Understory species response to partial harvesting in boreal riparian buffers

by

Cristina Spalvieri

A thesis submitted in partial fulfilment of the requirements for the degree of Master of Science in Biology

Department of Biology

Lakehead University
Thunder Bay, ON
November, 2009

THERE is a pleasure in the pathless woods,
There is rapture on the lonely shore,
There is society, where none intrudes,
By the deep sea, and music in its roar:
I love not man the less, but Nature more,
From these our interviews, in which I steal
From all I may be, or have been before,
To mingle with the Universe, and feel
What I can ne'er express, yet cannot all
conceal
  ~Lord Byron

Abstract

In order to preserve valuable riparian functioning, forest harvesting in Canada attempts to protect riparian areas through the application of a no-harvest buffer zone around water bodies, and more recently through the emulation of natural disturbance patterns. Partial harvesting with maintenance of understory vegetation may emulate natural disturbance better than clearcut harvesting with conventional intact riparian buffers. With most canopy gaps in the boreal forest being less than 100 m^2, small-scale canopy gap disturbance plays an important role in boreal forest dynamics. I studied the response of understory vegetation, including tree seedlings and saplings, to gaps created by partial harvesting in riparian buffers to i) assess the response of understory species to small gaps created by partial harvesting, and ii) investigate overstory replacement patterns in harvest gaps. I hypothesized that i) the boreal understory community would exhibit resilience to small-scale canopy disturbance due to leaf morphological plasticity which allows plants to adapt to gap-induced environmental changes, and ii) that tree seedlings/saplings would respond to gaps through increased growth of all seedlings and saplings and increased stem density of shade intolerant species.

Research was conducted in three mixedwood dominated watersheds located on the Canadian boreal shield in northern Ontario. Two watersheds were clearcut in the upland with retention of approximately 40 m riparian buffers. Three years prior to this research, partial harvesting within the buffers created canopy gaps ranging in size from 1-400 m^2. Gaps were classified as small (<20 m^2), medium (21-99 m^2) or large (>100 m^2). Some portions of the buffers were left unharvested. A third watershed with no recent record of disturbance was used as reference riparian forest. Understory species composition, richness, diversity, abundance, and evenness were compared among treatments on two levels: i) transect means of partially harvested buffers containing gaps, unharvested buffers, and reference forests; and ii) gap centred

quadrats compared with closed canopy quadrats in partially harvested and unharvested riparian buffer locations. Specific leaf area (leaf area per unit dry weight) and leaf dry matter content (leaf dry weight as a percentage of fresh weight) of four common understory species (*Clintonia borealis, Cornus canadensis, Vaccinium angustifolium,* and *Vaccinium myrtilloides*) were assessed in the centre of harvest gaps and along transects of unharvested stands. Stem density, basal diameter, and height of tree seedlings and saplings were compared among gaps, unharvested buffer and reference forest transects. Overstory structure was also tested to determine its influence on tree regeneration.

The hypothesis of understory resilience to small-scale canopy disturbance was supported. Understory species composition in terms of richness, abundance, diversity, and evenness did not differ significantly among partially harvested buffers, unharvested buffers, and reference forest. *Clintonia borealis, Cornus canadensis, V. angustifolium,* and *V. myrtilloides,* showed differences in specific leaf area and leaf dry matter content under closed canopy and in harvest gaps; supporting the hypothesis that boreal understory species use plasticity of leaf morphology to adapt to slight environmental changes. Consistent with my hypotheses, conifer seedlings/saplings were found in higher abundance under closed canopy than in gaps, but achieved larger sizes in gaps than under closed canopy. In larger gaps the proportion of hardwood regeneration was increased compared to conifers; with *Populus tremuloides* stem density and size positively correlated with gap area and overstory *Populus tremuloides* stem density. My results provide evidence that boreal understory species use morphological plasticity of leaves to confer resilience against small gap disturbance. However, partial harvesting can influence future overstory composition by enhanced growth of early successional canopy species such as *Populus tremuloides.*

To loving parents, great pets, and best friends.

Acknowledgements

Table of Contents

List of Tables

List of Figures

General Introduction

Disturbance is a driving force shaping ecosystems. Though historically natural disturbances such as wildfires have initiated stand replacement in boreal forests, anthropogenic disturbances such as timber harvesting have quickly replaced wildfire as the major disturbance of this region. Though both fire and clearcut harvesting are stand replacing disturbances there are key differences. Fire is usually a very large physical as well as a chemical disturbance which is sporadic and patchy in distribution resulting in 'soft' edges. Clearcuts are generally a smaller physical disturbance and linear in nature, resulting in the creation of 'hard' abrupt edges (Larrivée et al. 2008). In order to preserve natural forest structure and processes the Government of Ontario suggested that forest harvesting should emulate natural disturbance (OMNR 2001). Although the boreal forest is adapted to frequent stand replacing disturbance (i.e., fire), small gap dynamics play an important role in structuring boreal forests in the absence of such disturbance (Hansen et al. 1991; Greene et al. 1999). Canopy gaps commonly occur in the boreal forest and most are less than 100 m². Despite their prevalence small-scale gap disturbance has received relatively little attention until recently (Runkle 1990; Kneeshaw and Bergeron 1996; McCarthy 2001; Pham et al. 2004; Fraver and White 2005).

To preserve ecosystem integrity in riparian zones some unharvested riparian vegetation is kept as a buffer around water bodies (NCASI 2006). Riparian vegetation eases the transition between disturbed and undisturbed areas and can protect adjacent water bodies against dramatic increases in temperature (Hansen et al. 1991). Riparian buffers may emulate lower intensity fires which typically leave 10-20% of forest structure around streams and lakes (Lee et al. 2002; Nitschke 2005). Riparian buffers are meant to preserve riparian ecosystem functions and services such as regulating water quality, controlling soil erosion and sedimentation, moderating

stream temperature and light, and providing habitat for a multitude of floral and faunal communities (Hazlett *et al.* 2005). To ensure that the best management strategies are practised and riparian ecosystems continue to serve their functional role in the forest, in-depth analyses of riparian properties and functions are needed (Brosofske *et al.* 1997). Prescribed widths of riparian buffers (from stream edge to upland harvest area) are somewhat subjectively determined by the topography of the particular site, water body size and type, presence or absence of fish, potential downstream impacts, and aesthetic or recreational value of the area (Lee and Barker 2005). The result has been that conventional riparian buffers appear unnatural in the landscape, and there are concerns as to their efficacy (see MacDonald *et al.* 2004). One such concern is the chance for decreased stability of riparian buffers as they mature into old growth. There may be increased blowdown of trees due to the creation of a new edge and increased wind velocity (Reid and Hilton 1998). In addition, riparian buffers may not be effective in protecting many species due to large home ranges and the diversity of critical habitat required (Goates et al. 2007). Lack of scientific merit in prescribing buffer widths has provoked research regarding the effects of harvesting near riparian areas.

It has been suggested that partial harvesting with maintenance of understory vegetation may emulate wildfire effects better than that of clearcut harvesting with a conventional buffer (OMNR 2001). Partial harvesting has been permitted in riparian buffers up to three metres from water's edge but our knowledge is inadequate on the effect of partial harvesting on understory vegetation (OMNR 1988; Gea-Izquierdo *et al.* 2004). Partial harvesting involves the felling of individual or small groups of trees and as such, is considered a lower impact logging practice than clearcutting (Broadbent *et al.* 2006). Partial harvesting in riparian buffers may emulate fire more closely than clearcutting with retention of an intact buffer because of the patchy

distribution of fire in riparian areas. However, more evidence is needed to determine if partial harvesting can emulate natural disturbance patterns (Lee *et al.* 1997; Harrison *et al.* 2005).

Partial harvesting creates canopy gaps which play a major role in the functioning of riparian ecosystems by their influence on forest floor light, moisture, soil nutrients, understory development, and exposure to frost and winter injury (MacIsaac *et al.* 2006). A forest 'gap' is defined as an opening extending from the canopy layer down to two metres above the forest floor and marked by foliage surrounding the perimeter of this vertical column. To simplify, the canopy gap is the area of the forest floor directly under the canopy opening (Runkle 1982). Creation of gaps by partial harvesting may significantly alter forest microclimate by increasing air and soil temperature and decreasing moisture (Schumann *et al.* 2003). Gaps can influence floristic composition because microclimate differentially affects plant species growth and distribution (Brosofske *et al.* 1997). Gaps also influence soil nitrogen mineralization (Reynolds *et al.* 2000). Environmental changes incurred through gap creation can also cause shifts of dominant species; resulting in altered community composition and canopy structure (Forkner *et al.* 2006).

Understory plants undergo changes in community composition and dominance depending on intensity of and time since disturbance. Environmental factors such as light, soil moisture, and nutrients vary depending on gap size and directly influence understory species composition (McCarthy 2001; Galhidy *et al.* 2006). Therefore, gap size will determine what species can become established (Denslow 1987). Near-ground microclimate of gaps tend to favour growth of herbs and woody species (Schaetzl *et al.* 1989; Denslow and Spies 1990; Goldblum 1997). In particular, increased light after canopy disturbance can increase shrub growth (Domke *et al.* 2007). As a result of increased light penetration to the understory, gaps can provide habitat for

early successional species such as grasses and sedges, and other shade intolerant vegetation (Grushecky and Fajvan 1999; Felton *et al.* 2006). Small gaps may not provide enough light to stimulate the growth of light demanding species, and therefore continue to be dominated by shade tolerant species, while larger gaps can support less tolerant or shade intolerant species (McClure and Lee 1993).

Increased light in gaps also stimulates the growth of tree seedlings and saplings (Denslow 1987; Canham *et al.* 1990; Gilbert *et al.* 2001). Trees that grow as advance regeneration are suppressed under closed canopy; but are able to capitalize on increased light and grow rapidly to fill the canopy gap (Felton *et al.* 2006). There is a tendency for advance regeneration of shade tolerant species such as *Abies balsamea* to fill small gaps, while shade intolerant tree species such as *Populus tremuloides* colonize large gaps (Whitmore 1989; Frelich and Reich 1995; Kuuluvainen and Juntunen 1998; Kneeshaw and Bergeron 1998; 1999; Grushecky and Fajvan 1999; Hill *et al.* 2005). Some harvest gaps may be larger than natural gaps which may result in higher light exposure and higher recruitment of tree seedlings and saplings in harvested forests than in natural forests (Schumann *et al.* 2003; Felton *et al.* 2006). Some partial harvesting gaps, especially with single tree removal, may be too small to create the high light conditions needed to regenerate shade-intolerant species, and may not cause any noticeable shift in dominant vegetation (Crow *et al.* 2002; Domke *et al.* 2007). Because of the range of gap sizes that can result from partial harvesting, it is important to study harvest gaps across a size range corresponding to varying harvesting intensities.

My objective was to document the response of understory vegetation to a range of gap sizes created by partial harvesting within riparian buffers. Understanding how gaps across a size range impact riparian understory will help forest managers decide what intensity of harvest, if

any, is needed to achieve management objectives. My thesis is presented in two chapters. In chapter one I assess the resilience of understory species to gaps created by partial harvesting. In chapter two I present the results of canopy tree replacement patterns in harvest gaps. I hypothesized that i) boreal understory vegetation would exhibit resilience to small-scale canopy disturbance by utilizing plasticity of foliage to adapt to the gap environment, and ii) that canopy species would respond to harvest gaps through increased growth of seedlings and saplings in gaps, and increased stem density of shade intolerant hardwoods in larger gaps.

General Methods

Study area

I conducted research approximately 60 km south of White River, Ontario, Canada (48°21'5''N, 85°20'46''W). Located on the Canadian boreal shield, the area supports mixedwood forests with *Abies balsamea* and *Betula papyrifera* dominating the canopy. The dominant understory vegetation includes *Cornus canadensis, Vaccinium angustifolium, Clintonia borealis,* and *Pleurozium schreberi.* Climate in the region is characterized by long, cold winters and short, warm summers with snow cover generally occurring from November to May. The area is founded on Precambrian bedrock, and rocky outcrops are common. Soils are generally thin glacial tills, consisting mainly of Humo-Ferric podzols (Muto *et al.* 2009).

Experimental design

My study sites were located in three watersheds which are part of the White River Riparian Harvest Impact Project (WRRHIP) being conducted by Natural Resources Canada and other

partners. The objectives of the WRRHIP study were to investigate whether partial harvesting within riparian buffers could improve their stand quality and increase habitat complexity without compromising stream habitat and the biotic community. A single 1-3 order stream reach was studied in each watershed (Figure 1.2). Two of the watersheds were clearcut in the upland with riparian buffers 32-42 m wide and 370-840 m long. Some sections of the buffers were also partially harvested, while other sections were left intact as conventional unharvested riparian buffers. The partial harvests were indiscriminate of species and size of harvested trees, and created gaps ranging from 1-408 m^2 (Fig. 1.1). Logging was conducted using feller bunchers with grapple skidders in the winter of 2005, since winter harvesting minimizes site damage (Nichols *et al.* 1994; Schumann *et al.* 2003). Machine entry and movement corridors within the riparian buffers were restricted to 15 m wide with no movement within 3 m of the water's edge. The third watershed was undisturbed and considered as a reference forest. Stem density, height, and basal area of overstory trees in the three study treatments after harvesting are presented in Table 1.1.
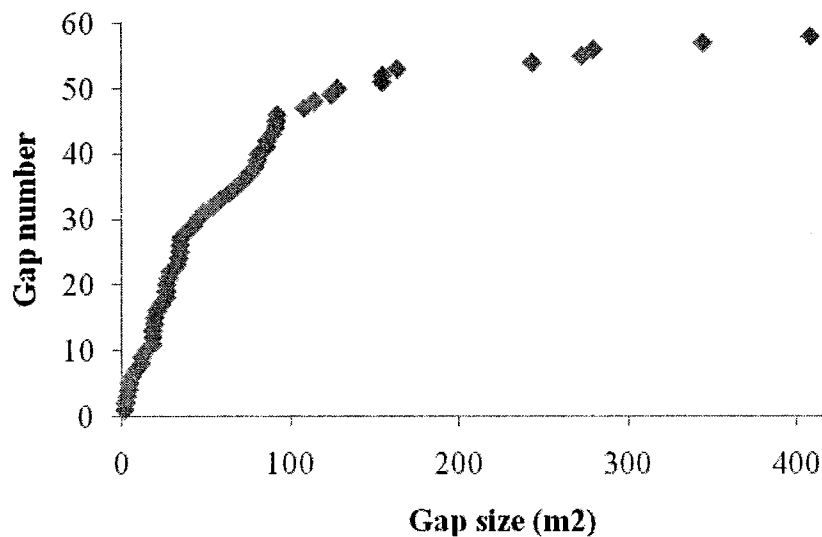
Figure 1.1. Distribution of gap sizes created by partial harvesting. Each point represents one of the 58 harvest gaps surveyed.
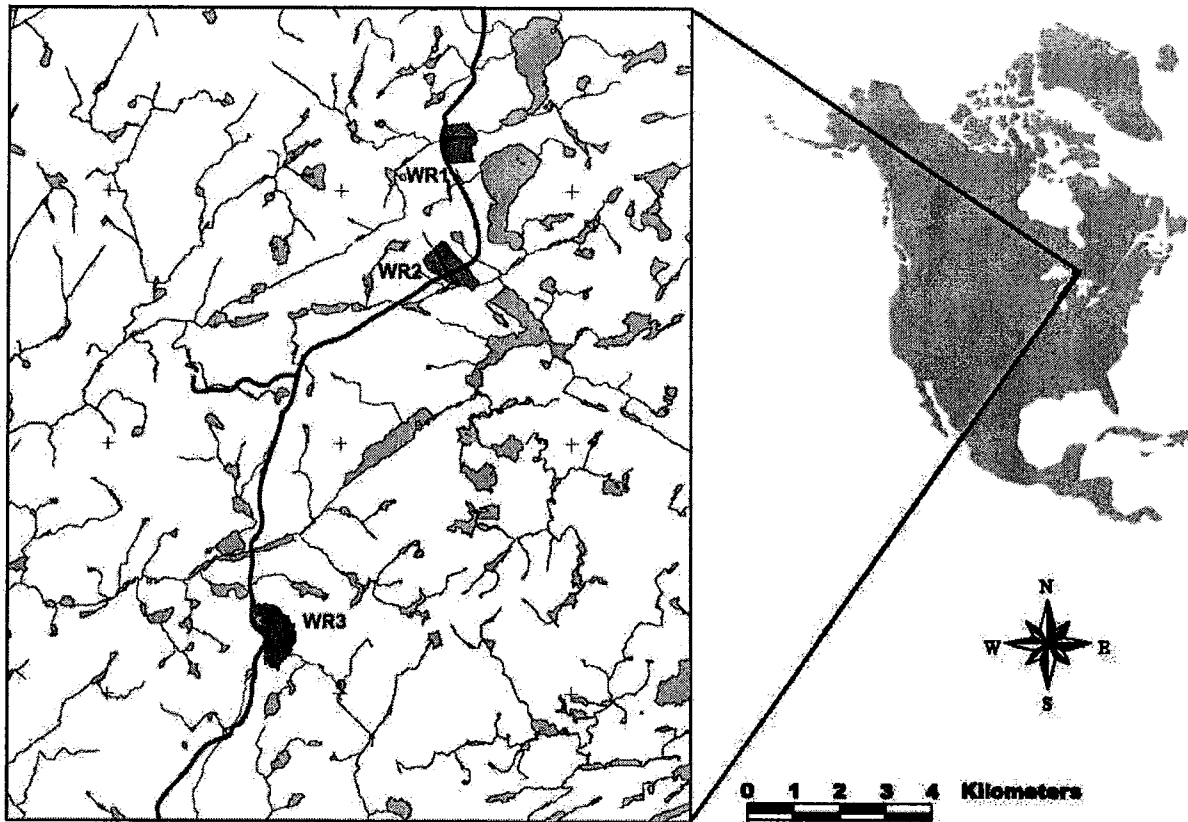
Figure1.2. Map of study area located on the Boreal Shield near White River, Ontario (between 48°21'5''N, 85°20'59''W and 48°13'47''N, 85°22'3''W). Sites were located in three watersheds shown by dark shading, one stream reach studied in each. The solid black line is a logging road. (Modified from Kreutzweiser *et al*. 2009).

Table 1.1. Mean stem density, height, and live tree basal area in partially harvested buffers containing gaps (large, medium, and small), unharvested buffers, and reference forest.

Treatment		Number of transects	Stem density/ha				Height (m)	Live basal area (m^2/ha)
			Abies balsamea	*Betula papyrifera*	*Picea spp.*	*Populus tremuloides*		
Partially harvested buffer	Large	12	278.7	548.5	251.7	17.9	12.2	18.5
	Medium	30	290.4	252.8	325.8	17.7	11.7	18.8
	Small	16	288.2	409.1	300.3	29.9	10.2	20.6
Unharvested buffer		6	237.9	371.0	659.4	20.4	13.1	26.2
Reference forest		7	683.33	594.05	240.4	14.3	12.21	22.7

Strengths and limitations of experimental design

In order to take advantage of the range of gap sizes created by partial harvesting transects were not randomly placed, instead each transect was deliberately placed passing through the centre of one harvest gap in partially harvested buffers. By passing a transect through only one gap, I assumed that differences in understory in partially harvested buffers compared with closed canopy unharvested buffers and reference forest could be attributed to a gap of a particular size. All transects were greater than 5 m from any other transect and on slopes less than 30 degrees. Sampling all suitable gaps resulted in unequal sample sizes among harvest treatments because there was an abundance of transects sampled within partially harvested buffers compared with fewer transects sampled in unharvested buffers and reference forest. My reason for studying fewer transects in unharvested buffers and reference forest was the low variability in community composition and site characteristics in these stands (personal observation). Most reference transects were located in a separate watershed than the partially harvested and unharvested buffer transects. Each transect was considered as a replicate, though many are located within the same stream reach, and therefore may not have been independent but biased by location. Since my study was constrained to the WRRHIP design, I assumed that transects in the reference watershed were representative of reference forests in general, independent of watershed. The scarcity and need for research on partial harvesting within riparian buffers, coupled with my confinement to the WRRHIP design and the impracticality of replicating harvest treatments, was my justification for accepting potentially non-independent replicates into this study (as in Groot *et al.* 2009). Since gap age and cause of gap-maker mortality are important in understory regeneration and are often ambiguous no natural gaps were included in this study. Another reason for not including natural gaps was that the specific research question of this thesis was to

determine how understory species respond to the introduction of harvest gaps. In order to answer this question most efficiently, it was simpler to compare harvest gaps with closed canopy forests so that in every respect, other than the presence of a gap, partially harvested transects were similar to unharvested buffers and reference forest. The assumption of similarity between closed canopy sections of partially harvested and unharvested buffers, and reference forest transects was my justification for sampling tree regeneration within harvest gaps in partially harvested buffers, but along transects in unharvested buffers and reference forest.

Chapter 1

Resilience of the boreal understory plant community to partial harvesting

Abstract

Most studies on gap dynamics in the boreal forest have focused on commercial tree regeneration, with little attention paid to understory species. Since riparian understory species provide essential ecosystem services, I investigated their response to gaps created by partial harvesting in riparian buffers. I hypothesized that boreal understory plants would show resilience to canopy gap disturbance caused by partial harvesting, and that their resilience could be attributed to morphological plasticity of leaves. I compared unharvested buffers and natural riparian forests with partially harvested buffers containing gaps ranging from 1-400 m^2 in area. Understory community composition, specific leaf area and leaf dry matter content of four common understory species (*Clintonia borealis*, *Cornus Canadensis*, *Vaccinium angustifolium*, and *Vaccinium myrtilloides*), and selected environmental variables were surveyed along transects passing through small (n=16, 1-20 m^2), medium (n=30, 21-99 m^2) and large (n=12, >100 m^2) gaps in partially harvested riparian buffers, and compared with six transects in unharvested buffers, and seven transects in a reference natural riparian forest. Partially harvested buffers, regardless of gap size, did not differ significantly from unharvested buffers or reference forest with respect to understory species composition and diversity. The results suggest that partial harvesting in riparian buffers did not have any significant impact on riparian plant communities when the majority of gaps created by harvesting were less than 100 m^2. The prediction of resilience of boreal understory species to small-scale canopy disturbance was supported. Specific leaf area (leaf area per unit dry weight) was greater under closed canopy than in gaps, while leaf dry matter content (leaf dry weight as a percentage of fresh weight) was lower. The data suggest that the common understory species studied responded to canopy gap formation by adjusting leaf morphology; and this plasticity may explain the ability of common boreal understory species to resist small-scale canopy disturbance.

Introduction

Canopy gaps play an important role in forest regeneration and as a result, most studies on gap dynamics focus on tree species, however forest understory species must also be considered (Kneeshaw and Bergeron 1999; Lahde *et al.* 1999; Coates 2002). Understory vegetation is an integral part of any ecosystem, influencing decomposition and nutrient cycling by contributing organic matter to the soil (Gilliam and Turrill 1993; Abe *et al.* 1995; Hazlett *et al.* 2005; Nilsson and Wardle 2005). Although understory shrubs and herbs are particularly sensitive to disturbance, little attention has been paid to understory regeneration in gaps (Moore and Vankat 1986; Collins and Pickett 1987; Hughes and Fahey 1991; Schumann *et al.* 2003). Canopy gaps can elicit response from understory communities by altering microclimate, which influences plant growth and distribution (Brosofske *et al.* 1997; McCarthy 2001). The near-ground microclimate of gaps tends to favour the growth of herbs and woody species (Schaetzl *et al.* 1989; Denslow and Spies 1990; Goldblum 1997). In particular the increase in light after canopy disturbance can increase shrub growth (Domke *et al.* 2007). As a result of increased light, gaps can provide habitat for early successional species, such as grasses and sedges, and other shade intolerant vegetation (Grushecky and Fajvan 1999; Felton *et al.* 2006). With cessation of transpiration by the gap maker tree, soil moisture increase in gaps (Galhidy *et al.* 2006). Larger gaps however, can experience decreased soil moisture and increased air and soil temperature due to increased, and prolonged, exposure to higher light in summer (Schumann *et al.* 2003). In winter greater exposure to frost in gaps can lead to understory winter injury (MacIsaac *et al.* 2006). Environmental changes incurred through gap creation can cause shifts of dominant species and alter community composition (Forkner *et al.* 2006). Understory plants undergo changes in community composition and dominance depending on the intensity of and time since

disturbance. Environmental factors such as light, soil moisture, and nutrients vary depending on gap size, and directly influence understory species composition (McCarthy 2001; Galhidy *et al.* 2006). Therefore, gap size will influence which species can become established (Denslow 1987). Small gaps may not provide enough light to stimulate the growth of light demanding species and therefore still favour shade tolerant species (Grushecky and Fajvan 1999), while larger gaps favour less tolerant or shade intolerant species (McClure and Lee 1993). Successional changes can be predicted if life history traits relating to establishment, longevity, and shade tolerance are taken into account (de Grandpre *et al.* 1993).

The response of plant communities to disturbance can be described in terms of resistance and resilience. Whereas, resistance is the ability of a community to remain unchanged despite disturbance, resilience is the ability of a post-disturbance community to return to pre-disturbance conditions, in terms of species composition and abundance (Westman 1978; de Grandpre and Bergeron 1997; Gunderson 2000). When disturbance intensity is low, understory communities may be able to resist changes through adaptations of individual plants. Specific leaf area and leaf dry matter content in particular, are important morphological traits related to plant photosynthetic capacity, competitive ability, and stress tolerance. The study of plant traits can aid in predictions of changes in plant species abundance associated with canopy disturbance (Wilson *et al.* 1999; Dahlgren *et al.* 2006)

Plants respond to environmental stress by being competitive, ruderal, stress tolerant or any combination of those three strategies. Stress tolerant plants contribute more energy to long-term survival than short-term resource capture and growth, contrary to competitive plants (Grime 1977). When conditions are favourable, stress tolerators are able to respond by allocating more resources to growth and sexual reproduction. However, these plants are able to tolerate less

favourable conditions by reallocating biomass to longer lived organs such as stems, roots, and rhizomes (Moola and Mallik 1998). Species that do not have biomass allocation plasticity cannot tolerate shade stress and are likely to be eliminated after canopy closure (Ricard and Messier 1996). Most boreal forest plant species are adapted to stand-replacing disturbance such as wildfire (Greene *et al.* 1999). Ericaceous plants, such as *Vaccinium* spp., are able to increase growth after overstory removal by fire and logging; this has been attributed to their ability to alter morphology and physiology with increased light availability (Marshall and Waring 1984; Messier and Kimmins 1991; Messier 1992; Mallik 1995). The study of how species respond to stress, and relief from stress, is important for forest management. For example, blueberries (*Vaccinium myrtilloides* and *V. angustifolium*) are important in the diets of many mammals and birds. Since *V. myrtilloides* and *V. angustifolium* often dominate the understory in boreal forests, and are sensitive to logging, it has been suggested that forestry practices such as gap creation by partial harvesting can improve wildlife habitat through light-related morphological and reproductive responses of these understory plants (Arimond 1979; Hall *et al.* 1979, Vander Kloet and Hall 1981, Balfour 1989; Hamilton *et al.* 1991; Freedman *et al.* 1993; Atlegrim and Sjoberg 1996, Hannerz and Hanell 1997).

With the objective of evaluating understory plant responses in partially harvested buffers compared to unharvested forests, I tested two hypotheses: i) if boreal understory species are resilient to small-scale gap based disturbance, then species abundance should not differ between closed canopy unharvested buffers and reference forest and partially harvested buffers across a range of gap sizes; and ii) if common understory plants are able to adjust leaf morphology after harvest gap-induced environmental changes, then those growing within harvest gaps should display differences in specific leaf area and leaf dry matter content compared with

conspecifics growing under a closed canopy; and that this response should be proportional to gap size.

Methods

Understory response to partial harvesting in riparian buffers

To assess the overall impact of partial harvesting on the riparian buffer plant community, I used transects running through harvest gaps in partially harvested buffers, and under the closed canopy of unharvested buffers and reference forest. Harvesting was conducted in the winter of 2005 and sampling occurred three years later in the summer of 2008. In partially harvested buffers 58 transects were run perpendicular to the stream, spanning the entire width of the buffer (from stream edge to cut edge), and passing directly through the centre of one harvest gap. This was done to capture the variability in canopy density across a range of gap sizes. Gaps occupied up to 75% of a transect if they were large (average 38%), up to 50% if they were medium (average 25%), and up to 20% if they were small (average 10%). Six transects were run perpendicular to the stream and for the entire width of the riparian buffer in areas which were clearcut in the upland but not partially harvested within the buffer. These represented conventional riparian buffers left after clearcut logging in the upland. To characterize vegetation and microclimate in undisturbed riparian forests, seven reference forest transects (40 m) were run perpendicular to the stream in riparian areas that had no harvesting within 100 m. There were no gaps within 5 m of any unharvested buffer or reference forest transects, and no additional gaps within 5 m of any partially harvested transect. Anderson and Leopold (2002) considered closed

canopy 5 m away from gaps in order to mitigate edge effects. I assumed that unharvested

transects more than 5 m away were not influenced by canopy gaps, and any significant

differences observed in partially harvested stands could be attributed to one particular gap. In

total 30 transects were sampled in watershed 1, with 10 passing through small gaps, 16 through

medium gaps, 4 through large gaps, and 3 through unharvested buffers. 28 transects were

sampled in watershed 2, with 6 passing through small gaps, 14 through medium gaps, 8 through

large gaps, 3 through unharvested buffers, and two through reference forest. Five transects were

sampled in watershed 3, all of which passed through reference forest (Fig. 1.3).

