THE INFLUENCE OF SITE TYPE AND HARVEST INTENSITY ON UNDERSTORY COMPOSITION IN BOREAL *PICEA MARIANA* (Mill.) B.S.P. FOREST COMMUNITIES IN NORTHWESTERN ONTARIO

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In closing, I dedicate this thesis to my children Devon, Linnaea and Sean who are following their own dreams, dedicating energy, enthusiasm and excellence to family, friendships, sport, the environment, writing, and art.

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ABSTRACT

Plant diversity and composition in boreal black spruce understory communities was assessed 15 years after the application of three harvest disturbance treatments on loam, sand and peat site types. The study was carried out on replicated uncut, tree-length, full-tree, and full-tree blade harvest treatments applied on 30 x 30 m treatment plots in six research areas in northwestern Ontario in 1995/96. A significant treatment x site type interaction effect on species diversity and abundance was found. Species richness and diversity increased after canopy removal on all site types. Species evenness after canopy removal was significantly different only on the loam sites. The retention of slash (tree-length) compared to its removal lead to a significant decrease in species diversity on loam sites; the reverse was observed on peat sites. Species composition shifts were most evident on sites where the surface O-layer was removed (full-tree blade) with increases in herbaceous cover including grasses still evident 15 years after treatments. Species evenness was only significantly different after full-tree blade compared to other harvest treatments on sand sites. Mineral soil exposure and the presence of ruderal species were still evident on both the loam and sand site types. Comparison of the soil seed bank with the composition of the 15 year old communities did not detect the presence of invasive or exotic species. Species diversity response did not comply with the intermediate disturbance hypothesis. There was some evidence of compliance with the mass ratio hypothesis on peat sites, with the continued dominance of the pre-harvest ericaceous shrub and sphagnum components.

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1.0 INTRODUCTION

1.1 Current Context of Disturbance Ecology

The dynamics of early successional boreal conifer forests are not well understood especially with respect to the long-term effects of forest management choices on plant biodiversity and composition (Hunt *et al.* 2003, Barbier *et al.* 2008, Puettmann *et al.* 2009, Paquette and Messier 2010, Schmiedinger *et al.* 2012). The application of different harvesting systems and post-harvest site and regeneration treatments creates different environmental conditions in which plant communities develop. Despite the known relationship between species composition (vegetation type) and site type in northern Ontario (e.g., Sims *et al.* 1996, Sims *et al.* 1989), the dynamics of young black spruce (*Picea mariana* (Mill.) BSP) forests, from establishment through to stand closure and early maturity, on different site types are not well understood (Hunt *et al.* 2003, Hart and Chen 2008, Schmiedinger *et al.* 2012). Loss of biodiversity and the proportional loss of ecosystem function have been identified as two of the major impacts humans have had on ecosystems in the last century (Chapin *et al.* 2000, Aubin *et al.* 2011, Wardle *et al.* 2012). In Canada, there is a growing recognition of the value of understory plants to post-harvest community development (Roberts and Gilliam 1995, Thomas *et al.* 1999, Hunt *et al.* 2003).

Interest in the diversity response to disturbance is, in part, due to the close association of different species to different environmental properties and to the critical role different species play in the provision of ecosystem services. The understory accounts for the majority of plant diversity in the boreal forest (de Grandpré and

Bergeron 1997, Bell and Newmaster 2002, Hunt *et al.* 2003, Robert 2004, Gilliam 2007) and has been shown to be an important driver of nutrient cycling (Metzger and Schultz 1984), productivity (Nilsson and Wardle 2005) and forest succession (Messier *et al.* 1998, Bell and Newmaster 2002, Hunt *et al.* 2003).

Understanding the factors that affect the diversity and composition of the understory in boreal forests is increasingly the subject of current research (Kurulok and Macdonald 2007, Lafleur et al. 2011, Wang and Chen 2010, Paquette and Messier 2011, Biswas and Mallik 2011, Pigeon and Mallik 2013). For example, Kurulok and Macdonald's 2007 study in Alberta compared stands burned by wildfire with those burned and salvage logged (2 to 34 years after disturbance) showing that species richness was significantly greater after salvage-logging, with higher shrub abundance, higher ruderal species presence, and lower abundance of fire-specialist seed banking species. Wang and Chen (2010) reported that species diversity, shade tolerance diversity, diameter and height diversity increased with increasing soil disturbance but fertilization or brush control had no effect on diversity in their study of 15 year-old black spruce plantations.

Biswas and Mallik's (2011) study compared boreal riparian (small streams) and upland communities subjected to low intensity (uncut forests), intermediate intensity (clearcut stands), and high intensity (clearcut plus soil scarification) disturbances. They showed that mean species richness per trait associated with disturbance tolerance progressively increased after intermediate and high disturbances, decreased for competitive traits and showed no discernable trend for generalist traits for the same comparisons in both upland and riparian communities.

Pigeon and Mallik (2013) found no significant differences in species diversity (Shannon's diversity H') related to disturbance type (p=0.78) or site properties (p=0.42) in 15-37 year old jack pine (*Pinus banksiana* Lamb.) communities in NW Ontario that grew after fire, clearcutting or clearcutting with mechanical site preparation plus prescribed burning. They did, however, find significant differences in species composition (MRPP, A=0.065, P=0.003) among the treatments. The communities with the two disturbances (fire plus mechanical site preparation) had higher early successional (deciduous) species derived from seed banking, wind dispersal, and alien origin when compared to wildfire or clearcut with mechanical site preparation sites, and that the latter showed no specific trait associations.

Paquette and Messier (2011) developed and ran structural equations with inputs from an extensive Quebec forest plot data set (1970 – 2010) and showed that beneficial interactions between species may be the most important mechanism in the more stressful environment of boreal forests, compared to competitive exclusion processes in the more productive temperate forests. Reich *et al.* (2012) reported that stand age and disturbance type prior to current stand origin had very little impact on vascular plant species composition or diversity data collected in northeastern Minnesota boreal forest stands (age 19-133 years old). In contrast, increased basal area reduced plot-scale species richness due to competitive exclusion from light, the most limiting resource, while at very low light levels, overall vascular understory cover was low which alleviated resource competition and resulted in an increase in species richness.

Hart and Chen (2008) reported on the response of boreal mixedwood forests (7-31 years post-harvest, 7-201 years post fire) showing that vascular species richness was lower in older stands but higher for nonvascular species. They also reported that total understory species composition and diversity in post-logged stands and post-fire stands were similar, but that logged sites had higher vascular species richness and lower nonvascular species richness, attributing this to higher pre-established rhizomatous species and few pyrophytic species on post-logged sites.

Both ecological experiments and observational studies have almost consistently shown that plant species response and effects are influenced by the disturbance regime and resource availability (Hooper *et al.* 2005, Reich *et al.* 2001). Different species possess different traits that facilitate preferential survival under different biophysical site conditions (Nilsson and Wardle 2005, Bell *et al.* 2011). It is well documented that key functions affecting productivity in forests include the availability of light (Messier *et al.* 1999, Reich *et al.* 2012), nitrogen (Reich *et al.* 1995, 1998, Finzi and Canham 2000) and the provision of water and nutrients for vegetative uptake and nutrient cycling. These, in turn, vary with soil texture, soil organic matter content and the suite of plant species growing on a given site and their abundance (Lavorel *et al.* 1997, Nilsson and Wardle 2005, Bell *et al.* 2011).

Ecologists are testing the validity of some of the historically influential frameworks in ecological theory related to the diversity response to disturbance and the productivity-diversity relationships. Many of the foundational concepts remain highly debated, both theoretically (Tokeshi and Schmid 2002, Li *et al.* 2004, Shea *et al.* 2004) and empirically (Frank and McNaughton 1991, Hooper *et al.* 2005, Fargione *et al.* 2007). In this thesis, I consider two of these - the intermediate disturbance hypothesis (IDH) and the mass ratio hypothesis (MRH) - that underpin much of our understanding of community response to disturbance and the relationship of diversity to disturbance.

IDH presents the hypothesis that diversity response follows a unimodal response pattern, with highest diversity at medium disturbance intensities and frequencies and lower diversity at both low and high levels (Connell 1978). The second theory, MRH, proposes that dominant species (defined by greatest biomass) on a given site, regulate key ecosystem functions that create or sustain conditions favorable to their continued dominance on a given site (Grime 1998). This appears to conflict with the IDH and can be problematic for land managers who have less comfort designing systems that sustain a dominant cover type or monoculture.

Despite the lack of conclusive evidence, there is widespread acceptance of the IDH and the assumption that high biodiversity equates with high productivity (Chapin 2000, Loreau 2000, Tilman *et al*. 2001, Cardinale *et al.* 2007). Highest richness is often, but not always associated with intermediate levels of biomass (Grime 1979, Grace et al. 2000, Keddy 2005,). The evidence to support a positive relationship between productivity and species richness is largely restricted to recently disturbed habitats (early successional communities) or on nutrient poor sites (Naeem et al. 1994, Tilman et al. 1996, Hector et al. 1999, Loreau and Hector 2001, Aarssen et al. 2003). On more fertile sites, or in later stages of succession, the relationship is often neutral or negative (Aarssen et al. 2003, Gross and Cardinale 2007, Laughlin et al. 2008). Many natural resource management policies and practices are designed to minimize risks to losses in diversity and by assumption to minimize loss of ecosystem productivity by sustaining community diversity. For example, the retention of biodiversity and maintenance of ecosystem productivity are the principles upon which sustainable forestry is practiced in Ontario (CFSA 1994, OMNR 2012). Yet our understanding of the impacts of current forestry practices on community assembly and plant diversity remain poorly understood (Roberts 2004, Gilliam 2007). Given that the IDH proposes that intermediate levels of disturbance is associated with high diversity, and the MRH contends that the dominant species (defined by biomass), not high diversity, is the key to sustaining ecosystem integrity, and productivity, it is important to understand where each of these hypotheses are most relevant (Grime 2001).

The study reported here investigates the effects of harvest disturbance (treatment types), site type, and their interaction, on plant community diversity and species composition in boreal black spruce forests 15 years after disturbance, using a well-structured replicated set of treatment plots established as part of a long-term research project in northwestern Ontario in the mid-1990's (Duckert and Morris 2001, Gordon *et al.* 2001). The results will contribute to furthering our understanding of the applicability of the IDH and to a lesser degree to MRH to the prediction of boreal understory plant community diversity and compositional response to disturbance on loam site types, sand site types, and peat site types under varying levels of biomass removal.

1.2 Geographic Setting: Ontario's Boreal Forests

Black spruce forests are well suited for studying plant community diversity response to disturbance for a number of reasons: 1) black spruce has a broad ecological amplitude dominating a wide range of soil/site conditions (Sims *et al.* 1990, 1996) and response can thus be examined on sites on a range of conditions, 2) the vegetation in boreal conifer forests has evolved in the presence of cyclical disturbances from fire, insect, disease and wind and groups of species display different strategies for surviving these disturbances (Rowe 1983), 3) these natural disturbances occur at different intensities and plant community response is known to vary as a function of this intensity (Haussler and Bergeron 2004), 4) boreal understory species, whose life cycles are relatively short, represent an important component of annual readily decomposable plant material and the largest proportion of above ground biomass in young post-disturbance boreal forest communities (Haussler and Bergeron 2004), 5) black spruce is a major commercial forest species and harvesting is an ongoing economic value to northwestern Ontario communities (MNR 2012), and 6) boreal forests have become the subject of growing interest given their important role in global biodiversity, carbon storage and mitigation of climate change (MNR 2012).

In Ontario, 17.7 million ha of forests representing about 41% of the province's total productive forest land has a prominent black spruce component (OMNR 2002, Chen and Wang 2006) currently accounting for 36% of the total volume growing stock by species group (OMNR 2012). Black spruce is one of the two main commercial conifer species harvested in Ontario representing 37% (4.95 million m^3 y^{-1}) of the total harvest volume

(13.5 million m^3 y^{-1}) in 2010/2011 (OMNR 2012). Fire (average 50 to 150 year cycle for Ecoregion 3W, Crins *et al.* 2010) and defoliation by spruce budworm are the prominent natural disturbances in these forests with the forest community species possessing a variety of adaptations to thrive in these disturbance environments (Rowe 1985, OMNR 2012). The proportion of productive forest annually disturbed by harvest averages 4% or 2.3 million ha y^{-1} which is similar to the average annual area disturbed by fire (3.8% per year, 2.2 million ha y^{-1}) (OMNR 2012). Current harvesting practices remove most of the overstory canopy then leave sites for natural regeneration or apply mechanical site preparation methods (patch scarification or disk trenching on mineral soils; winter shear -blading on some forested peatlands) that create favorable planting sites.

1.3 The Research Questions

Given land managers' mandate to sustain both biodiversity and ecosystem functions, they need to understand and predict the community response to the suite of approved forestry practices on different site types. Both the number of different species (diversity) and the types of species (species composition with their related specific traits, such as mode of reproduction, shade tolerance, growth form, growth rate, nutrient requirements) influence a community's response to disturbance. Given the wide geographic distribution of spruce and its important economic value, the results from this study will have broad application as input to forest harvest and silvicultural guides. For example, the results may lead to recommendations to modify harvest intensity by site-type, where required, to minimize the loss of native plant species diversity. This thesis examines the following questions:

1. Is there a significant disturbance effect of the level of biomass removal associated with harvesting treatments on plant diversity in boreal black spruce understory communities? If so, is this response consistent with the IDH or MRH?
2. Is there a significant disturbance effect of the level of biomass removal associated with harvesting treatments on species composition?
3. Are the effects, if any, consistent across site types?

A survey of plant species presence and abundance and key environmental site characteristics in boreal black spruce communities 15 years after the application of four harvesting disturbances with four levels of biomass removal, on three site types was carried out to study these questions. The treatments included uncut reference condition (UNCUT), tree-length harvesting (TL), full-tree harvesting (FT), and full-tree harvesting plus blading to remove the residual understory and the surface O-horizon (FTB). A full description of these harvesting treatments is provided in the methods section (Section 3.2) of this thesis.

The study examines both the overall community diversity response in terms of richness (R), evenness (E), two widely adopted indices [Shannon's (H') and Simpson's, (D)] and plant species composition response. The analysis was conducted at the alpha, or species level, with a follow-up examination of the response of groups defined by dominant reproductive strategies (seed, vegetative, both). Where significant response patterns were detected or where past research pointed out particular functional groups as important in structuring community reassembly, the elements were partitioned out for examination (e.g., ericaceous species compared to non-ericaceous species).

The results will: 1) provide quantitative data to evaluate the biodiversity effects of current harvesting systems on loam, sand and peat site types, 2) assess the effects of clearcut harvesting on biodiversity, 3) assist in furthering our understanding of disturbance ecology, and 4) provide information for updating provincial management guides for conserving biodiversity at the landscape and stand and site scales (OMNR 2010).

1.3.1 Formulation of Hypotheses

Two broad hypotheses provided the context for this study. Within each of these, specific hypotheses were constructed to test the influence of the retention or removal of biomass as implemented by the harvesting treatments on species diversity and species composition response: 1) the retention or removal of the overstory, 2), the retention or removal of the harvest residual branch and foliage material (fine woody material - FWM), and 3) the retention or removal of the understory vegetation and the surface organics (O - layer) after clearcut harvesting.

Hypothesis 1: There will be a significant disturbance-site type interaction on species diversity on loam, sand and peat site types. The response will be a linear increase in diversity from low to high disturbance on loam site types where favorable establishment and growing conditions will support species germination and survival on the exposed mineral soils after the high disturbance (i.e., inconsistent with IDH). The response will be unimodal on sand site types where the additional opportunities for establishment of sun-tolerant species among the pre-disturbance vegetation will increase species diversity at intermediate disturbances, but will be countered by the increased stress (microclimate fluctuations, drought on the sand) after high disturbance reducing the number of species able to establish (i.e., consistent with the IDH). The response on peat site types will be low in magnitude because of the overriding influence of the dominant ericaceous and sphagnum species suppressing the establishment and survival of all but a few species that can survive the wet acidic site conditions (i.e., consistent with the MRH).

Hypothesis 2: There will be a significant disturbance-site type interaction affecting plant species composition. Species compositional response will be highly variable on loam site types compared to sand and peat site types, reflecting the more rapid growth of which ever species are first to arrive on the more favorable loam-textured soils. The first species to arrive may vary from plot to plot. The predicted smaller pool of species able to establish, especially on the harsh conditions of the bare mineral soil or bladed peat mat, will reduce species diversity. The less than optimal growing conditions, will slow growth rates thus lengthening the opportunity for species to establish, leaving more time for the species that are best suited for these site conditions to establish and over time, dominate the plots.

On the sand site type, species adapted to disturbed open habitats will increase in diversity on the FTB sites, while forest species adapted to sheltered shady conditions will be absent. On the peat site type, ericaceous species will increase in abundance after TL and FT treatments, responding to the increased light availability when compared to the uncut forest, and will limit the number of other species on those sites. Graminoids, such as cottongrass (*Eriophorum* species) or Canada blue-joint grass (*Calamagrostis* *canadensis* (Michx) Beauv.) that are wind-dispersed in high numbers and then rapidly expand through vegetative clonal reproduction to form both a dense root mat and a dense foliage cover will have established and increased in abundance on FTB treatment limiting the ability of other vascular species to establish on these sites. In addition, the reestablishment of the pre-disturbance ericaceous shrub cover will originate from the vegetative reproduction of plants growing on the edge of the treatment plots.

This thesis is structured as follows. Section 2 will present the results of the literature review that summarizes the current relevance of the IDH and MRH in terrestrial disturbance ecology. This paper has already been published in Critical Reviews in Plant Sciences (Kershaw, H.M. and Mallik, A.U. 2013. Predicting plant diversity response to disturbance: applicability of the intermediate disturbance hypothesis and mass ratio hypothesis. Critical Reviews in Plant Science 32:383-395). Section 3 outlines the methods used for this study. Results are presented in Section 4 in two subsections: the first addresses hypothesis 1 and presents the results from the assessment of diversity response for total species, vascular species and life form groups; the second addresses hypothesis 2 and presents the results of the analysis of species presence and abundance (percent cover) at the taxonomic level. Section 5 presents a discussion of the findings integrating the results from the diversity and species composition assessments. Conclusions, including management implications and recommendations for future work, are presented in Section 6.

2.0 LITERATURE REVIEW - PREDICTING PLANT DIVERSITY RESPONSE TO DISTURBANCE: APPLICABILITY OF THE INTERMEDIATE DISTURBANCE HYPOTHESIS AND MASS RATIO HYPOTHESIS[1]

2.1 Introduction

There has been a growing interest in understanding and predicting post-disturbance plant community diversity and ecosystem function to achieve the objectives of sustainable ecosystem management (Roberts 2004, Tikina *et al.* 2010, Moore *et al.* 2012). A general assumption in this context is that maintenance of high biodiversity will ensure ecosystem sustainability and productivity (Chapin *et al.* 1997, Tilman *et al.* 1997, Mayfield *et al.* 2010). The predicted increase in natural disturbance, triggered by climate change and increased rate of resource extraction, compel us to better understand ecosystem response to disturbance intensity and frequency, particularly in forested and grassland ecosystems. Land managers need to predict how ecosystems might respond to certain management prescriptions and reject the ones that might reduce biodiversity and productivity. One must also understand the influences of post-disturbance high biodiversity and that of dominant species on ecosystem integrity and productivity on a site. This is known to vary with ecosystem type and site productivity (Kondoh 2001, Li *et al.* 2004, Hughes *et al.* 2007).

In theory, the distribution of plant species across the land- scape follows a set of principles known as the community assembly rules (*sensu* Keddy 1992). The typical patterns of community assembly and species diversity, however, shift with disturbance intensity and frequency and site productivity (Connell 1978, Craine 2005, Craine *et al.* 2007, Kohv *et al.* 2013). Several hypotheses have been developed over the past few

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[1] This section was published as: Kershaw and Mallik (2013). Some sections have been modified based on the external examiners review.

decades to predict and explain these patterns by integrating key drivers of post-disturbance plant colonization, establishment, resource acquisition and growth that collectively contribute to community assembly and succession. The Intermediate Disturbance Hypothesis (IDH - Connell 1978) and the Mass Ratio Hypothesis (MRH - Grime, 1998) are the two overarching concepts that predict plant community assembly response to disturbance (Craine 2005, Grime, 2007).

The IDH proposes that species diversity displays a hump- shaped response curve to disturbance, peaking at intermediate disturbance levels (Figure 2.1). This hypothesis is built on the premise that disturbance prevents highly competitive species from excluding other species from a community. This is attributed to a trade-off between a species' ability to compete and their ability to tolerate disturbance. At low levels of disturbance only the strongest competitors persist leading to low diversity. At very intense or frequent disturbance, only a few disturbance tolerant species from the regional species pool survive the less-than optimum growing conditions and colonize after each disturbance, which also yields low species diversity (Connell 1978, Roxburgh *et al.* 2004).

Only at intermediate disturbance levels is there a balance between competitive exclusion and ruderal species establishment. This favors the coexistence of competitive and disturbance tolerant species leading to maximum species diversity (Mackey and Currie 2001). This matches a parallel peak in plant biomass comprised of the cumulative biomass of a number of species (Figure 2.2). With time since disturbance, site biomass remains high, sustained by the surviving long-living shade tolerant species as the less tolerant species die out.

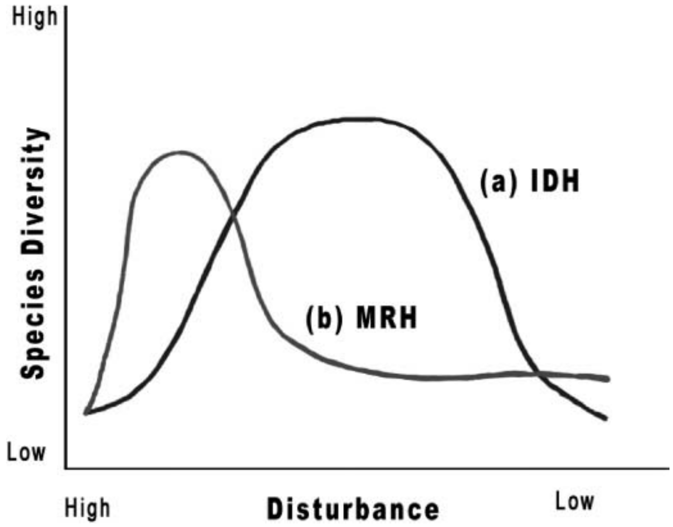

Figure 2.1 Predicted relationship between species diversity and disturbance in IDH and MRH. (a) Typical hump-shaped curve of species diversity-disturbance intensity/frequency/time since disturbance showing highest species diversity at intermediate level of intensity/frequency/time since disturbance while lowest diversity at the two extremes as per IDH. (b) Highest species diversity at high disturbance frequency/intensity/immediately after disturbance contributed by disturbance and stress tolerant and competition intolerant species. At less frequent/low intensity disturbance only stress tolerating and competitively superior species persist resulting low diversity as per MRH.

The Mass Ratio Hypothesis (MRH), on the other hand, pro- poses that the biological traits of the dominant species contributing to productivity (defined by biomass) are the critical regulators of ecosystem function (Grime 1998, McLaren and Turkington 2010). The MRH is built on the premise of a linear (increasing) response of one or a few species to biotic and abiotic site conditions after disturbance, and that the influence of the species that is best able to rapidly capture resources on key ecosystem functions is proportional to its biomass (Garnier *et al.* 2004, 2007, Vile *et al.* 2006, Mokany *et al.*

2008). This concept implies that a recently established species (after disturbance) has less influence on ecosystem function than the mature dominant species of the community. Given time, the species that is best able to rapidly reproduce and/or outgrow other species will influence the site proportional to its biomass. This could be either a newly introduced species after disturbance or the expansion of a pre-disturbance resident species. Thus, according to MRH, this key species will disproportionately modify the environmental conditions to favor its own survival through a positive feedback mechanism that creates conditions often less favorable to other species and hence create low species diversity (Polley *et al.* 2006, Mokany and Ash 2008).

The legacy left by the dominant species on a given site may also continue to influence ecosystem function proportional to its pre-disturbance abundance, long after the disturbance (Garnier *et al*. 2007). For example, when a pre-disturbance community was dominated by red raspberry (*Rubus idaeus* L.) or rapidly growing sedge (*Carex* spp.) prior to disturbance, the community will often initially recover as a young short-lived diverse community of ruderal species. This would rapidly transition to a shrub (raspberry) or sedge (*Carex* spp.) dominated community, originating from persistent underground reproductive structures. A second example would be the rapid establishment and dominance of jack pine (*Pinus banksiana* Lamb.) following fire, originating from the germination of seeds protected in residual serotinous pine cones from the pre-fire mature pine canopy (Greene *et al.* 1999). The shade created by the newly established jack pine community limits the survival of many post-disturbance colonizing species.

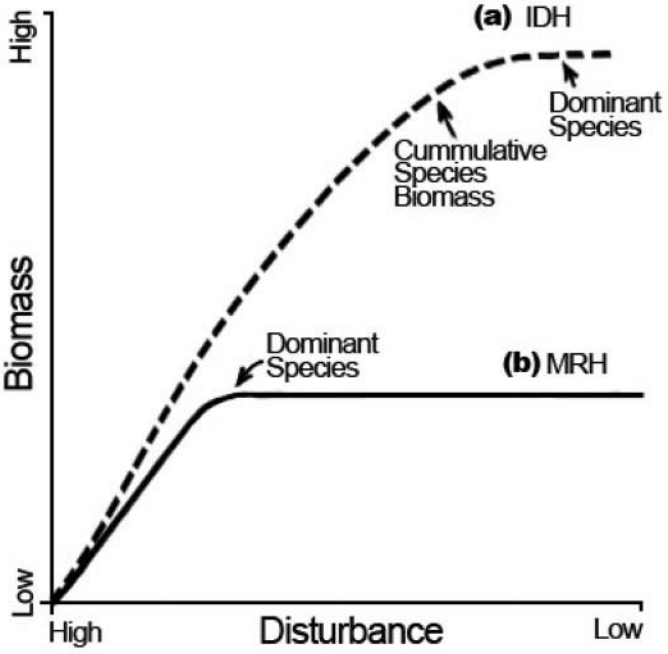

Figure 2.2 Predicted relationship between community productivity and disturbance in IDH and MRH. (a) Community productivity (biomass) increases with decreasing disturbance frequency/intensity/time since disturbance until it reaches an equilibrium at climax condition when mostly the long-lived species account for the community biomass, commonly observed in mineral rich productive sites as per IDH. (b) Community productivity (biomass) increases with decreasing disturbance frequency/intensity/time since disturbance until it levels when only a few stress tolerating competitive species achieve dominance and contribute most of the community biomass observed in organic rich, nutrient- poor acidic soil as per MRH.

The diversity response predicted by the MRH is displayed in Figure 2.1 showing that species diversity increases rapidly to a maximum, shortly after disturbance (with expectations that maximum diversity would be lower than that predicted by IDH) then progressively declines with time since disturbance or with decreasing intensity/frequency of disturbance as only a few stress tolerating competitive species dominate. The prediction is that this leads to a self-regulating stable community whose integrity is regulated by the dominant species (Polley *et al.* 2006, Mokany *et al.* 2008). This pattern contrasts with that predicted by the IDH that shows a much longer period of increasing diversity and a slower decline in diversity with time since disturbance. IDH is portrayed as a cyclic pattern of disturbances in terms of intensity and frequency, describing communities that become less stable with time (as diversity decreases) and more vulnerable to disturbance. It is commonly associated with fire-driven terrestrial ecosystems (Mackey and Currie 2001).

MRH is often associated with ecosystems with longer periods between major stand replacing disturbances. It proposes that biodiversity is held low by the dominance of one or a few species (see right side of the graph, Figure 2.1) and that this configuration sustains site productivity (Loreau 2000, Srivastava and Vellend 2005, Wright and Jones 2006, Kikvidze *et al.* 2011).

Ecosystems supporting periods of low biodiversity are not always less productive than earlier phases of higher biodiversity on the same sites (Loreau 2000, Srivastava and Vellend 2005; Wright and Jones 2006; Kikvidze *et al.* 2011). For example, communities dominated by a few ericaceous and sphagnum species can be relatively productive and remain stable for extended periods of time (Mallik *et al.* 2010, Siegwart-Collier and Mallik 2010). These few ericaceous species create soil conditions unfavorable for establishment of seed reproducing conifer and other species (Morris et al. 2009).

Both habitat and plant trait response to disturbance are key components of species diversity of an ecosystem (Grime 1977, Tilman *et al.* 1982, Tilman 1987, Grime *et al.* 1997, Meyers et al. 2001). They represent the fundamental components of abiotic filters (seedbed availability) and biotic filters (competitive exclusion) which are the inferred mechanisms of both IDH and MRH. The relationship between disturbance intensity and biodiversity, central to IDH, has lead to the principle that the maintenance of biodiversity following disturbance is pivotal for sustaining ecosystem integrity and productivity (see review by Srivastava and Vellend 2005). The influence of the disturbance – productivity (biomass) relationship, central to MRH supports the principle that the maintenance of dominant species is critical to sustaining ecosystem productivity and the presence of less abundant species has little relevance (Grime 1998, Loreau 2000, Wright and Jones 2006, Kikvidze *et al.* 2011).

Broader reviews of experimental work that examined the effects of disturbance on species diversity and productivity in a wide range of terrestrial and aquatic ecosystems have been conducted by Mackey and Currie (2001), Li *et al.* (2004) and Hughes *et al.* (2007). They report conformity to IDH rates as low as 16%. In the most recent review of 1000 studies on disturbance- diversity models, the authors reported that only 16% (160 studies) showed support for the IDH (Svennson *et al.* 2012). Despite this low conformity, they found over 3300 citations of IDH for all ecosystems combined (Web of Knowledge search up to 2010), with over 33% citations published in the past five years (2006 and 2010) (Svennson *et al.* 2012). Similarly, Hughes *et al.* (2007) reported low conformity to IDH in their review of 94 articles that examined the effects of disturbance on diversity (richness). They reported that only 18% of the experiments reviewed (23 out of 130) conformed to the classic humped-shape curve of IDH with highest conformity associated with marine macro-algal ecosystems (Hughes *et al.* 2007). They concluded that disturbance had variable effects on diversity.

The work of Hughes *et al.* (2007) followed an earlier review of observational and experimental studies by Mackey and Currie (2001), who reported that the most common disturbance - diversity response was positive, not hump-shaped. Bi-modal curves (c.f., Roxburgh *et al.* 2004, Potthoff *et al.* 2006, Bongers *et al.* 2009, Banitz *et al.* 2008, dos Santos *et al.* 2010), linear increasing or linear decreasing diversity response (c.f., Cadotte *et al.* 2006, Cadotte 2007) and those with no clear pattern (c.f., Svensson 2007, 2012, Bongers *et al.* 2009, dos Santos *et al.* 2011) are also reported. In a recent provocative opinion paper, Fox (2013) goes so far as suggesting outright abandonment of the IDH because of its lack of conformity with the hump shaped diversity-disturbance relationship. We suspect that in these assessments, two potential confounding factors, ecosystem type and site productivity might have been overlooked in determining the conformity of IDH.

In this review, we examine the applicability of IDH and MRH in predicting species diversity and productivity response patterns to disturbance in terrestrial ecosystems at local and regional scale. The lack of conformity to IDH reported in the literature for terrestrial ecosystems, the perception that environmental factors may influence conformity, and the different diversity response pattern to disturbance predicted by the IDH and MRH formed the basis of our review. We connect our conclusions to land management policy implications.

