. 1998; Hanssen et al. 2003). Inverting involves placing the humus layer at the bottom of furrows or pits and covering them with mineral soil. Mounding consists of the double action of first penetrating a mechanical shovel blade into the sub-surface mineral layers, then inverting the contents onto a mound. This creates both a pit of exposed mineral soil and an adjacent mound of mineral soil over the inverted humus layer. Scarification reduces advance regeneration (Bjorse 2000), which could be considered a net benefit as advance regeneration of white spruce is seldom dense.

Studies have shown significant enhancement of germinant and seedling establishment in cases where scarification preceded an abundant seed fall (Skoklefeldt 1995, Karlsson & Orlander 2000). Studying germination of white spruce following a mast year in 2002, Gielau (*2007-unpublished*) found far higher numbers of germinants in artificial pits and mounds created in the forest floor of a mixed spruce-aspen-jack pine stand than in unscarified (control) microsites. Eastham and Jull (1999) carried out patch scarification and disc-trenching of small patches and discovered higher numbers of

Engelmann spruce germinants (essentially the same species as white spruce) in a single tree retention cut versus a clear cut harvest treatment. Stewart et al. (2000) showed that strip scarification produced more seedlings than control plots following masting episodes. Like optimal seedbeds created by fire, freshly scarified patches do not maintain their desirable characteristics for long. They become shaded and cool, and the seedbeds generally become covered with broad leaves or mosses after one or two growing seasons (Pomeroy 1949; Winsa 1995). In summarizing the few North American studies of repeated sowing aimed at determining if first-year survivorship declined with time since scarification, Greene and Johnson (1998) concluded that seedbed remained useful for four years for small-seeded species, although this depended on the rate at which the leaf area index of hardwoods increased (Koroleff 1954; Bergsten 1988; Hytonen 1992). Similarly, Karlsson & Orlander (2000) and Orlander et al. (1996) concluded that the window for post-scarification regeneration was about three to four years long.

Some conflicting results appear between studies conducted during good seed years and low seed years. Eastham and Jull (1999) examined patch and selection cuts during a good seed year, and showed better regeneration compared to clearcuts. Karlsson and Nilsson (2005) showed that scarification and shelterwood treatments also fostered better germination and establishment during a good seed year. Further, Karlsson and Orlander (2000) found that germinant recruitment was increased considerably in situations where scarification immediately preceded an abundant seed fall. Karlsson et al. (2002) showed that mounding increased the density of birch and pine seedlings but did not cause a significant increase in Norway spruce density, probably because the study was conducted during a non-mast year for spruce.

These results lead to two approaches to the problem of using mast years to enhance white spruce regeneration. First, foresters could time scarification on *very small* cuts (thus obviating the dispersal constraint for the conifers) so that it occurs after the harvest but just before a masting episode. Second, understory scarification could occur in the summer just prior to the autumnal seedfall of a spruce mast crop, with harvesting occurring the first winter and germination the next growing season. Harvesting machinery would travel in between the well-marked scarification paths, previously established by a skidder. A variant on this second approach is that the harvest is delayed for several years so that initial recruitment cohort has time to develop into seedling- or sapling-sized advanced regeneration. This second approach should perhaps be avoided in dense aspen stands as the leaf fall in the *second* autumn after scarification will greatly reduce the size of the cohort.

Dynamics of white spruce with trembling aspen

In the boreal mixedwood forest of Abitibi-Temiscamingue, trembling aspen is one of the major competitors (and companions) of conifer species, including white spruce. While trembling aspen regenerates from root suckers following fire or logging (Perala 1990; Wang 2003), balsam fir and white spruce must reinvade fire-disturbed sites by seeding in from surviving residual trees within the disturbed area or from edges. Given that the shade-intolerant aspen suckers (clones) are very fast growing immediately after a canopy-replacing disturbance of harvest, the more slowly growing and more shade tolerant white spruce is invariably out-competed in the short-term as suppressed stems

under an aspen canopy (Lieffers & Stadt 1994). In addition to the white spruce regenerated immediately following disturbance, spruce can continue to recruit into a stand in pulses following subsequent mast year events, but in lesser numbers as seedbed quality generally deteriorates. Such late arriving spruce are usually found on the only available good seedbed: rotted wood (Stewart et al. 2001). Nonetheless, the number of spruce that establish long after a disturbance is usually much smaller than for the larger-seeded and much more shade tolerant balsam fir (Greene et al. 2002). Thus, suggestions such as those of these authors for a reliance on advance regeneration for post-harvest regeneration may be appropriate for fir but less so for white spruce, except perhaps in parts of western North America where white spruce advance regeneration is often quite dense under sparse aspen canopies. The deficiency of white spruce basal area in mixed stands of spruce and trembling aspen can result in a decrease in softwood production and annual allowable cut (Cumming et al. 2000).

Trembling aspen is harvested in northwestern Québec primarily for fabrication of oriented strand board (“chipwood”) and, until recently, laminated veneer lumber. Trembling aspen ceases net volume accrual and begins to undergo mortality from senescence generally from 60 to 100 years of age, whereas white spruce can still attain much more growth and survive well beyond this age (Cumming et al. 2000). In order to ensure a minimum of pole- to merchantable-sized spruce stems when the aspen component of a stand arrives at maturity, it is important that conifer recruitment occur early in stand development (Wang & Kembell 2005) and that stands containing aspen and spruce are harvested first for the aspen and later for the spruce..

White spruce and mixedwood management

Interest in establishing white spruce in the understory has grown recently as foresters imagine a genuine mixedwood silviculture (Lieffers et al. 1996). Considering both the difficulty and expense of plantation of white spruce in clearcuts, and the fact that white spruce regenerates naturally in the understory of aspen dominated stands, it would appear only logical that enhancement of natural regeneration under aspen be pursued as a silvicultural option. Semi-natural methods could be implemented in the boreal mixedwood forest to decrease regeneration costs and more closely align with forest ecosystem management “close to nature” principles (Lieffers et al. 1996). Moreover, it is possible that mixedwood-based management might even yield larger total stand volumes than pure stands (Kelty 1989; Légaré et al. 2004). Given the impressive recruitment of white spruce and balsam fir in 2007, this study will attempt to show the benefits of planning harvest cuts in the light of impending masting episodes.

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Chapter 2: The Seed Tree Retention Study

Introduction

White spruce (*Picea glauca* (Moench) Voss) is a commercially important and common species of the mesic, mixedwood boreal forest of the Abitibi Lowlands ecological region. Lacking asexual reproduction, soil or aerial seedbanks, or reliably dense seedling banks of advance regeneration, white spruce is generally difficult to regenerate to full stocking except by plantations (Lees 1964; Steill 1976; Greene et al. 1998; Stewart et al. 2000). Even with planting, obtaining adequate regeneration can be problematic (Lieffers et al. 1996). Moreover, planting is expensive (Greene et al. 2002) and herbicide use has been progressively phased out in Québec's crown forests; consequently, more emphasis is being placed on improving natural regeneration of white spruce, particularly as a result of increasing interest in both mixedwood and ecosystem management (Coates & Burton 1997; Harvey et al. 2002). In order for natural regeneration of white spruce to occur, four major conditions must exist, 1) a seed source within adequate dispersal distance of the seedbeds, 2) receptive seedbed evenly spaced across the area, 3) a favourable microclimate, and 4) minimal competition from other vegetation (Roe 1967; Lees 1972).

White spruce is a masting species, and produces large quantities of seed every 4-6 years (Stewart et al. 2000), with the intervening years yielding poor or virtually no cone crop (Coates et al. 1994; Nienstaedt & Zasada 1990). Even in a good seed year, the small seeds have very demanding seedbed requirements. Thin humus, leaf-free rotted wood, and exposed mineral soil are particularly good seedbeds (Zasada 1985; Coates et al.

1994; Delong et al. 1997; Greene & Johnson 1998; Wright et al. 1998) while broad-leaf and needle litter (Zasada 1985; Coates et al. 1994; Koroleff 1954; Simard et al. 1998) and deep feathermoss or thick organic substrate layers generally lead to very low recruitment (Nienstaedt & Zasada 1990; Delong et al. 1997; Charron & Greene 2002). It is assumed that, under natural conditions, dense white spruce cohorts are likely to occur only (1) when a mast crop is available soon after a wildfire before the favourable post-disturbance seedbeds are covered with plants, moss and leaf litter of the regenerating competitors (Purdy et al. 2002; Peters et al. 2005), or (2), in stands that have evaded fire for longer than the initially established trees' lifespan. In the latter situation, the moderately tolerant spruce germinant tends to establish on the rotted wood of fallen boles derived from long-fallen burnt stems or downed stems of the post-fire cohort (Purdy et al. 2002).

Decomposing wood offers stable moisture conditions (Day 1963; Harvey et al. 1978) and, because it is generally elevated, hardwood leaves that might smother the tiny (2 cm tall) spruce germinants do not generally accumulate (Koroleff 1954; Rowe 1955; Waldron 1966; Harmon & Franklin 1989; Delong et al. 1997). Another excellent seedbed is exposed mineral soil which favours seedling establishment by allowing rapid development of roots in a matrix with stable moisture availability (Winsa 1995; Delong et al. 1997; Karlsson & Orlander 2000; Wurtz & Zasada 2001; Hanssen et al. 2003). In an intact forest, rotted fallen logs are common whereas exposed mineral soil is quite rare except for sites exposed by episodic disturbances such as blow down, widespread animal burrowing, and wildfires (Delong et al. 1997).

Within clearcuts, many studies have shown that exposing mineral soil via site scarification significantly enhances the recruitment of white spruce compared to an

undisturbed organic layer (Winsa 1995; Karlsson & Orlander 2000; Hanssen et al. 2003; Wurtz & Zasada 2001). Nonetheless, exposed mineral soil, rotted wood, and thin humus in clearcut conditions result in much lower survivorship than their analogues in intact or post-fire stands because of, it is presumed, the lack of shading (higher summer soil temperatures and associated risk of desiccation) (Mullin 1963; Vyse 1981; Burdett et al. 1984). Both balsam fir and white spruce are linked with substrates where competition is low and moisture is abundant (Simard et al. 1998).

Aspen is typically a codominant species in early succession mixedwood stands. It regenerates prolifically through vegetative root sprouts, or suckers. Because of the reliable suckering (asexual regeneration via near-surface roots) of aspen (the typical codominant species of southern boreal mixedwood stands) in a recently burned or harvested area, the more tolerant and slow growing species such as white spruce often begin under a soon-dominant aspen cohort (Rowe 1955; Lieffers & Stadt 1994; in Stewart et al. 1998). Conventional management practices force another dynamic (at great expense) with mixedwood stands : white spruce is planted and herbicides are applied to aggressive competition from aspen and other hardwood shrubs.

In the context of mixedwood management, forest managers should take into account the natural dynamics between trembling aspen as the dominant canopy occupant, and the understory component of white spruce and (the less desirable) balsam fir. Seed tree retention harvesting, a variant of the traditional clear cut (Sullivan et al. 2001), retains a certain number of fairly evenly distributed mature stems of desired species that will then serve as seed sources for naturally regenerating a harvested site (Smith 1986; Coates et al. 1994; Lieffers & Beck 1994; Lyon & Robinson 1977). Combined with a

scarification treatment to increase the proportion of favourable seedbed, this approach can potentially increase natural regeneration to full stocking levels. Seed trees if not ulteriorly harvested, may also increase in structural diversity (Smith 1986) and serve other ecological functions.

One obvious possibility for the natural regeneration of white spruce would be to scarify a stand (perhaps 20% total coverage on the ground) just prior to a mast year. Nienstaedt & Zasada (1990) reported seed deposition ranges from 1000 to 4000 seeds/m² during mast years in white spruce-dominated stands, more than enough to supply high seed densities on scarified paths with fewer recruit numbers in the inter-path areas. Even if harvesting reduced residual tree density to 10% of its basal area/area—or with a mixed stand where spruce comprised about 10% of the basal area/area—a mast year still ought to provide 100-400 seeds/m² (Quaite 1956; Ball & Walker 1995; Stewart et al. 2000), which would barely provide for full stocking (Greene et al. 2002).

Mechanical scarification is a generally used in the boreal forest to assist artificial regeneration of harvested areas. A variety of machines exist but all are designed to move wood debris and organic layers and expose mineral soil, to favour site conditions for planting or seeding. The exposed mineral soil substrate has, relative to most other seedbeds, 1) greater surface soil moisture availability (Oleskog 1999), 2) higher soil temperature (Eastham & Jull 1999; Burgess et al. 1995), 3) greater nutrient availability (Dryness et al. 1998), and 4) reduced (at least for awhile) competing vegetation (Nilsson & Orlander 1999). It is no surprise therefore that understory scarification in a mast year has attained full stocking standards in most studies conducted thus far (Lees 1963, 1970; Skoklefeldt 1985; Desjardins 1988; Anon 1995; Eastham and Jull 1999; Stewart et al.

2000). It should be noted however that all of these examples have been simple field experiments rather than operations at the scale of a harvest block. Likewise, European shelterwoods coupled with scarification have often been successful in regenerating Scots pine (*Pinus sylvestris*); European beech (*Fagus sylvatica*) (Hagner 1962; Beland et al. 2000; Karlsson & Orlander 2000; Agestam et al. 2003; Karlsson & Nilsson 2004); and Norway spruce (Holgen & Hanell 2000; Nilsson et al. 2002).

Study Objectives

This study aims to answer the following questions: Given various silvicultural treatments following a seed-tree retention cut during a mast year, (1) Which substrate types (rotted wood, mineral soil, moss, humus, needles & fibric mix) are best for white spruce germination and first year germinant survival? 2) Which treatments (control, chipped, scarified, chipped and scarified) produce the greatest proportion of the best seedbed types, and therefore the best recruitment of white spruce? 3) How does age-specific survivorship vary by seedbed? 4) Can we devise a formula to predict the number of germinants as a function of source strength (using seeds/m² or as proxy residual basal area/area), and optimal substrate type and proportion? 5) What percentage of seed trees will succumb to windthrow? 6) How can foresters incorporate specific harvesting and site preparation treatments into their planning for sites with white spruce regeneration potential when mast years are not easily predicted? Although I focus on the more valuable white spruce, the recruitment of balsam fir will also be examined.