Every five meters along each transect I established a 1 m^2 quadrat within which I recorded

the percent cover of each species and selected environmental variables. An additional 1 m^2

quadrat was established in the centre of each gap. Microclimate measurements were taken

between 12:00 and 2:00 pm on clear days to mitigate diurnal fluctuations, and during the summer

months of July and August to negate seasonal fluctuations. A species list of understory species

encountered is presented in Appendix 1.18 (Chambers et al. 1996; Legasy 1995). The

environmental variables measured at breast height were canopy openness (determined using a

spherical densitometer), photosynthetically active radiation (PAR) (using a triple-sensor Apogee

BQM quantum meter by Apogee Instruments Inc., Logan, UT), relative humidity (RH), and air

temperature (using a digital humidity/temperature meter by VWR, model number: Q070757).
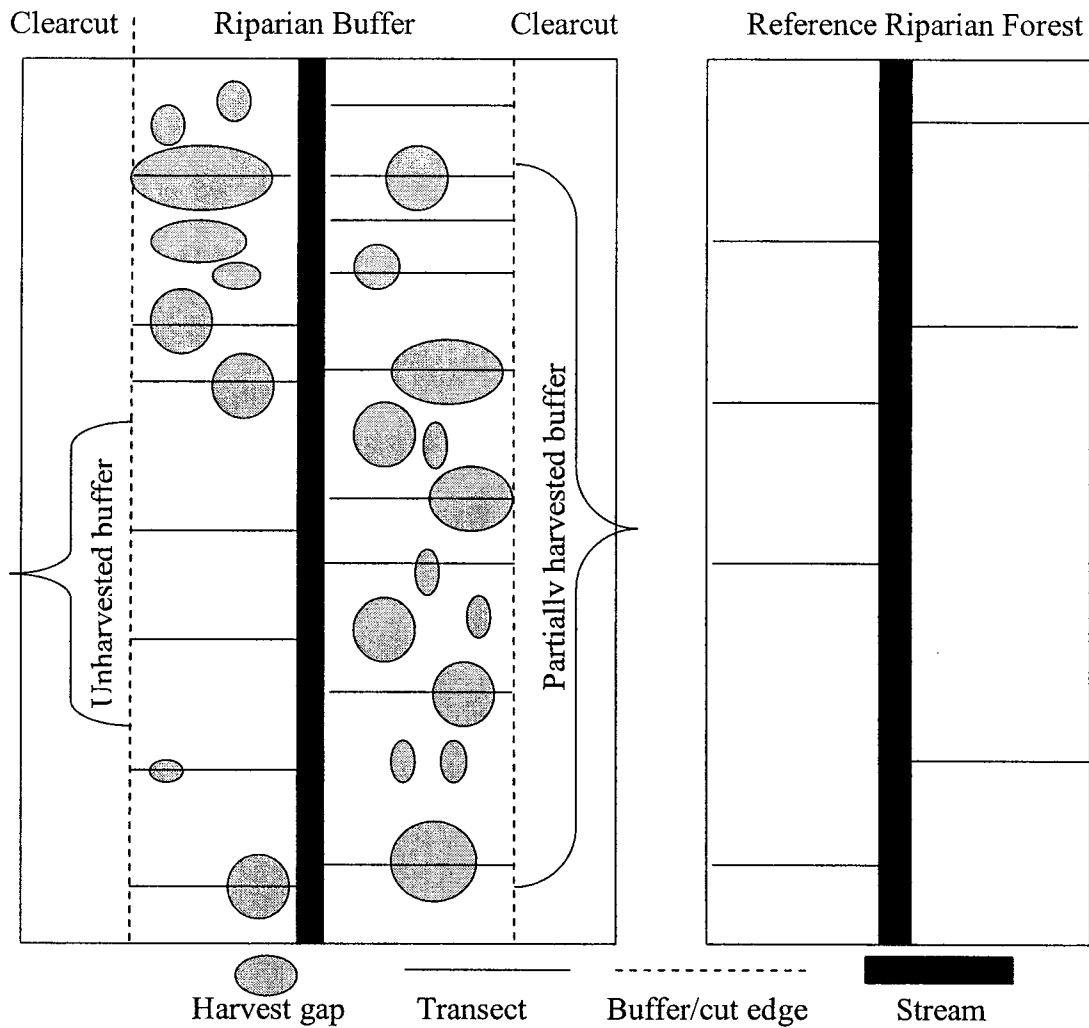
Figure 1.2. Sampling design illustrating the distribution of transects. Two watersheds were clearcut in the upland with partially harvested as well as unharvested riparian buffers. A third watershed had no record of recent disturbance and was used as reference riparian forest.

Ground surface temperature (using a digital humidity/temperature meter by VWR, model number: Q070757) and soil temperature (using a Fisher Scientific Traceable Thermometer, model number 15-0770961) were also recorded.

Understory response to gap size

In order to isolate the effect of gaps, quadrats located within harvest gaps were compared with quadrats located under closed canopy in partially harvested buffers, unharvested buffers,

and reference forest. To determine the role of gap size on understory community response the area of each harvest gap was measured and gaps were classified into three size classes: small (1-20 m^2), medium (21-99 m^2) and large (>100 m^2). Small gaps represent those smaller than those in some other studies on natural gaps (e.g., Dobrowolska and Veblen 2008). Medium gaps represent most of the natural gaps formed in boreal forests (McCarthy 2001). Large gaps represent those larger than most natural gaps. I studied 16, 30, and 12 small, medium, and large gaps respectively. Quadrats located within gaps were then compared among the three size classes.

Leaf morphological response to gap size

In order to infer leaf morphological adaptation to canopy gaps, leaves of four common species (*Cornus canadensis, Clintonia borealis, Vaccinium angustifolium,* and *Vaccinium myrtilloides*) were sampled from the 1 m^2 quadrat at the centre of each gap harvest gap in partially harvested buffers and compared with those sampled from quadrats located 5, 20, and 40 m from the stream along transects in unharvested buffers and reference forest. Ten randomly selected mature leaves were collected from *V. angustifolium, V. myrtilloides*, and *Cornus. canadensis*. Only five randomly selected leaves were collected from *Clintonia borealis* since the leaves were fewer and much larger than the other species. Specific leaf area and leaf dry matter content were compared between gaps and closed canopy quadrats, and among the gap size classes. Freshly collected leaves were pressed in the field to prevent damage in transport. Fresh leaves were weighed and repressed. Leaves were assumed to have reached constant mass after air drying at room temperature (25° C) for several months (Benfield 1996). After drying, leaves were again weighed and leaf area measurements were taken using WinFOLIA 2004a (Regent Instruments, Nepean, ON). Specific leaf area was determined as area (cm^2)/dry weight (g).

17

Leaf dry matter content was calculated as (dry weight/fresh weight) *100. Mean SLA and LDMC for each species per quadrat were used for analyses.

Data analyses

Understory species richness, abundance, Hill's diversity index, and Pielou's evenness index were calculated for each quadrat using percent cover data. From these data, average values were calculated for each transect. Richness was calculated as the total number of species present in each quadrat. Abundance was calculated as the sum of the cover values of all species in each quadrat. Hill's diversity index was used as an alpha diversity index due to its adequate sensitivity to both common and rare species (Jost 2006, 2007). All the plant species were placed into one of eight life-form groups: (tree seedlings/saplings; tall woody shrubs (potential to reach >1 m); low woody shrubs (not exceeding 1 m); herbaceous plants; graminoids (grass or sedge); pteridophytes (ferns and fern allies); bryophytes; and lichens. Richness, diversity, abundance, and evenness were calculated for each of the life-form groups and compared among harvest treatments.

Multivariate analyses of variance (MANOVA) with Duncan post-hoc tests were used to detect any significant difference in understory community response variables (richness, abundance, diversity, and evenness) among harvest treatments and gap sizes. The life-form groups were the multiple attributes in each MANOVA. Before analysis all variables were transformed using the natural logarithm in order to improve normality and homogeneity. Evenness of life-forms was tested with univariate analysis of variance (ANOVA) due to missing values that resulted from some life-forms not occurring together in all the plots.

Environmental variables were tested among treatments using MANOVA. Photosynthetically active radiation (PAR) was square-root transformed to improve normality and homogeneity. Kruskal-Wallis tests with Mann-Whitney post-hoc tests on individual attributes were used to confirm MANOVA results since canopy openness, relative humidity, air temperature, and ground surface temperature data did not meet homogeneity assumptions and PAR data could not be normalized with transformations.

Non-Metric Multidimensional Scaling (NMDS) (Clarke 1993), and multiple response permutation procedure (MRPP) (McCune and Grace 2002) were used to assess variation in understory species composition. Indicator species analysis was used to determine associations between species and treatments (gap sizes, unharvested buffers, and reference forests). Through indicator species analysis and indicator value (IV) is assigned to each species based on that species' relative abundance and frequency of occurrence in sites of a given group compared with sites of other treatment groups (Dufrene and Legendre 1997).

Specific leaf area (SLA) and leaf dry matter content (LDMC) were compared among treatments using one-way analyses of variance (ANOVA) and Tukey post hoc tests. The average LDMC and SLA was determined by combining the data of all four common understory species in each quadrat and compared among treatments. Regression models were fit to predict average leaf dry matter content and specific leaf area using the measured environmental variables. SPSS 16.0 (SPSS Inc. 2007) was used for analyses of variance and regressions. Non-metric multidimensional scaling, multiple response permutation procedures, and indicator species analyses were run using PC-Ord 5.10 (McCune and Mefford 2006).

Results

Understory community response along partially harvested and unharvested transects

The understory community of partially harvested buffers (with respect to species richness, abundance, diversity, and evenness) did not differ from unharvested buffers or reference forest (Table 1.2). Unharvested buffers had significantly lower richness than reference forest (MANOVA, $F_{2,68}=3.957$, p=0.024). Abundance, diversity, and evenness did not differ among treatments (MANOVA, $F_{2,68}=2.552$, p=0.085; $F_{2,68}=2.525$, p=0.088; $F_{2,68}=0.576$, p=0.565and respectively) (Fig. 1.4, A.1.1). Richness, abundance, diversity, and evenness of the life-form groups did not differ significantly among partially harvested buffers, unharvested buffers, and reference forest (Fig. 1.5, A. 1.2-1.5).

Understory species composition did not differ significantly among partially harvested buffers, unharvested buffers, and reference forest (MRPP, A=0.014, p=0.004) (A.1.6). Ordination of understory species data showed overlap of transects belonging to each treatment, and the heterogeneity of species within treatment groups was near that expected by chance. The ordination shows that rather than harvest treatment, canopy density and overstory species were the most important factors influencing understory species composition (Fig. 1.6). Much of the variation (46.5%) in species composition among sites was explained by Axis 2, which was negatively correlated with canopy density and positively correlated with overstory stem density of *Abies balsamea* and *Betula papyrifera*. Axis 1 explained 21.0 % of the variation in species composition among sites and was positively correlated with overstory stem density of *Populus tremuloides* and negatively correlated with relative humidity (Fig. 1.6, A. 1.7).
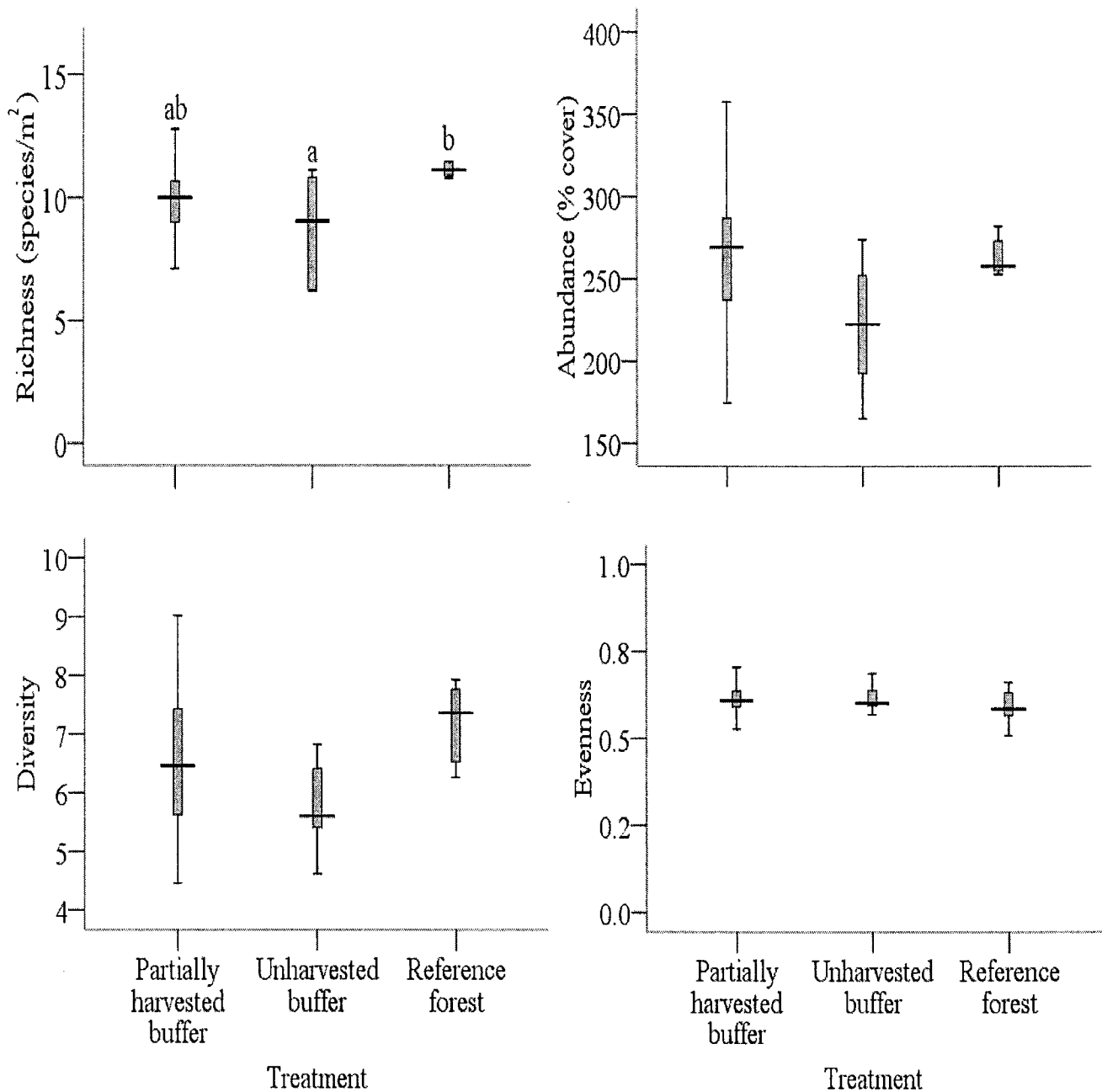
Figure 1.4. Transect means and standard errors of species richness, abundance, diversity, and evenness of understory plants in partially harvested buffers (n=58), unharvested buffers (n=6), and reference forest (n=7). Treatments sharing the same superscript, or no superscript, are not significantly different at the p=0.05 level. Abundance values exceeded 100% due to layering of understory plants.

Table 1.2. F statistics and p significance values for 3 MANOVAs (richness, abundance, and diversity) and 8 ANOVAs (evenness of each life-form) comparing partially harvested buffers (n=58), unharvested buffers (n=6), and reference forest (n=7). Life-form groups were the multiple attributes in each MANOVA.

	Richness		Abundance		Diversity		Evenness	
	$F_{(2,68)}$	p	$F_{(2,68)}$	p	$F_{(2,68)}$	p	$F_{(treatment,error)}$	p
Trees	0.070	0.932	0.587	0.559	0.012	0.989	$F_{(2,55)}$=0.620	0.542
Tall shrubs	1.194	0.309	1.917	0.155	0.573	0.566	$F_{(2,46)}$=0.759	0.474
Low shrubs	0.247	0.782	2.714	0.073	0.718	0.491	$F_{(2,68)}$=2.149	0.124
Herbs	1.887	0.159	1.012	0.369	1.112	0.335	$F_{(2,67)}$=0.612	0.545
Graminoids	2.750	0.071	1.092	0.341	1.494	0.232	$F_{(2,28)}$=0.696	0.507
Pteridophytes	1.137	0.327	1.723	0.186	0.498	0.610	$F_{(2,44)}$=0.956	0.392
Bryophytes	1.909	0.156	0.105	0.901	1.121	0.332	$F_{(2,67)}$=0.153	0.858
Lichens	0.605	0.549	0.218	0.805	0.076	0.927	$F_{(2,26)}$=1.222	0.311

Although overall understory composition did not significantly differ among treatments, many riparian species were significant indicators of reference forest, while riparian buffers (partially harvested and unharvested) had relatively few significant indicator species (Table 1.3).

Canopy openness and PAR were greater in partially harvested buffers than in both unharvested buffers and reference forest (MANOVA, $F_{2,55}$=25.002, p<0.001, and $F_{2,55}$=4.612, p=0.014 respectively). Unharvested buffers had greater canopy openness than reference forest. Relative humidity (RH) and temperature (air, surface, and soil) did not differ significantly among treatments (MANOVA, $F_{2,55}$=0.717, p=0.493, $F_{2,55}$=0.807, p=0.452, $F_{2,55}$=0.771, p=0.467, $F_{2,55}$=2.060, p=0.137 respectively) (Fig. 1.7, A.1.8).
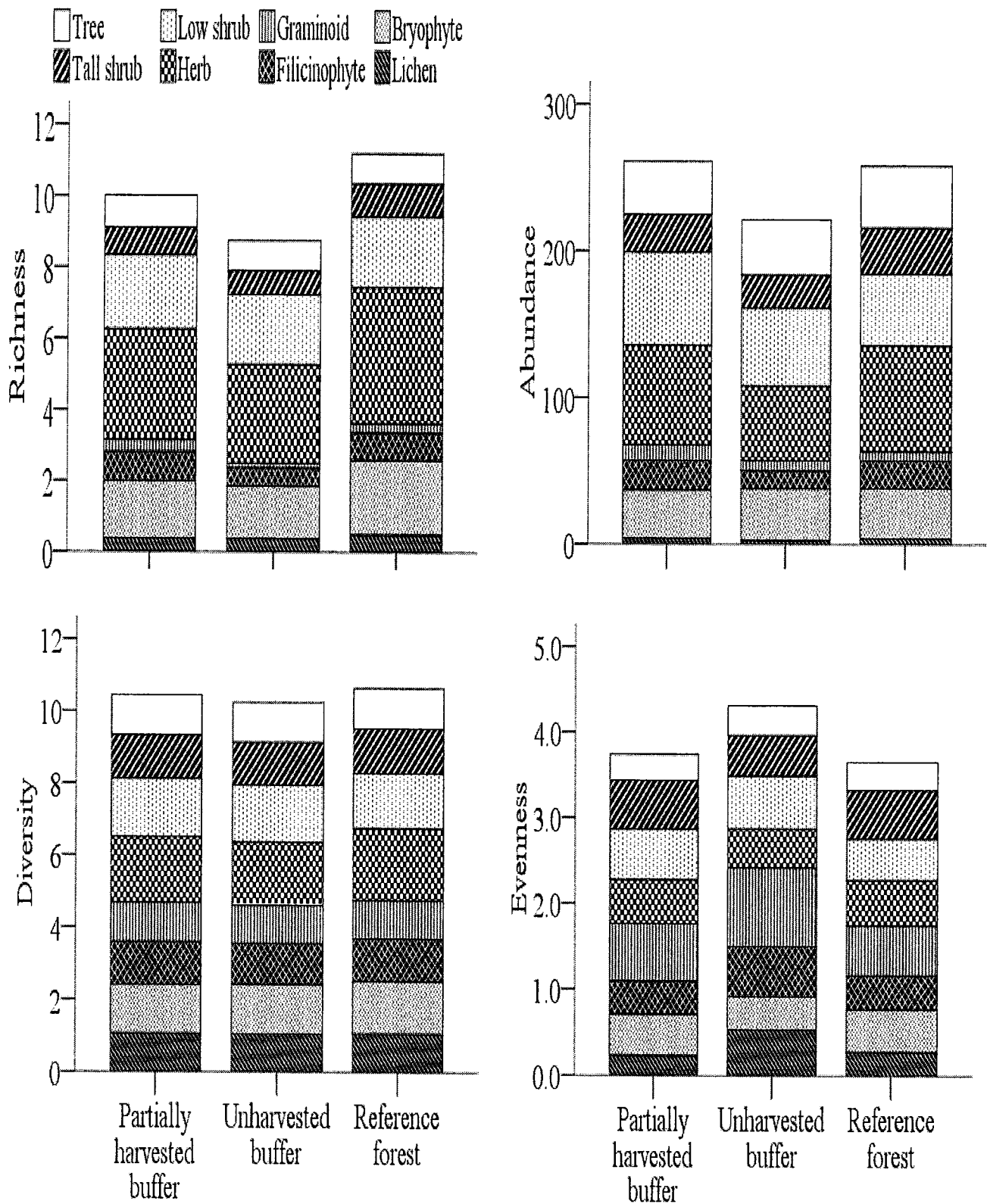
Figure 1.5. Transect mean of richness, abundance, diversity, and evenness of understory life-form groups did not significantly differ among partially harvested buffers (n=58), unharvested buffers (n=6), and reference forest (n=7).
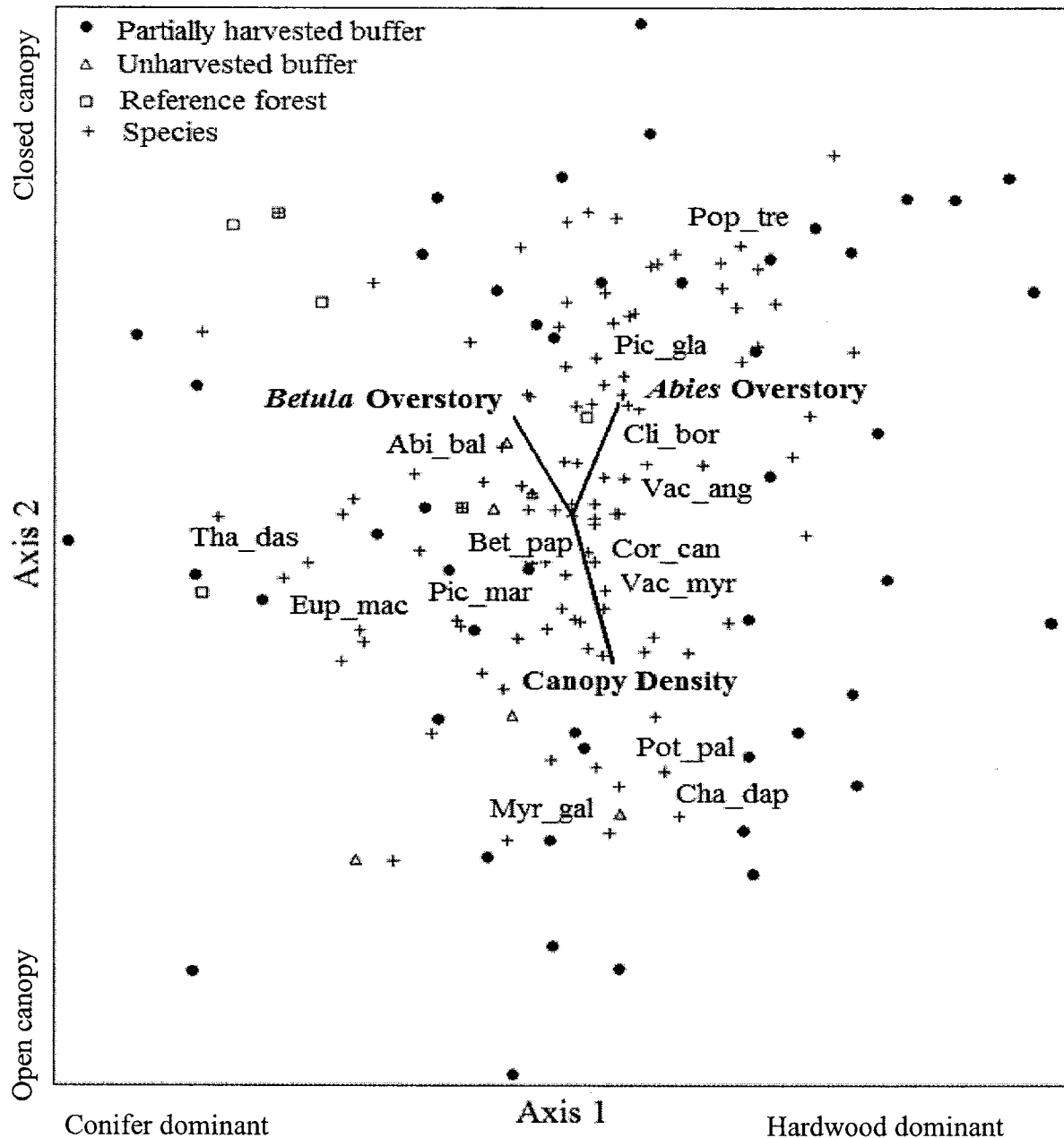
Figure 1.6. Non-metric multidimensional scaling ordination of understory species cover of partially harvested buffers (n=58), unharvested buffers (n=6), and reference forest (n=7) transects. The overlap of transects from different treatments indicates that they did not differ greatly in their understory composition. Canopy density, as well as overstory *Abies balsamea* and *Betula papyrifera* stem densities were more important in determining understory composition than harvest treatment.

Table 1.3. Indicator species of reference forest, unharvested buffers, and partially harvested buffers.

Indicator species	Indicator value	Significance *p≤0.05
Reference forest		
Gymnocarpium dryopteris	40.3	**0.005**
Gallium asperellum	35.7	**0.014**
Eupatorium maculatum	43.6	**0.014**
Lycopus uniflorus	47.9	**0.024**
Goodyera repens	37.4	**0.027**
Phegopteris connectilis	43.1	**0.027**
Thalictrum dasycarpum	43.5	**0.033**
Lycopodium lucidulum	49.5	0.056
Brachythecium spp.	49.3	0.069
Sorbus decora	42.8	0.114
Abies balsamea	41.5	0.193
Lycopodium dendroideum	40.6	0.096
Viola spp.	39.9	0.204
Cladonia spp.	37.8	0.471
Alnus incana	37.7	0.128
Rubus pubescens	35.3	0.177
Trientalis borealis	29.5	0.502
Picea glauca	28.1	0.141
Rubus idaeus	27.4	0.388

Table 1.3. Continued

Indicator species by treatment	Indicator value	Significance *p≤0.05
Unharvested buffer		
Pleurozium schreberi	56.7	**0.009**
Pteridium aquilinum	45.8	0.0528
Vaccinium myrtilloides	44.2	0.162
Picea mariana	43.5	0.130
Diervilla lonicera	42.8	0.242
Linnaea borealis	41.5	0.212
Amelanchier spp.	36.2	0.597
Maianthemum canadense	35.6	0.585
Chameaedaphne calyculata	34.7	0.151
Melampyrum lineare	29.7	0.176
Aralia nudicaulise	27.5	0.890
Partially harvested buffer		
Cornus canadensis	39.9	0.165
Vaccinium angustifolium	38.9	0.414
Clintonia borealis	37.8	0.604
Coptis trifolia	36.2	0.439
Epigea repens	36.1	0.275
Osmunda claytoniana	33.3	0.100
Athyrium felix-femina	31.8	0.231
Ledum groenlandicum	27.0	0.511
Betula papyrifera	26.4	0.685
Polytrichum juniperinum	26.3	0.176
Populus tremuloides	17.7	0.564
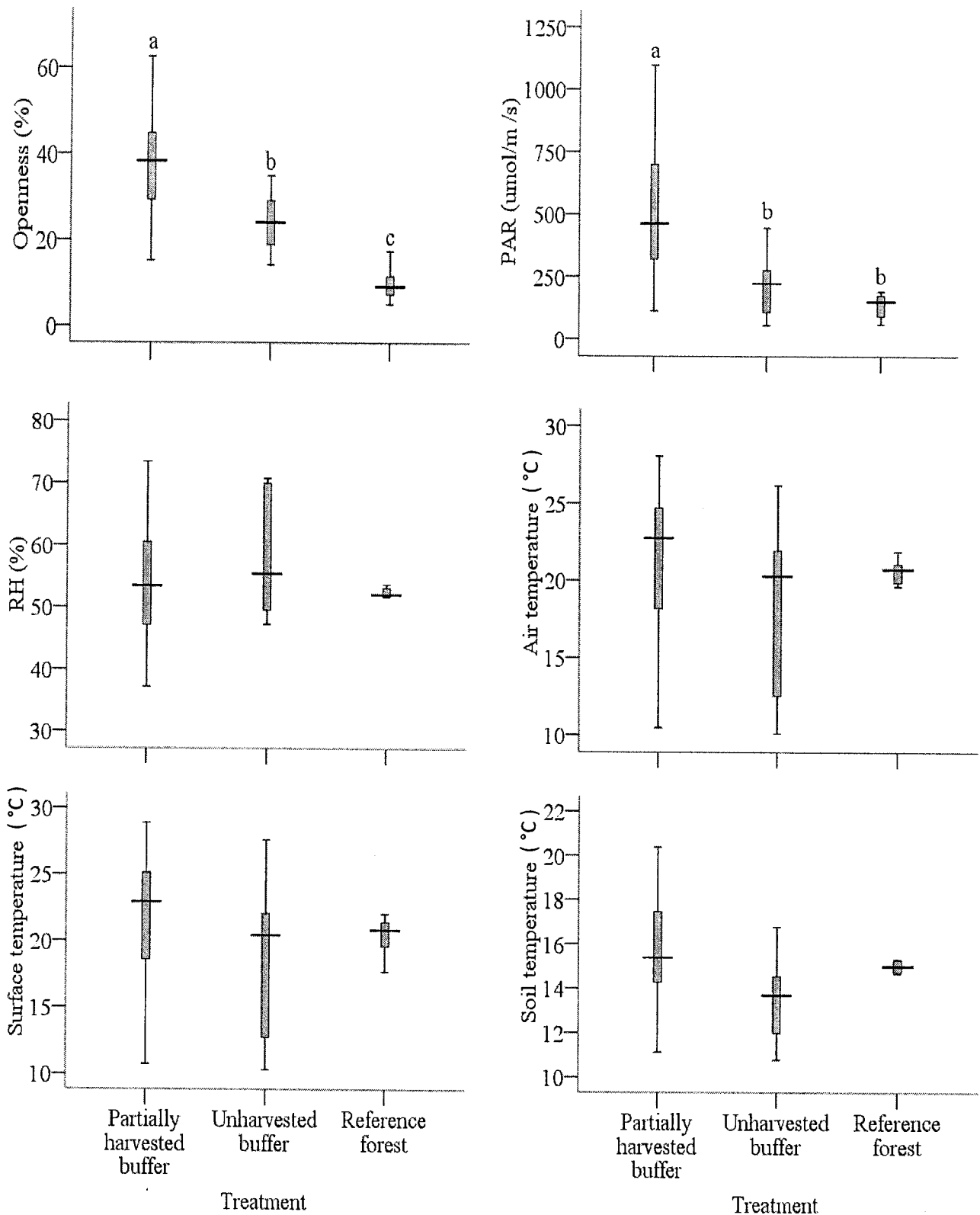
Figure 1.7. Transect means and standard errors of microclimate in partially harvested buffers (n=58), unharvested buffers (n=6), and reference forest (n=7). Treatments sharing the same superscript, or no superscript, are not significantly different at the p=0.05 level.