At the local scales, plant traits associated with reproduction, dispersal, growth and environmental constraints strongly influence community assembly and species composition over time (Belyea and Lancaster 1999, dos Santos *et al.* 2010). Our intent was to assess whether conformity to IDH and MRH was a function of ecosystem type, landscape type or site productivity. Conclusions from this review may foster a re-examination of current land management policies designed to create disturbances to maximize plant diversity on all site types to enhance ecosystem sustainability and productivity.

We anticipated that (1) the highest conformity of species diversity response to disturbance patterns with IDH in terrestrial ecosystems would be reported for grassland ecosystems occupying upland sites of intermediate productivity, and (2) that species diversity and productivity (biomass) response to time since disturbance would conform with the MRH in ecosystems of low productivity such as boreal peatland forests and upland alpine meadows. We predicted that the upland terrestrial sites of intermediate productivity would provide conditions that facilitate the coexistence of species with all three traits proposed by Grime (1977), competitive (C-species), stress tolerant (S-species), and ruderals (R-species). On nutrient-poor lowland sites, however, high moisture and low pH will limit nutrient availability and create conditions where, the ability of a species to survive despite limited resources may override any trends created by disturbance intensity/frequency. Similarly on xeric sites the limitation of moisture will restrict the rate of nutrient availability and create less than favorable conditions for many species to regenerate. Thus, environmental stress filters associated with these sites may limit the species pool regardless of disturbance intensity (Keddy 1992, Lavorel and Garnier 2002). On these sites, of cold, wet and nutrient poor conditions, a few species that can successfully establish and thrive through positive plant-soil feedbacks modify local conditions to favor their expansion after disturbance creating low species diversity consistent with the MRH.

2.2 Assessment of Biodiversity Response to Disturbance Models

2.2.1 Literature Search

In September 2011, we searched the ISI Web of Science^{SM} (Thompson Scientific, Stamford, CT) database using combinations of the following keywords: IDH, intermediate disturbance hypothesis, mass ratio hypothesis, MRH, Grime's mass ratio hypothesis, boreal, plant ecology, forestry, boreal forest, plant assembly, boreal understory, understory, and grasslands to select relevant papers on IDH and MRH for terrestrial ecosystems.

We limited our search to recent publications (1999 to 2011) because this captures the results of work that benefits from at least ten years of testing since the hypotheses were proposed with an equal scope for both searches. We acknowledge that the publications on IDH, first introduced in the 1970s (Connell 1978), have benefited from additional time for testing. We selected papers that tested or discussed IDH and/or MRH, including experimental results, observational studies, modelling and broader meta-analysis that focused on synthesizing the latest understanding of these two hypotheses. This contrasts with earlier reviews that limited their scope to reviewing only experimental and/or observational field studies in relation to the IDH alone (Li *et al.* 2004, Mackey and Currie 2011).

From the retrieved articles, 60 papers published over the past ten years were selected that met the following criteria: 1) the papers focused on terrestrial ecosystems, 2) research was designed to test the validity of IDH or MRH, and, 3) IDH or MRH were provided as explanatory theories for the research results. This excluded a large number of papers that dealt with aquatic ecosystems including benthic communities, plankton communities, and the field of microbiology.

We recorded the original author's interpretation of the results as to: 1) support for the IDH (response variable showing the classic hump-shaped curve), 2) rejection of the IDH, 3) support of MRH, 4) rejection of MRH, or 5) mixed or inconclusive. The ecosystem types identified as forests (boreal forest, boreal plantations, tropical or sub-tropical forest, temperate forests) or herbaceous (grassland, savannah, or alpine meadow). Landscape type was defined as upland, lowland, or mixed (a combination of upland and lowland terrain). The productivity of the ecosystem studied was assigned into four broad classes based on net primary productivity (NPP) by biome: high (tropical forest 925 g C $m^{-2}y^{-1}$); medium high (savannah and temperate forest 790 and 670 g C $m^{-2}y^{-1}$ respectively), medium (boreal forest and plantations, 355 g C $m^{-2}y^{-1}$ and 670 g C $m^{-2}y^{-1}$ respectively), and low (temperate grasslands 350 g C $m^{-2}y^{-1}$ and alpine meadow 105 g C $m^{-2}y^{-1}$) (http://daac.ornl.gov/ NPP/other files/worldnpp1.txt accessed August 2012). In addition, each paper was classified as: 1) designed to test the IDH, 2) IDH was a post-research compliance test, 3) designed to test MRH, or 4) MRH was a post-research compliance test. As per Mackey and Currie (2001) and Hughes *et al.* (2007), only those papers that dealt with disturbance effects on communities over a time scale that was relevant to the communities being studied were selected for further analysis.

2.2.2 Data Analysis

The 60 papers selected from the review were critically examined in relation to species diversity response to disturbance in terrestrial grassland or forest ecosystems (Table 2.1). An initial scan was carried out to determine if the distribution of emphasis in the suite of selected papers was weighted more towards IDH or to MRH. We then determined if compatibility with IDH or MRH were significantly associated with any of the three variables of interest: ecosystem type, landscape type, or site productivity. We ran a series of nonparametric tests of comparison of independent samples to test our hypothesis that conformance with IDH and MRH were a function of ecosystem type, landscape type, and site productivity. We applied the Kruskal-Wallis H Test to accept/reject the null hypothesis that the distribution of ecosystem type, landscape type, and site productivity is the same where IDH model held true and tested for significance at $\alpha = 0.05$ probability. We reran the same model for MRH. The nonparametric tests were only run on records that were based on field studies ($N = 50$, which included papers that reported on IDH and MRH). Only those results that rejected the null hypothesis are reported. All statistical tests were conducted using SPSS ver. 19.

2.3 Patterns of Biodiversity Response to Disturbance

2.3.1 Compliance and Deviations

Approximately 80% papers (48 out of 60 papers) met the screening criteria for IDH and 25% (15 of 60 papers) met the MRH criteria, when all papers reviewed were included. Four papers compared the disturbance response to both IDH and MRH and were counted for both IDH and MRH (this replication results in a total exceeding 100%). Over one-third (37%, 22 of 60 papers) reported experimental or observational results in herbaceous ecosystems (primarily grasslands and savannah) and 40% papers (24 of 60 papers) discussed disturbance response in forested ecosystems, the latter distributed between boreal (14 papers), temperate (5), or tropical (5) forests. The remaining papers were syntheses of published work (meta-analysis) and theoretical modelling. Because the papers reporting on herbaceous communities were almost exclusively from grassland ecosystems, testing the degree of conformance with the response model to types of communities was not carried out on this subset of the data.

Of the papers that examined the validity of IDH approximately 46% reported compliance (n = 22 out of 48), and 17% (n = 8 out of 48) rejected IDH. The remaining papers (37%) were inconclusive, with most authors reporting weak conformance.

Among the 15 papers referring to MRH eight papers (53%) reported conformity with MRH, four (27%) explicitly rejected it. The remaining three papers (20%) reported mixed results. Explicit reference to MRH was uncommon in the disturbance ecology literature with fewer than 10% (194 of 2100 references) referring to MRH based on a broad search using the key words, community assembly and disturbance ecology within the Web of Science search engine.

2.3.2 Is Compliance Associated With Ecosystem?

Selecting only those papers that reported on field studies ($n = 50$), we ran a nonparametric test of independent samples using the Kruskal-Wallis Test (because the data were not suitable for parametric analysis) to see if ecosystem type, landscape type, or productivity class was associated with compliance of IDH or MRH. The null hypothesis was rejected for productivity class at $p < 0.05$ level ($p = 0.028$) and landscape type ($p = 0.0037$) but retained for ecosystem type ($p = 0.656$). Our exploration of the data suggests that more detailed examination of the relationship of compliance with IDH and MRH with environmental variables would be helpful in furthering our understanding of ecosystem response to disturbance patterns. Visual inspection of scatter plots showed that MRH compliance was more common on sites of low productivity. Given the small size of the data set for field based studies ($n = 8$) no quantitative analysis was carried out.

2.4 Relevance of IDH and MRH to Land Management

2.4.1 Reasons for Compliance or Deviation

We set out to assess the current state of empirical support for the widely used hypotheses, IDH and MRH, that relate ecosystem disturbance to biodiversity and ecosystem stability, in order to determine if conformance to each hypothesis is related to ecosystem type, landscape type or site productivity. We found that conformance of

IDH reported in past reviews ranged from 16 to 21% when considered all ecosystem types together. This contrasts with our findings, which showed that conformance in studies conducted in terrestrial ecosystems was 46%, whereas 17% reported noncompliance and the remaining studies reporting inconclusive or weak conformity. Studies in temperate and tropical forests showing clear conformance of IDH were very few, but the proportion was equal (4 of 8 studies; 3 of 6 studies). Very few studies tested or explained their results with the MRH (*N* = 10 for studies that reported field results), half reporting non-conformity and half reporting compliance.

We found that only two studies were specifically designed to test the IDH or MRH hypotheses. Most studies reframe their conclusions into these hypotheses as an explanation of the observed patterns. The first paper by Mokany *et al.* (2008), examined the diversity hypothesis (the diversity of organisms in a community influence ecosystem processes, for example by complementary resource use) and the MRH (ecosystem processes are determined primarily by the functional traits of dominant species) as an explanation of the observed variation in ecosystem processes in a temperate native grassland. They demonstrated that the key traits of dominant species predicted the effect of plants on ecosystem processes, consistent with MRH. They reported a poor correlation of species richness with productivity. Responses reported for other studies of productive grasslands showed linear increases in species richness with increased grazing, no response, or decreases attributed to the complexity of interactions (Proulx and Asit 1998, Polley *et al.* 2006). Another example of these complex interactions was the

Table 2.1 Studies published between 1999 and 2011 that illustrate the evidence of conformity or rejection of IDH and MRH for terrestrial plant communities.

Hypothesis Conformity	Ecosystem Type	Landscape Type	Study Type	References
Accept IDH	Boreal Forest	Upland, mixed	Field Studies	Hauessler et al., 2002; Jobidon et al., 2004; Mandryk and Wein, 2006; Hart and Chen, 2008; Biswas and Mallik, 2010; Heikkinen and Makippaa, 2010
Accept IDH	Boreal and Montane	Conifer Upland	Field Experiments	Roberts and Zhu, 2002; Widenfalk and Weslien, 2009; Peter and Harington, 2009; Wang and Chen, 2010
Accept IDH	Temperate Forest	Upland	Field Studies	Jobidon et al., 2004; Suzuki, 2008; Zinck et al., 2010
Accept IDH	Tropical and Sub-Tropical Forest	Upland	Field Studies	Molino and Sabatier, 2011; Nzunda, 2011
Accept IDH	Tropical	Mixed	Modeling Literature Review	Sheil and Burslem, 2003
Accept IDH	Grassland, Savannah	Upland	Field Studies	Smith and Knapps, 2003; Leis et al., 2005; Peterson and Reich, 2008;
Accept IDH	Grassland	Upland	Field Experiments	Martin-Queller et al, 2011
Accept IDH	Alpine Meadow	Upland	Field Studies	Mark and Whigham, 2011
Weak support IDH	Boreal Forest	Upland	Field Experiments	Manninen et al., 2009
Weak support IDH	Boreal Peatlands and Temperate Riparian	Lowlands	Field Experiments	Benscoter and Vitt, 2008; Moore and Franklin, 2011
Weak support IDH	Temperate	Upland	Field Studies	Palmer et al., 2000; McWethy et al., 2010
Weak support IDH	Tropical Forest	Upland	Field Studies	Koehler and Huth, 2007; Lindenmayer *et al*., 2008; Bongers *et al*., 2009
Weak support IDH	Grassland	Upland	Field Studies	Warren-Rhodes *et al*., 2007
Weak support IDH	Grassland, Savannah	Upland	Field Experiments	Beckage and Stout, 2000; Dupre and Diekmann, 2001; Sasaki *et al*., 2009; Vicente *et al.,* 2010
Weak support IDH	Terrestrial (Boreal, temperature, grassland)	NA	Models, Metanalysis	Cordonnier *et al*., 2006; Kadmon and Benjamini, 2006; Hughes *et al.*, 2007; Koehler and Huth, 2007; Dos Santos *et al.*, 2010; Kikvidze *et al.*, 2011
Reject IDH	Temperate Forest	Upland	Field Experiments	Langhans *et al.*, 2010
Reject IDH	Temperate and Tropical Grassland/Savanna	Upland	Field Experiments	Li *et al.*, 2004; Mokany *et al.*, 2008; O'Bryan *et al.*, 2009; Loiola *et al.*, 2010
Reject IDH	Grassland	Upland	Field Studies	Warren-Rhodes *et al.*, 2008; Langhans *et al.*, 2010
Reject IDH	Variety	Mixed	Models, Metanalysis	Mackey and Currie, 2001; Whittaker *et al.*, 2001, Shea *et al.*, 2004
Accept MRH	Boreal	Upland	Field Experiments	Gilbert *et al.*, 2009
Accept MRH	Grassland	Upland	Field Studies	Garnier *et al.*, 2004; Srivastava and Vellend, 2005, Polly *et al.*, 2006, Cortez *et al.*, 2007 Mokany *et al.*, 2008; O'Bryan *et al.*, 2009, Pakeman *et al.*, 2010, 2011
Weak Support MRH	Grassland	Upland	Lab and/or Field Experiment	Vile *et al.*, 2006; Sasaki and Lauenroth, 2011
Reject MRH	Boreal Forest – Heath	Lowland	Field studies	Bloom and Mallik, 2006; Mallik *et al.*, 2010
Reject MRH	Variety	Variety	Models, Metanalysis	Loreau 2000; Whittaker *et al.*, 2001; Hooper *et al., 2005*

variation of within and inter-biotic reactions associated with edible vs. non-edible species ratios leading to uneven grazing pressures. Linearity in responses and conformity with MRH were commonly reported for both very productive sites and nutrient-poor sites, for example, diversity and productivity studies in very productive grasslands (Polley *et al.* 2006, Diaz *et al.* 2007).

A second paper presented the results of a species removal experiment that tested the effect of early-successional species on the recruitment of dominant species in disturbed North American grasslands and in turn how this affects nitrogen retention in soil-plant systems (Polley *et al.* 2006). The data showed that production and accumulation of nitrogen by plants declined after the removal of early season annuals in proportion to the contribution of annuals to above-ground biomass and nitrogen, consistent with MRH.

Both IDH and MRH models were commonly used as a reference for comparison with observations of species diversity response to gradients of disturbance (Biswas and Mallik 2010) or to predict ecosystem response in the context of climate change (dos Santos *et al.* 2010). Molino and Sabatier (2001) explained observed species diversity in tropical forests ten years after disturbance in French Guiana with IDH. Biswas and Mallik (2010, 2011) explained species diversity-functional diversity relationships of boreal riparian plant communities in response to disturbance intensity with reference to IDH. Hart and Chen (2008) similarly explained observed plant diversity in boreal mixedwood forests in northwestern Ontario with IDH, concluding that the response pattern was not always consistent with the model.

In reviewing the specific papers where conformance with IDH or MRH was reported as an explanatory model, greater compliance with IDH was reported for studies conducted on well-drained mineral-soil uplands than for those studying poorly drained, often organic lowland or moisture-limited dry mineral- soiled landscapes, consistent with our hypothesis. However, compliance with MRH was also higher for upland sites than poorly drained lowland sites, contrary to our initial hypothesis. This may be an artifact of the small number of studies reviewed. The MRH is rarely reported in forest ecosystems with the exception of conifer forests with ericaceous understory in nutrient-poor sites with thick organic horizons. In these communities, the traits of dominant ericaceous species (e.g., *Rhododendrum groenlandicum* (Oeder) Kron & Judd, *Kalmia angustifolia L.*, *Empetrum* spp., *Vaccinium* spp.), have been shown to be the key drivers of core ecosystem functions (c.f., Lamb and Mallik 2003, Mallik 2003, Heikkinen and Makipaa 2010, Mallik *et. al.* 2012, Siegwart-Collier and Mallik 2010). Contradictory evidence or interpretation of the evidence is often reported for these ecosystem types. For example, with respect to forest productivity, MRH was rejected in a study of fire-driven boreal *Picea mariana (Mill.)* Britton, Sterns & Poggenburg-*Kalmia angustifolia* communities in eastern Newfoundland (Mallik *et al.* 2010). The authors reported that under non-severe fire regimes the subordinate ericaceous shrub species reproduce rapidly by vegetative means to dominate post-disturbance sites by pre-empting the regeneration niche of the pre-disturbance dominant species, black spruce, leading to a decline in the establishment and abundance of black spruce. Thus the multilayered forest communities get converted into structurally simpler ericaceous heath (Mallik 2003).

The stability and productivity of *Kalmia* heath is still under investigation.

Others have reported both compliance and non-compliance attributing to the interplay of above-and below-ground biomass/carbon distribution within the complex multidimensional peatland ecosystem (Belyea and Baird 2006). This complexity includes vertical and horizontal zonation, fluctuations in resource supplies, and strong self-organization structures. Collectively these contradictions make it very difficult to successfully model community changes and test compliance with predictive hypotheses in these habitats.

Ecosystem response to disturbance on sites with shallow soils was also often in non-compliance with both IDH and MRH, displaying an early (skewed) peak in diversity when both non-vascular and vascular species are considered, then a rapid decline as tree cover develops (Bell and Newmaster 2002). Where lichen and bryophytes were major contributors to diversity, the response patterns were further complicated by species-specific responses to disturbance and the presence of refugia within larger disturbed patches that played a key role in species diversity recovery (Newmaster and Bell 2002, Nilsson and Wardle 2005, Petersen and Drewa 2009). This may be a confounding factor in future studies of testing the universality of IDH. The discovery of DNA markers are redefining phyllogenetic relationships (Webb *et al.* 2006). With increased precision in plant identification, species diversity may in fact, be greatest at higher levels of disturbance or on sites of more intense disturbance where a wide variety of graminoids, bryophytes, and lichen often thrive. This will depend on the response of species functional groups to disturbance.

Scale can also be a confounding factor. The IDH is most appropriately applied at local and regional scales (Connell 1978). The probability of a large number of species finding suitable habitat in a heterogeneous landscape is greater than a uniform one exposed to a consistent moderate disturbance. Resource heterogeneity is thought to be the dominant driver of diversity at the landscape level and early stages of succession, with resource important in mature stages (Ricklefs and Ricklefs 1977, Cornwell and Grubb 2003, Bartels 2010). Scale, which varies with the metric being tested, variation in the period of competitive exclusion among functional groups and habitat diversity generated by spatially correlated disturbances (Cadotte *et al.* 2006, dos Santos *et al.* 2011) further influence and complicate the interpretation of results (Whittaker *et al.* 2001, Colwell *et al.* 2004).

The effects of the site productivity - disturbance interactions on species diversity continue to challenge ecologists (Abrams 1995, Mackey and Currie 2001, Mittelbach *et al.* 2001, Kadmon and Benjamini 2006). The Dynamic Equilibrium Hypothesis addresses the productivity dimension of ecosystem response to disturbance and is accepted by some as an underlying premise of the IDH (Huston and Wolverton 2009). It assumes the following key unimodal relationships: (1) between species diversity and disturbance and, (2) between species diversity and productivity. This leads to a negative relationship between diversity and productivity on less productive sites and a positive relationship on fertile sites (McWethy *et al.* 2010). As a consequence, sites with scarce resources are often dominated by a few generalists and stress tolerant specialists (Siegwart-Collier and Mallik 2010). Fertile sites are often populated by species with a broader spectrum of traits with narrower niche widths. This leads to higher diversity until the more competitive species outcompete others and diversity declines as a result (McWethy *et al.* 2010).

2.4.2 Relevancy of IDH to Land Management

Overall much of the lack of conformity to IDH is attributed to the misapplication of the hypothesis in the following four areas: (i) applying the test to only a portion of the disturbance continuum (short-time frame, narrow disturbance regime), (ii) testing only a portion of a biological ecosystem (e.g., dominant vascular, nonvascular, woody species) (Bongers *et al.* 2009), (iii) poor assessment of disturbance impacts (see review by Li *et al.* 2004) and variability in the nature of the disturbance regime such as logging versus wildfire effects (Cochrane *et al.* 2004, Bongers *et al.* 2009), and (iv) variation in ecosystem composition in terms of functional groups which in turn leads to variation in the biotic response to disturbance (Bongers *et al.* 2009, dos Santos *et al.* 2011).

The fire-driven boreal forests provide a suitable natural ecosystem for studying disturbance-diversity responses. Fire cycles vary from infrequent (150 to 500 years) in peatlands to short (20 to 120 years) fire-free intervals on shallow upland sites and fire intensity varies from light ground fires to intense stand replacing crown fires (Heinselman 1973, Bergeron *et al.* 2002). Fire selectively removes less fire-tolerant species leaving those with strong fire resistance (e.g., thick bark, below-ground resprouting structures) and modifies surface soil. Vegetation re- colonization occurs from species with traits that favor reinvasion on burned areas from aerial and soil seed banks (de Grandpre and Bergeron 1997, Lavorel and Garnier 2002) with subsequent evolution of the community varying as a function of the initial post-fire seedbed condition (Mallik *et al.* 2010, Siegwart- Collier and Mallik 2010).

The rationale for current forest harvesting models in the boreal forest aimed at resource extraction and biodiversity protection is strongly linked to the IDH (McWethy *et al.* 2010), yet very few studies were designed to specifically test the validity of the model in the boreal forest. The support for this approach was largely based on implicit references to the IDH as an explanatory hypothesis (see Newmaster *et al.* 2007, Hart and Chen 2008; Biswas and Mallik 2010). There was often a discussion of predicted or tested "drivers" of a disturbance response and incidental reference to consistency or deviation from the IDH pattern. The research questions were rarely designed to test the IDH and in most cases only a small section of a disturbance gradient was examined.

The IDH is a key principle on which best management practices for the maintenance of biodiversity are designed. The IDH has also been proposed as a way to represent the relative degree of ecosystem degradation associated with silvicultural treatments in the boreal forest. The criteria for defining the degree of degradation remains subjective in the absence of data that identify "tipping points" between acceptable and unacceptable degree of disturbance in different communities. In practice, an arbitrary value of 60% of the maximum value of the metrics studied is often selected (Haeussler *et al.* 2002). Yet, what might be more critical is deviation from the shape of the response curve rather than absolute change in maximum species diversity.

2.4.3 Relevancy of MRH to Land Management

Testing of the MRH is more involved than IDH. Data on the number, relative abundance, and identity of species in a community are collected along with ecosystem functional response such as biomass, nutrient concentrations or, carbon storage (Grime 1998, Garnier *et al.* 2004). If the traits of the dominant species are known and quantified, and models exist to predict changes in the abundance of those species with specific environmental conditions, then predictions can be made regarding the impact of disturbance on changes to key ecosystem processes (often productivity), regardless of the cause (Smith and Knapp 2003, Diaz *et al.* 2007). This has been applied in Europe as a management tool to test the impact of land management activities and policies (Diaz *et al.* 2007).

Evidence from laboratory experiments, long-term field trials and large experiments in natural systems provided support for MRH (Jones *et al.* 1994, Wardle *et al.* 1998, 1999, Garnier *et al.* 2004, Hooper *et al.* 2005, Vile *et al.* 2006, Diaz *et al.* 2007). It is increasingly proposed to explain the link between species response traits, effect traits, and ecosystem functions. The few exceptions reported were often attributed to species acting as ecosystem engineers or keystone species with specialized traits that disproportionately influenced the growing conditions for other species (Hooper *et al.* 2005, Vile *et al.* 2006).

The a priori effect on plant community composition is a significant factor (Vile *et al.* 2006). As such, the timing of disturbance has a critical influence on the effects on community assembly. It influences both abiotic and biotic responses, for example the mortality of resident species, the propagule supply and ultimately the suite of species available to recolonize. This in part explains the differences in communities that establish following similar intensities and types of disturbance. Priority effects often lead to a positive short-term increase in species diversity that in turn influence ecosystem processes (e.g., primary productivity and nutrient retention). This short-term increase in phenotypic trait variation at the initial post-disturbance establishment phase at times facilitate dominance by select species with extreme traits (Loreau 2000). For example, in forests growing on thick organic layers, *Kalmia angustifolia* L. and *Rhododendron groenlandicum* (Oeder) Kron & Judd are able to expand and dominate the site, creating conditions less favorable for the survival and establishment of conifer and other primarily seed reproducing species (Mallik *et al.* 2010). What is less well understood with MRH, are the longer term ecological implications for the potential reduction in the redundancy of species that possess similar stress tolerating traits (as per the insurance hypothesis – see Petchey *et al.* 1999, Petchey and Gaston 2002, Naeem and Wright 2003) and ignores the need to re- examine the validity of the stability-complexity debate (Loreau 2000).

As with IDH, there is widespread acceptance of MRH but relatively few studies have directly tested and quantified the underlying assumptions across a variety of sites (Lavorel and Garnier 2002, Diaz *et al.* 2007, Pakeman and Marriott 2010, Pakeman et al. 2011). There is some indication that the hypothesis is so widely accepted that it is no longer a priority to test for compliance in terrestrial plant ecology. The few direct tests have shown that the effects of species removal on productivity and soil nutrients can be predicted by specific traits of individual species (Polley *et al.* 2006). These studies showed that net primary productivity, litter decomposition rate, soil total carbon and nitrogen are strongly correlated with weighted (by abundance) mean traits including leaf dry matter content (LDMC), specific leaf area (SLA) and leaf nitrogen concentration (Garnier *et al.* 2004). Other studies have shown that above-ground net primary productivity can be predicted from species-level measures of relative growth rate (Vile *et al.* 2006), that community weighted mean LDMC is strongly related to litter decomposition (Cortez *et al.* 2007) and that mean trait values were better predictors of ecosystem processes than measures of functional diversity or richness (Mokany *et al.* 2008). Pakeman and Marriott (2010) from a decomposition study testing the MRH in grasslands, re- ported that 48% of the variation in mass loss of leaf litter of single species and mixtures of several species was explained by LDMC alone. They found that LDMC provided accurate predictions of vegetation level decomposition rates as per the MRH, with greater predictive value than diversity. Despite this, thresholds of what levels of shifts in species composition and their associated decomposition rates lead to significant loss in key ecosystem functions, remained unknown.

The results of two decades of experimental work reviewed by Cardinale *et al.* (2009) using 44 experiments that controlled richness demonstrated how plant diversity affects biomass production. Only 12% of the experiments reported higher values for total biomass from mixed species compared to the single most productive species. However, overall, mixed species produced, on average, 1.7 times more biomass than monocultures. Higher values were reported in 79% of all experiments. This is consistent with the principle of complementarity, where community productivity is augmented by the interaction among biological processes among multiple species (Callaway *et al.* 2005, Sullivan *et al.* 2007). This adds to the confusion between the values of higher diversity versus the MRH where the dominant species play the critical role. The majority of articles that referenced MRH were conducted in herb-dominated ecosystems (grasslands and savannah) designed to better understand successional regulation of productivity and to predict changes in species composition through species removal experiments (Polley *et al.* 2006). These studies were often built on earlier community assembly work (Hooper and Vitousek 1997, Wardle *et al.* 1999, Diaz *et al.* 1998, 2003, Wardle and Grime 2003, Hooper *et al.* 2005).

2.5 Challenges in Interpreting Compliance and Deviation

One important gap in empirical support for both MRH and IDH is found in communities with high bryophyte and lichen components. In cold biomes bryophytes and lichens contribute substantially to above-ground biomass and organic matter (Hilli *et al.* 2010, Gornall *et al.* 2011), host nitrogen-fixing fungi and bacteria (Crews *et al.* 2001); bryophytes influence photosynthesis (Solheim *et al.* 1996, Raghoebarsing *et al.* 2005), modify microclimate (Lortie *et al.* 2004, Hilli *et al.* 2010), influence mineralization rates (Sedia and Ehrenfeld 2006) and reduce soil erosion by forming biological crusts (Harper and Belnap 2001). They also form important feedbacks with soil biota, facilitating and competing with vascular plants (Sedia and Ehrenfeld 2006, Cornelissen *et al.* 2007). Despite these known effects on succession, many studies of MRH seem to ignore this component of the vegetation.

A gap also exists in testing the IDH in terms of both species and functional richness response of cryptograms. Where they are included in studies, records often varied in precision, with many species grouped to report at the genus level. Interpreting results is also complicated by the temporal and spatial variability of individual species' response to concurrent shifts in the function of key traits as site factors, including changes in biogeochemical processes and community composition (Bates *et al.* 2000, van Wijk *et al.* 2004, Cornelissen *et al.* 2007). Cryptograms are often both the primary colonizers on highly disturbed sites with extremely harsh growing conditions, but some of them also thrive on very stable communities where disturbance events are widely spaced. As such we suspect that the abundance response curve to disturbance intensity would be concave rather than convex (see Mallik *et al.* 2010). This may help explain why the IDH model does not consistently hold in boreal forest ecosystems where the cryptogamic layer can act as a barrier of post-disturbance colonization.

Land managers today are faced with the challenge of predicting ecosystem response that considers predominantly non-vascular species. This group of plants are predicted to show the greatest change (decrease) in abundance, biomass and composition as a result of global warming (Callaghan *et al.* 2004). Vascular plant cover is predicted to expand at the expense of lichen and other non-Sphagnum mosses in cold biomes due to increases in soil nitrogen and phosphorus availability (van Wijk *et al.* 2004, Cornelissen *et al.* 2007). Experiments testing global warming on Sphagnum species confirmed increases up to 33% in Sphagnum biomass as snow depths increase, but caution that the total area of peatlands is likely to decline as drought increases (Dorrepaal *et al.* 2004). There were no reports on the consequences of these changes to ecosystem function.

The underlying assumptions in IDH are often challenged where plant population growth rates are low or high (Grime 1977, 1998, Bongers *et al.* 2009). In plant communities dominated by species with rapid growth rates, species diversity often peaks at high disturbance levels. Where communities are dominated by plant species with slow growth rates and low reproduction rates, richness often peaks at lower disturbance levels (Lavorel and Garnier 2002, dos Santos *et al.* 2011) adding more to the complexity.

Plants have important "after-life effects" on ecosystem processes (DeLuck *et al.* 2007). Microbially mediated litter de- composition determines the immobilization and mineralization of nutrients. This creates direct feedbacks that determine net primary productivity and helps explain why decomposition studies have not shown consistent effects of plant diversity on decomposition rates (Hart *et al.* 1993, Knops *et al.* 2001); nutrient availability (Tilman 1985, Tilman *et al.* 1996, 1997, Diaz *et al.* 1999, 2003) and mineralization (Hooper and Vitousek 1997). These inconsistencies and debates point to a need to test the underlying assumptions and predictions of MRH to confirm its universality.

2.6 Conclusions

Based on our review of 60 relevant papers, we conclude that the IDH provides a common template for comparing biodiversity response to disturbance on upland sites of moderate to high productivity. There was insufficient rigour to the field studies and too few studies in forested communities to make a definitive link to specific ecosystem type. Although IDH has been widely accepted as a model relating biodiversity to ecosystem disturbance, very few studies were specifically designed to test the validity of this model. The MRH is a less frequently cited hypothesis that examines biodiversity-biomass response to disturbance in relation to dominant species. It is particularly applicable to poorly drained organic rich and less productive sites. As with IDH, very few studies were specifically designed to test this hypothesis. There is a need for new studies specifically designed to test the validity of both IDH and MRH. The shape and amplitude of these models could serve as early warning signs of change in species composition and ecosystem function that would be useful to land managers. Strong empirical support for these hypotheses will bring confidence to their use in natural resource management.

