UNIVERSITY OF QUÉBEC IN MONTRÉAL

ABUNDANCE AND GROWTH OF SHRUB AND TREE SPECIES IN THE BALSAM FIR – YELLOW BIRCH DOMAIN, UNDER VARYING LEVELS OF LANDSCAPE SPATIAL HETEROGENEITY

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ABONDANCE ET CROISSANCE DES ARBRES ET ARBUSTES DANS LA SAPINIÈRE À BOULEAU JAUNE EN FONCTION DE DIFFÉRENTS NIVEAUX D'HÉTÉROGÉNÉITÉ SPATIALE DU PAYSAGE

MÉMOIRE
PRÉSENTÉE
COMME EXIGENCE PARTIELLE
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PAR
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QUOTES

"All we can do is to search for the falsity content of our best theory."

- Karl Popper

"From this evolutionary perspective, what really determines the species richness of shade tolerant and gap species in a particular local tree community is the richness of the regional species pool and the abundance of shady and gap habitats in the metacommunity over long periods of time."

- Stephen Hubbell, 2005

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RÉSUMÉ GÉNÉRAL

Traditionnellement, les décisions en écologie sont prises en présumant que la structure spatiale de peuplements forestiers est homogène. Or, dans la sapinière à bouleau jaune, la mortalité individuelle des arbres et les perturbations qui génèrent des trouées, telles les épidémies de la tordeuse des bourgeons de l'épinette ou les coupes partielles, changent continuellement la structure spatiale interne des peuplements. Nous posons comme hypothèse que l'hétérogénéité spatiale joue un rôle important sur la dynamique des peuplements en modifiant la distribution spatio-temporelle de la lumière, ce qui a pour effet d'accentuer ou non l'abondance et la croissance d'arbustes qui peuvent intervenir sur la succession des arbres. Nous avons utilisé un indice d'hétérogénéité spatiale pour identifier 12 paysages de 1 km^2 présentant différents niveaux d'hétérogénéité (hétérogène, modéré et homogène). Dans ces paysages, des données d'abondance et de croissance d'espèces d'arbustes et de la régénération d'espèces d'arbres ont été prises dans des trouées de différentes tailles et sous couvert forestier. Nos résultats indiquent que le noisetier à long bec est deux fois plus abondant dans les paysages hétérogènes et que le bouleau jaune est trois fois plus abondant dans les paysages d'hétérogénéité modérée que dans les paysages fortement hétérogènes. Notre recherche indique que les forêts hétérogènes contiennent significativement moins d'arbres et plus d'arbustes en régénération que les paysages moins hétérogènes. Cependant, ni la compétition par les arbustes et ni la croissance de la régénération des arbres ne diffèrent entre les paysages avec différents niveaux d'hétérogénéité, suggérant que les mécanismes de dispersion et d'établissement seraient successibles d'être à la base des patrons observés.

GENERAL ABSTRACT

Traditionally, ecological studies have assumed that the spatial structures of forests are homogenous. However, in the Balsam fir – Yellow birch forest type, individual mortality, spruce budworm outbreaks and partial cuts continuously re-shape the forest structure at different scales. We propose that the spatial heterogeneity of forest structures at the landscape scale plays an important role in stand dynamics by influencing regeneration of both tree seedlings and shrubs and their subsequent growth. We hypothesize that the spatial heterogeneity of landscapes will be an indicator of the spatio-temporal distribution of light, that will then accentuate or not the growth and abundance of species. We used a spatial heterogeneity index to identify 12 landscapes of $1km^2$, presenting three different levels of heterogeneity (heterogeneous, moderate heterogeneity, homogenous). In these landscapes, abundance and growth data for shrub and tree species regeneration were taken in canopy gaps of various sizes and under forest cover. Our results indicate that hazelnut is two times more common in heterogeneous landscapes and that yellow birch is three times more abundant in moderate heterogeneity landscapes when compared to heterogeneous landscapes. Our results show that heterogeneous forests contain significantly less overall tree regeneration and that they also contain significantly more total amount of shrubs when compared to less heterogeneous forests. However, neither the competition from shrubs, nor the growth of tree and shrub regeneration, were different in the landscape heterogeneity levels. This may mean that dispersal and establishment mechanisms may be important toward the observed patterns.

CHAPTER I

GENERAL INTRODUCTION

1.1 Introduction

Current forest management and underlying silvicultural theory, are not operating at the same level of complexity as forest ecology (Puettmann et al. 2008). This is likely due to the biocomplexity observable from the macroscopic to the microbiotic spatial scales. We can define heterogeneity as "the spatially structured variability of a property of interest, which can be a categorical or quantitative" (Wagner and Fortin, 2005). The heterogeneous pattern observed in natural landscapes is due to the "underlying landform, climatic and edaphic conditions, disturbance regime, activities of living organisms, and cumulative historical events that have taken place over time" (Coulson and Tchakerian, 2010). Many attributes can be used in the characterization of the spatial heterogeneity of forests (McElhinny et al. 2005).

Due in part to spruce budworm outbreaks and the gap phase forest, the horizontal structure of the southern mixedwood forest is extremely complex and heterogeneous. Characterization of this heterogeneity can explain some of the variability inherent in forest dynamics. Landscape structures that are characterized as homogenous, would require a straightforward silvicultural prescription, landscape structures described as heterogeneous would benefit from a finely scaled human intervention that is consistent with the forest patch level of complexity. A greater amount of ground level manipulations would be required in heterogeneous stands, with the eventual goal of returning the forest to a more productive state.

1.2 Degraded stands in the Balsam fir – Yellow birch domain

Knowledge of appropriate management of mixedwood dynamics and regeneration practices are not conclusive (Prévost et al. 2003). With regards to yellow birch, this might be because it has not been sufficiently studied in the northern part of its range (Gastaldello et al. 2007). The over simplification of past management practices treated mixed stands as pure stands (Prévost et al. 2003). The management difficulties in the mixedwood forest include the challenge of maintaining mixedwood status after interventions, as the composition tends toward hardwood or softwood content (Kneeshaw and Prévost, 2007). In the Québec mixedwood forests, hardwood content has been shown to increase at the expense of softwood content (Doyon and Varady-Szabo, 2012). Specifically, partial cutting in this bioclimatic domain has increased the abundance of tolerant hardwood species (Doyon and Varady-Szabo, 2012). Also, the reduction of old forests results in a simplification of the age structure of the forests (Doyon and Varady-Szabo, 2012). Interventions in this region are difficult because of the differences in reproduction methods, growth rates, shade tolerances and longevity amongst species (Prévost et al. 2003). Complications also arise when considering species specificity for soil types, drainage regimes and differential survival after disturbances (Prévost et al. 2003). Some of the most important factors limiting the productivity of yellow birch include the ecological site suitability, harvest timing, residual forest cover, seed tree availability and germination microsites (Nolet et al. 2001).

Contributing to the open canopy structure that is susceptible to degradation in our particular study area was high graded diameter limit harvests (selection of high quality stems) conducted from the 1960s to the 1980s and the latest spruce budworm outbreak (Sabbagh et al. 2002, Doyon and Lafleur, 2004). The spruce budworm outbreak of the 1970s increased light levels to the benefit of competitive species (Prévost et al. 2003). Until the 1980s, the use of diameter limit harvesting methods throughout the northeast of North America degraded numerous yellow birch stands (Metzger and Tubbs, 1971). Efforts to regenerate yellow birch could be hampered by the low vigor of residual seed trees after diameter limit harvesting (Bédard and Majcen, 2003). This cutting method often resulted in high-grading, wherein forestry operations would harvest the trees with the greatest genetic fitness, thus denying them the chance to seed-in future generations of trees (Bédard and Majcen, 2003). High-grading and spruce budworm outbreaks resulted in yellow birch stands with a meager volume of 30 to 50m³/ha and large amounts of non-commercial competitive species (Prévost et al. 2003). Heavily cut areas due to diameter limit cutting suffered a decline in seedling and sapling stocking, potentially resulting in as much as half of the study quadrats being dominated by shrubs (Metzger and Tubbs, 1971). In the absence of human activity, these forests can have a volume at stand maturity of 200 m³/ha (Prévost et al. 2003).

Degraded sites have an open forest canopy structure with a recalcitrant, dense shrub underlayer (*sensu* Royo and Carson, 2006). Competition from non-commercial species such as mountain maple, beaked hazelnut and hobblebush (*Viburnum alnifolium*) will be established as advance regeneration under the canopy (Prévost, 2008). Other competitive species such as pin cherry (*Prunus pennsylvanica*) and raspberry (*Rubus idaeus*) will rely on the seed bank (Prévost, 2008). The potential area of degradation is extensive especially in the mixedwood forest, as mountain maple is distributed in all but pure conifer and tolerant hardwood stands (Vincent, 1965). Mountain maple can persist in the understory for up to 60 years (Vincent, 1965). The seedlings of white spruce and balsam fir were less abundant and were smaller in height when in the presence of competitive shrubs such as mountain maple (Kneeshaw et al. 2012). Other reports indicate that in the boreal mixedwood forest, mountain maple can persist through all stages of succession (Aubin et al. 2005). Harvesting, especially clearcutting, has been found to contribute to the spread of the shrub mountain maple (Archambault et al. 1998). Species diversity at the stand and patch level have been found to decrease due to high shrub stocking and high hazelnut density after logging, when compared to natural disturbances (Kemball et al. 2005). Hazelnut has been shown to respond in greater densities after logging than after fire or spruce budworm outbreak (Kemball et al. 2005).

1.3 Disturbance and succession

The Balsam fir – Yellow birch mixedwood forest covers an area larger than 86 500 km² (Ministère des Resources Naturelles du Québec, 1994). Prominent tree species include balsam fir (*Abies Balsamea*), white spruce (*Picea glauca*), yellow birch (*Betula alleghaniensis*) and white birch (*Betula papyrifera*). Balsam fir is a shade tolerant, large seeded conifer that may live until 200 years and is considered late successional, with a regeneration strategy of saturating the forest understory with seedlings (Burns and Honkala, 1990, Kneeshaw and Prévost, 2007). The intermediately shade tolerant white spruce is a late succession species that can live up to 350 years of age and seldom disperses its seed farther than 50m (Burns and Honkala, 1990). Yellow birch is intermediately shade tolerant, it produces small well dispersed seeds, and it succeeds in succession due to its longevity (350 years) (Burns and Honkala, 1990, Kneeshaw and Prévost, 2007). White birch produces small well dispersed seeds and also reproduces vegetatively from basal sprouts, it is a shade intolerant pioneer species, and is short lived, rarely surpassing 140 years of age (Burns and Honkala, 1990). The midtolerant shrub mountain maple (*Acer spicatum*) mainly reproduces by basal sprouts and stem layering and can reach a maximum age of 53 years (Jobidon, 1995, Archambault et al. 1998, Humbert et al. 2007). Hazelnut (*Corylus cornuta*) is able to reproduce by seed (large seeds predated on and dispersed by small mammals) or by underground roots, it is midtolerant and has a life expectancy of up to 40 years (Jobidon, 1995, Humbert et al. 2007).

Gap dynamics in the Balsam fir – Yellow birch bioclimatic domain are caused by tree senescence, insect epidemics and windthrow (Prévost et al. 2003). The natural fire cycle in western Québec is approximately 188 to 314 years, with historically longer fire cycles in the south and the east (Grenier et al. 2005). Major spruce budworm outbreaks have occurred in the region in 1910, 1945 and 1980 (Bouchard et al. 2006). The spruce budworm outbreak in 1910 appeared to have been mild in northern and southern regions, the outbreak in 1950 appeared to cause high levels of mortality in the southern region and the 1980 outbreak appeared to have caused heavy mortality in the northern region (Bouchard et al. 2007). Spruce budworm outbreaks can lead to "a stand replacing effect in balsam fir-dominated stands, to the emergence of multi-level canopy structures in mixed boreal stands and quasi-gap dynamics in mixed hardwood stands" (Bouchard et al. 2005). White birch and balsam fir appear to be correlated with mixed boreal stands, whereas hazelnut, red maple and mountain maple were more abundant in mixed hardwood stands (Pominville et al. 1999, Bouchard et al. 2005). Older forests may be more susceptible to insect outbreak because of the increased conifer content and aging balsam fir stands that are less vigorous (Pominville et al. 1999, Kneeshaw et al. 2012).

Partial cutting has been found to restrain mountain maple abundance and allow it to increase its cover for only a couple of years (Bourgeois et al. 2004). Selection cutting however, may not meet the regeneration requirements of yellow birch or white spruce, species that require the creation of canopy gaps through group selection cutting. Although white birch is typically considered an early succession species, it has also been reported to represent the majority of hardwood content in older mixedwood stands, perhaps due to its well-dispersed seed or sprouting ability (Prévost et al. 2003, Frelich and Reich, 1995). It is possible that the character of the southern mixed forest, and valuable tree species such as yellow birch would not be expected to return to the forest for 250 years after clearcutting (Hébert, 2003). After stand replacing fires, balsam fir and white cedar (*Thuja occidentalis*), both species that have poor seed dispersal and use layering to reproduce, will slowly gain in importance over the next 150-200 years (Burns and Honkala, 1990, Frelich and Reich, 1995). White spruce is very susceptible to fire, as its seed source is eliminated within the burnt area (Burns and Honkala, 1990). Although most ecologists believe that yellow birch reproduces primarily in small and medium sized gaps, some evidence suggests that the species may be maintained by large disturbances (Woods, 2000).

1.4 Gap ecology

In openings larger than 400m², yellow birch will face greater competition and only be found around the patch edges (Zillgit and Eyre, 1945, Eyre and Zillgit, 1953). A literature review recommends gap openings of 400m² to 2400m² for yellow birch regeneration (Burns and Honkala, 1990). Conversely, it has also been found that 5000m² was the maximum gap size to regenerate yellow birch (Prévost, 2008). Other work shows yellow birch regeneration density to increase with increasing gap sizes over 800m² (Kneeshaw and Prévost, 2007). Anthropogenic gaps may result in more yellow birch microsites due to soil scarification. Successful yellow birch regeneration seems to require a tradeoff between favorable large gap sizes and unfavorable competition from shrubs. Balsam fir seedling density has been found to be negatively associated with increasing gap sizes (Kneeshaw and Bergeron 1998). Birch and white spruce reacted positively to increasing gap size (Kneeshaw and Bergeron 1998). Mountain maple, red maple and hobblebush regeneration density increased with increasing gap size (Kneeshaw and Prévost, 2007). Total shrubs in the largest size class also increased with increasing gap size (Kneeshaw and Prévost, 2007).

The gap partition hypothesis suggests that canopy gaps of different sizes or various positions within gaps may lead to microclimates and species specialization (Kneeshaw and Bergeron, 1999, Raymond et al. 2006). In southern boreal forests, seedlings and saplings of balsam fir and white cedar have been associated with the southern part of canopy gaps, while aspen was more abundant in the north of gaps (Kneeshaw and Bergeron, 1999). In another study located in the Sugar maple - Yellow birch bioclimatic domain, yellow birch seedlings were found to be more abundant in the southwest and northwest of gap locations compared to the east (Raymond et al. 2006). The centre and north of the gaps are subject to temperature extremes (Raymond et al. 2006). Yellow birch seedlings in particular have better survival along the edges of the openings, likely due to reduced water stress (Prévost et al. 2010).

The optimal regeneration niche may be confronted with such paradoxes as the possible requirement for moisture to aid germination, but light to allow for canopy admittance. Essentially, the location with increased light does not correspond to the location with increased water. Over time, the different stages of tree development may display different optimal responses to the resource levels available within different positions in a gap as well as within different gap sizes. Gaps also change over time, with peak light levels in large gaps being in the middle of a gap, while in smaller gaps peak light levels are closer to the north (Gendreau-Berthiaume and Kneeshaw, 2009).

1.5 Landscape heterogeneity of spatial structures

The forest structure is complex in part due to: competition, different plant functional traits, environmental factors, disturbances and interactions with animals (McElhinny et al. 2005). The internal structure of natural stands is likely to be more complex than managed stands (Kuuluvainen et al. 1996). Patch heterogeneity is typically a characteristic of landscapes (Coulson and Tchakerian, 2010). Intact landscapes have fewer, large matrix areas, whereas disturbed landscapes have large quantities of smaller patches (Mladenoff et al. 1993). At the landscape scale, an early successional forest may have a greater number of forest types, smaller patch sizes and a smaller range of patch sizes giving it more heterogeneous patterns than an old growth forest (Mladenoff et al. 1993). There appears to be more patches in disturbed landscapes, and patch complexity was found to be lower in disturbed landscapes when compared to old growth forests (Mladenoff et al. 1993).

Some controversy surrounds the debate on whether structural heterogeneity confers biological diversity (Neumann and Starlinger, 2001). One study specifies the stage between forest perforation and forest fragmentation, wherein both early succession and late succession species would mingle, to consequently be of high species richness (Spies et al. 1994). However, heterogeneity of forest canopies has been shown to foster biodiversity and habitat creation in the short term. A large diversity of patches, at a fine scale (0.1 to 0.5ha), contribute to a high abundance of species, when compared to large homogenous patches (Carey, 2003). Even-aged management reduces spatial heterogeneity and biodiversity (Carey, 2003). In another study, high structural complexity was also shown to be positively associated with the richness of plant species (Proulx and Parrott, 2008). Stands composed of a large variety of tree heights are likely to contain higher diversity of species (Zenner, 2000). High heterogeneity of horizontal and vertical stand structures increases biodiversity (Pommerening, 2002). In summary, Coulson and Tchakerian (2010) state that "reduced habitat heterogeneity and fragmentation diminish species diversity".

1.6 Plant community processes in heterogeneous environments

Patch size may influence whether the available resources within a patch are sufficient for the survival, growth, reproduction and persistence of a particular organism (Coulson and Tchakerian, 2010). Large patches would provide protection from extreme weather events, thus providing large organisms, with long life spans, slow development and low rates of population growth (k-strategists) a refuge (Coulson and Tchakerian, 2010). Conversely, small patches that are more vulnerable to extreme weather events may be populated by small organisms, with short life spans, fast development and high rates of population growth (r-strategists or edge species) (Coulson and Tchakerian, 2010).

The term metapopulation can be defined as the extinction, establishment and interaction of local populations (Hanski and Gilpin, 1991). The size of a metapopulation can be the number or proportion of occupied patches (Hanski and Gilpin, 1991). The proportion of patches occupied can be dependent on the size of local populations (Hanski and Gilpin, 1991). There is an important difference to be made regarding the dynamics between and within metapopulations (Kotliar and Wiens, 1990, Levin, 1992). Conceptual links can be made between metapopulation theory, island biogeography and inquiries on the dynamics of species in patchy environments (Hanski and Gilpin, 1991). Work done on island biogeography stated that species diversity on islands depended on colonization and extinction events: large islands would attract more colonists and also have lower rates of extinction (MacArthur and Wilson, 1967).

The spatial competition hypothesis (also know as the competitor - colonizer hypothesis) seeks to prove that the coexistence between species is enhanced by species investment in either competition (large seeds, poor dispersal ability, shade tolerance, long life span, vegetative reproduction) or dispersal (small seeds, dispersal ability, shade intolerant, short life span) (Tilman, 1994, Hubbell, 2005). In theory, there should be as many species as there are limiting resources (Tilman, 1994). However, when neighborhood competition and random dispersal are taken into account, multiple species coexistence is ensured even with only a single resource (Tilman, 1994). This coexistence is explained because greater dispersal of less competitive species ("fugitive species") persist in sites where superior competitors are not present (Tilman, 1994). Neighborhood interactions and local dispersal may increase intraspecific competition and decrease interspecific competition, and may in turn contribute to the coexistence of species (Tilman, 1994).