Understory community response in harvest gap and closed canopy quadrats

Large gaps and unharvested buffers had lower species richness than reference forests (MANOVA, $F_{5,488}$=3.770, p=0.002). Unharvested buffers also had lower diversity ($F_{5,488}$=3.012, p=0.011) than reference forest, and lower abundance (MANOVA, $F_{5,488}$=3.222, p=0.007) than all treatments with the exception of large gaps. Evenness did not differ among any of the treatments (MANOVA, $F_{5,488}$=1.240, p=0.289) (Fig. 1.8, A. 1.9).

Medium-sized gaps had significantly greater richness of low shrubs than small gaps. Small gaps had significantly greater richness of pteridophytes than large gaps and unharvested buffers. Closed canopy quadrats of partially harvested buffers had greater pteridophyte richness than unharvested buffers. Unharvested buffers had significantly lower richness of herbs and bryophytes than reference forest. Large gaps had lower richness of herbs than reference forest. The richness of trees, tall shrubs, graminoids, and lichens did not differ significantly among quadrats (Table 1.4, Fig. 1.9, A. 1.10).

Medium gaps had greater abundance of low shrubs than unharvested buffers and reference forest. Medium gaps also had greater abundance of bryophytes than unharvested buffers and closed canopy quadrats of partially harvested buffers. Large gaps had significantly lower abundance of pteridophytes than small gaps and closed canopy quadrats of partially harvested buffers. The abundance of trees, tall shrubs, herbs, graminoids, and lichens did not differ among quadrats (Table 1.4, Fig. 1.10, A.1.11).

Medium gaps had significantly greater diversity of low shrubs than unharvested buffers. Unharvested buffers also had lower diversity of pteridophytes and lichens than closed canopy quadrats of partially harvested buffers, and lower diversity of herbs than reference forest. Large

gaps had lower diversity of pteridophytes than the closed canopy quadrats of partially harvested buffers (Fig. 1.11, A. 1.12). None of the life-forms significantly differed among quadrats with respect to their evenness (Table 1.4, A. 1.13).
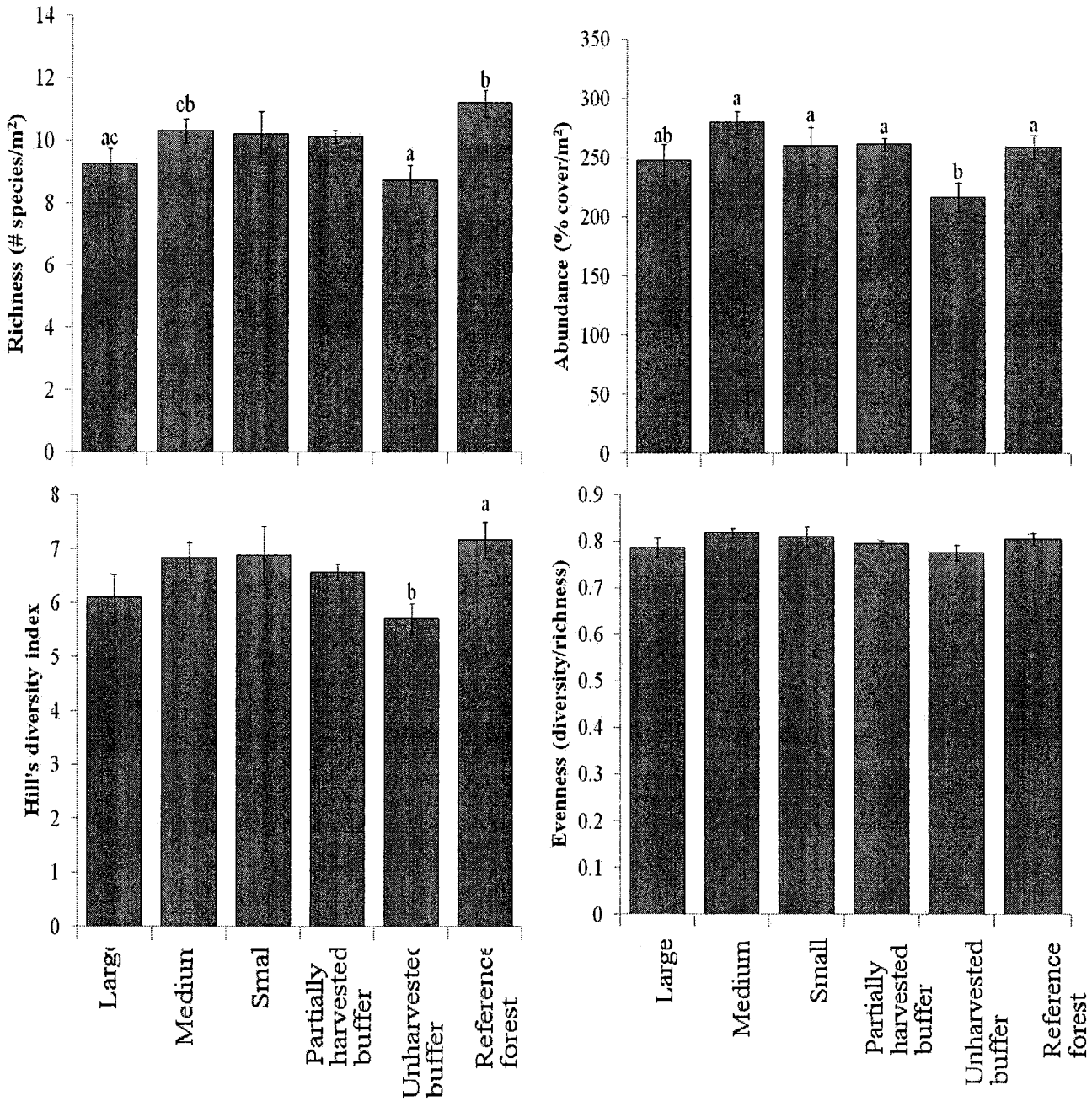
Figure 1.8. Mean and standard error (+/- 1) of understory species richness, abundance, diversity, and evenness in gaps (large n=32, medium n=59, and small n=24) and closed canopy quadrats in partially harvested buffers (n=257), unharvested buffers (n=58), and reference forest (n=66). Unlike superscripts indicate statistically significant differences, while no superscripts indicate lack of significant difference.

Figure 1.9. Mean richness/m^2 of life-forms in gaps (large n=32, medium n=59, and small n=24) and closed canopy quadrats in partially harvested buffers (n=257), unharvested buffers (n=58), and reference forest (n=66). Strata without labels or sharing the same labels (a,b, and c) within life-forms are not significantly different at the p=0.05 level.
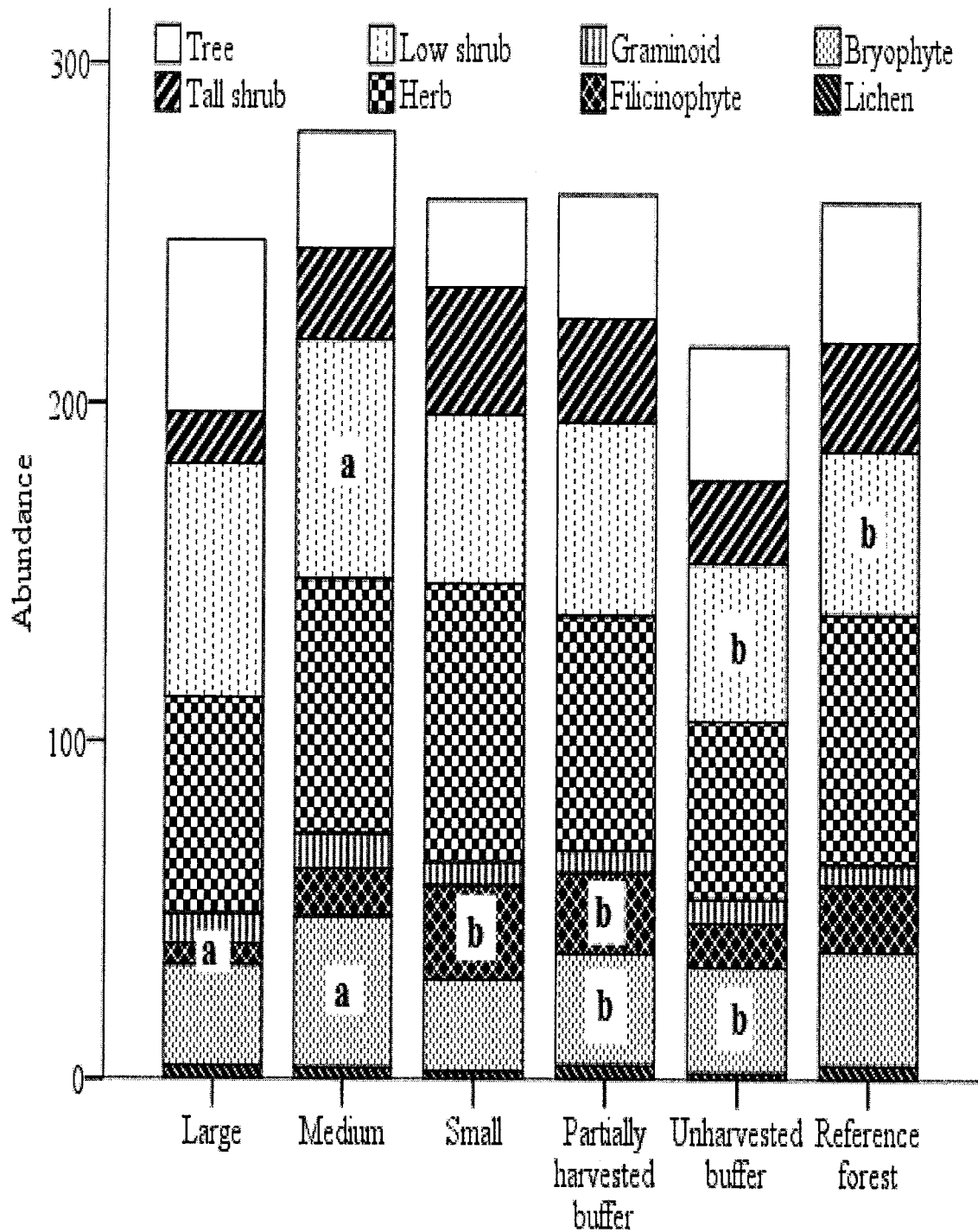
Figure 1.10. Mean abundance (percent cover/m^2) of life-forms in gaps (large n=32, medium n=59, and small n=24) and closed canopy quadrats in partially harvested buffers (n=257), unharvested buffers (n=58), and reference forest (n=66). Unlike labels (a and b) within a life-form stratum indicate statistically significant differences, while no labels or identical labels indicate a lack of significant difference at the p=0.05 level.
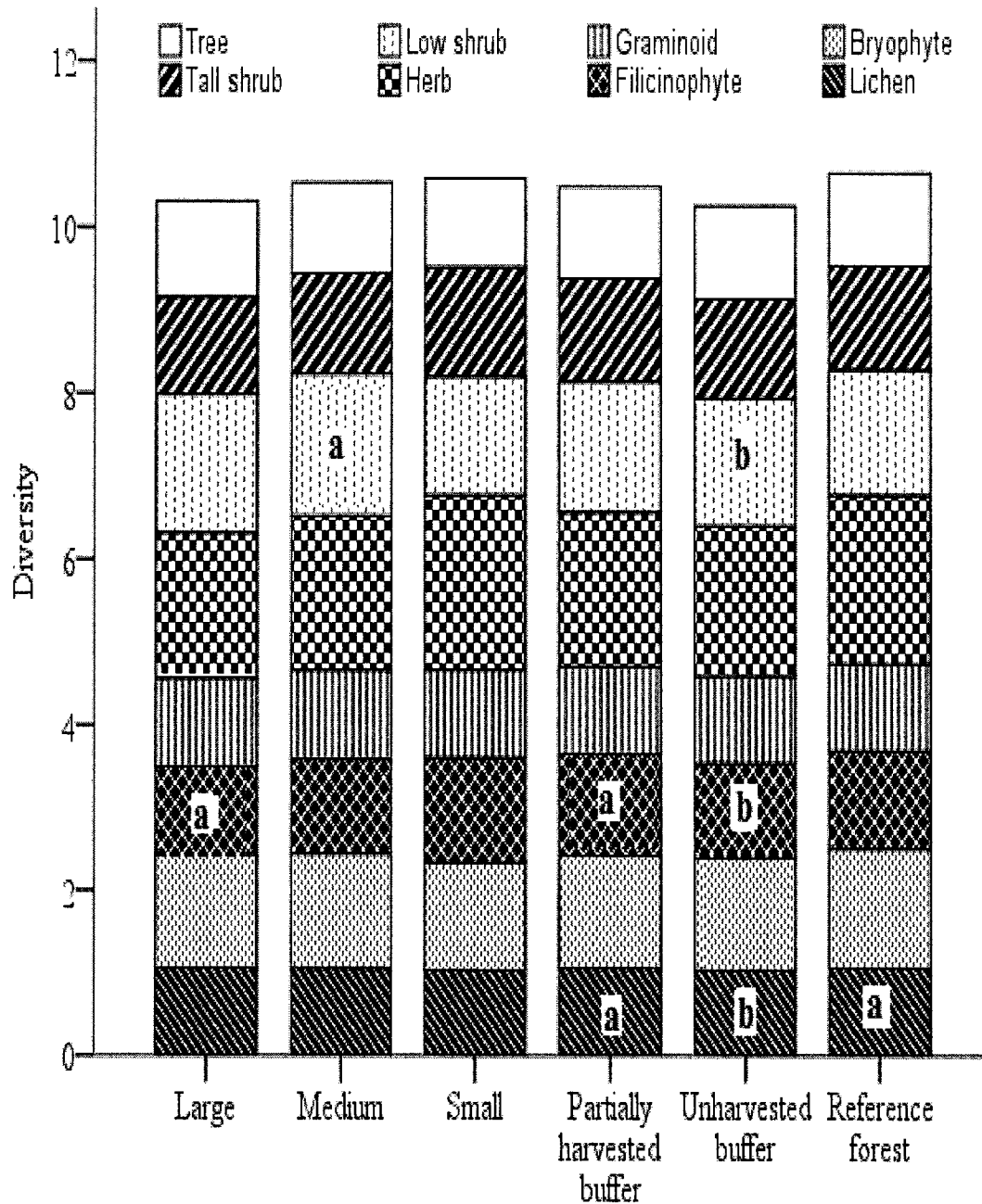
Figure 1.11. Mean diversity of life-forms in gaps (large n=32, medium n=59, and small n=24) and closed canopy quadrats in partially harvested buffers (n=257), unharvested buffers (n=58), and reference forest (n=66). Unlike labels (a and b) within a life-form stratum indicate statistically significant differences, while no labels or identical labels indicate a lack of significant difference at the p=0.05 level.

Table 1.4. F statistics and p significance values for richness, abundance, diversity and evenness MANOVAs of life-forms in gaps (large n=32, medium n=59, and small n=24) and closed canopy quadrats in partially harvested buffers (n=257), unharvested buffers (n=58), and reference forest (n=66).

	Richness		Abundance		Diversity		Evenness	
	$F_{(5,490)}$	p	$F_{(5,490)}$	p	$F_{(5,490)}$	p	$F_{(treatment, error)}$	p
Tree	1.028	0.400	1.363	0.237	1.093	0.364	$F_{(5,92)}=2.261$	0.055
Tall shrub	1.699	0.133	1.821	0.107	2.088	0.066	$F_{(5,92)}=1.963$	0.092
Low shrub	2.926	**0.013**	3.970	**0.002**	3.254	**0.007**	$F_{(5,316)}=1.691$	0.136
Herb	3.568	**0.004**	2.226	0.051	2.468	**0.032**	$F_{(5,411)}=1.196$	0.310
Graminoid	1.439	0.209	0.798	0.551	1.200	0.308	$F_{(5,15)}=2.463$	0.081
Pteridophyte	4.300	**0.001**	4.300	**0.001**	4.621	**<0.001**	$F_{(5,90)}=1.070$	0.382
Bryophyte	2.508	**0.029**	2.337	**0.041**	1.267	0.277	$F_{(5,249)}=0.470$	0.798
Lichen	1.067	0.378	0.917	0.470	2.298	**0.044**	$F_{(5,17)}=1.274$	0.320

Canopy density was significantly higher in reference forest than all other treatments, and lower in large and medium gaps than all other treatments. Small gaps and closed canopy quadrats of partially harvested buffers had significantly lower canopy density than unharvested buffers and reference forest, but significantly higher than large and medium gaps (MANOVA, $F_{5,362}=55.629$, $p<0.001$). Photosynthetically active radiation (PAR) was significantly higher in all gaps than in unharvested buffers and reference forest. Closed canopy quadrats of partially harvested buffers

also had significantly higher PAR than unharvested buffers and reference forest, but lower than large and medium gaps (MANOVA, $F_{5,362}=17.685$, $p<0.001$). Relative humidity (RH) was significantly lower in large gaps than small gaps, closed canopy quadrats of partially harvested buffers, and unharvested buffers. Small gaps and unharvested buffers had significantly higher relative humidity than reference forest, and unharvested buffers also had significantly higher relative humidity than medium gaps (MANOVA, $F_{5,362}=4.224$, $p=0.001$) (Fig. 1.12). Air temperature and ground surface temperature were significantly higher in large gaps than small gaps, unharvested buffers, and reference forest (MANOVA, $F_{5,362}=5.555$, $p<0.001$, and $F_{5,362}=5.792$, $p<0.001$ respectively). Air temperature was significantly lower in unharvested buffers than gaps and closed canopy of partially harvested buffers. Soil temperature was significantly higher in large gaps than all treatments except medium gaps; and significantly lower in unharvested buffers than all treatments (MANOVA, $F_{5,362}=8.437$, $p<0.001$) (Fig.1.13, A.1.14).

Plasticity of leaf morphology

Specific leaf area of *Cornus canadensis* (ANOVA, $F_{4,70}=13.209$, $p<0.001$) and *Vaccinium angustifolium* was greater in unharvested buffers and reference forest than all gaps (ANOVA, $F_{4,49}=25.803$, $p<0.001$). Specific leaf area of *Vaccinium myrtilloides* was greater in reference forest than all gaps, and greater in unharvested buffers than in medium and large gaps (ANOVA, $F_{4,38}=13.495$, $p<0.001$). Specific leaf area of *Clintonia borealis* was only significantly lower in medium gaps than in unharvested buffers and reference forest (ANOVA, $F_{4,52}=4.955$, $p=0.002$) (Fig. 1.14, A.1.15).
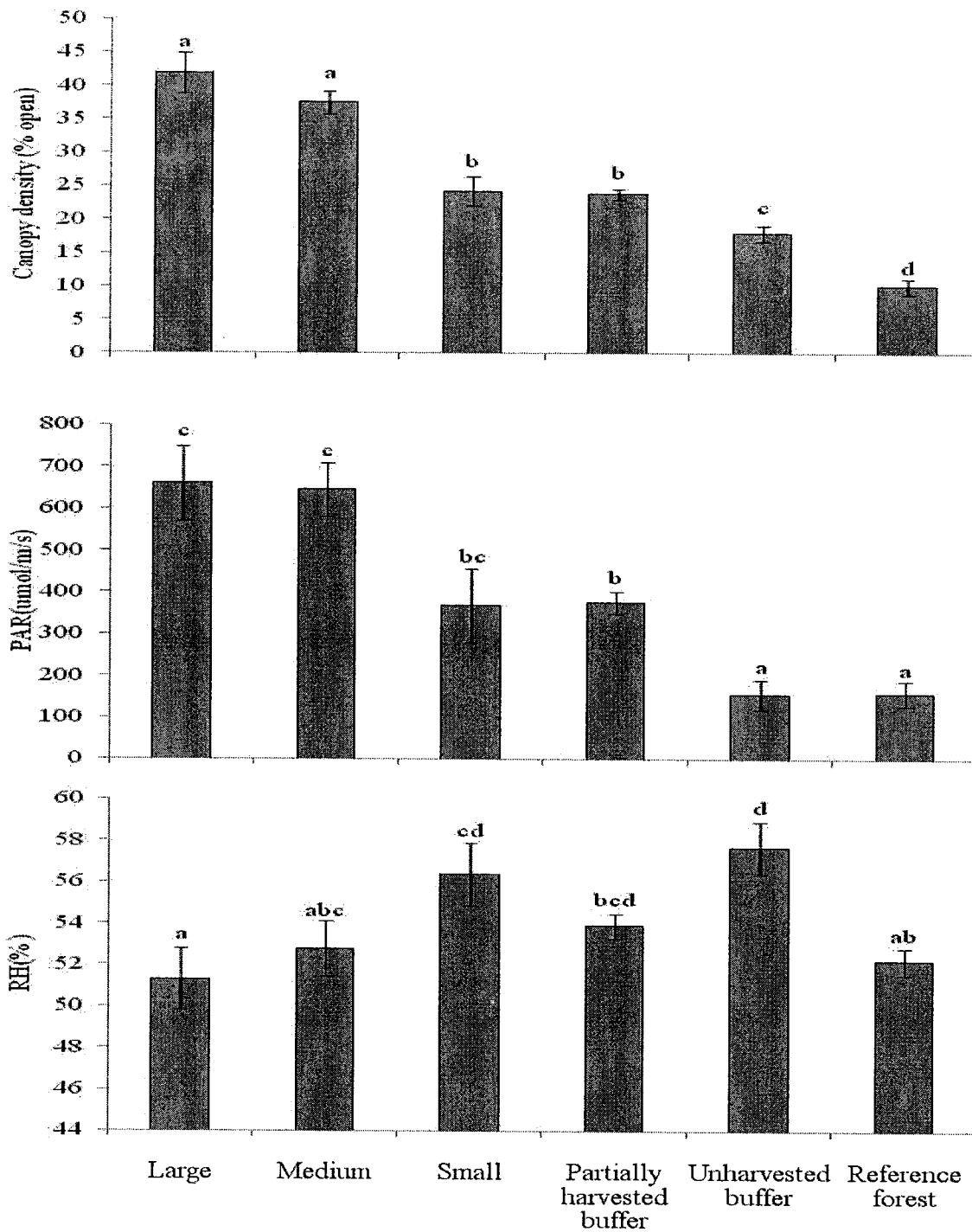
Figure 1.12. Mean and standard error of microclimate in gaps (large n=32, medium n=59, and small n=24) and closed canopy quadrats in partially harvested buffers (n=257), unharvested buffers (n=58), and reference forest (n=66). Groups sharing the same superscript are not significantly different at the p=0.05 level.
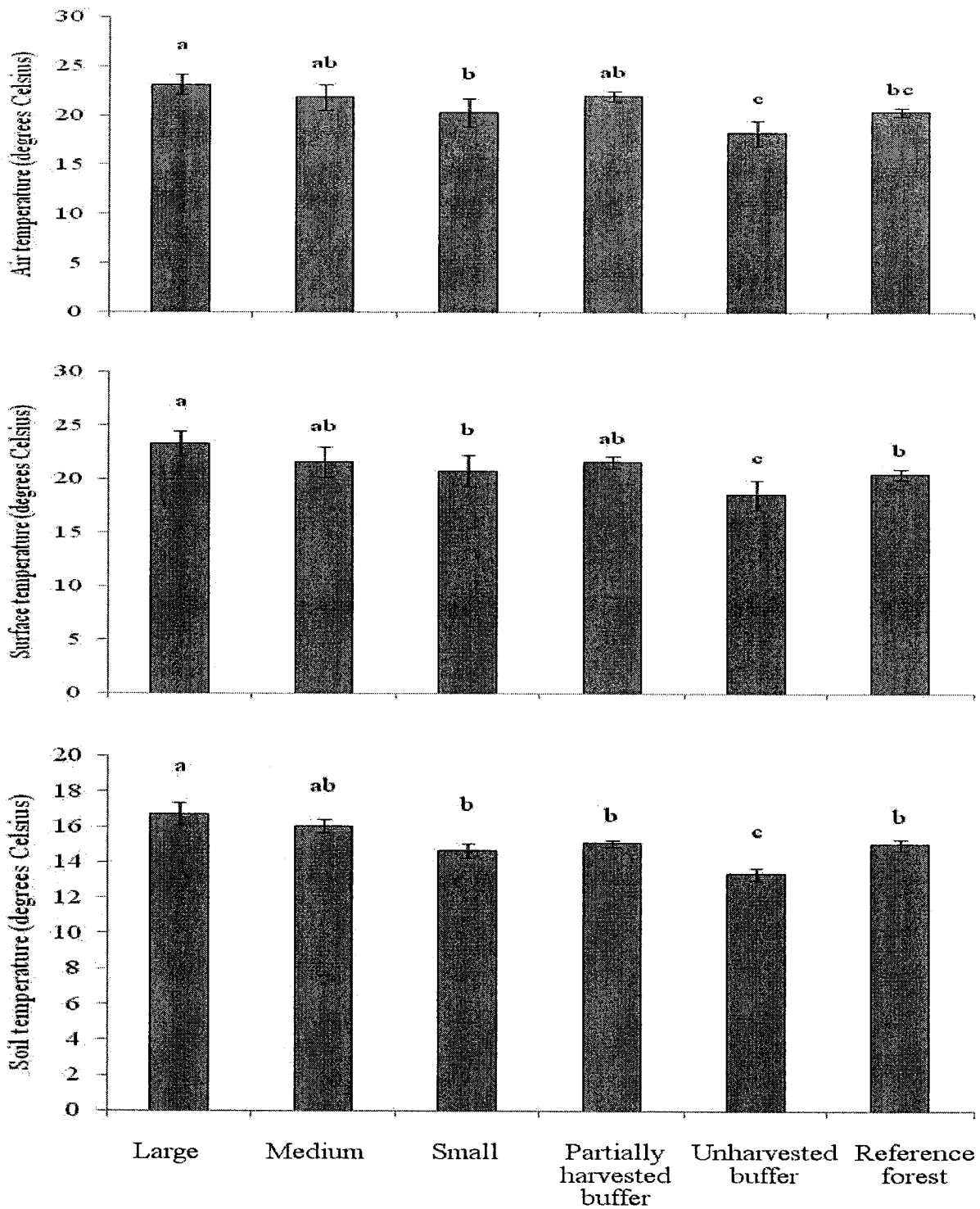
Figure 1.12. Mean and standard error of microclimate in gaps (large n=32, medium n=59, and small n=24) and closed canopy quadrats in partially harvested buffers (n=257), unharvested buffers (n=58), and reference forest (n=66). Groups sharing the same superscript are not significantly different at the p=0.05 level.