3.0 METHODS

3.1 The Study Areas: Long-Term Site Productivity (LTSP) Research Plots

The study was designed and carried out within the Ontario Ministry of Natural Resources - Long-term Site Productivity (OMNR-LTSP) project, established as a condition of Ontario's Class Environmental Assessment (EA) for Timber Harvesting to investigate the impact of full-tree harvesting on soil productivity and biodiversity (Duckert and Morris 2001, Gordon *et al.* 2001). The EA Board determined that evidence in support of concerns associated with full-tree harvesting (i.e., increased nutrient removals and loss of biodiversity) was contradictory rather than conclusive. As a result, approval for harvesting trees on Crown land was dependent on meeting a number of Terms and Conditions (T&C) one of which, T&C 101, stated: "OMNR shall design and implement a study pertaining to the effects of full-tree harvest and full-tree chipping on long-term forest productivity".

The resulting OMNR-LTSP project in northwestern Ontario was designed and implemented to study ecosystem processes within the black spruce working group to track biogeochemical and plant community changes after harvest in order to meet this EA requirement (Gordon *et al.* 1993). The initial focus was on the identification and assessment of key processes involved in nutrient cycling over a wide range of black spruce site types, including those believed to be sensitive to removals of organic matter. Based on the existing literature and expert opinion, sensitive sites were identified as well-drained medium to coarse sands, shallow soils over bedrock and poorly drained peat soils (Morris 1997, Kershaw *et al.* 1996). This thesis addresses the second objective, to document the recovery patterns of the plant communities to better understand biodiversity response, by examining the response of understory biodiversity on three of the suspected sensitive site types: sand, loam (these experimental sites were shallow till deposits over bedrock) and peat.

The OMNR-LTSP study areas (Figure 3.1) were selected in 1991, followed by two years of pre-harvest inventory assessment (1992-1993) and three years of nutrient process-oriented studies on three intensive sites (1993-1996). A series of experimental harvests were carried out in 1994/95 using a common design (see Section 3.2). A detailed description of the experiment is provided in the LTSP establishment report (Duckert and Morris 2001). OMNR continues to conduct a detailed post-harvest monitoring program to assess post-disturbance recovery (Duckert and Morris 2001, Whaley, OMNR, pers. comm. September 20, 2013).

3.2 Harvest Treatments

During the late winter of 1994 and winter of 1995 (Gordon *et al.* 1993, Duckert and Morris 2001), harvest treatments, resulting in increasing levels of biomass removal, were randomly applied and replicated three times in 30 x 30 m plots in black spruce - dominated communities at six study sites, representing three site types: loam, sand, and peat. These three site types represent both upland mineral forests (loam and sand site types) and forested peatlands (peat site type). Table 3.1 summarizes the pre-treatment stand conditions; Table 3.2 summarizes pre-harvest nutrient pools in the organic and mineral layers. Photographs (Figures 3.2, 3.3, and 3.4) show the pre-disturbance, reference (UNCUT) forests on loam, sand and peat site types, respectively.

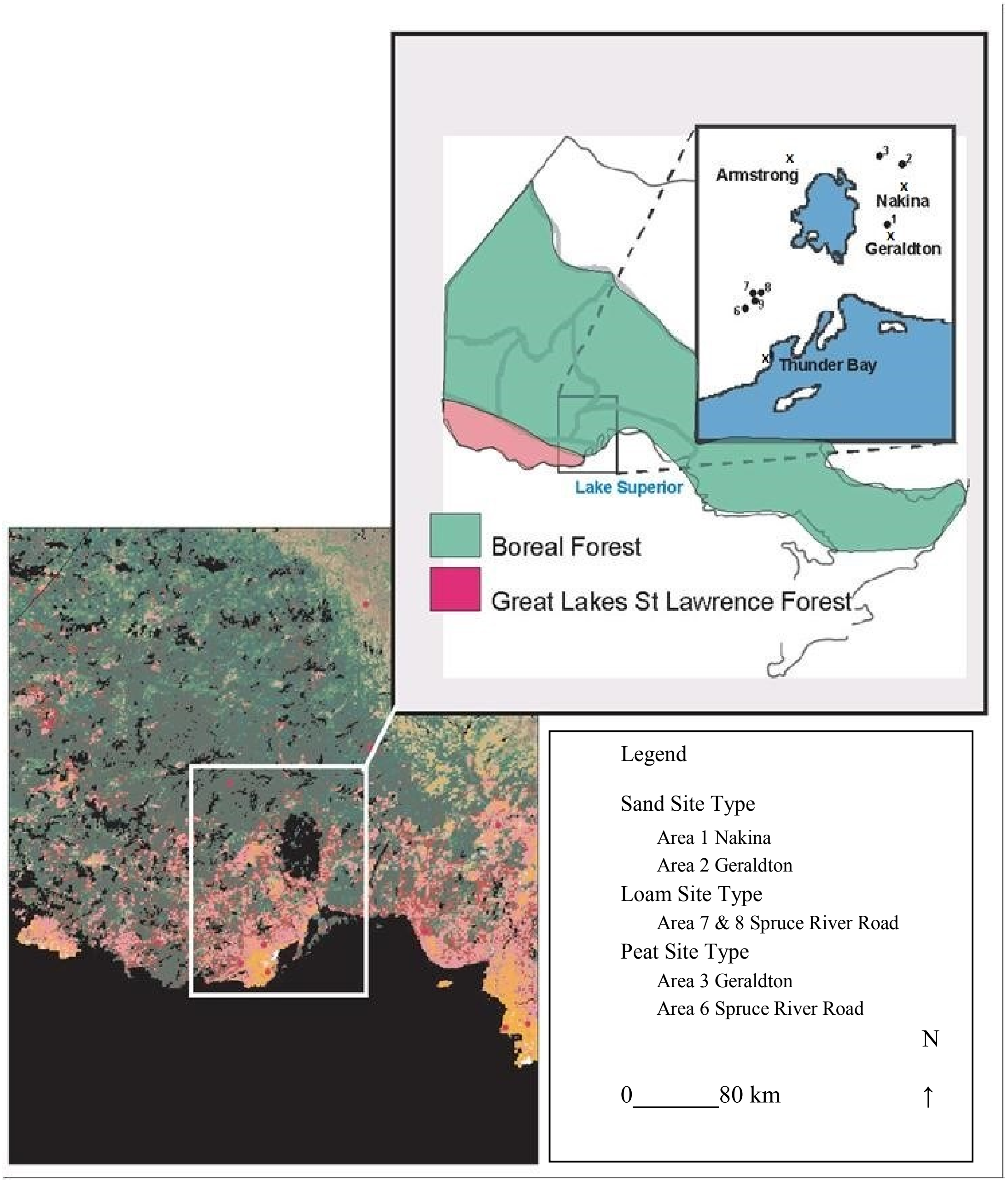

Figure 3.1 Location of the study areas (2013 Ontario EFRI imagery; inset map adapted from Duckert and Morris 2001).

Table 3.1 Preharvest stand characteristics for loam, sand, and peat site types (adapted from Duckert and Morris 2001).

Area (A) Number	Species Composition	Site Index	Age (yrs-as of 1994)	Stems ha^{-1}	Forest Description	Soil Description
Loam Site Type						
Rep 1 (A8)	Sb_{10}	12.8	100	1342	Spruce-pine/ feathermoss	Fresh, shallow, loam
Rep 2 (A9)	Sb_{10}	12.5	100	2619	Spruce-pine/ feathermoss	Fresh, shallow, loam
Sand Site Type						
Rep 1 (A1)	Sb_6Pj_4	14.9	107	956	Pine-spruce mixed wood	Fresh, deep, fine sandy
Rep 2 (A2)	Sb_7Pj_3	11	115	1513	Pine-spruce mixedwood	Dry, deep, coarse sandy
Peat Site Type						
Rep 1 (A3)	Sb_{10}	10.9	70	2924	Black spruce, poor swamp	Moist to wet, organic, over silty clay
Rep 2 (A6)	Sb_{10}	10.5	125	1705	Black spruce, poor swamp	Wet, organic over fine silt loam

Note: site index (at age 50), Morris unpublished data; A=Study areas, see Figure 3.1 for locations.

Table 3.2 Total pre-harvest carbon (T ha^{-1}) and nutrients (kg ha^{-1}) in the surface O-horizons and upper 20 cm mineral soil layer for loam, sand and peat site types.

Horizon	Site Type	C	N	P	K	Ca	Mg
Organic							
	Loam	96.0	2076.6	10.4	127.3	307.9	70.4
	Sand	127.3	2768.4	22.9	204.2	541.5	92.6
	Peat	205.7	3611.8	30.9	201.1	2284.3	390.0
Upper 20cm mineral							
	Loam	19.0	736.0	5.0	39.0	557.5	138.6
	Sand	19. 5	598.3	10.1	36.7	248.0	41.7
	Peat	0	0	0	0	0	0

Figure 3.2 Loam site type: Pre-treatment uncut black spruce forest with a *Pleurozium-Sphagnum* understory on loam soil.

Figure 3.3 Sand site type: Pre-treatment uncut black spruce forest with a *Pleurozium schreberi* understory on sandy soil.

Figure 3.4 Peat site type: Pre-treatment uncut black spruce forest (poor swamp) with a low shrub (*Rhododendron groenlandicum*) and continuous *Pleurozium-Sphagnum* understory on organic soil.

Harvest treatments were: 1) tree-length (TL) delimbed at stump; 2) full-tree (FT) delimbed at roadside and, 3) full-tree and blade (FTB) where vegetation and the upper O-horizons were removed. These represent low, medium and high biomass removal disturbances, respectively, for the purposes of this study. Harvesting was conducted using a feller buncher, grapple skidder and delimber system; a D8 bulldozer removed all plant material and surface O-horizons after the harvest for the blading treatment (FTB). Figure 3.5 provides photographs of three harvest treatments and post-treatment site conditions.

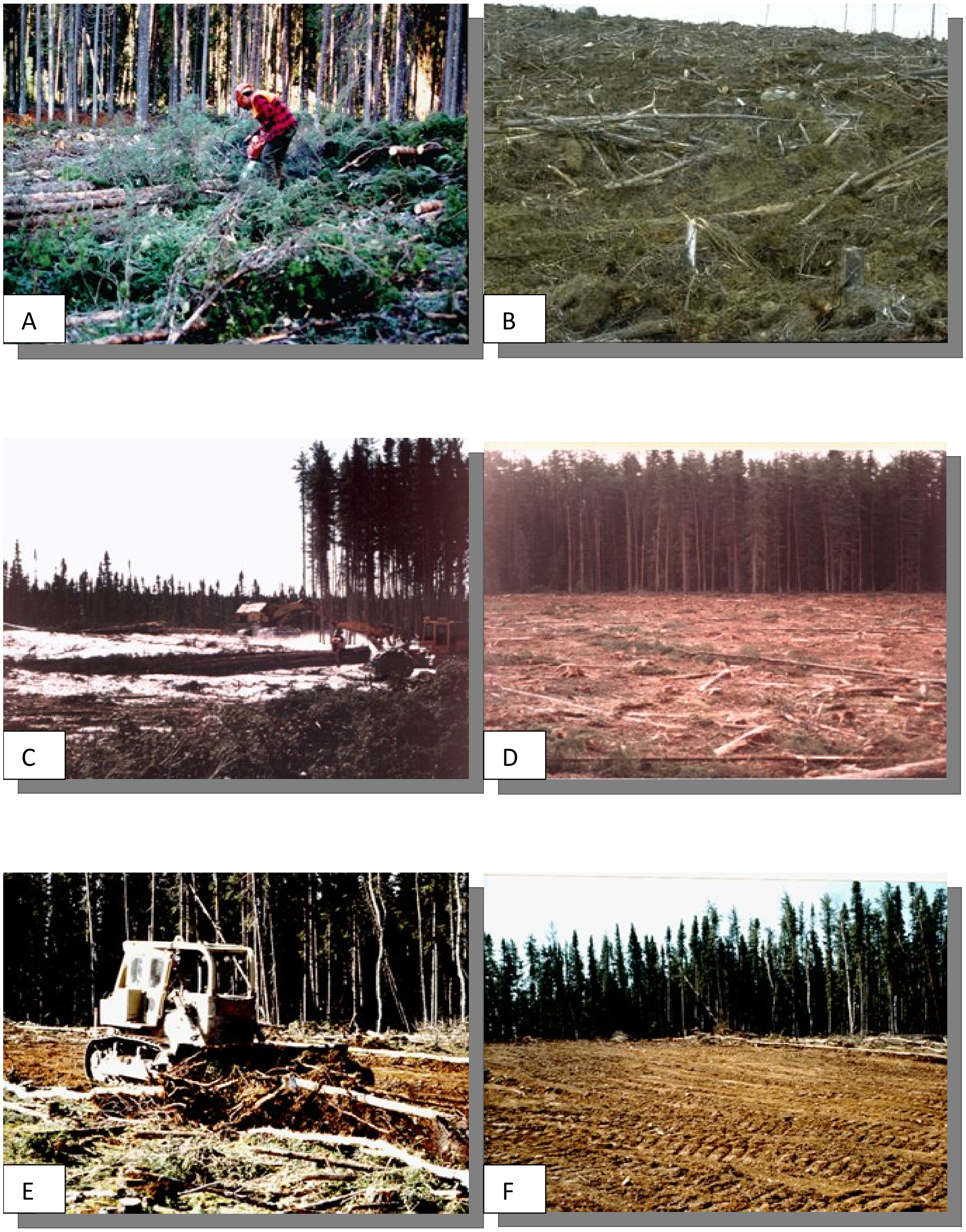

Figure 3.5 Harvest treatments (1994) and conditions after treatment (1995) for tree-length (TL) - low intensity (A, B); full-tree (FT) - medium intensity (C, D) and full-tree plus blade (FTB) - high intensity (E, F) disturbance.

Operationally, the TL harvesting system removed the merchantable stems only, leaving fine (FWM) and coarse woody material (CWM) on site. FT harvesting systems removed both the central trunk and the fine, live branch material. FTB removed the above ground portions of the trees, shrubs, and herbs, plus the upper surface organic layers (10-20 cm on mineral soils; 20 – 25 cm Of (fibric layer) on peat soils). The degree of the removal of the O-horizons also varied as a function of the terrain, presence of stones and boulders, deeper rooted stumps and variation in soil moisture, with greatest uniformity achieved on sand site types. The objective of the FTB treatment was to physically remove all above ground vegetation and most of the reproductive structures located in the surface organic layer.

The average residual biomass left after the treatments was reported as about 38 Mg ha^{-1} (loam), 32 Mg ha^{-1} (sand) and 28 Mg ha^{-1} (peat) after TL harvests, dropping by at least 40% to 24 Mg ha^{-1} (loam), 19 Mg ha^{-1} (sands) and 15 Mg ha^{-1} (peat) after FT harvests. A further decline in residual biomass was recorded after the FTB treatment (averaging <0.2 Mg ha^{-1} across all site types in the original LTSP experimental sites), with higher values (up to 15 Mg ha^{-1}) reported for the loam sites due to the operational challenges on the shallower soils (Duckert and Morris 2001, Morris, unpublished data). The higher biomass values on the loam and sand sites relative to the peat sites was largely a reflection of lower branch and foliage biomass associated with the shorter, smaller trees on the poorly drained peat sites.

Conventional harvesting was carried out on the 20-metre buffer strips surrounding and between the treatment plots to minimize edge effects. Overwintered containerized black spruce seedlings were planted on three of the four 15 x 15 m sub-plots of each treatment plot at 2 x 2 m spacing (50 seedlings per sub-plot) in the spring following harvesting (either 1994 or 1995 depending on the location).

Four 50 x 50 m uncut plots at each study location were marked for reassessment to monitor for any broad regional shifts in species composition such as an unpredicted insect or disease infestation or climate events that might modify plant community assembly, separately from the treatment effects. The extra replicate and larger plot size (50 x 50 m) were designed to minimize risks of loss of these mature plots from blow down.

3.3 Field Sampling Methods

3.3.1 Experimental Layout

As per the original OMNR-LTSP design (Figure 3.6), each study area utilized the 30 x 30 m treatment plots with treatments randomly applied to create 3 replicates per treatment per study area. Data presented in this thesis was collected from nine treatment plots (3 each of TL, FT, FTB) and 3 UNCUT reference plots in each of two study areas per site type. Where blow down was excessive in Area 2, temporary 50 x 50 m plots were established, as replacements, at least one mature tree-length from the cut edge to minimize edge effects

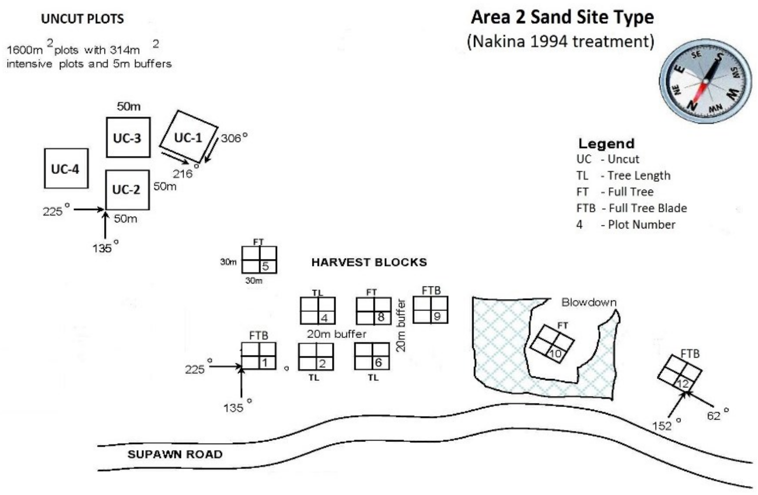

Figure 3.6 Experimental layout of the treatment plots for one study area (adapted from diagram in OMNR 2001).

Vegetation and associated environmental parameters were assessed in four 2 x2 m quadrats established around a permanent stake in the centre of each sub-plot (Figure 3.7). Data from all four quadrats (i.e., sampling units) were averaged for one observation per sub-plot. Data from all four sub-plots were then averaged for plot means (i.e., experimental units). The same approach was taken with the UNCUT plots but, in this case within each 25 x 25 m sub-plot. Because these sub-plots did not have center stakes the central position in each sub-plot was located by measuring.

3.3.2 Environmental Parameters

On each 2 x 2m quadrat, ocular estimates of physical and biotic environmental site parameters were recorded and mean sub-plot and plot levels values calculated (described previously). The parameters were selected to characterize seedbed and post-disturbance conditions created by the harvest treatments and included exposed mineral soil, litter cover by type (conifer, deciduous), total lichen cover, bryophyte cover by sub-category [feathermoss (*Pleurozium schreberi* (Brid.) Mill., *Ptilium crista-castrensis* (Hedw.) DeNot, *Hylocomium splendens* (Hedw.), sphagnum, pioneer moss (*Polytrichum* spp., *Ceratodon* spp., *Pohlia* spp.)], fine woody material (FWM, <10 cm diameter), and coarse woody material (CWM, >10 cm diameter).

Plot level basal area (BA) m^{-2} ha^{-1} values (15 years after harvest), provided by OMNR, were used in the subsequent analysis to examine the relationship between shading and species presence and abundance. Basal area has been shown to strongly correlate to light availability and provides an objective measurable variable (see Reich *et al.* 1998, Comeau 2001). The BA values were calculated using either measured or estimated root collar diameter (rcd). A formula to convert dbh to rcd was based on regression analysis of data collected on both dbh and rcd for 30 to 50 trees in each area.

Mean depth of the surface O-horizon was calculated by averaging 9 measurements in each sub-plot, one near the central stake with additional measurements taken at 8 principal compass points around the stake and equivalent distances to the plot boundaries (Figure 3.7). This measure should provide an indication of the quality of the seedbed for germination and the probability that plant vegetative reproductive structures remain on-site.

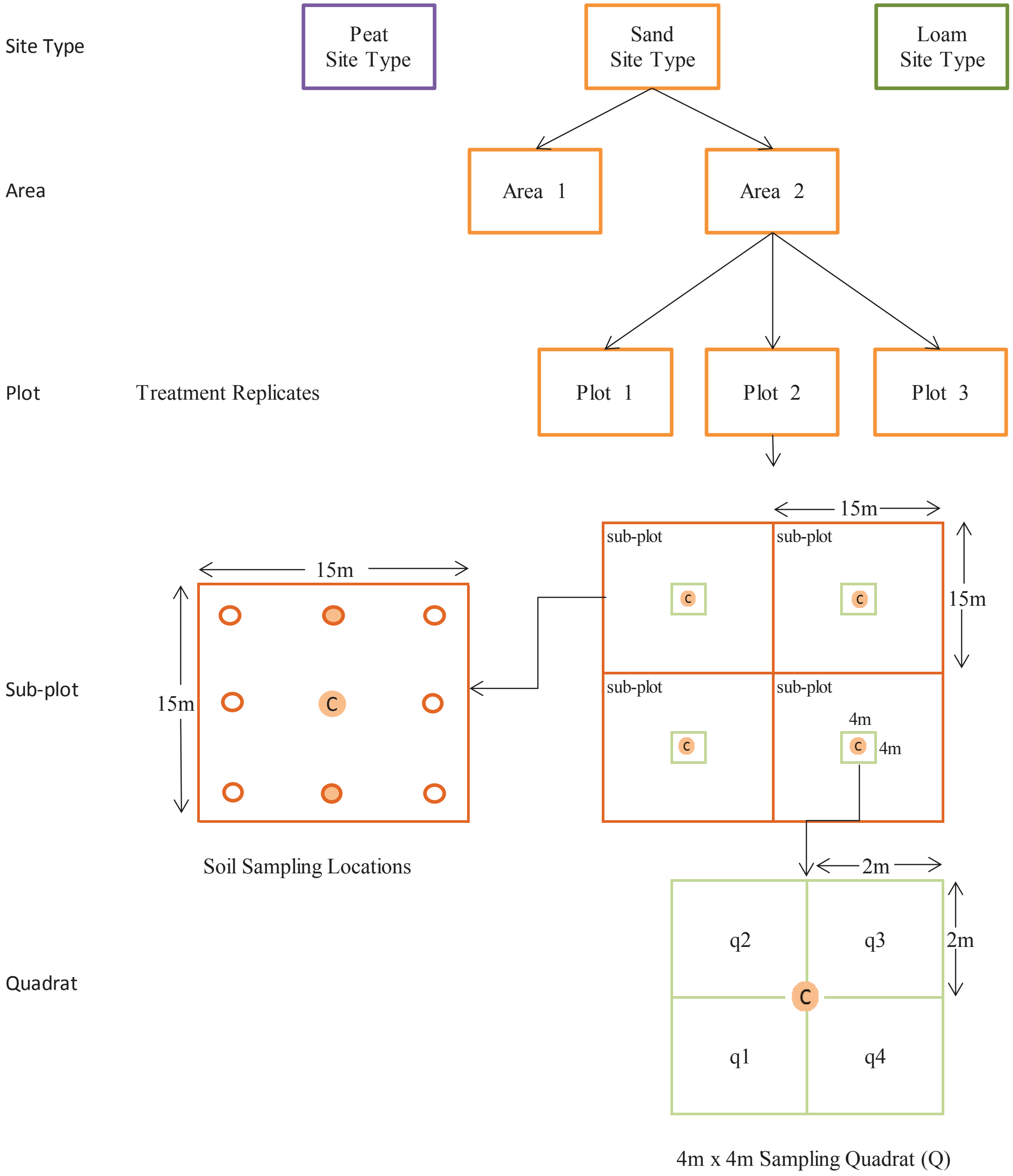

Figure 3.7 Schematic displaying sampling layout. All plant presence and abundance data, canopy closure, and surface soil environmental data was collected at the 2 x 2m quadrat level, averaged to give one value per sub-plot then averaged again to give one value per plot, thus resulting in 18 observations (3 x 2 x 3). per treatment type over all three sites (6 observations per treatment/site type combination). C - centre stake, O (circles) - soil sample locations

3.3.3 Soil sampling

Soil samples for the assessment of nutrient pools and pH were collected from 3 locations in each sub-plot along a central transect (Figure 3.7), and taken immediately to the lab for analysis. Samples for bulk density assessment were taken adjacent to the central stake in each subplot using a 48 ml metal sampling tool. Samples for the mineralizable nitrogen assessment were collected from the O-horizon and top 10 cm of the mineral soil from half of the treatment sub-plots (near the central stake) in 2008. This sampling quantity fit the time and budget for data collection and laboratory analysis and allowed for duplicate samples from each treatment unit.

3.3.4 Plant Inventory

Species identification and an occular estimate of abundance (cover) for each vascular plant, lichen and moss species were recorded for each 2 x 2m quadrat (Figure 3.7). All estimates of cover were done by the author to increase consistency. All vascular and non-vascular species were tallied to the species level where possible; samples of any unknown species were collected for later identification and verification. Nomenclature for vascular species follows the Ontario Plant List (NHIC 2008) and the Northern Ontario Plant database (Meades *et al.* 2013); mosses follow Ireland and Ley (1992); and lichens follow Brodo *et al.* (2001). Voucher specimens were collected for deposit in the herbarium at Lakehead University.

Plant species were further categorized by 1) life form layer (i.e., tall shrub (1.5 - 3 m), low shrub (<1.5m), herb, graminoid, lichen, and moss) and 2) dominant reproductive strategy (seed, vegetative, seed + vegetative). Fern and fern allies (*Lycopodium*, *Equisetum*) exhibited <1% occurrence on the sites and therefore were included in the graminoid layer for analysis purposes. Life forms were used in comparing pre-disturbance seed bank composition (methods described in Section 3.4) to that of the 15-year post disturbance communities. The proportional abundance of each of life form group was calculated by dividing the total cover of species in the life form group by the total vascular plant cover in each plot. A similar approach was used to calculate the proportional abundance of individual species used in the graphical comparison of the proportional abundance of seed bank species with the 15 year post-disturbance community.

3.4 Sampling and Processing Procedures for Soil Seed Bank Assessment

Surface soil samples, collected in 1992-93 from all three site types prior to harvest, were used in a germination experiment, conducted in the Lakehead University greenhouse and carried out by OMNR, to assess the seed bank species composition. Soil samples were collected within 2 x 2m sampling units that were greater than 3m from the edge of any future treatment units, using GPS coordinates to mark the sample locations. A soil sample was extracted at the centre of the 2 x 2m quadrat, using a 10cm deep, 6cm wide tulip planting tool (300 ml) to cut and extract a sample of surface LFH and a second sample of the upper mineral soil.

Soils were subjected to cold temperatures (0-5 ˚C) for 30 to 90 days to break physiological dormancy of seeds, a time suitable for the majority of the seed banking species in the study area (Schopmeyer 1974, Baskin and Baskin 1989). Soils were then placed in the greenhouse to promote germination of seeds. Conditions were set at an 8 to 12 hour photoperiod and 20-30 ˚C night-day temperature to mimic conditions required for germination for the majority of northwestern Ontario plant species (Hills and Morris

1992). For species that could not be identified after 6 weeks, seedlings were transferred to larger pots to grow until identification could be made. Because of the challenge of identifying graminoids to the species level during the germination trial, these groups were recorded as Poaceae (*Poa*) and sedges (*Carex*) in the original greenhouse trial (Morris, unpublished). As such these groupings were carried forward in the comparison of the pre-disturbance seed bank composition with the 15 year post-disturbance plant community.

Germination success over time was plotted (Figure 3.8) to confirm that the duration of the experiment was sufficient for maximum germination. After six weeks, and the marked decline in germination, the soils were reworked by hand and monitored for further germination, to see if this soil mixing stimulated any further germination. As a result of a very low germination rate per sample, the values were pooled for each site type during the original greenhouse trial (Morris, unpublished data).

The results of the greenhouse trial provided the data for the proportional abundance of species in the seed bank for each site type, used in this study. The seed bank species-level data was also grouped by life form category to compare the proportional abundance of each life form in the seed bank with the proportional abundance of life form groups in the 15 year-post harvest communities for each treatment (TL, FT, FTB) and for each site type (See Section 4.5).

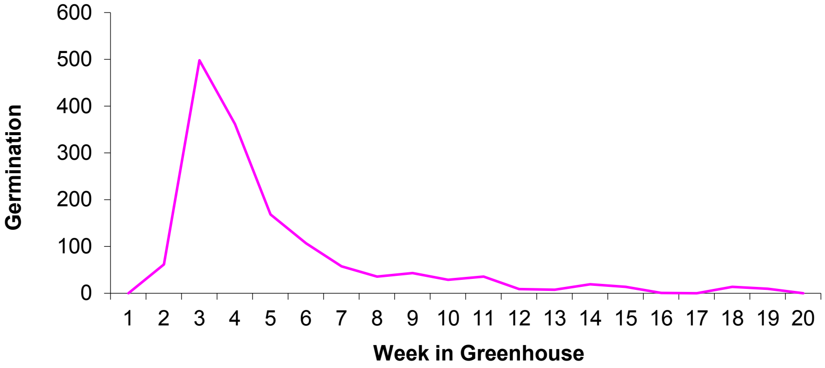

Figure 3.8. Number of germinants per week from the total soil seed bank collection from all sites combined (unpublished data, MNR).

3.5 Laboratory Analysis of Soil Properties

3.5.1 Chemical Analysis

Acidity was measured on fresh organic and mineral soil samples using a 2:1 paste (0.01 M $CaCl_2$) as per Kalra and Maynard (1991).

Elements analyzed included total carbon (TC), total nitrogen (TN), phosphorus (Brays P), and exchangeable potassium (K), calcium (Ca), and magnesium (Mg). Samples were air dried. Organic samples were hand ground after cones and branch fragments > 2 cm in diameter were removed. Mineral soil samples were sieved (2 mm) to remove coarse fragments. Bulk density measurements were done by OMNR as part of the ongoing monitoring of these trials.

Chemical analysis was done at the Ontario Forest Research Institute (OFRI) laboratory using standard procedures as per Kalra and Maynard (1991) as follows: for total C - dry combustion on a LECO CNS-2000 analyzer, total N - semi-micro Kjeldahl digestion procedure analyzed on a TrAAcs; P - Bray's No. 1 (an acid/fluoride extractant), and cations - 10% HNO_3 acid digestion followed by analysis on a Varian Vista Pro inductively coupled argon plasma spectrometer (ICP). Quality Control (QC) measures included running an in-house OFRI standard after every 20 samples. In addition, Quality Assessment (QA) procedures were in place, with every sample run in duplicate (up to 10% variance accepted). Total C, TN, P, Ca and Mg pools, by horizon, were calculated as horizon depth (cm) x elemental concentrations (mg kg^{-1}) x fine fraction bulk density (g cm^{-3}), adjusted for coarse fragment content, then converted to a kg ha^{-1} basis (Mg ha^{-1} for TC).