Study Area

This study was conducted in the 80 km² Lake Duparquet Research and Teaching Forest (FERLD is the French acronym) in the Abitibi region, situated approximately 45 km northwest of Rouyn-Noranda (48 30' N, 79 20'W, altitude ca. 300 m). A mosaic of deciduous, mixed and coniferous stands characterizes this portion of Abitibi. The study area is located within the western balsam fir-white birch bioclimatic subdomain of the boreal forest (Robitaille & Saucier 1998). Balsam fir (*Abies balsamea* (L.) Mill) is the dominant species in mature forests and is associated with white spruce (*Picea glauca* (Monech) voss), trembling aspen (*Populus tremuloides* Michx.-especially in younger stands), and paper birch (*Betula papyrifera* Marsh) (Harvey et al. 2002). Grey Luvisol formed in glaciolacustrine clays are the dominant soil type in the region (Vincent & Hardy 1977). The mean annual precipitation is 828 mm, and mean annual temperature is 0.6° C, with a mean frost-free period of 64 days (Environment Canada 1982).

The stands used in the seed tree retention cut originated from a fire in 1760 and were seriously affected by the last spruce budworm outbreak (1970-1987). This disturbance, resulting in extensive fir mortality, left open stands dominated by residual white spruce, birch, aspen, and cedar, and a regeneration layer composed predominately of previously-suppressed balsam fir. As these soils are quite productive, they are characterized by heavy vegetative competition, which quickly reappears after cutting. Some dominant shrub species are mountain maple (*Acer spicatum* (Lamb)), hazelnut (*Corylus cornuta* Marsh.) speckled alder (*Alnus rugosa*), Viburnum (*Viburnum* spp.),

raspberry (*Rubus idaeus* L.), and willow (*Salix*) species. The main herbaceous species are wild sarsaparilla (*Aralia nudicaulis* L.), touch-me-not (*Impatiens capensis*), and broad-leaved aster (*Aster macrophyllus* L.)

Methodology

Harvesting Treatment

Stands in the study area were harvested using a seed-tree retention system in the winter of 2005-06 prior to the extraordinarily large seed crop that matured in late August 2006. The cut was replicated three times in three separate blocks. The surface areas of the scarification treatment (parcels within) blocks varied (Table 2.1). Approximately 25 mature white spruce seed trees per hectare were left, roughly evenly dispersed through the cutovers, to act as seed sources. Several mature stems of other species (i.e. eastern white cedar, balsam fir, white birch) were left standing as well.

Table 2.1: Approximate surface area (m²) of treatment with the three blocks.

Block	Treatment	Approx. Surface Area
		m ²
1	Control	2975
	Chipped	4830
	Scarified	3825
	Chipped & Scarified	4365
2	Control	5000
	Chipped	5395
	Scarified	5375
	Chipped & Scarified	4612.5
3	Control	5750
	Chipped	4500
	Scarified	4025
	Chipped & Scarified	4600

As shown in Table 2.2, basal area per area (m^2/m^2) differed little among treatments for white spruce. Balsam fir basal area per area measurements were smaller than white spruce and varied far more among the treatments; there was almost an order of magnitude difference in basal area per area. Basal area per area was calculated with this formula:

$$\text{BA/A} = \frac{\pi r^2}{\text{area of treatment}}, \text{ where } r = \text{DBH (diameter at breast height in cm)} / 200.$$

Table 2.2: Total basal area/area (m^2/m^2) measurements (multiplied by 10 000) of white spruce and balsam fir in each treatment within each block.

Block	Treatment	BA/A	
		White Spruce	Balsam Fir
1	Control	3.4001	0.5072
	Chipped	2.3256	0.0000
	Scarified	2.9591	0.0403
	Chipped & Scarified	2.6684	0.0000
2	Control	0.7333	0.1630
	Chipped	3.0510	0.0306
	Scarified	0.6114	0.3195
	Chipped & Scarified	2.0395	0.1788
3	Control	1.5206	0.0883
	Chipped	1.6345	0.0671
	Scarified	0.7903	0.0677
	Chipped & Scarified	1.1008	0.1974

Site-preparation Treatments

Three site preparation treatments were applied in the summer of 2006 in each of three blocks in a complete block design: 1) chipping, 2) disk trenching scarification, and 3) chipping followed by disk trenching. The harvest treatment in winter 2005-06 with no subsequent site preparation was the fourth (control) treatment of the experiment. The chipping treatment was applied in July 2006, and the disk scarification in August 2006. Both treatments occurred before the onset of the mast crop abscission season in late August 2006. The chipping was done by a horizontally mounted chipper on an excavator. This treatment chipped all standing live and dead vegetation (small, residual trees and woody shrubs) and harvest debris down to the soil, without actually making direct contact with the surface organic layer. Disk trenching in each of the three blocks was done with a Donaren scarifier mounted behind a skidder; and consisted of two rotary disks penetrating into the mineral layer, turning over the organic surface layer, exposing mineral soil and mixing the mineral and organic layers in two parallel furrows with each pass of the machine. It was assumed that chipping prior to disk trenching—the combined treatment—would improve the action (and effect) of the trenching alone, by reducing the quantity of coarse woody stems, branches and dead wood that otherwise reduced the capacity of the disks to penetrate into and mix the soil layers. The control treatment consisted merely of the harvesting and, as such, had a relatively heavy cover of understory shrubs in 2006 and 2007 compared to the other treatments.

Seed Rain Monitoring

To obtain an estimate of the seed rain during the 2006 mast year, 16 mesh (opening = 1.7 mm) and wood seed traps, each 0.5m² in area and elevated 0.7 m above the ground, were placed within each block, (4 traps/treatment/block), for a total of 48 traps. Trap contents were collected five times during the non-winter months: September 21, 2006, November 1, 2006, May 2, 2007, July 14, 2007, and December 8, 2007. Trap contents were dried after each collection and white spruce, white birch, balsam fir, and white cedar seeds and spruce cones were counted. Seeds easily dislodged from intact cones found in traps were counted as well. Predator proof/exclusion measures were not taken into account in the design of the seed traps.

Germinant, vegetation and substrate inventories

The first germinant recruitment census was conducted in August 2007. Three transects 20.5 m long and 1 m wide were established within each treatment (in each block). To avoid a bias with the microtopography created by the Donaren scarifier, transects were positioned perpendicular to the furrows created by the machine. Transect starting and ending points within each treatment were chosen using a random numbers table, and identified with wooden stakes. In all, 36 transects were established in the three blocks combined. At every 0.5 m point along transects, the type of substrate and depth was noted, and the number of layers of broad leaves was determined by vertically skewering the ground surface and then counting the number of leaves. Within each consecutive 0.5 m² area along the transects, the number of germinants (white spruce and balsam fir) and the number of white spruce cones were counted. The substrate type in

which each germinant was growing was also noted. In addition, the percent cover of vegetation types (e.g.: mountain maple, raspberry, beaked hazelnut, alder) and the relative abundance of mineral soil and decomposed wood visible on the ground was recorded as: class 1 (present below 5 % cover), class two (5-25%), class three (26-50%), class four (51- 75%), and class five (76-100%).

First year, over-winter survival of germinants was monitored using another set of transects in June of 2008 under the assumption that germination occurring within the 2007 transect areas would be the same 5m away within the same treatment. With the exception of vegetation cover and cone count, the same inventory was conducted as in 2007 only rather than three transects, two new transects were run per treatment per block.

Data Analysis

Effects of treatment on substrate types

To assess how post-harvest site preparation treatments affected seedbed conditions, the proportions of each substrate type were compared among treatments. The proportion of each substrate type was first calculated by combining the number of uniform points characterizing that type along a transect, and then dividing it by the total points (N=42) distributed uniformly along the transect. By lumping blocks together, this gave 9 measurements of substrate type abundance for each treatment (N=36, 3 transects per treatment x 3 blocks x 6 substrate types).

The main substrate types encountered were mineral soil, sod (in the form of thick mats of dead vegetation or plant roots moved about by machinery), Oh (humus), fibric substrate type (F), decomposed wood, firm wood, moss, decomposing leaves, a thin layer of moss on decomposing wood, a mixture of needle litter and fibrous duff, and a mixture of disintegrated woody material and fibric humus substrate type. The F is part of the O (organic) horizon and is characterized by the presence of filamentous fungi, and the accumulation of partly decomposed material (i.e. twigs, roots, woody substances, etc.). Humus (located underneath F) is also part of the O horizon, but is characterized by unrecognizable, decomposed organic matter. The substrate type 'fibric humus' represents the mixing of both layers. Because 'thin moss on decomposed wood' was very infrequently observed, it was lumped with the type 'decomposed wood'. Similarly, 'decomposing leaves', mixture of 'disintegrated woody material and fibric humus', and 'sod' were lumped with humus. For simplicity, 'F' which was lumped with 'needle &

humus mix' was not considered in our analyses due to the relatively low recruitment numbers in summer of 2007. Rare and lethal substrate types (i.e. water, rocks) were eliminated from the analyses.

Separate model I one-way ANOVAs were used to determine differences in substrate type proportions (mineral soil, decomposed wood, humus, firm wood and moss) between the different treatments. Post-hoc Tukey (HSD) tests were performed to determine which treatments differed significantly from one another for each substrate type. All statistics were performed using SPSS (version 10.1) except for the post hoc Tukey tests for adjusted densities and for the multiple regression analyses, which were conducted with JMP (SAS version 7). Due to a well-balanced experimental design, all statistical tests in this study were performed assuming that the possible violations of the assumptions of normality do not have serious consequences on the legitimacy of probability statements (Glass 1972). In this study, non-parametric tests gave similar probability values to the parametric tests. Therefore, we chose to report the results from the parametric tests only.

Effects of substrate type (and treatment) on germinant and first year seedling densities

The number of germinants per each substrate type was summed for transects. Due to a relatively low abundance or poor quality (or both combined), substrate types which showed low germinant recruitment numbers (needle & humus mix, moss and firm wood) were not analyzed. Consequently, the effects of optimal seedbed types (mineral soil, decomposed wood and humus) on white spruce and balsam fir germinant and first year seedling densities were analyzed using two way ANOVAs with replication, separated by

treatment (N=108 for germinants; N=72 for seedlings). Post-hoc Tukey tests determined which substrate types differed significantly from one another, in each treatment. Balsam fir average seedling densities were transformed with the log function prior to the ANOVA test.

Effects of treatment on germinant recruit densities

Average densities of white spruce and balsam fir germinants were first transformed with the square root function to better meet assumptions of normality. One way ANOVAs were then performed to determine differences between treatments (N=36) followed by a post-hoc Tukey test which determined which treatments differed significantly from one another.

Regardless of the differences in recruitment success on each substrate type, and the varied proportions of substrates within each treatment, the best treatment scenario ought to have the greatest recruit density or (similarly) the best stocking value (*see* definition: Helms 1998). The stocking of white spruce and balsam fir was assessed by grouping 8 half-meter squared (0.5 m^2) consecutive units in the transect data to create the (Québec) softwood regeneration of standard 4 m^2 . Note that these 4 m^2 areas were not shaped like standard regeneration inventory plots. In Québec, “full stocking” has been defined as an area with greater than 60% stocked plots (with a stocked plot defined as one containing at least one stem of a commercially valuable species) (Greene et al. 2002). Although both white spruce and balsam fir are merchantable species, we will estimate stocking separately for the two species.

Effect of treatment on adjusted germinant densities

In order to properly assess a seedbed type's success in recruiting germinants, it does not suffice to simply compare total germinant numbers between each seedbed type, considering that the quantity of each seedbed type varies. Densities were therefore adjusted to take into account the relative abundances of each substrate type. That is,

$$D_i = N_i N_{ui} / (A_t N_u)$$

where D_i is the adjusted density (germinants per m^2 on the i^{th} seedbed type), N_i is the number of recruits found on that type, N_{ui} is the number of uniform points of that type, A_t is the total area (m^2) examined along the transect, and finally N_u is the total number of uniform points (any seedbed type) found along the transect. These adjusted densities were transformed by rank averaging, and then one way ANOVAs were used to determine treatment (N=36) and substrate type (N=108) differences. If there was a significant effect, post-hoc Tukey (HSD) tests were performed. Note that these adjusted densities will be directly proportional to the survivorship from seed to germinant as long as one can assume that seed densities did not vary as a function of seedbed type. This assumption is reasonable given the even distribution of seed trees spread out in the study blocks.

Effect of treatment and substrate types on survivorship

The survivorship for seedlings on seedbed i was calculated by dividing the total number of seedlings (2008) by the total number of germinants found growing in the same seedbed type in 2007. One way ANOVAs were then used to compare survivorship between substrate types (N=72) and between the different treatments (N=24). Similarly, post hoc Tukey tests were performed if the F statistic was significant.

Effects of treatment on seedling densities

A one way ANOVA was used to determine differences in spruce and fir seedling densities (assessed in summer 2008) between treatments. A post-hoc Tukey test was used to determine which treatments differed significantly from each other.

To analyze the extent of over-winter mortality of germinants, comparisons were made between the number of germinants recruited in 2007 and seedling numbers of the same cohort present in 2008 by using students T-tests.

Seed rain assessment

The rate of seed fall was derived by dividing the average number of seeds/m² by the number of days elapsed since the start of the masting period (~ August 21, 2006 for batch one) or the days elapsed since the first collection date (for batch two). To determine whether seed rain densities differed significantly between treatments and blocks, a two way ANOVA (random block) was performed (N=12). Also, Spearman correlations were conducted to test relationships between BA/A and seeds/m² for white spruce and balsam fir (N=12). A positive correlation between seeds/m² and BA/A (both are estimates of seed crop size) would indicate that basal area could be used as a proxy for seed trap data to estimate seed rain.