In the Yellow birch – Balsam fir domain, the inferior competitor yellow birch may be excluded from mountain maple invaded sites. Yellow birch would not be able to seed-in due to intense competition for light, and cannot grow as fast as vegetative shrubs. The vegetative shrubs would be dispersal limited compared to wind dispersed seeds. Once yellow birch reaches the canopy it is ensured dominance due to its long life span or large space occupancy ratio (Kneeshaw and Prévost, 2007). This example implies that large amounts of small patches and gap openings will create a heterogeneous landscape that may favor light loving, short lived, pioneer and clonal species.

1.7 Species growth

Mountain maple growth in newly formed canopy openings tended to be superior to balsam fir growth (Kneeshaw et al. 2012). Balsam fir seedlings have been documented to grow better under any tree species, when compared to growth under mountain maple (Kneeshaw et al. 2012). Seedlings of white spruce and fir grew to smaller heights in the presence of competitive shrubs, specifically mountain maple and total competition (Kneeshaw et al. 2012). Furthermore, balsam fir seedling mortality was higher under mountain maple (82%) when compared to mortality under other tree species (19%) (Kneeshaw et al. 2012). Because the light levels were similar under mountain maple cover, when compared to general tree species cover (5-15%), it was not clear if the increased mortality was due underground competition, or variability in gap size (> variability under mountain maple cover) (Kneeshaw et al. 2012).

Absolute values for height growth 20 years after clearcutting indicate average height for yellow birch and white birch to be > 4m, average height for mountain maple and balsam fir to be > 1m and < 2m, and average height of white spruce and sugar maple to be < 1m (Archambault et al. 1998). White birch attained an average height of 2.73m, whereas white spruce reached an average height of only 0.32m, 6 years after scarification (Delagrange and Nolet, 2009). This indicates that white spruce does not have the same growth strategy as another midtolerant species, the yellow birch. The height growth of white birch (30 to 45cm per year) and yellow birch (30 to 50cm per year) over five years was inferior to pin cherry (*Prunus pensylvanica*) (40 to 50cm per year) but superior to both mountain maple (30cm per year) and balsam fir (20 to 30cm per year) (Laflèche et al. 2000).

The greatest white spruce growth can be observed at full light, at 50% light levels, the height decreased by 25% in 10 year old seedlings (Burns and Honkala, 1990). White spruce was not able to survive in light levels below 15% (Burns and Honkala, 1990). Balsam fir growth is positively correlated with the photon flux density, with growth increasing with increasing exposure to sunlight (Parent and Messier, 1995). However, balsam fir growth becomes less correlated with increasing light levels, as it is believed that the influence of other factors (humidity, soil water and nutrients) on height growth are amplified (Parent and Messier, 1995). Some evidence suggests that mountain maple growth responds less well to light levels above 60% (Aubin et al. 2005). Yellow birch and sugar maple were shown to increase growth with increasing light, yellow birch was reported to have higher growth than sugar maple (Beaudet and Messier, 1998). Other studies indicate that yellow birch, sugar maple and red maple have a similar growth response in their first 50 years of growth (Burns and Honkala, 1990). Yellow birch can be expected to outperform sugar maple on poorly drained soils (Burns and Honkala, 1990).

1.8 Hypotheses

Our objective was to determine the role of landscape heterogeneity in influencing the abundance and growth of shrub and tree species. We base our work on the supposition that there is a causal chain wherein the landscape heterogeneity would affect local competition, which would in turn affect plant growth, plant survival and finally plant density (Figure 1.1).

Our first hypothesis, presented in Chapter 2, is that (1) heterogeneous landscapes contain a greater density of competitive shrubs, because of the greater concentration of gap openings present in heterogeneous landscapes. Because of this increased competition, tree species will be less abundant in heterogeneous landscapes than in homogenous ones. Tree populations will be more capable of colonizing homogenous sites than shrub populations, due to larger distances between the gap openings and greater dispersal capacities. Our measure of landscape heterogeneity is assumed to capture the previous dynamic of small disturbances that have occurred in the forest.

Our second hypothesis, presented in Chapter 3 is that (2) the growth of five key species: mountain maple, white birch, yellow birch, white spruce and balsam fir, will vary as a function of the levels of landscape spatial heterogeneity. We expect seedling growth to be negatively influenced in heterogeneous landscapes by a persistent understory shrub layer in canopy openings and under forest cover. To control the response of growth, we evaluate the effects of other factors, such as the gap position, competition, microtopography and browsing.

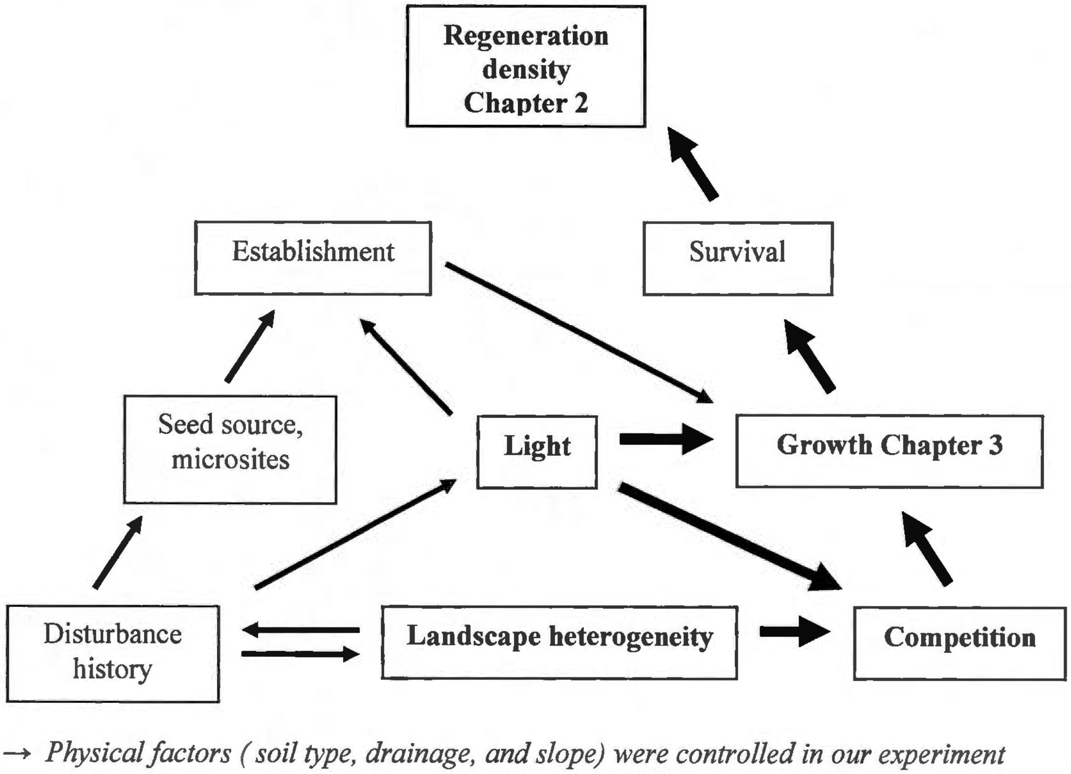


Figure 1.1. Conceptual model of the forest dynamics in the Balsam fir – Yellow birch bioclimatic domain

CHAPTER II

LANDSCAPE HETEROGENEITY OF FOREST STRUCTURES INTERACT WITH LOCAL FACTORS TO AFFECT TREE AND SHRUB REGENERATION DYNAMICS IN BALSAM FIR – YELLOW BIRCH FORESTS

2.1 Introduction

Modern silviculture is largely based on theories that may not be adapted to contemporary challenges in ecological thinking (Puettmann et al. 2008). A new philosophical and practical approach toward forest ecosystem management that views the forest as a complex adaptive system is required (Puettmann et al. 2008). The heterogeneous pattern observed in natural landscapes is due to the "underlying landform, climatic and edaphic conditions, disturbance regime, activities of living organisms, and cumulative historical events that have taken place over time" (Coulson and Tchakerian, 2010). We can define heterogeneity as "the spatially structured variability of a property of interest, which can be a categorical or quantitative" (Wagner and Fortin, 2005). Patch heterogeneity can typically be characteristic of landscapes (Coulson and Tchakerian, 2010).

The southern mixedwood forest exhibits predominantly small scale disturbances such as individual tree mortality, insect outbreaks and windthrow, which contribute to gap dynamics primarily responsible for the regeneration of trees (Prévost et al. 2003). Because mixedwood forests can contain species of different sizes and development stages, they can also be considered relatively heterogeneous, especially at the scale of silvicultural intervention (Prévost et al. 2003). The over simplification of past management practices treated mixed stands as pure stands (Prévost et al. 2003). The management difficulties in the mixedwood forest include the challenge of maintaining mixedwood status after interventions, as the composition tends toward hardwood or softwood content (Kneeshaw and Prévost, 2007). The heterogeneity of the forest structure was increased by high graded diameter limit harvests (selection of high quality stems) conducted from the 1960s to the 1980s and a recent spruce budworm outbreak (1980s) (Metzger and Tubbs, 1971, Sabbagh et al. 2002, Doyon and Lafleur, 2004).

Researchers suggest that the character of the southern mixedwood forest and valuable trees such as yellow birch (*Betula alleghaniensis*) would not return for up to 250 years after clearcutting (Hébert, 2003). Multiple studies identify disturbance as the causal factor in high competitive shrub abundances and the delayed return of tree species regeneration (Archambault et al. 1998, Laflèche et al. 2000, Kemball et al. 2005). Heavily cut areas have been found to display lower amounts of seedling and sapling stocking, and competitive shrub invasion (Metzger and Tubbs, 1971, Royo and Carson, 2006). Vegetative shrubs such as mountain maple (*Acer spicatum*) have been shown to persist through all successional stages (Aubin et al. 2005). Competition from shrub species such as mountain maple and beaked hazelnut (*Corylus cornuta*) will be pre-established as advance regeneration under the canopy (Prévost, 2008). It is possible that heterogeneous structures at the landscape level, are an indication of the accumulation of disturbance events, that may cause a buildup of vegetative shrub populations. We identify portions of the landscape as different heterogeneity levels. We presume that landscapes that demonstrate a greater heterogeneity of forest patches, are consequently more disturbed (Mladenoff et al. 1993).

To explain in part the dynamics of forest ecosystems, it is possible that plant species coexistence is maintained by species investment in either competition or dispersal abilities. This coexistence is explained because greater dispersal of less competitive species ("fugitive species"), persist in sites where superior competitors are not present (Tilman, 1994). The landscape heterogeneity of forest structures may confer differential oppurtunities for colonizers and competitors. Essentially, "what really determines the species richness of shade tolerant and gap species in a particular local tree community is the richness of the regional species pool and the abundance of shady and gap habitats in the metacommunity over long periods of time" (Hubbell, 2005). We are interested in the metapopulation, a term which can be defined as the extinction, establishment and interaction of local populations (Hanski and Gilpin, 1991). Important conceptual links have been made between metapopulation theory and island biogeography (Hanski and Ovaskainen, 2003). Work done on island biogeography stated that species diversity on islands depended on colonization and extinction events: large islands would attract more colonists and also have lower rates of extinction (MacArthur and Wilson, 1967). Similarly, large patches would provide protection from extreme weather events, thus allowing larger organisms, with longer life spans, slow development and low rates of population growth (k-strategists) a refuge (Coulson and Tchakerian, 2010). Conversely, small patches that are more vulnerable to extreme weather events may be populated by smaller organisms, with shorter life spans, fast development and high rates of population growth (r-strategists or edge species) (Coulson and Tchakerian, 2010).

Our research specifically looks at the effect that landscape level processes may have on local phenomena such as tree abundance. We propose the hypothesis that heterogeneous landscapes contain a greater density of competitive shrubs, because of the greater concentration of gap openings present in heterogeneous landscapes. The increased turnover rate of heterogeneous landscapes, allows latent understory shrub communities to persist and rapidly expand when presented with a canopy opening. Studies have shown that species as far away as 30m from a gap opening, may experience an increase in growth (Kneeshaw et al. 2012). Because of this increased shrub competition, tree species will be less abundant in heterogeneous landscapes than in homogenous ones. Tree populations will be more capable of colonizing homogenous sites than shrub populations, due to larger distances between the gap openings and greater dispersal capacities. Our measure of landscape heterogeneity is assumed to capture the previous dynamic of small disturbances that have occurred in the forest.

2.2 Methods

2.2.1 Study site

Our study site is located in the Réserve Faunique La Vérendrye, in between the boreal mixedwood forest to the north and the northern hardwood forest zones to the south, in the area corresponding to the Balsam fir – Yellow birch bioclimatic domain (Figure 2.1) (Saucier et al. 1998). The mixedwood forests in these areas are dominated by balsam fir

(*Abies balsamea*), yellow birch, white spruce (*Picea glauca*) and white birch (*Betula papyrifera*). Other species that occur in the area include black spruce (*Picea mariana*), white pine (*Pinus strobus*), white cedar (*Thuja occidentalis*), trembling aspen (*Populus tremuloides*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*) and large tooth aspen (*Populus grandidentata*). In the absence of fire, mesic-xeric hilltops are often dominated by sugar maple, upper slope mesic sites are mixed and dominated by yellow birch, lower slope mesic sites are dominated by conifer species (balsam fir or white cedar) and imperfectly drained sites are dominated by black spruce (Bouchard et al. 2006).

The mean annual precipitation at Maniwaki is 908.8mm (including 238.3cm as snow) and the mean annual temperature is 3.7 °C. The natural fire cycle in western Québec is approximately 188 to 314 years, with historically longer fire cycles in the south and the east (Grenier et al. 2005). Major spruce budworm outbreaks have occurred in the region in 1910, 1945 and 1980 (Bouchard et al. 2006). In northern Outaouais, the topography is flat with some small hills and an abundance of small lakes.

2.2.2 Landscape selection

Our study site consists of 12 sampled landscapes, 1km² in area, with 3 levels of heterogeneity: homogenous, moderate and heterogeneous. The heterogeneity index was applied to the entire study region, while the specific landscapes (1km²) were selected based on bio-physical conditions using ArcGIS (ESRI 2006) (Table 2.1). Our selection process included measures to reduce environmental heterogeneity. Our first criterion was the selection of forest polygons with at least 50% yellow birch - balsam fir - white birch composition. Previous disturbance included light spruce budworm damage of balsam fir in all landscapes. The landscapes also had different human footprints including selection cuts (years 1967 - 1969), diameter limit cuts (1989), and group selection cuts (1995, 2003).

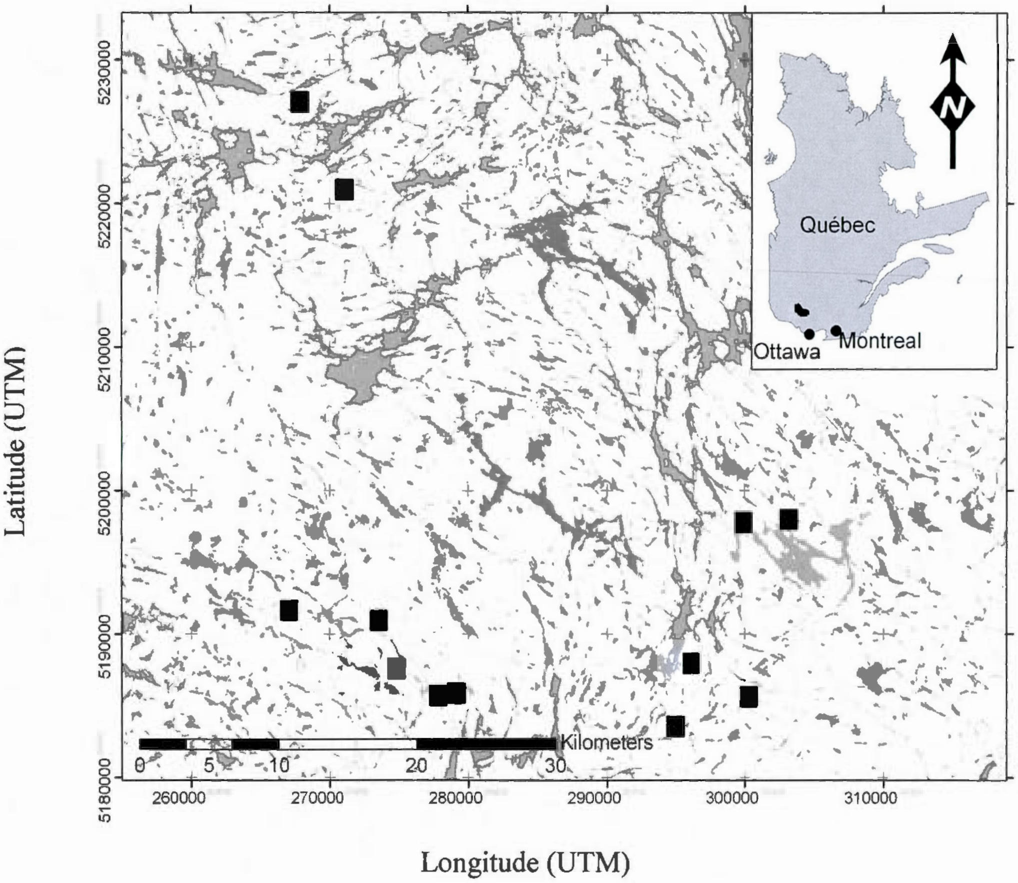


Figure 2.1. The 12 landscapes sampled in our study are located in the Réserve Faunique La Vérendrye

Table 2.1. Selection of bio-physical conditions required for a landscape to be retained for selection

Forest composition	Drainage	Soil deposit	Water bodies	Roads accessibility
> 50% Yellow birch, Balsam fir, White birch	Dominance mesic, medium	> 70% till	< 10% in each landscapes	No further than 3 km from a landscape

We selected stands with a density of poor (C) to very poor (D) and a stand age of 70 years (JIN) or 90 years and more (VIN). This was to ensure that our landscapes were not degraded due to recent harvesting, but instead were not productive (low tree densities) for a long time. We selected sites with a predominantly medium drainage regime, and with similar percentages of other drainage types. We selected for standard till deposits (1A > 1m till, 1m > 1AR > 0.5m till). We included landscapes with a soil type of at least 20% of 1A and 20% 1AR for a total of 70% between them. We selected landscapes that had < 10% standing water. Any landscapes that were further than 3km from a road were not considered due to access limitations, and the landscapes had to be minimally 100ha in size. Approximately 100 landscapes were admissible once our selection process was complete, heterogeneity values were calculated and landscapes were ranked by heterogeneity. Lastly, visual inspection of the landscapes using aerial photographs allowed us to check for irregularities.

2.2.3 Spatial heterogeneity characterization

We used Québec Ministry of Natural Resource and Wildlife 4th decadal forest inventory maps (MRNF 2007) to characterize landscape heterogeneity. Heterogeneity was assessed using indicators applied in a 100ha circular window around the central pixel. We selected this size of window as it is about one order of magnitude greater than the average stand size in the area (stand size ranging from 0.1 to 122ha). The spatial analysis was conducted after transforming the vector stand polygonal coverage into a 1 ha cell raster. A floating window of 100ha was then performed using the neighborhood analysis function in ArcGIS (ESRI 2006).

For assessing the four heterogeneity indicators that were computed to inform as to the variability of structures of forest communities in the landscape:

a) The first indicator we used was the <u>average stand size</u>. Multiple disturbances fragment forest communities into smaller stands, making them different in their composition and structure. Therefore, the smaller the average size, the more heterogeneous the landscape is likely to be. (Mladenoff et al. 1993)

b) The second indicator was the area-weighted average stand tree density. A more frequently disturbed forest landscape is more likely to show many stands with low stand tree density, particularly if the major disturbance types often exhibit a moderate severity. In the forest inventory, stand tree density is characterized using 4 classes (25-40%, 41-60%, 61-80%, 81-100%) and we used the mid-value of each class (32%, 50, 70%, 90%) for computing the area-weighted density average inside the 100ha window.

c) The third indicator looks at the variety (richness) of stand structures, as described by the combination of height and density. The disturbance types acting in the landscapes spanned a wide variety of severities (spruce budworm outbreaks and timber harvesting), generating residual stands with different stand structures. A disturbed landscape exhibits a greater variety of stand structures. In the forest inventory, stand height is described using 6 classes. Therefore, stand structure can be described by 24 combinations of density (4) and height (6). A variety count was performed using the neighborhood analysis.

d) The last indicator used the Shannon-Weaver (1963) information index to characterize the diversity of stand structures in the landscape. This indicator is computed similarly to the previous one, by looking at the different density and height class combinations, but takes into account the proportion of the area covered by each combination, thereby capturing the evenness aspect of the diversity of structures.