3.5.2 Anaerobic Nitrogen Determination

Mineralizable N, using an anaerobic incubation method, was measured to provide an index of potentially available N (Powers 1980). After standard processing (as per Kalra and Maynard 1991), 10 grams of each air dried, sieved, mineral sample or 5 grams of each air dried organic sample was placed in individual pill bottles and filled with 50 ml of deionized water. The samples were gently stirred to ensure they were well mixed. The bottles were then sealed and randomly placed in an incubator for 14 days at 30 ˚C (as per Binkley *et al.* 1990). After samples were removed from the incubator, 50 ml of 4 M KCl solution was added to yield a 2 M KCl solution (Binkley *et al*. 1990). Samples were then placed on a shaker table for one hour at 180 rpm (as per Druhar 2005). Extractions were then completed using a vacuum flask and Buchner funnel with Fisher-Scientific brand Q2 filters. Fifty ml of the extractant was stored in a labelled sterile centrifuge tube and placed in the freezer until analysis for NH_4 using a Technicon

Instruments Autoanalyzer II in the Forest Resources and Soil Testing Laboratory at Lakehead University a few weeks later. All lab equipment was thoroughly rinsed three times with distilled water between sample extractions and all other Standard QC and QA procedures followed. Analysis was only conducted for ammonium and net ammonification values are reported, calculated as described for nutrient pools. Testing for nitrates was not necessary as nitrate is not generally produced under anaerobic conditions (Boone 1992).

3.6 Quantitative Analysis

3.6.1 Assessment of Community Diversity 15 Years after Harvesting Disturbance

Diversity Measures

Differences in understory alpha diversity, [species richness (R), evenness (E), Shannon's Diversity (H') and Simpson's Diversity (D)] were calculated using the formulae provided in the PCOrd vers. 6 software (McCune and Grace 2002, McCune and Mefford 2011) and shown below. Simpson's index was selected as a relatively stable value, regardless of sample size, as the addition or loss of rare species does not strongly affect the index (Magurran 2004, McCune and Mefford 2011). Shannon's diversity index, sensitive to both sampling size and changes in rare species, was included to allow for comparison of results to the majority of other published papers in the field (Hunt *et al.* 2004, Fukami *et al.* 2005).

Species Richness (R): R is the number of different species present per unit area commonly reported in the ecological literature (Tramer 1969, McCune and Grace 2002).

Evenness (E): E provides information on the relative abundance of the species present in a given group. The values range from 0 to 1, where if E=1, then all species are present in equal abundance. The formula used was Pielou's J (Pielou 1966, 1975, Hill 1997) as follows:

$$E=J= H'/\ln R \quad [1]$$

where: H' is Shannon's diversity index and R is average species richness of the data set of interest.

*Shannon's Diversity Index (H')***:** H' quantifies the entropy or uncertainty in a species data set for a defined group (Shannon and Weaver 1963). It is based on the assumption that as the number of species present in a group increases, the more equal their proportional abundances become, and therefore the more difficult it is to correctly predict which species will be the next one in a string. H' quantifies this uncertainty associated with predicting the species in a given group and is calculated as follows:

$$H' = \sum p_i \ln p_i \quad [2]$$

where: p_i is the proportion of individuals belonging to the *i*th species in the data set of interest.

Simpson's Diversity Index (D): This index measures the chance that two species drawn at random will be the same (Simpson 1951). The values range from 0 to 1. When all species are present in equal abundance then D equals 1/R. It is calculated as follows:

$$D = 1 - \sum(p_i * p_i) \quad [3]$$

where: p_i is the proportion of individuals belonging to the *i*th species in the data set of interest.

Species richness and diversity data were reviewed to check for conformity to the normal distribution. Parametric tests were run on raw data and log transformed data, where required, to meet assumptions of normality.

Statistical Approach

Diversity measures were first analyzed as a randomized complete block design with three replicates of four levels of organic matter removal treatments applied within each of two areas (blocks) nested within three site types using a 2-way ANOVA with the following General Linear Model (GLM)

$$Y_{ijkl} = \mu + ST_i + BK(ST)_{(i)j} + HT_k + ST{*}HT_{ik} + \varepsilon_{(ijk)l}, \qquad [4]$$

where: Y_{ijkl} is the average value of the given response variable for the l^{th} replicate plot within the k^{th} harvest treatment within the j^{th} study area (random factor) within the i^{th} site type, μ is the overall mean, ST_i is the fixed effect of the i^{th} site type ($i = 3$), $BK(ST)_{(i)j}$ is the random effect of the j^{th} study area within the i^{th} site type ($j = 2$), HT_k is the fixed effect of the k^{th} harvest treatment ($k = 3$ or 4), $ST{*}HT_{ik}$ is the interaction of the i^{th} site type with the k^{th} harvest treatment, and $\varepsilon_{(ijk)l}$ is the random effect of the l^{th} replicate plot within the i^{th} site type within the j^{th} study area within the k^{th} harvest treatment ($l = 3$ or 4). The number of treatments varied with the questions being posed, set at 4 when the UNCUT treatment was included, and 3 when the response variables being examined were limited to differences among the harvest treatments (TL, FT, FTB).

The 2-way ANOVAs were performed with the GLM procedure in the DATA DESK software, version 6 (Velleman 1997). The analysis of richness (count data) was run with the raw data as recommended by O'Hara and Kotzke (2010). Evenness and D were log transformed to meet the requirements for normality and homogeneity for the analysis. This was followed by carrying out orthogonal contrasts in SPSS (vers. 21) to detect where the differences occurred (see below).

Significant effects of ST*HT interactions were further investigated by running separate 1-way ANOVAs for each site type followed by orthogonal contrasts run in SPSS (vers. 21)(see below). The ANOVA were run with the GLM procedure in the DATA DESK software, version 6 (Velleman 1997).

Orthogonal Contrasts

Orthogonal contrasts were designed to answer the following ecological questions: 1) does harvesting alone (i.e., removal of the overstory) affect understory species diversity in boreal black spruce - dominated communities? 2) does the removal or retention of the forest floor and O-horizon affect understory diversity in black spruce - dominated stands?, and 3) does the removal or retention of fine and coarse woody material affect understory diversity? (Table 3.3). The sand site type data set for all species did not meet the assumptions of equal variance for species richness as is common for this type of community data. Log, ln, and square root transformations did not correct this problem. The results are presented, noting this limitation in the data set. .

Table 3.3. Orthogonal contrasts to examine the effect of key ecological conditions on species richness (R), evenness (E), Shannon's diversity (H') and Simpson's diversity (D).

	Contrast	Treatment Coefficient				
		λ_1	λ_2	λ_3	λ_4	$\sum \lambda$
L_1	Reference vs. Harvested	-3	1	1	1	0
L_2	Forest Floor Retained *vs.* Removed	0	1	1	-2	0
L_3	Coarse & Fine Slash Retained vs. Coarse Slash Only	0	1	-1	0	0

Subscripts are: λ_1 Reference (UNCUT), λ_2 Tree-length harvest (TL) which retains fine woody material (FWM) on site, λ_3 Full-tree harvest (FT) which removes coarse (CWM) and fine woody material (FWM) from the site, λ_4 Full-tree plus blade to remove forest floor treatment (FTB).

Reproductive Trait Response to Treatments

Each vascular plant species was categorized by dominant reproductive strategy (seed, vegetative, combined) as reported in a data set of functional traits developed collaboratively in the Department of Biology, Lakehead University (unpublished, Mallik 2011) and cross-checked with reference to the USDA data base and Plants of Northern Ontario data base (Meads 2013). The number of species in a given sampling unit grouped under each of the three dominant reproductive strategies provided the richness values used in the analysis. Richness (vascular species) associated with each of the three categories of dominant reproductive strategy was then subjected to 2-way ANOVA using equation 4 to assess plant species response to harvest treatment and site type (ST*HT). The test was carried out in SPSS vers. 20 (IBM 2011).

3.6.2 Assessment of Species Composition 15 Years after Harvest Treatments

PerMANOVA

Using the plot level data, multivariate analysis of variance (PerMANOVA) procedures were used to test for differences in understory species composition among the harvest treatments and site types. PerMANOVA is a permutation-based multivariate analysis of variance that is applicable where non-Euclidean distance measures (such as Sorensen distance) are used in multifactor designs (Anderson 2001). The test applies the mathematical rule that "the sum of squared distances between points and their centroid is equal to (and can be calculated directly from) the sum of squared interpoint distances divided by the number of points" (Anderson 2001). (PerMANOVA, often recommended for plant community data, was selected because it avoids the assumptions of linear species response and normally distributed errors which are often not met in plant community data (Anderson 2001).

A two-way PerMANOVA was run with the harvested treatment data set (HT * ST) using Sorensen's (Bray Curtis) distance measure to determine if the degree of similarity in the species composition of communities was attributed to harvest treatment (HT), site type (ST), or their interaction. When significant interactions were detected or if the response to HT differed with ST, one-way PerMANOVA for each site type was used to test for significant HT differences in species composition. Tests were also run to detect significant ST effects for a given HT when there was a significant interaction. The tests were run at the recommended number of 4999 permutations for a test of $\alpha = 0.05$ (McCune and Grace 2002).

3.6.3 Indicator Species Analysis (ISA)

Given the results of the ANOVAs and the orthogonal contrasts, indicator species analysis (ISA), as described by Dufrêne and Legendre 1997) was used to determine whether any particular plant species showed significant association with the different HT treatments on each of the site types. The analysis was carried out on each site type separately because both the ANOVA and PERMANOVA tests detected strong HT * ST interactions. This method combines information on both the presence (relative frequency of a species in a given group in relation to other groups) and abundance (concentration of a species in a given group) of a given species. A perfect indicator species (IS), assigned a score of 100, is one that is always present on that site-treatment condition and not present on other conditions. Statistical significance of indicator values (IV) was determined with 10,000 Monte Carlo permutations to compare results with those expected by chance. ISA was conducted with PCord vers. 6 (McCune and Mefford 2011).

3.6.4 Ordination: Non-Metric Multidimensional Scaling (NMS)

An unconstrained ordination (non-metric multidimensional scaling, NMS) was used to display the dispersion of plant species communities (matrix of species presence and abundance) in relation to each other in a multi-dimensional ordination space (Kruskal and Wish 1978, McCune and Grace 2002). NMS is well-suited for data, such as that found in this study, that are non-normal and discontinuous and is strongly recommended for the analysis of plant community data (McCune and Grace 2002, Clarke 1993). The ordination tests were run with the full data set (all species, vascular and nonvascular species) and for the vascular species data set for all site types together and for each site type, separately, in PCOrd vers. 6 (McCune and Mefford 2011). The tests were run using the slow and thorough settings, selecting the Sorensen distance measure, random starting coordinates, up to 6 axes, and 500 iterations. Species that occurred with <1% total cover in the data set or only occurred on one plot were excluded from this analysis. Tests were repeated ten times to confirm trends as recommended by McCune and Grace (2002).

Joint plots of key environmental factors (R>0.2) were superimposed on the NMS ordinations to detect the presence of any strong gradients. Variables that represent light availability, degree of soil disturbance, seedbed conditions, and nutrient availability, all of which have been reported to be key drivers of species establishment after disturbance in boreal conifer forests (c.f., Roberts 2007, Hart and Chen 2008, Kohv *et al*. 2013, Reich *et al*. 2012), were selected. Tree basal area (BA- $m^2 ha^{-1}$) was selected to represent degree of light availability (Reich et al. 2012). Degree of soil disturbance (i.e., mean depth of surface O-horizon and percent mineral soil exposure for sand, loam site types and non-moss cover for peat site types), percent fine woody material (FWM) cover, total feathermoss, and sphagnum cover were selected to represent seedbed condition. Feathermoss and sphagnum cover were also selected, along with shrub cover, to represent the residual pre-disturbance understory layer as per Roberts 2007), Total graminoid cover and pioneer moss cover were selected to represent post-disturbance ground cover response. Mineralizable N and 15 year soil acidity (pH CaCl) were selected to represent soil productivity. To aid interpretation, the axes were orthogonally rotated so that axis 1 aligned with the strongest vector. Vector fitting (Dargie 1984) was used to study correlations between environmental factors and the ordinations.

3.6.5 Analysis of Seed Bank Species Presence

Comparison of Seed Bank with 15 year Post-harvest Community Diversity Measures

This work was carried out to study the differences in the composition of viable seeds in the seed bank (at the time of treatment) to the composition of post-harvest communities among site types and harvest types. Separate graphs were prepared showing the proportional abundance of each species (relative to total vascular plant cover excluding trees), compared to the proportional abundance of viable seed counts for that species in the seed bank to look for differences based on site type and harvest treatment.

The presence of a species in a post-treatment community and in the pre-disturbance seed bank per se does not prove that the species originated from the seed bank. The inclusion of the FTB treatment (where the seed bank was largely removed), however, provided an opportunity to show where species established from off-site propagules. The relationship between presence of a species in the seed bank and presence in the community on the TL and FT treatment can only be presented as observations, not causal. The origin of the plant species in the 15 year post-disturbance community may be parent plants in the pre-disturbance forest in, or adjacent to the treatment plots. Plant size is another factor that is considered when relating the proportional abundance of a species in the seed bank with that of the post-disturbance community. A comparison of proportional presence in the seed bank with proportional presence based on species presence/absence data provided a second approach for studying the role of the seed bank in post-disturbance community development.

A comparison of the pre-disturbance seed bank to the 15 year post-disturbance plant community was carried out using graphical representation of the proportional abundance of each life form and key species. The selection of species to examine was based on dominance in the seed bank, common species among the site types, and selected indicator species. Because pooling of study area results within site types was necessary to obtain adequate sample sizes, it was not possible to conduct formal statistical analyses on the data set.

It is often the abundance (cover) and life form rather than the diversity of species that influence the rate of development of both the overstory and understory plant community after disturbance. This analysis provides another line of evidence that increases our understanding of the response of communities to disturbance and the contribution of the pre-disturbance forest legacy (the relative abundance of vascular species in the seed bank and their position in the post-disturbance community) in structuring communities.

4.0 RESULTS

4.1 Environmental Parameters

While relationships between environmental parameters and species are explored later using NMS ordination and Indicator Species Analysis, a brief description of mean values and trends is presented here. Forest floor and soil conditions 15 years after treatment varied with site type and harvest treatment (Table 4.1). The most consistent trends with respect to soil nutrient properties were linked to site rather than harvest type. The mean values for the environmental parameters organized by site type can be found in Appendix III.

Physical Properties: Mineral soil exposure is highly variable ranging from 1.1 % (loam FT) to over 50% (sand, FTB). Although this parameter was estimated on peat sites, there was, as expected, little to no exposed mineral soil. Reflecting site and area variability, mineral soil exposure ranged from 1% to 20% after TL and FT on loam and sand site types, respectively. Mean mineral soil exposure continued to be high (44 and 54%) on FTB treatments on loam and sand site types, respectively, (Table 4.1).

There could have been confounding effects of incomplete removal of the surface O-horizon during the blading treatment on the more undulating loam site types interspersed with areas of exposed bedrock. Despite differences in the thickness of the LFH layers associated with site type, mean depths on TL and FT sites on the same site type were within 1.1 cm of each other.

Table 4.1 Fifteen-year physical, biotic and chemical environmental parameters for loam, sand and peat site type (mean values with standard error in brackets, soil nutrients for total soil (20 cm), except mineralizable NH_4 for F-horizon.

A Field Observations - Physical Properties

Harvest		Mineral Soil Exposure		Mean Depth of LFH		Coarse Woody Material (CWM)		Fine Woody Material (FWM)		Conifer Litter		Deciduous Litter	
Treatment	Site Type	% cover	range	(cm)	range	% cover	range	% cover	range	% cover	range	% cover	range
Tree Length	Loam	4.8 (1.3)	0-7.5	9.3 (1.5)	4.9-14.2	14.9 (3.6)	7-27	11.6 (1.7)	5.8-15	9.4 (5.9)	0-30	5.7 (2.9)	0-15
	Sand	18.7 (5.6)	0-40	5.9 (0.6)	3.7-7.3	12.5 (2.6)	1-20	13.3 (6.5)	0-40	7.0 (3.07)	1-18	2.3 (1.6)	0-10
	Peat	0.0	0.0	0.0	0.0	7.1 (1.7)	12-11	3.8 (1.8)	0-12	4.3 (2.2)	5-15	16.0 (5.6)	4.8-40.3
Full Tree	Loam	1.1 (0.9)	0-6.3	10.4 (1.4)	6.8-15.4	16.1 (5.4)	1-40	7.5 (3.6)	0-28	37.3 (12.0)	0-90	16 (10.0)	0.5-75
	Sand	4.8 (3.1)	0-120	5.4 (0.7)	3.9-7.2	4.2 (0.8)	3-3	6.6 (1.8)	0.9-12	43.7 (12.5)	0.5-32.5	0.6 (0.3)	0-2
	Peat	0.2 (0.2)	0-1	0.0	0.0	3.2 (1.1)	0-56.3	1.3 (0.8)	0-4.5	2.8 (1.1)	0-6.5	5.5 (1.4)	2-11.8
Full Tree Blade	Loam	43.6 (17.4)	0-90	7.5 (0.6)	6-8.6	10.8 (2.0)	4-20	1.7 (1.6)	0-8	28.6 (10.3)	0-50	3 (0.9)	1-5
	Sand	54.0 (17.0)	0-99	0.1 (0.1)	0-0.3	3.9 (2.0)	0.4-12	0.2 (0.2)	0-1	16.0 (7.3)	0-45	20.8 (15.1)	0-95
	Peat	0.0	0.0	0.0	0.0	3.1 (1.8)	0.6-12	1.0 (0.4)	0-3	0.3 (1.7)	0-75	15.6 (5.3)	0-30

B Field Observations - Biotic Elements

Harvest		Basal Area		Pioneer Moss		Feathermoss		Sphagnum		Total Moss		Total Lichen	
Treatment	Site Type	m^2ha^{-1}	range	% cover	range	% cover	range	% cover	range	% cover	range	% cover	range
Tree Length	Loam	2.6 (0.3)	1.4-3.4	10.0 (6.3)	0-30	0.3 (0.133)	0-0.6	0.0	0.0	12.3 (7.2)	0.3-30	2.3 (1.5)	0-8
	Sand	7.4 (1.5)	4.4-13.8	15.5 (9.8)	0-60	30.833 (11.0)	0-75	0.0	0.0	46.3 (11.1)	7-80	1.8 (0.6)	5-4
	Peat	1.4 (0.5)	0.5-3.1	1.5 (0.5)	0-3.3	9.3 (2.8)	1-20	55.9 (11.8)	15.5-90	66.1 (9.8)	28.8-93	2.3 (1.1)	0-5.7
Full Tree	Loam	5.2 (0.8)	3.0-7.9	21.5 (11.0)	0-80	10.1 (5.6)	0-32.5	1.6 (1.6)	0-11.3	33.1 (11.9)	5-80	5.6 (2.1)	5-16.7
	Sand	11.2 (0.8)	9.0-14.6	5.6 (2.1)	1-14	23.8 (11.4)	1-70	0.0	0.0	38.7 (13.1)	2.2-84	13.2 (5.6)	2-31.4
	Peat	0.7 (0.1)	0.3-1.1	2.1 (1.5)	0-9.3	6.4 (3.5)	0-19.8	64.9 (14.5)	11.5-95	73.4 (10.4)	40-96	1.7 (0.7)	0-3.7
Full Tree Blade	Loam	9.7 (1.2)	6.6-15.0	3.5 (1.3)	0-8	0.0	0.0	46.5 (19.4)	0-90	52.9 (20.6)	0-90	12.5 (1.3)	8-15.2
	Sand	9.2 (1.5)	4.8-14.0	17.9 (8.5)	0-55	12.2 (7.9)	0-49	0.0	0.0	21.3 (7.7)	2.5-5.5	1.8 (0.4)	0-2.5
	Peat	0.5 (1.7)	0.9-1.0	2.3 (0.9)	0-5.3	0.5 (0.4)	0-2.3	69.4 (7.1)	50-95	71.5 (8.1)	50-100	0.9 (0.4)	0-2.5

Table 4.1(cont'd) Fifteen-year physical, biotic and chemical environmental parameters for loam, sand and peat site type (mean values with standard error in brackets, soil nutrients for total soil, except mineralizable NH_4 for F-horizon.

C- Soil Chemical Properties

Harvest type		pHCaCl		pH Water		Mineralizable N, NH_4		Total N	
	Site Type	mean (SE)	range	mean (SE)	range	kgha^{-1}	range	kgha^{-1}	range
Tree Length	Loam	3.6 (0.2)	3.1-4.0	5.0 (0.1)	4.6-5.3	13.1 (2.45)	9.0-25.1	3017.2 (355.1)	1998.1-4146.1
	Sand	3.7 (0.1)	3.2-4.2	5.1 (0.1)	4.5-5.6	10.2 (1.8)	4.3-14.6	1558.3 (202.4)	1025.8-2325.1
	Peat	3.7 (0.3)	2.9-4.3	4.8(0.4)	3.8-5.8	31.1 (11.2)	3.4-58.9	3619.0 (647.0)	1779.6-5006.9
Full Tree	Loam	4.0 (0.1)	3.7-4.4	5.1 (0.1)	4.9-5.6	8.0 (0.2)	1.9-14.6	3696.0 (470.0)	1626.5-5962.2
	Sand	3.9 (0.2)	3.9-0.2	5.2 (0.2)	4.8-7.5	9.0 (1.5)	4.7-12.6	1706.6 (264.5)	1213.1-2925.4
	Peat	3.6 (0-.3)	3.2-4.6	4.8 (0.3)	4.3-5.73	21.9 (6.2)	7.6-42.9	2424.0 (593.3)	1189.0-4297.0
Full Tree Blade	Loam	4.2 (1.0)	4.0-4.5	5.5 (0.1)	5.1-5.9	1.8 (0.9)	0-5.2	2451.0 (352.9)	1771.1-4101.3
	Sand	4.5 (0.2)	4.1-5.2	5.7 (0.1)	5.3-6.1	0.0	0.0	605.7 (100.3)	337.3-1025.8
	Peat	3.9 (0.3)	2.9-4.4	5.0 (0.3)	4.0-5.6	41.2 (11.4)	6.5-72.9	2399.7 (280.9)	1641.1-3708.1

Harvest type		TC total soil		Bray's P		K		Ca		Mg	
	Site Type	Mgha^{-1}	range	kgha^{-1}	range	kgha^{-1}	range	kgha^{-1}	range	kgha^{-1}	range
Tree Length	Loam	101.3 (13.4)	57.3-134.2	7.1 (0.5)	5.6-9.1	549.1 (70.9)	281-789.8	7503.2 (3508.9)	1940.4-24883.	649.4 (293.3)	108.0-2039.6
	Sand	52.5 (8.2)	24.3-73.2	11.0 (1.6)	6.7-15.7	70.4 (8.4)	46.7-105.1	640.0 (169.6)	360.4-1465.4	60.6 (12.5)	32.0-119.8
	Peat	146.0 (17.6)	100.1-208.1	5.8 (1.1)	3.9-9.7	1027.7 (641.7)	82.5-3543.4	2009.3 (1193.8)	102.6-5880.1	353.9 (102.1)	110.0-669.1
Full Tree	Loam	116.9 (15.1)	50.8-159.1	5.6 (0.3)	4.8-6.6	740.2 (116.1)	379.3-1160.2	14661.6 (3330.0)	3693.1-22480.	618.3 (114.0)	267.8-949.7
	Sand	59.9 (7.7)	44.3-95.1	13.3 (3.333)	5.5-25.9	72.8 (4.8)	56.1-87.6	534.5 (102.6)	259.8-899.4	66.2 (12.0)	34.6-103.0
	Peat	130.7 (23.9)	74.6-205.8	3.9 (0.8)	2.4-6.1	712.7 (300.1)	67.8-1735.3	1192.3 (831.2)	79.9-4378.0	305.2 (81.7)	160.1 - 618.2
Full Tree Blade	Loam	74.0 (11.8)	53.6-131.1	5.5 (1.1)	2.1-9.7	490.6 (105.6)	225.6-829.6	22652.2 (7081.7)	6350.1-55532.	760.7 (161.9)	310.4-1230.7
	Sand	14.9 (2.4)	8.7-24.3	12.0 (4.6)	3.9-34.17	35.7 (3.4)	23.3-46.7	272.5 (94.5)	75.7-677.5	25.4 (7.5)	5.9-57.9
	Peat	119.2 (4.7)	103.9-135.9	3.4 (0.5)	2.3-5.4	701.4 (423.5)	48.3-2724.8	1865.1 (780.3)	89.1-3702.3	359.2 (78.4)	114.1 - 585.6

Percent cover of CWM and FWM declined with increasing harvesting intensity on all site types. FWM values after FT treatments were just over half of those recorded on TL plots, and percent cover of FWM on FTB plots was <2% on all sites. Total values were similar on the upland sites (loam, sand site types) with notably lower values on peat site types (e.g., CWM cover after TL was estimated at 14.9%, 12.5%, and 7.1%; FWM cover was 11.6%, 13.3%, and 3.8%, on loam, sand, and peat site types, respectively). Percent cover of conifer litter on the sand and loam site types was higher after FT and FTB compared to TL. For example, on loam sites the percent cover of conifer litter was 9.4, 37.3%, and 28.6% for the TL, FT and FTB plots. Percent cover of conifer litter cover on peat sites was half of that recorded on loam sites after TL (4.3%) and more than 10 times lower for FT (2.8%) and FTB (0.3%) values. Percent cover of deciduous leaf litter was high after FTB treatments on sand (20.8%) and peat (15.6%) sites but sparse (3%) on loam site types.

Biotic Elements

Basal Area: Overall, mean BA values increased from the peat (mean 0.8 m^2 ha^{-2}), to loam (mean 5.7 m^2 ha^{-2}) to sand (9.3 m^2 ha^{-2}) site types. On loam sites, BA increased with increasing harvest intensity (2.6 m^2 ha^{-2}TL, 7.4 m^2 ha^{-2} FT, 9.7 FTB) (APPENDIX III). On sands, BA peaked at intermediate harvest intensities (11.2 m^2 ha^{-2} FT) and on peat sites BA declined as harvest intensity increased (1.4 TL, 1.35 m^2 ha^{-2} FTB). Photographs of a plot from a loam site type 15 years after the TL, FT and FTB treatments show the differences among the treatments (Figure 4.1).

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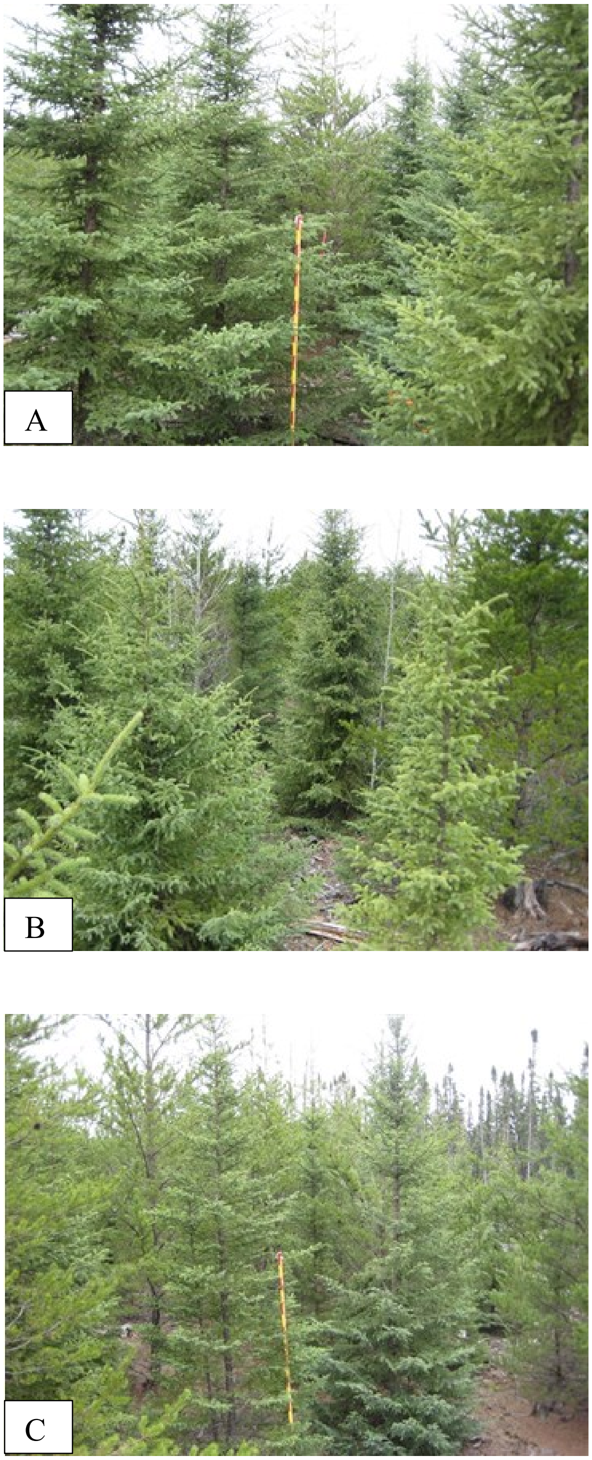

Figure 4.1 Plant communities 15 years after:A- tree-length (TL), B-full-tree (FT) and C-full-tree blade (FTB) treatments on the loam site type.

Moss and Lichen: Overall total moss was highest on peat sites driven by % sphagnum. Feathermosses were highest on sand sites regardless of harvest treatment and pioneer mosses were lowest on peat sites. There was a reduction in feathermoss cover on FTB treatments compared to TL on all site types (e.g., 30.8%, TL, 12.2%, FTB sand site types, Table 4.1). Lichen presence was variable, however overall values were lowest on TL plots and highest on sand after FT (13.2%) and on loam after FTB (12.5%)

Chemical Properties:

pH: Mean soil pH (CaCl) values increased with harvest intensity on loam (3.7 TL, 4.0 FT, 4.2 FTB) and sand (3.8 TL, 3.9 FT, 4.6 FTB) with little change on peat (3.7 TL, 3.6 FT, 3.9 FTB) site types.

Mineralizable Nitrogen: Mineralizable nitrogen (NH_4, kg ha^{-1}) values for the F-horizon declined with increasing harvest intensity on the loam and sand site reflecting the removal of the surface organic layer. Values (for the Of layer) were variable, and much higher, on the peat site type. Values for the mineral soil layer did not show a detectable response to treatment intensity and are not reported.

Total Soil Nitrogen (TN): Total soil total N (kg ha^{-1}) decreased 20 to 30% after FTB when compared to TL on loam and peat and was 40% lower when compared to TL on sand site types. Interestingly, TN was highest on the FT treatments for the loam and sand site types.

Total Soil Carbon (TC): Total soil C was consistently low on the sand sites and high on the peat sites. Highest values on loam and sand were recorded on the FT sites (117 and 60 Mg ha-1, respectively), followed by TL (101 and 52 Mg ha-1, respectively) and FTB

(74 and 15 Mg ha-1, respectively). Values on peat sites declined approximately 10% with each increase in harvesting intensity.

Bray's Phosphorus (P): Brays P values were approximately 20% lower after FTB (5.5 kg ha^{-1}) compared to TL (7.1 kg ha^{-1}) on loam, were higher on sand (FTB 13.3 kg ha^{-1}) compared to TL (11 kg ha^{-1}). Values were lower after FTB (3.4 kg·ha^{-2}) compared to TL (5.8 kg·ha^{-2}) on peat site types.

Potassium (K): K pools in kg·ha^{-2} were similar after TL and FT on sands (70 kg·ha^{-2}, 73 kg·ha^{-2}, respectively), then dropped to half the value (36 kg·ha^{-2}) on FTB site types. On loam sites K values fell by 40% after FTB, when compared to FT, and on sand site types fell by approximately 50%. On peat site types, K was highest on TL plots (1027.7 kg·ha^{-2} compared to 701.4 FTB).