Recruitment models

The following predictors of recruit density were inputted into a multiple regression model using the stepwise regression function in JMP (SAS) software:

seeds/m², basal area per area, and the product of the proportion of optimal seedbeds (p) with basal area per area or seeds/m² (p * BA/A or p * seeds/m²). The proportion of optimal seedbed was formulated by counting the number of uniform points characterizing non-optimal (fresh leaf litter and sod) and lethal substrate types (rocks, water, and firm wood) and by subtracting that figure from the total number of sampled points in each treatment to arrive at the remaining proportion of optimal seedbeds. These included: mineral soil, decomposed wood, humus, moss, moss on decomposing wood, decomposed wood & fibric mix, F and 'needle & humus mix'. Because the variables (seeds/m²), and BA/A are both estimators of potential seed input into the system, it may be considered redundant to use both in the regression model.

Results

Effects of treatment on substrate types

The abundance of the different substrate types, particularly mineral soil, varied between treatments (Figure 2.1). A one way ANOVA indicated a significant difference in mineral soil availability between the treatments ($F=8.502$, $df=3, 32$, $p<0.001$). Post-hoc Tukey tests revealed that the scarified treatment showed significantly greater proportions of mineral soil than both the control ($p<0.001$) and chipped ($p=0.002$) treatments. Similarly, the chipped & scarified treatment also showed greater mineral soil availability than both the control ($p<0.001$) and chipped ($p=0.004$) treatments. While mineral soil accounted for 25% in the chipped & scarified treatment, this was not significantly different from the mineral soil present in the scarified treatment (12%; $p=0.994$).

The proportion of firm wood also differed significantly between treatments ($F=6.387$, $df=3,32$, $p=0.002$): the chipped treatment contained significantly more of this lethal substrate type compared to the control ($p=0.001$), scarified ($p=0.19$), and chipped & scarified ($p=0.036$) treatments. The quantity of decomposed wood did not differ significantly between treatments ($F=2.862$, $df=3,32$, $p=0.052$).

The proportion of humus, which included decomposed leaves (especially abundant in the control) differed significantly between treatments ($F=12.395$, $df=3,32$, $p<0.001$), with the control treatment showing significantly more amounts than the scarified ($p<0.001$), chipped ($p=0.010$) and chipped & scarified ($p<0.001$) treatments. Proportions did not significantly differ between the chipped and both the scarified and chipped & scarified treatments ($p>0.05$).

The availability of moss also significantly differed between treatments ($F=8.767$, $df=3,32$, $p<0.001$). The Tukey analyses revealed that the only significant differences occurred between the control and both the scarified ($p<0.001$), and chipped & scarified ($p=0.001$) treatments.

Disk trenching had a positive effect in exposing mineral soil; this is evident looking at the large amounts of mineral soil available in the scarified (12%) and chipped & scarified (25%) treatments, and thus the significantly lower mineral soil availability present in the non-scarified scenarios: the control (0.5%) and chipped (6.6%) treatments.

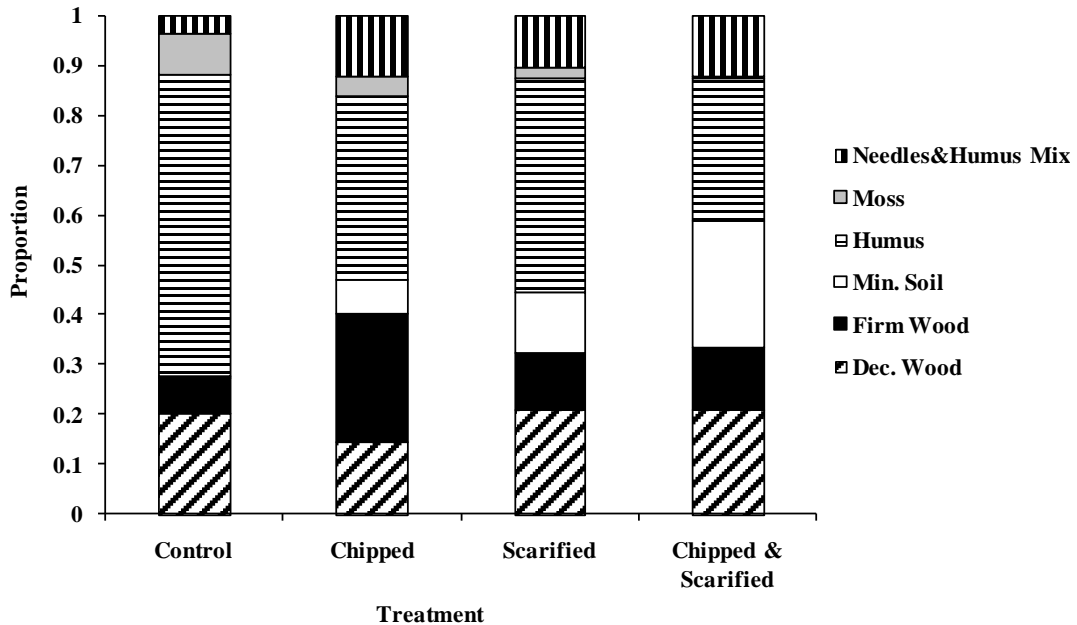


Figure 2.1: Proportions of substrate types (N=36) in each treatment.

Effects of treatment and substrate type on germinant and first year seedling densities

White Spruce

There were significant effects of both treatment ($F=9.671$, $df=3$, $p<0.001$; Figure 2.2) and substrate type ($F=3.748$, $df=2$, $p=0.027$) on white spruce germinant densities. A significant interaction between treatment and substrate type ($F=2.424$, $df=6$, $p=0.032$) implies that the recruit success on different substrate types was contingent on the type of treatment applied. The effect of treatment on white spruce seedling densities was also significant ($F=3.677$, $df=3$, $p=0.017$; Figure 2.3), although substrate type had no significant effect on seedling densities ($F=2.745$, $df=2$, $p=0.072$). In addition, there was no significant interaction ($F=0.899$, $df=6$, $p=0.502$) between treatment and substrate type on the survivorship of spruce seedlings into summer 2008. Substrate type seems not to have any effect on survivorship; rather other factors (i.e. light availability) may be involved.

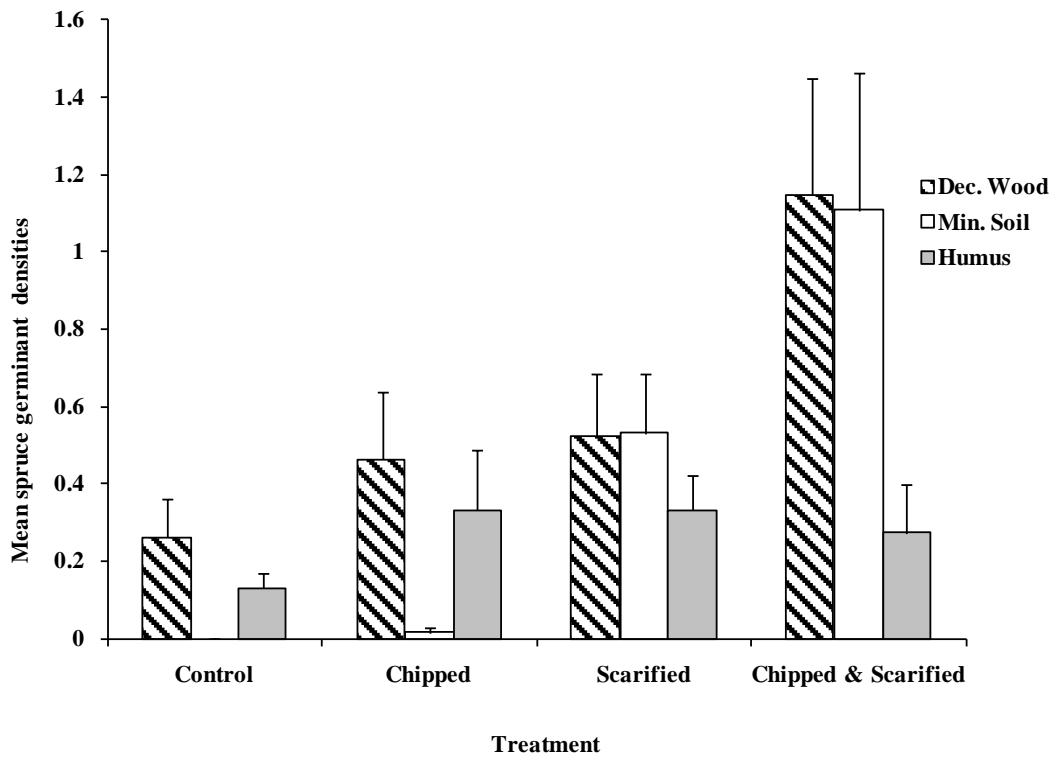


Figure 2.2: Means (per m²; with mean standard error (SE) bars) of white spruce germinant densities (N=36) in decomposed wood, mineral soil, and humus, per treatment.

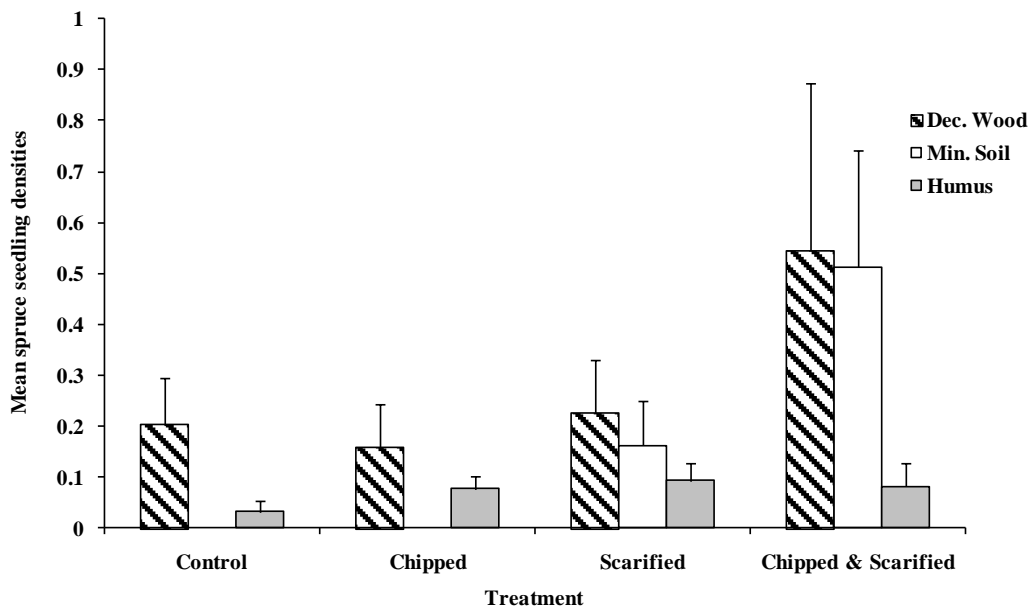


Figure 2.3: Means (per m²; with mean standard error (SE) bars) of spruce seedling densities (N=24) in decomposed wood, mineral soil and humus, per treatment.

Post hoc Tukey tests on treatment effects showed that germinant densities differed significantly between the control and chipped & scarified treatments ($p < 0.001$); the scarified and chipped & scarified treatments ($p = 0.040$); and between the chipped and the chipped & scarified treatments ($p = 0.001$). There was no significant difference in spruce germinant recruit densities between the control and scarified ($p = 0.091$). Interestingly, there were no significant differences in spruce seedling densities in 2008 (Figure 2.3) between any treatments, with the exception of the control and chipped & scarified treatments ($p = 0.028$).

Post-hoc Tukey analyses on substrate type revealed that decomposed wood and humus had significantly different spruce germinant densities ($p = 0.020$), while the differences were not significant between mineral soil and decomposed wood ($p = 0.282$), and mineral soil with humus ($p = 0.455$). Finally, there were no significant differences in spruce seedling (Figure 2.3) densities between substrate types (*all* $p > 0.05$).

Balsam Fir

While there was a significant effect of substrate type on the densities of balsam fir germinants ($F = 5.809$, $df = 2$, $p = 0.004$; Figure 2.4), there was no significant effect of treatment ($F = 1.346$, $df = 3$, $p = 0.264$). There was barely a significant interaction between treatment and substrate type on fir recruit densities in 2007 ($F = 2.199$, $df = 6$, $p = 0.050$). There was no significant effect of either treatment ($F = 0.056$, $df = 2$, $p = 0.949$) or substrate type ($F = 1.028$, $df = 3$, $p = 0.402$) on fir seedling survivorship in 2008 (Figure 2.5); nor was

there a significant interaction between treatment and substrate type ($F=0.228$, $df=6$, $p=0.919$). Post-hoc Tukey tests revealed that there were no significant differences in balsam fir germinant recruit densities, nor on fir seedling survivorship, between all treatments (*all* $p>0.05$).