The effects of the individual indicators on the heterogeneity of the spatial structures are summarized in Table 2.2. The landscape spatial heterogeneity global index was then calculated by combining these four previous indicators, based on equal worth of each of the four variables. We then considered spatial heterogeneity values < 37% to represent relatively homogenous landscapes, 37 to 57% to represent moderate heterogeneity landscapes, while heterogeneous landscapes had values of > 60%.

Table 2.2. A summary of the effects of the four indicators on the spatial heterogeneity index

Stand heterogeneity	Stand size	Density	Variety	Diversity
Homogenous landscapes	Large	High	Low	Low
Heterogeneous landscapes	Small	Low	High	High

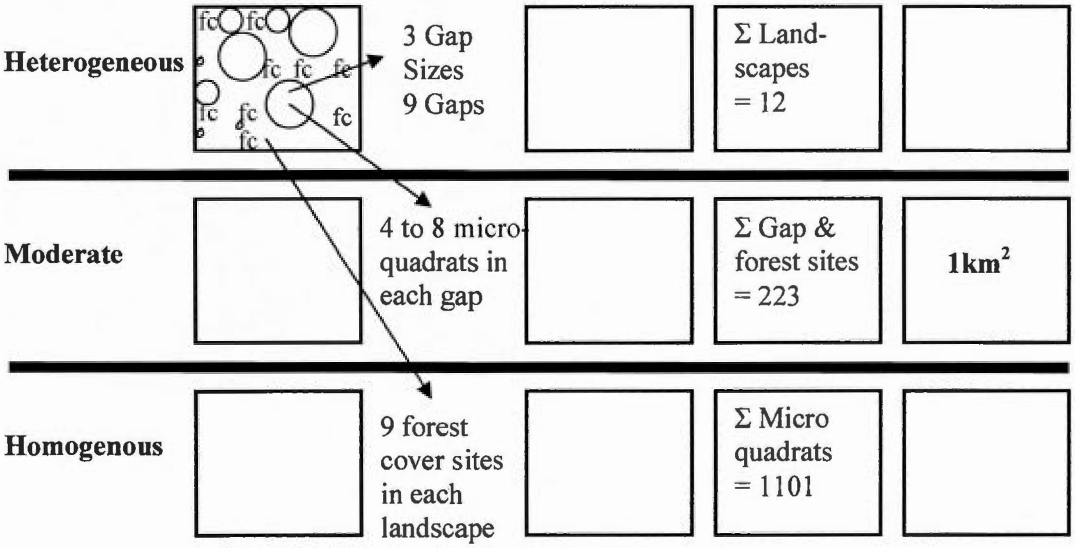


Figure 2.2. Experimental design, twelve 1km^2 landscapes

2.2.4 Site sampling

Within each of the 12 landscapes, there were 18 sampling sites, 9 of these sites were in canopy gap areas and 9 were under forest canopy. Within the 9 gap sites there were 3 different gap size intervals considered, all replicated 3 times (Figure 2.2). The 3 gap sizes were: small (50-200m^2), medium (201-600m^2) and large (601m^2+). Both gap sampling areas and forest cover sampling areas contained microquadrats. There were a constant number of 4, 5m^2 microquadrats in the forest cover sites and variable numbers of 4 to 8 microquadrats in the gap areas. The microquadrats were set along geographic compass directions called gap positions (north east, north west, south east, south west).

Sampling in gap sites

In each of the 12 landscapes, 9 gap sites were sampled, with 3 replicates of each gap size class. Gap area was field-measured assuming an elliptical shape (area= πab). The longer axis (*a*) was chosen to align with the north east or north west direction using a compass and the center was located (*a*/2), then the axis *b* was measured perpendicularly to the center of axis *a*. Measurements of the axes were conducted assuming that the gap area ends at the vertical projection of the canopy tree. The tree that represents the edge of the gap must be at least 75% the height of the surrounding gap trees to be considered part of the canopy and not inside the gap. In this study we did not consider the extended gap area (Gendreau-Berthiaume and Kneeshaw, 2009). It is possible that the largest potential axis in the gap was not always used, because we set the axes along compass directions.

In the small gap size class, 2 microquadrats were located at a distance of *a*/4 and 2 microquadrats were located at a distance of *b*/4, to the north east, the north west, the south east, and the south west, from the center of axis *a* or *b*. In medium sized gaps, 6 microquadrats were placed, with 4 microquadrats on the longer axis (*a*/6 and 2*a*/6 distance from centre of axis *a*) and 2 on the shorter axis (*b*/4 distance from the centre of axis *b*). In large gap size classes, 4 microquadrats were located on both axis *a* and axis *b* for a total of 8 microquadrats (*a*/6, 2*a*/6, *b*/6 and 2*b*/6 distance from the centre of each respective axis) (Figure 2.3). Microquadrat area was $5m^2$ (radius = 1.26m), but the area was increased to $19.95m^2$ (radius = 2.52m) for yellow birch, white birch and white spruce, 3 less frequently observed trees species that were focal to this research. This adjustment was done to avoid a sampling bias for common species as well as to reduce the amount of zeros in the dataset. Individuals were assigned to one of the three following size classes; seedling: height > 20cm, DBH (diameter at breast height) < 1cm , sapling: $1cm < DBH \leq 9cm$, and pole sizes: $DBH \geq 9.1cm$. Because of vegetative reproduction, and the small stature of shrub adults, the terms seedling and sapling were in reference to plant size and not the life stage. Basal sprouts of white birch or mountain maple were counted as one individual.

Sampling in forest cover sites

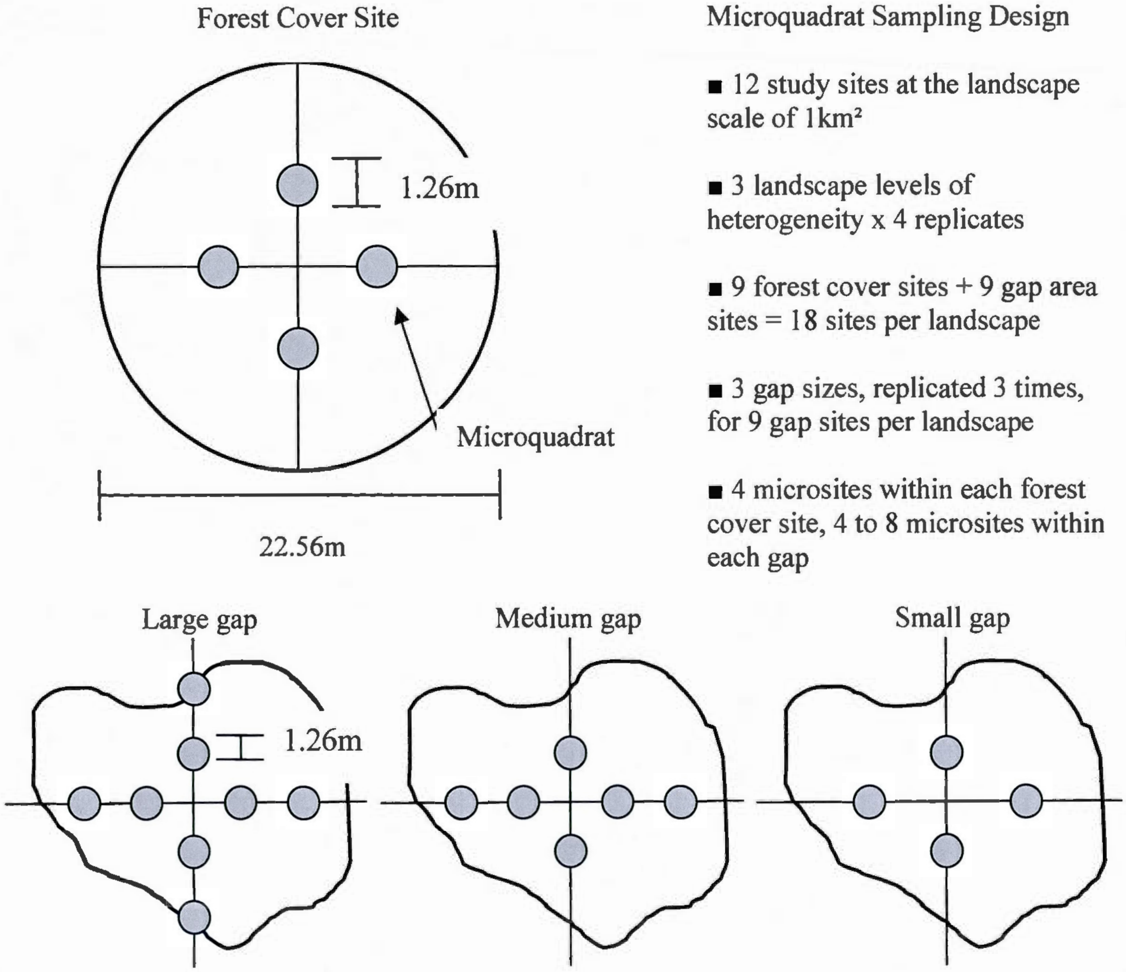
Vegetation data was also gathered under forest cover. In each of the 12 landscapes, 9 circular plots (radius = 11.28m, area = 400m²) were randomly distributed along four 1 km transects. Plots were all under forest cover (basal area > 6 m^2/ha) on mesic sites. Sampling included recording the species and the DBH of all trees. Within each plot there were 4 microquadrats, positioned at 5m from the center along the four cardinal directions. Microquadrat sampling was done in exactly the same manner as in gaps.

2.2.5 Data analysis

Stem density values (number of individuals/unit area) were obtained by summing up the individuals in all the microquadrats of a sample site (gap or forest cover) and then by dividing that sum by the area of all the microquadrats in that site combined. Data were grouped at different levels including species by size class and group of species (shrub and trees) for testing the main hypothesis. The independent variables in our databases included 3 heterogeneity levels (categorical), 4 gap size categories (under forest cover and the three gap size classes) and gap size (m²).

We tested the main treatment effects of gap size, landscape spatial heterogeneity and interactions on stem density with a Poisson mixed regression using R software (version 2.1.3.0) (R Development Core Team, 2011). All analyses using the Poisson mixed regression were calculated with the random factor as the landscape and the site nested within the landscape. The resulting predicted values and their confidence intervals were charted and can be read according to the technique presented in Cummings (2009). Separate tests had to be done for main effects and interaction effects of the Poisson mixed regression to calculate the probabilities using a multiple comparison test (Zuur et al. 2009). There was no simple procedure that computes Poisson mixed regression whole model probabilities or the percent of variability that the model explains (Zuur et al. 2009). The density of shrubs was plotted against the density of tree regeneration using a simple linear regression using JMP software (version 7.0.1) (JMP, 2007). The effects of landscape heterogeneity, categorical gap size and interactions, on the measured gap size were analyzed with an ANOVA mixed model using

JMP. The effects of spatial heterogeneity on the basal area and mean tree DBH in forest plots were analyzed with a one factor ANOVA mixed model using JMP.



Microquadrat Sampling Design

- 12 study sites at the landscape scale of 1km²
- 3 landscape levels of heterogeneity x 4 replicates
- 9 forest cover sites + 9 gap area sites = 18 sites per landscape
- 3 gap sizes, replicated 3 times, for 9 gap sites per landscape
- 4 microsites within each forest cover site, 4 to 8 microsites within each gap

Figure 2.3. An overview of the sampling design in gap and forest cover sites

2.3 Results

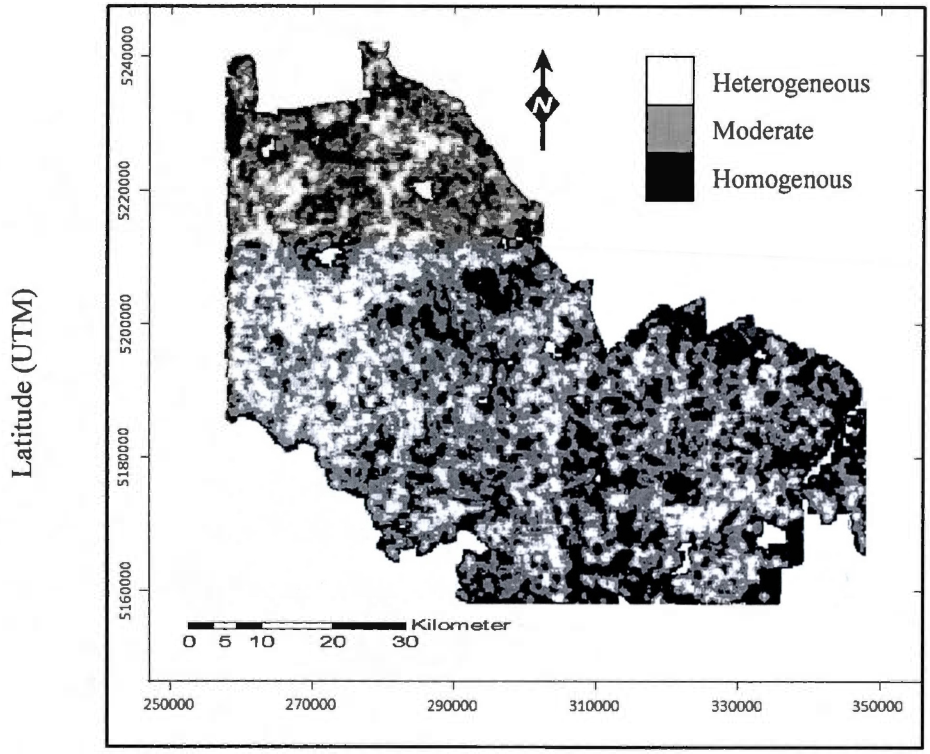
2.3.1 Characterization of the spatial heterogeneity of the landscape

The global spatial heterogeneity index varies for the selected landscapes, from 18% to 76%, with higher percentages indicating more heterogeneous landscapes (Table 2.3). Among the four heterogeneity indicators forming the global spatial heterogeneity index, only stand structure variety and stand structure diversity were correlated ($r = 0.917$, $P(f) < 0.001$). More heterogeneous zones occurred in the northwestern part of the entire study area, while the southeast portion of the study area is much less heterogeneous (Figure 2.4). More heterogeneous pockets seem to be linked with higher road density.

Table 2.3. Percent heterogeneity values, the four indicators are given equal weight, higher percentages indicate more heterogeneous landscapes.

Site	Diversity	Variety	Density	Stand size	Heterogeneity	Category
27	16.66	20.36	24.694	15.15	76.87	Heterogeneous
1	15.22	19.57	19.33	11.68	65.8	Heterogeneous
82	24.74	25	6.58	9.32	65.64	Heterogeneous
72	17.32	14.17	15.15	18.91	65.56	Heterogeneous
50	11.22	9.14	20.68	19.9	60.94	Moderate
60	9.12	15.67	23.5	8.73	57.02	Moderate
89	9.42	9.34	4.55	18.62	41.93	Moderate
2	4.62	6.09	14.13	13.07	37.92	Moderate
70	12.8	10.9	12.52	1.12	37.41	Homogenous
86	7.2	5.08	8.68	8.85	29.81	Homogenous
10	0	0.02	17.55	5.68	23.25	Homogenous
81	4.46	6.68	5.77	1.22	18.14	Homogenous

Source: Roy et al. (2011)



Source: Roy et al. (2011)

Figure 2.4. Map of the landscape spatial heterogeneity (SH) index applied in a circular window of 100 ha in the forest management units 73-51 and 73-52 in Québec. The black SH values at the border of the study area are an artifact of the neighborhood analysis.

2.3.2 Difference in gap size, basal area and mean DBH by spatial heterogeneity level

The gap sizes within the three different spatial heterogeneity levels were not significantly different (F ratio = 0.21, P(f) = 0.8146) (Table 2.4). Furthermore, the gap sizes (numerical) were not significantly different when considering the interaction between the terms spatial heterogeneity and gap size (categories) (F ratio = 1.13, P(f) = 0.3443). Neither the basal area, nor the DBH mean of the trees measured in the forest plots were different among spatial heterogeneity levels (Table 2.5). Basal area was around 31 m^2/ha and mean DBH around 21 cm.

Table 2.4. Average gap size (m^2) within the different spatial heterogeneity levels

Average gap size (m^2) in the landscapes within different spatial heterogeneity levels				
P(f)	F ratio	Heterogeneous	Medium	Homogenous
0.9449	0.06	405m^2	382m^2	357m^2

Table 2.5. Basal area and mean DBH in forest sites by spatial heterogeneity levels

Basal area (m^2/ha) by spatial heterogeneity levels				
P(f)	F ratio	Heterogeneous	Moderate	Homogenous
0.7681	0.27	29.49	30.73	32.7
DBH mean (cm) by spatial heterogeneity levels				
P(f)	F ratio	Heterogeneous	Moderate	Homogenous
0.7685	0.27	20.56	21.82	21.68

2.3.3 Tree and shrub density groups respond to landscape spatial heterogeneity and interactions with gap size

Overall shrub seedling densities were greater in heterogeneous landscapes, with more than 30 000 individuals per hectare in heterogeneous landscapes and less than 20 000 individuals per hectare in homogenous landscapes (Figure 2.5a). Shrub seedling density decreased as the landscape became more homogeneous; we detected a significantly greater density in heterogeneous sites when compared to homogenous sites ($P(z) = 0.0066$, Z value = 2.71) (Figure 2.5a). Conversely, tree species seedling density was less abundant in heterogeneous sites when compared to homogenous landscapes ($P(z) = 0.0202$, Z value = 2.32) (Figure 2.5a). Tree saplings were also less abundant in heterogeneous sites when compared to moderate heterogeneity landscapes ($P(z) = 0.0351$, Z value = 2.11) (Figure 2.5b). No statistically significant interactions were observed as ranks of density by gap size class were relatively the same whatever the heterogeneity level for the shrub and the tree groups, (Figures 2.6a-d). Tree sapling density decreased with increasing shrub sapling densities ($P(f) = 0.0156$) but the relationship was weak ($R^2 = 0.02$) (Figure 2.7).