Leaf dry matter content of *Clintonia borealis* was greater in medium gaps than in small
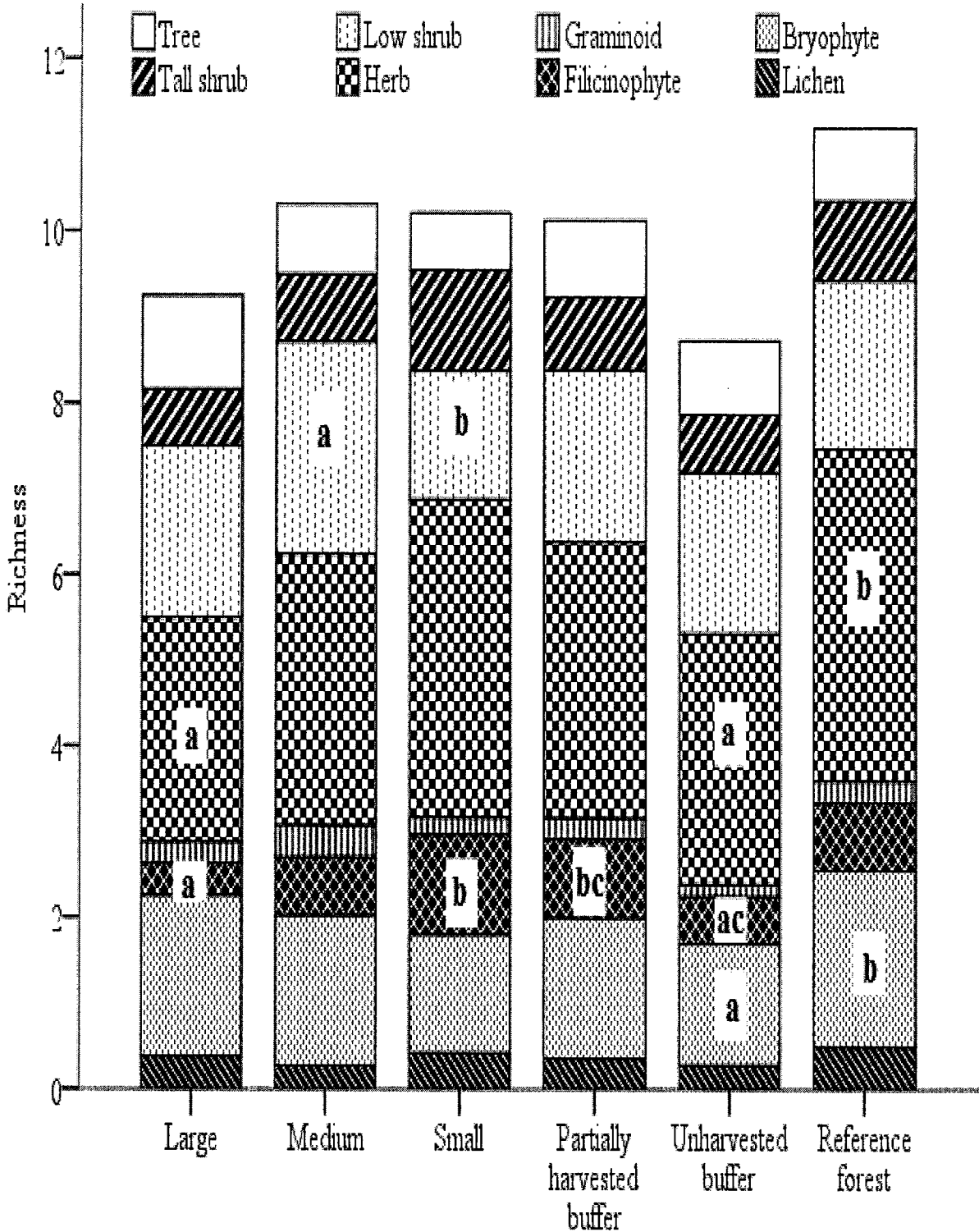
gaps, unharvested buffers and reference forest (ANOVA, $F_{4,52}=5.889$, $p=0.001$). Leaf dry matter

content of *Cornus canadensis* (ANOVA, $F_{4,69}=4.147$, $p=0.005$), *V. angustifolium* (ANOVA,

$F_{4,46}=20.251$, $p<0.001$), and *V. myrtilloides* (ANOVA, $F_{4,36}=30.422$, $p<0.001$) was greater in all

gaps than in unharvested buffers and reference forest (Fig. 1.15, A.1.16).

Average specific leaf area was negatively correlated with gap size (regression, $r^2=0.186$,

$p=0.002$), and average leaf dry matter content was positively correlated with gap size(regression,

$r^2=0.232$, $p<0.001$) (Figs. 1.16 and 1.17 respectively) (A1.17).
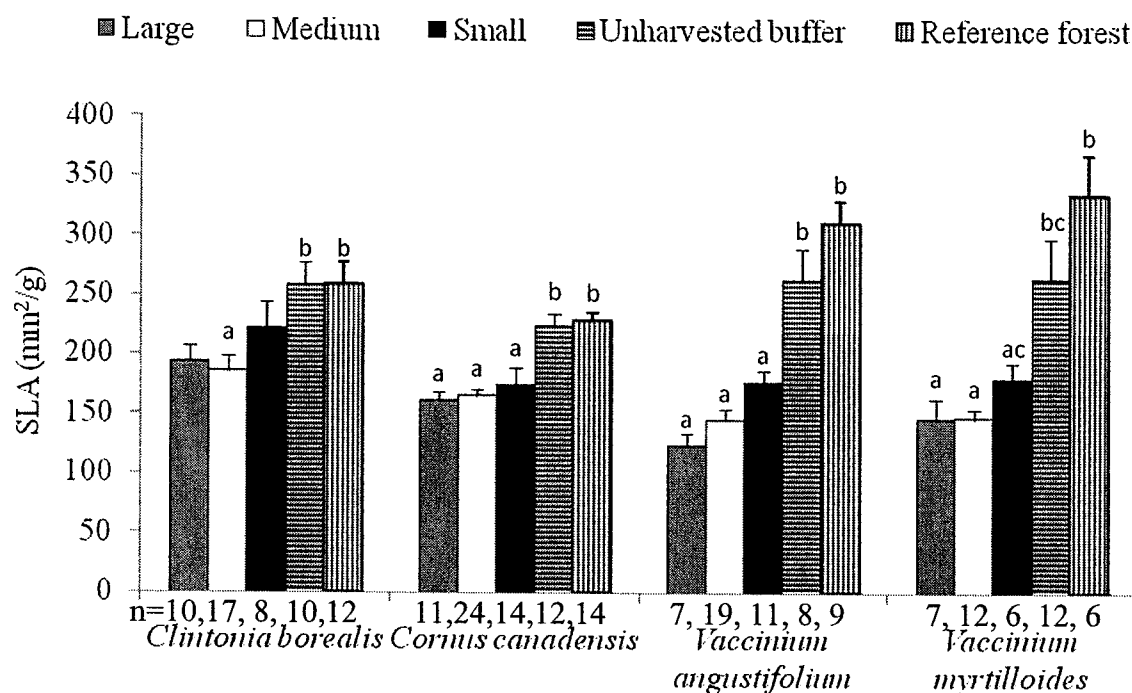
Figure 1.14. Mean specific leaf area and standard error of four common understory species
found in large, medium, and small gaps, and in unharvested buffers and reference forest.
Columns within a species sharing the same superscript, or without any superscript, are not
significantly different at the $p=0.05$ level.
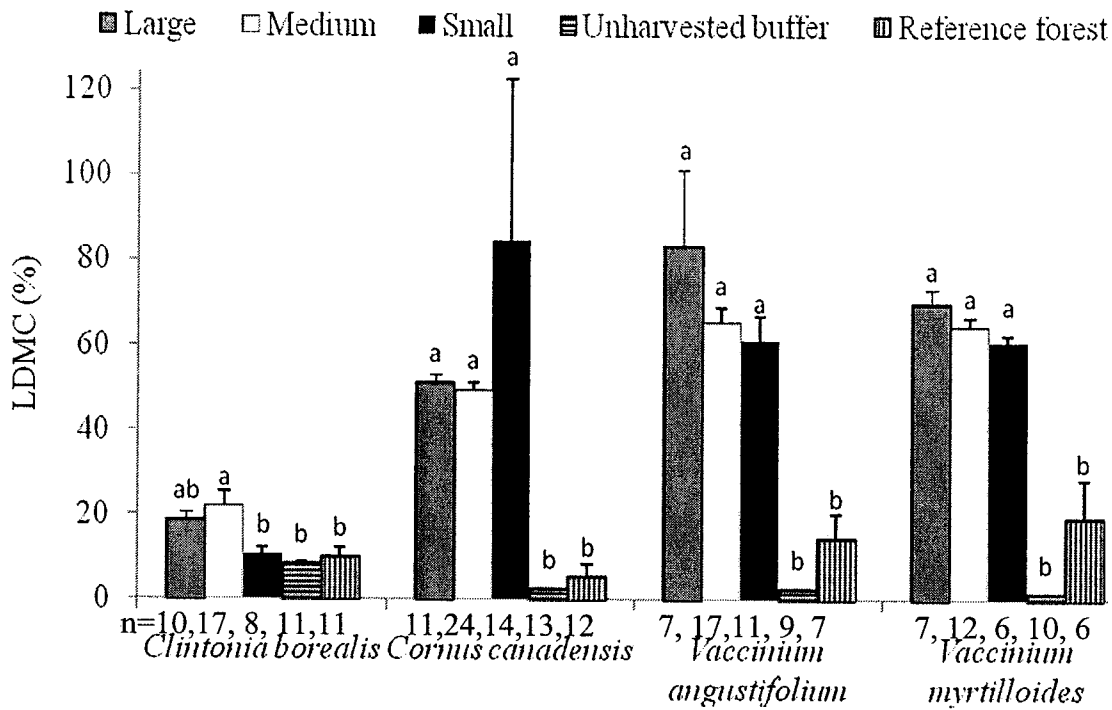
Figure 1.15. Mean leaf dry matter content and standard error for four common understory species found in large, medium, and small gaps, and in unharvested buffers and reference forest. Columns within a species sharing the same superscript, or without any superscript, are not significantly different at the p=0.05 level.
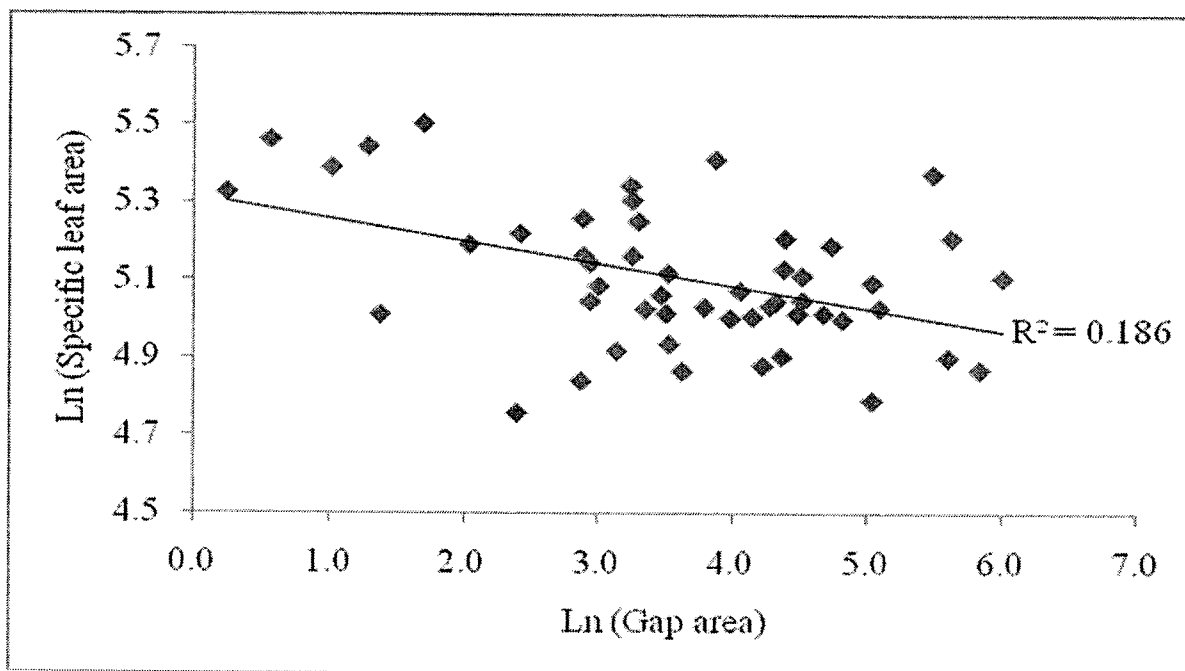
Figure 1.16. Average specific leaf area of four common understory plants was negatively correlated with gap area on a logarithmic scale (r^2=0.186, p=0.002).
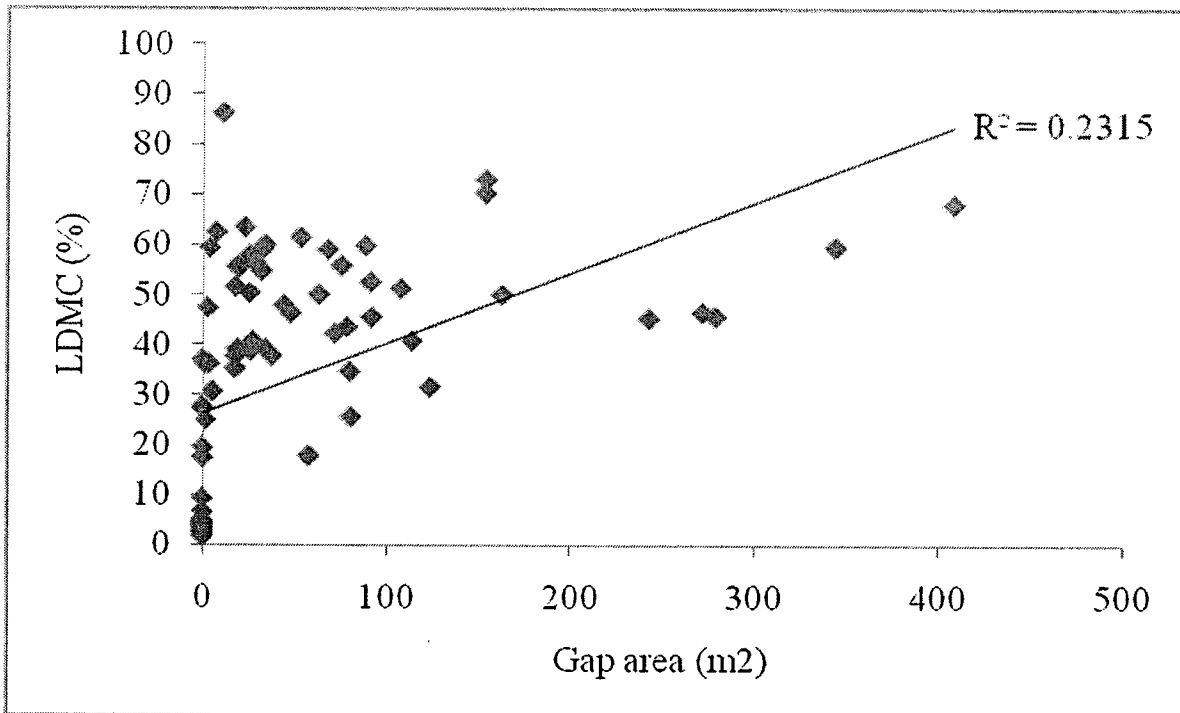
Figure 1.17. Average leaf dry matter content of four common understory species was positively correlated with gap area (r^2=0.232, p<0.001).

Discussion

Partially harvested buffers were not significantly different from unharvested buffers or

undisturbed riparian forests with respect to understory species composition, richness, abundance,

diversity, or evenness. However, unharvested buffers were lower in species richness, abundance,

and diversity than reference forest and partially harvested buffers. This may suggest that the

creation of gaps by partial harvesting in riparian buffers can increase their heterogeneity;

however it is more likely a function of the selection of sites for partial harvesting. Although sites

were selected to minimize among-site variability, most of the sections of riparian buffers that

were left unharvested were due to machine inaccessibility. Rocky outcrops and steeper slopes in those areas may explain lower richness, abundance, and diversity in unharvested buffers.

None of the life-form groups (trees, tall shrubs, low shrubs, herbs, graminoids, pteridophytes, bryophytes, and lichens) showed any significant difference in richness, abundance, diversity, and evenness among unharvested buffers, reference forest, and partially harvested buffers. The results suggest that the creation of harvest gaps (1-400 m^2) within riparian buffers does not significantly impact understory plant communities in the surrounding closed canopy. It is important to note, however, that many riparian species were significant indicators of reference forests, while buffers did not have many significant indicator species. This may raise concerns that important species could be lost even with the retention of a riparian buffer, and should be a special focus of future studies. However, since all reference transects were located in a separate watershed than partially harvested and unharvested buffers it is possible that indicator species were exhibiting partiality to the location rather than the treatment.

With the exception of lower richness in large gaps, overall species richness, abundance, diversity, and evenness did not significantly differ among gaps of varying size and the closed canopy of partially harvested buffers and reference forest. However, a few significant differences were noted for specific life-form groups. Large gaps had significantly lower herb and pteridophyte richness than reference forest. Medium gaps had the highest richness, abundance, and diversity of low shrubs. Small gaps had the lowest richness of low shrubs, but the highest richness of pteridophytes. Small gaps had significantly greater richness of pteridophytes than unharvested buffers. Small gaps and the closed canopy of partially harvested buffers containing small gaps also had significantly greater abundance of pteridophytes than large gaps. Higher richness and abundance of pteridophytes in small gaps compared with larger

40

gaps suggests that gaps greater than 20 m^2 may provide sub-optimal habitat for pteridophytes due to increased exposure, and potential moisture loss. Bryophyte abundance was highest in medium gaps; this may be explained by the favourable microclimate achieved in medium gaps. Medium gaps received significantly higher light than closed canopy quadrats, but had higher canopy density, therefore potentially lower moisture loss and temperature fluctuations than large gaps.

With the exception of canopy density, gaps did not significantly differ in microclimate. The lack of compositional differences among gaps can be explained by the maintenance of microclimate in gaps within the tolerance range of the gap inhabiting species. Gaps could cause community changes due to altered microclimate when they are large. Schumann *et al.* (2003) showed a correlation between gap size and species abundance and diversity; however the gaps they surveyed were mostly larger than those analysed here (36-3393 m^2). Fahey and Puettmann (2008) found that gaps as large as 0.4 ha in Douglas Fir (*Psuedotsuga menziesii*) forests did not have any significant influence on understory plants, however those gaps would have been more sheltered by tall perimeter trees than those in boreal forests. Average canopy height at my sites was 12 m. If gaps are not large enough to introduce competitive early successional species, then it is not likely that any change of understory species composition should occur due to gap formation (Grushecky and Fajvan 1999; Fahey and Puettmann 2008). It is possible that the gaps created by partial harvesting did not alter microclimate enough to affect understory species.

The boreal forest is adapted to large scale disturbances such as fire and insect defoliation. These disturbances result in a mosaic of open and closed canopies and result in heterogeneity of the landscape which is reflected in high species richness, with a mix of early and late successional species (de Grandpre and Bergeron 1997). The lack of compositional change between partially harvested buffers with gaps of varying size and the closed canopy of

unharvested buffers and reference riparian forest support the hypothesis that boreal understory communities have resilience to fine scale canopy disturbance. Though insufficient time since disturbance might explain the lack of compositional differences, another possibility is that the adaptation of boreal species to stand replacing disturbance makes them resistant to fine scale disturbances, such as small harvest gaps. The morphological plasticity of common understory species may allow them to maintain abundance in the face of disturbance by adapting to the altered environment in gaps.

The alteration in microclimate did not result in significant community differences among gaps of varying size, however it was great enough to affect leaf morphology of individual plants growing in the centre of gaps. In boreal forests at northern latitudes, the highest light levels are expected to occur in the centre of large gaps, and slightly north of the centre in smaller gaps (Gendreau-Berthiaume and Kneeshaw, In Press). Specific leaf area (SLA) of all four species was higher in unharvested buffers and reference forest than in gaps. SLA is an indication of photosynthetic efficiency of plants (Hunt 1982). Higher SLA in shade indicates the leaves were thin with large surface areas to maximize light capture (Moola and Mallik 1998). Leaf dry matter content was higher in gaps than under closed canopy. Leaf dry matter content is a good predictor of a plant's resource capture and usage strategy; it is related to the structural support of the leaf, and herbivory defense (Wilson *et al.* 1999). The increase of leaf dry matter content in gaps could have an impact on litter quality since it reflects the amount of lignin and fibre in the leaves, and thus their decomposability (Fortunel *et al.* 2009).

The observed plasticity of specific leaf area and leaf dry matter content between gaps and closed canopies suggest that the four common understory species studied responded to canopy gap formation by altering their leaf morphology. Plasticity allows shade tolerant species to

survive under low light, and respond with greater reproductive efforts under more favourable conditions (Vander Kloet and Hall 1981; Chazdon 1985, Messier 1992, Messier and Puttonen 1995). By adjusting leaf morphology, *Clintonia borealis, Cornus canadensis, Vaccinium angustifolium*, and *V. myrtilloides* could maintain abundance in gaps at levels similar to those in unharvested forests. The lack of compositional change, coupled with the leaf morphological differences observed among gaps and unharvested forests support the hypothesis that common boreal understory plants may be able to adapt to canopy gap creation, through plasticity of leaf morphological traits. The results of this study suggest that understory plants in this region may show resilience to smaller-scale disturbances such as gap creation. Historically, boreal forests have been shaped by large stand replacing disturbance such as wildfire, and the resilience to gap creation observed in this study suggests that understory plants in this region are adapted to the historic disturbance regime.

Chapter 2

Tree regeneration in harvest gaps created by partial harvesting

Abstract

Natural disturbance pattern emulation continues to be an objective of boreal forest management. Consistent with that objective, partial harvesting in riparian buffers may become a viable option for sustainable silviculture. Prior to implementing partial harvesting in riparian buffers as a best management practice, the ecological impacts of such practice must be evaluated. I investigated the effect of partial harvesting on regeneration of canopy species (*Abies balsamea, Betula papyrifera, Picea glauca, Picea mariana,* and *Populus tremuloides*) by testing the hypothesis that growth of tree seedlings/saplings would be enhanced in gaps, and that stem density of shade intolerant hardwoods would increase with gap size. I surveyed gaps in mixedwood riparian areas near White River, in north western Ontario. The gaps were created by partial harvesting three years prior to this study. The gaps ranged in size from 1.3 to 408 m² in forests averaging 12 m in height. I surveyed stem density, basal diameter, and height of tree seedlings and saplings in 58 gaps. Regeneration under closed canopy in unharvested stands was characterized in 1 m² quadrats positioned every 5 m along 40 m riparian transects. Tree seedling and sapling regeneration was compared among gap size classes (small: 1-20 m², medium: 21-99 m², and large: >100m²), and contrasted with regeneration under closed canopy in unharvested buffers and undisturbed reference forests. Multiple regression and Spearman correlations were used to determine associations between tree regeneration and stand characteristics (gap size, microclimate, and overstory composition). Conifer seedlings and saplings had higher stem density under closed canopy, but were larger (greater height and basal diameter) in gaps, supporting the hypothesis of enhanced growth in gaps. As predicted, *Populus tremuloides* density and size was positively correlated with increasing gap area and overstory stem density of conspecifics. As a result, higher intensity overstory removal in larger gaps increased the proportion of hardwood to conifer regeneration. These results suggest that gaps created by partial harvesting can be used to stimulate tree regeneration of early successional species such as *Populus tremuloides*; and that stem density of conifers will decrease in gaps, likely due to competition from *Populus tremuloides* and other light demanding species.

Introduction

Canopy gaps are important in determining forest structure, particularly in the absence of stand replacing disturbance (McCarthy 2001; Dobrowolska and Veblen 2008). Senescence or disturbances such as wind and insect defoliation result in a range of gaps from the death of single to many trees. This frees up growing space for seedlings or suppressed trees to be recruited into the forest canopy. Small-scale canopy disturbances only affect a few trees at a time. Those disturbances often result in uneven-aged stand structure and greater species diversity (Forcier 1975; Runkle 1982; Lertzman 1992; Grushecky and Fajvan 1999; Woods 2000). Despite their ubiquity and acknowledged relevance in stand perpetuation, relatively little is known about the dynamics of tree regeneration in small canopy gaps in the boreal forest (Schumann et al. 2003). Even less is known about the impacts of small canopy gaps created by partial harvesting in riparian buffers.

Most gaps in the boreal forest are less than 100 m² (McCarthy 2001). This small-scale canopy gap disturbance has received relatively little research attention until recently (Runkle 1990; Kneeshaw and Bergeron 1996; McCarthy 2001; Pham et al. 2004; Fraver and White 2005). In the last decade research on natural gap dynamics in the boreal forest has mostly focused on large scale canopy disturbances such as insect defoliation and wind (Pham et al. 2004; de Romer et al. 2007). Tree regeneration in gaps less than 20 m² in area has received little attention (e.g., Dobrowolska and Veblen 2008). Most studies were conducted retrospectively with initial regeneration response inferred many years later (Kneeshaw and Bergeron 1998; Noguchi and Yoshida 2007). More research is needed to examine how overstory tree mortality resulting in small gaps affects the establishment and growth of canopy trees, and how understory

species respond to canopy openings (Coates and Burton 1997; Archambault *et al.* 1998; Felton *et al.* 2006).

In order to preserve natural forest structure and processes the Government of Ontario has suggested that forest harvesting should emulate natural disturbance patterns. It has been suggested that partial harvesting with maintenance of understory vegetation may emulate fire better than clearcut harvesting leaving a conventional riparian buffer (OMNR 2001). However, the response of understory vegetation to small gaps created by partial harvesting in riparian forests remains undocumented. The unique microclimate and suite of species in riparian areas may cause recruitment patterns to differ from those in upland areas. Riparian areas have been described as the most productive part of a forest. The riparian zone is characterized by high soil moisture and soil nutrients which help enhance regeneration of tree species. However, greater growth of tall shrubs and hardwood species in riparian areas may inhibit conifer regeneration due to competition (Minore and Weatherly 1994).

Gaps created by partial harvesting in riparian areas change several biophysical properties that influence regeneration. The increase in light reaching the forest floor after canopy removal is a strong factor, accelerating the growth of many species (Seng *et al.* 2004). Increased light stimulates the growth of tree seedlings, advance regeneration of trees, and other light demanding species (Denslow 1987; Canham *et al.* 1990; Gilbert *et al.* 2001). Advance regeneration mediated by vegetative growth responds differently to gap creation than seedlings (Stewart *et al.* 1991). Trees that grow as advance regeneration are suppressed under a closed canopy but are able to capitalize on increased light and grow to fill the canopy gap (Felton *et al.* 2006). Therefore, this mode of regeneration can often inhibit the growth of competing species (Dobrowolska and Veblen 2008). The physiological and morphological plasticity of shade

tolerant species, allows them to respond quickly to slight changes in the forest floor environment, such as increased light and temperature (McCarthy 2001). Rapid shrub growth in large canopy gaps overtime can quickly re-close the gaps and inhibit tree seedling growth due to competition for light and space (Archambault *et al.* 1997; Felton *et al.* 2006; Domke *et al.* 2007). However, in smaller gaps where the light is insufficient to stimulate shrub growth, advance tree regeneration may out-compete shrubs (Alaback and Tappeiner, 1991). Gaps can also be filled by lateral growth from surrounding canopy trees (Runkle 1990). To account for resource use both spatially and temporally, gap characteristics such as gap size and age are other important factors impacting tree regeneration and must be considered in forest management (Coates and Burton 1997; Kneeshaw and Bergeron 1998).

The growth strategies of specific tree species also have a major role in controlling recruitment of canopy species, especially in mixedwood forests where both shade tolerant and intolerant species can prevail through niche partitioning (Schnitzer and Carson 2001; Kneeshaw and Prevost 2007). A general assumption for boreal mixedwoods is that there is a tendency for advance regeneration of shade tolerant species such as *Abies balsamea* to fill small gaps, while shade intolerant tree species such as *Populus tremuloides* colonize large gaps (Whitmore 1989; Frelich and Reich 1995; Kuuluvainen and Juntunen 1998; Kneeshaw and Bergeron 1998; 1999; Grushecky and Fajvan 1999; Hill *et al.* 2005). Very large gaps can support a range of vegetation, with shade intolerant species in the centre and increasingly more shade tolerant species growing at the edges of the gap (McClure and Lee 1993). Another assumption is that the dominant overstory species will greatly influence subsequent canopy recruitment, with canopy species usually replacing themselves (Burns and Honkala 1990; Sirois 1997; Newton and Jolliffe 1998; Cumming *et al.* 2000; Pham *et al.* 2004; Dobrowolska and Veblen 2008).