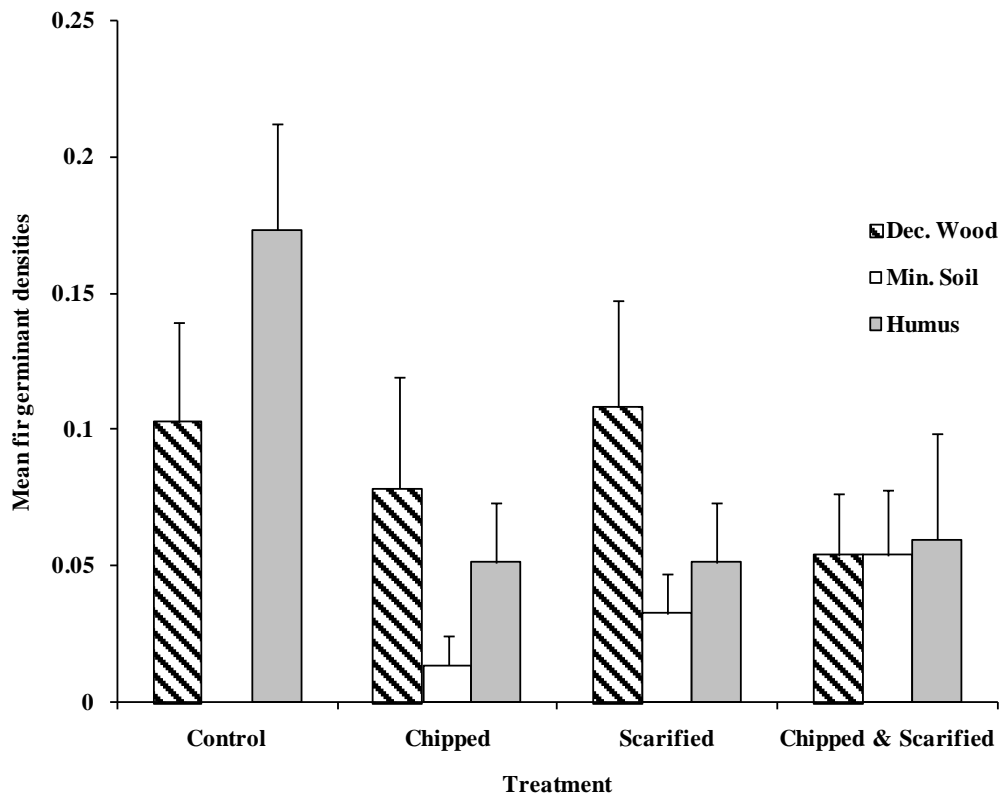


Figure 2.4: Means (per m²; with mean standard error (SE) bars) of fir germinant densities (N=36) in decomposed wood, mineral soil and humus, per treatment.

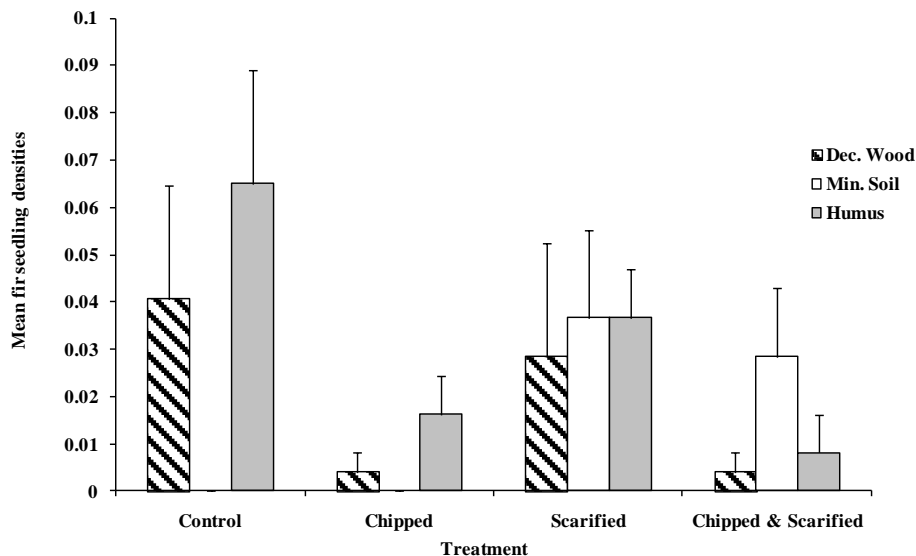


Figure 2.5: Means (per m²; with mean standard error (SE) bars) of fir seedling densities (N=24) in decomposed wood, mineral soil and humus, per treatment.

Post-hoc Tukey tests revealed significant differences in balsam fir germinant recruit densities between decomposed wood and mineral soil ($p=0.01$), and between mineral soil and humus ($p=0.013$). There was no significant difference between humus and decomposed wood ($p=0.995$). Regarding fir seedling densities, there were no significant differences between the three substrate types (*all* $p>0.05$).

Effects of treatment on overall germinant recruit densities

White Spruce

A one way ANOVA on the square root- transformed spruce germinant data showed that the treatments differed significantly in their spruce germinant densities (Figure 2.6; $F=12.168$, $df=3,32$, $p<0.001$). Post-hoc Tukey tests showed that white

spruce germinant densities differed significantly between the control and scarified ($p=0.007$); and the chipped & scarified ($p<0.001$) treatments. There were no significant differences in spruce germinant densities between the scarified treatment with the chipped ($p=0.278$) and likewise with the chipped & scarified ($p=0.135$) treatments. The chipped & scarified treatment showed significantly greater spruce germinant numbers than the chipped treatment ($p=0.002$) and control treatment ($p=0.000$). While the control treatment was also significantly different from the scarified treatment ($p=0.007$), it did not differ significantly from the chipped treatment ($p=0.351$).

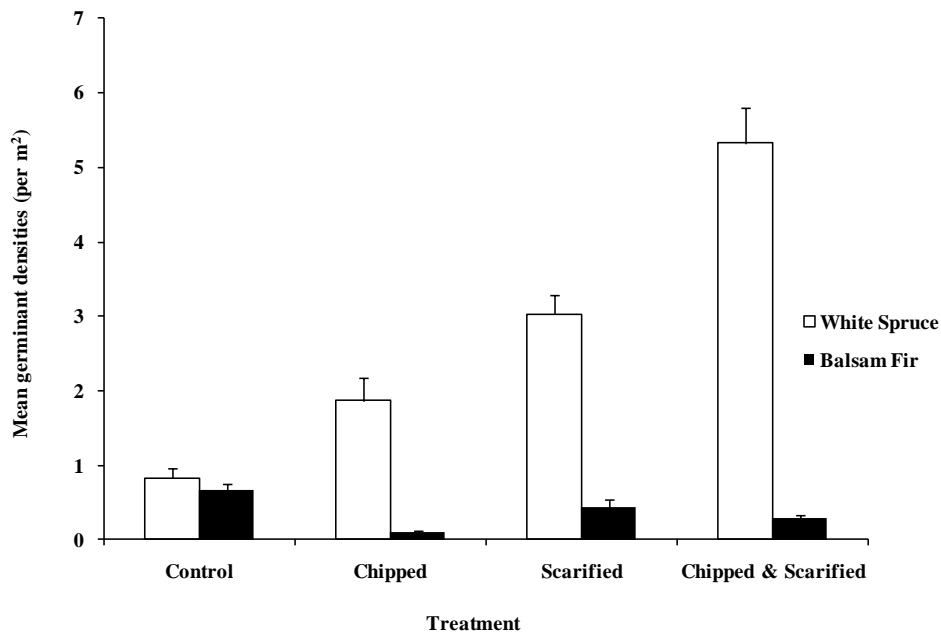


Figure 2.6: Mean densities (per m²; with mean standard error (SE) bars) of white spruce and balsam fir germinants (N=36) per treatment in 2007.

Balsam Fir

A one way ANOVA on square root-transformed germinant densities showed significant differences between treatments (Figure 2.6; $F=10.11$, $df=3, 32$, $p=0.018$). Post hoc tests showed that fir densities were significantly different between the control and chipped treatments ($p=0.001$) and between the scarified and chipped treatments ($p=0.049$). While the control treatment had greater fir densities than the other treatments, it did not differ significantly from the second best treatment (scarified, $p=0.485$).

Effects of treatment on adjusted germinant densities

White Spruce

The chipped & scarified treatment showed the greatest mean adjusted spruce density (Figure 2.7) in decomposed wood ($13.7/m^2 \pm 3.9$), followed by the chipped treatment ($6.9/m^2 \pm 2.5$) and the scarified treatment ($3.6/m^2 \pm 0.8$). Adjusted densities for decomposed wood differed significantly between treatments ($F=3.456$, $df=3,32$, $p=0.0278$). A Tukey test revealed that the control was significantly different from the chipped & scarified treatment ($p<0.05$). Although the chipped & scarified treatment had the greatest adjusted density of the four treatments, it did not have significantly greater densities than the chipped or scarified treatments. The greatest mean adjusted spruce densities in mineral soil occurred in the scarified treatment ($11.7/m^2 \pm 5.9$), followed by the chipped & scarified treatment ($7.9/m^2 \pm 1.3$). Densities in mineral soil also differed significantly between treatments ($F=39.422$, $df=3,32$, $p=0.001$). Although there was no

significant difference between the scarified and chipped & scarified treatments ($p=0.145$) these two differed significantly from the control and chipped treatments (*all* $p<0.05$). There was no significant difference between the control and chipped treatments ($p=0.456$). With regards to humus, the greatest densities occurred in the scarified treatment ($7.1/m^2 \pm 2.8$). White spruce adjusted densities growing in humus differed significantly between treatments ($F=3.0989$, $df=3,32$, $p=0.0409$). A post hoc Tukey test indicated a significant difference between the control and scarified treatments ($p=0.0451$).

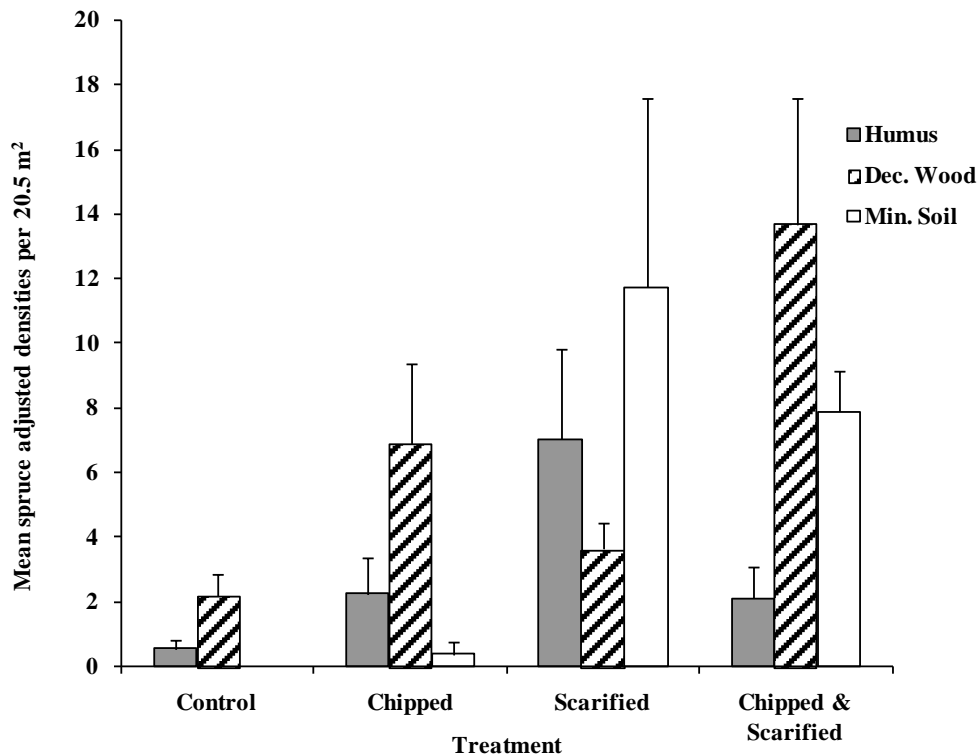


Figure 2.7: The mean adjusted densities (with mean standard error bars (SE) per 20.5 m²) of white spruce germinants growing in each substrate type, in each treatment (N=36). Adjusted density = (no. germinants in seedbed i * total no. uniform points) / (total transect area*uniform points of seedbed i).

Balsam Fir

The mean fir adjusted densities for decomposed wood were found greatest in both the control ($1.1/\text{m}^2 \pm 0.4$) and chipped ($1.0/\text{m}^2 \pm 0.4$) treatments (Figure 2.8), while densities were smaller in the scarified ($0.6/\text{m}^2 \pm 0.2$) and chipped & scarified ($0.4/\text{m}^2 \pm 0.2$) treatments. Fir densities were generally low and there was no significant difference between treatments ($F=0.882$, $df=3, 32$, $p=0.460$). The greatest densities of fir in mineral soil occurred in the scarified treatment ($1.1/\text{m}^2 \pm 0.4$), followed by the chipped & scarified treatment ($0.4/\text{m}^2 \pm 0.2$). Overall, there was a significant difference in densities in mineral soil between the treatments ($F=4.160$, $df=3,32$, $p=0.0135$). A post-hoc Tukey test revealed a significant difference between the control and chipped & scarified treatments, and likewise between the control and the scarified treatments (*all* $p<0.05$). Similarly, the chipped treatment differed significantly from the scarified and chipped & scarified treatments ($p=0.005$). No germinants were surveyed on mineral soil in the control or chipped treatment, while there was no significant difference between the scarified and chipped & scarified treatments ($p=0.084$). Overall, the greatest adjusted densities occurred in humus, and particularly in the scarified treatment ($1.3/\text{m}^2 \pm 0.9$), followed by the control ($0.7/\text{m}^2 \pm 0.3$). There was no significant difference between treatments with regards to adjusted densities of balsam fir growing in humus ($F=1.415$, $df=3,32$, $p=0.256$), and in decomposed wood ($F=0.646$, $df=3,32$, $p=0.591$).