Total Soil Calcium (Ca): Total soil Ca was higher on the FTB treatments when compared to TL on loam, and lower on sand and peat sites.

Total Soil Magnesium (Mg): Mg was highest on loam sites (618 to 761 kg ha-1), and lowest on sand sites (25 to 66 kg ha-1) with peat sites in the middle.

4.2 Species Diversity Measures

Overall, post-harvest values for richness, evenness, Shannon's H' and Simpson's D for all species and for the vascular species data set increased on the loam and peat site types, but not the sand site type (Table 4.2, 4.3). Orthogonal contrasts (Table 4.4) helped to identify the key ecological factors that contributed to these changes. In very general terms, the removal of the forest canopy through harvesting led to significant differences in all four diversity metrics. Removing or retaining the forest floor had no effect on the loam or peat sites but led to changes in E, H' and D on sand types. Retention or removal of the CWM led to significant changes in R but again only on the loam and peat sites.

Table 4.2 Mean diversity indices for UNCUT forests (SE- standard error) found on loam, sand and peat site types (richness values for 2 m x 2m quadrats).

Diversity Measure		Site Type					
		Loam		Sand		Peat	
		Mean	(SE)	Mean	(SE)	Mean	(SE)
Richness	All Species	14.30	(1.8)	19.50	(2.1)	13.70	(1.3)
	Vascular Species	7.50	(1.4)	12.83	(1.10)	8.50	(1.80)
Evenness	All Species	0.58	(0.05)	0.61	(0.02)	0.70	(0.03)
	Vascular Species	0.45	(0.06)	0.69	(0.04)	0.73	(0.06)
Shannon's H'	All Species	1.50	(0.20)	1.80	(0.04)	1.80	(0.18)
	Vascular Species	0.88	(0.19)	1.76	(0.13)	1.43	(0.12)
Simpson's D	All Species	0.70	(0.05)	0.73	(0.01)	0.74	(0.06)
	Vascular Species	0.42	(0.08)	0.73	(0.05)	0.69	(0.04)

Two-way ANOVA for the four metrics (all species and vasculars) including the UNCUT plots indicated significant effects of the ST*HT interaction for all comparisons (Table 4.5) as well as HT main effects for seven of the eight comparisons. The interaction pattern varied with the metric and the grouping of species used (i.e., all species or vascular species only). Figure 4.2 illustrates this variability for richness.

Table 4.3 Mean diversity indices 15 years after harvest disturbance associated with loam, sand and peat site types (SE-standard error); richness per 2m x 2m quadrat.

Diversity Measure		HT	Site Type loam Mean (SE)	 sand Mean (SE)	 peat Mean (SE)
Richness	All Species	TL	21.29 (1.70)	22.50 (2.13)	30.00 (4.08)
		FT	25.00 (3.52)	33.50 (2.00)	24.33 (2.50)
		FTB	23.33 (2.67)	28.17 (6.40)	28.67 (5.00)
	Vascular	TL	13.00 (1.23)	7.60 (1.07)	16.17 (2.40)
		FT	12.60 (2.90)	11.50 (3.90)	15.17 (3.40)
		FTB	16.67 (2.39)	14.50 (3.35)	15.83 (2.90)
Evenness	All Species	TL	0.74(0.03)	0.59(0.03)	0.67(0.02)
		FT	0.72(0.02)	0.63(0.02)	0.74(0.02)
		FTB	0.71(0.03)	0.76(0.06)	0.70(0.03)
	Vascular	TL	0.67 (0.04)	0.76 (0.06)	0.66 (0.03)
		FT	0.67 (0.02)	0.58 (0.06)	0.77 (0.02)
		FTB	0.65 (0.03)	0.75 (0.06)	0.76 (0.03)
Shannon's H'	All Species	TL	2.33 (0.12)	1.18 (0.08)	2.52 (0.13)
		FT	2.27(0.11)	2.13 (0.22)	2.49 (0.17)
		FTB	2.43(0.19)	2.39 (0.21)	2.55 (0.12)
	Vascular	TL	1.78 (0.16)	1.43 (0.11)	2.16 (0.18)
		FT	2.11 (0.13)	1.57 (0.26)	2.12 (0.10)
		FTB	1.92 (0.19)	1.89 (0.23)	2.48 (0.11)
Simpson's D	All Species	TL	0.84 (0.02)	0.72 (0.04)	0.86 (0.02)
		FT	0.87 (0.02)	0.78 (0.04)	0.86 (0.03)
		FTB	0.86 (0.03)	0.86 (0.02)	0.87 (0.02)
	Vascular	TL	0.75 (0.04)	0.68 (0.04)	0.81 (0.03)
		FT	0.81 (0.02)	0.64 (0.08)	0.83 (0.02)
		FTB	0.76 (0.04)	0.78 (0.04)	0.88 (0.01)

HT =Harvest treatment, TL= tree length, FT= full tree and FTB= full tree blade

Table 4.4 Orthogonal contrast results for the effect of disturbance type on all species diversity for three site types.

Contrasts	Richness R		Evenness E		Diversity H'		Diversity D	
	t	Sig.	t	Sig.	t	Sig	t	Sig.
Loam Sites:								
Unharvested vs. Harvested	*4.1*	**0.001**	3.86	**0.001**	4.88	**<0.001**	4.87	**<0.001**
Forest floor retained vs. Removed	-0.28	0.78	0.46	0.65	0.81	0.94	-0.13	0.99
Coarse and fine slash retained vs. CWM only	-2.2	**0.04**	0.337	0.74	-1.01	0.32	-0.71	0.49
Sand Sites:								
Unharvested vs. Harvested	1.95	**0.07**	1.7	0.12	2.93	**0.01**	2.5	**0.03**
Forest floor retained vs. Removed	-0.12	0.91	-3.1	**0.02**	-1.9	0.1	-3.5	**0.006**
Coarse and fine slash retained vs. CWM only	-0.12	0.91	-0.07	0.95	-0.06	0.95	-0.43	0.68
Peat Sites:								
Unharvested vs. Harvested	4.76	**<0.001**	-0.005	0.1	4.14	**0.001**	3.08	**0.006**
Forest floor retained vs. Removed	-0.68	0.51	0.05	0.96	-0.29	0.78	-0.28	0.78
Coarse and fine slash retained vs. CWM only	2.27	**0.03**	-1.84	0.08	0.17	0.87	-0.06	0.96

Recognizing that UNCUT plots were statistically different from their harvested counterparts and in order to better capture significant differences between harvest treatments, two-way ANOVA was run without the UNCUT data (Table 4.6). In this case, the interaction (ST*HT) was only significant in 5 of 12 comparisons with the HT main effect identified only once and that where there was a significant ST*HT interaction. Site type alone was a significant main effect only for non-vascular richness and vascular Shannon's H' and Simpson's D. Evenness of all, vascular and non-vascular species was the most consistently affected variable. The relationship of species composition values with environmental variables were examined with NMS ordination and are discussed in Section 5.

4.2.1 Canopy Disturbance

Based on the orthogonal contrasts (for all species), the removal of the overstory by harvesting significantly increased R, H and D on all three site types (R, p=0.001, p=0.07, p=<0.001; H, p<0.001, p=0.01, p=0.001; D, p=<0.001, 0.03, 0.006 for loam, sand, peat site types, respectively)(Table 4.4). The test also showed a significant effect on E on loam (p=0.001) but not sand (p=0.34) or peat (p=0.1) site types.

Both total species R and vascular R increased after overstory removal on all three site types (Tables 4.3 and 4.4). R values in the uncut forests were very similar for loam and peat site types (R=14.3, 13.7 total species; R=7.5, 8.5 for vascular species. On sand site types, both total and vascular R (19.5, 12.8) were higher compared to loam and peat site types.

When E values for UNCUT treatments were compared among the site types, values were highest on peat sites (all species E=0.70; vascular species E=0.73) suggesting that the species present occurred with relatively even abundance, with lower values on sand (E=0.61 and 0.69) and loam sites (E=0.58, 0.45) for all species and vascular species, respectively. The removal of the overstory only lead to a significant difference with harvested plots on the loam site type (p=0.001).

Table 4.5 Two-way ANOVA to test for differences in species diversity measures on loam, sand and peat site types (all treatments).

Diversity Measure		Source	df	Mean Square	F-ratio	P
Species Richness	All Species	ST	2	306.79	0.86	0.51
		BK	3	362.91	2.90	**0.04**
		HT	3	1244.33	9.95	**≤0.0001**
		ST*HT	6	316.46	2.53	**0.03**
		Error	57	125.12		
		Total	71			
	Vascular Species	ST	2	298.18	1.01	0.46
		BK	3	295.74	5.16	**0.003**
		HT	3	517.05	9.02	**≤0.0001**
		ST*HT	6	230.66	4.03	**0.002**
		Error	57	57.30		
		Total	71			
Evenness	All Species	ST	2	0.02	1.99	0.280
		BK	3	0.01	1.94	0.130
		HT	3	0.03	4.80	**0.005**
		ST*HT	6	0.02	3.82	**0.003**
		Error	57	0.006		
		Total	71			
	Vascular Species	ST	2	0.08	4.02	0.14
		BK	3	0.02	1.63	0.19
		HT	3	0.03	2.18	0.10
		ST*HT	6	0.04	3.51	**0.005**
		Error	57	0.01		
		Total	71			
Shannons H'	All Species	ST	2	0.67	1.34	**0.04**
		BK	3	0.50	3.92	**0.01**
		HT	3	2.03	15.97	**≤0.0001**
		ST*HT	6	0.26	2.03	0.08
		Error	57	0.13		
		Total	71			
	Vascular Species	ST	2	1.15	4.44	0.13
		BK	3	0.26	1.60	0.20
		HT	3	1.80	11.22	≤0.0001
		ST*HT	6	0.70	4.34	**0.001**
		Error	57	0.16		
		Total	71			
Simpson's D	All Species	ST	2	0.03	1.10	0.06
		BK	3	0.03	5.13	0.24
		HT	3	0.07	13.79	**0.04**
		ST*HT	6	0.01	2.25	**0.05**
		Error	57	0.005		
		Total	71			
	Vascular Species	ST	2	0.09	6.35	0.08
		BK	3	0.01	1.18	0.33
		HT	3	0.12	10.11	≤0.0001
		ST*HT	6	0.07	5.69	**≤0.0001**
		Error	57	0.01		
		Total	71			

ST- site type (loam, sand, peat) BK(ST) site type rep

Table 4.6 Two-way ANOVA to test for differences in species diversity measures on loam, sand and peat site types (harvest treatments only)

Diversity Measure		Source	df	Sum of Squares	Mean Square	F-ratio	P
Species Richness	All Species	ST	2	1285.14	642.57	2.19	0.26
		BK	3	879.90	293.30	1.85	0.15
		HT	2	143.46	71.73	0.45	0.64
		ST*HT	4	1140.76	285.19	1.80	0.15
		Error	42	6668.08	158.76		
		Total	53	10028.80			
	Vascular Species	ST	2	973.06	486.53	2.42	0.24
		BK	3	603.622	201.21	2.84	**0.05**
		HT	2	168.36	84.18	1.19	0.32
		ST*HT	4	724.48	181.12	2.56	**0.05**
		Error	42	2976.88	70.88		
		Total	53	6030.59			
	Non-vascular	ST	2	141.89	70.95	49.84	**0.01**
		BK	3	4.27	1.42	0.03	0.99
		HT	2	82.45	41.23	0.95	0.39
		ST*HT	4	105.29	26.32	0.61	0.66
		Error	42	1821.64	43.37		
		Total	53	2149.20			
Evenness	All Species	ST	2	0.06	0.03	10.53	**0.04**
		BK	3	0.01	0.00	0.49	0.69
		HT	2	0.03	0.01	2.41	0.10
		ST*HT	4	0.75	0.02	3.26	**0.02**
		Error	42	0.24	0.01		
		Total	53	0.41			
	Vascular Species	ST	2	0.07	0.04	1.03	0.46
		BK	3	0.11	0.04	3.91	**0.02**
		HT	2	0.04	0.03	2.24	0.12
		ST*HT	4	0.15	0.04	4.16	**0.01**
		Error	42	0.39	0.01		
		Total	53	0.67			
	Non-vascular	ST	2	0.24	0.12	1.58	0.34
		BK	3	0.23	0.08	2.65	0.06
		HT	2	0.05	0.03	0.89	0.42
		ST*HT	4	0.42	0.11	3.64	**0.01**
		Error	42	1.22	0.03		
		Total	53	2.15			

Table 4.6 (cont'd) Two-way ANOVA to test for differences in species diversity measures associated with site type and harvest types.

Diversity Measure		Source	df	Mean Square	F-ratio	p
Shannons H'	All Species	ST	2	1.27	8.75	0.06
		BK(ST)	3	0.15	1.12	0.35
		HT	2	0.26	2.00	0.15
		ST*HT	4	0.21	1.59	0.20
		Error	42	0.13		
		Total	53			
	Vascular Species	ST	2	1.89	35.76	**0.01**
		BK(ST)	3	0.05	0.31	0.82
		HT	2	0.34	2.01	0.15
		ST*HT	4	0.14	0.85	0.50
		Error	42	0.17		
		Total	53			
	Non-vascular	ST	2	0.49	0.97	0.47
		BK(ST)	3	0.51	1.37	0.26
		HT	2	0.15	0.40	0.67
		ST*HT	4	0.30	0.81	0.53
		Error	42	0.37		
		Total	53			
Simpson's D	All Species	ST	2	0.05	8.31	0.06
		BK(ST)	3	0.01	1.46	0.24
		HT	2	0.01	3.50	**0.04**
		ST*HT	4	0.01	2.63	**0.05**
		Error	42	0.00		
		Total	53			
	Vascular Species	ST	2	0.09	15.14	**0.03**
		BK(ST)	3	0.01	0.61	0.62
		HT	2	0.02	2.05	0.14
		ST*HT	4	0.01	1.39	0.25
		Error	42			
		Total	53			
	Non-vascular	ST	2	0.11	1.89	0.29
		BK(ST)	3	0.06	1.43	0.25
		HT	2	0.02	0.38	0.69
		ST*HT	4	0.06	1.41	0.25
		Error	42	0.04		
		Total	53			

ST - site type (loam, sand, peat); BK(ST) site type rep

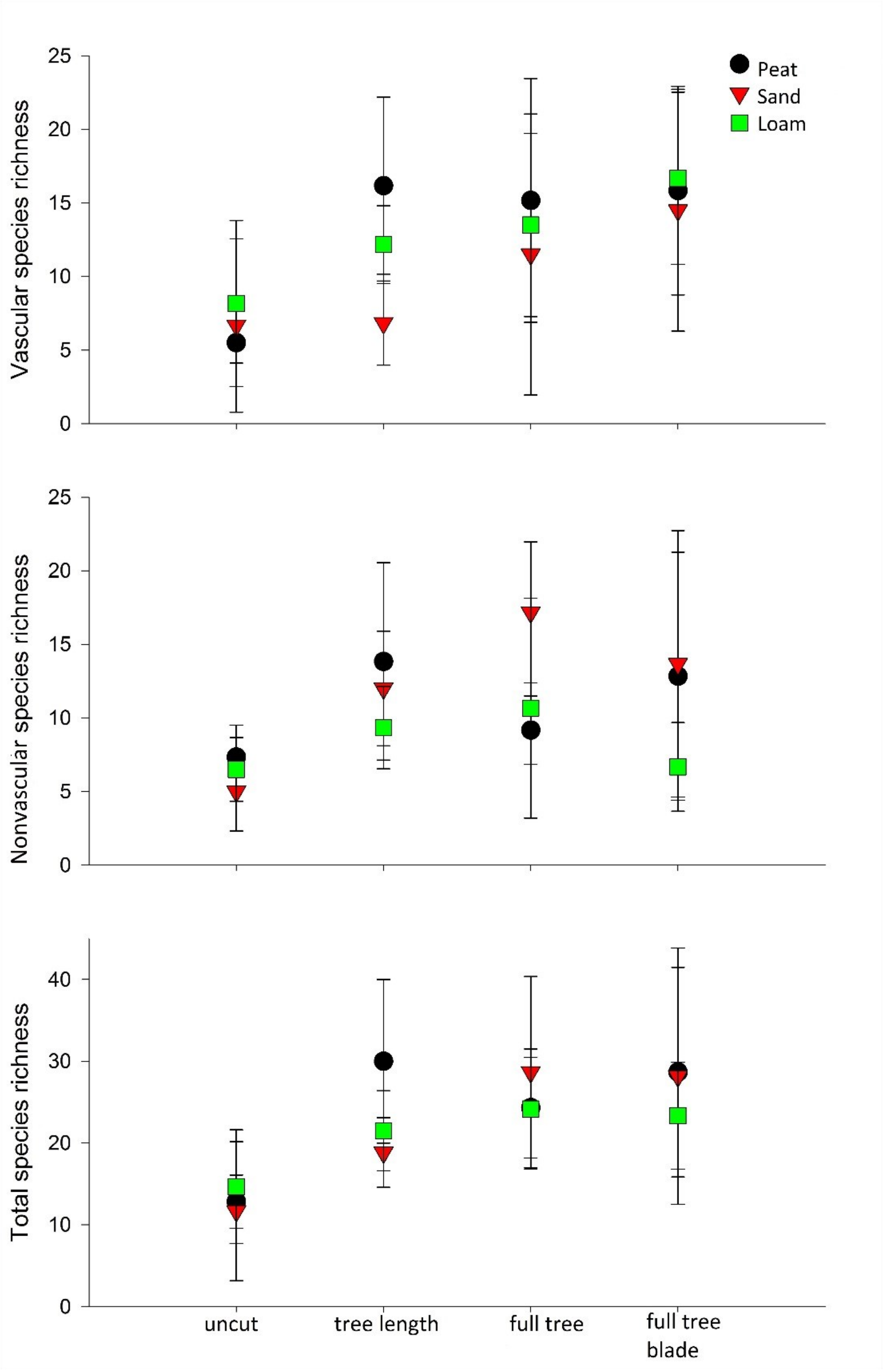

Figure 4.2 Species richness 15 years after three levels of harvesting intensity on loam, sand and peat site types.

4.2.2 Ground Layer Disturbance

The results of the orthogonal contrasts showed that the removal of the forest floor (FTB *vs*. TL and FT) did not have a significant effect on 15 year post-disturbance total plant diversity indices on loam or peat site types (Table 4.4, all values of $p > 0.5$) over and above the effects of the removal of the overstory and FWM. For example, R (all species) was estimated as 23.1 after TL and FT treatments and 23.3 after the removal of the surface O-horizons (FTB) on loam, 28 for TL and FT and 28.2 for FTB on sand and 27.1 (TL and FT) and 28.7 (FTB) on peat sites). FTB was also associated with a significant response in E ($p=0.02$) and D (0.006) on sand site types. E was estimated as 0.61 (all species) after TL and FT increasing to 0.76 after FTB treatments on sands.

4.2.3 Fine Woody Material (FWM) Disturbance

The removal of FWM had a positive effect on total species R ($p=0.04$) but not on other indices on the loam site type (all p values > 0.3, Table 4.4) with values increasing from 21 (TL) to 25 (FT) (Table 4.3). On peat site types, the removal of FWM was associated with a decrease in R from 30 (TL) to 24 (FT) ($p=0.03$).

4.3 Reproductive Strategy Response

Two-way ANOVA for the vascular species data set (for harvested data only) showed significant ST*HT interaction effects for groups that rely primarily on vegetative reproduction ($p=0.002$) but not for those employing seed reproduction or those that rely on both seed and vegetative strategies (Table 4.7). The results showed a significant effect of harvest treatment on richness for seed-reproduction ($p \leq 0.0001$) and those that rely on both reproductive strategies ($p=0.001$).

Table 4.7 Two-way ANOVA of dominant reproductive strategy richness for vascular species for all treatments

Source	df	Mean Square	F	p
Seed Reproduction				
Site type (ST)	2	45.17	1.34	0.38
Block (BK)	3	33.76	3.07	0.04
Harvest Treatment (HT)	3	130.37	11.84	**<0.0001**
Harvest treatment x Site type (HT*ST)	6	4.6	0.42	0.86
Error	57	11.02		
Total	71			
Vegetative Reproduction				
Site type (ST)	2	106.17	2.51	0.23
Block (BK)	3	42.28	6.63	≤0.001
Harvest Treatment (HT)	3	5.5	0.86	0.47
Harvest treatment x Site type (HT*ST)	6	25.72	4.03	**0.002**
Error	57	6.38		
	71			
Seed and Vegetative Reproduction				
Site type (ST)	2	2.89	0.36	0.73
Block (BK)	3	8.06	4.88	0.004
Harvest Treatment (HT)	3	9.89	5.99	**0.001**
Harvest treatment x Site type (HT*ST)	6	1.11	0.67	0.67
Error	57	1.65		
	71			

p= level of significance; df=degrees of freedom,

4.4 Species Composition and Abundance

A two-way PerMANOVA run with the harvested data set showed significant ST*HT interaction effects for all species (p=0.01) and the vascular species (p=0.05) (Table 4.8). As a result, separate one-way PerMANOVA were run. These results showed significant differences in total species composition among the harvest treatments for each site type (loam, p=0.02, sand, p<0.001 and peat p=0.04; Table 4.9). This result could be attributed to differences in vascular species composition among the HT for loam (p=0.03) and peat (p=0.02) but not sand (p=0.19) site types.

Table 4.8 Permutation multivariate analysis (PerMANOVA) results for 15th year understory all species and vascular species cover

Data Set	Source	df	Mean Square	F-ratio	p
All Species					
	ST	2	2.664	12.132	<0.001
	HT	2	0.552	2.516	0.001
	ST x HT	4	0.364	1.660	0.01
	Residual	45	0.220		
	Total	53			
Vascular					
	ST	2	2.094	9.044	<0.001
	HT	2	0.488	2.107	0.09
	ST x HT	4	0.333	1.439	0.05
	Residual	45	0.232		
	Total	53			

4.4.1 Indicator Species Analysis

Significant indicator species (IS) in pre-disturbance (UNCUT) forests on all site types were the shrub *Gaultheria hispidula* (L.) Muhl. ex Bigelow (p=0.02, 0.003, 0.02 on loam, sand, and peat site types, respectively), and *Pleurozium schreberi* (p=0.001, 0.001, 0.01 on loam, sand, and peat site types, respectively) (Table 4.10). *Gaultheria* is a slow growing, shade-tolerant creeping ericaceous shrub and *P. schreberi* is a common shade- tolerant feathermoss. *Linnaea borealis* L., a native evergreen dwarf shrub, was an additional IS on the loam and sand site types (p=0.07 and 0.003 respectively).

Relatively few IS were identified for TL treatments. *Vaccinium angustifolium* Aiton (p=0.04), a deciduous ericaceous low shrub (p=0.04) and fireweed (*Epilobium angustifolium* p=0.10) for loam and *Alnus incana* (L.) Moench, (p=0.02) a tall shrub

Table 4.9 Permutation multivariate analysis (1-way PerMANOVA) results for 15th year all species and vascular species understory cover by site type

Site Type	Data Set	Source	df	Mean Square	F-ratio	p
Sand	All Species					
		HT	2	0.56	2.29	<0.001
		Residual	15	0.25		
		Total	17			
	Vascular					
		HT	2	0.36	1.26	0.19
		Residual	15	0.29		
		Total	17			
Loam	All Species					
		HT	2	0.40	1.76	0.02
		Residual	15	0.23		
		Total	17			
	Vascular					
		HT	2	0.39	1.93	0.03
		Residual	15	0.20		
		Total	17			
Peat	All Species					
		HT	2	0.32	1.72	0.04
		Residual	15	0.19		
		Total	17			
	Vascular					
		HT	2	0.41	1.97	0.02
		Residual	15	0.21		
		Total	17			

with nitrogen fixing properties on peat site types. There were no significant indicator species associated with the sand site type.

With FT harvest, the greatest variety of IS were associated with the loam site types (6 species): two trees (*Populus tremuloides* Michx., p=0.003 and *Pinus banksiana* Lamb*.,* p=0.02), one low shrub, *Vaccinium myrtilloides* Michx. (p=0.01), one grass, Canada blue-joint grass, *Calamagrostis canadensis* (Michx.) P. Beauv. (IV=49.4, p=0.07) and the ruderal herb *Tragopogon pratense* L. (p=004). On sands, the IS was *P. banksiana* (p=0.02); and on peat soils, *Cladina* spp., a reindeer lichen (p=0.01).

Four IS were associated with the highest disturbance treatments (FTB) on loam and sand site types. The IS on loam sites included *Salix* (p=0.01) and two ruderal herbs, *Anaphalis margaritaceae* (L.) Benth. & Hook (p=0.08) and *Hieracium aurantiacum L.* (p=0.04), both indicators of open disturbed habitats. On sand site types, the IS were *Betula papyrifera* Marsh. (p= 0.06), a pioneer tree species, and the ruderal herb, *Symphyotrichum ciliolatum* (Lindl.) A. Love & D. Love (p=0.007), both wind-dispersed species well-adapted to germinating on mineral soil substrates, providing moisture conditions at the time of germination are favourable. Two pioneer moss species, well adapted to full to partial sunlight and disturbed mineral soils, *Ceratodon purpureus* (Hedw.) Brid. and *Pohlia nutans* (Hedw.) Lindb., grouped for the analysis, were IS of sand sites after FTB (p=0.04).

On the peat site types, 17 IS were associated with the FTB treatments. This included two deciduous trees (*B. papyrifera* and *Larix laricina*) and two tall shrub species (*Alnus, Salix*) that are well adapted to growing in full-sunlight conditions after disturbance. Five herbs indicative of disturbed soils were identified, including the post-fire species *E. angustifolium*, and species common to roadsides including *H. aurantiacum* and *A. margaritacea*. Graminoids were also identified as significant indicators including cottongrass (*Eriophorum* spp.), and Canada blue-joint grass (*C. canadensis*) and common cattail (*Typha latifolia*). Alder was also identified as a significant indicator of TL with no vascular species identified as significant indicators of FT treatments.

Table 4.10. Indicator species found on loam, sand and peat sites for uncut (UNCUT), tree-length (TL), full-tree (FT) and Full-tree blade (FTB) treatments.

Site Type	Life Form	Species	UNCUT			Tree-Length			Full-Tree			Full-Tree Blade		
			IV	f	p	IV	f	p	IV	f	p	IV	f	p
Loam	Tree and tall shrub													
		Picea mariana	67.0	100	**<0.001**									
		Pinus banksiana							46.7	100	**0.02**			
		Populus tremuloides							69.4	100	**0.003**			
		Salix spp.										57.6	83	**0.01**
	Low shrub													
		Gaultheria hispidula	62.6	83	**0.02**									
		Linnaea borealis	43.5	50	**0.07**									
		Rubus pubescens							55.1	67	**0.06**			
		Vaccinium angustifolium				54.8	100	**0.04**						
		V. myrtilloides							60.7	67	**0.01**			
	Herb													
		Anaphalis margaritaceae										40.2	50	**0.08**
		Epilobium angustifolium				49.6	100	**0.1**						
		Hieracium aurantianum										73.6	100	**0.04**
		Tragopogon pratense							50	50	**0.04**			
	Graminoid													
		Calamagrostis canadensis							49.4	67	**0.07**			
	Moss	*Pleurozium shreberi*	83.2	100	**<0.001**									
	Lichen													
		Cladonia spp.										48	100	**0.08**
Sand	Tree and tall shrub													
		Betula papyrifera										46.6	67	**0.06**
		Picea mariana												
		Pinus banksiana							57.6	100	**0.02**			
	Low shrub													
		Gaultheria hispidula	72.3	83	**0.003**									
		Linnaea borealis	61.2	100	**0.02**									
		Rosa acicularis	45.0	67	**0.08**									
		Vaccinium angustifolium										66.7	67	**0.007**
		Vaccinium myrtilloides	59.6	83	**0.04**									
	Herb													
		Cornus canadensis	47.4	100	**0.06**									
		Maianthemum canadense	53.6	100	**0.02**									
		Symphyotrichum ciliolatum										65.4	67	**0.007**
	Gramoid													
	Moss													
		Pleurozium shreberi	58.4	100	**<0.001**									
		Ceratodon & Pohlia										48.9	50	**0.04**
	Lichen													

Table 4.10 cont'd. Indicator species found on loam, sand and peat sites for uncut (UNCUT), tree-length (TL), full-tree (FT) and Full-tree blade (FTB) treatments.

Site Type	Life Form	Species	UNCUT			Tree-Length			Full-Tree			Full-Tree Blade		
			IV	f	p	IV	f	p	IV	f	p	IV	f	p
Peat	Tree and tall shrub													
		Picea mariana	57.7	86	**0.01**									
		Alnus incana				49.3	83	**0.02**						
		Larix laricina										63.4	80	**0.02**
		Betula papyrifera										40	40	**0.04**
		Salix spp.										53	80	**0.02**
		Alnus crispa										41	60	0.05
	Low Shrub													
		Gaultheria hispidula	53.2	100	**0.02**									
		Chamaedaphne calyculata										61	100	**<0.001**
		Kalmia polifolia										56.7	80	**0.03**
	Herb													
		Solidago uliginosa										75.6	80	**0.02**
		Epilobium angustifolium										48	80	**0.03**
		Anaphalis margaritaceae										40	40	**0.04**
		Hieracium aurantianum										40	40	**0.04**
		Viccia cracca										40	40	**0.04**
	Graminoid													
		Scirpus spp.										80	80	**0.005**
		Poa										61.1	100	**0.01**
		Eriophorum spp.										60.9	100	**0.01**
		Calamagrostis canadensis										58.2	80	**0.01**
		Typha latifolia										40	40	**0.04**
	Moss													
		Pleurozium shreberi	47.8	86	**0.1**									
		Sphagnum spp.	49.2	100	**0.07**							47.4	100	**0.08**
	Lichen													
		Cladina spp.							57.4	100	**0.01**			

Bold - signficant at p≤0.1, IV = Indicator Value, f=relative frequency of occurrence, p=probability

4.5 Soil Seed Bank

The number of germinants was highest (687) from collections taken from the sand, intermediate on loam (377), and lowest on the peat (94) site types (Appendix IV). The results of a comparison of the proportional distribution of species in the seed bank compared to the proportional distribution of these species in the 15 year old plant communities are presented by ST in Figures 4.3 (loam site type), 4.4 (sand site type), and 4.5 (peat site type). *Carex* (sedge) and *Poa* (grass) species were the most abundant species in the soil seed bank, accounting for 25 to 60 % of the total germinants. The species in the figures are presented based on similar proportional abundance in the seed bank.

4.5.1 Loam Site Type

Sixteen plant species and one unidentified species were present in the seed bank. *Carex* (sedge) and *Poa* (grass) species were the most abundant species in the pre-disturbance soil seed bank (Figure 4.3). Sixty-two percent of these species were observed in the treatment plots. Their presence in plant communities 15 years after harvest varied with treatment: 56%, 56% and 44% after TL, FT and FTB treatments, respectively. Those species that were absent included *Diervilla lonicera* (shade-tolerant deciduous shrub), *Chamaedaphne calyculata* (evergreen ericaceous species), three herbs that reproduce primarily from rhizomes, namely *Corydalis sempervirens, Geranium bicknellii* and *Oxalis montana* (Pavek 1992). *Chenopodium album* (Lamb's quarters), an annual seed –origin species of European origin characterized by rapid growth and seed banking properties of seeds retaining their viable beyond 40 years was also absent.