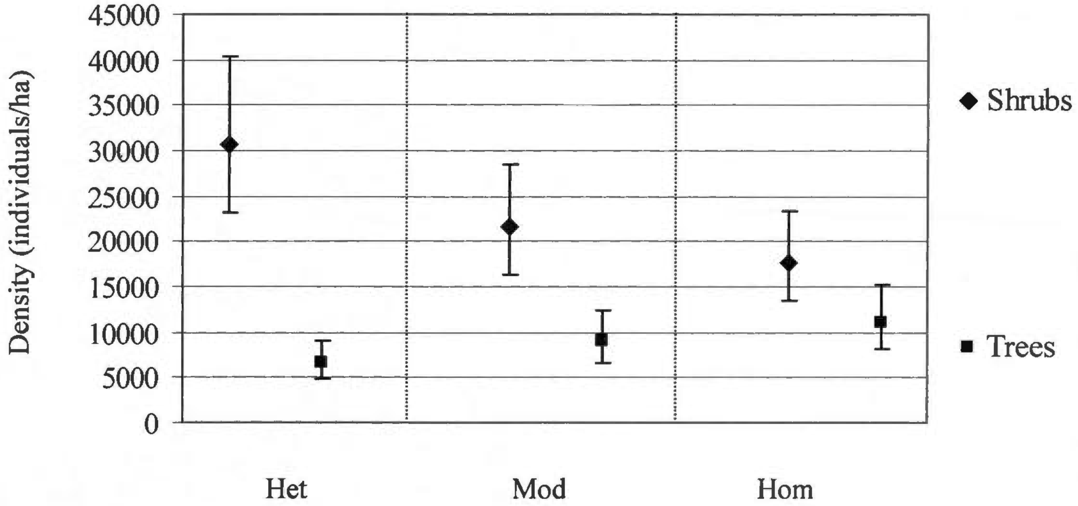


Figure 2.5a. Density response of shrub and tree seedlings to spatial heterogeneity levels [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom), Poisson mixed regression predicted values with confidence intervals]

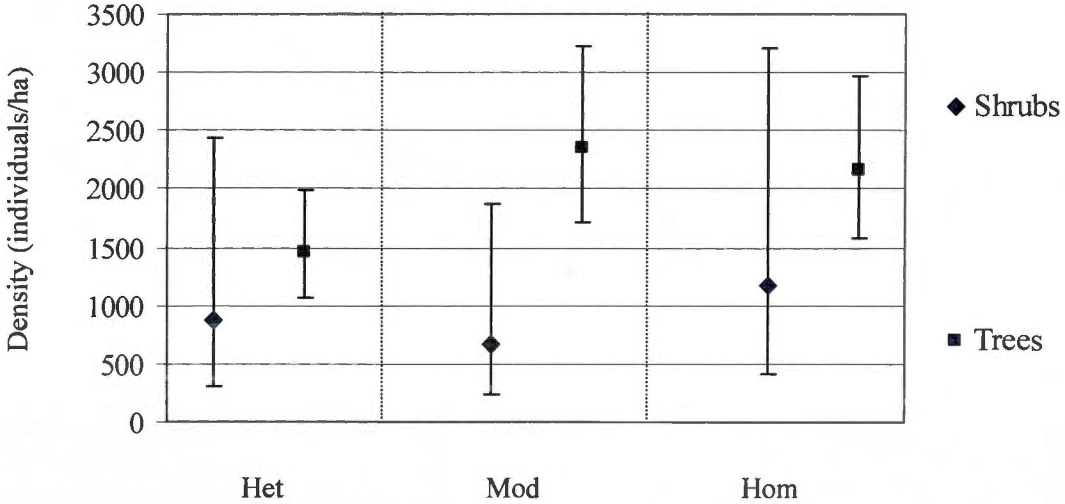


Figure 2.5b. Density response of shrub and tree saplings to spatial heterogeneity levels [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom), Poisson mixed regression predicted values with confidence intervals]

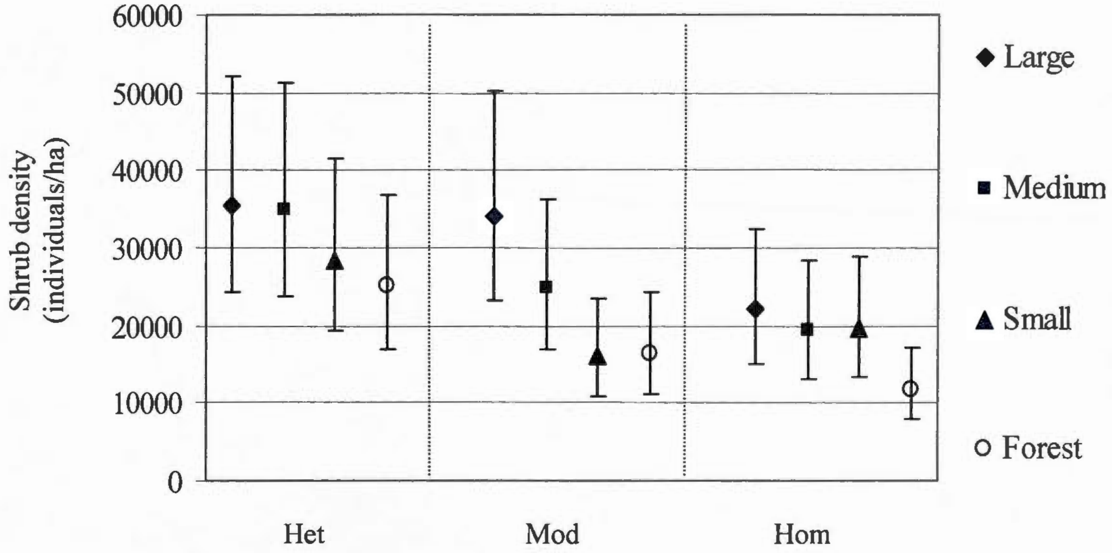


Figure 2.6a. Density response of shrub seedlings to the interaction of spatial heterogeneity levels [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom)] and gap size [Poisson mixed regression predicted values with confidence intervals]

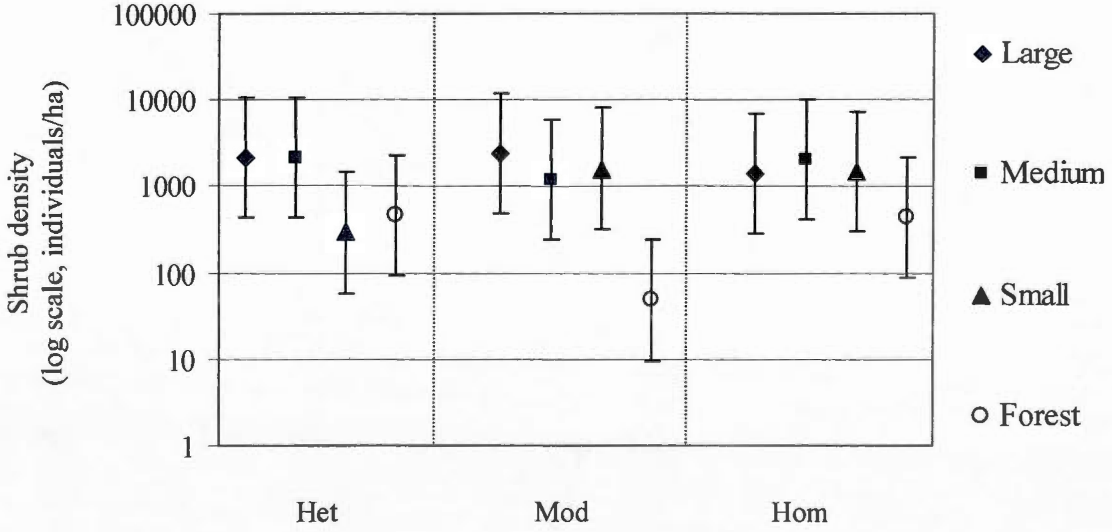


Figure 2.6b. Density response of shrub saplings to the interaction of spatial heterogeneity levels [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom)] and gap size [Poisson mixed regression predicted values with confidence intervals]

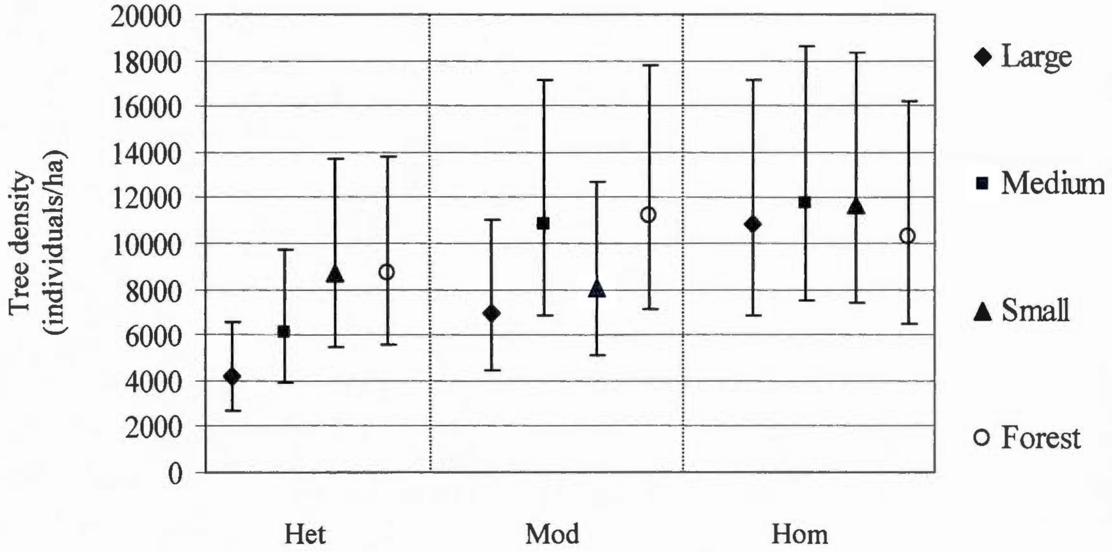


Figure 2.6c. Density response of tree seedlings to the interaction of spatial heterogeneity levels [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom)] and gap size [Poisson mixed regression predicted values with confidence intervals]

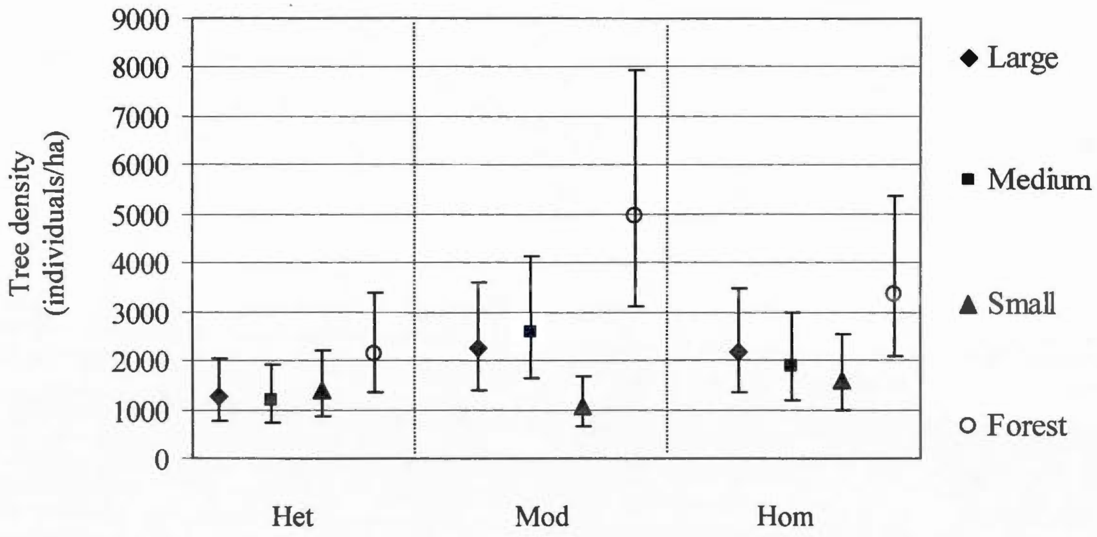


Figure 2.6d. Density response of tree saplings to the interaction of spatial heterogeneity levels [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom)] and gap size [Poisson mixed regression predicted values with confidence intervals]

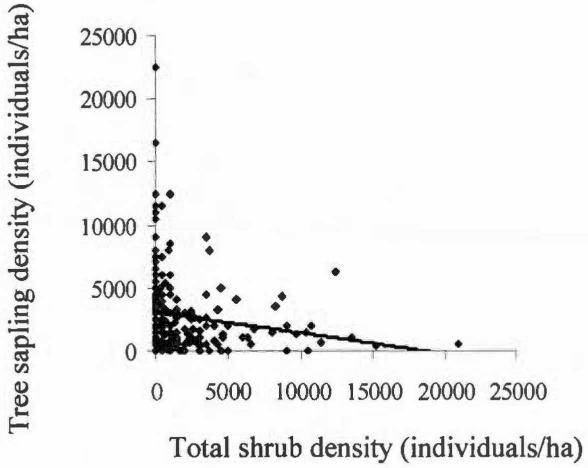


Figure 2.7. Tree sapling density as a function of shrub sapling density [simple regression]

2.3.4 Density response of tree and shrub species to landscape spatial heterogeneity

Red maple and balsam fir were the most abundant tree seedlings (> 1000 individuals/ha), as well as saplings (> 100 individuals/ha except for red maple in heterogeneous landscapes), in the sampled plots. We observed that yellow birch, sugar maple and white spruce densities were noticeably lower in heterogeneous landscapes (Figure 2.8a). We observed significantly fewer yellow birch seedlings and saplings in heterogeneous landscapes when compared to moderate heterogeneous (seedling: P(f) = 0.0002, Z value = 3.696; sapling: P(f) = 0.0003, Z value = 3.618) and homogenous landscapes (seedling: P(f) = 0.0087, Z value = 2.624; sapling: P(f) = 0.0029, Z value = 2.973) (Figures 2.8a-b). White spruce, another mid-tolerant species, had seedling densities significantly less abundant in heterogeneous landscapes when compared to homogenous landscapes (P(f) = 0.0006, Z value = 3.419) (Figure 2.8a). Although not detected as significant, some species also showed important density differences between landscape heterogeneity levels that are worth mentioning. The seedlings of sugar maple tended to be more numerous in homogenous systems (Figure 2.8a). The densities of the shrubs hazelnut and mountain maple were greater than any of the tree species. Hazelnut and *Viburnum cassinoides* seedling stem densities showed a non significant, positive tendency towards being more abundant in the heterogeneous landscapes (Figures 2.8c-d).

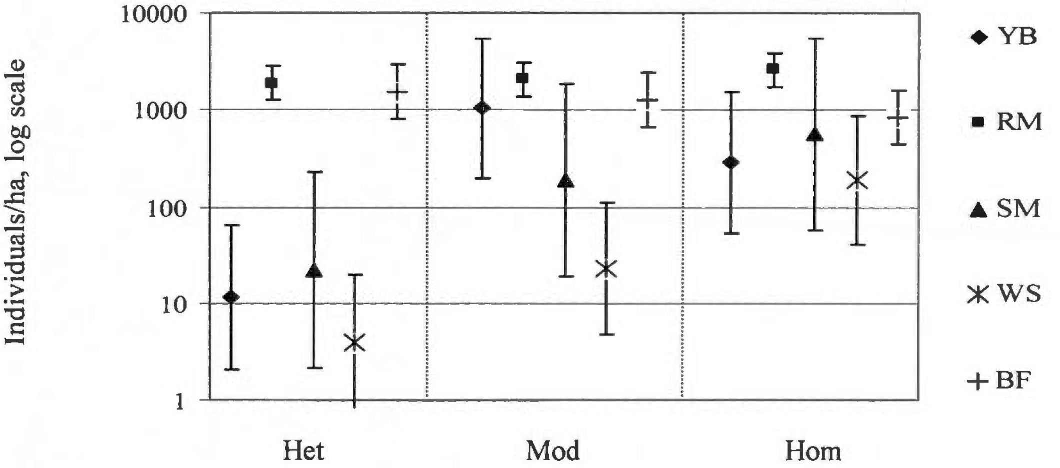


Figure 2.8a. Density response of tree species seedlings [yellow birch (YB), red maple (RM), sugar maple (SM), white spruce (WS) and balsam fir (BF)] to spatial heterogeneity levels [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom), Poisson mixed regression predicted values with confidence intervals]

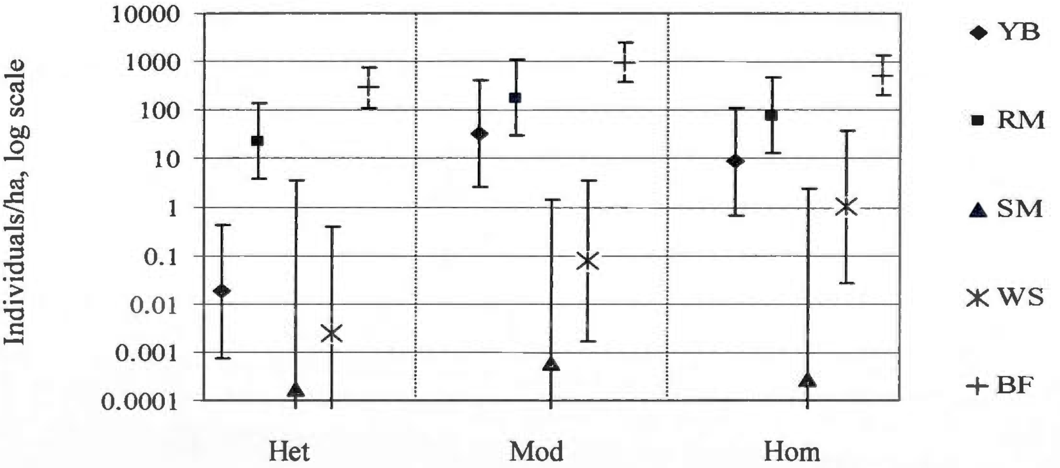


Figure 2.8b. Density response of tree species saplings [yellow birch (YB), red maple (RM), sugar maple (SM), white spruce (WS) and balsam fir (BF)] to spatial heterogeneity levels [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom), Poisson mixed regression predicted values with confidence intervals]

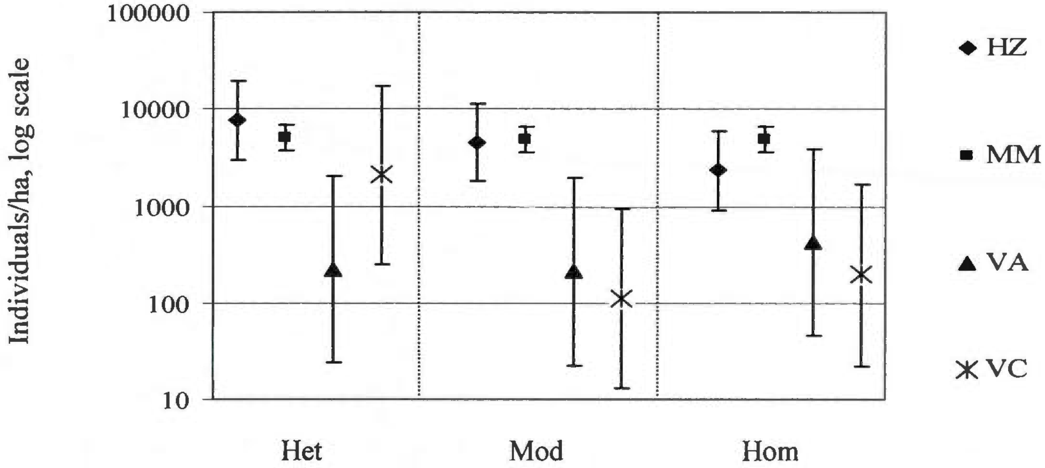


Figure 2.8c. Density response of shrub species seedlings [hazelnut (HZ), mountain maple (MM), *Viburnum alnifolium* (VA) and *Viburnum cassinoides* (VC)] to spatial heterogeneity levels [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom), Poisson mixed regression predicted values with confidence intervals]

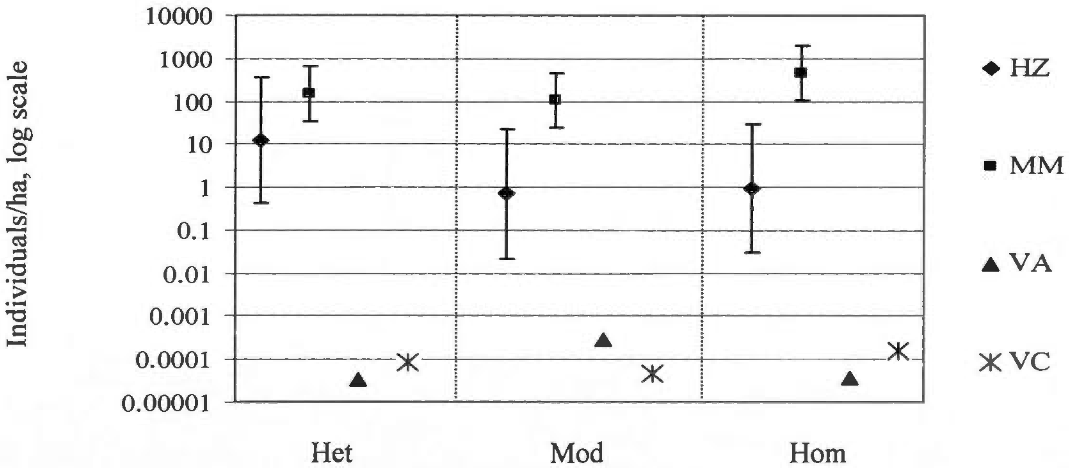


Figure 2.8d. Density response of shrub species saplings [hazelnut (HZ), mountain maple (MM), *Viburnum alnifolium* (VA) and *Viburnum cassinoides* (VC)] to spatial heterogeneity levels [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom), Poisson mixed regression predicted values with confidence intervals]

2.3.5 Density response of tree and shrub species to gap size

The seedlings of the intermediately shade tolerant yellow birch, were significantly less abundant in forest cover sites, when compared to small gaps (P(f) = 0.0073, Z value = 2.683), medium gaps (P(f) = 0.0116, Z value = 2.524), and large gaps (P(f) = 0.0004, Z value = 3.513) (Figure 2.9a). Yellow birch saplings were less abundant in forest sites than large gap sites (P(f) = 0.0037, Z value = 2.904) (Figure 2.9b). The seedlings of another intermediately shade tolerant species, white spruce, were more abundant in forest sites than medium gap sites (P(z) = 0.0463, Z value = 1.993) (Figure 2.9a). Seedlings of the shade tolerant red maple were significantly less abundant in large gaps relative to forest sites (P(f) = 0.0023, Z value = 3.04) and small gaps (P(z) = 0.0276, Z value = 2.20) (Figure 2.9a). The seedlings of another shade tolerant species, balsam fir, were more common in forest sites when compared to small gap sites (P(z) = 0.0341, Z value = 2.119) (Figure 2.9a). Balsam fir saplings were significantly more common in forest sites (P(z) = 0.0001, Z value = 4.280), large gap sites (P(z) = 0.0020, Z value = 3.089) and medium gap sites (P(z) = 0.0100, Z value = 2.575) when compared to small gap sites (Figure 2.9b). We also found significantly more white cedar seedlings in forest sites when compared to small gaps (P(z) = 0.0259, Z value = 2.228) and medium gaps (P(z) = 0.0367, Z value = 2.089) (*data not shown*).