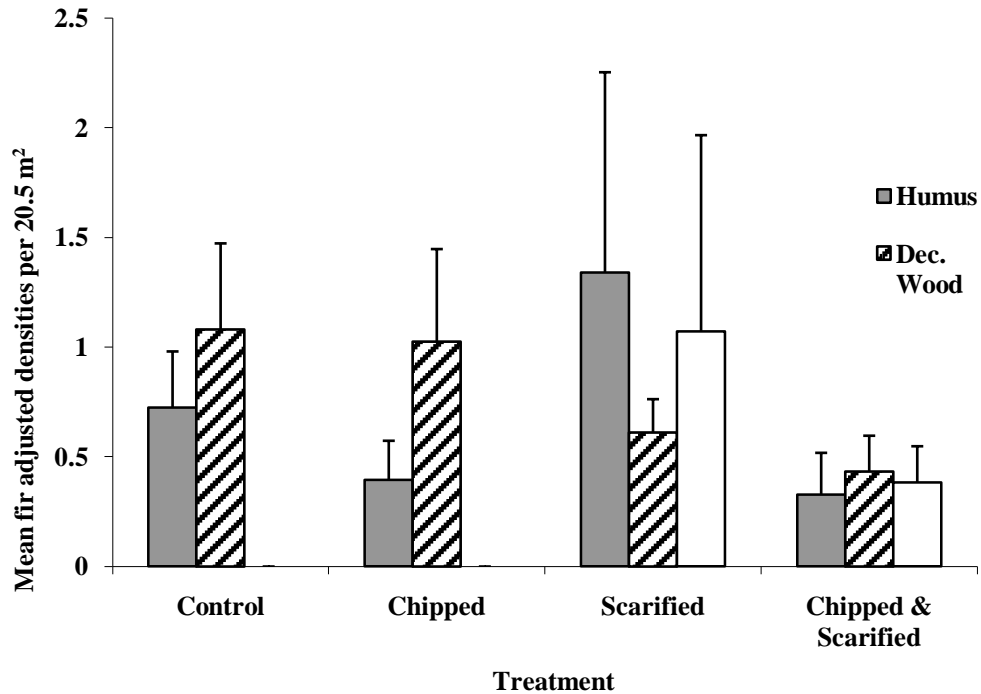


Figure 2.8: The mean adjusted densities (with mean standard error bars (SE) per 20.5 m²) of balsam fir germinants (N=36) growing in each substrate type, in each treatment. Adjusted density = (no. germinants in seedbed *i* * total no. uniform points) / (total transect area*uniform points of seedbed *i*).

Effects of substrate type on adjusted densities

White spruce

A one-way ANOVA and Tukey test revealed significant differences in spruce adjusted densities (N=27) between all substrate types (Figure 2.7) in the control treatment ($F = 29.759, df=2,24, p < 0.0001; all p < 0.05$). There were no significant differences in adjusted densities between substrate types in the scarified treatment ($F=0.277, df=2,24, p=0.761$). However, there were significant differences between substrate types in the

chipped treatment ($F=13.272$, $df=2,24$, $p=0.0001$), with significant differences occurring between decomposed wood and mineral soil ($p=0.0094$) and between mineral soil and humus ($p=0.021$). There was no significant difference between decomposed wood and humus ($p=0.085$). There was a significant difference in densities between seedbeds in the chipped & scarified treatment ($F=10.293$, $df=2,24$, $p=0.0006$), with significant differences occurring between decomposed wood and humus ($p=0.032$), and also between mineral soil and humus ($p=0.0345$). There was no significant difference in spruce adjusted densities between decomposed wood and mineral soil ($p=0.234$).

Balsam Fir

There were no significant differences in balsam fir adjusted densities ($N=27$) between substrate types (Figure 2.8) in both the scarified ($F=1.357$, $df=2,24$, $p=0.277$) and the chipped & scarified treatments ($F=0.168$, $df=2,24$, $p=0.847$). There was a significant difference between seedbeds in the control ($F=12.038$, $df=2,24$, $p=0.0002$). A Tukey test revealed that mineral soil was significantly different from humus and decomposed wood, with roughly nil adjusted densities (all $p<0.05$). The chipped treatment also showed significant differences between seedbed types ($F=7.586$, $df=2,24$, $p=0.0028$). The post hoc test confirmed significant differences between mineral soil (adjusted densities were nil) and decomposed wood and humus (all $p<0.05$). Humus and decomposed wood was not significantly different from mineral soil (all $p>0.05$).

Effects of treatment on seedling densities

White Spruce

After the first growing season (Figure 2.9), over-winter mortality of white spruce seedlings occurred in all treatments, with a considerable decrease in seedling numbers in the ‘chipped’ treatment (63%). Interestingly, the lowest mortality rate occurred in the control treatment (23%), while the ‘scarified’ and ‘chipped & scarified’ treatments showed higher mortality rates (58% and 55%, respectively).

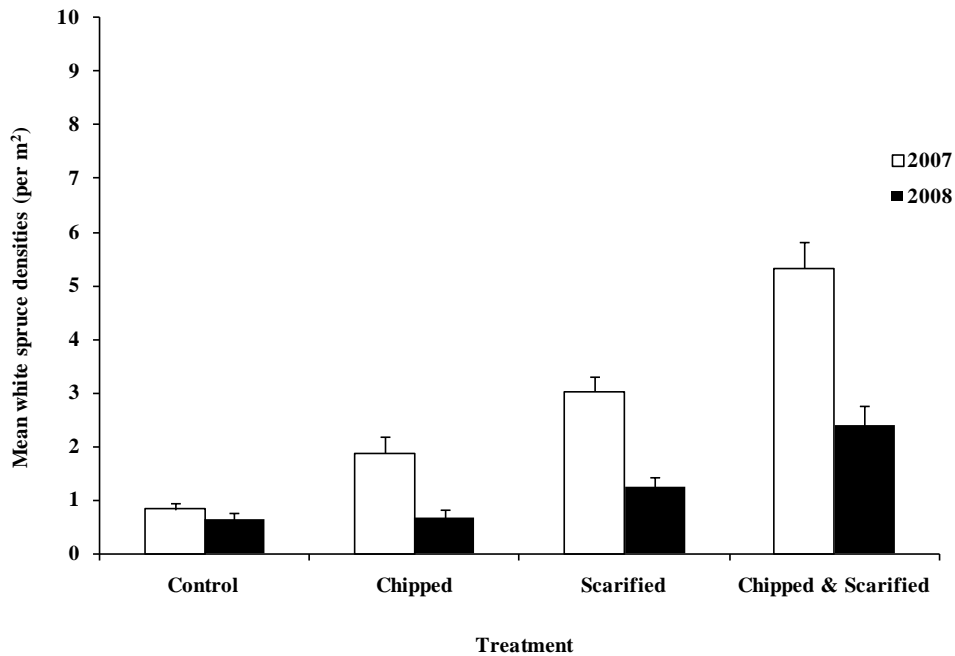


Figure 2.9: Mean densities (per m²; with standard error bars (SE)) of white spruce germinants in 2007 (N=36) and seedlings in 2008 (N=24) in all treatments.

There was a significant difference between treatments with regard to white spruce seedling densities ($F=3.84$, $df=3,20$, $p=0.025$). Tukey tests revealed that white spruce

seedling densities only differed significantly between the control and chipped & scarified treatments ($p=0.030$).

Balsam Fir

Similar to white spruce, balsam fir showed significant over-winter mortality rates (Figure 2.10). Mortality affected more than half of balsam fir germinants in three of the four treatments: control (65%), chipped (58%) and ‘chipped & scarified’ (65%).

Interestingly, the scarified treatment experienced 45% mortality, which resulted in the control and scarified treatments showing very similar final mean fir seedling densities. The chipped treatment contained the lowest fir seedling densities, while the ‘chipped and scarified’ treatment showed the second lowest densities.

There was a significant difference between treatments in regards to balsam fir seedling densities ($F=4.531$, $df=3,20$, $p=0.014$). Tukey tests revealed that balsam fir seedling densities differed only between the scarified and chipped treatments ($p=0.013$).

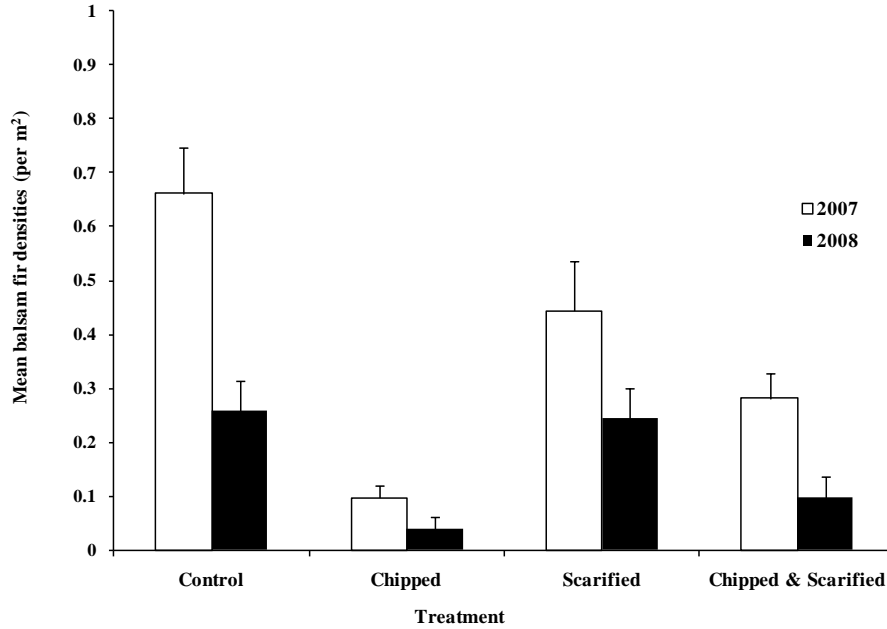


Figure 2.10: Mean densities (per m²; with mean standard error bars (SE)) of balsam fir germinants in 2007 (N=36) and seedlings in 2008 (N=24) in all treatments.

Effects of treatment on first year survivorship (germinant-to-seedling)

White Spruce

One way ANOVAs on ranked averages of spruce survivorship values (Figure 2.11) revealed no significant differences in spruce survivorship between treatments on both decomposed wood ($F=0.9056$, $df=3,20$, $p=0.456$) and humus ($F=0.444$, $df=3,20$, $p=0.725$). Yet, treatment effects did differ significantly on mineral soil ($F=14.348$, $df=3,20$, $p=0.0001$). A post hoc Tukey test showed that the chipped & scarified treatment differed significantly (much greater survivorship value) from both the control and chipped treatments (*all* $p<0.05$).

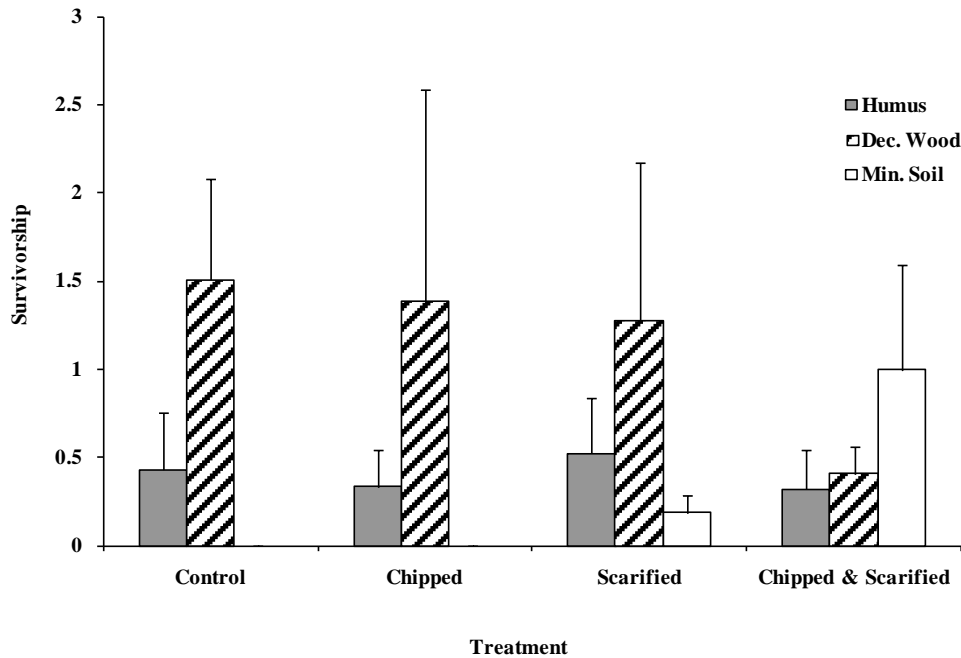


Figure 2.11: Mean survivorship values, with mean standard error bars (SE), (no. of seedlings/no. of germinants) of white spruce in each substrate type (N=72), separated by treatment (N=24).

Balsam Fir

One way ANOVAs on ranked averages of balsam fir actual survivorship values (Figure 2.12) revealed no significant differences between treatments on both decomposed wood ($F=0.950$, $df=3,20$, $p=0.4354$) and mineral soil ($F=0.668$, $df=3,20$, $p=0.4559$). There was however a significant difference in survivorship on humus between treatments ($F=3.180$, $df=3,20$, $p=0.0463$). A Tukey test showed that the difference was only significant between the control and chipped & scarified treatments ($p=0.0023$).

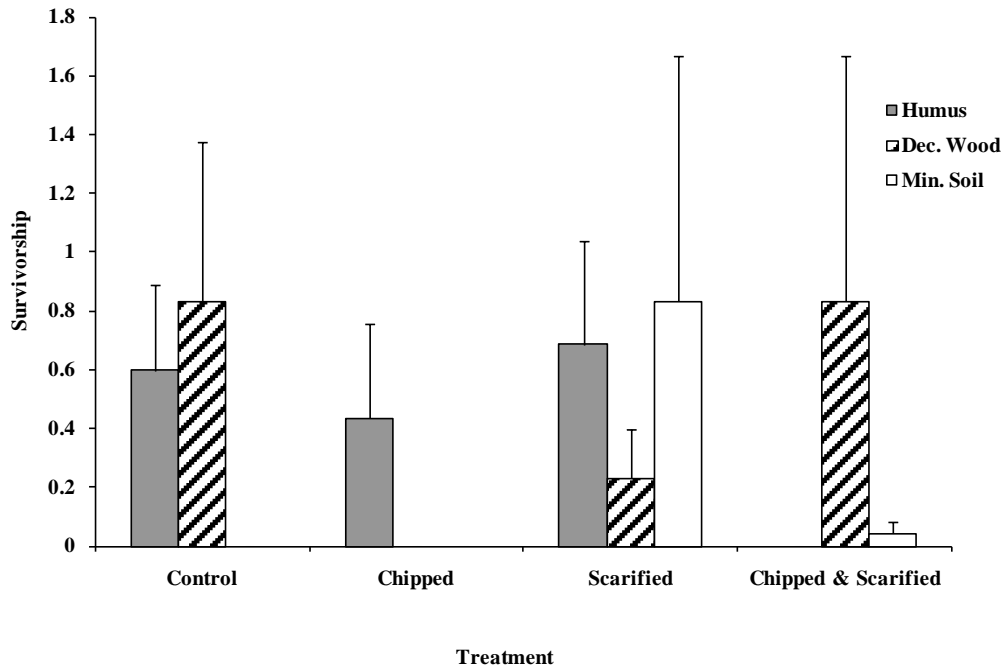


Figure 2.12: Mean survivorship values (no. of seedlings/no. of germinants) with mean standard error bars (SE) of balsam fir for each substrate type (N=72), separated by treatment (N=24).