Sedge presence was highest on the FTB sites where the surface O-horizons were removed; *Poa* presence was highest after FT treatments. Sedges represented an average of 314.3 germinants per m^{-3} and grass species 132.63 germinants per m^{-3}.

The relative proportion of herbaceous species in the seed bank was very low with an average of 17.2 germinants m^{-3} consisting of 5 species including two moderately shade-tolerant forest herbs including (*O. montana*) which propagates primarily vegetatively from rhizomes and less commonly by seed, and *Viola renifolia*. The presence of these herb species in the 15-year old plant communities is negligible to absent. *O. montana* was not observed in any of the post-treatment plots.

The woody species present in the soil seed bank were diverse, but represented a small proportion of the seed bank. *G. hispidula* represented a very small proportion of the seed bank, but had increasing prominence in the plant communities as harvest intensity increased (Figure 4.3). Its presence may represent expansion of pre-disturbance plants as shading re-established on the TL and FT sites. On the FTB site, its presence may represent vegetative growth from small residual patches adjacent to stumps or rocks that were missed in the treatment. *Ribes* species and *Rubus idaeus* L. are well-known seed banking species which retain their viability for decades. Their representation in the 15 year old plant communities on the loam soils was proportionally greater than their presence in the seed bank, showing their highest proportional abundance after the treatments that retain the surface organic layers (TL, FT).

The seeds from the ericaceous species, *C. calyculata* Moench, were present in the seed bank (1.3 germinants m^{-3}) but had negligible presence in the 15 year old plant communities on the loam site types. Similarly, the presence of the deciduous low shrub, *D. lonicera* Mill. in the seed bank (2.7 germinants m^{-3}) was not evident in the 15 year old communities. *B. papyrifera* Marsh. (white birch) seed was present in the seed bank (4 germinants m^{-3}) and showed some presence in the 15 year old communities after the intermediate disturbance treatments (FT).

4.5.2 Sand Site Type

Sedges (*Carex)* represented the highest proportion (57%) of the soil seed bank (519.9 germinants m^{-3}), but had a very low proportional presence 15 years after the harvest treatments were applied (Fig. 4.4). *G. hispidula*, had a low proportional representation in the soil seed bank (0.3%) and a high proportional presence in post harvested communities, particularly in the FT (3.8%) and FTB (3.9%) treatments. The tall shrub *Cornus stolonifera* had a low presence of viable seed in the seed bank but was not recorded in the post-treatment plant communities. Two annual herbs, *O. montana* and *Convolvulus arvensis* represented less than 2% of the viable seed in the soil seed bank, and were not recorded in the plant communities. The common post-fire herb, *E. angustifolium*, was recorded in the TL treatment plots but was absent in the seed bank.

4.5.3 Peat Site Type

Sedge (*Carex*) and grass (*Poa*) species represented a high proportion of the soil seed bank (38.3 and 28.0? %, respectively) as well as a high proportion in the 15-year old plant communities particularly on FTB plots (8, 36%, respectively) with low cover on the TL (5%) and FT (10%) (Figure 4.5). The origin of the plants on the FTB plots would be largely from migration onto the site, as the majority of the seed bank would have been by removed by shear blading. The ericaceous low shrub *G. hispidula*, estimated at

5.6% of the seed bank, was present on all treatments with greatest cover on the TL (3%) and lowest on FT (0.7%) treatments. *Chamaedaphne* represented 4.5% of the seed bank composition, yet it represented a large proportion of the post-treatment communities, particularly after FTB (23.7%), suggesting seed origin establishment. The post-fire herb, *E. angustifolium* was present in small numbers in the seed bank (1.1%), with a small representation in the TL (0.2%) and FTB (0.2%) treatments. The origin of the latter would have been from off-site, most likely from wind dispersal Similarly the origin of the *B. papyrifera* on the FT sites is similarly most likely from wind-dispersed seeds or resprouting from a residual pre-disturbance individual, given both its absent on both the TL and FTB plots and the rapid decline in the viability of birch seeds in the seed bank within days of dispersal. Two annual herbs *O. montana* and *G. bicknelli,* adapted to full sunlight and often germinating on exposed mineral soil, were not observed in the plant communities, despite a presence in the soil seed bank.

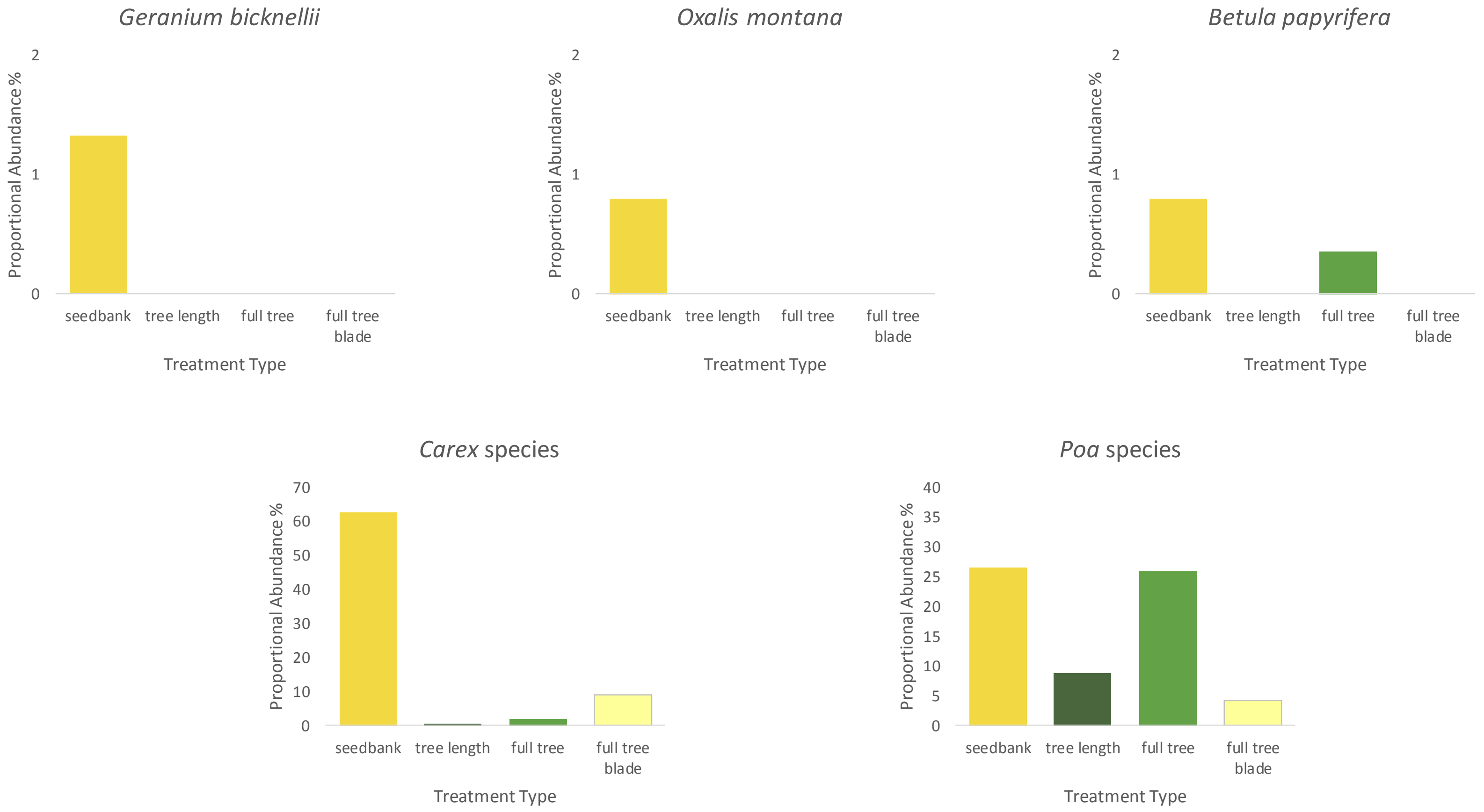

Figure 4.3. Proportional distribution of seed bank species in pre-disturbance forests compared to 15 year proportional abundance in plant communities on loam site type.

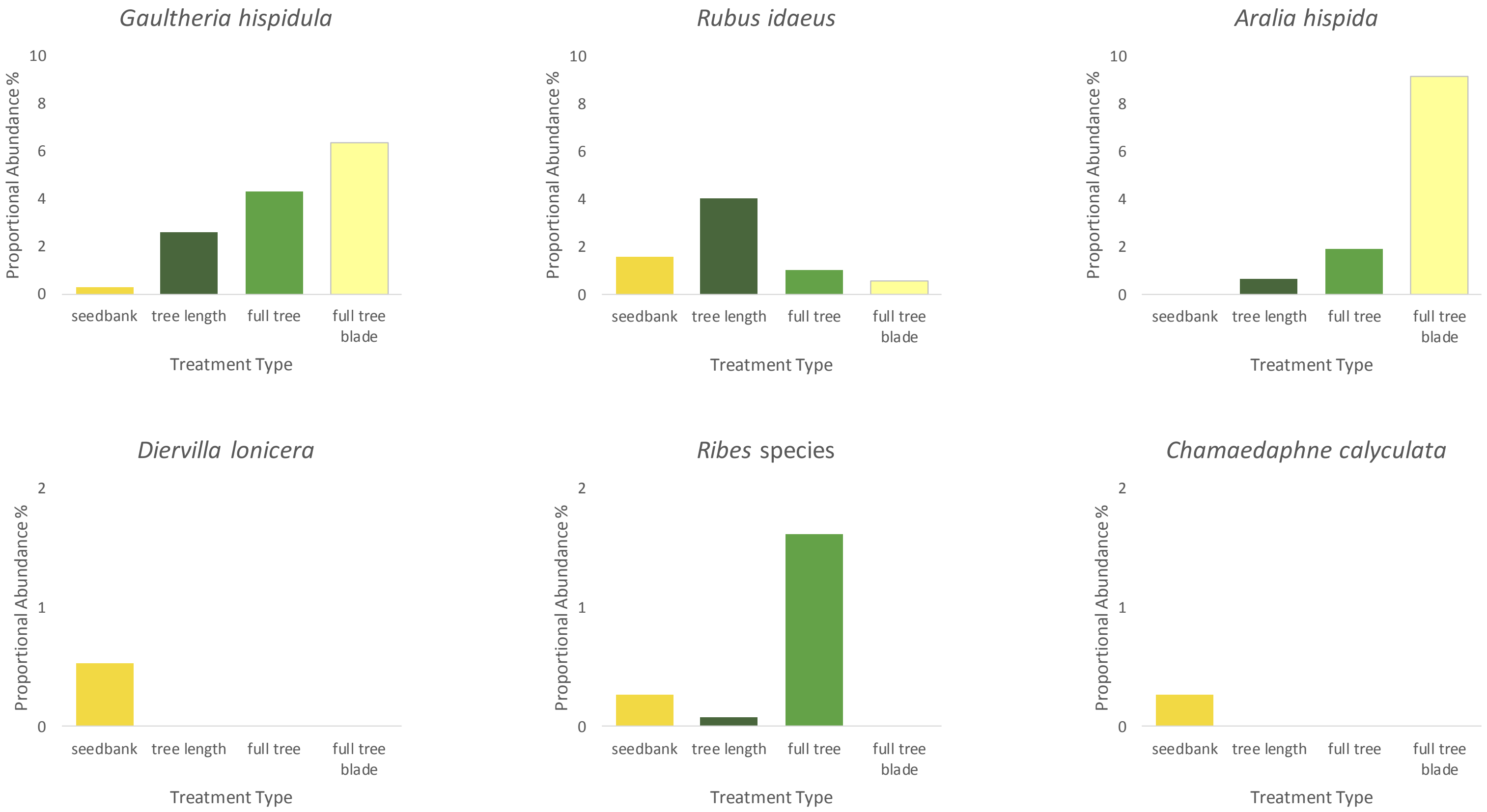

Figure 4.3 (cont'd). Proportional distribution of seed bank species in pre-disturbance forests compared to 15 year proportional in the loam site type.

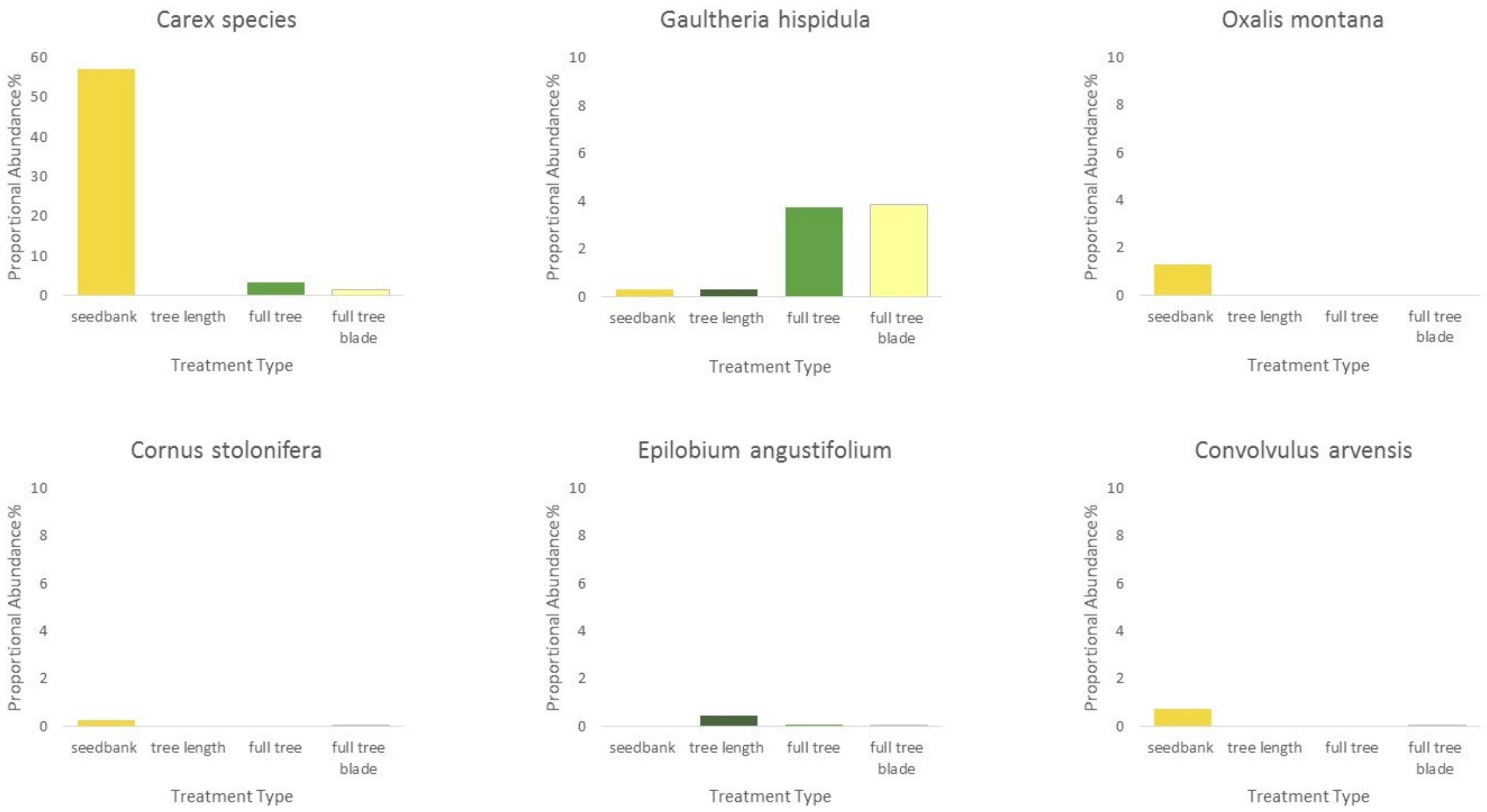

Figure 4.4 Proportional distribution of seed bank species in pre-disturbance forests compared to 15 year proportional abundance in plant communities on sand site type.

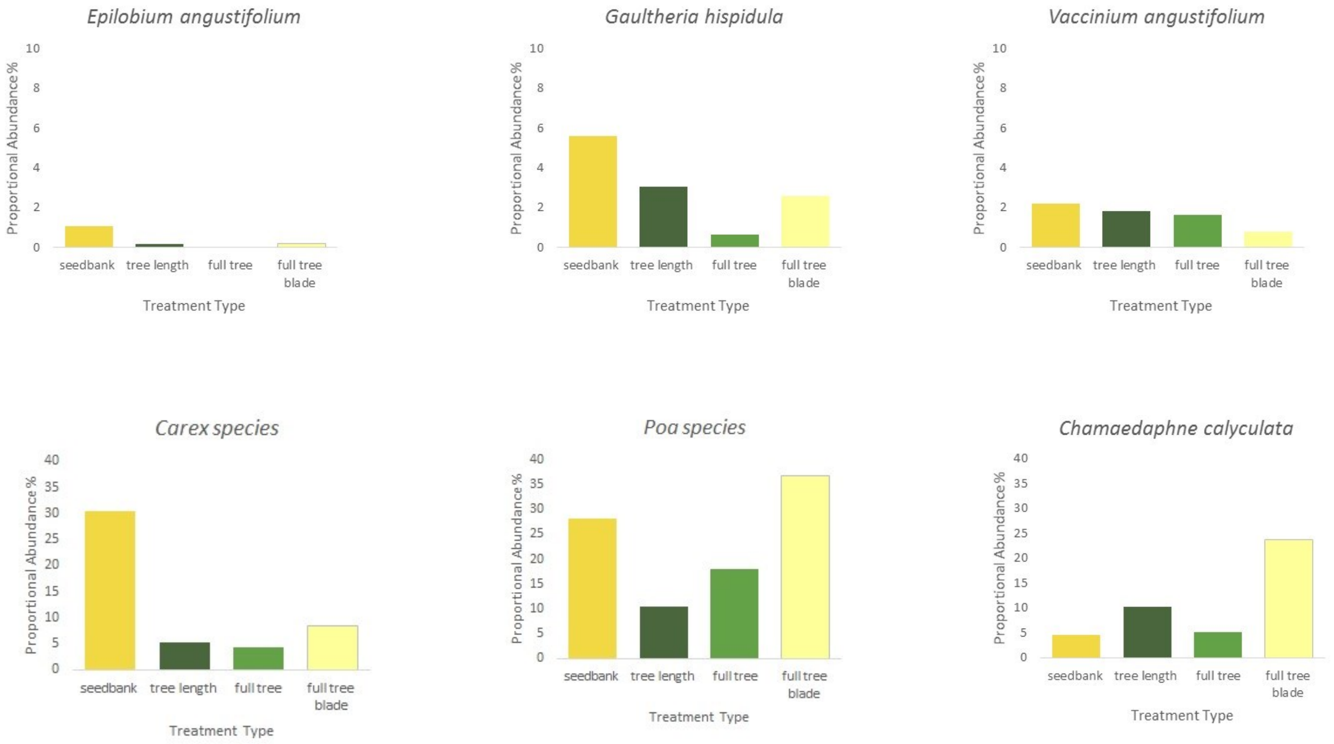

Figure 4.5 Proportional distribution of seed bank species in pre-disturbance forests compared to 15 year proportional abundance in plant communities on peat site type.

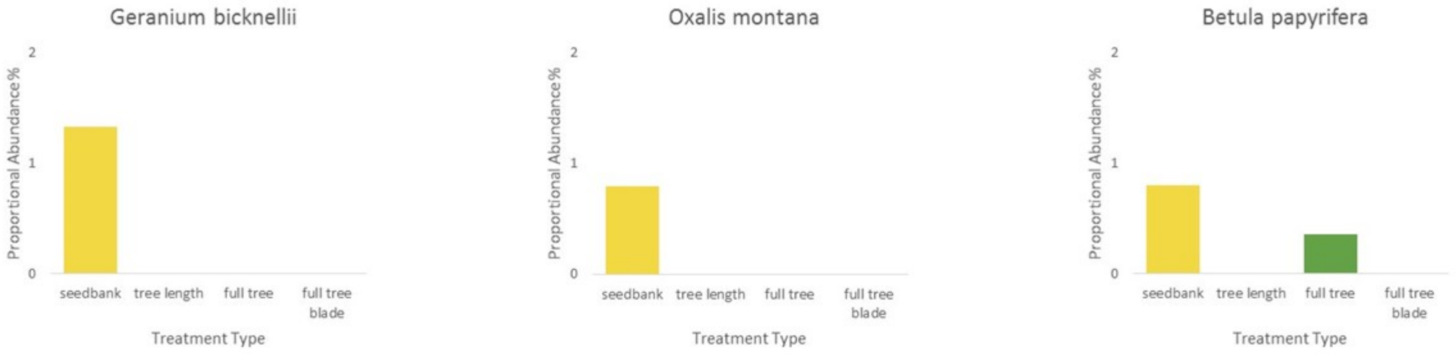

Figure 4.5 (cont'd) Proportional distribution of seed bank species in pre-disturbance forests compared to 15 year proportional abundance in plant communities on peat site type.

4.6 Relationship of Environmental Variables with Plant Community Composition

4.6.1 All Types Combined

The NMS ordination for the total plant list for all three site types and all treatments identified a best-fit three dimensional solution with a final stress of 14.12 (Figure 4.6A). Axis 1, 2 and 3 accounted for 22, 41 and 14% of the variation (total 77.6%). The distribution shown on the strongest axes (Axis 1 and 2) showed a clustering of the peat site types in the upper right quadrant associated with deeper O-layers and higher total herbaceous cover separate from the loam and sand site types, regardless of harvest treatment. The uncut plots also clustered together in the upper left quadrant associated, as expected with higher basal area (BA). The loam site type plots tended to cluster in the lower central portion of the ordination and the sand site type plots closer to both Axis 1 and 2. These results are consistent with the results of the ANOVA analysis and the ISA showing a soil type x harvest treatment (ST*HT) interaction.

The NMS ordination for the total plant list for all three site types (harvest treatments only) identified a best-fit three dimensional solution with a final stress of 14.08 , which is within the bounds of acceptable solutions for this analytical technique (McCune and Grace 2002) (Figure 4.6B). Axis 1 accounted for 48% of the variation, and axes 2 and 3 an additional 19% and 10 % of the total variation, respectively. The ordination is consistent with the results of the ANOVA analysis and the ISA showing a ST*HT interaction. There is a distinct clustering of peat site type plots in the left hand portion of the ordination. The loam and sand site types show a less distinct pattern, although the sand plots extend into the lower portion of the ordination. Harvest treatments are intermixed, with FTB plots concentrated in the upper portion of the ordination, and with treatments often clustered in groups.

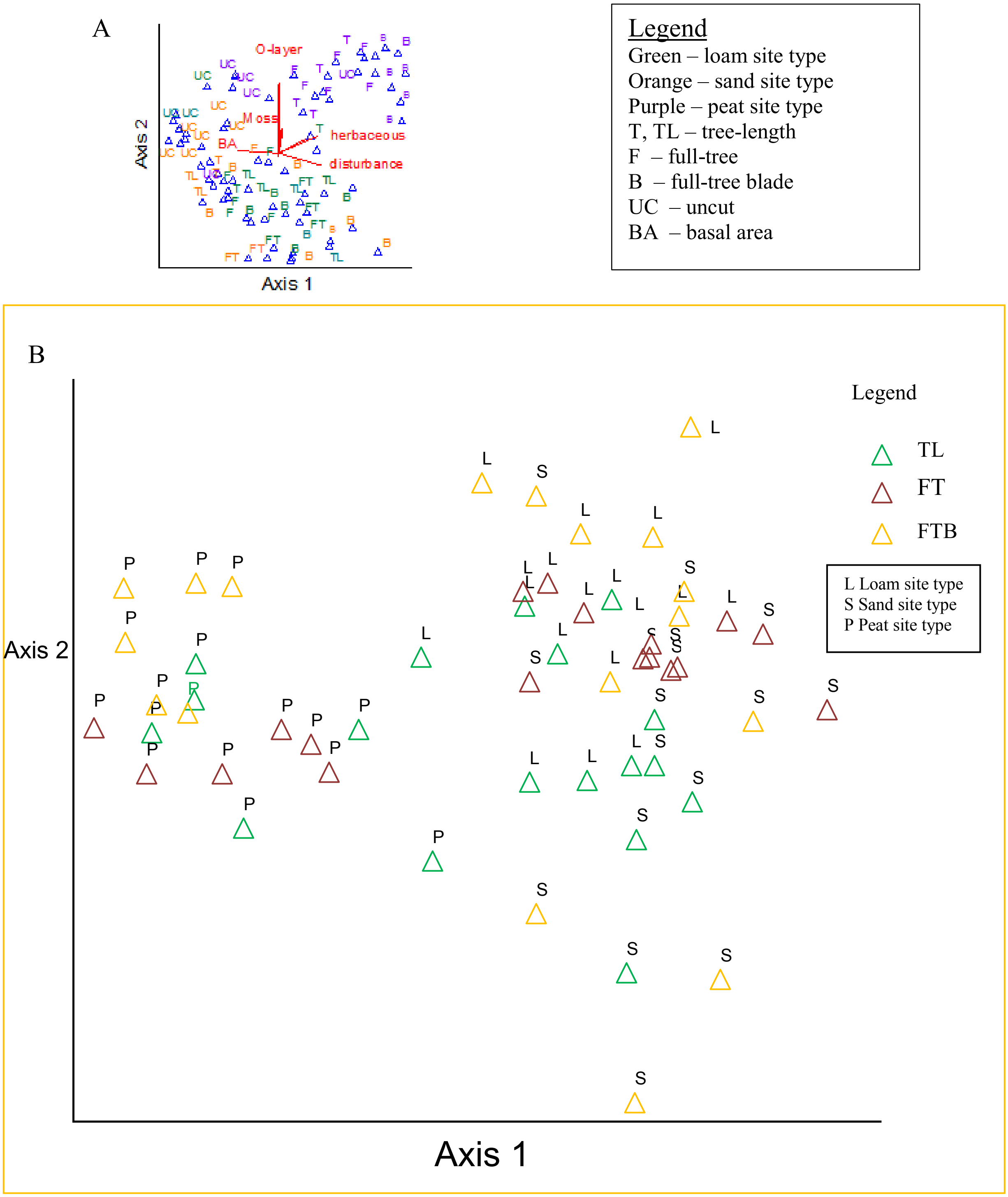

Figure 4.6 NMS ordination (Axis 1 and 2) for all species showing the distribution of species composition by site type and harvest treatment. A. including UNCUT treatments, B. harvested treatments only

4.6.2 Loam Site Type

The NMS ordination for the total plant list for the loam site type (harvest treatments only) found a best-fit three dimensional solution with a final stress of 13.28, which is within the bounds of acceptable solutions for this analytical technique (Figure 4.7A). The harvest treatments are overlain on the ordination in Figure 4.7B to show the relationship of treatment to the ordination results. Strong environmental vectors are overlain on the ordination showing the relationship of the 15 year basal area of tree species (BA), total moss cover (MOSS), depth of surface O-layer (LFH), pH, average mineralizable N values for the surface O-layer (FNH_4), and total pioneer moss cover (POL). The first axis represented 47.7 % of the variation; Axis 2 accounted for an additional 18% of the variability. The first axis shows a gradient from lower to higher basal area from the central position to the left axis, and higher to lower mineralizable N from the central position to the right side of the ordination. Axis 2 shows a gradient from higher to lower total moss cover from the central position to the lower portion of the ordination space, similar to the gradient in pH. A similar outcome was achieved when the vascular data set was analysed, with a resultant best-fit 3-dimensional solution, with a stress of 13.93.

The relative abundance and distribution of key indicator species in the ordination space are displayed. The low shrub and herb species indicator species of TL treatments (*V. angustifolium*, *E. angustifolium, respectively*), characterized by strong vegetative propagation strategies, showed greatest abundance in the lower right hand quarter of the ordination space (Figure 4.7 G, H). The sun-tolerant and seed-origin jack pine (*P. banksiana*) showed a wide distribution with greatest abundance in the left and centre of the ordination space, associated with high BA (D). The resprouting trembling aspen (*P. tremuloides*), an indicator species of FT treatment showed a limited distribution in the left centre of the ordination space (Figure 4.7 E). *Salix* spp., an indicator species for FTB treatments, showed a dispersed distribution (Figure 4.7F), strongly associated with the dispersed pattern of the FTB plots (Figure 4.7B). The distribution of the ruderal herb, *H. auriantiacum* (J), a strong indicator species of FTB plots, showed a limited dispersion of abundance in the lower right corner of the ordination space.

4.6.3 Sand Site Type

A meaningful solution for the total species and the vascular species data set for harvested treatments only for the sand site types were not found, despite running the analysis on both raw scored and transformed data (square root transformed, log transformed, ln transformed). The analysis was also run after excluding outliers or species that occurred with less than 1% cover or less than 5% frequency. A one dimensional solution with high final stress levels (>35%) did not provide any meaningful ecological information. The lack of solution may reflect the wide variability within each treatment type in the data set.

4.6.4 Peat Site Type

The NMS ordination lead to a best-fit 3-dimensional solution for the total species data set with a final stress of 8.85, and a 2-dimensional solution when the vascular species data set was analysed, with a final stress of 13.2. When total species were considered, Axis 1 accounted for 54% of the variation and axes 2 and 3 an additional 30% and 8% (Figure 4.8). When vascular species only were considered (not shown), Axis 1 accounted for 40.6% of the variation, and axis 2 accounted for 41.9% of the variation. For the total species data set, Axis 1 represented a weak gradient from high to lower basal area from the centroid towards the left axis, and high to lower total moss cover from upper (TL treatments) to central positions (FTB treatments). A weaker trend was found diagonally (A) with increasing total moss (MOSS) cover from the centroid to the upper right corner, and a weak gradient in magnesium and total soil pH. A gradient from

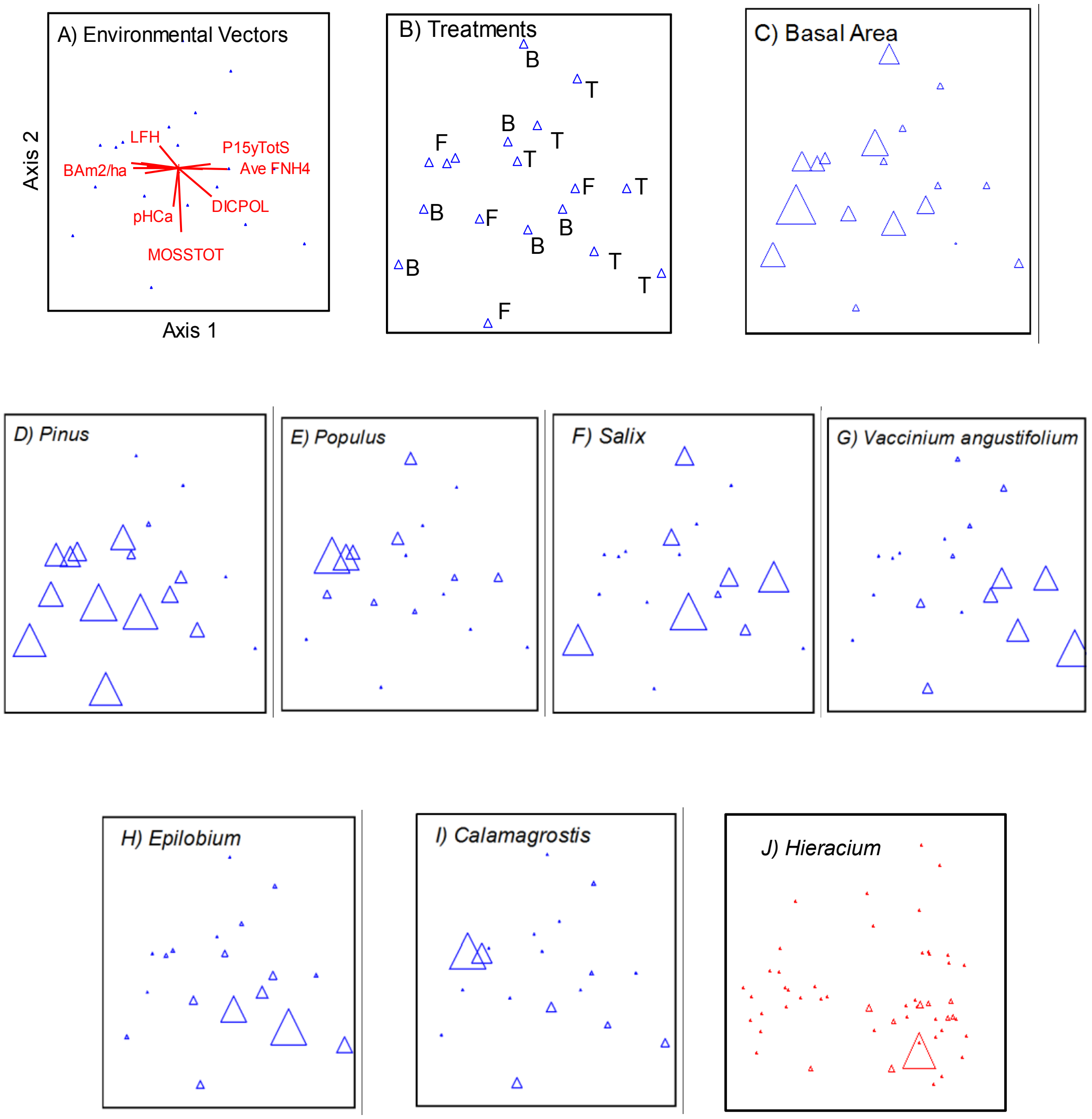

Figure 4.7 Loam Site Type: NMS (axis 1 and 2) ordination results for the total species data set showing (A) Harvest Treatment plots overlain with significant environmental vectors (r .> 0.02):, (B) Harvest Treatments, (C) Basal area of tree species (year 15), and relative abundance of indicator species (D-J) Size of triangles represent amount or proportional abundances of species. Codes: T-tree length, F - full-tree, B - full-tree blade.