Seedlings of the intermediately shade tolerant hazelnut, were significantly more plentiful in large gap sites when compared to forest sites (P(z) = 0.0195, Z value = 2.336) (Figure 2.9c). Hazelnut seedlings were more plentiful in large (P(z) = 0.0003, Z value = 3.631) and medium gaps (P(z) = 0.0012, Z value = 3.234) when compared to small gaps (Figure 2.9c). Hazelnut saplings were more abundant in large (P(z) = 0.0001, Z value = 3.971, P(z) = 0.0429, Z value = -2.024) and medium gaps (P(z) = 0.0005, Z value = 3.499, P(z) = 0.0095, Z value = -2.595) when compared to forest and small gap sites (Figure 2.9d). Seedlings of the intermediately shade tolerant mountain maple, were significantly more abundant in large gap sites when compared to forest gaps (P(z) = 0.0434, Z value = 2.019) (Figure 2.9d).

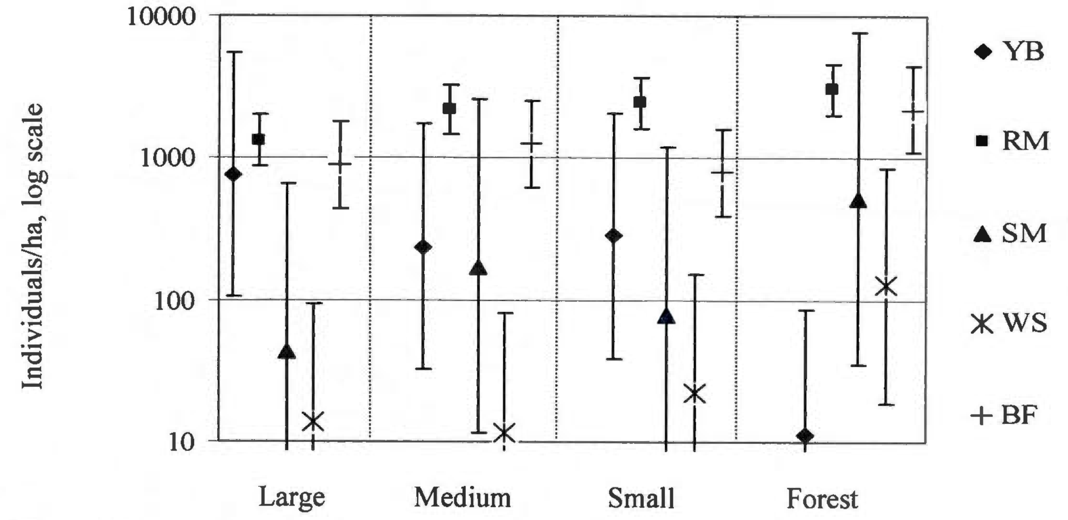


Figure 2.9a. Density response of tree species seedlings [yellow birch (YB), red maple (RM), sugar maple (SM), white spruce (WS) and balsam fir (BF)] to gap size [Poisson mixed regression predicted values with confidence intervals]

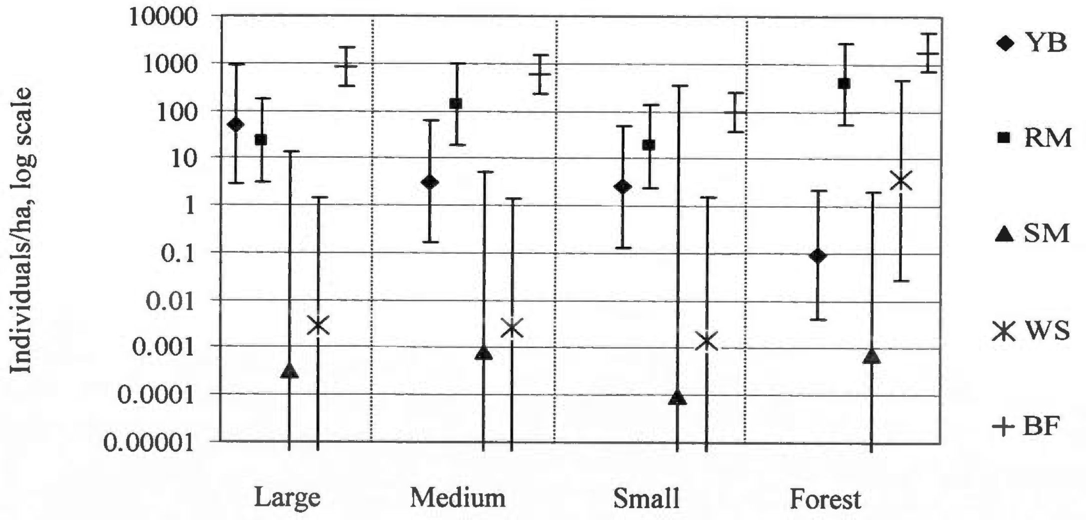


Figure 2.9b. Density response of tree species saplings [yellow birch (YB), red maple (RM), sugar maple (SM), white spruce (WS) and balsam fir (BF)] to gap size [Poisson mixed regression predicted values with confidence intervals]

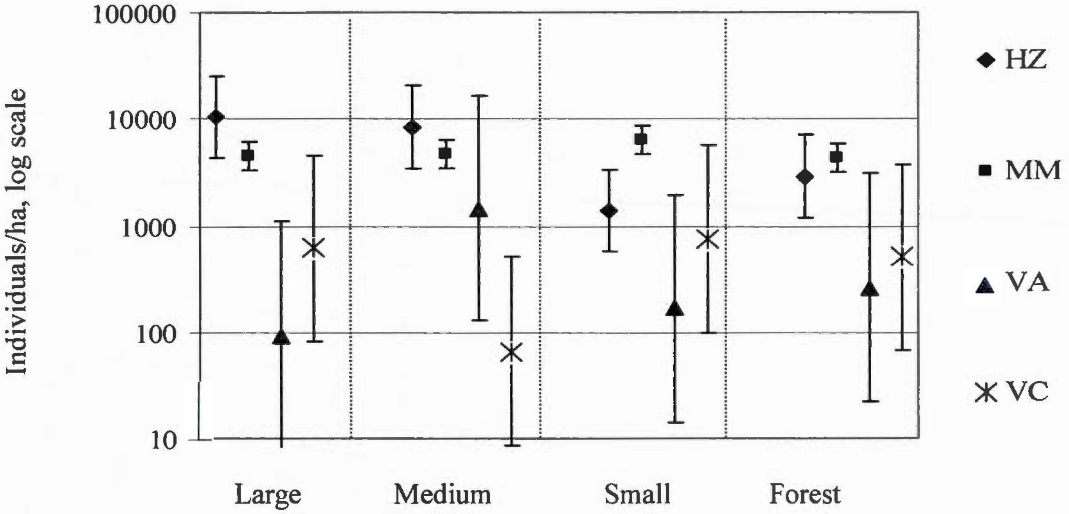


Figure 2.9c. Density response of shrub species seedlings [hazelnut (HZ), mountain maple (MM), *Viburnum alnifolium* (VA) and *Viburnum cassinoides* (VC)] to gap size [Poisson mixed regression predicted values with confidence intervals]

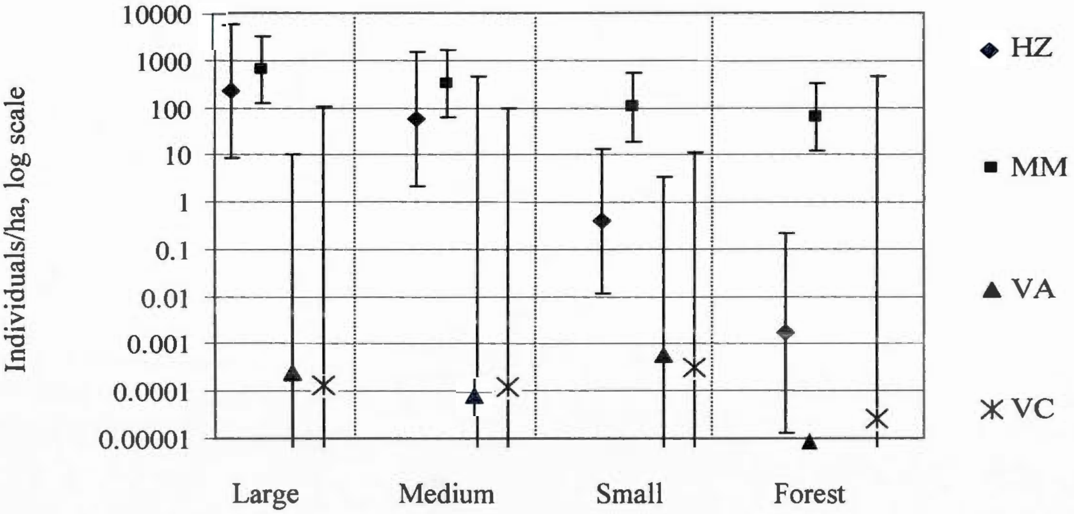


Figure 2.9d. Density response of shrub species saplings [hazelnut (HZ), mountain maple (MM), *Viburnum alnifolium* (VA) and *Viburnum cassinoides* (VC)] to gap size [Poisson mixed regression predicted values with confidence intervals]

2.3.6 Density response of tree and shrub species to the interaction between spatial heterogeneity and gap size

Looking at the interaction between the spatial heterogeneity and gap size for yellow birch seedlings, we can see that three of the four lowest values are in heterogeneous systems, thus suggesting that heterogeneous landscapes had fewer yellow birch seedlings, when comparing densities within the same gap size (Figure 2.10a). Specifically, we measured higher seedling densities in gaps of medium size situated within moderate heterogeneity landscapes, when compared to medium gaps in heterogeneous landscapes ($P(z) = 0.0421$, Z value = 3.318) (Figure 2.10a). Red maple seedlings were more frequently observed in large gaps in homogenous systems, when compared to large gaps in heterogeneous systems ($P(z) = 0.0183$, Z value = -3.573) (Figure 2.10b). Balsam fir seedlings were more abundant in small gaps in heterogeneous systems when compared to small gaps in homogenous ones ($P(z) = 0.0259$, Z value = 3.473) (Figure 2.10c). Also, balsam fir saplings were more common in small gaps in moderate heterogeneity systems, compared to those in heterogeneous systems ($P(z) = 0.0303$, Z value = 3.428) (Figure 2.10d).

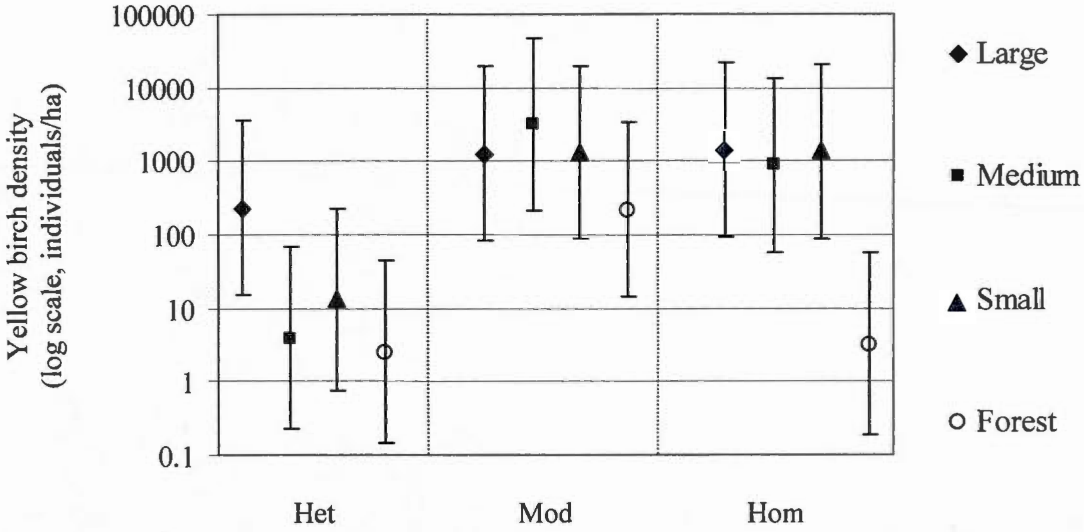


Figure 2.10a. Yellow birch seedling density as a function of the interaction between spatial heterogeneity [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom)] and gap size [Poisson mixed regression predicted values with confidence intervals]

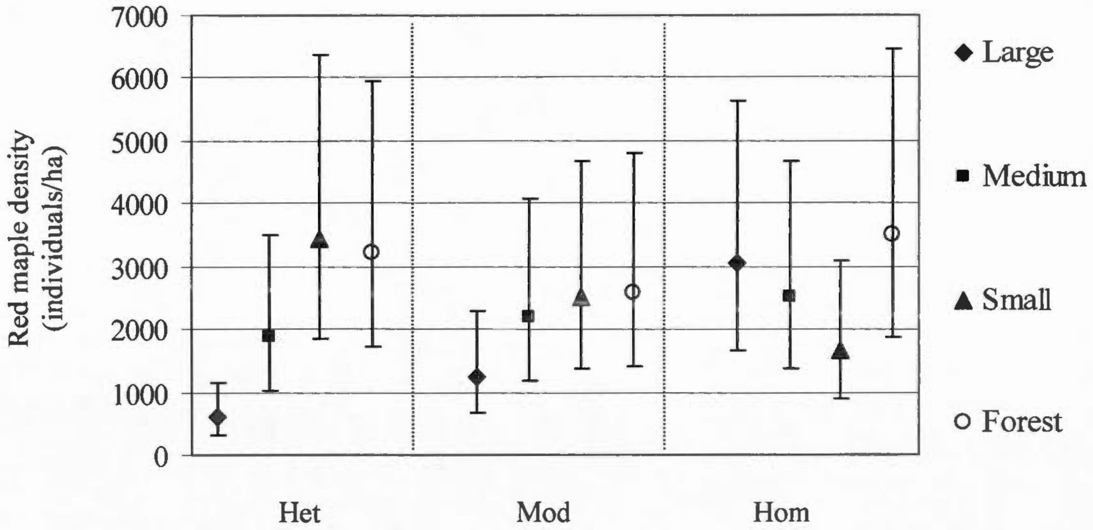


Figure 2.10b. Red maple seedling density as a function of the interaction between spatial heterogeneity [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom)] and gap size [Poisson mixed regression predicted values with confidence intervals]

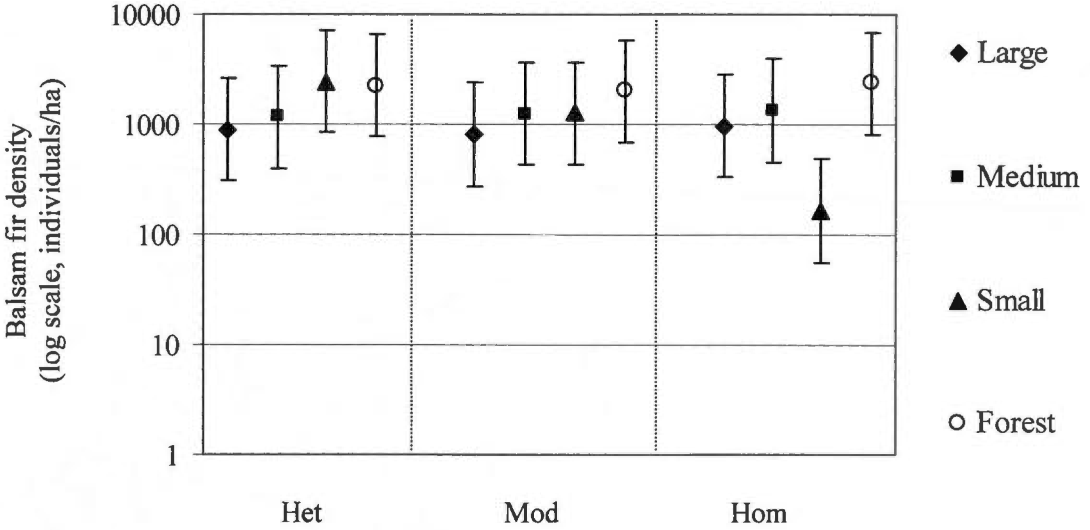


Figure 2.10c. Balsam fir seedling density as a function of the interaction between spatial heterogeneity [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom)] and gap size [Poisson mixed regression predicted values with confidence intervals]

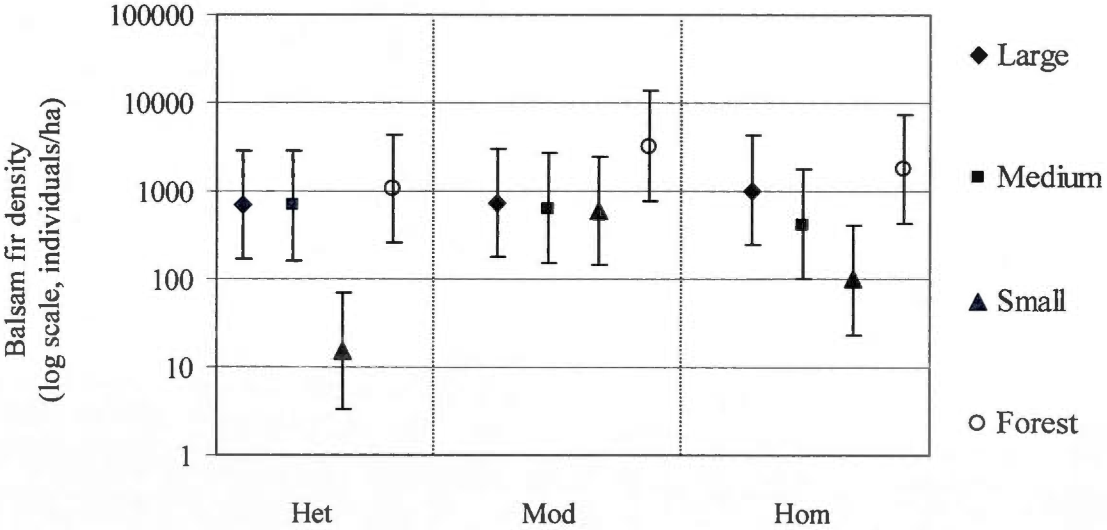


Figure 2.10d. Balsam fir sapling density as a function of the interaction between spatial heterogeneity [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom)] and gap size [Poisson mixed regression predicted values with confidence intervals]

2.4 Discussion

2.4.1 Competitors, colonizers and the heterogeneity of landscapes

We found that local forest regeneration, within the same gap size (and similar light environments), was different according to the landscape context, here described by the level of spatial heterogeneity of stand structures. Specifically, the evidence demonstrates greater average abundance of shrub regeneration, and significantly lower average abundance of tree regeneration, in heterogeneous landscapes (Figures 2.5a-b). We observed more than two times as many shrub seedlings under forest cover in heterogeneous landscapes, when compared to shrub seedlings under forest cover in homogenous landscapes (Figure 2.6a). Also, we observed more than two times as many tree seedlings in large gaps in homogenous landscapes, when compared to large gaps in heterogeneous landscapes (Figure 2.6c).