Effects of substrate types on first year survivorship (germinant-to-seedling)

White Spruce

Spruce first year survivorship values (Figure 2.11) were significantly different in the control treatment ($F=7.568$, $df=2,21$, $p=0.005$). The Tukey test showed no significant differences between humus and decomposed wood, and between humus and mineral soil (*all* $p>0.05$), even though mineral soil had a zero survivorship value. There was a significant difference between mineral soil and decomposed wood ($p=0.003$).

There was no significant difference in survivorship values between substrate types in the

scarified ($F=1.057$, $df=2,21$, $p=0.372$), chipped ($F=1.679$, $df=2, 21$, $p=0.220$) and chipped & scarified ($F=1.638$, $df=2,21$, $p=0.227$) treatments.

Balsam Fir

There were significant differences in fir survivorship (Figure 2.12) between substrate types in the control treatment ($F=5.022$, $df=2,21$, $p=0.021$). Mineral soil, having no seedlings, was significantly different from both humus and decomposed wood ($p<0.0001$), whereas there was no significant difference between humus and decomposed wood ($p=0.093$). There was a significant difference between seedbed types in the chipped treatment ($F=4.747$, $df=2,21$, $p=0.025$). Both decomposed wood and mineral soil had no survivorship values in the chipped treatment; humus had significantly higher survivorship values than the other two (*all* $p<0.05$). There were no significant differences in survivorship between types in the scarified ($F=1.282$, $df=2,21$, $p=0.306$) and chipped & scarified ($F=0.504$, $df=2,21$, $p=0.614$) treatments.

White Spruce Stocking

In 2007, all treatments achieved full stocking of white spruce germinants (Figure 2.13), with the scarified and 'chipped & scarified' treatments attaining 98% and 100% spruce stocking, respectively. The control and chipped treatments were stocked at 71% and 78%, respectively. In 2008, full stocking was maintained in all treatments except the control, which, because of high over-winter mortality, dropped to 53% stocking.

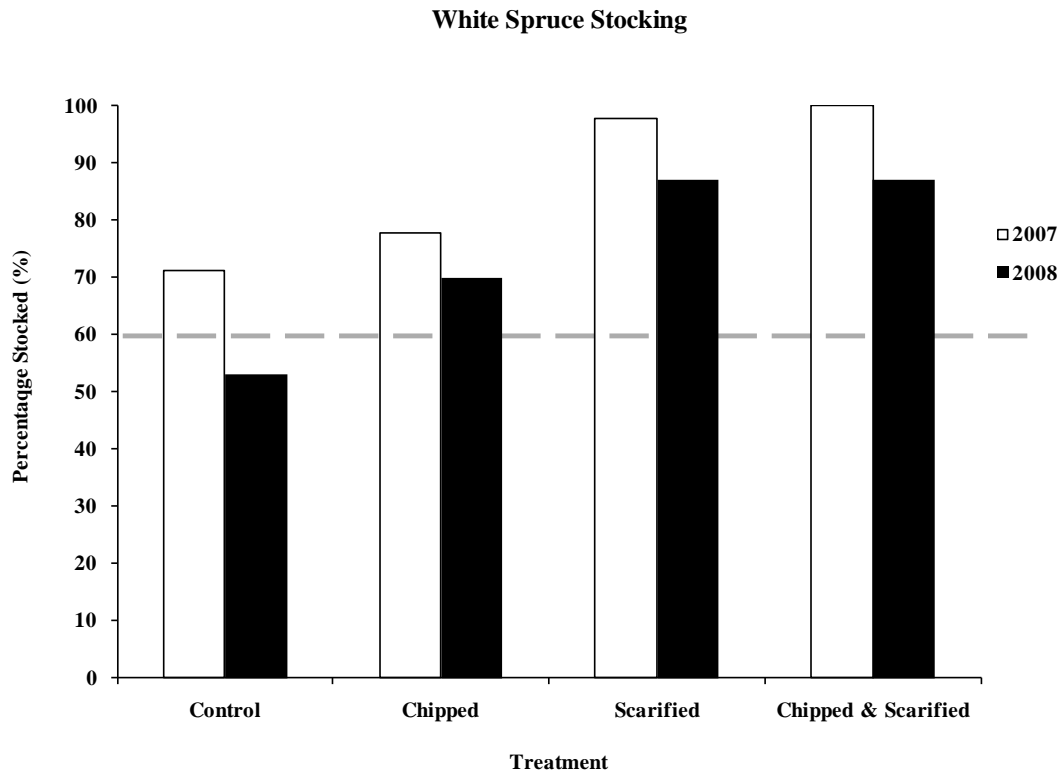


Figure 2.13: Stocking (based on 4m² plots) of white spruce based on the censuses of germinant number in 2007 and seedling number in 2008. The dotted line represents the 60% full stocking level standard in Quebec. Sample sizes vary: N=45 (2007); N=30 (2008).

Balsam Fir Stocking

For balsam fir in 2007 (Figure 2.14), only the control and scarified treatments attained full stocking (at 69% and 60%, respectively). In 2008, neither treatment achieved full stocking of balsam fir, with the ‘chipped & scarified’ treatment dropping by 24%.

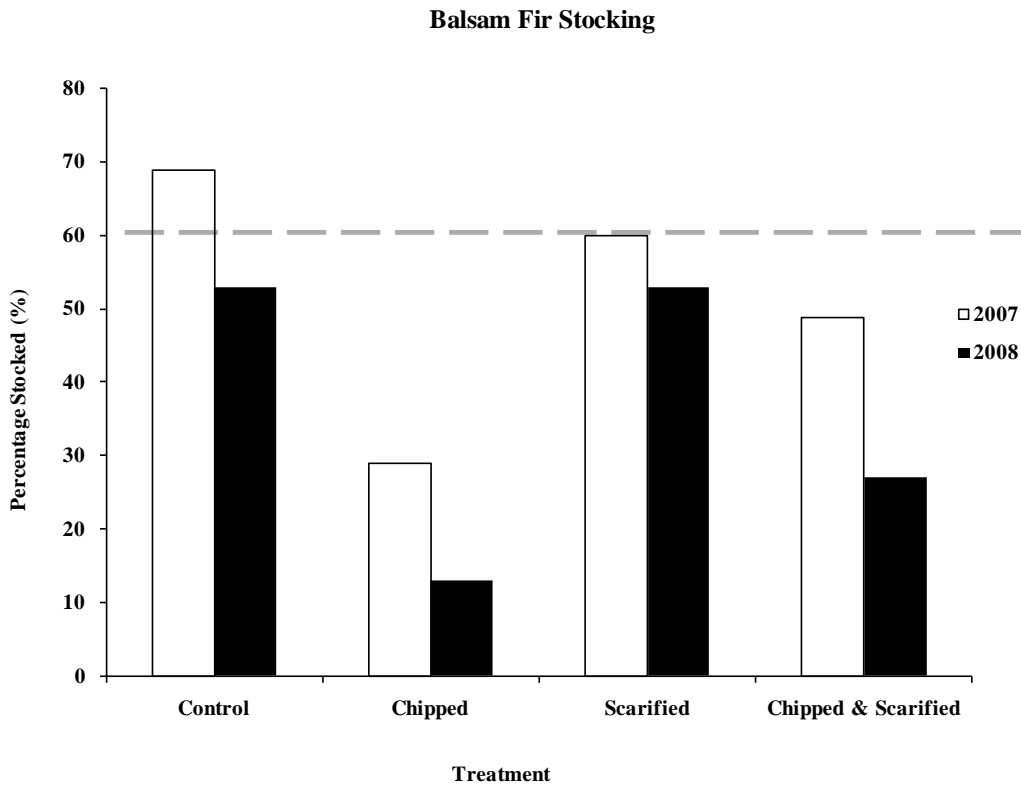


Figure 2.14: Stocking (4m² area) of balsam fir based on the censuses of germinant number in 2007 and seedling number in 2008. The dotted line represents the 60% full stocking level standard in Quebec. Sample sizes vary: N=45 (2007); N=30 (2008).

Seed Count Assessment

From the start of the masting episode in September 2006 to the end in December 2007, an average 1022 spruce abscised seeds per m² (Figure 2.15). Essentially all of these were derived from the 2006 crop as the 2007 crop for white spruce was extremely poor. There were sharp declines in white spruce seeds with each successive collection date from September 2006 to December 2007. From late August to September 21, 2006, approximately 600 seeds/m² (58% of the total number) were deposited. Forty days later,

average seed count had diminished to half the previous number (€300 seeds/m²), and again roughly half that amount was assessed in May (€150 seeds/m²).

As with spruce, fir had an extremely poor crop in 2007 and thus essentially all our seed collection data is for the 2006 mast crop. Balsam fir demonstrated a similar decline, although with much smaller magnitudes. From September 2006 to December 2007, there was on average a total of 46 balsam fir seeds/m², or 460 000 seeds/hectare.

The random block ANOVA revealed no significant difference in white spruce seed densities between the different treatments ($F=2.259$, $df=3,11$, $p=0.182$), and there was no significant difference between blocks ($F=3.651$, $df=2,11$, $p=0.092$). For balsam fir, the ANOVA revealed no significant difference in fir seed densities between the different treatments ($F=0.970$, $df=3,11$, $p=0.466$), and similar to spruce, there was no significant difference between blocks ($F=0.618$, $df=2,11$, $p=0.570$).

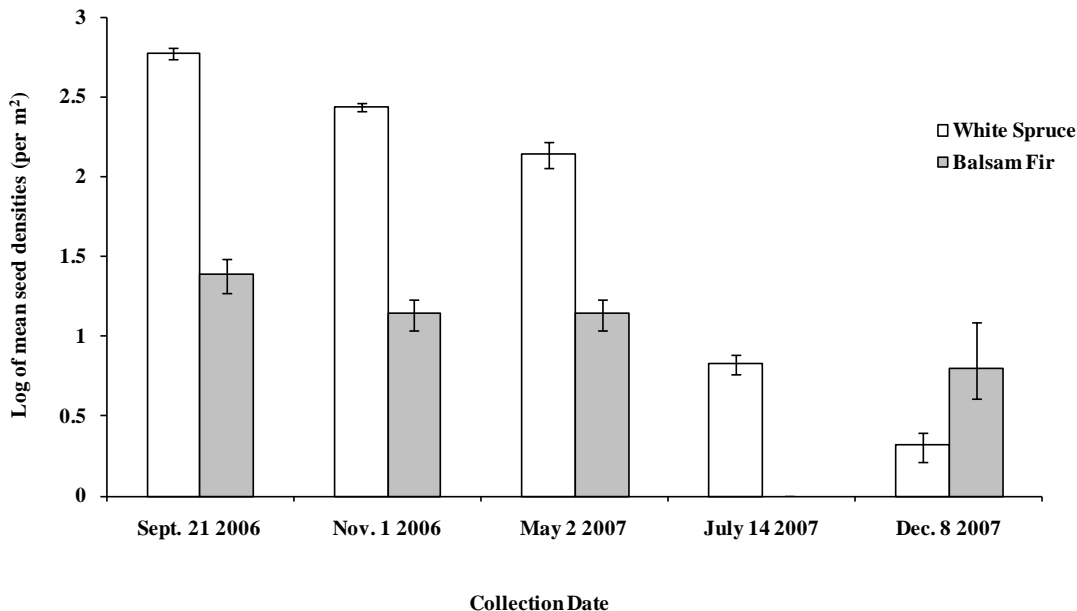


Figure 2.15: Log of mean densities of white spruce and balsam fir seeds/m² (with log of mean standard error (+/- SE) bars) based on trap contents collected on the five different dates (N=48 traps).

Transforming seed tallies into rates (seeds/m²/day), white spruce trees dispersed their seeds at high rates prior to the beginning of the winter (Figure 2.16). Balsam fir seed fall rates were similar to those of white spruce, steadily declining after September 21, 2006. However in the case of balsam fir, there was a large increase between July 14, 2007 and December 8, 2007 (i.e. the second autumn after the crop matured).

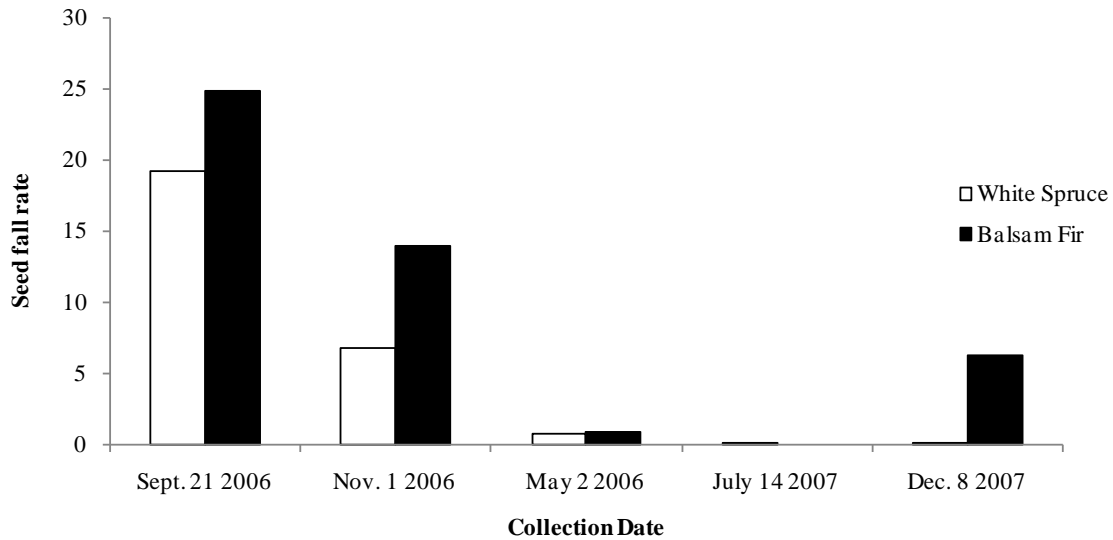


Figure 2.16: Rates of white spruce and balsam fir seed fall (seeds/m²/day since previous collection date or since the traps were first installed).