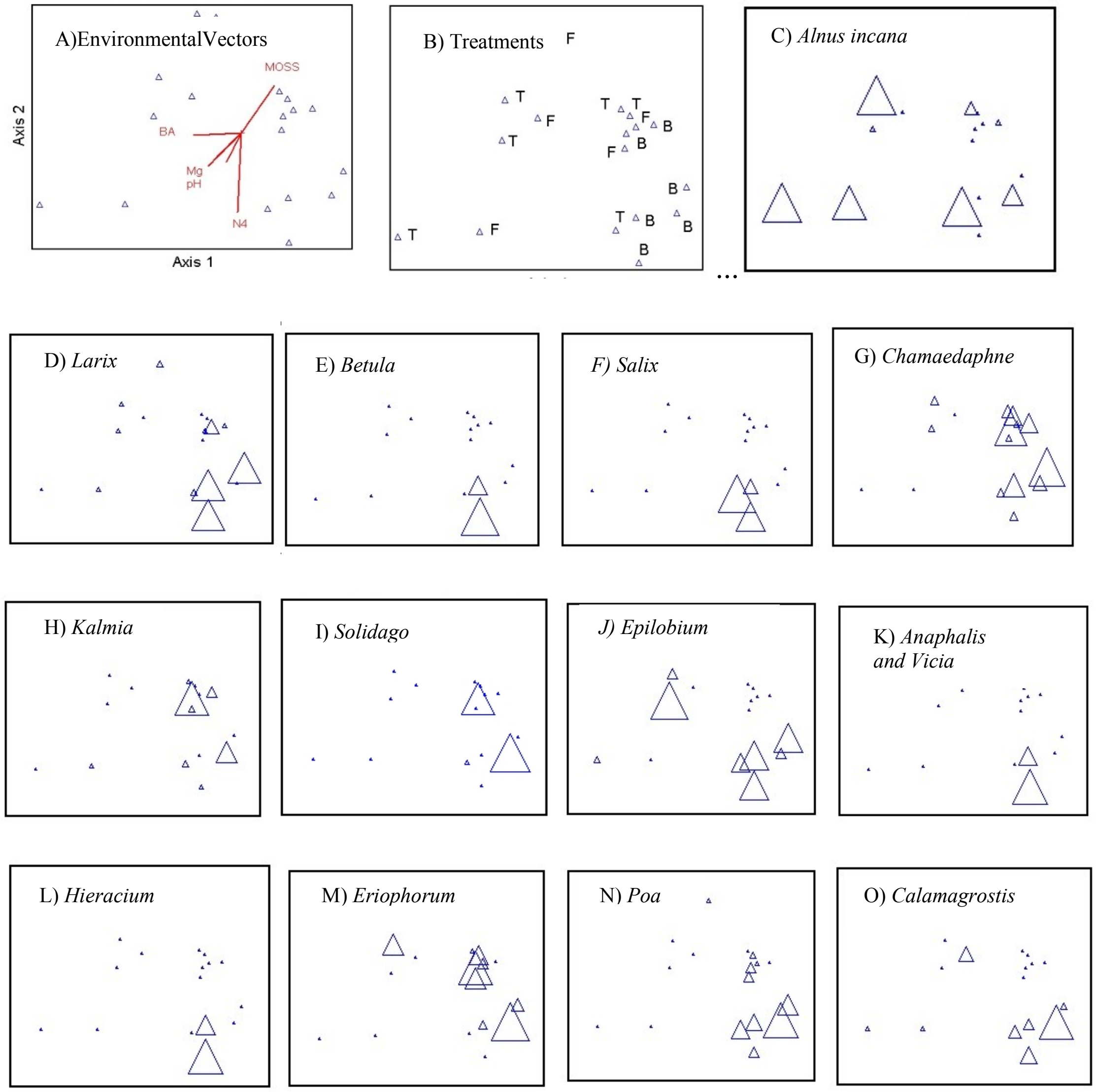

Figure 4.8 Peat Site Type: NMS ordination (axis 1 and 2) of all species data set overlain by dominant environmental vectors (A). Harvest treatments denoted in (B). Each data point represents a plot level mean. Triangle size represents proportional abundance of cover of indicator species of TL (*Alnus incana* (C), and FTB treatments (D-O). The distribution of *Scirpus* overlapped with *Calamagrostis* and is not shown.). Codes: T=tree-length, F= full-tree, B = full-tree blade plots. Year 15 BA-tree basal area, MOSS-total moss cover, NH4 mineralizable N from surface O-layer; Mg-total soil magnesium, pH – average soil pH.

higher to lower mineralizable N was also found in the solution, from the centroid to the lower portion of the ordination (A), running parallel to axis 2. The distribution of the key indicator species relative to the ordination is shown in Figure 4.8 by a series of bubble plots, where the size of triangles representing the proportional abundance of each species. *A. incana* (C), an indicator species of TL treatments, shows greater abundance on the TL and reduced abundance (smaller triangles) on the FTB (B) plots (Figure 4.8B and C). Indicator species of the FTB plots showed multiple-patterns of distribution. The distribution and abundance of the seed-origin conifer *L. laricina* (D), white birch (*B. papyrifera* –E) and shrub (*Salix*, E), all indicators of the FTB sites, overlapped with that of the exotic ruderal herb *H. aurantiacum (L*) and other seed-origin ruderal herbs (e.g., *Anaphalis* and *V*. *cracca*- K). Graminoid distributions (N and O) overlapped, with abundance concentrated in the lower right quadrant of the ordination space, strongly associated with the FTB sites. Cottongrass (*E. vaginatum*) showed pockets of additional abundance on other treatments as well (M vs. B). The vegetatively propagated shrubs *C. calyculata* (G) and *K. polifolia* (G) showed a strong association with each other, lying on the right-hand portion of the ordination space, with some affiliation with *S. uliginosa* (I).

5.0 DISCUSSION

5.1 Species Diversity

Both the ANOVA and perMANOVA analyses consistently identified a significant ST*HT interaction with respect to species diversity and species composition supporting the need for a site-type specific examination of harvesting disturbance impacts. A better understanding of the differential effects of overstory removal and different ground disturbances on plant community response will aid in the refinement of site specific forestry prescriptions to retain diversity of native plant species best adapted to local conditions. The initial establishment phase of plant communities has important long-term implications for stand development through succession (Turner *et al.* 1997, Fu *et al.,* 2007, Newmaster *et al.* 2007, Jeffries et al. 2010) and a strong influence on longer term forest development in the boreal forest (Frelich 2002, Nilson and Wardle 2005, Gauthier et al. 2010).

The orthogonal contrast results showed that overstory removal had a more consistent effect on post-harvest understory community diversity than did the varying levels of ground disturbance imposed by the harvest treatments. The removal of the overstory doubled both vascular and total species richness on all site types, which was attributed to an increase in shrub, herb, graminoid and nonvascular species richness. Overstory removal also increased both Shannon's and Simpson's diversity indices, whereas species evenness showed less of a response. This is consistent with other studies of diversity response to overstory removal when total species richness was selected as the index, although declines in forest species richness are also reported. For example, Newmaster *et al.* (2007) in Ontario, reported that harvesting (without site preparation) increased richness by 9-13% when compared to the adjacent uncut forest in a study of mixedwood forests in Ontario reported. Hart and Chen (2008) reported higher species richness values (22.6, 21.5, and 22.7) for older-aged (>72 years of age) communities when compared to younger (7- year old) boreal conifer mixedwoods (19.8 and 17.1 for vascular species), however their findings were reported for a relatively large sample unit size, the sum of species richness in 10 x 1 m^2 plots. Differences in findings are often attributed to the timing of the assessment with richness often low immediately after disturbance, climbing to a maximum at some point between disturbance events and then declining (Roberts 2007). Other differences can be attributed to the varying size of the unit in which species richness is measured and reported for.

The low diversity in the mature (UNCUT) forests for both total and vascular species richness in this study (vascular species mean R 7.5 ± 1.4, loam, 12.7±1.1 sand, 8.5 ±1.8 peat) are somewhat higher, but within the range of values reported in others studies for boreal black spruce forests. For example Paquette and Messier (2011) in their study using the Quebec (eastern Canada) forest survey dataset of over 12,324 plots of undisturbed boreal forest stands reported mean species richness of 3.3 ± 1.7 (range 1-11). Biswas and Mallik (2011) reported mean richness for uncut mature boreal forests at 2.9 ± 2.1 SD (Riparian) and 3.0 ± 2.3 (upland) in their study in northwestern Ontario. The low diversity is often attributed to compositional stability maintained by black spruce, ericaceous shrub and feathermoss and/or sphagnum dominance and competitive exclusion of other species (Bartemucci *et al.* 2006). The dominant tree cover maintains low light levels in the understory and the continuous bryophyte ground cover provides a poor seedbed for most species (de Grandpré *et al.* 1993).

It is a logical prediction that the removal of the tree layer and even minor disturbances to the ground cover, will provide opportunities for other species to establish, and that both the species composition and magnitude of changes will differ on different site types. It is well documented that different environmental filters operate on different site types (Grime 1979, Halpern and Spies 1995, Nilsson and Wardle 2005). For example on forested peatlands, the dominance of ericaceous shrubs further limit the survival and growth of other species through allelopathic effects (Inderjiit and Mallik 2002, Morris *et al.* 2009).

The interaction of two drivers of alpha diversity, the removal of overstory and ground surface disturbance, is consistent with earlier findings (e.g., Halpern and Spies 1995, Rees and Juday 2002, Schmiedinger *et al.* 2012). Differences in the magnitude of response reported in different studies are often attributed to differences in time since disturbance for the disturbed study areas and the age of the adjacent reference forest condition, physical damage to pre-existing plants, and changes to local microclimate conditions as a result of the treatments. (Halpern 1988, 1989, Roberts and Gilliam 1995, Roberts 2007). As forests age, the continuous canopy often breaks up creating canopy gaps that lead to increased local diversity reported for some old growth forests (Deans et al. 2003, Kneeshaw and Gauthier 2003, Bergeron and Fenton 2012).

The results of this study appear to conflict with the findings of Fleming and Baldwin (2008) who reported that soil disturbance provided greater increases in overall richness and woody species diversity than canopy openings. The difference can be explained in the harvesting methods and the dominant tree species (tolerant hardwoods), which in this study was clear-cutting that removed 100% of the canopy as opposed to partial cutting practices in their study in the southern boreal tolerant hardwood forests.

Post-harvest soil disturbance effects on species diversity and composition varied with site type and harvest intensity. Roberts (2007) also points out that the amount of slash on the floor may affect herbaceous layer response and that this factor should be explicitly studied in harvest impact studies. With limited surface soil disturbance, the understory vascular species cover is dominated by species that primarily establish vegetatively, keeping diversity low on sand and loam site types after TL treatments, and similar to the pre-disturbance forest community.

At intermediate disturbance intensities (FT), the removal of FWM material on loam site types, increased overall diversity (21.29 TL vs. 25 FT) with no significant effect on vascular species richness (13 TL), 12.6 FT). The pattern for Shannon's diversity showed an increase for vascular H ' (2.3 TL vs. 2.3 FT) and increase for vascular (1.8 TL vs. 2.1 FT) while Simpson's indices (D) showed little change (0.8 TL, 0.9 FT, all species; 0.8, 0.8 vascular species). On peat sites, the removal of the FWM reduced R (30 TL, 24.3 FT for the total data set, 16.2 TL, 15.2 FT for vascular species). The pattern for species diversity indices was similar, showing higher values for H' on TL plots when compared to FT plots on peat sites. As such, the retention of FWM had a negative effect on species richness and diversity on loam and positive effect on peat site types.

Other studies have shown that the reduction in slash increases diversity by creating more favorable germination sites and conditions for growth for species that require warmer soils by removing the additional insulating effect of the fine slash (De Grandpré and Bergeron 1997, De Grandpré *et al.* 2003). On loam site types, the retention of FWM favoured the dominance of the pre-disturbance forest species most probably by maintaining partially shaded, cool moist surface conditions. In contrast on the peat site types, the removal of the overstory combined with the residual FWM on the surface, would have created variable site conditions on the stress-prone peat sites enabling the entrance of new species, and reducing the dominance of the pre-disturbance species.

The lack of a significant effect of the removal of the forest floor and surface organic layer on diversity indices on the loam soils (as shown by orthogonal contrasts) could be attributed to the relatively rapid reestablishment of surface O-horizons (LFH 7.5 cm ± 0.6, Table 4.1) on these finer textured soils over the 15 years since the disturbance. This appears to have supported a more abundant plant cover where competitive mechanisms come into play, favouring the more competitive perennial species including *G. hispidula*, sedges and grasses at the expense of ruderal colonizing species. Unlike the decrease in nonvascular and vascular herbaceous and woody species diversity after increased surface soil disturbance (as defined by mineral soil exposure) reported by Newmaster *et al*. (2007), this study found that total and vascular species richness was not significantly different from sites with little soil disturbance (total species richness). In fact on sand site types, richness significantly increased.

Richness on the drier sand site types increased as disturbance intensity increased. R remained low on the TL treatments where the FWM would have ameliorated the full exposure of the ground surface to temperature and moisture stresses immediately after harvest, favouring the pre-disturbance species. Field observations further showed that a variety of lichen (*Cladina*, *Cladonia*) species and a few vascular forest species colonized pockets of desiccated moss adjacent to larger cut stumps on plots where the FWM had been removed. With the removal of surface organics, species with stress-tolerant traits established on all site types. The high diversity of species recorded on the sand site types, is in part due to wider presence a variety of ruderal (invasive) traits that rapidly establish and reproduce after disturbance. This is consistent with the slower recovery of the surface horizons and the thinner LFH layers associated with higher fire disturbance frequencies on the drier sandy site types in the boreal forest when compared to forested peatlands favoring the cyclic presence of ruderal species (Bonan and Shugart 1989, Pastor and Mladenoff 1992, DeGrandpré *et al*. 1993, Bergeron *et al.* 2002, Bergeron and Fenton 2012).

Many of the indicator species on the FTB sites produce abundant, widely disseminated seeds well suited to germinating on disturbed soils such as *A. margaritaceae* (L.) Benth. & Hook f.and *H. aurantiacum* L., but fail to create a continuous plant cover, thus leaving niche space for a wider variety of species to establish (most accounted for less than 2% cover). Nonvascular species with affinities for disturbed soils, such as *C. purpureus* (Hedw.) Brid. and *P. nutans* (Hedw.) Lindb. also contributed to increases in R. The strong relationship between species composition and mineral soil exposure suggest that germination and seedling survival play an important role in community dynamics in boreal conifer communities (Rowe 1985, Turner *et al.* 1997, Kemball *et al.* 2006, MacDonald 2007).

On peat soils, the study showed that species diversity doubled with overstory removal but was not significantly affected by harvest disturbance intensity. An examination of the shifts in species composition was more insightful of changes that occurred in the communities after the different treatments. Grass and sedge cover (particularly *Eriophorum* spp. and *C. canadensis*) increased and low shrub cover decreased after the treatments that removed the ground layer and the surface O-horizons. The low shrub component in the uncut plots consisted of ericaceous shrub species that rely on vegetative reproduction strategies, where the perenating structures were removed with the FTB treatment. Figure 4.1 of species richness shows a consistent shallow concave pattern to the response to disturbance intensity with lower values at intermediate disturbances for total species, vascular species, and nonvascular richness response inconsistent with IDH. Although FTB reduced low shrub species richness, it increased herb richness particularly on sand site types.

Based on regeneration strategies, vegetative species richness appears more responsive to harvest intensity than seed producing species, as shown in the ANOVA results (Table 4.6). This may in part be an artifact of the analysis where richness, not diversity (which would include cover values) provided the input. Even small surface soil disturbances across the treatments would provide opportunities for the incidental establishment of seedlings. In contrast the highest disturbance treatment, FTB, removed many of the vegetative reproductive structures which, in boreal conifer shrub species, primarily lie in the surface organic horizon or within the upper 10 cm of the mineral soil (Hauessler *et al.* 2002, Mallik 2003, Six and Halpern 2008). Thus diversity of plant species relying primarily on vegetative propagation would be reduced as plant cover re-established slowly from parent propagules from adjacent vegetation.

This pattern of increasing species diversity with increased soil disturbance in young black spruce communities is consistent with the findings of Wang and Chen (2010) who showed that increasing soil disturbance through site preparation resulted in higher species diversity and shade tolerance diversity in black spruce and white spruce plantations. It is also consistent with the knowledge that many boreal tree and herb species require mineral soil exposure for germination and that the abundance of individual herbaceous species on the sand site type each occur with low abundance (i.e., 95% of herbs present with less than 1% cover). As such, no individual species outcompeted other species to limit their presence. The lower vascular species richness on the low disturbance treatments reflects their absence of surface soil disturbance, which thus reduces the pool of candidate species.

5.2 Species Composition

5.2.1 Canopy Retention

There was considerable overlap in the significant understory indicator species (IS) for uncut plots among the three site types (Table 4.9). *G. hispidula* (p=0.02, 0.003, 0.02 on loam, sand, and peat site types, respectively) and feathermoss *P.shreberi* (p=0.001, 0.001, 0.01 loam, sand, peat) were common indicator species (IS) in the UNCUT forests. *L. borealis* L., was a second significant low shrub indicator on the loam and sand (p=0.07, 0.003, respectively) site types. Both vascular species are trailing prostrate shrubs that regenerate primarily from underground stolons lying within or at the interface between the mineral soil and moss (Howard 1993, USDA, ARS 2013) with root crowns located in or just beneath the surface O-horizons that support shallow (0.3 cm) fibrous root systems. They are slow growing, able to tolerate both low and high light (2% sub-canopy light), low nutrient levels, a wide range of pH (4-6.5) and medium anaerobic tolerance (Howard 1993, USDA, ARS 2013). Stolon production for *L. borealis* begins between age 5 and 10 with increases in cover not occurring prior to this (Antos *et al.* 1984). They are both fire avoiders, surviving only in small patches of residual moist unburned pockets (Howard 1993). Sexual reproduction is very rare, with occasional records of seedlings in burned or disturbed sites (Antos *et al.* 1984, Eriksson 1992, Howard 1993). *G. hispidula* seeds were present in the seed bank of all three site types in this study, with *L. borealis* seeds recorded only on the peat site types. Given their biology, the presence of both species on FTB sites would have originated from immigration onto the site.

Additional species were identified as significant indicators of UNCUT treatments for the sand site type including two common forest herb species, *C. canadensis* L. (p=0.06) and *M. canadense* Desf. (p=0.02) and two deciduous shrubs, *V. myrtilloides* Michx. (p=0.04) and *R. acicularis* Lindl. (p=0.08). All four species regenerate by vegetative means, well suited to propagation on the continuous moss carpet of mature black spruce forest communities. *R. acicularis,* is particularly resilient to surface soil disturbances, regenerating from widespread rhizomes that can extend to depth of 30 cm and support clones over an area of 10 to 20 m^2, with individual clones reported to survive for over 100 years. As such, this species has a long legacy in black spruce forest communities growing on sandy soils (Calmes *et al.* 1982, Crane 1990). Given the deep rhizomes, this species could regenerate vegetatively after the FTB treatment. In addition, *R. acicularis* can successfully reproduce from seed, although the seed displays deep dormancy with germination stimulated by disturbance (Calmes *et al.* 1982).

PerMANOVA revealed a substantial interaction effect (p=0.001) between site type and harvest intensity on the composition of species, with greater compositional differences in the low shrub layer and graminoid layer on peat site types, as previously noted. Similar interactions were less evident for species richness or diversity, with only Simpson's diversity index (D) showing a significant effect. That the interaction has a stronger effect on species composition than diversity is consistent with the perspective that disturbance impacts on understory communities commonly reflect changes in relative species abundance rather than species presence or absence (Metzger and Schultz 1984, Elliot and Swank 1993, Haeussler *et al*. 2004).

5.2.2 Removal of the Overstory and Fine Woody Material

Very few indicator species were associated with the low disturbance treatment (TL) where the FWM was left on-site. *V. angustifolium* (IV=55, p=0.04), a deciduous ericaceous shrub, and the perennial post-disturbance herb *E. angustifolium* (IV=49.6, p=0.1) were IS of TL on loam site types. It is probable that *V. angustifolium* represented enhanced growth after overstory removal and the latter a response of seed germination from the soil seed bank in combination with colonization by its abundant wind-dispersed seed. No significant IS of FT were associated with the sand site type. *A. incana* (L.) Moench, a tall shrub, was an IS of TL treatments on the peat site type. This species in all probability represents a residual from the pre-disturbance forest.

The greatest variety of significant indicator species were associated with the intermediate disturbances (FT) on the loam site types (6 species, Table 12B). This abundance is consistent with the IDH hypothesis that suggests that species richness is maximal at intermediate disturbances. Two IS are common early successional boreal tree species (*P. tremuloides* IV=69.4, p=0.003 and *P. banksiana* IV=46.7, p=0.02), the first, which regenerates vegetatively from structures lying close to the surface of the soil. *V. myrtilloides* (IV=60.7, p=0.01), *C. canadensis* (IV=49.4, p=0.07) and the ruderal herb *T. pretense* L.(IV=50, p=004) can tolerate both partial to high light levels, thus indicative of these sites where the tree cover is re-establishing creating a mosaic of light conditions (Lieffers and MacDonald 1993). It is likely that the presence of these species reflects a combination of initial establishment from the seed bank, combined with wind dispersal (in the case of *C. canadensis* and *T. pretense*).

On the sand site type, *P. banksiana,* was a significant indicator of the FT (p=0.1) treatment, whose origin is likely from on-site seed released after harvest. On peat soils, unexpectedly, reindeer lichen (*Cladina* spp.) was a FT IS associated (p=0.01), perhaps associated with the warmer microsites created with the removal of both the overstory and the FWM from the site.

5.2.3 Removal of the Surface Organic Layer (FTB)

PerMANOVA, indicator species analysis (ISA), and the examination of the pre-treatment soil seed bank showed that the removal of the surface O-horizons (FTB) had greater effect on post-harvest understory community composition than the retention of FWD on sand and peat site types. Berger *et al.* (2004) and Fleming and Baldwin (2008) also reported that the degree of ground disturbance had the greatest positive influence on species richness and composition.

Soil disturbance, at its most extreme, removes aboveground vegetation, many of the vegetative reproductive structures, and the majority of the soil seed bank (Roberts and Dong 1993). In addition, it also alters microclimatic conditions (Singh *et al.* 2008) and nutrient supply (Simard *et al*. 2001), consistent with the results of this study that showed changes in nutrient pools as a response to high disturbance intensity. In general, the removal of the surface O-horizon increased soil pH in this study, which in turn created more favorable conditions for nutrient availability, yet it also lowered mineralizable nitrogen (by removing surface) layers). Lagerstrom et al. (2007) noted that in the absence of disturbance (fire) N accumulates at a rate of approximately 1.8 kg ha^{-1} $year^{-1}$ in boreal forests of northern Sweden, with active biological N_2 fixation in late-successional systems (biological fixation by *P. shreberi*). This elevates N:P ratios, and reduces available nutrients, often notably phosphorus leading to a decline in forest productivity.

The removal of this surface O-horizon, triggers primary succession, providing opportunities for community revitalization or degradation. The exposed mineral soil, still representing more than one-third of ground surface conditions on sand and loam site types, provides suitable seedbed conditions for many of the boreal understory species to establish (Roberts and Zhu 2002, Reyes et al. 2010).

IS associated with the highest disturbance treatments (FTB) ranged from 4 on loam, 4 on sand and 17 IS on peat site types. All four IS on loam site types are indicators of open disturbance habitats (*Salix*, p=0.01; *A. margaritaceae*, p=0.08; *H.aurantiacum, 0.04*). The percent cover of these latter two ruderal herbs is relative low (<2% cover) although the cover of *H. aurantiacum* continued to form small colonies on some sub-plots. These species would have established as migrant species, well adapted to establishment on mineral soil substrates in full sunlight. *H. aurantiacum* may be a species of concern, with respect to displacing native herb colonization. It reproduces vegetatively in the centre of the colony and sexually on the periphery, thus both intensifying and expanding its presence (Stone 2005). It is tolerant of drought and heat stress, well suited to establish on the post FTB sites (Duncan *et al.* 2005). Its' limited presence on the majority of the plots indicates that, as the tree canopy closes in, its presence will continue to decline as shading increases. Studies comparing seed bank to plant communities in boreal forests in Sweden (Granström 1982, Schimmel and Granström 1996) also reported its minor presence in the seed bank and 16year old black spruce communities, yet it was absent in boreal mixedwood seed banks in northwestern Ontario studied by Qi and Scarratt (1998).

The IS on the sand site type included the pioneer tree species, *B. papyrifera* (0.06), and the ruderal herb, *S. cilolatum* (0.007), both wind-dispersed species well-adapted to germinating on mineral soil substrates, providing moisture conditions at the time of germination are favorable (Reyes et al. 2010). Two pioneer moss species well adapted to disturbed mineral soils, *C. purpureus* and *P. nutans*, grouped for the analysis were IS of sand sites after FTB (p=0.04) These species often establish after severe fire, but are gradually displaced by shade tolerant moss as the overstory tree cover establishes.

Many of the understory species associated with the removal of the surface organic layers are ubiquitous species, common in many anthropogenically disturbed habitats and include post-fire specialists (e.g., *C. purpureus*, *E. angustifolium*). Similar observations that high disturbance favours ubiquitous weedy species and graminoids were reported by Kurulok and MacDonald (2007) in their study of post-fire salvaged boreal communities. The concern that harvesting disturbances will threaten the retention of post-fire specialists (c.f., Hart and Chen 2008) was not strongly apparent in this study, although the presence of the post fire species, *G. bicknellii* in the seed bank, was not evident in the 15 year old plant communities. It is reasonable to assume that the species present in the seed bank that also occurred in the post-disturbance communities, will contribute seed to replenish the soil seed bank.

Of greater concern are the plant communities associated with the low disturbance treatment (TL) where the majority of the species had strong closed-forest affinities. It is reasonable to predict that the composition of the viable seed in the seed bank of these post-TL harvested forests, in the absence of mechanical site preparation, fire or other catastrophic disturbances, will reduce in diversity over time because of the absence of surface soil conditions that facilitate the establishment of a variety of seed banking species. The longevity of the seed bank on a particular site needs to exceed the time between disturbances that can promote the establishment of the species present in the seed bank (Granström 1982, Mladenoff 1990).

The response varies with life form and with dominant reproductive strategy. Previous harvesting impact studies (e.g., Halpern 1988, Hughes and Fahey 1991, Roberts and Zhu 2002, Ramovs and Roberts 2003) have shown that changes in the herbaceous layer are directly related to ground disturbance intensity (Roberts 2007). The herbaceous layer in many of the studies (plants <1m tall), often include several life forms that may respond differently to disturbance, namely tree seedlings, low shrubs and herbaceous species (Roberts and Gilliam 1995). Harper and MacDonald 2002 found decreased abundance of shrubs but increased abundance of herbaceous species near the edge of clearcuts in the second year after harvesting.

Low shrubs typically survive disturbances of low to moderate severity in boreal forests (De Grandpré *et al.* 2003). However, where harvesting is accompanied by ground layer disturbance, low shrub cover many be reduced disproportionately because their perenating buds are located further above the ground (Roberts 2007). Roberts (2007) points out the importance of tracking low shrubs and herbaceous species separately in harvesting disturbance studies so that the interactions between disturbance severity and growth forms can be identified.

Approximately 30% of the species tallied on the sites contributed to less 2% cover on all of the site types. *E. angustifolium*, often very abundant in the first few years after disturbance, was absent from the soil seed bank and was absent or negligible in terms of relative abundance in the 15 year old post disturbance communities. It was present in trace amounts in the seed bank study of Qi and Scarrat (1998) in northwestern Ontario boreal stands, and represented less than 1.1% of the measured seed rain.

Forest floor disturbance affected both structural and compositional diversity within secondary successional pathways in this study on sand site types, and has been commonly reported in other related studies (Jobidon 1990, Archibold *et al*. 2000, Pelzer *et al.* 2000, Bok and Van Rees 2002, Haeussler *et al*. 2002, Jobidon et al. 2004, Newmaster *et al.* 2007). What varied in this study was that the removal of this layer did not have a significant effect on species diversity on loam and peat site types, when assessed 15 years after the disturbance, which conflicts with the findings of the above authors. This may be attributed to the shorter time frames of many of the other studies which examined the response with the first six years after forest floor disturbance (c.f., Newmaster *et al*. 2007, 5 years), the reestablishment of the tree layer and the re-development of the surface LFH layer on the loams site types. The percentage of mineral soil exposure on the loam and sand sites were similar to those reported by Newmaster *et al.* (2007) ranging from (7 to 52%).

Plants also have important “after-life effects” on ecosystem processes (DeLuck *et al.* 2007). This has been documented on peatlands where the ericaceous species have modified soil chemistry that favours ericaceous species survival over other species groups. An important after life in boreal forests are present in the soil seed bank.