Recent attention to small-scale boreal forest gap dynamics has been beneficial in illuminating natural regeneration and species replacement patterns in older, relatively undisturbed stands. However, most studies have been limited by considering uneven aged gaps with unclear mechanisms of gap formation, incomplete or gradual canopy removal, and unknown initial regeneration response (Kneeshaw *et al.* 1998; Hill *et al.* 2005; Dobrowolska and Veblen 2008). Management recommendations have been made based on the retrospective study of older, naturally formed canopy gaps, rather than conclusive studies on small gaps created deliberately by partial harvesting. Some harvest gaps may be larger than natural gaps, which may result in higher light exposure and higher recruitment of tree seedlings and saplings in partially harvested forests than natural forests (Schumann *et al.* 2003; Felton *et al.* 2006). Some partial harvests, especially with single tree removal, may result in gaps too small to create the high light conditions needed to regenerate shade-intolerant species and may not cause any noticeable shift in dominant vegetation (Crow *et al.* 2002; Domke *et al.* 2007). Because of the range of gap sizes that can result from partial harvesting, it is important to study harvest gaps across a size range corresponding to varying harvesting intensities. Sites with larger gaps can be expected to deviate more from closed canopy conditions than sites with smaller gaps (Price and Price 2006). I hypothesized that: if microclimate, especially light, differs depending on gap size then gap size is also expected to influence tree regeneration by i) enhancing the growth of seedlings and saplings, and ii) promoting the establishment of shade intolerant species in higher light environments corresponding with larger gaps.

Methods

Role of gap size on tree regeneration

A gap represents the opening in the canopy greater than the natural spacing between crowns, delimited by the edges of surrounding canopy trees, as vertically projected to the forest floor (Runkle 1982). In this study I considered gaps created by partial harvesting in riparian buffers. In total I surveyed 58 harvest gaps ranging from 1.3 m^2 (single tree removal) to 408 m^2 (multiple tree removal). I determined canopy gap area using the formula for area of an ellipse (A=π*(long axis*short axis)/4), by measuring the longest and shortest perpendicular distances between overstory branches above the harvest stumps, i.e., area of open sky over the gap maker stump(s) (Runkle 1992).

To determine the influence of gap size on tree regeneration I measured the area of each gap and the gaps were classified into three size classes: small (n=16, 1-20 m^2), medium (n=30, 21-99 m^2) and large (n=12, >100 m^2). Small gaps represent those smaller than those in some other studies on natural gaps (e.g., Dobrowolska and Veblen 2008). Medium gaps represent most of the natural gaps formed in boreal forests (McCarthy 2001). Large gaps represent those larger than most natural gaps. I compared tree seedling and sapling height, basal diameter, and stem densities among the three gap size classes. I also measured tree seedling and sapling height, basal diameter, and stem density in quadrats of unharvested stands to assess tree regeneration in the absence of gaps.

In the centre of all large gaps over 100 m^2 I placed a 10 x 10 m plot to characterize tree regeneration. In small and medium gaps less than 100 m^2 I assessed tree regeneration in the entire gap area. I assessed regeneration by counting all seedlings and saplings (trees <5 cm

diameter at breast height) per species, and grouping them into height classes (0-0.49 m, 0.5-2 m, and >2 m) as in Hill *et al.* (2005). Basal diameter (bd) of the three tallest saplings, over 1 m, of each species for each gap was also recorded. From these data, stem density (stems/m^2), proportion of hardwood to conifer juveniles (hardwood density/conifer density), maximum height, and maximum basal diameter were determined for each gap. Under closed canopy, tree regeneration was quantified in 1 m^2 quadrats positioned every 5 m along transects set up in unharvested stands. These transects were run perpendicular to a stream and spanned the width of the unharvested buffers, or 40 m in the case of reference forest without an adjacent clearcut. All transects were positioned on slopes less than 30 degrees, and were not located within 5 meters of any gaps following Andersen *et al.* (2002). Quadrat data were pooled along each transect to calculate a mean value of each regeneration variable measured for each of the 13 unharvested stands (unharvested buffers, n = 6; and reference forest, n = 7).

A 10 m wide belt transect was used to characterize overstory structure and composition. These belt transects were centered on each gap in partially harvested buffers and spanned the width of the buffer running perpendicular from the stream. In unharvested buffers and reference forest, these 10 m bands were centered on those transects discussed above (Fig. 1.2). Stand structure was characterized by recording each species and measuring diameter at breast height for each tree, and estimating the height of three average trees for each species. Height was estimated using trigonometry by estimating the angle to the top of the tree using a clinometer-fitted compass, measuring the distance to the base of the tree with a tape measure, and adjusting for the height difference between the compass at eye level and the base of the tree.

Data Analysis

Multivariate analysis of variance (MANOVA) with Duncan *post hoc* tests were used to detect any significant differences in tree seedling/sapling stem density among treatments. Kruskal-Wallis and Mann Whitney U tests were used to confirm the results of MANOVA since data could not be normalized with transformations. Kruskal-Wallis and Mann Whitney U tests were also used to determine significant differences in seedling/sapling height and basal diameter among treatments. Associations were also identified between tree regeneration and stand characteristics using multiple regression and Spearman correlations. The aforementioned tests were run with SPSS 16.0 (SPSS Inc. 2007). Tree seedling and sapling stem densities were ordinated using non-metric multidimensional scaling (slow and thorough setting) and correlated with the environmental variables (Clarke 1993). Multiple response permutation procedure (MRPP) was used to detect significant differences in the composition of tree seedlings/saplings among treatments (McCune and Grace 2002). Indicator species analyses were run in order to determine the association of certain tree species with environment. Through indicator species analysis and indicator value (IV) is assigned to each species based on that species' relative abundance and frequency of occurrence in sites of a given group compared with sites of other treatment groups (Dufrene and Legendre 1997). Non-metric multi-dimensional scaling, MRPP, and indicator species analysis were run with PC-Ord 5.10 (McCune and Mefford 2006). The critical alpha was set at 0.05, and results were reported as significant if $p<0.05$.

Results

Tree seedling and sapling composition

Abies balsamea was the most prevalent seedling/sapling encountered in the research area (with an overall density of 7667 stems/ha); with *Picea mariana* (2570 stems/ha), *Populus tremuloides* (794 stems/ha), *Betula papyrifera* (635 stems/ha), and *Picea glauca* (325 stems/ha) occurring at lower densities. Most sites were dominated by *A. balsamea*. Unharvested buffers and reference forest also had a large component of *Picea mariana* regeneration (Fig. 2.1). However, if *Populus tremuloides* existed in the surrounding overstory, seedlings and saplings of that species tended to dominate, particularly in large gaps (personal observation). Gaps of varying size, unharvested buffers, and reference forest significantly differed in their composition of tree seedlings/saplings, with the heterogeneity within groups being significantly less than that expected by chance (MRPP, A=0.157, p<0.001, A.2.1). Reference forest had higher stem density of *A. balsamea* (MANOVA, $F_{4,66}$=10.892, p<0.001) than all gap sizes, and higher stem density of *Picea mariana* (MANOVA, $F_{4,66}$=7.399, p<0.001) than medium and large gaps. Unharvested buffers also had higher stem density of *Picea mariana* than medium and large gaps, and higher stem density of *B. papyrifera* (MANOVA, $F_{4,66}$=3.305, p=0.016) than reference forest, small, and medium gaps. Stem density of *Picea glauca* (MANOVA, $F_{4,66}$=1.464, p=0.223) and *Populus tremuloides* (MANOVA, $F_{4,66}$=0.829, p=0.511) did not differ significantly among gaps of varying size and unharvested forest (Fig. 2.1, A.2.2).

From an ordination of tree seedlings/saplings, stem density was found to be associated with both the understory environment, and the overstory canopy composition. Axis 1 explained 49.1% of the variation in seedling/sapling densities among treatments and was negatively

correlated with canopy openness, gap area, and photosynthetically active radiation (PAR). Axis

2 explained 34.6% of the variation in seedling/sapling densities among treatments and was

negatively correlated with overstory *A. balsamea* and *Populus tremuloides*. *Abies balsamea*

seedling and sapling density was positively correlated with Axis 1. *Picea mariana* was

positively correlated with Axis 2, while *Populus tremuloides* was negatively correlated with Axis

2. Conifer seedlings and saplings were ordinated closer to reference forest and unharvested

buffers than to gaps. Hardwood seedlings and saplings were associated with greater canopy

openness. Overstory *A. balsamea* and *Populus tremuloides* were the two most important factors

influencing seedling and sapling stem density. *Populus tremuloides* seedling and sapling stem

density was influenced more by the surrounding overstory than the understory environment, with

higher stem density correlated with a greater overstory component of conspecifics. *Populus*

tremuloides seedling and sapling stem density was highly correlated with a higher overstory

component of mature *Populus tremuloides*. *Abies balsamea* seedling and sapling stem density

was also positively correlated with a greater overstory component of conspecifics. *Picea glauca,*

Picea mariana, and *B. papyrifera* seedling and sapling stem density were not correlated with

overstory conspecifics, but were negatively correlated with higher overstory components of both

A. balsamea and *Populus tremuloides* (Fig.2.2, A.2.3, A.2.4). *Abies balsamea* and *Picea*

mariana seedlings and saplings were significant indicator species of reference forests (indicator

value=44.7 and 45.7 respectively, $p<0.05$). *Picea glauca, Populus tremuloides,* and *B.*

papyrifera were not significantly indicative of any treatment (indicator values=13.1, $p=0.90$; 9.5,

$p=0.75$; and 26.9, $p=0.22$ respectively) (A.2.5).

Regeneration was found to be associated with both overstory conspecifics and canopy

gap area (A.2.4, A.2.9). The hardwood to conifer regeneration ratio increased significantly with

increasing gap size and overstory *Populus tremuloides* stem density (Regression, r^2=0.253,

p<0.001, A.2.6). With greater proportions of overstory stem density consisting of *Populus*

tremuloides, seedling/sapling regeneration was dominated by hardwoods rather than conifers

(Fig. 2.3). In particular, *Populus tremuloides* had higher seedling/sapling density with greater

proportions of mature *Populus tremuloides* in the overstory (Fig. 2.4). The proportion of overall

hardwood regeneration was not significantly correlated with gap size alone.
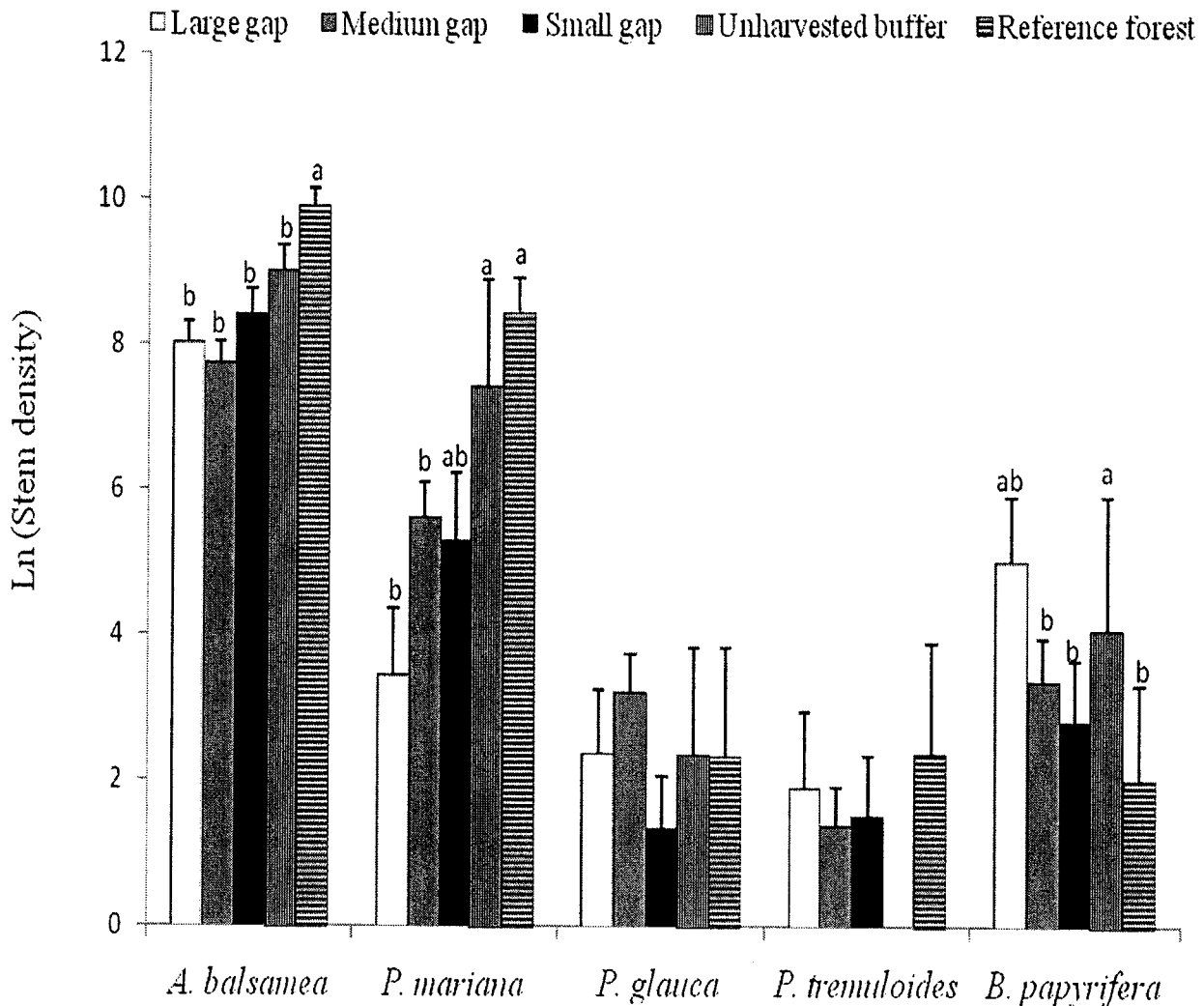
Figure 2.1. Stem densities (mean and standard error on a logarithmic scale) of tree seedlings/saplings growing in large (n=12), medium (n=30), and small gaps (n=16), unharvested buffers, and reference forest. For each species, columns with the same superscripts are not significantly different at p<0.05 as indicated in a multivariate analysis of variance and Tukey post-hoc multiple comparison tests.
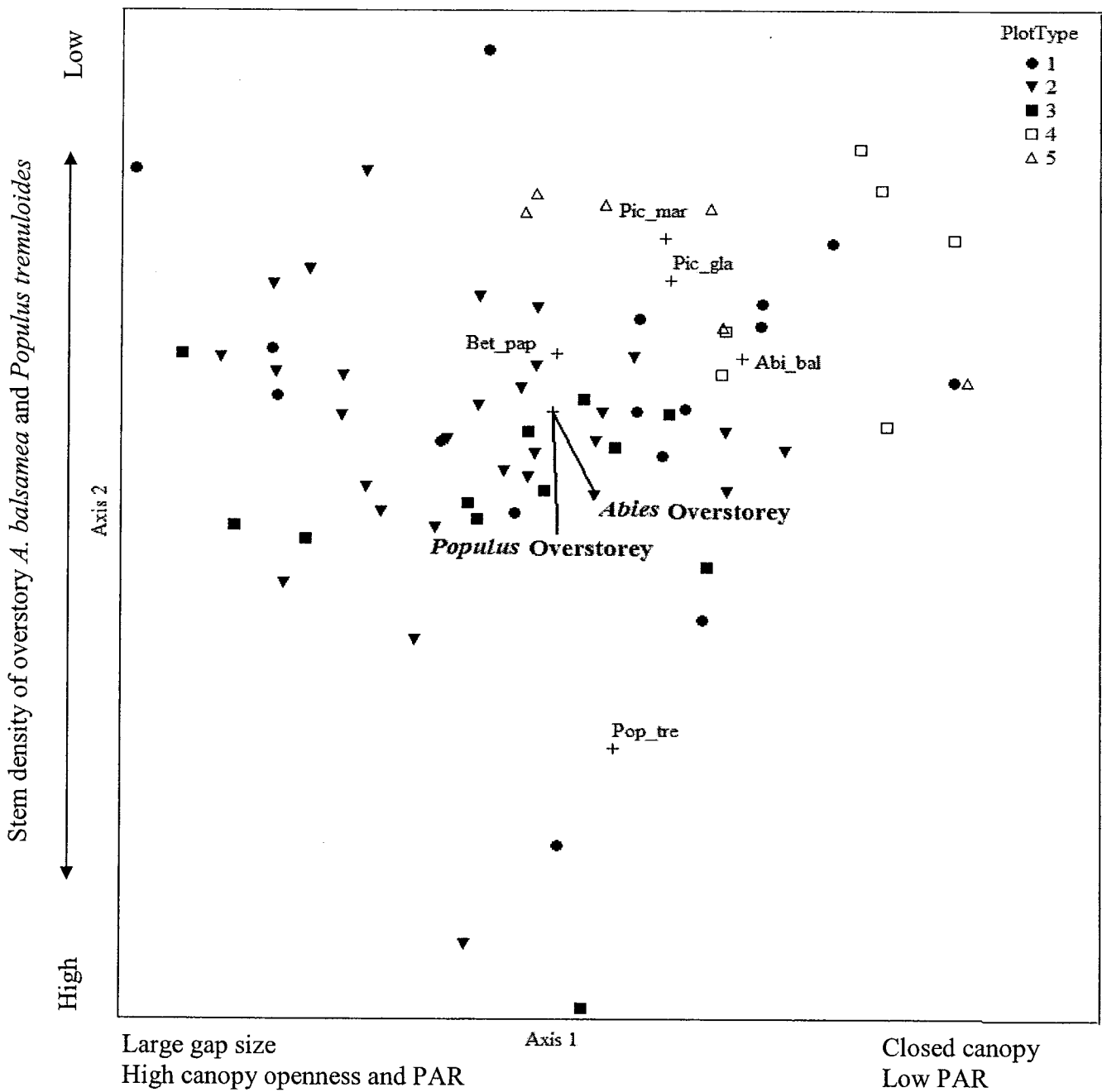
Figure 2.2 Non metric multidimensional scaling ordination explaining 83.7% of the variation in tree seedling and sapling stem density among small gaps (1), medium gaps (2), large gaps (3), reference forest (4), and unharvested buffers (5). Most unharvested sites are located in the top right corner, as are the conifer seedlings.
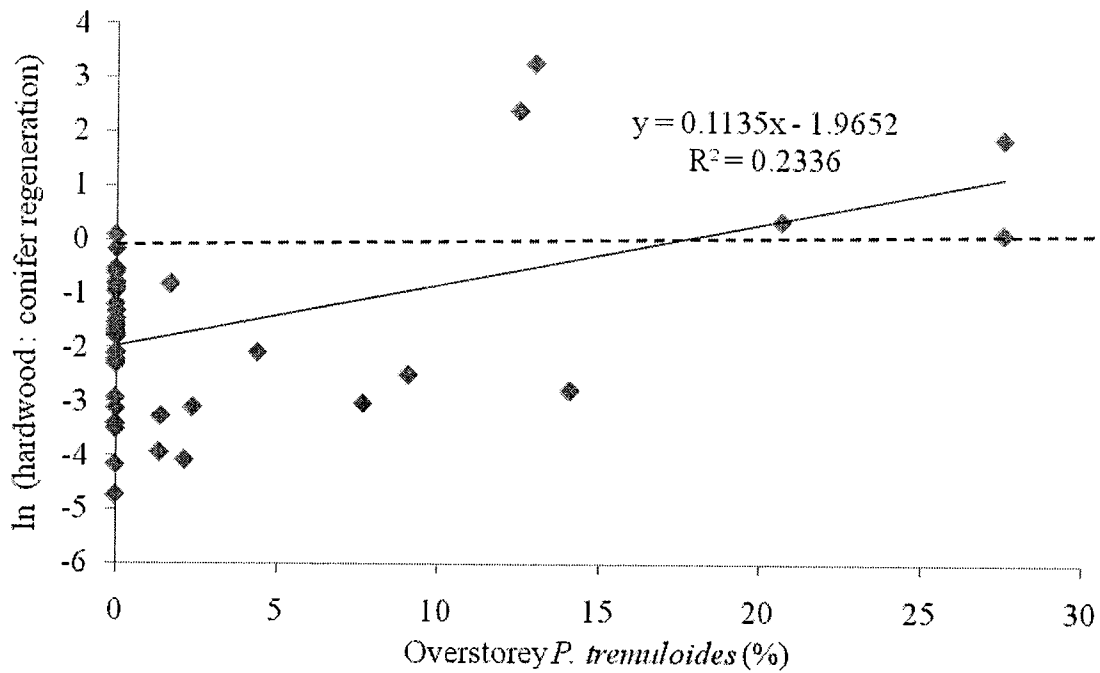
Figure 2.3. Scatterplot showing that the hardwood to conifer ratio of tree seedlings and saplings increases with increasing proportions of overstory *Populus tremuloides*.
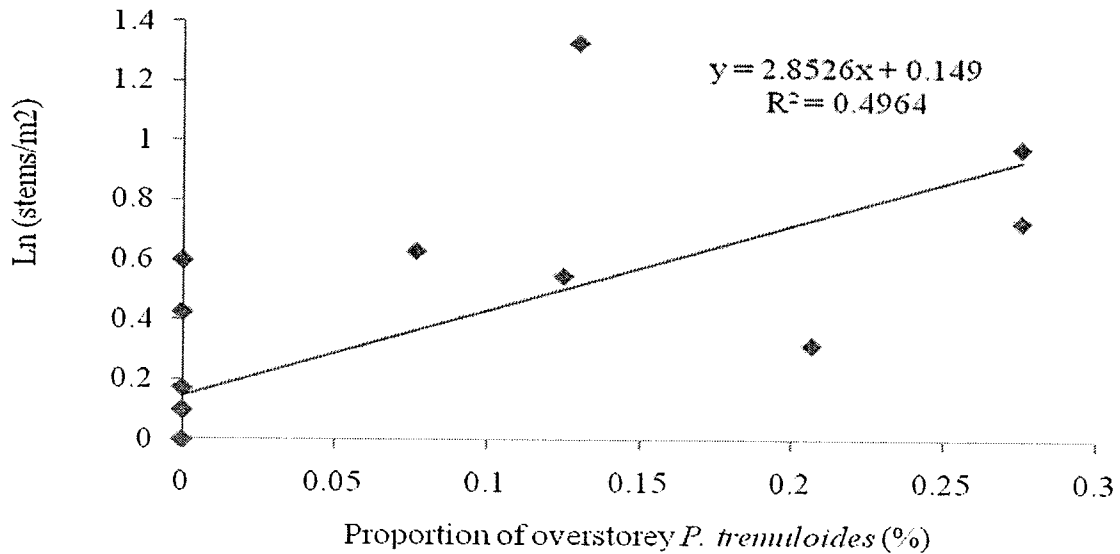
Figure 2.4. Significant linear relationship between understory and the proportion of overstory stem density of *Populus tremuloides* using a logarithmic scale.

Sapling height and basal diameter

Picea mariana saplings attained greater maximum height in medium gaps than in reference forest or large gaps (Kruskal-Wallis, χ^2=14.022, p=0.007). None of the other tree species differed significantly among gaps and unharvested plots with respect to their maximum sapling height (Fig. 2.5, A.2.7). The maximum basal diameter of *A. balsamea* saplings was significantly lower in unharvested buffers than in small and medium gaps, as well as reference forest (Kruskal-Wallis, χ^2=11.163, p=0.025). *Picea mariana* saplings in small and medium sized gaps achieved larger basal diameters than those in reference forest (Kruskal-Wallis, χ^2=16.599, p=0.002), (Fig. 2.6, A.2.8).

In general, conifer (*Abies balsamea* and *Picea mariana*) seedling and sapling stem densities were negatively correlated with canopy gap area (Spearman rank correlation, rho= -0.476 and -0.480, respectively, p<0.001). However, *Populus tremuloides* sapling height and basal diameter were positively correlated with canopy gap area (Spearman rank correlation, rho= +0.536 and +0.541, respectively, p<0.05). Basal diameter of *Picea mariana* saplings was also positively correlated with gap area (Spearman rank correlation, rho= +0.378, p=0.012). Stem density of *A. balsamea* and *Populus tremuloides*, as well as height and basal diameter of *A. balsamea*, were positively correlated with the proportion of conspecifics in the overstory (Spearman rank correlation, rho= +0.274, +0.409, +0.262 and +0.781, respectively, p<0.05). Seedling/sapling stem density of *Picea mariana* was negatively correlated with that of *Populus tremuloides* (Spearman rank correlation, rho= -0.329, p=0.005). In addition, basal diameter of *Picea mariana* saplings was negatively correlated with seedling/sapling stem density of *A. balsamea* (Spearman rank correlation, rho= -0.387, p=0.01), (A.2.9).

□ Large gap ▨ Medium gap ■ Small gap ▤ Unharvested buffer ▥ Reference forest
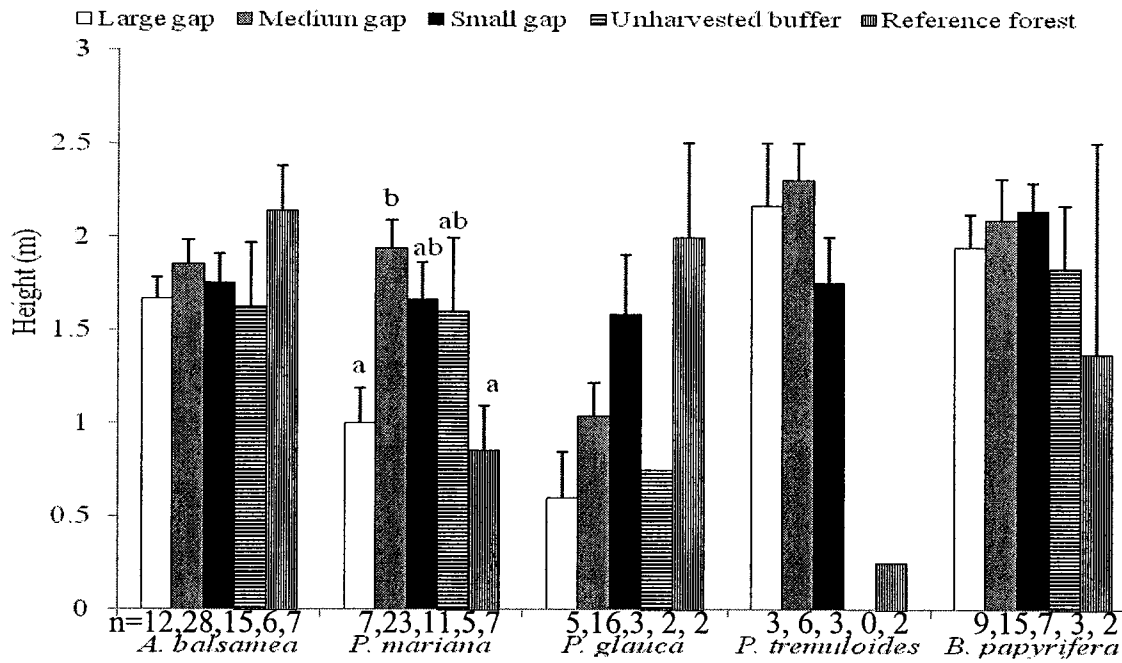
Figure 2.5. Maximum height (mean and standard error) of tree saplings compared among gaps, unharvested buffers, and reference forest. For each species, columns with the same superscript, or no superscript, are not significantly different at the p=0.05 level.