White Spruce Cone Fall Assessment

For the period between September 2006 and December 2007, on average 32 cones per m² were counted in the traps (Note: not all these cones were empty; filled seeds were commonly found among the scales, especially in the autumn of 2006). White spruce cone abscission peaked prior to September 21, 2006 (Figure 2.17). An even larger number of cones abscised during the winter (before May 2, 2007) and cone fall continued into December 2007, but in smaller amounts.

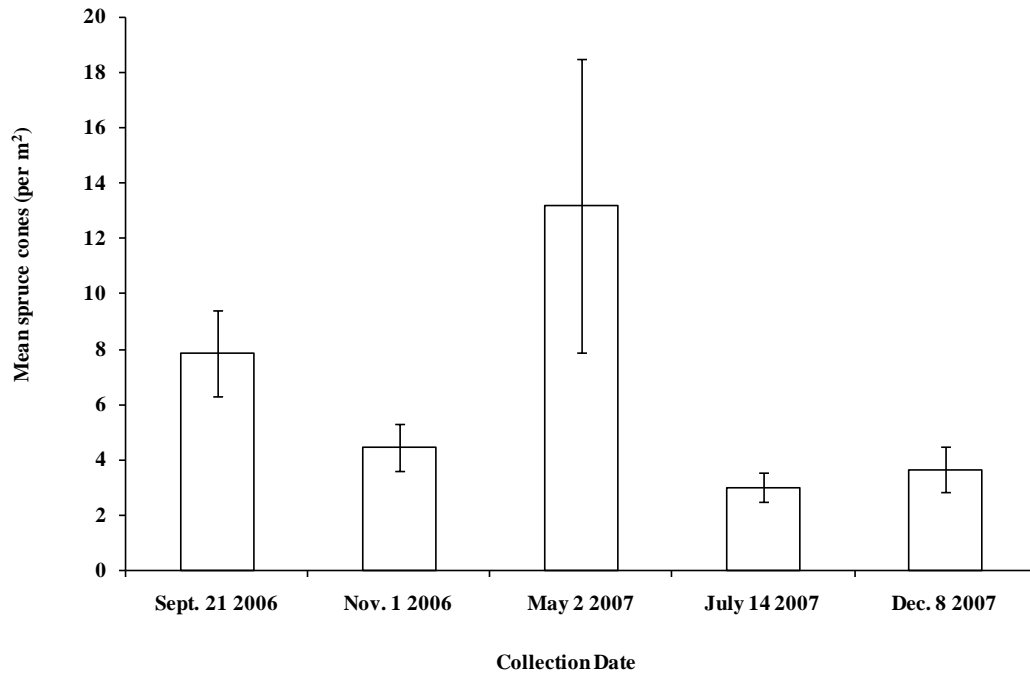


Figure 2.17: Mean densities of white spruce cones (per m²; with mean standard error bars) counted in each batch collected on the five different dates (N=48 traps).

Similar to the seed fall schedule, the spruce cone drop rate (cones/m²/day) was highest in September, steadily decreasing thereafter (Figure 2.18).

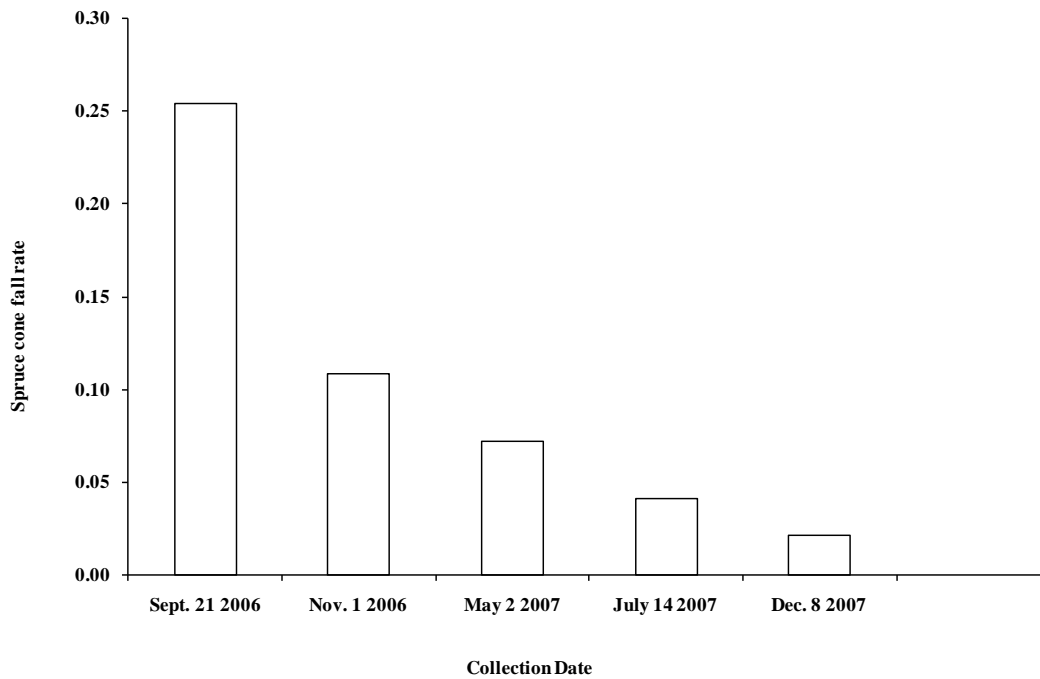


Figure 2.18: White spruce cone fall rate (number of cones/m²/days since last collection date or since the traps were first installed).

Correlations between BA/A and seeds/m²

There was no significant correlation between white spruce basal area/area and seeds/m² for the traps ($r=0.195$, $p=0.5436$, $N=12$, Figure 2.19). Likewise, there was no significant correlation between balsam fir basal area and seed density ($r=0.140$, $p=0.681$, $N=11$, Figure 2.20).

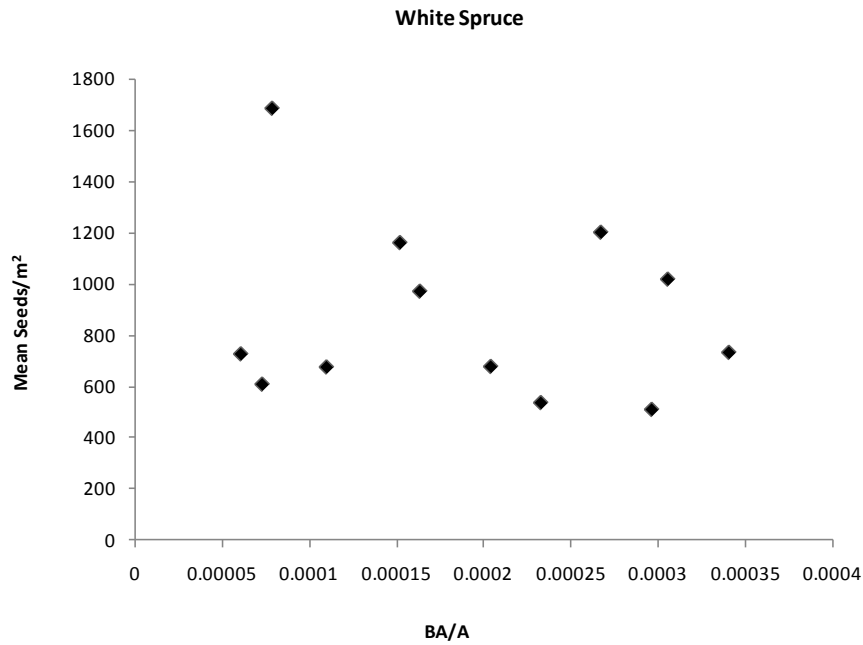


Figure 2.19: Relationship between white spruce basal area/area and average number of seeds/m² (N=12).

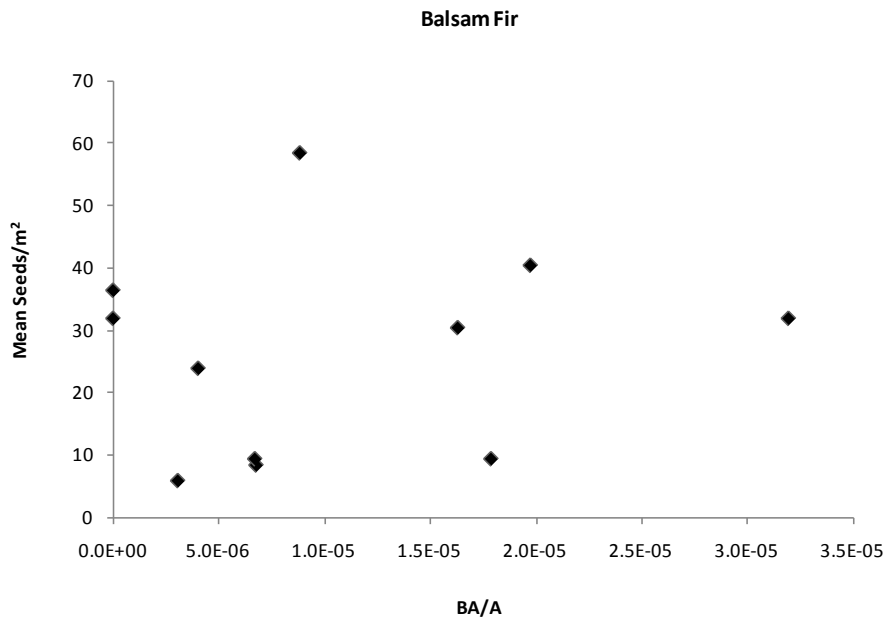


Figure 2.20: Relationship between balsam fir basal area/area and average number of seeds/m² (N=11).

Recruitment Models

White Spruce

As a predictor in a multiple regression, the combination of the product 'p*seeds' with BA/A (where p is the proportion of good seedbeds (mineral soil, humus, decomposed wood) along the transects; "seeds" is seeds/m² from the traps near each transect; BA/A is the basal area per area in the vicinity of each transect) gave the highest correlation for the prediction of white spruce germinant recruitment ($r=0.717$; $p=0.00004$, Table 2.3). Note: we used both BA/A and seeds/m² as they were showed previously they to be uncorrelated. The best single predictor was BA/A ($r=0.598$; $p=0.000241$).

Balsam Fir

Given the lack of a significant correlation between balsam fir seeds/m² and BA/A, both these factors could be included in the stepwise regression models. Similar to white spruce, although not quite the same, the best model for predicting balsam fir recruitment numbers was the product 'p*BA/A' coupled with seeds/m² ($r=0.447$; $p<0.00066$; Table 2.3). For a regression with a single predictor, the product 'p*BA/A' was the best for predicting balsam fir germinant densities ($r=0.447$; $p=0.0073$).

Table 2.3: Regression models in order of highest to lowest correlation (r). The first model is the best model for predicting both white spruce and balsam fir germinant density [One variable, v=30 (r critical = 0.426); two variables, v=30 (r critical = 0.349); v=35 (r critical = 0.397)].

White spruce			
Model	No.	r	p
	variable(s)		
p*seeds, with BA/A	2	0.717	0.00004
seeds, with BA/A	2	0.689	0.00003
p*BA/A, with seeds	2	0.616	0.00015
BA/A	1	0.598	0.00113
P*Seeds	1	0.536	0.00133
p* BA/A	1	0.529	0.00617
seeds/m2	1	0.451	0.00943
Balsam Fir			
Model	No.	r	p
	variable(s)		
p*BA/A, with seeds	2	0.447	0.0066
p*BA/A	1	0.441	0.0073
p*seeds, with BA/A	2	0.437	0.0074
p* seeds	1	0.437	0.0074
BA/A, with seeds	2	0.399	0.0088
seeds	1	0.377	0.0200
BA/A	1	0.371	0.0217

Windthrow of Seed Sources Following Harvest

Few of the seed trees fell during this experiment. For white spruce, 16 of 114 trees (14%) were toppled by the summer of 2008, 3 years after harvesting (Table 2.4). For fir, the percentage of fallen seed sources, 5% (1 of 20 trees), was also low. However, granted the abscission schedule for the seeds of these two species, the important period

for wind throw is from the harvest to the winter of 2006-07. During this period, only 2 of 114 white spruce trees fell (2%) and no fir trees were lost.

Table 2.4: Windthrown white spruce and balsam fir seed trees (with DBH (mm) measurements) showing the time when the tree was recorded as downed.