We suggest that spatial heterogeneity represents a surrogate for landscape level disturbance, with heterogeneous landscapes being more disturbed. Natural disturbances are responsible for creating some large homogenous patches and other smaller heterogeneous patches, with anthropogenic factors accelerating these processes (Mladenoff et al. 1993, Spies et al. 1994). We acknowledge that heterogeneous landscapes may have important differences in land use and natural disturbance history which may be a primary cause of the difference in tree recruitment (Coulson and Tchakerian, 2010). Our work can be placed within the larger context of research providing the links between degraded landscapes and abundant shrub populations (Royo and Carson, 2006). However, the linear regression between superior shrub density and inferior tree density, although significant, explained a very small percent of the variability (Figure 2.7). To optimize this relationship, it may have been necessary to further separate the shrub and tree groups with regards to their functional groups. Nevertheless, it is likely that the competitive relationship between shrub and tree regeneration is more complex than a simple linear relationship.

We propose that the reduced amount of shrubs in homogenous landscapes is likely the combination of dispersal limitation, weak establishment and limited persistence abilities of the shrubs (Hanski and Gilpin, 1991, Tilman, 1994). Gap openings in homogenous landscapes were less frequently distributed throughout the landscape; competitive shrubs were less able to survive over long periods shadowed under the forest cover and had limited access to canopy openings created by small-scale disturbance. Naturally, at the landscape level, the patch size influenced the persistence of certain organisms (Coulson and Tchakerian, 2010). In homogenous landscapes, tree species regenerated in greater numbers because they were able to either disperse their seeds long distances or persist as seed trees due to their long life span (Coomes and Grubb, 2003, Kneeshaw and Prévost, 2007). Heterogeneous landscapes would magnify the ability of certain shrubs to maintain "dormant" colonies (sit and wait strategy) in otherwise inhospitable closed forest habitats, the shrubs can then reproduce readily when an opening occurs in their vicinity, either vegetatively or by short dispersal distance (Aubin et al. 2005, Royo and Carson, 2006). Species that perform vegetative reproduction would be more competitive directly after a disturbance, as long as the disturbance does not affect their root structure (Laflèche et al. 2000). Species that reproduce using small seeds may be less viable in a competitive environment (Coomes and Grubb, 2003). We acknowledge that although shrub dominance may be isolated at different points in time, over large time scales, with the absence of anthropocentric disturbances, trees and not shrubs would be likely to occupy positions of dominance due to maximum height and age capabilities (Kneeshaw and Prévost, 2007).

2.4.2 Density response to gap size

We documented significant and important effects on species densities due to different gap sizes. The primary effect observed was superior species densities in either forest cover or gap sites depending on shade tolerance. Yellow birch seedlings and saplings were statistically less present in forest sites, remaining consistent with the literature (Woods, 2000, Kneeshaw and Prévost, 2007) (Figures 2.9a-b). Shade tolerant balsam fir seedlings and saplings, and white cedar seedlings were more frequently found in forest cover sites, all consistent with the scientific literature (Kneeshaw and Bergeron 1998, Kneeshaw et al. 2006) (Figures 2.9a-b). Shade tolerant red maple seedlings were more frequently found in forest cover sites, contrary to previous research (Kneeshaw and Prévost, 2007) (Figure 2.9a). Positive white spruce seedling response to forest cover sites was inconsistent with the literature, as the intermediately shade tolerant species has been shown to be more present in large gap sizes

(Kneeshaw and Bergeron 1998) (Figure 2.9a). Hazelnut regeneration was more apparent in large and medium gaps when compared to small gaps and forest sites, which was not unexpected due to its shade tolerance status (Humbert et al. 2007) (Figures 2.9c-d). Mountain maple sapling regeneration was more abundant in large gaps, when compared to forest sites, consistent with what other researchers have found (Kneeshaw and Prévost, 2007) (Figure 2.9d).

2.4.3 Separating the effects of light and spatial heterogeneity

One of the difficulties in this project was to isolate the effect of landscape heterogeneity from percent light as some collinearity between these two factors could arise. By measuring the density of various species in different gap sizes within the 3 heterogeneity levels, we hoped to capture the species response to spatial heterogeneity within similar light environments, therefore allowing us to extract the light variable from our landscape heterogeneity of spatial structures variable. Within the same gap size categories, yellow birch seedling densities were always lower in heterogeneous landscapes (Figure 2.10a). Red maple seedlings as well responded to the interaction of factors, with more individuals in large gaps in homogenous landscapes than large gaps in heterogeneous ones (Figure 2.10b).

Because we defined heterogeneous landscapes as having higher variability in tree density and higher variability in tree height, they may as a result be more luminous in canopy gaps or forest cover sites. The edges of the canopy gaps in heterogeneous landscapes may be less consistent in height and density and therefore more luminous. Nevertheless, increased light entering the forest canopy does not translate into an increase in light at the ground and shrub layer, and may in fact result in increased competition and less light at that layer. Interestingly, some of our results have provided us with evidence that there is limited collinearity between the two main factors in terms of effects. Firstly, basal area and average tree DBH for sampled plots under forest cover were not different among the spatial heterogeneity levels, although the heterogeneous sites did have slightly lower average basal areas (Table 2.5). Secondly, gap sizes between the spatial heterogeneity levels were not significantly different, although the average gap size in heterogeneous systems was approximately 50 m^2 larger on average than those in homogenous systems ($50m^2$ is a perceptible difference between small gaps, but inconsequential regarding larger gaps) (Table 2.4). The absence of differences for these two variables related to gap size suggest that differences in light availability at the time of sampling was probably not the primary factor behind the observed effect of spatial heterogeneity.

The primary factors related to the ground layer vegetation include stand age, basal area, crown cover, fertility, species composition and topography (Pitkanen, 1997). Our landscape selection process included only stands that were greater than 70 years, thus only mid-succession stands were selected. Basal area as mentioned before was not significantly different within the different heterogeneity levels, and consideration of crown cover was included in our analyses as the factor gap size. Furthermore, we managed to maintain control of site conditions (fertility, drainage regimes, water body proportion), and the general forest domain or composition was controlled within the 12 landscapes (Table 2.1). Lastly, having added a landscape variable as a random factor in the mixed Poisson regression procedure, ensured that the observed responses were not due to differences in the sampled landscapes.

2.4.4 Conclusion

Our work demonstrated an effect of landscape spatial heterogeneity on tree and shrub, seedling and sapling density. This work has implications toward the regenerative patterns that can be observed in heterogeneous forests. The composition and integrity of these forests may be compromised in the short term, higher shrub densities may mean less germination and establishment opportunities for commercially and ecologically important tree species. It is also possible that shrubs are unable to saturate forests and gap openings situated in homogenous landscapes due to dispersal, establishment and persistence limitations. These results have direct implications toward forest managers as their decisions may impact the metapopulation dynamic of competitive shrubs. Heterogeneous forest structures at the landscape level are due to elevated natural and anthropogenic disturbance. Landscape spatial heterogeneity may be linked to succession, albeit not in a linear fashion. Homogenous landscapes may be composed of young or older even aged stands. Heterogeneous landscapes may be composed of disturbed stands, or old aged stands that have irregular canopy heights. Moderate heterogeneity landscapes may be stands entering old age gap dynamics forests.

Future work should consider that light levels in homogenous and heterogeneous landscapes may not be the same at different heights and that this may differentially affect species establishment and growth. The relationship between different disturbance agents and our definition of spatial heterogeneity also warrants further study. Although our work identified patterns of species densities associated with a novel landscape level factor, further work on the processes and functional traits that are responsible for the observed patterns is essential. Spatial heterogeneity may be useful in situations where the landscape is so disturbed that the disturbance agents themselves are no longer relevant to natural succession. Instead a summation of landscape disturbance becomes relevant; the landscape heterogeneity of spatial structures.

CHAPTER III

GROWTH OF SPECIES REGENERATION AS A FUNCTION OF GAP SIZE AND SPATIAL HETEROGENEITY

3.1 Introduction

Degraded forests have an open canopy structure with a recalcitrant, dense shrub underlayer (*sensu* Royo and Carson, 2006). Although different shrub species have evolved different ways to exploit short periods of sunlight, fast vegetative growth is possibly more effective than germination in the short-term. The potential area of degradation is extensive especially in the mixedwood forest, as shrub species such as mountain maple are distributed in all but pure conifer and tolerant hardwood stands (Vincent, 1965). Harvesting, especially clearcutting, has been found to contribute to the spread of the shrub mountain maple (*Acer spicatum*) (Archambault et al. 1998). Mountain maple can suppress spruce (*Picea sp.*) and balsam fir (*Abies balsamea*) regeneration for decades, and can persist in the understory for up to 60 years (Vincent, 1965). Other reports indicate that in the boreal mixedwood forest, mountain maple can persist through all stages of succession (Aubin et al. 2005). Mountain maple growth in newly formed canopy openings tends to be superior to balsam fir growth (Kneeshaw et al. 2012). Balsam fir seedlings have been documented to grow better under any tree species, when compared to growth under mountain maple (Kneeshaw et al. 2012). Furthermore, balsam fir seedling mortality was higher under mountain maple (82%) when compared to mortality under other tree species (19%) (Kneeshaw et al. 2012). Hazelnut (*Corylus cornuta*) has been shown to respond in greater densities after logging than after fire or spruce budworm outbreak (Kemball et al. 2005). Previous work shows that the total density of shrub species was found to be significantly greater in landscapes with heterogeneous spatial structures, while total tree species density was found to be significantly lower in the same heterogeneous landscapes (Chapter 1, Markgraf, 2012). Further questions regarding the processes involved in shrub invasion remain.

Heterogeneous patterns are naturally observed in the forest ecosystem (Coulson and Tchakerian, 2010). Intact landscapes have fewer, large matrix areas, whereas disturbed landscapes have large quantities of smaller patches (Mladenoff et al. 1993). Patch size may influence whether the resources available within the patch are sufficient for the survival, growth, reproduction and persistence of a particular organism (Coulson and Tchakerian, 2010). Within this chapter we propose the hypothesis that the growth and height of species will be differentially affected by landscape heterogeneity. We suggest that heterogeneous landscapes will shelter higher levels of competition, which will negatively affect tree seedling growth, thus explaining why we observed lower levels of tree regeneration in heterogeneous landscapes. In order to investigate the effects of landscape heterogeneity, other factors (gap size, gap position, competition, browsing, microsite conditions and microtopography) have been measured to provide a control on the response variable.

3.2 Methods

3.2.1 Study site

Our study site is located in the Réserve Faunique La Vérendrye, in between the boreal mixedwood to the north and the northern hardwood forest zones to the south, in the area corresponding to the Balsam fir – Yellow birch bioclimatic domain (Saucier et al. 1998). The mixedwood forests in these areas are dominated by balsam fir. Yellow birch (*Betula alleghaniensis*), white spruce (*Picea glauca*) and white birch (*Betula Papyrifera*) are also present in the stands. Other species that occur in the area include black spruce (*Picea mariana*), white pine (*Pinus strobus*), white cedar (*Thuja occidentalis*), trembling aspen (*Populus tremuloides*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*) and large tooth aspen (*Populus grandidentata*). In the absence of fire, mesic-xeric hilltops are often dominated by sugar maple, upper slope mesic sites are mixed and dominated by yellow birch, lower slope mesic sites are dominated by conifer species (balsam fir or white cedar) and imperfectly drained sites are dominated by black spruce (Bouchard et al. 2006).

The mean annual precipitation at Maniwaki is 908.8mm (including 238.3cm as snow) and the mean annual temperature is 3.7 °C. The natural fire cycle in western Québec is approximately 188 to 314 years, with historically longer fire cycles in the south and the east (Grenier et al. 2005). Major spruce budworm outbreaks have occurred in the region in 1910, 1945 and 1980 (Bouchard et al. 2006). In northern Outaouais, the topography is flat with some small hills and an abundance of small lakes.

3.2.2 Landscape selection

Our study site consists of twelve sampled landscapes, 1 km^2 in area, with 3 levels of heterogeneity (homogenous, moderate and heterogeneous). We selected our study landscapes (1km^2) on the basis of the following criteria based on the GIS tool ArcGIS (ESRI 2006). Our selection included measures to reduce environmental heterogeneity. Our first criterion was the selection of forest polygons with at least 50% yellow birch - balsam fir - white birch composition. Previous disturbance included light spruce budworm damage of balsam fir in all landscapes. The landscapes also had different human footprints including selection cuts (years 1967 - 1969), diameter limit cuts (1989), and group selection cuts (1995, 2003). We selected stands with a density of poor (C) to very poor (D) and a stand age of 70 years (JIN) or 90 years and more (VIN). This was to ensure that our landscapes were not degraded due to recent harvesting, but instead had low tree densities for a long time. We selected sites with a dominance of medium drainage regime, and with similar percentages of other drainage types. We selected for standard till deposits (1A > 1m till, 1m < 1AR > 0.5m till). We included landscapes with a soil type of at least 20% of 1A and 20% 1AR for a total of 70% between them. We selected landscapes that had < 10% standing water. Any landscapes that were further than 3km from a road were not considered due to access limitations.

3.2.3 Spatial heterogeneity characterization

We used Québec Ministry of Natural Resource and Wildlife 4th decadal forest inventory maps (MRNF 2007) to characterize landscape heterogeneity. Heterogeneity was assessed using indicators applied in a 100 ha circular window around the central pixel. We selected this size of window landscape as it is about one order of magnitude greater than the average stand size in the area (stand size ranging from 0.1 to 122 ha). The spatial analysis was conducted after transforming the vector stand polygonal coverage into a 1 ha cell raster. A floating window of 100 ha was then performed using the neighborhood analysis function in ArcGIS (ESRI 2006). This process is described in greater detail in Section 2.2.3., Chapter 2, Markgraf (2012). The landscape spatial heterogeneity global index was calculated by combining the four indicators based on equal worth of each of the four variables: average stand size, average stand density, the variety of stand structures in terms of average stand height and average stand density and the diversity in terms of average stand density and average stand height. We then considered spatial heterogeneity values < 37% to represent relatively homogenous landscapes, 37 to 57% to represent moderate heterogeneity landscapes while heterogeneous landscapes had values of > 60 (Table 2.3, Chapter 2, Markgraf, 2012).

3.2.4 Site sampling

Within each of the 12 landscapes, there were 18 sample sites, 9 of these sites were in canopy gap areas and 9 were under forest cover. Within the 9 gap sites there were 3 different gap size intervals considered, all replicated 3 times. Both gap sampling areas and forest cover sampling areas contained microquadrats. There were 4, $5m^2$ microquadrats in the forest cover sites and a variable number of 4 to 8 microquadrats in the gap areas. The microquadrats were set along geographic compass directions called gap positions (north east, north west, south east, south west). We used 3 gap sizes; small ($50\text{-}200m^2$), medium ($201\text{-}600m^2$) and large ($601m^2$+).

The gap area was field-measured assuming an elliptical shape (area= πab). The longer axis (*a*) was chosen to align to the north east or north west direction using a compass and the center was located (*a*/2), then the axis *b* was measured perpendicularly to the center of axis *a*. Measurements of the axes were done assuming that a gap ends at the edge of the canopy tree branches. The tree that represents the edge of the gap must be at least 75% the height of the surrounding gap trees to be considered a part of the canopy and not inside the gap. In this study we do not consider the extended gap area (Gendreau-Berthiaume and Kneeshaw, 2009). It is possible that the largest potential axis in the gap was not always used, because we set the axes along compass directions.

In the small gap size class, 2 microquadrats were located at a distance of *a*/4 and 2 microquadrats were located at a distance of *b*/4, to the north east, the north west, the south east, and the south west, from the center of axis *a* or *b*. In medium sized gaps, 6 microquadrats were placed, with 4 microquadrats on the longer axis (*a*/6 and 2*a*/6 distance from centre of axis *a*) and 2 on the shorter axis (*b*/4 distance from the centre of axis *b*). In large gap size classes, 4 microquadrats were located on both axis *a* and axis *b* for a total of 8 microquadrats (*a*/6, 2*a*/6, *b*/6 and 2*b*/6 distance from the centre of each respective axis). Microquadrat area was $5m^2$ (radius = 1.26m), but the area was increased to $19.95m^2$ (radius = 2.52m) for yellow birch, white birch and white spruce, three less frequently observed trees species that were focal to this research. This adjustment was done to avoid a sampling bias for common species as well as to reduce the amount of zeros in the dataset. Individuals were assigned to one of the three following size class: seedling: height $>$ 20cm, DBH (diameter at breast height) $<$ 1cm , sapling: 1cm $<$ DBH $\leq$ 9cm, and pole: DBH $\geq$ 9.1cm. Because of vegetative reproduction, and the small stature of adult shrubs, the terms seedling and sapling were in reference to plant size and not the life stage.

We measured growth, height, establishment position and percent cover of competition overtopping the largest individual of five key species (yellow birch, white birch, mountain maple, balsam fir and white spruce) in the microquadrats of gap and forest cover sites. The previous year's growth was measured from the leading stems last observable growth scar, to the tip of the branch. Saplings that were over 5 meters tall were sometimes impossible to measure and so either the next tallest individual was sampled if available, or no data was taken for growth and height measurements in that particular case. The cover of overtopping competition was estimated using cover classes (0, 25%, 50%, 75%, and 100%), representing the percent foliage above the selected individual in a 0 to 6m column of the size of the crown of the individual. Microtopography position was the difference in height measured from the lowest point in the microquadrat to the point where the individual was established. Establishment site (rock, log, pit or mound) and signs of browsing (branches are cleanly cut) were also documented for each sampled individual.

3.2.5 Data analysis

The independent variables included 3 heterogeneity levels (high, moderate and low) and 4 gap size categories (under forest cover and the three gap size classes). Other sub-treatments included competition (categorical and numerical), establishment site (categorical), microtopography position (numerical) and browsing (categorical). Analysis of species establishment on microsites with 5 categories (no microsite, rock, log, pit or mound) was impossible due to lack of data. For analysis, establishment site categories were grouped into soil microsite and non-soil microsite (rock, log, pit or mound).