□ Large gap ▨ Medium gap ■ Small gap ▤ Unharvested buffer ▥ Reference forest
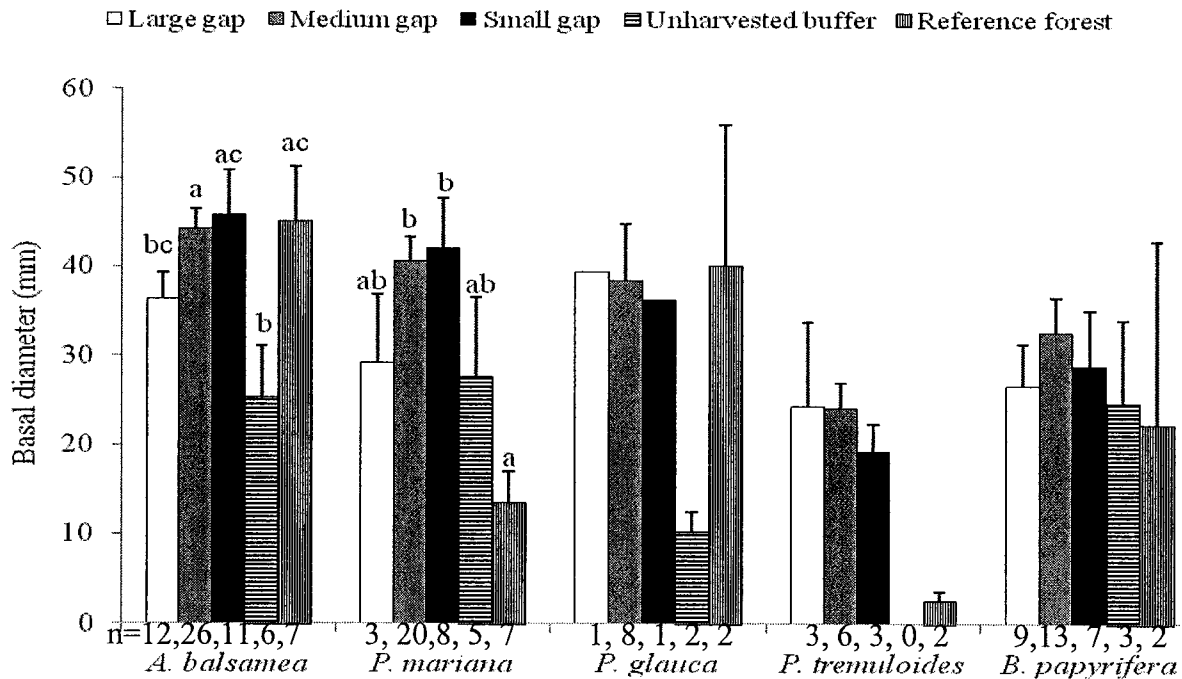
Figure 2.6. Maximum basal diameter (mean and standard error) of tree saplings compared among gaps, unharvested buffers, and reference forest. For each species, columns with the same superscript, or no superscript, are not significantly different at the p=0.05 level.

Discussion

Contrary to other studies (e.g., Hill *et al.* 2005; de Romer *et al.* 2007), my results indicate that the creation of small canopy gaps in boreal riparian buffers can influence tree regeneration with respect to seedling and sapling composition, density, and size. Consistent with my hypothesis, the ratio of juvenile hardwoods to conifers was higher in larger gaps particularly with *Populus tremuloides* abundant in the overstory. However, gap size was not found to be the most important factor influencing hardwood seedling/sapling stem density. Light-demanding *Populus tremuloides* juveniles, particularly individuals taller than 2 m, exhibited a positive correlation with gap area as well as overstory *Populus tremuloides*. As in Dobrowolska and Veblen (2008), *Populus tremuloides* juveniles grew taller and in higher density in larger gaps than under more closed canopy conditions. No *Populus tremuloides* saplings >1 m in height were recorded in unharvested buffers or reference forest. As saplings approach 2 m in height, their physiological demands may be too great for shaded environments, as photosynthesis rather than root suckering from parent trees becomes more important (Messier *et al.* 1999). If partial harvesting creates large gaps there might be an increase in shade intolerant hardwoods such as *Populus tremuloides* in the harvested buffers, especially if conspecifics are prevalent in the overstory (Kneeshaw and Bergeron 1999). Conversely, shade tolerant conifer juveniles were present in higher density under the closed canopy of unharvested stands than under the higher light environments of gaps in the partially harvested buffers. Conifer juveniles displayed a negative correlation with canopy gap area as observed by Kneeshaw and Bergeron (1998), and Noguchi and Yoshida (2007). Differences in juvenile stem density under closed and open canopies may exist due to differences in competition for resources between conifer and hardwood juveniles (Dobrowolska 1996; Roy *et al.* 2000). If opportunistic hardwood species such as *Populus tremuloides* are able to

outcompete conifer species in the early stages of gap regeneration by having higher initial growth rates, then conifer species would achieve greater success through a shade tolerant strategy of suppressing height growth and persisting under closed canopies (Hill *et al.* 2005).

My hypothesis of seedlings/saplings achieving larger sizes in gaps was generally supported. Despite being present in significantly lower abundance, *Picea mariana* juveniles had greater maximum height and basal diameter in small and medium harvest gaps than under closed canopy, or in large gaps. These results are consistent with the response of *Picea rubens* reported by Burns and Honkala (1990). This was also true for *Populus tremuloides* for which all gap sizes had larger individuals than unharvested stands. Dobrowolska and Veblen (2008) also found that juvenile trees were taller in harvest gaps than closed canopy forests. Juvenile trees appear to grow better in harvest gaps if they are able to establish there without competitors. Small and medium sized gaps may allow shade tolerant conifers to experience accelerated growth by offering slight increases in light and growing space, free from competition from light demanding species (Alaback and Tappeiner, 1991). Juveniles observed in small and medium gaps, as opposed to large gaps, were mostly larger than their counterparts in other locations. Even under closed canopies, conifer seedlings and saplings can take advantage of the higher light available each season before leaf initiation and after leaf senescence of coexisting deciduous species (Waring and Franklin 1979). Another possible explanation for the increase in size of conifers in small and medium, but not large gaps, could be that harvesting equipment damaged advance regeneration of conifers in larger gaps which were essentially machine movement corridors (Groot and Houba 1995). In addition, the amount of useable light may actually be less in large gaps than smaller gaps since large gaps may experience photoflux densities well above levels needed for photosynthesis (Wayne and Bazzaz 1993).

In addition to gap size, overstory stand composition also exerted influence over juvenile tree recruitment. *Abies balsamea* juveniles occurred at higher density and were larger when growing in association with greater proportions of their conspecifics. *Populus tremuloides* juveniles occurred in greater densities in correlation with stands having greater proportions of overstory conspecifics. Dobrowolska and Veblen (2008) also noted the same observation with respect to *Abies alba*, *Picea abies*, and *Populus tremula*. These results are consistent with other investigations reporting a similar trend of self-replacement of canopy species (Burns and Honkala 1990; Sirois 1997; Newton and Jolliffe 1998; Cumming *et al.* 2000; Pham *et al.* 2004). However, the larger size under conspecifics may be an artefact of older juveniles being sampled if their conspecifics are dominant because they have been established in a particular area for a long time, especially for *A. balsamea* which grows as advance regeneration under closed canopy (Archambault et al. 1998). It is likely that *Populus tremuloides* occurred at higher densities and were larger under conspecific overstory because *Populus tremuloides* can reproduce by sprouting and the juveniles are able to access nutrients through parent root suckers (Messier *et al.* 1999; USDA Plant Database 2009).

In contrast, stem densities of 0.5-2 m tall *Betula papyrifera* showed a negative correlation with the proportion of mature *B. papyrifera* in the overstory. This could be because *B. papyrifera* is an early successional, shade intolerant species (Burns and Honkala 1990). Despite the amount of parent trees in the stand, their juveniles require high light environments and exposed mineral soil for successful establishment (Campbell and Hawkins 2004). The harvest gaps I surveyed may not have been large enough to provide sufficient light for them, considering the height of the perimeter trees (12 m) around the gap. Dobrowolska and Veblen (2008) also noted the same observation for *Betula pendula*. Since the affected juveniles were < 2 m tall, they

may have been undergoing self-thinning (Simard and Zimonick 2005). With greater proportions of parent trees in the stand, perhaps more seedlings were initially produced after harvesting than in other stands, leading to greater pressure from intraspecific competition, and resulting in higher rates of juvenile mortality. Since no data were collected on seedling ages or from deceased individuals, this can only be suggested as a speculation. However, interspecific competition is less important for vegetatively regenerating *B. papyrifera,* since it grows out of a parent stem, and does not have to compete as much for growing space, light, and nutrients compared to the conifer advance regeneration (Greene *et al.* 1999). Other factors such as herbivory can also limit tree regeneration, especially for hardwood species (Suominen *et al.* 1999). Roy *et al.* (2000) documented that moose (*Alces alces*) browsing resulted in a high percentage of injuries to juvenile trees two to five years after harvesting. According to the United States Department of Agriculture (USDA) Plant Database (2009), *B. papyrifera* has high palatability for browsing animals, such as moose. Moose were observed near my study sites; therefore moose browsing could be a likely factor limiting *B. papyrifera* regeneration.

As expected, stem density of shade tolerant conifer juveniles was negatively correlated with gap area, occurring in higher densities in smaller gaps and under closed canopies. Shade intolerant pioneer species, *Populus tremuloides*, were taller and they occurred in higher densities in positive correlation with larger canopy gap areas. *Betula papyrifera*, another pioneer species, did not show any significant correlation with gap size, likely because the gaps surveyed were too small to support juvenile recruitment for that species. Due to the response of *Populus tremuloides*, the ratio of hardwood to conifer juveniles increased with the presence of *Populus tremuloides* in the overstory, and to a lesser extent, with increasing gap size. Gaps under 100 m^2 created by partial harvesting can enhance the growth of some conifers by slight increases in

growing space and light. However, a shift from conifer to hardwood dominance can occur with the introduction of large canopy gaps to riparian buffers where a parent crop exists in the adjacent overstory. *Populus tremuloides* can establish in gaps less than 100 m^2, but its proportion will be larger in large gaps.

The results of my study have implications for boreal mixedwood management. The creation of gaps by partial harvesting in riparian buffers can impact tree regeneration. Unharvested buffers and reference forest surveyed in this study were dominated by conifer seedlings/saplings even if the overstory was mixedwood. The establishment of the early successional hardwood, *Populus tremuloides*, in gaps can improve the heterogeneity of riparian buffers. The efficacy of partial harvesting to emulate natural disturbance patterns needs to be investigated in future research. After fire, species such as *Pinus banksiana* and *Populus tremuloides*, tend to dominate initially. As the stand matures, shade tolerant species such as *Abies balsamea* and *Picea* spp. increase in abundance (Bergeron 2000). The perpetuation of mixedwood in partially harvested buffers, due to the establishment of *Populus tremuloides* in gaps, could represent emulation of natural succession following stand replacing disturbance. The size of harvest gaps followed natural gap patterns to an extent; however the similarity in distribution of gaps in partially harvested buffers and natural gap distribution remains to be determined. Most of the harvest gaps were of comparable size to natural gaps, 41-141 m^2 (McCarthy 2001). Future research should investigate the prevalence of natural gaps in riparian areas, and compare with the size and distribution of gaps in partially harvested buffers. More research is needed to assess the emulation of natural gap dynamics by partial harvesting.

General Discussion and Conclusions

My results show that partial harvesting within riparian buffers may not impact understory species composition but can cause significant shifts in juvenile tree recruitment within gaps. Partially harvested buffers, regardless of gap size, were not significantly different from unharvested buffers or reference forest with respect to understory species composition and diversity. These results suggest that partial harvesting in riparian buffers did not have any significant impact on riparian plant communities when the majority of gaps created by harvesting were less than 100 m^2, supporting the hypothesis of boreal understory resilience to small-scale canopy disturbance.

Microclimate varied only slightly among treatments. Some of the gaps surveyed were large enough to alter microclimate, but the microclimate of gaps probably still remained within the tolerance range of the inhabiting species. Fahey and Puettmann (2008) also found that gaps as large as 0.4 ha did not have any significant influence on understory plants. If gaps are not large enough to introduce competitive early successional species, then it is not likely that any changes in understory composition should occur due to gap formation (Grushecky and Fajvan 1999; Fahey and Puettmann 2008). This suggests that gaps could cause community changes due to altered microclimate when they are large, however the changes in microclimate that occur when gaps are small are not large enough to affect understory species in this region. I suspected that the adaptation of boreal species to disturbance makes them resistant to fine-scale disturbances, such as gap creation by partial harvesting. If boreal plant communities consist of species that have wide ranges of tolerance for environmental variables such as light, moisture, and temperature then the community should be able to adapt to environmental changes without

experiencing major shifts in species composition, provided that the disturbance does not alter microclimate beyond the tolerance limits of the species.

Although understory communities in riparian buffers did not seem to be affected by partial harvesting, individual plants growing in harvest gap centers did display significant morphological differences in specific leaf area and leaf dry matter content from their counter parts growing under closed canopy. Specific leaf area was greater under closed canopy, as shown by Moola and Mallik (1998), and leaf dry matter content was greater in large gaps. The increase of leaf dry matter content in gaps could have an impact on litter quality since it reflects the amount of lignin and fibre in the leaves, and thus their decomposability (Fortunel *et al.* 2009). This, in addition to the increase of juvenile hardwoods in gaps, may impact organic inputs from riparian areas into streams. This aspect should be considered in future studies. Understory species respond to canopy gap formation by adjusting morphological efforts in such a way that allows them to persist in the face of disturbance. The findings of this study suggest that common boreal understory plants are able to be resilient to fine-scale disturbances, in part, through plasticity of leaf morphology.

Canopy species however, can experience shifts in dominance even when the majority of harvest gaps are small. Shade tolerant conifer juveniles were negatively correlated with gap area, growing larger and at higher densities in smaller gaps and under closed canopies. The shade intolerant pioneer, *Populus tremuloides* occurred in higher densities and were taller, in positive correlation with larger canopy gap areas. *Betula papyrifera*, another pioneer species, did not show any significant correlation with gap size; likely because the gaps surveyed were too small to support juvenile recruitment for this species. Due mostly to the response of *Populus tremuloides*, the ratio of hardwood to conifer juveniles was greater in gaps than under a closed

canopy. This result has important implications for management because it shows that partial harvesting in riparian buffers can alter stand composition. Anthropomorphically created gaps under 100 m^2 with slight increases in light can enhance the growth of some conifer species. However, a shift from conifer to hardwood dominance can occur with the introduction of larger gaps to riparian buffers. *Populus tremuloides* can establish in gaps under 100m^2, but their proportions are expected to increase with increasing gap area, particularly if the surrounding stand contains overstory conspecifics.

Literature cited

Abe, S., Masaki, T., and Nakashizuka, T. 1995. Factors influencing sapling composition in canopy gaps of a temperate deciduous forest. Vegetation **120:** 21-31.

Alaback, P., and Tappeiner, J. 1991. Response of western hemlock (*Tsuga heterophylla*) and early huckleberry (*Vaccinium ovalifolium*) seedlings to forest windthrow. Can. J. For. Res. **21:** 534-539.

Anderson, K., and Leopold, D. 2002. The role of canopy gaps in maintaining vascular plant diversity at a forested wetland in New York state. J. Torrey Bot. Soc. **129:** 238-250.

Archambault, L., Morissette, J., and Bernier-Cardou, M. 1998. Forest succession over a 20-year period following clearcutting in balsam fir yellow birch ecosystems of eastern Quebec, Canada. For. Ecol. Manage. **102:** 61-74.

Atlegrim, O., and Sjoberg, K. 1996. Response of bilberry (*Vaccinium myrtillus*) to clear-cutting and single-tree selection harvests in uneven-aged boreal *Picea abies* forests. For. Ecol. Manage. **86:** 39-50.

Balfour, P. 1989. Effects of forest herbicides on some important wildlife forage species. FRDA Report 020, BC Ministry of Forests, Victoria, B.C.

Benfield, E.F. 1996. Methods in stream ecology. pp. 582. Academia Press, Toronto, ON, Canada.

Bergeron, Y., and Harvey, B. 1997. Basing silviculture on natural ecosystem dynamics: An approach applied to the southern boreal mixedwood forest of Quebec. For. Ecol. Manage. **92:** 235-242.

Bergeron, Y. 2000. Species and stand dynamics in the mixedwoods of Quebec's southern boreal forest. Ecology **81:**1500-1516.

Broadbent, E., Zarin, D., Asner, G., Pena-Claros, M., Cooper, A., and Littell, R. 2006. Recovery of forest structure and spectral properties after selective logging in lowland Bolivia. Ecol. Appl. **16:** 1148-1163.

Brosofske, K., Chen, J., Naiman, R., and Franklin, J. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. Ecol. Appl. **7:** 1188-1200.

Burns, R., Honkala, B. 1990. Silvics of North America. Volume I. Conifers. USDA Fores Service. Washington D.C., USA.

Campbell, K., and Hawkins, C. 2004. Effect of seed source and nursery culture on paper birch (Betula papyrifera) uprooting resistance and field performance. For. Ecol. Mngmt. **196:** 425-433.

Canham, C., Denslow, J., Platt, W., Runkle, J., Spies, T., and White, P. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical Forests. Can. J. For. Res. **20:** 620-631.

Chambers, B., Legasy, K., and Bentley, C. 1996. Forest plants of central Ontario. Lone Pine Publishing, Toronto, ON., Canada.

Chazdon, R. 1985. Leaf display, canopy structure, and light interception of 2 understory palm species. Am. J. Bot. **72:** 1493-1502.

Clarke, K.R. 1993. Nonmetric multidimensional analyses of changes in community structure. Aus. J. Ecol. **18:** 117-143.

Coates, K. 2002. Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. For. Ecol. Manage. **155:** 387-398.

Coates, K., and Burton, P. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. For. Ecol. Manage. **99:** 337-354.

Collins, B., and Pickett, S. 1987. Influence of canopy opening on the environment and herb layer in a northern hardwoods forest. Vegetation **70:** 3-10.

Crow, T., Buckley, D., Nauertz, E., and Zasada, J. 2002. Effects of management on the composition and structure of northern hardwood forests in Upper Michigan. For. Sci. **48:** 129-145.

Cumming, S., Schmiegelow, F., and Burton, P. 2000. Gap dynamics in boreal aspen stands: Is the forest older than we think? Ecol. Appl. **10:** 744-759.

de Roemer, A., Kneeshaw, D., and Bergeron, Y. 2007. Small gap dynamics in the southern boreal forest of eastern Canada: Do canopy gaps influence stand development? J. Veg. Sci. **18:** 815-826.

Dahlgren, J., Eriksson, O., Bolmgren, K., Strindell, M., Ehrlen, J. 2006. Specific leaf area as a superior predictor of changes in field layer abundance during forest succession. J. Veg. Sci. **17:** 577-582.

de Grandpre, L., Gagnon, D., and Bergeron, Y. 1993. Changes in the understory of Canadian southern boreal forest after fire. J. Veg. Sci. **4:** 803-810.

de Grandpre, L., Bergeron, Y. 1997. Diversity and stability of understory communities following disturbance in the southern boreal forest. Ecology **85:** 777-784.

Denslow, J. 1987. Tropical rain-forest gaps and tree species-diversity. Annu. Rev. Ecol. Syst. **18:** 431-451.

Denslow, J., and Spies, T. 1990. Canopy gaps in forest ecosystems - an introduction. Can. J. For. Res. **20:** 619-619.

Dobrowolska, D., and Veblen, T. 2008. Treefall-gap structure and regeneration in mixed *Abies alba* stands in central Poland. For. Ecol. Manage. **255:** 3469-3476.

Domke, G., Caspersen, J., and Jones, T. 2007. Light attenuation following selection harvesting in northern hardwood forests. For. Ecol. Manage. **239:** 182-190.

Dufrene, M., and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs **67:** 345-366.

Fahey, R., and Puettmann, K. 2008. Patterns in spatial extent of gap influence on understory plant communities. For. Ecol. Manage. **255:** 2801-2810.

Felton, A., Felton, A.M., Wood, J., and Lindenmayer, D. 2006. Vegetation structure, phenology, and regeneration in the natural and anthropogenic tree-fall gaps of a reduced-impact logged subtropical Bolivian forest. For. Ecol. Manage. **235:** 186-193.

Forcier, L. 1975. Reproductive strategies and co-occurrence of climax tree species. Science **189:** 808-810.

Forkner, R., Marquis, R., Lill, J., and Le Corff, J. 2006. Impacts of alternative timber harvest practices on leaf-chewing herbivores of oak. Conserv. Biol. **20:** 429-440.

Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Freitas, H., Golodets, C., Jouany, C., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V.P., Quetier, F., Robson, M., Sternberg, M., Theau, J., Thebault, A., and Zarovali, M. 2009. Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. Ecology **90:** 598-611.

Fraver, S., and White, A. 2005. Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine. J. Veg. Sci. **16:** 597-610.

Freedman, B., Morash, R., and Mackinnon, D. 1993. Short-term changes in vegetation after the silvicutural spraying of glyphosate herbicide onto regenerating clearcuts in Nova-Scotia, Canada. Can. J. For. Res. **23:** 2300-2311.

Frelich, L., and Reich, P. 1995. Neighborhood effects, disturbance, and succession in forests of the western Great-Lakes region. Ecoscience **2:** 148-158.

Galhidy, L., Mihok, B., Hagyo, A., Rajkai, K., and Standovar, T. 2006. Effects of gap size and associated changes in light and soil moisture on the understory vegetation of a Hungarian beech forest. Plant Ecol. **183:** 133-145.

Gea-Izquierdo, G., Pastur, G., Cellini, J., and Lencinas, M. 2004. Forty years of silvicultural management in southern *Nothofagus pumilio* primary forests. For. Ecol. Manage. **201:** 335-347.

Gendreau-Berthiaume, B., and Kneeshaw, D. In press. Influence of gap size and position within gaps on light levels. Int. J. For. Res.

Gilbert, G., Harms, K., Hamill, D., and Hubbell, S. 2001. Effects of seedling size, El Nino drought, seedling density, and distance to nearest conspecific adult on 6-year survival of *Ocotea whitei* seedlings in Panama. Oecologia **127**: 509-516.

Gilliam, F., and Turrill, N. 1993. Herbaceous layer cover and biomass in a young versus a mature stand of a central Appalachian hardwood forest. Bul. Torrey Bot. Club **120**: 445-450.

Goldblum, D. 1997. The effects of treefall gaps on understory vegetation in New York State. J. Veg. Sci. **8**: 125-132.

Greene, D., Zasada, J., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., and Simard, M. 1999. A review of the regeneration dynamics of North American boreal forest tree species. Can. J. For. Res. **29**: 824-839.

Grime, J. 1977. Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. **111**: 1169-1194.

Goates, M., Hatch, K., and Eggett, D. 2007. The need to ground truth 30.5 m buffers: A case study of the boreal toad (*Bufo boreas*). Biological Conservation **138**: 474-483.

Groot, J., and Houba, V. 1995. A comparison of different indexes for nitrogen mineralization. Biol. Fertility Soils **19**: 1-9.

Groot, A., Man, R., and Wood, J. 2009. Spatial and temporal patterns of *Populus tremuloides* regeneration in small forest openings in northern Ontario. Forestry Chronicle 85: 548-557.

Grushecky, S., and Fajvan, M. 1999. Comparison of hardwood stand structure after partial harvesting using intensive canopy maps and geostatistical techniques. For. Ecol. Manage. **114**: 421-432.

Gunderson, L. 2000. Ecological resilience-in theory and application. Ann. Rev. Ecol. Syst. **31**: 425-439.

Hall, I., Aalders, L., Nickerson, N., and Vanderkloet, S. 1979. Biological flora of Canada .1. *Vaccinium angustifolium* Ait, sweet lowbush blueberry. Can. Field-Nat. **93**: 415-430.

Hamilton, A., Bryden, C., and Clement, C. 1991. Impacts of glyphosate application on grizzly bear forage production in the coastal western hemlock zone. B.C. Min. For.

Hannerz, M., and Hanell, B. 1997. Effects on the flora in Norway spruce forests following clearcutting and shelterwood cutting. For. Ecol. Manage. **90**: 29-49.

Hansen, A., Pate, J., and Hansen, A. 1991. Growth and reproductive performance of a seeder and a resprouter species of *Bossiaea* as a function of plant-age after fire. Annals of Botany **67**: 497-509.

Harrison, R., Schmiegelow, F., and Naidoo, R. 2005. Stand-level response of breeding forest songbirds to multiple levels of partial-cut harvest in four boreal forest types. Can. J. For. Res. **35**: 1553-1567.

Hazlett, P., Gordon, A., Sibley, P., and Buttle, J. 2005. Stand carbon stocks and soil carbon and nitrogen storage for riparian and upland forests of boreal lakes in northeastern Ontario. For. Ecol. Manage. **219**: 56-68.

Hill, S., Mallik, A., and Chen, H. 2005. Canopy gap disturbance and succession in trembling aspen dominated boreal forests in northeastern Ontario. Can. J. For. Res. **35**: 1942-1951.

Hughes, J., and Fahey, T. 1991. Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. J. Ecol. **79**: 605-616.

Hunt, R. 1982. Plant growth curves. University Park Press, Baltimore, pp 248.

Jost, L. 2006. Entropy and diversity. Oikos **113**: 363-375.

Jost, L. 2007. Partitioning diversity into independent alpha and beta components. Ecology **88**: 2427-2439.

Kneeshaw, D., and Bergeron, Y. 1999. Spatial and temporal patterns of seedling and sapling recruitment within canopy gaps caused by spruce budworm. Ecoscience **6**: 214-222.

Kneeshaw, D., and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology **79**: 783-794.

Kneeshaw, D., and Bergeron, Y. 1996. Ecological factors affecting the abundance of advance regeneration in Quebec's southwestern boreal forest. Can. J. For. Res. **26**: 888-898.

Kneeshaw, D., and Prevost, M. 2007. Natural canopy gap disturbances and their role in maintaining mixed-species forests of central Quebec, Canada. Can. J. For. Res. **37**: 1534-1544.

Kuuluvainen, T., and Juntunen, P. 1998. Seedling establishment in relation to microhabitat variation in a windthrow gap in a boreal *Pinus sylvestris* forest. J. Veg. Sci. **9**: 551-562.

Lahde, E., Laiho, O., Norokorpi, Y., and Saksa, T. 1999. Stand structure as the basis of diversity index. For. Ecol. Manage. **115**: 213-220.

Larrivee, M., Drapeau, P., and Fahrig, L. 2008. Edge effects created by wildfire and clear-cutting on boreal forest ground dwelling spiders. For. Ecol. Manage. **255**: 1434-1445.

Lee, C., Wickneswari, R., Mahani, M., and Zakri, A. 2002. Effect of selective logging on the genetic diversity of *Scaphium macropodum*. Biological Conservation **104**: 107-118.

Lee, P., and Barker, T. 2005. Impact of riparian buffer guidelines on old growth in western boreal forests of Canada. Forestry **78**: 263-278.

Lee, P., Crites, S., Nietfeld, M., VanNguyen, H., and Stelfox, J. 1997. Characteristics and origins of deadwood material in aspen-dominated boreal forests. Ecol. Appl. **7**: 691-701.

Legasy, K. 1995. Forest plants of northeastern Ontario. Lone Pine Publishing, Edmonton, AB., Canada.

Lertzman, K. 1992. Patterns of gap-phase replacement in a sub-alpine, old-growth forest. Ecology **73**: 657-669.

Macdonald, E., Burgess, C., Scrimgeour, G., Boutin, S., Reedyk, S., and Kotak, B. 2004. Should riparian buffers be part of forest management based on emulation of natural disturbance? For. Ecol. Manage. **187**: 185-196.

MacIsaac, D., Comeau, P., and Macdonald, S. 2006. Dynamics of regeneration gaps following harvest of aspen stands. Can. J. For. Res. **36**: 1818-1833.

Mallik, A.U. 1995. Conversion of temperate forests into heaths - Role of ecosystem disturbance and ericaceous plants. Environ. Manage. **19**: 675-684.

Marshall, J.D., and Waring, R.H. 1984. Conifers and broadleaf species - stomatal sensitivity differs in western Oregon. Can. J. For. Res. **14**: 905-908.

McCarthy, J. 2001. Gap dynamics of forest trees: A review with particular attention to boreal forests. Environmental Reviews **9**: 1-59.

McClure, J.W., and Lee, T.D. 1993. Small-scale disturbance in a northern hardwoods forest - effects on tree species abundance and distribution. Can. J. For. Res. **23**: 1347-1360.

McCune, B. and Grace, J. B. 2002. Analysis of Ecological Communities. MjM Software, Gleneden Beach , Oregon, U.S.A.

Messier, C. 1992. Effects of neutral shade and growing media on growth, biomass allocation, and competitive ability of *Gaultheria shallon*. Can. J. Bot. **70**: 2271-2276.

Messier, C., and Puttonen, P. 1995. Growth, allocation, and morphological responses of *Betula pubescens* and *Betula pendula* to shade in developing scots pine stands. Can. J. For. Res. **25**: 629-637.

Messier, C., and Kimmins, J.P. 1991. Aboveground and belowground vegetation recovery in recently clear-cut and burned sites dominated by *Gaultheria shallon* in coastal British-Columbia. For. Ecol. Manage. **46:** 275-294.

Messier, C., Doucet, R., Ruel, J.C., Claveau, Y., Kelly, C., and Lechowicz, M.J. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. Can. J. For. Res. **29:** 812-823.

Minore, D. and Weatherly, H.G. 1994. Effects of partial bark removal on the growth of Pacific yew. Can. J. For. Res. **24:** 860-862.

Moola, F.M., and Mallik, A.U. 1998. Morphological plasticity and regeneration strategies of velvet leaf blueberry (*Vaccinium myrtilloides* Michx.) following canopy disturbance in boreal mixedwood forests. For. Ecol. Manage. **111:** 35-50.

Moore, M.R., and Vankat, J.L. 1986. Responses of the herb layer to the gap dynamics of a mature beech-maple forest. Am. Midl. Nat. **115:** 336-347.