Block	Treatment	Species	DBH (mm)	Status		
				Autumn 2006	Summer 2007	Summer 2008
1	Chipped	Spruce	380	DOWN	-	-
		Spruce	477	-	-	DOWN
		Spruce	360	-	-	DOWN
		Spruce	358	DOWN	-	-
	Scarified	Spruce	364	-	-	DOWN
2	Chipped	Spruce	279	-	DOWN	-
		Spruce	237	-	-	DOWN
	Scarified	Spruce	288	-	DOWN	-
		Spruce	308	-	-	DOWN
	Chipped & Scarified	Spruce	324	-	DOWN	-
		Spruce	290	-	-	DOWN
Spruce		256	-	-	DOWN	
3	Control	Spruce	295	-	-	DOWN
		Spruce	260	-	-	DOWN
	Chipped	Spruce	375	-	-	DOWN
	Scarified	Fir	138	-	-	DOWN
Chipped & Scarified	Spruce	410	-	-	DOWN	

Discussion

Effects of treatment on substrate types

Site preparation of surface soil layers and chipping created varying proportions of substrate types in the different treatments. Of particular interest were the quantities of mineral soil and rotted wood, reported to be the best seedbeds for spruce regeneration. Although the difference was not significant, the scarified treatment produced only about half the amount of mineral soil (12%) created by the ‘chipped and scarified’ treatment (25%). Chipping prior to disk trenching, in the combined treatment, provided the added effect of improving the action (and response) of the trenching by reducing the quantity of coarse woody stems, branches and dead wood that otherwise reduced the capacity of the disks to penetrate into and mix the soil layers, thereby increasing the amount of exposed mineral soil. The control demonstrated how rare mineral soil is in intact forests: in this case, around 0.5% of the ground cover.

Rotted wood varied little among treatments, averaging about 17%. Humus was the most common seedbed ranging in percentage cover from 27% (chipped & scarified) to about 60% (control). The added cost of chipping may not to justify its use to promote spruce survivorship.

Effects of treatment and substrate type on germinant densities

Given that spruce seed supply did not differ significantly between blocks and treatments while the proportions of mineral soil seedbed varied considerably, the greater spruce germinant densities present in the scarified and chipped & scarified treatments

were probably due to the increased availability of mineral soil produced by site preparation. The densities of white spruce were very high when mineral soil was available (in the scarified and chipped & scarified treatments), around 0.5 germinants in the scarified and 1.8 germinants/m² in the chipped & scarified treatment. Rotted wood also recruited very well in every treatment, providing a recruitment of ≈ 1.2 germinants/m² in the chipped & scarified treatment.

Effects of treatment and substrate type on adjusted densities

The adjusted densities of spruce germinants, indicated modest seedbed-specific differences among treatments. With three seedbed types (sufficiently abundant to warrant an ANOVA) and 4 treatments, there were 6 significant differences among 18 pair-wise possibilities. Four of these differences involved the control. There were no significant differences between the scarified and chipped & scarified treatments. It is difficult to conclude from this whether the treatment has a systematic effect on the quality of the seedbed type. In the scarified and chipped & scarified treatments where mineral soil was successful in recruiting spruce germinants, there was no significant difference in seedbed recruitment quality between mineral soil and decomposed wood.

Balsam fir being several magnitudes smaller than those for white spruce, primarily owing to fewer seed trees being present, a smaller masting effort and dispersal constraints. Interestingly, despite the expensive site preparation, the control treatment recruited the greatest number of fir germinants in 2007. This is likely due mainly to the larger seed rain in that treatment or possibly because of the moderating influence of residual vegetation on reducing stress from high temperatures and desiccation. The

scarified treatment showed the next best fir recruitment while, surprisingly the chipped & scarified treatment showed very low recruitment, probably due to smaller seed rain.

There were no significant differences between treatments with regards to adjusted densities of balsam fir in humus or in decomposed wood. However mineral soil recruited significantly greater fir densities in the scarified and chipped & scarified treatments compared to the other treatments. Of 18 pair-wise comparisons, there were significant differences for only three (and these only for the control versus the other treatments on mineral soil). Adjusted densities for balsam fir were higher in humus and decomposed wood in all treatments, with no significant differences between each other. In the scarified and chipped & scarified treatments, where mineral soil was the most successful of the four treatments, mineral soil was not the superior seedbed type for fir; rather it was humus in the scarified treatment and decomposed wood in the chipped & scarified treatment. Based on the spruce data, the main contrasts concern (1) the control rather than the three treatments where seedbeds were manipulated by machinery; and (2) between mineral soil and the other two optimal seedbed types.

Effects of treatment and substrate type on first-year survivorship

Considerable over-winter mortality of both fir and spruce occurred in all treatments. The differences in white spruce seedling densities were significant between the chipped & scarified treatment (greater densities) versus the chipped and control treatments. However, unlike spruce germinant recruitment, there was no effect of substrate type on spruce seedling density between treatments. Likewise, there was no effect of treatment or substrate type on balsam fir seedling densities.

Regarding the actual survivorship results, spruce survivorship from germinant to next-summer seedling provided less dramatic differences among seedbeds similar results were reported by Charron and Greene (2002). There was little difference in the survivorship values for spruce among decomposed wood (averaging ~ 1.1) and humus (averaging ~ 0.4). Apart from the chipped & scarified treatment (where mineral soil had the highest, although not significant, spruce survivorship values), spruce had consistently better survivorship in decomposed wood in the other three treatments, however it was only significant in the control. The average spruce survivorship ratio was 0.6 between the scarified and chipped & scarified treatments. Fir germinant-to-seedling survivorships were much higher on mineral soil and decomposed wood, which showed relatively similar survivorship values (mineral soil in the scarified treatment, and decomposed wood in the chipped and scarified treatment; with no significant difference between the treatments: ~0.8). The chipped treatment only had survivorship in humus (~0.4). Fir survivorship in humus was very similar between all treatments as well (~0.6) with the exception of the chipped & scarified treatment (i.e. zero survivorship in humus). Fir showed great survivorship in all three substrate types, but the best substrate type varied in a given treatment (i.e. decomposed wood had the highest survivorship values in the control and chipped & scarified treatments; humus was the best in the chipped treatment; mineral soil had the highest values in the scarified treatment). Given these results, we suggest that seedbed type has at best a weak effect on first-winter survivorship. Not only is survivorship approaching an upper bound (1.0) but it will likely depend greatly on other factors that were not measured in this study (e.g. Calogeropoulos et al. 2004) and other stochastic events (leaf smothering, browsing, flooding, etc.).

It is well documented that mineral soil, thin humus and decomposing wood provide the best seedbed for the germination of various small-seeded species like white spruce (Foster 1985; Williams & Johnson 1992; Charron 1998; Greene and Johnson 1998, 1999, 2000; Purdy et al. 2002). Averaging across the treatments, these three seedbeds were essentially equally good substrates for germination that is, adjusted densities will be proportional to seed to seedling survivorship. Generally, the three substrates were poorer on the control and chipped treatments than on the other two, but it is not at all clear why this difference should exist. Fir also had generally equally good survivorship (as adjusted germinant densities) on the three best substrates. Unlike spruce, the control and chipped treatments did not tend to engender poorer substrates. This less variable performance reflects presumably the difference in germinant size (accruing from the difference in seed size) characterizing these two species (Greene et al. 2007). Differences in stocking necessarily reflected differences in seedling density. Spruce had full stocking (about 70-85%) for all treatments except the control. By contrast, fir never had full stocking; only the control and scarified treatments came close.

Seed rain assessment and timing of site preparation

Seed fall occurred primarily from late August to November 1, 2006 (second seed collection batch), accounting for about 85% of all spruce and fir seeds. The rate of seed abscission declined sharply with time except for a surprising increase for fir in the last half of 2007. In short, essentially all seeds were on the ground available for germination in the late spring following a mast year. In consequence, it is crucial that the substrate treatments occur prior to late August of the mast year.

Cumulative seed density in the traps was about 1000 seeds/m² for spruce and about 50 seeds/m² for fir. Given the 13-fold difference in basal area/area for these two species, and the fact that spruce seeds are about 4 times smaller than fir seeds (Greene et al. 2002; Greene & Johnson 1994), then it follows that these two species had about equally large mast years. This conclusion tallies with the unpublished data of D.F. Greene for these two species in eastern Canada: the differences in cones/basal area for individual trees were only what might be expected given that seed number scales with seed mass as the exponent -0.58 (Greene and Johnson 1994).

Relationship between BA/A and seeds/m²

Neither species showed the expected positive relationship between basal area/area and seeds per m². In the literature, although the relationship is reported to be weak, it is nonetheless unusual for it to be insignificant (Calogeropoulos et al. 2004). It is unlikely that the problem is a dramatic influx of seeds from the adjacent intact stands (the dispersal distances are not great) because (1) casual inspection indicated that the adjacent stands had similar amounts of spruce and fir basal area/area as the harvested blocks, and (2) as already mentioned, the ratio of seeds or cones to basal area (the latter based only on residual trees within the blocks) is at worst half of what might be expected from intact stands in this area in that year (D.F. Greene, unpublished data). The origin of this discrepancy is simply not understood.

Wind throw

Windthrow was common; of the 114 spruce seed trees in the experimental blocks, 16 toppled between 2006-2008, accounting for 14% of the seed trees. This percentage is high relative to studies of seed tree cuts where the typically higher density of residuals reduces wind speed. For example, in a shelterwood study, Jull et al. (1997) noted a windthrow loss of only about 2% in two years. The other reason our loss to wind was so high could well be the clay soils as they are more prone to shearing of the root mat when strong winds are accompanied by heavy rain.

Nonetheless, only five of these spruce trees fell early in the autumn of 2006 with the bulk of their seeds still in the cones. These stems were not considered for estimates of BA/A, in the prediction of seeds/m², or in the correlation between the two variables. They only accounted for about 5% of the expected seed supply given their contribution to the basal area/area originally present following the harvest. It would seem then that rapid seed dissemination in the early autumn means that wind throw will not greatly reduce the expected seed supply.

Recruitment Models

Our modeling attempt added little to our understanding as the obvious predictors (BA/A as a proxy for shading, deposited seed density, and the relative abundance of the better seedbeds) did not indicate any dramatic hierarchy of effects. Choosing a simple model that would also be easiest to estimate for spruce, the product of the proportion of good seedbeds and basal area per area provided an r^2 of 0.28. Note that the former (at least for exposed mineral soil) can be prescribed as the scarification intensity (proportion

of the area modified by the equipment) while the latter is under the control of the company as it harvests. As for fir, this same predictor would explain 19% of the variation.

Including seeds density as a second predictor does not greatly enhance the correlation for either species. Thus, unlike with Calogeropoulos et al (2003), knowing the small-scale seed density, rather than using basal area as a proxy, was not especially useful.

Conclusions

Typically, scarification produces a variety of effects, especially in clay-rich soils. Certain parts of the scarified areas (in both the scarified and ‘chipped and scarified’ treatments) contained ruts where water accumulated during wet periods, usually in the spring and autumn. In some parts of the replicates, water remained in the ruts during the summer, although most of the water disappeared in mid-July. Water accumulation in the ruts would have proven deadly for seeds and even fatal for germinant survival, and might explain the high germinant mortality rates in the ‘chipped & scarified’ treatment. Even balsam fir had the greatest germinant mortality rate in the ‘chipped & scarified’ treatment (65%). Because mortality due to standing water in ruts was not included in our data collection, our modeling success was necessarily poorer than it might otherwise have been.

Management Implications

Despite the low proportion of explained variance, a forester could use these results to forecast (perhaps with a safety factor) the required combination of residual basal area per area (combined with knowledge of the average cones per basal area that year) and scarification intensity that would provide a minimally acceptable seedling density. A constant amount could be added to the proportion of good seedbeds to account for the expected contribution of moss and rotted wood that were not on the scarification paths.

While adequate stocking was generally obtained for spruce, nonetheless the densities of spruce and (even more so) fir recruits were far lower than have been observed in other experiments with seedbed manipulation in advance of a mast year (e.g. Stewart et al, 2000; Eastham & Jull 1999; Karlsson & Orlander 2000; Karlsson & Nilsson 2005). The difference was that we used, essentially, a clearcut; the few standing spruce and fir provided very little shade and in consequence survivorship values were relatively poor. Thus, we have shown that it is possible to achieve full stocking of spruce even with a clearcut, so long as about 7% of the residual area consists of the target species. Note that this conclusion is unaltered if we lump fir recruits with spruce recruits, as is commonly done in stocking surveys, because fir contributed little to either the summed recruit number or the summed basal area/area.

For the humid eastern boreal forests of North America, we conclude that a cut in a predominantly-aspen forest with about 7% spruce and fir basal area/area with pre-abscission (mid-August or earlier) scarification (with or without other substrate manipulations such as chipping) will result (barely) in full stocking of second summer

seedlings. Of course, some mortality will still occur for this recruited second-summer cohort but that loss will be, relative to what happened in the preceding two years, relatively small (Calogeropoulos et al. 2003).

Putting our result in perspective, our rate of stocking with only about 2 m²/ha for seed sources (about 25 trees/ha) was extraordinarily good when compared with the literature on seed tree retention cuts (where a mast year is not a key factor). Estimates of the residual basal area of white spruce required to ensure proper stocking range from 4.4 m²/ha (Ball and Walker 1995) to 17.2 m²/ha (Waldron 1959). Clearly, the success of these few source trees was a reflection of the extraordinary size of the 2006 seed crop.

We point out that, in some ways, barely achieving the minimal stocking is to be preferred to having a huge recruit density as the latter would require a subsequent thinning intervention (Greene et al. 2002). The trade-off here of course is that just achieving a minimum threshold for full stocking runs the risk (not estimated here) of obtaining *inadequate* stocking. In any case, if greater stocking is desired, the forester can merely leave more spruce basal area per area or scarify a greater percentage of the block.

Presently there is no model for predicting mast year occurrence, apart from a weather cue (dry, warm spring) prior to the year of seed abscission, which would trigger the flowering (Koenig and Knops 2000). Pragmatically, mast years are noticed in the year in which they occur. Unfortunately, this technique of understory scarification in a mast year requires foresters to occasionally ignore their forest management plans and rapidly hire people to scarify and cut in stands that were scheduled to be cut later. Clearly, a model that could predict a mast year based on weather characteristics at the time of reproductive bud initiation one year before would be of great use. Conversely,

regular monitoring of barely-developed reproductive buds on branches of trees felled in normal harvesting operations in the autumn could be used to estimate the size of next year's crop.

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