The data for growth were log(x+1) transformed to insure that the data were normal and homocedast. We used a 2 factor ANOVA mixed model with interactions, for testing the effects of gap size and the landscape spatial heterogeneity, with the landscape as the random factor. Tukey tests (when the main effect was significant) and contrast tests (when the main effect was not significant) were used to evaluate the probability that categories relevant to our hypotheses were different. Analyses of factors related to growth (competition, browsing, microsite conditions and microtopography) were conducted to control factors other than gap size and spatial heterogeneity. In some cases, data were insufficient for some treatment combinations to be tested or residuals did not comply with the requirement for normality or absence of heterocedasticity. Because of this, one level ANOVA mixed models were tested for each treatment separately (interactions were not considered). Analysis using the average growth of species as a function of competition (categorical), establishment site (categorical) and browsing (categorical) were done using one factor ANOVA mixed models. The differences between categories for the factor competition were elucidated with the use of the Tukey test and contrast tests. The data for establishment site and browsing was sometimes not sufficient for analysis. Analysis regarding the height (square root transformed) of species regeneration, the microtopography position (log(x+1) transformed) and the percent competition (log(x+1) transformed) of 5 species were evaluated as a function of the two factors, spatial heterogeneity and gap size using 2 factor ANOVA mixed models, probabilities were assigned using the Tukey test and contrast tests. The exclusion of forest sites from the data was done for the growth response to the percent competition. This was because the percent competition was seen as a redundant measurement under forest cover (it was always documented as 100% competition under forest cover). Lastly, we tested the presence or absence of browsing as a function of the spatial heterogeneity levels using a Chi square test. All analyses in this section were completed with the help of JMP software (version 7.0.1) (JMP, 2007).

3.3 Results

3.3.1 Growth response of species regeneration to spatial heterogeneity, gap size and their interaction

The seedling growth of white spruce was the only species among size class combinations that was significantly related to spatial heterogeneity (Table 3.1). White spruce seedling growth was inferior in heterogeneous landscapes when compared to homogenous or moderate heterogeneity landscapes (Figure 3.1a). Contrast tests revealed that balsam fir sapling growth was greater in heterogeneous landscapes when compared to moderate heterogeneity ones (Figure 3.1b). The effect of gap size (forest cover, small, medium and large gaps) on growth was significant for yellow birch sapling, and mountain maple seedling and sapling growth (Table 3.1). In general, growth increases as gap size increases but the response is not always of the same magnitude and does not necessarily follow the same pattern (Figures 3.2a-b). Contrast tests revealed that yellow birch seedling growth was significantly higher in medium gaps when compared to small gaps (Figure 3.2a). Yellow birch saplings showed greater growth in large and medium gap sites when compared to small gaps (Figure 3.2b, predicted values and variability were reduced for small gaps when compared to actual values due to the random factor). Yellow birch sapling growth was greater in large and medium gaps when compared to small gaps (P(f) = 0.0262, F ratio = 5.45) (Figure 3.2b). Mountain maple seedling growth was significantly higher in the gap sites by more than double of what was observed under forest cover (Figure 3.2a). Mountain maple saplings had greater growth in medium gap sites when compared to sites under forest cover (Figure 3.2b). Further contrast testing revealed that mountain maple saplings had significantly reduced growth in forest sites when compared to the three gap sizes (P(f) = 0.0046, F ratio = 8.27) (Figure 3.2b). Contrast tests also revealed that balsam fir seedling growth showed higher growth in large gap environments, when compared to medium gaps, small gaps and forest sites but the difference was very small (<1cm) (Figure 3.2a). Balsam fir growth at the seedling stage was the only species that responded significantly (P(f) = 0.0235) to the gap area (m^2) simple regression, but the relationship was very weak (R^2 = 1 %).

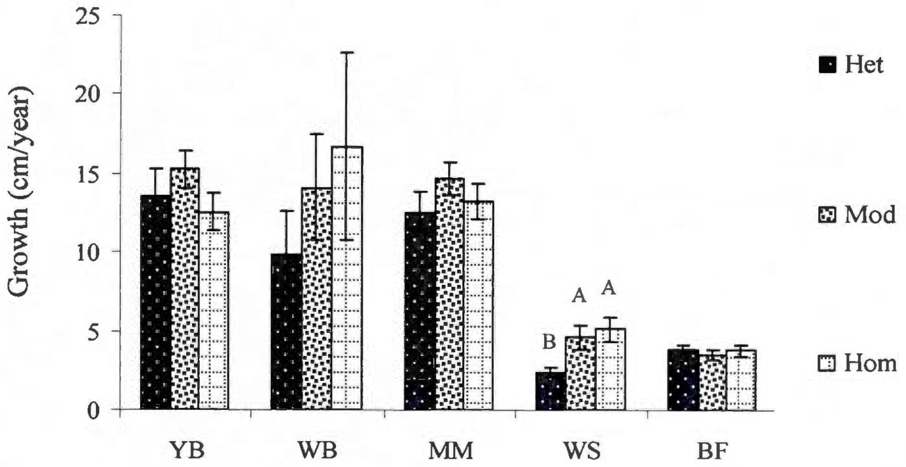


Figure 3.1a. Seedling growth of 5 species [yellow birch (YB), white birch (WB), mountain maple (MM), white spruce (WS) and balsam fir (BF)] as a function of spatial heterogeneity [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom), capital letters indicate significantly different Tukey tests, lower case letters indicate significantly different contrast tests, actual values with standard error]

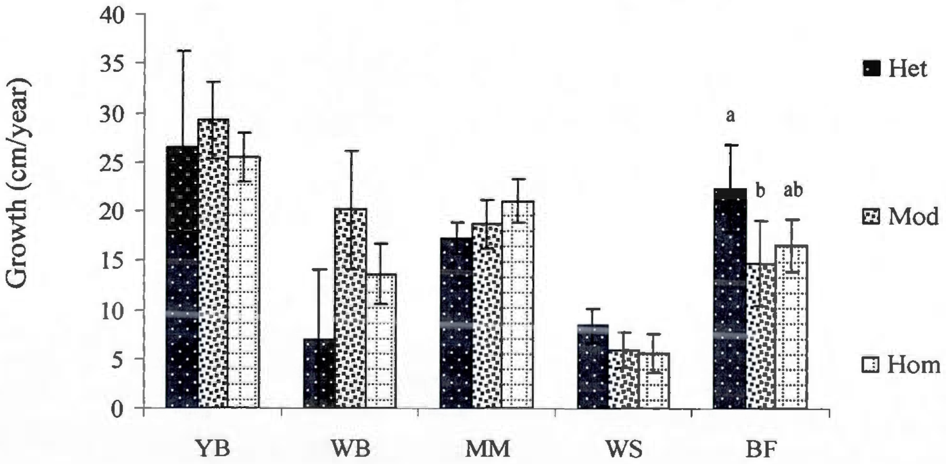


Figure 3.1b. Sapling growth of 5 species [yellow birch (YB), white birch (WB), mountain maple (MM), white spruce (WS) and balsam fir (BF)] as a function of spatial heterogeneity [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom), capital letters indicate significantly different Tukey tests, lower case letters indicate significantly different contrast tests, actual values with standard error]

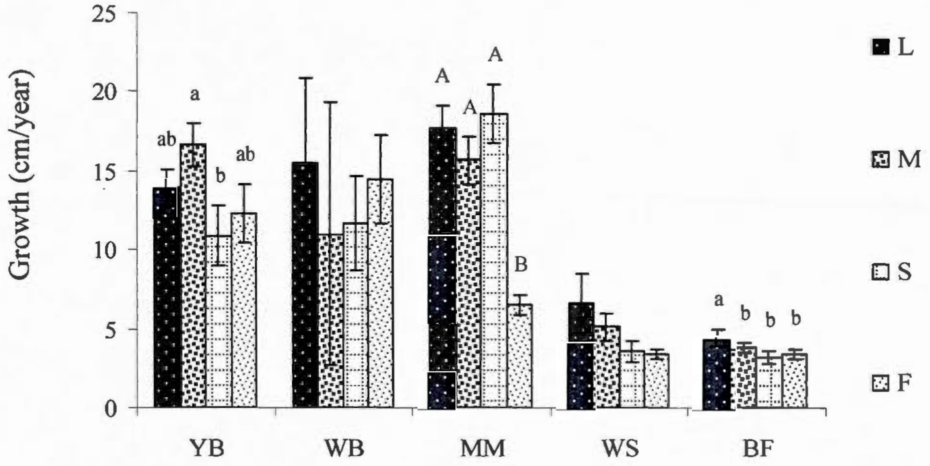


Figure 3.2a. Seedling growth of 5 species [yellow birch (YB), white birch (WB), mountain maple (MM), white spruce (WS) and balsam fir (BF)] as a function of gap size [large (L), medium (M), small (S) and forest sites (F), capital letters indicate significantly different Tukey tests, lower case letters indicate significantly different contrast tests, actual values with standard error]

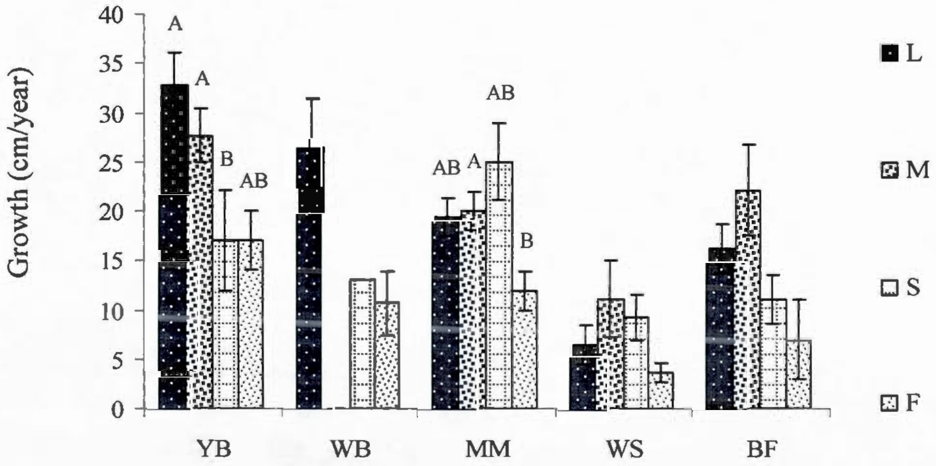


Figure 3.2b. Sapling growth of 5 species [yellow birch (YB), white birch (WB), mountain maple (MM), white spruce (WS) and balsam fir (BF)] as a function of gap size [large (L), medium (M), small (S) and forest sites (F), capital letters indicate significantly different Tukey tests, lower case letters indicate significantly different contrast tests, actual values with standard error]

Table 3.1. Growth response of species regeneration to spatial heterogeneity (SH) and gap size (GS) [ANOVA mixed model]

Species growth	P(f)	F ratio	n
Yellow birch seedling growth			
SH	0.7920	0.24	187
GS	0.2310	1.45	187
SH* GS (*interaction term*)	0.4693	0.94	187
Yellow birch sapling growth			
SH	0.3326	1.65	38
GS	0.0056	5.14	38
Mountain maple seedling growth			
SH	0.4349	0.91	471
GS	0.0001	28.30	471
SH* GS	0.7585	0.56	471
Mountain maple sapling growth			
SH	0.8736	0.14	177
GS	0.0364	2.91	177
SH* GS	0.2649	1.29	177
White spruce seedling growth			
SH	0.0262	4.57	71
GS	0.3451	1.13	71
SH* GS	0.3653	1.11	71
White spruce sapling growth			
SH	0.8816	0.13	22
GS	0.6279	0.60	22
Balsam fir seedling growth			
SH	0.0694	0.07	423
GS	0.0528	2.59	423
SH* GS	0.2159	1.39	423
Balsam fir sapling growth			
SH	0.1263	2.79	57
GS	0.4163	0.97	57

3.3.2 Growth response of species to microtopography position, establishment site, browsing and competition

The microtopography position, as expressed by the difference in height from the lowest position in the microquadrat to the position occupied by the stem, was not significantly related to growth for any of the species size class combinations as tested by a simple regression (*data not presented*). As well, the establishment site categories (soil microsites *versus* non-soil microsites such as rocks, decaying logs and pit and mound microtopography) did not yield any significant response from species growth (Table 3.2, Figures 3.3a-b). Nevertheless, species growth was always inferior on non-soil microsites (Figures 3.3a-b). Yellow birch was present on non-soil microsites 39% and 16% of the time for seedlings and saplings respectively (Table 3.2). White birch was also often observed on non-soil microsites (seedlings: 27%, saplings: 19%) (Table 3.2). Yellow birch seedling used decaying logs the most frequently (28%), followed by mounds (8%) and finally rocks (3%) (Figure 3.4).

Browsing significantly affected the growth of yellow birch seedlings and saplings, as well as white birch seedlings (Table 3.2, Figures 3.5a-b). Mountain maple seedling growth was not significantly affected by browsing (Figure 3.5a). The species size class that was the most browsed was white birch seedlings (30% of the time), followed by yellow birch seedlings (20%) and mountain maple seedlings (14%) (Table 3.2). Browsing at the sapling stage was less important (Table 3.2). Browsing was found to be almost significantly related to spatial heterogeneity, with more browsing in heterogeneous landscapes (P(f) = 0.0512, ChiSquare = 5.95) (Figure 3.5c).

In general, all species grew slower under increasing competition. Based on our measure of competition, the growth of seedlings and saplings of balsam fir and mountain maple were significantly and negatively affected by competition (Table 3.3). Balsam fir seedlings and saplings had inferior growth when competition was 100%, when compared to no competition (Figures 3.6a-b). Contrast tests showed that balsam fir seedlings had significantly superior growth in no competition situations when compared to all the other classes (P(f) = 0.0024, F ratio = 9.40) (Figure 3.6a). Mountain maple seedlings and saplings grew better under 0, 25% and 50% competition when compared to 100% competition

(Figures 3.6a-b). Contrast tests provided us with evidence that white spruce growth was best in no competition situations when compared to the other categories combined (Figure 3.6a).

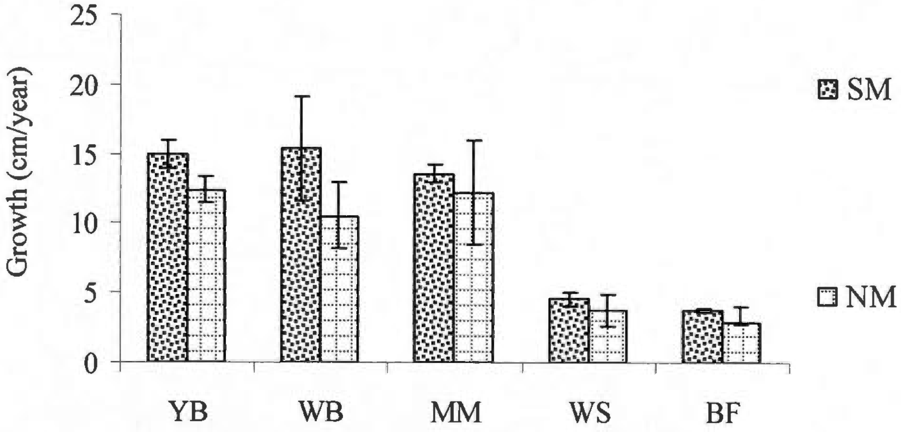


Figure 3.3a. Seedling growth of 5 species [yellow birch (YB), white birch (WB), mountain maple (MM), white spruce (WS) and balsam fir (BF)] as a function of the establishment site [soil microsite (SM) and non-soil microsite (NM), capital letters indicate significantly different Tukey tests, lower case letters indicate significantly different contrast tests, actual values with standard error]

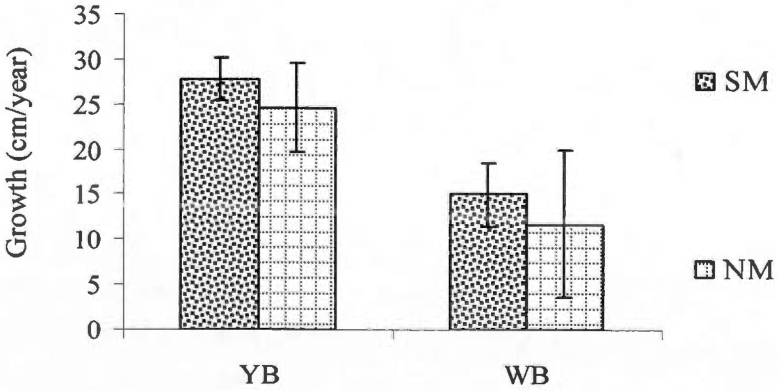


Figure 3.3b. Sapling growth of 2 species [yellow birch (YB) and white birch (WB)] as a function of the establishment site [soil microsite (SM) and non-soil microsite (NM), capital letters indicate significantly different Tukey tests, lower case letters indicate significantly different contrast tests, actual values with standard error]

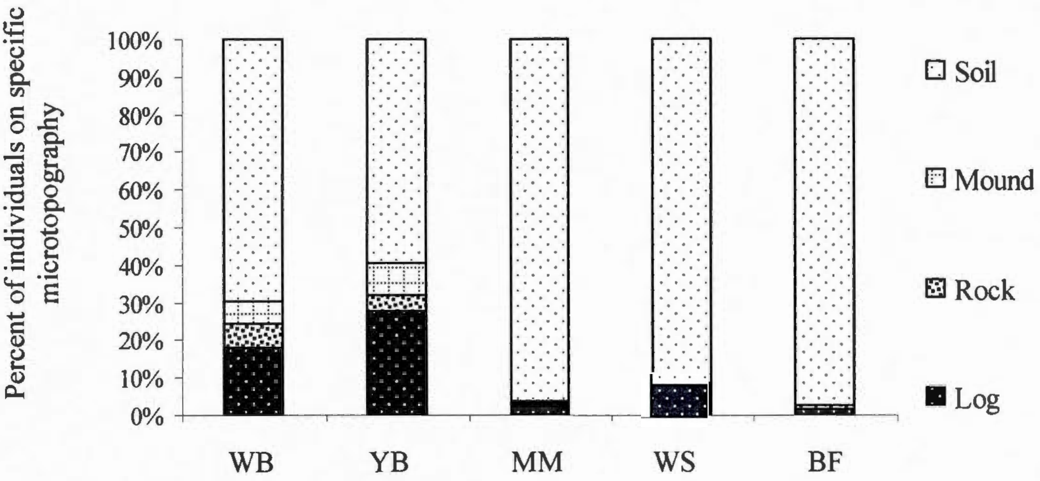


Figure 3.4. Microtopographic features associated with the abundance of seedlings of 5 species [white birch (WB), yellow birch (YB), mountain maple (MM), white spruce (WS) and balsam fir (BF)]

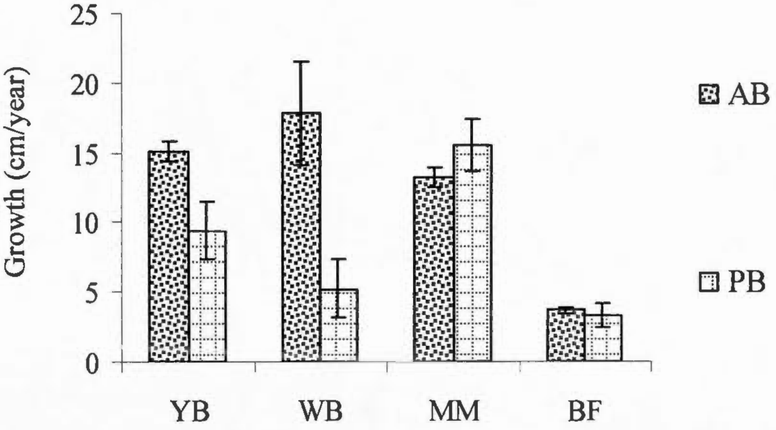


Figure 3.5a. Seedling growth of 4 species [yellow birch (YB), white birch (WB), mountain maple (MM) and balsam fir (BF)] as a function of browsing [absence of browsing (AB) and presence of browsing (PB), capital letters indicate significantly different Tukey tests, lower case letters indicate significantly different contrast tests, actual values with standard error]