5.2.4 Alien and Invasive Species Concerns

Forest harvesting and associated forest floor disturbances have been attributed to increasing opportunities for the establishment of alien plant species, relative to the species affiliated with natural forests, with an increase (Battles *et al*. 2001, Ramovs and Roberts 2003) or no significant change (Thomas *et al.* 1999, Haeussler and Bergeron 2004, Newmaster *et al*. 2007), in species richness or abundance of these plants being reported. As an example from this study, although present in the seed bank, the presence of the exotic *C. arvensis* L. was not realized in the 15 year old plant community and the majority of the herbaceous species each accounted for less than 1% cover.

This is consistent with the findings of other recent studies. Very little encroachment of alien species associated with forest floor disturbance in boreal conifer plantations was reported by Bock and Van Rees (2002) or Newmaster *et al*. (2007). Others have reported the incidental presence of the grass species *Agrostis gigantea* Roth. (redtop) and *Poa pratense L. – (*Kentucky bluegrass) in plantations, which are both common in fields and roadsides and used for soil stabilization in Ontario. Hunt *et al*. (2003) reported the presence of *Taraxacum officinale* F. H. Wigg. (dandelion) in plantations in the Limestone Lake area of NW Ontario and other ruderal species cover but noted that their presence declined notably over 20 years as shade tolerant moss and herbaceous species established. This is consistent with the general belief that early-successional herb species decline as light availability decreases proportional to the development of the overhead tree canopy develops leading to (Slayter 1977, Peter and Harrington 2009, de Grandpré *et al.* 2011). *H. aurantiacum* L.*, T. officinale*, and *Achillea millefolium* L. were present in the study sites, but represented <1% of total cover. The lack of significant colonization and persistence in the treatment areas is likely associated with the distance from major agricultural and urban landscapes, distance from major highways, and the absence of alien plant populations in the adjacent forest (Parker *et al.* 2002, Haeussler *et al*. 2004, Newmaster *et al.* 2007).

Concerns with the rapid establishment of species that were represented in the seed bank appear unfounded based on the results. In addition, the abundance in the seed bank was not always a predictor of the plant community composition 15 years after disturbance. For example sedges and grasses had a very low presence (<10%) on all three treatments on loam site types and had its greatest presence on FTB sites on both the loam and peat site types, despite accounting for >60 and 25% of the seed bank, respectively. It is a reasonable assumption that the origin of this cover on the FTB sites, is of wind-blown seed origin, rather than the soil seed bank as the residual surface O-horizon with the seed bank was removed in the blading treatment. Similarly the seeds from the ericaceous species, *C. calyculata*, and the deciduous low shrub, *D. lonicera* were well represented in the seed bank but had negligible presence in the post-disturbance plant communities.

Other species showed a distribution that was not predicted, for example white birch seed was present in the seed bank, but has a very short period of viability. It presence after the intermediate treatments (FT) is most likely from more recent immigration onto the site, or from a residual presence prior to harvesting. Seed rain measurements by Qi and Scarratt (1998) showed white birch represented 76.1% of the seed rain with sedges accounting for 13.6%. Herbaceous species overall had very little presence in both the seed bank and the post-disturbance plant communities.

In contrast, a few of the low shrub species produce seeds that retain their viability for decades. These species are able to respond to disturbances that create conditions favorable for their re-establishment, for example *Ribes, Rubus pubescens* Raf. and *R. idaeus*. On the loam soils, their proportionally abundance was greater than their presence in the seed bank on treatments that retain the surface organic layers (TL, FT). The seeds of these species lie lower in the organic layer together with *D. lonicera* and *Aralia nudicaulis,* facilitating rapid response after disturbance (Qi and Scarratt 1998).

Surprisingly *G. hispidula*, despite a low proportional representation in the soil seed bank, showed a high proportional presence in the 15-year old post-harvest communities on the sandy site types. It is likely that the origin of this presence was from residual patches after TL and FT and both seed germination and vegetative propagation from residual patches or adjacent vegetation.

On both the loam and peat site types, species with ruderal characteristics (seed origin, light tolerance) established after the removal of the surface O-horizons creating communities distinct from the residual understory community that consisted largely of species able to regenerate vegetatively, with reproductive structures lying within or close to the surface O-horizons. The lack of differences on the sand site type 15 years after harvesting was not expected. It may reflect the presence of moisture limitations for vascular species on these sites once the canopy was removed, regardless of the presence or absence of the surface O-horizon.

5.3 Compliance with IDH and MRH

Total species richness was highest after medium intensity disturbance treatments (FT) on loam (25 ± 3.5 SE) site types consistent with the IDH (Table 4.5). On sand sites, however, highest R was recorded on both medium (FT) and high intensity treatments (FTB) (33.5 ± 2, 28.17 ± 2) when compared to low disturbance (TL) treatments inconsistent with IDH (Table 4.4). On peat site types, R was highest on both low and high intensity treatments (30 ± 4.1, 28.67 ± 5, respectively), and lower at intermediate disturbances (FT), creating a concave response to disturbance intensity pattern, inconsistent with IDH. These results are presented within the context of the definition of level of disturbance as defined for this study and may not represent the full spectrum of the disturbance regime in boreal plant communities. The levels of disturbance intensity studies were those for three levels of biomass removals after full overstory removal (clear-cut) and did not examine the response of species richness after partial canopy removal, or local individual tree disturbances.

The pattern of species response was consistent with the IDH only when viewed as mean total species richness on loam and sand site types, or in terms of total or vascular species Simpson’s diversity index on loam site types. The more common pattern was to see a statistically insignificant difference in diversity metrics among the treatments or to see higher diversity after the highest disturbances. These responses are consistent with the results of the literature review which also showed that compliance occurred in fewer than half the studies in terrestrial ecosystems.

The underlying assumptions in IDH are often challenged where plant population growth rates are low or high (Grime 1977, 1998, Bongers *et al.* 2009). In plant communities dominated by species with rapid growth rates, species diversity often peaks at high disturbance levels. Where communities are dominated by plant species with slow growth rates and low reproduction rates, richness often peaks at lower disturbance levels (Lavorel and Garnier 2002, dos Santos *et al.* 2011) adding more to the complexity. This was the finding in this study for peat site types where species richness was highest after TL disturbances, although other diversity measures were similar regardless of intensity of disturbance (e.g., Simpson's diversity values were even across all disturbance intensities, Table 4.2). The results of the study demonstrated that the pattern of response is as much a function of the diversity measure adopted and the selection of which groupings of plant species one choses to study, as is the disturbance intensity.

Regardless, we did find the IDH model useful as an initial framework for examining and comparing community diversity response to the three harvest disturbance intensities. The model was cautiously applied to aid in interpreting the pattern of response to harvest disturbance intensity among the three site types, recognizing the post-disturbance communities had not all reached the same stage of canopy closure and thus were not entirely comparable. The height growth of the tree cover on the peat site types was particularly limited, reflected in the low BA and low values for canopy closure. Caution in placing too much emphasis on the model to explain the pattern of response was also premised on the low compliance rate reported in other studies, as noted in the literature review.

The mass ratio hypothesis was useful as a conceptual model for understanding differences in species diversity, composition and evenness in both the pre-disturbance forest community and the FTB sites, however this study was not designed to test the theory. The high dominance of black spruce, ericaceous shrub and sphagnum cover in the reference UNCUT communities is consistent with the concepts of MRH. It was a useful concept to consider in tracking the response of ericaceous shrub cover and graminoid cover. Other studies have shown that the effects of losing a functional group is not solely dependent on the group's dominance, and that the study of response in terms of group identity plays a critical role in determining the effects of diversity loss (McLaren and Turkinton 2010). The classical CRS (competition, ruderal, stress) model of Tilman (1985) which looks at species composition in terms of adaptability to environmental stresses, open mineral soil habitats, and fully occupied sites where competitive processes come into play was a practical framework for examining the differences in community composition after the three harvest treatments on the three site types.

This study contributes to better understanding the contribution of the soil seed bank to post-disturbance community composition on different site types. It also showed that species that are abundant in the soil seed bank are not always the source of the presence of that species in the post-disturbance community. The FTB treatment provided an opportunity to study this dimension.

6.0 CONCLUSION

This study set out to answer three questions about the effect of harvesting intensity on understory species diversity, composition, and response pattern in boreal black spruce forests:

1. Is there a significant disturbance effect of the level of biomass removal associated with harvesting treatments on plant diversity in boreal black spruce understory communities? If so, is this response consistent with the IDH or with MRH?
2. Is there a significant disturbance effect of the level of biomass removal associated with harvesting treatments on species composition?
3. Are the effects, if any, consistent across site types?

The results show that there is a significant harvest disturbance effect of four levels of biomass removal on plant diversity in boreal black spruce understory communities with the most significant effect produced by removing the forest canopy. The response across all three site types was positive when the diversity of 110 year old communities was compared to that of 15 year post-disturbance communities. Canopy removal increased the diversity of a range of plant life form groups including moss, lichen, herb, shrub, and tree species composition.

The effect of the removal of the surface organic horizon on species diversity was site specific with a significant negative effect on species evenness (E) and Simpson's diversity (D) on sandy site types. The effect on overall diversity indices for loam and peat site types was not significant. The effect of the retention or removal of coarse and fine woody material on diversity had an opposite effect on loam when compared to peat sites, with species richness decreasing on loam and increasing on peat sites. It is most likely that the retention of this material on the peat sites created drier elevated seedbed and substrate opportunities for species to establish and survive that are less successful establishing in a saturated moss mat, or competing with the presence of dominant ericaceous shrub species that are known to modify surface soil conditions (allelpathy).

The analysis showed that the IDH concept that richness is greatest at intermediate disturbance intensities, is at best, a useful conceptual model for comparing diversity responses among different site types. For most sites, diversity did not follow the classic unimodal response, but rather increased with increasing harvest disturbance intensity (FTB). The diversity response of groups defined by reproductive classes (to reflect species composition groups) also failed to respond consistently with the pattern predicted by the IDH.

The study was not well designed to test the mass ratio hypothesis response as the focus was not on evaluating biomass response. Assumptions can be made, however, that the of individual species on the peat site types (e.g., *Rhododendron groenlandicum*) that were prominent in the UNCUT forests and the low diversity of other species after canopy removal (TL) is in alignment with the belief that a few species regulate the environment to favour their continued presence at the expense of new entrants.

With respect to answering the second question regarding the effect of increased disturbance intensity on species composition, the results indicate that there was a significant treatment effect. Graminoids increased where the woody material and/or the surface organic layers were removed (FT and FTB); low shrub cover, particularly for species that regenerate from underground rhizomes, increased where this layer was retained. Unexpectedly, herb diversity and total lichen cover did not show a distinct pattern with harvest intensity, although there were some individual species associations. This in part may reflect the presence of small patches of suitable habitat for the establishment of both species groups from post-treatment disturbance, including disturbances associated with the presence of residual stumps on-site. The effects on species compositional shifts were greater and more insightful of ecological process responses than diversity response, as has been reported by others.

To answer the third question posed, the effects were not consistent across all site types, although there were some commonalities. The statistical tests applied showed that there was a significant site type x harvest treatment effect on the four diversity measures.

The removal of the surface organic layer lead to a significant difference in species evenness and diversity (D) only for the sand site types where evenness decreased. This in part may reflect the presence of ruderal species (e.g., *Lathyrus, Achillea, Hieracium*) occurring with very low cover contrasting with clonal species (*Gaultheria, Epilobium, Vaccinium*) that form larger patches. On sites where the shrub cover and surface feathermoss layer remained in-tact (TL, FT), the dominant species formed a more even distribution. The response of communities to the retention of residual coarse and fine woody material on site (TL) was positive on the peat but negative on loam sites. On the peat sites the woody material provided drier elevated habitat for species that were uncommon on the continuous sphagnum mat.

The presence and distribution of species recorded on the loam and sand site types overlapped, often occurring with each other in ordination space. As expected, species tolerant of wet, acidic conditions present on the peat sites were absent to sparse on the other site types. The distribution of species recorded in the peat treatment plots clustered together into a distinct pattern in the ordinations.

The removal of the overstory had a greater effect on post-harvest vascular and nonvascular species diversity and species composition than the retention or removal of the forest floor and surface O-horizons or the retention or removal of fine woody material. After harvesting, the effects of the removal of the organic layer and the removal of FWM are site type specific, and have a differential effect as a function of life form. Increases in mineral soil exposure and low levels of tree basal area (as a surrogate for degree of light availability) were associated with increased cover and diversity of grasses, herbs, and lichen. The retention of the surface organic layers favoured the dominance of low shrubs and resulted in reduced overall diversity.

Mean surface organic layer thickness on the full-tree bladed sites is deeper on the loam compared to the sand site types. In tandem with this, is the development of a more continuous ground cover on these finer textured soils where competitive processes often reduce the success of herbaceous species adapted to open habitats. The cover on the sandy site types on the bladed sites remains sparse, with a continued presence of exposed mineral soil receptive to colonization by ruderal species. These species are often present as individual plants or small clonal patches which contribute to a low cover value. Pioneer moss species of low stature such as *P. nutans* and *C. purpureus* and sun-tolerant *Polytrichum* species are also present on these sites, often in small patches. On sites where the tree canopy is well established, plant cover often remained low under the shade.

On peat site types, complete recovery of the pre-disturbance plant cover distribution had not occurred over the period of the study. Overall rate of tree growth on peat soils is slow (as shown by the low BA values for all post-harvest plots) which resulted in large canopy openings. The lack of deep shade from a closed canopy and the removal of the continuous moss and pre-disturbance dominant low shrub cover by FTB treatments, created favorable establishment sites for a wide variety of vascular and nonvascular species. This increased species richness values and the number of indicator species on these treatment sites. The results suggest that the inclusion of more intensive disturbances on forested peatlands may assist in the revitalization of the growing environments. The presence of seed-origin species, such as *L. laricina* and *Eriophorum* species, although they shift the community from a pure black spruce low shrub sphagnum composition to a more diverse community, may improve the growing conditions by reducing the concentration of soil allelopathic compounds associated with a dominant ericaceous cover and sustaining more favorable soil pH levels.

The study showed that the removal of the overstory and the removal of the surface O-horizons significantly increased species diversity on both the peat and sand site types, introducing primarily native plant species with affinities for open disturbed habitats that will contribute seed back into the soil seed bank. The contribution of the seed bank to post-disturbance recovery of plant communities is an integral part of boreal community development. The study highlights the role of disturbance in diversifying species in terms of increasing the proportion of species in different life forms, with different reproductive traits, and well known differences in rooting depths, flowering and fruiting periods, dispersal mechanisms, and wildlife values. There was little evidence that alien species persist as the forest cover establishes, and no evidence of the introduction of invasive species of concern. It is important to point out that the study areas are located some distance away from major urban population centres where the source of alien species with invasive properties primarily lies. It should also be noted that this study could not examine the presence or absence of any loss of any species with affinities for old-growth forest structures, as the study focused on the response of communities 15 years after disturbance.

The study provided evidence that there is a strong interactive effect between harvest intensity and site type, suggesting that harvest treatment impacts will be site type specific, as should harvesting and silvicultural prescriptions. Consistent with the results of the literature review, there was no evidence to suggest that the IDH is a universal hypothesis that can be applied as a predictive model when comparing disturbance intensity response of species diversity over a time period that is less than a full life cycle of the dominant cover.

During the study, it was noted that the diversity of species was often associated with the presence of residual stumps, exposed roots, and larger coarse woody material. Future studies could provide more insight into the effect of harvesting and post-harvest practices by examining the contribution these materials have on species diversity response on the three site types. The association is not only direct by providing substrate for seedling germination and vascular and nonvascular species establishment, but adds to the diversity of local habitat conditions providing periodic shade and different moisture conditions. The results of this study can contribute to the ongoing refinement of forest silvicultural and harvesting prescriptions.

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APPENDIX I LIST OF ABBREVIATIONS AND GLOSSARY OF TERMS

ANOVA	Analysis of variance
B	bladed
BA	basal area ($m^{-2}ha^{-1}$)
C	carbon
CNFER	Centre of Northern Forest Ecosystem Research (OMNR)
$CaCl_2$	calcium chloride
CWM	coarse woody material > 10 cm in diameter; woody material left on-site after harvesting
D	Simpson's diversity index (Simpson 1951)
EA	environmental assessment
EP	environmental parameters, this referred to the elements that were measured to help characterize seedbed conditions and important resources for growth.
ES	ecosite
FEC	Forest Ecosystem Classification system (as per Racey *et al.* 1996)
FF	forest floor
FT	full-tree, referring to a harvest where the above-ground portion of the tree is removed and moved to roadside, considered a medium disturbance in

	this thesis
FTB	full-tree harvest plus blading, referring to a harvest where the above ground portion of the tree is removed followed by the removal of all residual understory vegetation including the moss and the upper 20 cm of the soil (removing the surface organic layers) by a bull-dozer equipped with a blade; considered a high disturbance in this thesis.
FWM	fine woody material, <10 cm diameter material that includes branches and tops left on-site after harvesting
GLM	general linear model
H'	Shannon's diversity index (Shannon and Weaver 1963
HD	high disturbance, FTB is considered a HD in this thesis
ha	hectare
IS	indicator species analysis
kg	kilograms
L	litter
LD	low level of disturbance, in this thesis TL harvesting is considered a LD
LFH	surface organic layer, litter, fibric and humus layers
LTER	long-term ecological research
m	meter
MD	medium level of disturbance, in this thesis FT harvest is considered a MD

Mg	Magnesium
N	Nitrogen
NaCl	Sodium chloride
NH_4	ammonium respectively, representing mineralizable nitrogen in this thesis
NMS	non-metric multidimensional scaling ordination technique
NO_2 NO_3	nitrite, nitrate respectively
O-horizon	surface organic layer in a soil profile
Of	fibric organic layer
O-layer	organic layer located at the surface of the soil
OM	organic matter
OMNR	Ontario Ministry of Natural Resources
P	phosphorus
PAR	photosynthetically active radiation
PC	phenolic compound
PC	principal components analysis
PerMANOVA	nonparametric analysis method to
Plot	30 x 30 m treatment unit

Quadrat	4 x 4 m sampling unit on which plant species presence/absence and environmental parameters were recorded
R	species richness
Site Type	term referring to the black spruce forest community types in which the six study areas were located. There are three site types each associated with a dominant soil texture: loam site type, sand site type, and peat site type.
SMS	estimated mean square, statistical term
SS	shallow soil types as defined in the Forest Ecosystem Classification System (as per Racey *et al.* 1996)
Study Area	experimental areas in which the treatment applications occurred.
Sub-plot	15 x 15 portion quartile of each treatment plot
Sub-quadrat	2 x 2 m sampling quadrat
TC, TN	total carbon, total nitrogen
TL	tree-length, considered a low disturbance in this thesis
Total Species	vascular and nonvascular species, at times referred to as “all species”.
TSC	total soluble carbon
UNCUT	reference forest condition

APPENDIX II. LIST OF TREE SPECIES PRESENT IN THE STUDY.

List of tree species

Balsam fir	*Abies balsamea* (L.)
Black spruce	*Picea mariana* (Mill.) B.S.P.
Jack pine	*Pinus banksiana* Lamb
Larch	*Larix laricina* (Du Roi) K. Koch
Trembling aspen	*Populus tremuloides* Michx.
White birch	*Betula papyrifera* Marsh.

APPENDIX III. ENVIRONMENTAL PARAMETERS BY SITE TYPE

Harvest		Mineral Soil Exposure		Mean Depth of LFH		Coarse Woody Material (		Fine Woody Material (FWM)		Conifer Litter		Deciduous Litter	
Treatment	Site Type	% cover	range	(cm)	range	% cover	range	% cover	range	% cover	range	% cover	range
Tree Length	Loam	4.8 (1.3)	0-7.5	9.3 (1.5)	4.9-14.2	14.9 (3.6)	7-27	11.6 (1.7)	5.8-15	9.4 (5.9)	0-30	5.7 (2.9)	0-15
Full Tree	Loam	1.1 (0.9)	0-6.3	10.4 (1.4)	6.8-15.4	16.1 (5.4)	1-40	7.5 (3.6)	0-28	37.3 (12.0)	0-90	16 (10.0)	0.5-75
Full Tree Blade	Loam	43.6 (17.4)	0-90	7.5 (0.6)	6-8.6	10.8 (2.0)	4-20	1.7 (1.6)	0-8	28.6 (10.3)	0-50	3 (0.9)	1-5
Tree Length	Sand	18.7 (5.6)	0-40	5.9 (0.6)	3.7-7.3	12.5 (2.6)	1-20	13.3 (6.5)	0-40	7.0 (3.07)	1-18	2.3 (1.6)	0-10
Full Tree	Sand	4.8 (3.1)	0-12	5.4 (0.7)	3.9-7.2	4.2 (0.8)	3-3	6.6 (1.8)	0.9-12	43.7 (12.5)	0.5-32.5	0.6 (0.3)	0-2
Full Tree Blade	Sand	54.0 (17.0)	0-99	0.1 (0.1)	0-0.3	3.9 (2.0)	0.4-12	0.2 (0.2)	0-1	16.0 (7.3)	0-45	20.8 (15.1)	0-95
Tree Length	Peat	0	0	0	0	7.1 (1.7)	12-11	3.8 (1.8)	0-12	4.3 (2.2)	5-15	16.0 (5.6)	4.8-40.3
Full Tree	Peat	0.2 (0.2)	0-1	0	0	3.2 (1.1)	0-56.3	1.3 (0.8)	0-4.5	2.8 (1.1)	0-6.5	5.5 (1.4)	2-11.8
Full Tree Blade	Peat	0	0	0	0	3.1 (1.8)	0.6-12	1.0 (0.4)	0-3	0.3 (1.7)	0-75	15.6 (5.3)	0-30

B Field Observations - Biotic Elements

		Basal Area		Pioneer Moss		Feathermoss		Sphagnum		Total Moss		Total Lichen	
		m2ha-1	range	% cover	range	% cover	range	% cover	range	% cover	range	% cover	range
Tree Length	Loam	2.6 (0.3)	1.4-3.4	10.0 (6.3)	0-30	0.3 (0.133)	0-0.6	0	0	12.3 (7.2)	0.3-30	2.3 (1.5)	0-8
Full Tree	Loam	5.2 (0.8)	3.0-7.9	21.5 (11.0)	0-80	10.1 (5.6)	0-32.5	1.6 (1.6)	0-11.3	33.1 (11.9)	5-80	5.6 (2.1)	5-16.7
Full Tree Blade	Loam	9.7 (1.2)	6.6-15.0	3.5 (1.3)	0-8	0	0	46.5 (19.4)	0-90	52.9 (20.6)	0-90	12.5 (1.3)	8-15.2
Tree Length	Sand	7.4 (1.5)	4.4-13.8	15.5 (9.8)	0-60	30.833 (11.0)	0-75	0	0	46.3 (11.1)	7-80	1.8 (0.6)	5-4
Full Tree	Sand	11.2 (0.8)	9.0-14.6	5.6 (2.1)	1-14	23.8 (11.4)	1-70	0	0	38.7 (13.1)	2.2-84	13.2 (5.6)	2-31.4
Full Tree Blade	Sand	9.2 (1.5)	4.8-14.0	17.9 (8.5)	0-55	12.2 (7.9)	0-49	0	0	21.3 (7.7)	2.5-5.5	1.8 (0.4)	0-2.5
Tree Length	Peat	1.4 (0.5)	0.5-3.1	1.5 (0.5)	0-3.3	9.3 (2.8)	1-20	55.9 (11.8)	15.5-90	66.1 (9.8)	28.8-93	2.3 (1.1)	0-5.7
Full Tree	Peat	0.7 (0.1)	0.3-1.1	2.1 (1.5)	0-9.3	6.4 (3.5)	0-19.8	64.9 (14.5)	11.5-95	73.4 (10.4)	40-96	1.7 (0.7)	0-3.7
Full Tree Blade	Peat	0.5 (1.7)	0.9-1.0	2.3 (0.9)	0-5.3	0.5 (0.4)	0-2.3	69.4 (7.1)	50-95	71.5 (8.1)	50-100	0.9 (0.4)	0-2.5

C- Soil Chemical Properties

		pHCaCl		pH Water		Mineralizable N, NH 4		Total N		Bulk density (F-layer)		Bulk Density (B-layer)	
Harvest type	Site Type	mean (SE)	range	mean (SE)	range	kgha-1	range	kgha-1	range	g cm^{-3}	range	g cm^{-3}	range
Tree Length	Loam	3.6 (0.2)	3.1-4.0	5.0 (0.1)	4.6-5.3	13.1 (2.45)	9.0-25.1	3017.2 (355.1)	1998.1-4146.1	0.14 (0.008)	0.01-0.19	1.06(0.04)	0.87-1.24
Full Tree	Loam	4.0 (0.1)	3.7-4.4	5.1 (0.1)	4.9-5.6	8.0 (0.2)	1.9-14.6	3696.0 (470.0)	1626.5-5962.2	0.18 (0.008)	0.15-0.2	1.19(0.09)	0.69-1.59
Full Tree Blade	Loam	4.2 (1.0)	4.0-4.5	5.5 (0.1)	5.1-5.9	1.8 (0.9)	0-5.2	2451.0 (352.9)	1771.1-4101.3	0.18 (0.01)	0.12-0.26	1.16(0.04)	0.96-1.38
Tree Length	Sand	3.7 (0.1)	3.2-4.2	5.1 (0.1)	4.5-5.6	10.2 (1.8)	4.3-14.6	1558.3 (202.4)	1025.8-2325.1	0.19 (0.009)	0.14-0.22	1.15(0.04)	0.92-1.31
Full Tree	Sand	3.9 (0.2)	3.9-0.2	5.2 (0.2)	4.8-7.5	9.0 (1.5)	4.7-12.6	1706.6 (264.5)	1213.1-2925.4	0.21(0.011)	0.15-0.26	1.27(0.04)	1.14-1.5
Full Tree Blade	Sand	4.5 (0.2)	4.1-5.2	5.7 (0.1)	5.3-6.1	0	0	605.7 (100.3)	337.3-1025.8	0.20(0.006)	0.19-0.21	1.24(0.03)	1.14-1.33
Tree Length	Peat	3.7 (0.3)	2.9-4.3	4.8(0.4)	3.8-5.8	31.1 (11.2)	3.4-58.9	3619.0 (647.0)	1779.6-5006.9	0.15(0.009)	0.13-0.17	1.42(0.05)	1.27-1.52
Full Tree	Peat	3.6 (0-.3)	3.2-4.6	4.8 (0.3)	4.3-5.73	21.9 (6.2)	7.6-42.9	2424.0 (593.3)	1189.0-4297.0	0.16(0.03)	0.10-0.21	1.53(0.03)	1.48-1.61
Full Tree Blade	Peat	3.9 (0.3)	2.9-4.4	5.0 (0.3)	4.0-5.6	41.2 (11.4)	6.5-72.9	2399.7 (280.9)	1641.1-3708.1	1.49(0.009)	1.48-1.52	1.49(0.01)	1.48-1.52

		TC total soil		Bray's P		K		Ca		Mg	
		Mgha-1	range	kgha-1	range	kgha-1	range	kgha-1	range	kgha-1	range
Tree Length	Loam	101.3 (13.4)	57.3-134.2	7.1 (0.5)	5.6-9.1	549.1 (70.9)	281-789.8	7503.2 (3508.9)	1940.4-24883.0	649.4 (293.3)	08.0-2039.6
Full Tree	Loam	116.9 (15.1)	50.8-159.1	5.6 (0.3)	4.8-6.6	740.2 (116.1)	79.3-1160.	14661.6 (3330.0)	3693.1-22480.0	618.3 (114.0)	67.8-949.7
Full Tree Blade	Loam	74.0 (11.8)	53.6-131.1	5.5 (1.1)	2.1-9.7	490.6 (105.6)	25.6-829.	22652.2 (7081.7)	6350.1-55532.9	760.7 (161.9)	10.4-1230.7
Tree Length	Sand	52.5 (8.2)	24.3-73.2	11.0 (1.6)	6.7-15.7	70.4 (8.4)	46.7-105.1	640.0 (169.6)	360.4-1465.4	60.6 (12.5)	32.0-119.8
Full Tree	Sand	59.9 (7.7)	44.3-95.1	13.3 (3.333)	5.5-25.9	72.8 (4.8)	56.1-87.6	534.5 (102.6)	259.8-899.4	66.2 (12.0)	34.6-103.0
Full Tree Blade	Sand	14.9 (2.4)	8.7-24.3	12.0 (4.6)	3.9-34.17	35.7 (3.4)	23.3-46.7	272.5 (94.5)	75.7-677.5	25.4 (7.5)	5.9-57.9
Tree Length	Peat	146.0 (17.6)	100.1-208.1	5.8 (1.1)	3.9-9.7	1027.7 (641.7	2.5-3543.	2009.3 (1193.8)	102.6-5880.1	353.9 (102.1)	10.0-669.1
Full Tree	Peat	130.7 (23.9)	74.6-205.8	3.9 (0.8)	2.4-6.1	712.7 (300.1)	7.8-1735.	1192.3 (831.2)	79.9-4378.0	305.2 (81.7)	60.1 - 618.2
Full Tree Blade	Peat	119.2 (4.7)	103.9-135.9	3.4 (0.5)	2.3-5.4	701.4 (423.5)	48.3-2724.	1865.1 (780.3)	89.1-3702.3	359.2 (78.4)	14.1 - 585.6

APPENDIX IV. AVERAGE NUMBER OF GERMINANTS FOR SEED COLLECTED FROM SOIL SEED BANK ON LOAM, SAND, AND PEAT SITE TYPES

Species	**Common Name**	**Loam**	**Sand**	**Peat**
		Germinants m^{-2}	Germinants m^{-2}	Germinants m^{-2}
Aralia hispida Vent.	Bristly sarsaparilla	0	1.325	0
Betula papyrifera Marshall	White birch	3.98	14.59	4
Carex species	Sedges	313.005	519.905	35.48
Chamaedaphne calyculata (L.) Moench	Leatherleaf	1.325	0	5.305
Chenopodium album L.	Lambsquarters	1.325	0	0
Convolvulus arvensis L.	Field bindweed	0	6.63	0
Coptis trifolia (L.) Salisbury	Goldthread	0	0	0
Cornus stolonifera L. syn. *Cornus sericea* L. ssp. *sericea*	Redosier dogwood	0	2.655	0
Corydalis semperiren s (L.) Pers.	Pale corydalis	1.325	11.935	9.5
Diervilla lonicera Mill.	Bush honeysuckle	2.65	187.005	0
Epilobium angustifollium L. syn. *Chamerion angustifolium*	Fireweed	0	0	1.325
Gaultheria hispidula (L.) Muhl. Ex Big.	Creeping snowberry	1.325	2.655	6.655
Geranium bicknellii Brit.	Bicknell's cranesbill	6.63	14.59	0
Linnaea borealis L.	Twinflower	0	0	2.655
Maianthemum canadense Desf.	Canada mayflower	0	0	0
Melampyrum lineare Desr.	Cow-wheat	0	1.325	0
Oxalis montana Raf.	Mountain woodsorrel	3.98	11.935	6.825
Picea mariana (Mill.) Brit., Sterns & Pog.	Black spruce	1.325	0	0
Poa spp.		132.63	84.88	32.935
Ribes spp.	Current	1.325	0	0
Rubus idaeus L.	Wild red raspberry	7.955	31.83	4
Rubus pubescens Raf.	Dewberry	13.265	0	0
Unkown		5.305	17.24	6.805
Vaccinium angustifolium Aiton	Low bush blueberry	0	2.655	2.5