Muto, E.A., Kreutzweiser, D. P., and Sibley, P.K. 2009. The influence of riparian vegetation on leaf litter inputs to boreal shield streams: implications for partial-harvest logging in riparian reserves. Can. J. For. Res. **39:** 917-927.

National Council for Air and Stream Improvement, Inc. (NCASI). 2006. Structural and functional roles of riparian management areas in maintaining stream values in the Acadian forest. Technical Bulletin No. 922. Research Triangle Park, N.C.: NACASI, Inc.

Newton, P.F., and Jolliffe, P.A. 1998. Temporal size-dependent growth responses within density-stressed black spruce stands: Competition processes and budworm effects. For. Ecol. Manage. **111:** 1-13.

Nichols, M.T., Lemin, R.C., and Ostrofsky, W.D. 1994. The impact of 2 harvesting systems on residual stems in a partially cut stand of northern hardwoods. Can. J. For. Res. **24:** 350-357.

Nilsson, M.C., and Wardle, D.A. 2005. Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. Frontiers in Ecology and the Environment **3:** 421-428.

Nitschke, C.R. 2005. Does forest harvesting emulate fire disturbance? A comparison of effects on selected attributes in coniferous-dominated headwater systems. For. Ecol. Manage. **214:** 305-319.

Noguchi, M., and Yoshida, T. 2007. Regeneration responses influenced by single-tree selection harvesting in a mixed-species tree community in northern Japan. Can. J. For. Res. **37:** 1554-1562.

Ontario Ministry of Natural Resources (OMNR). 1998. Timber Management Guidelines for the Protection of Fish Habitat. Queen's Printer for Ontario, Toronto, Ontario, Canada.

Ontario Ministry of Natural Resources (OMNR). Forest Management Guide for Natural Disturbance Pattern Emulation. 2001. Queen's Printer for Ontario, Toronto, Ontario, Canada.

Pham, A.T., de Grandpre, L., Gauthier, S., and Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. Can. J. For. Res. **34**: 353-364.

Price, M. and Price, C.. 2006. Creaming the best, or creatively transforming? Might felling the biggest trees first be a win-win strategy? Forest Ecology and Management **224**: 297-303.

Reid, L.M. and Hilton, S. 1998. Buffering the buffer. USDA Forest Service Gen. Tech. Rep. PSW-GTR-168.

Reynolds, P.E., Thevathasan, N.V., Simpson, J.A., Gordon, A.M., Lautenschlager, R.A., Bell, W.F., Gresch, D.A., and Buckley, D.A. 2000. Alternative conifer release treatments affect microclimate and soil nitrogen mineralization. For. Ecol. Manage. **133**: 115-125.

Ricard, J.P., and Messier, C. 1996. Abundance, growth and allometry of red raspberry (*Rubus idaeus* L) along a natural light gradient in a northern hardwood forest. For. Ecol. Manage. **81**: 153-160.

Runkle, J.R. 1990. Gap dynamics in an Ohio *Acer-Fagus* forest and speculations on the geography of disturbance. Can. J. For. Res. **20**: 632-641.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North-America. Ecology **63**: 1533-1546.

Schaetzl, R.J., Burns, S.F., Johnson, D.L., and Small, T.W. 1989. Tree uprooting - Review of impacts on forest ecology. Vegetation **79**: 165-176.

Schnitzer, S.A., and Carson, W.P. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology **82**: 913-919.

Schumann, M.E., White, A.S., and Witham, J.W. 2003. The effects of harvest-created gaps on plant species diversity, composition, and abundance in a Maine oak-pine forest. For. Ecol. Manage. **176**: 543-561.

Seng, H.W., Ratnam, W., Noor, S.M., and Clyde, M.M. 2004. The effects of the timing and method of logging on forest structure in peninsular Malaysia. For. Ecol. Manage. **203**: 209-228.

Simard, S.W., and Zimonick, B.J. 2005. Neighborhood size effects on mortality, growth and crown morphology of paper birch. For. Ecol. Manage. **214:** 251-265.

Sirois, L. 1997. Distribution and dynamics of balsam fir (*Abies balsamea* [L.] Mill.) at its northern limit in the James Bay area. Ecoscience **4:** 340-352.

Stewart, G.H., Rose, A.B., and Veblen, T.T. 1991. Forest development in canopy gaps in old-growth beech (*Nothofagus*) forests, New-Zealand. J. Veg. Sci. **2:** 679-690.

Suominen, O., Danell, K., and Bryant, J.P. 1999. Indirect effects of mammalian browsers on vegetation and ground-dwelling insects in an Alaskan floodplain. Ecoscience **6:** 505-510.

Waring, R.H., and Franklin, J.F. 1979. Evergreen coniferous forests of the Pacific Northwest. Science **204:** 1380-1386.

Wayne, P.M., and Bazzaz, F.A. 1993. Birch seedling responses to daily time courses of light in experimental forest gaps and shadehouses. Ecology **74:** 1500-1515.

Westman, W.E. 1978. Measuring inertia and resilience of ecosystems. Bioscience **28:** 705-710.

Whitmore, T.C. 1989. Canopy gaps and the 2 major groups of forest trees. Ecology **70:** 536-538.

Wilson, P.J., Thompson, K., and Hodgson, J.G. 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. New Phytol. **143:** 155-162.

Woods, K.D. 2000. Dynamics in late-successional hemlock-hardwood forests over three decades. Ecology **81:** 110-126.

Appendix 1.1. Multivariate analysis of variance for overall species richness, abundance, diversity, and evenness of understory species along transects in partially harvested buffers, unharvested buffers, and reference forest.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.	Observed power
Corrected Model	Richness	19.359	2	9.679	3.957	0.024	**0.692**
	Abundance	8529.829	2	4264.915	2.552	0.085	0.494
	Diversity	6.528	2	3.264	2.525	0.088	0.489
	Evenness	0.003	2	0.001	0.576	0.565	0.142
Intercept	Richness	2741.719	1	2741.719	1.121E3	<0.001	1.000
	Abundance	1679455.951	1	1679455.951	1.005E3	<0.001	1.000
	Diversity	1159.215	1	1159.215	896.723	<0.001	1.000
	Evenness	10.143	1	10.143	4.635E3	<0.001	1.000
Treatment	Richness	19.359	2	9.679	3.957	**0.024**	**0.692**
	Abundance	8529.829	2	4264.915	2.552	0.085	0.494
	Diversity	6.528	2	3.264	2.525	0.088	0.489
	Evenness	0.003	2	0.001	0.576	0.565	0.142
Error	Richness	166.346	68	2.446			
	Abundance	113650.720	68	1671.334			
	Diversity	87.905	68	1.293			
	Evenness	0.149	68	0.002			
Total	Richness	7305.942	71				
	Abundance	4828227.377	71				
	Diversity	3142.192	71				
	Evenness	26.649	71				
Corrected Total	Richness	185.705	70				
	Abundance	122180.550	70				
	Diversity	94.433	70				
	Evenness	0.151	70				

Appendix 1.2. Multivariate analysis of variance for life-form richness of understory species along transects in partially harvested buffers, unharvested buffers, and reference forest.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.	Observed Power
Corrected Model	Tree	0.004	2	0.002	0.070	0.932	.067
	Tall shrub	0.116[b]	2	0.058	1.194	0.309	.196
	Low shrub	0.016[c]	2	0.008	0.247	0.782	.079
	Herb	0.222[d]	2	0.111	1.887	0.159	.409
	Graminoid	0.154[e]	2	0.077	2.750	0.071	.497
	Pteridophyte	0.170[f]	2	0.085	1.137	0.327	.213
	Bryophyte	0.188[g]	2	0.094	1.909	0.156	.466
	Lichen	0.044[h]	2	0.022	0.605	0.549	.147
Intercept	Tree	10.406	1	10.406	379.602	<0.001	1.000
	Tall shrub	8.334	1	8.334	171.001	<0.001	1.000
	Low shrub	32.372	1	32.372	977.593	<0.001	1.000
	Herb	55.074	1	55.074	935.641	<0.001	1.000
	Graminoid	1.148	1	1.148	40.885	<0.001	1.000
	Pteridophyte	6.904	1	6.904	92.502	<0.001	1.000
	Bryophyte	25.993	1	25.993	527.688	<0.001	1.000
	Lichen	2.898	1	2.898	80.212	<0.001	1.000
Treatment	Tree	0.004	2	0.002	0.070	.932	.067
	Tall shrub	0.116	2	0.058	1.194	.309	.196
	Low shrub	0.016	2	0.008	0.247	.782	.079
	Herb	0.222	2	0.111	1.887	.159	.409
	Graminoid	0.154	2	0.077	2.750	.071	.497
	Pteridophyte	0.170	2	0.085	1.137	.327	.213
	Bryophyte	0.188	2	0.094	1.909	.156	.466
	Lichen	0.044	2	0.022	0.605	.549	.147

Appendix 1.2. Continued.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square
Error	Tree	1.864	68	0.027
	Tall shrub	3.314	68	0.049
	Low shrub	2.252	68	0.033
	Herb	4.003	68	0.059
	Graminoid	1.909	68	0.028
	Pteridophyte	5.075	68	0.075
	Bryophyte	3.350	68	0.049
	Lichen	2.456	68	0.036
Total	Tree	29.504	71	
	Tall shrub	24.787	71	
	Low shrub	88.675	71	
	Herb	142.206	71	
	Graminoid	6.781	71	
	Pteridophyte	26.307	71	
	Bryophyte	68.022	71	
	Lichen	8.982	71	
Corrected Total	Tree	1.868	70	
	Tall shrub	3.430	70	
	Low shrub	2.268	70	
	Herb	4.225	70	
	Graminoid	2.063	70	
	Pteridophyte	5.245	70	
	Bryophyte	3.538	70	
	Lichen	2.500	70	

Appendix 1.3. Multivariate analysis of variance for life-form abundance of understory species along transects in partially harvested buffers, unharvested buffers, and reference forest.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.	
Corrected Model	Tree	0.314[a]	2	0.157	0.587	0.559	.105
	Tall shrub	2.741[b]	2	1.370	1.917	0.155	.137
	Low shrub	0.908[c]	2	0.454	2.714	0.073	.341
	Herb	0.352[d]	2	0.176	1.012	0.369	.245
	Graminoid	1.908[e]	2	0.954	1.092	0.341	.320
	Pteridophyte	2.079[f]	2	1.040	1.723	0.186	.211
	Bryophyte	0.067[g]	2	0.034	0.105	0.901	.060
	Lichen	0.278[h]	2	0.139	0.218	0.805	.090
Intercept	Tree	356.349	1	356.349	1.334E3	<0.001	1.000
	Tall shrub	246.753	1	246.753	345.209	<0.001	1.000
	Low shrub	421.925	1	421.925	2.522E3	<0.001	1.000
	Herb	461.158	1	461.158	2.653E3	<0.001	1.000
	Graminoid	95.516	1	95.516	109.316	<0.001	1.000
	Pteridophyte	186.539	1	186.539	309.055	<0.001	1.000
	Bryophyte	317.357	1	317.357	992.593	<0.001	1.000
	Lichen	48.619	1	48.619	76.314	<0.001	.993
Treatment	Tree	0.314	2	0.157	0.587	0.559	.105
	Tall shrub	2.741	2	1.370	1.917	0.155	.137
	Low shrub	0.908	2	0.454	2.714	0.073	.341
	Herb	0.352	2	0.176	1.012	0.369	.245
	Graminoid	1.908	2	0.954	1.092	0.341	.320
	Pteridophyte	2.079	2	1.040	1.723	0.186	.211
	Bryophyte	0.067	2	0.034	0.105	0.901	.060
	Lichen	0.278	2	0.139	0.218	0.805	.090

Appendix 1.3. Continued.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square
Error	Tree	18.169	68	0.267
	Tall shrub	48.606	68	0.715
	Low shrub	11.378	68	0.167
	Herb	11.818	68	0.174
	Graminoid	59.416	68	0.874
	Pteridophyte	41.043	68	0.604
	Bryophyte	21.741	68	0.320
	Lichen	43.322	68	0.637
Total	Tree	898.896	71	
	Tall shrub	706.535	71	
	Low shrub	1178.422	71	
	Herb	1226.175	71	
	Graminoid	358.874	71	
	Pteridophyte	584.895	71	
	Bryophyte	842.999	71	
	Lichen	162.929	71	
Corrected Total	Tree	18.483	70	
	Tall shrub	51.347	70	
	Low shrub	12.286	70	
	Herb	12.170	70	
	Graminoid	61.324	70	
	Pteridophyte	43.123	70	
	Bryophyte	21.808	70	
	Lichen	43.599	70	

Appendix 1.4. Multivariate analysis of variance for life-form diversity of understory species along transects in partially harvested buffers, unharvested buffers, and reference forest.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.	
Corrected Model	Tree	<0.001[a]	2	6.597E-5	0.013	0.987	.052
	Tall shrub	0.015[b]	2	0.007	0.502	0.607	.129
	Low shrub	0.060[c]	2	0.030	0.580	0.563	.143
	Herb	0.261[d]	2	0.130	1.178	0.314	.250
	Graminoid	0.013[e]	2	0.007	1.503	0.230	.310
	Pteridophyte	0.017[f]	2	0.008	0.494	0.612	.128
	Bryophyte	0.065[g]	2	0.032	1.200	0.308	.254
	Lichen	<0.001[h]	2	<0.001	0.073	0.930	.061
Intercept	Tree	34.108	1	34.108	6.778E3	<0.001	1.000
	Tall shrub	40.584	1	40.584	2.735E3	<0.001	1.000
	Low shrub	68.520	1	68.520	1.318E3	<0.001	1.000
	Herb	95.204	1	95.204	860.696	<0.001	1.000
	Graminoid	31.136	1	31.136	7.144E3	<0.001	1.000
	Pteridophyte	37.489	1	37.489	2.207E3	<0.001	1.000
	Bryophyte	53.162	1	53.162	1.972E3	<0.001	1.000
	Lichen	30.525	1	30.525	1.218E4	<0.001	1.000
Treatment	Tree	<0.001	2	6.597E-5	0.013	0.987	.052
	Tall shrub	0.015	2	0.007	0.502	0.607	.129
	Low shrub	0.060	2	0.030	0.580	0.563	.143
	Herb	0.261	2	0.130	1.178	0.314	.250
	Graminoid	0.013	2	0.007	1.503	0.230	.310
	Pteridophyte	0.017	2	0.008	0.494	0.612	.128
	Bryophyte	0.065	2	0.032	1.200	0.308	.254
	Lichen	<0.001	2	<0.001	0.073	0.930	.061

Appendix 1.4. Continued.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square
Error	Tree	0.342	68	0.005
	Tall shrub	1.009	68	0.015
	Low shrub	3.535	68	0.052
	Herb	7.522	68	0.111
	Graminoid	0.296	68	0.004
	Pteridophyte	1.155	68	0.017
	Bryophyte	1.833	68	0.027
	Lichen	0.170	68	0.003
Total	Tree	88.085	71	
	Tall shrub	104.773	71	
	Low shrub	187.008	71	
	Herb	246.634	71	
	Graminoid	83.163	71	
	Pteridophyte	100.390	71	
	Bryophyte	133.381	71	
	Lichen	78.856	71	
Corrected Total	Tree	0.342	70	
	Tall shrub	1.024	70	
	Low shrub	3.595	70	
	Herb	7.782	70	
	Graminoid	0.309	70	
	Pteridophyte	1.172	70	
	Bryophyte	1.897	70	
	Lichen	0.171	70	

Appendix 1.5. Summary of univariate analyses of variance for life-form evenness of understory species along transects in partially harvested buffers, unharvested buffers, and reference forest.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	Tree	0.022	2	0.011	0.646	0.528
	Tall shrub	0.025[a]	2	0.013	0.820	0.447
	Low shrub	0.037[a]	2	0.018	2.063	0.135
	Herb	0.005[a]	2	0.003	0.605	0.549
	Graminoid	0.092[a]	2	0.046	0.785	0.466
	Pteridophyte	0.029[a]	2	0.015	1.074	0.350
	Bryophyte	0.004[a]	2	0.002	0.183	0.834
	Lichen	0.085[a]	2	0.043	1.163	0.328
Intercept	Tree	2.972	1	2.972	174.665	<0.001
	Tall shrub	5.626	1	5.626	366.390	<0.001
	Low shrub	9.434	1	9.434	1.066E3	<0.001
	Herb	7.641	1	7.641	1.739E3	<0.001
	Graminoid	6.267	1	6.267	106.335	<0.001
	Pteridophyte	5.378	1	5.378	392.861	<0.001
	Bryophyte	6.190	1	6.190	577.264	<0.001
	Lichen	1.711	1	1.711	46.585	<0.001
Treatment	Tree	0.022	2	0.011	0.646	0.528
	Tall shrub	0.025	2	0.013	0.820	0.447
	Low shrub	0.037	2	0.018	2.063	0.135
	Herb	0.005	2	0.003	0.605	0.549
	Graminoid	0.092	2	0.046	0.785	0.466
	Pteridophyte	0.029	2	0.015	1.074	0.350
	Bryophyte	0.004	2	0.002	0.183	0.834
	Lichen	0.085	2	0.043	1.163	0.328

Appendix 1.5. Continued.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square
Error	Tree	0.936	55	0.017
	Tall shrub	0.706	46	0.015
	Low shrub	0.602	68	0.009
	Herb	0.294	67	0.004
	Graminoid	1.650	28	0.059
	Pteridophyte	0.602	44	0.014
	Bryophyte	0.718	67	0.011
	Lichen	0.955	26	0.037
Total	Tree	8.240	58	
	Tall shrub	17.503	49	
	Low shrub	26.451	71	
	Herb	19.854	70	
	Graminoid	14.791	31	
	Pteridophyte	13.677	47	
	Bryophyte	16.342	70	
	Lichen	5.152	29	
Corrected Total	Tree	0.958	57	
	Tall shrub	0.732	48	
	Low shrub	0.639	70	
	Herb	0.300	69	
	Graminoid	1.743	30	
	Pteridophyte	0.632	46	
	Bryophyte	0.722	69	
	Lichen	1.040	28	

Appendix 1.6. Summary table of MRPP results testing the difference in composition among partially harvested buffers, unharvested buffers, and reference forest.

		T	A	p
Observed delta	59.821420	-3.4580630	0.01386831	0.00380320
Expected delta	60.662709			

Appendix. 1.7. Environmental variables correlated with the main axes of an NMDS ordination of understory species in partially harvested buffers, unharvested buffers, and reference forest.

Axis:	1		2		3	
	r	r^2	r	r^2	r	r^2
Canopy density	0.268	0.072	-0.539	0.290	-0.309	-0.186
PAR	0.185	0.034	-0.186	0.035	0.082	-0.172
RH	-0.124	0.015	0.157	0.025	0.134	0.043
Air temperature	-0.096	0.009	-0.019	<0.001	-0.374	-0.307
Surface temperature	-0.307	0.094	-0.147	0.022	0.021	-0.205
Soil temperature	0.131	0.017	-0.115	0.013	-0.176	-0.052
Soil moisture	-0.031	0.001	0.275	0.076	0.058	0.056
Gap area	0.113	0.013	0.062	0.004	-0.017	-0.062
A. balsamea	0.283	0.080	0.463	0.214	0.348	0.270
B. papyrifera	-0.319	0.102	-0.209	0.189	0.128	0.064
Picea glauca	-0.045	0.002	-0.027	0.019	0.152	0.140
Picea mariana	0.070	0.005	0.078	0.019	-0.223	-0.207
Populus tremuloides	0.251	0.063	0.077	0.063	0.428	0.219

Appendix 1.8. Multivariate analysis of variance for microclimate along transects in partially harvested buffers, unharvested buffers, and reference forest.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	Canopy density	4961.734	2	2480.867	25.002	<0.001
	RH	109.041	2	54.520	0.717	0.493
	Air temperature	112.961	2	56.481	0.807	0.452
	Surface temperature	112.125	2	56.062	0.771	0.467
	PAR	1120.065	2	560.032	4.612	0.014
	Soil temperature	0.076	2	0.038	2.060	0.137
Intercept	Canopy density	15404.884	1	15404.884	155.252	<0.001
	RH	81845.454	1	81845.454	1.076E3	<0.001
	Air temperature	125353.500	1	125353.500	1.790E3	<0.001
	Surface temperature	127040.540	1	127040.540	1.748E3	<0.001
	PAR	7432.412	1	7432.412	61.207	<0.001
	Soil temperature	205.315	1	205.315	1.106E4	<0.001
Treatment	Canopy density	4961.734	2	2480.867	25.002	<0.001
	RH	109.041	2	54.520	0.717	0.493
	Air temperature	112.961	2	56.481	0.807	0.452
	Surface temperature	112.125	2	56.062	0.771	0.467
	PAR	1120.065	2	560.032	4.612	0.014
	Soil temperature	0.076	2	0.038	2.060	0.137
Error	Canopy density	5457.383	55	99.225		
	RH	4181.923	55	76.035		
	Air temperature	3851.033	55	70.019		
	Surface temperature	3997.549	55	72.683		
	PAR	6678.686	55	121.431		
	Soil temperature	1.021	55	0.019		
Total	Canopy density	72076.515	58			
	RH	176578.704	58			
	Air temperature	282510.673	58			
	Surface temperature	286870.182	58			
	PAR	33666.024	58			
	Soil temperature	448.876	58			

Appendix 1.9. Multivariate analysis of variance of overall richness, abundance, diversity, and evenness of understory species in gaps and closed canopy quadrats.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.	Observed power
Corrected Model	Richness	4.029	5	0.806	3.770	0.002	.936
	Abundance	113.960	5	22.792	3.222	0.007	.889
	Diversity	0.009	5	0.002	1.240	0.289	.442
	Evenness	2.731	5	0.546	3.012	0.011	.864
Intercept	Richness	3062.731	1	3062.731	1.433E4	<0.001	1.000
	Abundance	70927.486	1	70927.486	1.003E4	<0.001	1.000
	Diversity	510.262	1	510.262	3.417E5	<0.001	1.000
	Evenness	2087.308	1	2087.308	1.151E4	<0.001	1.000
Treatment	Richness	4.029	5	0.806	3.770	0.002	.936
	Abundance	113.960	5	22.792	3.222	0.007	.889
	Diversity	0.009	5	0.002	1.240	0.289	.442
	Evenness	2.731	5	0.546	3.012	0.011	.864
Error	Richness	104.300	488	0.214			
	Abundance	3451.909	488	7.074			
	Diversity	0.729	488	0.001			
	Evenness	88.493	488	0.181			
Total	Richness	5489.000	494				
	Abundance	128027.000	494				
	Diversity	887.839	494				
	Evenness	3738.318	494				
Corrected Total	Richness	108.329	493				
	Abundance	3565.869	493				
	Diversity	0.738	493				
	Evenness	91.225	493				

Appendix. 1.10. Multivariate analysis of variance of life-form richness in gaps and closed canopy quadrats.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.	Observed power
Corrected Model	Tree	0.397	5	0.079	1.028	0.400	.368
	Tall shrub	0.795	5	0.159	1.699	0.133	.589
	Low shrub	1.751	5	0.350	2.926	0.013	.852
	Herb	3.246	5	0.649	3.568	0.004	.921
	Graminoid	0.305	5	0.061	1.439	0.209	.508
	Pteridophyte	2.150	5	0.430	4.300	0.001	.964
	Bryophyte	1.819	5	0.364	2.508	0.029	.784
	Lichen	0.287	5	0.057	1.067	0.378	.382
Intercept	Tree	510.228	1	510.228	6.599E3	<0.001	1.000
	Tall shrub	498.523	1	498.523	5.329E3	<0.001	1.000
	Low shrub	810.982	1	810.982	6.778E3	<0.001	1.000
	Herb	1160.464	1	1160.464	6.377E3	<0.001	1.000
	Graminoid	343.468	1	343.468	8.109E3	<0.001	1.000
	Pteridophyte	471.464	1	471.464	4.714E3	<0.001	1.000
	Bryophyte	724.703	1	724.703	4.997E3	<0.001	1.000
	Lichen	372.166	1	372.166	6.922E3	<0.001	1.000
Treatment	Tree	0.397	5	0.079	1.028	0.400	.368
	Tall shrub	0.795	5	0.159	1.699	0.133	.589
	Low shrub	1.751	5	0.350	2.926	0.013	.852
	Herb	3.246	5	0.649	3.568	0.004	.921
	Graminoid	0.305	5	0.061	1.439	0.209	.508
	Pteridophyte	2.150	5	0.430	4.300	0.001	.964
	Bryophyte	1.819	5	0.364	2.508	0.029	.784
	Lichen	0.287	5	0.057	1.067	0.378	.382

Appendix 1.10. Continued.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square
Error	Tree	37.889	490	0.077
	Tall shrub	45.842	490	0.094
	Low shrub	58.632	490	0.120
	Herb	89.169	490	0.182
	Graminoid	20.753	490	0.042
	Pteridophyte	49.011	490	0.100
	Bryophyte	71.061	490	0.145
	Lichen	26.346	490	0.054
Total	Tree	931.000	496	
	Tall shrub	908.000	496	
	Low shrub	1495.000	496	
	Herb	211<0.001	496	
	Graminoid	62<0.001	496	
	Pteridophyte	896.000	496	
	Bryophyte	1331.000	496	
	Lichen	672.000	496	
Corrected Total	Tree	38.286	495	
	Tall shrub	46.637	495	
	Low shrub	60.383	495	
	Herb	92.415	495	
	Graminoid	21.058	495	
	Pteridophyte	51.162	495	
	Bryophyte	72.879	495	
	Lichen	26.633	495	

Appendix. 1.11. Multivariate analysis of variance of life-form abundance in gaps and closed canopy quadrats.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.	Observed power
Corrected Model	Tree	90.833	5	18.167	1.363	0.237	.483
	Tall shrub	104.293	5	20.859	1.821	0.107	.624
	Low shrub	184.142	5	36.828	3.970	0.002	.948
	Herb	116.178	5	23.236	2.226	0.051	.726
	Graminoid	18.154	5	3.631	0.798	0.551	.288
	Pteridophyte	175.767	5	35.153	4.300	0.001	.964
	Bryophyte	94.550	5	18.910	2.337	0.041	.750
	Lichen	8.486	5	1.697	0.917	0.470	.329
Intercept	Tree	7317.768	1	7317.768	549.138	<0.001	1.000
	Tall shrub	5047.001	1	5047.001	440.540	<0.001	1.000
	Low shrub	13774.816	1	13774.816	1.485E3	<0.001	1.000
	Herb	17230.289	1	17230.289	1.651E3	<0.001	1.000
	Graminoid	1063.339	1	1063.339	233.803	<0.001	1.000
	Pteridophyte	3174.065	1	3174.065	388.221	<0.001	1.000
	Bryophyte	7530.015	1	7530.015	930.580	<0.001	1.000
	Lichen	794.094	1	794.094	428.954	<0.001	1.000
Treatment	Tree	90.833	5	18.167	1.363	0.237	.483
	Tall shrub	104.293	5	20.859	1.821	0.107	.624
	Low shrub	184.142	5	36.828	3.970	0.002	.948
	Herb	116.178	5	23.236	2.226	0.051	.726
	Graminoid	18.154	5	3.631	0.798	0.551	.288
	Pteridophyte	175.767	5	35.153	4.300	0.001	.964
	Bryophyte	94.550	5	18.910	2.337	0.041	.750
	Lichen	8.486	5	1.697	0.917	0.470	.329

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square
Error	Tree	6529.703	490	13.326
	Tall shrub	5613.638	490	11.456
	Low shrub	4545.976	490	9.278
	Herb	5115.149	490	10.439
	Graminoid	2228.522	490	4.548
	Pteridophyte	4006.203	490	8.176
	Bryophyte	3964.954	490	8.092
	Lichen	907.103	490	1.851
Total	Tree	19187.000	496	
	Tall shrub	14773.000	496	
	Low shrub	28725.000	496	
	Herb	34787.000	496	
	Graminoid	4046.000	496	
	Pteridophyte	10407.000	496	
	Bryophyte	17208.000	496	
	Lichen	2368.000	496	
Corrected Total	Tree	6620.537	495	
	Tall shrub	5717.931	495	
	Low shrub	4730.119	495	
	Herb	5231.327	495	
	Graminoid	2246.676	495	
	Pteridophyte	4181.970	495	
	Bryophyte	4059.504	495	
	Lichen	915.589	495	

Appendix. 1.12. Multivariate analysis of variance of life-form diversity in gaps and closed canopy quadrats.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.	Observed power
Corrected Model	Tree	0.022	5	0.004	1.093	0.364	.391
	Tall shrub	0.091	5	0.018	2.088	0.066	.694
	Low shrub	0.274	5	0.055	3.254	0.007	.892
	Herb	0.383	5	0.077	2.468	0.032	.777
	Graminoid	0.019	5	0.004	1.200	0.308	.428
	Pteridophyte	0.175	5	0.035	4.621	<0.001	.975
	Bryophyte	0.083	5	0.017	1.267	0.277	.451
	Lichen	0.024	5	0.005	2.298	0.044	.742
Intercept	Tree	598.823	1	598.823	1.470E5	<0.001	1.000
	Tall shrub	632.043	1	632.043	7.235E4	<0.001	1.000
	Low shrub	726.787	1	726.787	4.312E4	<0.001	1.000
	Herb	817.126	1	817.126	2.633E4	<0.001	1.000
	Graminoid	585.377	1	585.377	1.863E5	<0.001	1.000
	Pteridophyte	615.812	1	615.812	8.126E4	<0.001	1.000
	Bryophyte	670.910	1	670.910	5.096E4	<0.001	1.000
	Lichen	581.509	1	581.509	2.839E5	<0.001	1.000
Treatment	Tree	0.022	5	0.004	1.093	0.364	.391
	Tall shrub	0.091	5	0.018	2.088	0.066	.694
	Low shrub	0.274	5	0.055	3.254	0.007	.892
	Herb	0.383	5	0.077	2.468	0.032	.777
	Graminoid	0.019	5	0.004	1.200	0.308	.428
	Pteridophyte	0.175	5	0.035	4.621	<0.001	.975
	Bryophyte	0.083	5	0.017	1.267	0.277	.451
	Lichen	0.024	5	0.005	2.298	0.044	.742

Appendix 1.12. Continued.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square
Error	Tree	1.996	490	0.004
	Tall shrub	4.281	490	0.009
	Low shrub	8.259	490	0.017
	Herb	15.209	490	0.031
	Graminoid	1.539	490	0.003
	Pteridophyte	3.713	490	0.008
	Bryophyte	6.451	490	0.013
	Lichen	1.004	490	0.002
Total	Tree	1042.783	496	
	Tall shrub	1105.877	496	
	Low shrub	1276.095	496	
	Herb	1427.406	496	
	Graminoid	1018.855	496	
	Pteridophyte	1085.209	496	
	Bryophyte	1175.096	496	
	Lichen	1014.264	496	
Corrected Total	Tree	2.018	495	
	Tall shrub	4.372	495	
	Low shrub	8.533	495	
	Herb	15.592	495	
	Graminoid	1.558	495	
	Pteridophyte	3.889	495	
	Bryophyte	6.535	495	
	Lichen	1.027	495	

Appendix 1.13. Summary of univariate analyses of variance for life-form evenness of understory species in gaps and closed canopy quadrats.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	Tree	0.229	5	0.046	2.261	0.055
	Tall shrub	0.337	5	0.067	1.963	0.092
	Low shrub	0.235	5	0.047	1.691	0.136
	Herb	0.116	5	0.023	1.196	0.310
	Graminoid	0.419	5	0.084	2.463	0.081
	Pteridophyte	0.158	5	0.032	1.070	0.382
	Bryophyte	0.067	5	0.013	0.470	0.798
	Lichen	0.225	5	0.045	1.274	0.320
Intercept	Tree	7.195	1	7.195	355.714	<0.001
	Tall shrub	19.728	1	19.728	574.437	<0.001
	Low shrub	61.345	1	61.345	2.206E3	<0.001
	Herb	72.590	1	72.590	3.752E3	<0.001
	Graminoid	4.591	1	4.591	134.972	<0.001
	Pteridophyte	5.641	1	5.641	191.407	<0.001
	Bryophyte	34.324	1	34.324	1.210E3	<0.001
	Lichen	1.537	1	1.537	43.550	<0.001
Treatment	Tree	0.229	5	0.046	2.261	0.055
	Tall shrub	0.337	5	0.067	1.963	0.092
	Low shrub	0.235	5	0.047	1.691	0.136
	Herb	0.116	5	0.023	1.196	0.310
	Graminoid	0.419	5	0.084	2.463	0.081
	Pteridophyte	0.158	5	0.032	1.070	0.382
	Bryophyte	0.067	5	0.013	0.470	0.798
	Lichen	0.225	5	0.045	1.274	0.320

Appendix 1.13. Continued.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square
Error	Tree	1.861	92	0.020
	Tall shrub	3.160	92	0.034
	Low shrub	8.788	316	0.028
	Herb	7.952	411	0.019
	Graminoid	0.510	15	0.034
	Pteridophyte	2.652	90	0.029
	Bryophyte	7.065	249	0.028
	Lichen	0.600	17	0.035
Total	Tree	14.643	98	14.643
	Tall shrub	40.981	98	
	Low shrub	124.527	322	
	Herb	127.912	417	
	Graminoid	7.857	21	
	Pteridophyte	30.737	96	
	Bryophyte	67.985	255	
	Lichen	3.845	23	
Corrected Total	Tree	2.090	97	
	Tall shrub	3.497	97	
	Low shrub	9.023	321	
	Herb	8.068	416	
	Graminoid	0.929	20	
	Pteridophyte	2.810	95	
	Bryophyte	7.132	254	
	Lichen	0.825	22	

Appendix 1.14. Multivariate analysis of variance for microclimate in gaps and closed canopy quadrats.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	Canopy density	58.167	5	11.633	55.629	<0.001
	RH	.490	5	0.098	5.792	<0.001
	Air temperature	.461	5	0.092	5.555	<0.001
	Surface temperature	.590	5	0.118	4.224	0.001
	PAR	120.790	5	24.158	17.685	<0.001
	Soil temperature	1.114	5	0.223	8.437	<0.001
Intercept	Canopy density	1994.009	1	1994.009	9.535E3	<0.001
	RH	3789.474	1	3789.474	2.241E5	<0.001
	Air temperature	3774.318	1	3774.318	2.274E5	<0.001
	Surface temperature	3342.066	1	3342.066	1.196E5	<0.001
	PAR	5538.297	1	5538.297	4.054E3	<0.001
	Soil temperature	1609.380	1	1609.380	6.097E4	<0.001
Treatment	Canopy density	58.167	5	11.633	55.629	<0.001
	RH	0.490	5	0.098	5.792	<0.001
	Air temperature	0.461	5	0.092	5.555	<0.001
	Surface temperature	0.590	5	0.118	4.224	0.001
	PAR	120.790	5	24.158	17.685	<0.001
	Soil temperature	1.114	5	0.223	8.437	<0.001

Appendix 1.14. Continued.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square
Error	Canopy density	75.704	362	0.209
	RH	6.123	362	0.017
	Air temperature	6.008	362	0.017
	Surface temperature	10.116	362	0.028
	PAR	494.495	362	1.366
	Soil temperature	9.556	362	0.026
Total	Canopy density	3622.339	368	
	RH	6655.084	368	
	Air temperature	6631.680	368	
	Surface temperature	5908.708	368	
	PAR	10315.474	368	
	Soil temperature	2826.354	368	
Corrected Total	Canopy density	133.871	367	
	RH	6.612	367	
	Air temperature	6.469	367	
	Surface temperature	10.706	367	
	PAR	615.285	367	
	Soil temperature	10.670	367	

Appendix 1.15. Summary of univariate analyses of variance for specific leaf area of four common understory species in gaps and along transects in unharvested stands.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	*Clintonia borealis*	60649.807	4	15162.452	4.955	0.002
	Cornus canadensis	59853.285	4	14963.321	13.209	<0.001
	V. angustifolium	234715.112	4	58678.778	25.803	<0.001
	V. myrtilloides	281983.076	4	70495.769	13.495	<0.001
Intercept	*Clintonia borealis*	2677391.812	1	2677391.812	874.973	<0.001
	Cornus canadensis	2532088.540	1	2532088.540	2.235E3	<0.001
	V. angustifolium	1983388.060	1	1983388.060	872.162	<0.001
	V. myrtilloides	1783215.511	1	1783215.511	341.349	<0.001
Treatment	*Clintonia borealis*	60649.807	4	15162.452	4.955	0.002
	Cornus canadensis	59853.285	4	14963.321	13.209	<0.001
	V. angustifolium	234715.112	4	58678.778	25.803	<0.001
	V. myrtilloides	281983.076	4	70495.769	13.495	<0.001
Error	*Clintonia borealis*	159118.408	52	3059.969		
	Cornus canadensis	79296.364	70	1132.805		
	V. angustifolium	111431.111	49	2274.104		
	V. myrtilloides	198512.712	38	5224.019		
Total	*Clintonia borealis*	2986707.045	57			
	Cornus canadensis	2774388.532	75			
	V. angustifolium	2351391.133	54			
	V. myrtilloides	2561750.357	43			
Corrected Total	*Clintonia borealis*	219768.216	56			
	Cornus canadensis	139149.649	74			
	V. angustifolium	346146.224	53			
	V. myrtilloides	480495.788	42			

Appendix 1.16. Summary of univariate analyses of variance for leaf dry matter content of four common understory species in gaps and along transects in unharvested stands.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	*Clintonia borealis*	1862.233	4	465.558	5.889	0.001
	Cornus canadensis	63791.216	4	15947.804	4.147	0.005
	V. angustifolium	40456.259	4	10114.065	20.251	<0.001
	V. myrtilloides	28278.687	4	7069.672	30.422	<0.001
Intercept	*Clintonia borealis*	10435.269	1	10435.269	131.999	<0.001
	Cornus canadensis	102508.821	1	102508.821	26.654	<0.001
	V. angustifolium	94231.803	1	94231.803	188.680	<0.001
	V. myrtilloides	70787.257	1	70787.257	304.608	<0.001
Treatment	*Clintonia borealis*	1862.233	4	465.558	5.889	0.001
	Cornus canadensis	63791.216	4	15947.804	4.147	0.005
	V. angustifolium	40456.259	4	10114.065	20.251	<0.001
	V. myrtilloides	28278.687	4	7069.672	30.422	<0.001
Error	*Clintonia borealis*	4110.901	52	79.056		
	Cornus canadensis	265370.888	69	3845.955		
	V. angustifolium	22973.610	46	499.426		
	V. myrtilloides	8365.960	36	232.388		
Total	*Clintonia borealis*	18578.333	57			
	Cornus canadensis	453785.053	74			
	V. angustifolium	187692.472	51			
	V. myrtilloides	118368.225	41			
Corrected Total	*Clintonia borealis*	5973.135	56			
	Cornus canadensis	329162.103	73			
	V. angustifolium	63429.869	50			
	V. myrtilloides	36644.647	40			

Appendix 1.17. Multiple linear regression models for specific leaf area and leaf dry matter content.

Dependent Variable	Predictor Variable	Unstandardized Coefficients		Standardized Coefficients	t	Sig.	R^2
		B	Std. Error	(Beta)			
Ln (Specific Leaf Area)	Constant	5.314	0.067		79.704	<0.001	0.186
	Ln (Gap area)	-0.058	0.017	-0.431	-3.346	0.002	
Leaf Dry Matter Content	Constant	26.405	2.669		9.894	<0.001	0.232
	Gap area	0.140	0.029	0.481	4.878	<0.001	

Appendix 1.18. Species list of understory plants surveyed June-August 2008 near White River, ON.

Species

Trees	**Shrubs cont'd**	**Shrubs cont'd**
Abies_balsamea	*Gaultheria_procumbens*	*Viburnum_edule*
Acer_rubrum	*Ledum_groenlandicum*	*Viburnum_trilobum*
Betula_papyrifera	*Linnaea_borealis*	
Larix_laracina	*Lonicera_sp*	
Picea_glauca	*Prunus_pensylvanica*	
Picea_mariana	*Prunus_virginiana*	
Pinus_banksiana	*Ribes_glandulosum*	
Populus_tremuloides	*Ribes_hirtellum*	
Shrubs	*Ribes_triste*	
Acer_spicatum	*Rosa_acicularis*	
Alnus_crispa	*Rubus_acaulis*	
Alnus_incana	*Rubus_idaeus*	
Amelanchier_sp	*Rubus_pubescens*	
Chamaedaphne_calyculata	*Salix_discolor*	
Cornus_stolonifera	*Salix_sp*	
Corylus_cornuta	*Sambucus_racemosa*	
Diervilla_lonicera	*Sorbus_decora*	
Epigea_repens	*Vaccinium_angustifolium*	
Gaultheria_hispidula	*Vaccinium_myrtilloides*	

Appendix 1.18. Cont'd

Herbs

Apocynum_androsaemifolium
Aralia_hispida
Aralia_nudicaulis
Aster_macrophyllus
Aster_nemoralis
Clintonia_borealis
Coptis_trifolia
Cornus_canadensis
Drosera_rotundifolia
Epilobium_angustifolium
Eupatorium_maculatum
Fragaria_virginiana
Gallium_asperellum
Gallium_triflorum
Goodyera_repens
Iris_versicolor
Lycopus_uniflorus
Mainthemum_canadense
Melampyrum_lineare
Mentha_arvensis
Mertensia_paniculata
Mitella_nuda
Monotropa_uniflora
Myrica_gala
Petasites_frigidus
Polygonum_cilinode
Potentilla_palustris
Scutellaria_galericulata
Solidago_uliginosa
Spirea_sp
Streptopus_roseus
Thalictrum_dasycarpum
Trientalis_borealis
Trillium_cernum
Viola_blanda
Viola_renifolia
Viola_septentrionalis

Graminoids

Agrostis_gigantean
Bromus_ciliatus
Calamagrostis_canadensis
Cinna_latifolia
Graminoid_sp
Carex_disperma
Carex_intumescens
Carex_michauxiana
Carex_sp
Carex_trisperma
Deschampsia_flexiosa
Elymus_repens
Eriophorum_angustifolium
Juncus_sp
Scirpus_atrovirens
Scirpus_sp

Pteridophytes

Athyrium_filix-femina
Equisetum_pratense
Equisetum_sylvaticum
Dryopteris_carthusiana
Gymnocarpium_dryopteris
Lycopodium_annotinum
Lycopodium_clavatum
Lycopodium_dendroideum
Lycopodium_digitatum
Lycopodium_lucidulum
Osmunda_claytoniana
Phegopteris_connectilis
Pteridium_aquilinum

Bryophytes

Aulacomnium_palustre
Brachythecium_sp
Callicladium_haldanianum
Ceratodon_purpureus
Climacium_dendroides
Dicranum_flagellare
Dicranum_fuscescens
Dicranum_montanum
Dicranum_polysetum
Dicranum_scoparium
Dicranum_sp
Hypnum_pallescens
Plagiomnium_medium
Pleurozium_schreberi
Ptilium_crista-castrensis
Rhizomnium_pseudopunctatum
Rhizomnium_punctatum
Rhodobryum_roseum
Rhytidiadelphus_triquetrus
Sanionia_uncinata
Scorpidium_scorpiodes
Sphagnum_angustifolium
Sphagnum_capillifolium
Sphagnum_fuscum
Sphagnum_girgensohnii
Sphagnum_magellanicum
Sphagnum_rivular
Sphagnum_squarosum
Thuidium_delicatulum

Lichens

Cladina_mitis
Cladina_rangiferina
Cladina_sp
Cladonia_cristatella
Cladonia_sp
Hypogymnia_physodes
Parmelia_sulcata
Usnea_sp.

Appendix 2.1. Summary table of MRPP results testing the difference in tree seedling/sapling composition among gaps, unharvested buffers, and reference forest.

		T	A	p
Observed delta Expected delta	9532.8167 11308.267	-9.6278666	0.15700463	<0.00100037

Appendix 2.2. Multivariate analysis of variance of tree seedling/sapling stem density in gaps, unharvested buffers, and reference forest.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.	Observed power
Corrected Model	A. balsamea	23.874	4	5.969	10.892	<0.001	1.000
	B. papyrifera	0.177	4	0.044	3.305	0.016	0.814
	Picea glauca	0.034	4	0.008	1.464	0.223	0.430
	Picea mariana	5.195	4	1.299	7.399	<0.001	0.994
	Populus tremuloides	0.187	4	0.047	0.829	0.511	0.251
Intercept	A. balsamea	55.480	1	55.480	101.247	<0.001	1.000
	B. papyrifera	0.347	1	0.347	25.938	<0.001	0.999
	Picea glauca	0.088	1	0.088	15.398	<0.001	0.972
	Picea mariana	7.995	1	7.995	45.550	<0.001	1.000
	Populus tremuloides	0.362	1	0.362	6.411	0.014	0.704
Treatment	A. balsamea	23.874	4	5.969	10.892	<0.001	1.000
	B. papyrifera	0.177	4	0.044	3.305	0.016	0.814
	Picea glauca	0.034	4	0.008	1.464	0.223	0.430
	Picea mariana	5.195	4	1.299	7.399	<0.001	0.994
	Populus tremuloides	0.187	4	0.047	0.829	0.511	0.251
Error	A. balsamea	36.166	66	0.548			
	B. papyrifera	0.882	66	0.013			
	Picea glauca	0.378	66	0.006			
	Picea mariana	11.584	66	0.176			
	Populus tremuloides	3.730	66	0.057			

Appendix 2.2. Cont'd

Source	Dependent Variable	Type III Sum of Squares	df
Total	*A. balsamea*	101.778	71
	B. papyrifera	1.345	71
	Picea glauca	0.486	71
	Picea mariana	21.468	71
	Populus tremuloides	4.365	71
Corrected Total	*A. balsamea*	60.040	70
	B. papyrifera	1.059	70
	Picea glauca	0.411	70
	Picea mariana	16.779	70
	Populus tremuloides	3.917	70

Appendix 2.3 a: R-squared for Axis 1 and Axis 2 of a non-metric multidimensional scaling ordination of juvenile tree species using Sorensen (Bray-Curtis) distance measure.

	R-Squared	
Axis	Increment	Cumulative
1	0.446	0.446
2	0.403	0.848

Appendix 2.3 b: Othogonality of a non-metric multidimensional scaling ordination of juvenile tree species using Sorensen (Bray-Curtis) distance measure.

Axis pair	r	Orthogonality,% = $100(1-r^2)$
1 vs 2	0.101	99.0

Appendix 2.4: Correlations of variables with ordination axes.

	Axis 1			Axis 2		
Environmental Variable	r	r-squared	tau	r	r-squared	tau
Gap area	-0.319	0.102	-0.356	-0.351	0.123	-0.342
Canopy Openness	-0.348	0.121	-0.284	-0.267	0.072	-0.233
Soil Moisture	0.119	0.014	0.125	0.005	<0.001	-0.032
Surface temperature	0.046	0.002	0.096	0.091	0.008	0.052
Air temperature	-0.209	0.044	-0.184	0.124	0.015	0.017
Relative humidity	0.284	0.081	0.211	0.013	<0.001	-0.018
PAR	-0.325	0.106	-0.222	-0.029	0.001	-0.043
Overstory Species						
A. balsamea	0.299	0.090	0.236	-0.434	0.189	-0.282
B. papyrifera	0.167	0.028	0.099	0.150	0.022	0.070
Picea glauca	0.279	0.078	0.205	0.052	0.003	0.051
Picea mariana	-0.205	0.042	-0.179	0.014	<0.001	0.019
Populus tremuloides	0.108	0.012	0.169	-0.506	0.256	-0.169
Seedling/Sapling						
A. balsamea	0.818	0.669	0.824	0.280	0.078	0.158
B. papyrifera	0.011	<0.001	-0.098	0.190	0.036	0.045
Picea glauca	0.260	0.068	-0.021	0.348	0.121	0.149
Picea mariana	0.306	0.093	0.083	0.569	0.324	0.721
Populus tremuloides	0.106	0.011	0.045	-0.710	0.505	-0.427

Appendix 2.5: Indicator species analysis of plot types (small gaps, medium gaps, large gaps, unharvested control buffers, and undisturbed reference forests) using juvenile tree species.

| Species | Max. Group | Observed Indicator Value (IV) | IV from randomized groups | | Significance (p) |
			Mean	Standard deviation	
A. balsamea	Reference	44.7	29.4	4.38	0.0050
B. papyrifera	Control	26.9	22.6	6.85	0.2200
Picea glauca	Reference	13.1	20.7	7.41	0.9008
Picea mariana	Reference	45.7	29.6	6.99	0.0292
Populus tremuloides	Large gap	9.5	14.4	6.93	0.7522

Appendix 2.6. Multiple linear regression model for the proportion of hardwood and conifer seedlings/saplings in gaps and unharvested stands.

| Dependent Variable | Predictor Variable | Unstandardized Coefficients | | Standardized Coefficients | t | Sig. | R^2 |
		B	Std. Error	(Beta)			
H:C	Constant	-0.568	0.489		-1.161	0.250	
	Populus tremuloides	26.343	6.261	0.446	4.207	<0.001	0.253
	Gap area	0.012	0.004	0.282	2.660	0.010	

Appendix 2.7 a: Kruskal-Wallis test of significant difference in juvenile tree height among plot types (small gaps, medium gaps, large gaps, unharvested control buffers, and undisturbed reference forests).

	A. balsamea	B. papyrifera	Picea glauca	Picea mariana	Populus tremuloides
Chi-Square	3.594	2.157	6.862	14.022	6.397
Degrees of freedom	4	4	4	4	3
Asymp. Significance (p)	0.464	0.707	0.143	0.007	0.094

Appendix 2.7 b: Mann-Whitney U tests were used to identify significant differences in *Picea mariana* juvenile tree height among plot types (small gaps, medium gaps, large gaps, unharvested control buffers, and undisturbed reference forests).

	Med vs Ref	Med vs Large
Mann-Whitney U	22.500	25.500
Wilcoxon W	50.500	53.500
Z	-3.024	-2.875
Asymp. Sig. (2-tailed)	0.002	0.004
Exact Sig. [2*(1-tailed Sig.)]	0.003	0.005

Appendix 2.8 a: Kruskal-Wallis test of significant difference in juvenile tree basal diameter among plot types (small gaps, medium gaps, large gaps, unharvested control buffers, and undisturbed reference forests).

	A. balsamea B. papyrifera	Picea glauca	Picea mariana	Populus tremuloides
Chi-Square	11.163	1.603	5.207	16.599	5.343
Degrees of freedom	4	4	4	4	3
Asymp. Significance (p)	0.025	0.808	0.267	0.002	0.148

Appendix 2.8 b: Mann-Whitney U tests were used to identify significant differences in *A. balsamea* juvenile tree basal diameter among plot types (small gaps, medium gaps, large gaps, unharvested control buffers, and undisturbed reference forests).

	Small vs Con	Med vs Large	Med vs Con	Con vs Ref
Mann-Whitney U	9.000	92.000	20.000	6.000
Wilcoxon W	30.000	170.000	41.000	27.000
Z	-2.412	-2.010	-2.800	-2.143
Asymp. Sig. (2-tailed)	0.016	0.044	0.005	0.032
Exact Sig. [2*(1-tailed Sig.)]	0.015	0.045	0.003	0.035

Appendix 2.8 c: Mann-Whitney U tests were used to identify significant differences in *Picea mariana* juvenile tree basal diameter among plot types (small gaps, medium gaps, large gaps, unharvested control buffers, and undisturbed reference forests).

	Small vs Ref	Med vs Ref
Mann-Whitney U	3.000	4.00
Wilcoxon W	31.000	32.000
Z	-2.893	-3.652
Asymp. Sig. (2-tailed)	0.004	<0.001
Exact Sig. [2*(1-tailed Sig.)]	0.002	<0.001

Appendix 2.9 a: Significant Spearman correlations between regeneration variables and environmental variables.

Regeneration Variable		Spearman Correlation Coefficient	Environmental Variable	Sig.
Juvenile stem density (stems/ha)	Proportion of hardwoods	+0.329	Soil temperature	0.026
	A. balsamea	+0.329	Relative humidity	0.012
		-0.476	Gap area	<0.001
	Picea mariana	-0.480	Gap area	<0.001
		-0.520	Soil moisture	0.027
	Populus tremuloides	-0.318	Surface temperature	0.023
		-0.357	Air temperature	0.006
Abies balsamea	Stems 0-0.5 m tall	-0.545	Gap area	<0.001
		-0.363	Soil temperature	0.009
	Stems 0.5-2 m tall	-0.401	Gap area	0.001
		-0.363	Soil temperature	0.012
	Stems >2 m tall	-0.321	Gap area	0.006
Betula papyrifera	Stems 0.5-2 m tall	-0.317	Relative humidity	0.015
	Maximum diameter	-0.560	Soil temperature	0.008
Picea glauca	Stems >2 m tall	-0.319	Soil temperature	0.029
	Maximum height	-0.416	Gap area	0.028
Picea mariana	Stems 0-0.5 m tall	-0.404	Gap area	<0.001
		-0.263	Relative humidity	0.046
	Stems 0.5-2 m tall	-0.367	Gap area	0.002
	Maximum diameter	+0.378	Gap area	0.012
Populus tremuloides	Stems 0-0.5 m tall	-0.242	Gap area	0.042
		-0.386	Surface temperature	0.005
	Stems 0.5-2 m tall	-0.414	Air temperature	0.001
		-0.267	PAR	0.043
	Stems >2 m tall	-0.339	Surface temperature	0.015
		-0.352	Air temperature	0.007
	Maximum height	+0.536	Gap area	0.048
	Maximum diameter	+0.541	Gap area	0.046

Appendix 2.9 b: Significant Spearman correlations between regeneration variables and overstory composition.

Regeneration Variable		Spearman Correlation Coefficient	Overstory Species	Sig.
Juvenile stem density (stems/ha)	A. balsamea	+0.274	A. balsamea	0.021
		+0.261	Picea spp.	0.028
	B. papyrifera	-0.270	Populus tremuloides	0.023
		-0.263	A. balsamea	0.027
	Picea glauca	-0.349	Populus tremuloides	0.003
	Picea mariana	-0.297	A. balsamea	0.012
	Populus tremuloides	+0.419	A. balsamea	0.013
		+0.409	Populus tremuloides	<0.001
Abies balsamea	Stems 0-0.5 m tall	+0.287	Picea spp.	0.015
		+0.295		0.012
	Stems 0.5-2 m tall	+0.278	A. balsamea	0.019
	Stems >2 m tall	+0.287		0.015
	Maximum height	+0.262		0.031
	Maximum diameter	+0.781		0.010
Betula papyrifera	Stems 0.5-2 m tall	-0.334	B. papyrifera	0.004
Picea glauca	Stems 0-0.5 m tall	-0.234		0.050
	Stems 0.5-2 m tall	-0.288	Populus tremuloides	0.015
	Maximum height	+0.455		0.015
Picea mariana	Stems 0-0.5 m tall	+0.824	Picea spp.	<0.001
		-0.294	Populus tremuloides	0.013
	Stems 0.5-2 m tall	-0.278	A. balsamea	0.019
	Stems >2 m tall	-0.284		0.016
	Maximum height	-0.319	Picea spp.	0.020
	Maximum diameter	-0.315		0.047
		-0.304	A. balsamea	0.040
Populus tremuloides	Stems 0-0.5 m tall	+0.299	Picea spp.	0.011
		+0.250	A. balsamea	0.036
		+0.373		0.001
	Stems 0.5-2 m tall	-0.284	B. papyrifera	0.016
		+0.430	Populus tremuloides	<0.001
	Stems >2 m tall	+0.306	A. balsamea	0.010

Appendix 2.9 c: Significant Spearman correlations among tree seedlings and saplings.

Regeneration Variable		Spearman Correlation Coefficient	Juvenile Tree Species	Sig.
Juvenile stem density (stems/ha)	Proportion of hardwoods	-0.342	*A. balsamea*	0.004
		+0.612	*B. papyrifera*	<0.001
		-0.355	*Picea mariana*	0.003
		+0.552	*Populus tremuloides*	<0.001
	Populus tremuloides	-0.329	*Picea mariana*	0.005
Abies balsamea	Stems 0-0.5 m tall	+0.686	*A. balsamea*	<0.001
		-0.390	*B. papyrifera*	0.001
		+0.323	*Picea mariana*	0.006
	Stems 0.5-2 m tall	+0.573	*A. balsamea*	<0.001
		-0.258	*B. papyrifera*	0.030
		+0.239	*Picea mariana*	0.045
	Stems >2 m tall	+0.369	*A. balsamea*	0.002
		-0.251	*B. papyrifera*	0.035
Betula papyrifera	Stems 0-0.5 m tall	+0.234	*B. papyrifera*	0.049
	Stems 0.5-2 m tall	+0.567		<0.001
	Stems >2 m tall	+0.551		<0.001
	Maximum height	+0.440		0.007
	Maximum diameter	+0.366		0.033
Picea glauca	Stems 0-0.5 m tall	+0.587	*Picea glauca*	<0.001
	Stems 0.5-2 m tall	+0.746		<0.001
		+0.312	*Picea mariana*	0.008
	Stems >2 m tall	+0.244	*Picea glauca*	0.040
Picea mariana	Stems 0-0.5 m tall	+0.824	*Picea mariana*	<0.001
		-0.294	*Populus tremuloides*	0.013
	Stems 0.5-2 m tall	-0.373		0.001
		+0.828	*Picea mariana*	<0.001
	Stems >2 m tall	+0.298		0.012
	Maximum diameter	-0.387	*A. balsamea*	0.010
Populus tremuloides	Stems 0-0.5 m tall	+0.353	*Populus tremuloides*	0.003
	Stems 0.5-2 m tall	-0.374	*Picea mariana*	0.001
		+0.780	*Populus tremuloides*	<0.001
	Stems >2 m tall	+0.599		<0.001
		-0.241	*A. balsamea*	0.043
	Maximum diameter	+0.576	*B. papyrifera*	0.031