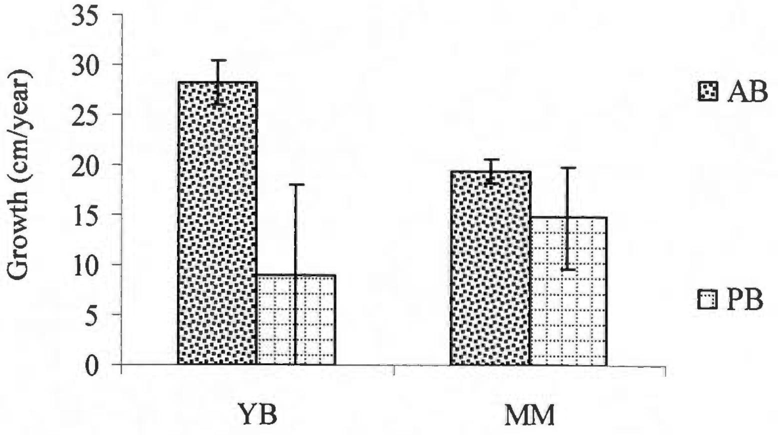


Figure 3.5b. Sapling growth of 2 species [yellow birch (YB) and mountain maple (MM)] as a function of browsing [absence of browsing (AB) and presence of browsing (PB), capital letters indicate significantly different Tukey tests, lower case letters indicate significantly different contrast tests, actual values with standard error]

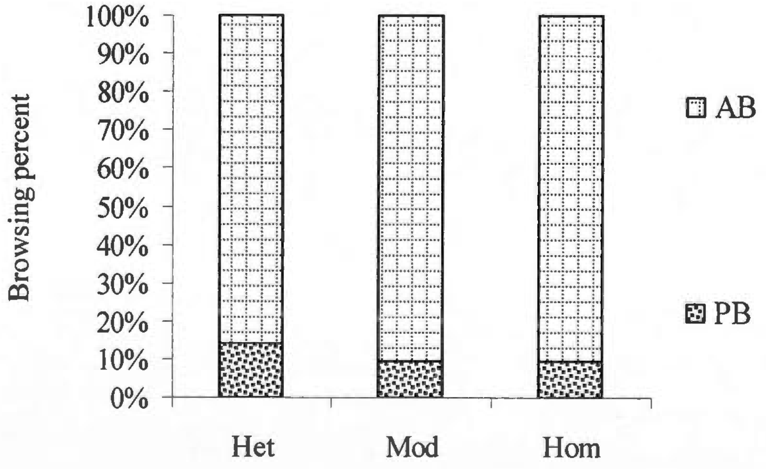


Figure 3.5c. Browsing percent for three species seedlings [yellow birch, white birch and mountain maple, absence of browsing (AB) and presence of browsing (PB)] as a function of spatial heterogeneity [heterogeneous (Het), moderate (Mod), homogenous (Hom), actual values]

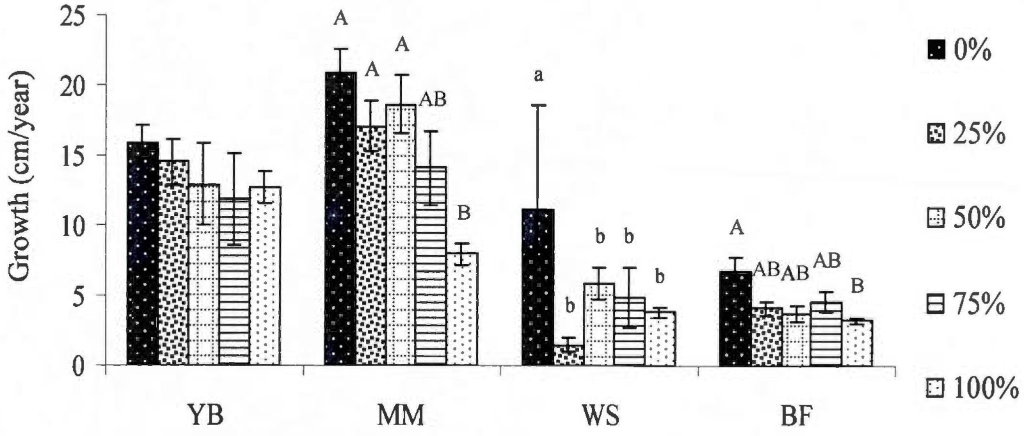


Figure 3.6a. Seedling growth of 5 species [yellow birch (YB), white birch (WB), mountain maple (MM), white spruce (WS) and balsam fir (BF)] as a function of percent competition [capital letters indicate significantly different Tukey tests, lower case letters indicate significantly different contrast tests, actual values with standard error]

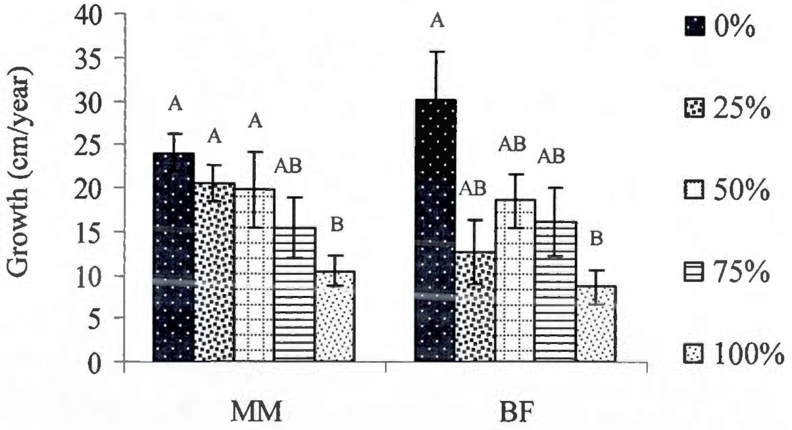


Figure 3.6b. Sapling growth of 2 species [mountain maple (MM) and balsam fir (BF)] as a function of percent competition [capital letters indicate significantly different Tukey tests, lower case letters indicate significantly different contrast tests, actual values with standard error]

Table 3.2. Growth response of species regeneration to establishment site (ES) and browsing (BR) [not available (NA), ANOVA mixed model]

Species growth	Proportion browsed or on establishment sites	n	P(f)	F ratio
Yellow birch seedlings				
ES	39%	187	0.4908	0.48
BR	20%	187	0.0001	43.30
Yellow birch saplings				
ES	16%	38	0.3374	0.95
BR	5%	38	0.0072	8.23
White birch seedlings				
ES	27%	37	0.9245	0.01
BR	30%	37	0.0029	10.63
White birch saplings				
ES	19%	16	0.6952	0.16
BR	13%	16	0.0698	6.52
Mountain maple seedlings				
ES	4%	471	0.4392	0.60
BR	14%	471	0.9670	0.01
Mountain maple saplings				
ES	0%	177	NA	NA
BR	7%	177	0.1026	2.69
White spruce seedlings				
ES	8%	71	0.6837	0.17
BR	1%	71	0.3896	0.75
Balsam fir seedlings				
ES	4%	423	0.1565	2.01
BR	3%	423	0.6399	0.22

Table 3.3. Growth response of species regeneration to the percent competition [not available (NA), ANOVA mixed model]

Species growth	P(f)	F ratio	n
Yellow birch seedling growth			
Competition	0.1844	1.57	166
Yellow birch sapling growth			
Competition	0.3648	1.15	31
Mountain maple seedling growth			
Competition	0.0009	4.84	294
Mountain maple sapling growth			
Competition	0.0001	6.77	136
White spruce seedling growth			
Competition	0.0909	2.19	40
White spruce sapling growth			
Competition	NA	NA	12
Balsam fir seedling growth			
Competition	0.0012	4.70	237
Balsam fir sapling growth			
Competition	0.0401	2.73	54

3.3.3 Response of height, competition and microtopography position to gap size and spatial heterogeneity

There was no significant species height response to spatial heterogeneity (Figures 3.7a-b). Important trends were observed for yellow birch (> 30cm) and white birch (> 80cm) seedlings to have inferior height in heterogeneous landscapes when compared to homogenous landscapes (Figure 3.7a). Height did vary significantly with gap size for some species (Table 3.4). Mountain maple seedling and sapling height was smaller under forest cover than in any of the gap sites (Figures 3.7c-d). Balsam fir seedling height was significantly affected by gap size, with the height of specimens being significantly greater under forest cover than medium or small gaps (Figure 3.7c). White spruce saplings were also significantly smaller under forest cover than either large or medium gaps (Figure 3.7d).

The competition experienced by the five key species did not significantly differ among gap sizes or spatial heterogeneity levels for any of the species size class combinations (Table 3.5). The microtopography position (the difference in height from the lowest position in the microquadrat to the position occupied by the individual) was not significantly related to the gap sizes or spatial heterogeneity levels (*data not presented*).

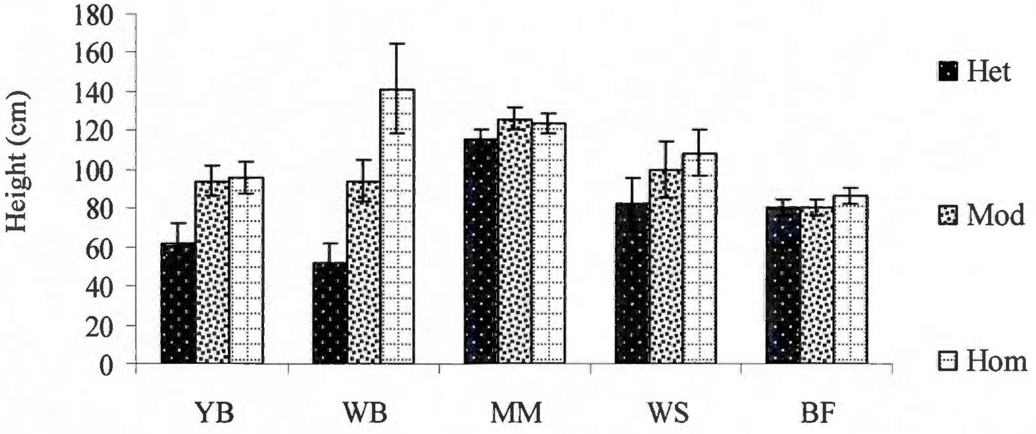


Figure 3.7a. Seedling height of 5 species [yellow birch (YB), white birch (WB), mountain maple (MM), white spruce (WS) and balsam fir (BF)] as a function of spatial heterogeneity [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom), capital letters indicate significantly different Tukey tests, lower case letters indicate significantly different contrast tests, actual values with standard error]

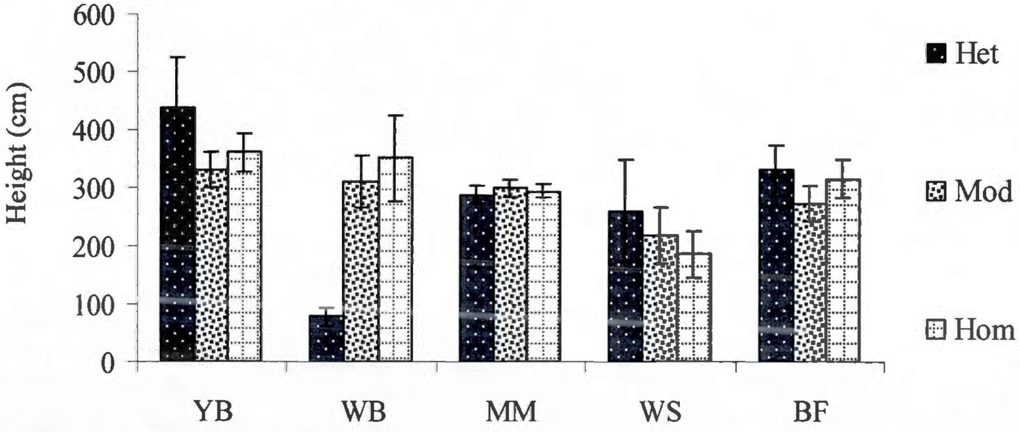


Figure 3.7b. Sapling height of 5 species [yellow birch (YB), white birch (WB), mountain maple (MM), white spruce (WS) and balsam fir (BF)] as a function of spatial heterogeneity [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom), capital letters indicate significantly different Tukey tests, lower case letters indicate significantly different contrast tests, actual values with standard error]

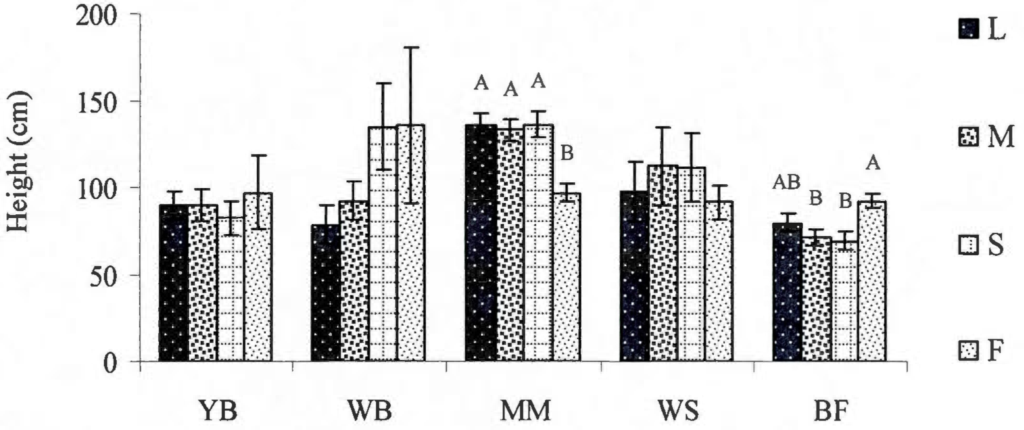


Figure 3.7c. Seedling height of 5 species [yellow birch (YB), white birch (WB), mountain maple (MM), white spruce (WS) and balsam fir (BF)] as a function of gap size [large (L), medium (M), small (S) and forest sites (F), capital letters indicate significantly different Tukey tests, lower case letters indicate significantly different contrast tests, actual values with standard error]

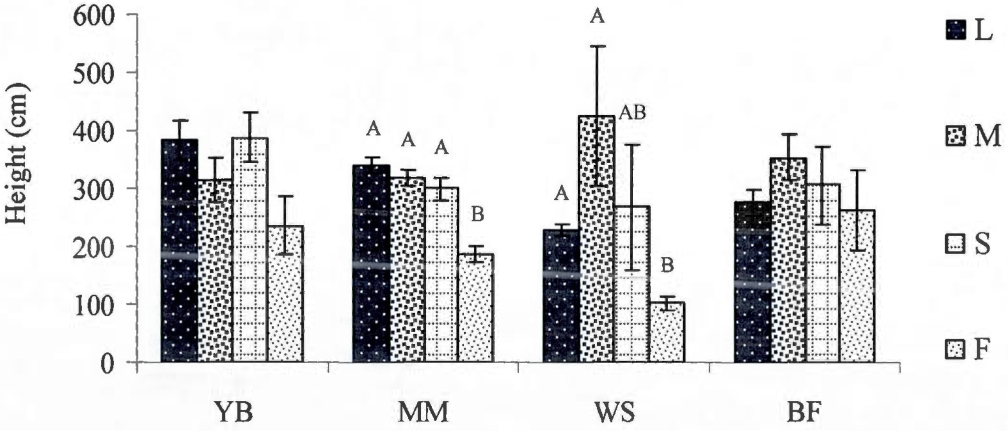


Figure 3.7d. Sapling height of 4 species [yellow birch (YB), mountain maple (MM), white spruce (WS) and balsam fir (BF)] as a function of gap size [large (L), medium (M), small (S) and forest sites (F), capital letters indicate significantly different Tukey tests, lower case letters indicate significantly different contrast tests, actual values with standard error]

Table 3.4. Height response of species regeneration to spatial heterogeneity (SH) and gap size (GS) [ANOVA mixed model]

Species height	P(f)	F ratio	n
Yellow birch seedlings			
SH	0.2332	1.78	187
GS	0.9980	0.01	187
Yellow birch saplings			
SH	0.6384	0.48	39
GS	0.2924	1.29	39
White birch seedlings			
SH	0.1612	18.74	37
GS	0.1673	1.97	37
Mountain maple seedlings			
SH	0.8369	0.18	474
GS	0.0001	14.90	474
Mountain maple saplings			
SH	0.9178	0.09	179
GS	0.0001	32.90	179
White spruce seedlings			
SH	0.6164	0.51	72
GS	0.9212	0.16	72
White spruce saplings			
SH	0.9948	0.01	22
GS	0.0047	7.63	22
Balsam fir seedlings			
SH	0.5856	0.58	425
GS	0.0035	4.61	425
Balsam fir saplings			
SH	0.2337	2.42	57
GS	0.2142	1.64	57

Table 3.5. Response of species regeneration percent competition to spatial heterogeneity (SH) and gap size (GS) [not available (NA), ANOVA mixed model]

Species competition	P(f)	F ratio	n
Yellow birch seedlings			
SH	0.8781	0.1323	167
GS	0.0621	3.75	167
Yellow birch saplings			
SH	0.2251	1.75	32
GS	0.5490	0.61	32
White birch seedlings			
SH	0.7481	0.29	29
GS	0.6429	0.45	29
Mountain maple seedlings			
SH	0.5653	0.61	294
GS	0.2903	1.24	294
Mountain maple saplings			
SH	0.5071	0.76	137
GS	0.3537	1.04	137
White spruce seedlings			
SH	0.7654	0.27	40
GS	0.4254	0.88	40
White spruce saplings			
SH	0.6224	0.52	12
GS	0.2788	2.23	12
Balsam fir seedlings			
SH	0.8213	0.20	237
GS	0.1282	2.07	237
Balsam fir saplings			
SH	0.4140	2.42	54
GS	0.2401	1.47	54

3.4 Discussion

3.4.1 Growth response of species regeneration to spatial heterogeneity and gap size

The scientific literature provides evidence that highly disturbed stands exhibit elevated levels of shrub abundance and competition (Post, 1970, Archambault et al. 1998, Laflèche et al. 2000). Shrub species are able to establish dense underlayers in degraded stands (Royo and Carson, 2006). Mountain maple can suppress tree regeneration for over 50 years and can persist through all stages of succession (Vincent, 1965, Aubin et al. 2005). Hazelnut has been shown to respond in greater densities after logging than after fire or spruce budworm outbreak (Kemball et al. 2005). Despite the evidence in the literature, growth response to spatial heterogeneity was variable. White spruce seedling growth had significantly lower growth in heterogeneous landscapes (Figure 3.1a). Balsam fir saplings however, had superior growth in heterogeneous landscapes (Figure 3.1b). These observations may be partially explained by white spruce seedling growth being negatively influenced by a shrub layer in heterogeneous landscapes, whereas balsam fir saplings would have been above the shrub layer in heterogeneous landscapes, however we cannot confirm this mechanism (Figures 3.1a-b).

Growth of species regeneration responded predictably toward gap size, all species except mountain maple showed maximum growth in either large or medium gaps. Our work thus provides some additional evidence to support the different effects among gap openings and forest sites, although differential response within gap sizes was not evident (Kneeshaw and Bergeron, 1998, 1999). Species growth did respond to presence or absence of canopy openings, but we might wonder why the numerical gap size (m^2) was only important for balsam fir at the seedling stage (Table 3.1). Lack of response regarding the growth of species with respect to the gap area and gap size class was likely due to the irregular shapes of naturally formed gaps, different time since disturbance and variable average regeneration height.

3.4.2 Growth response to microtopography position, establishment site, browsing and competition

The microtopography position (the difference in height from the lowest position in the microquadrat to the position occupied by the individual) and the establishment site (soil microsites versus non-soil microsites such as rocks, decaying logs and pit and mound microtopography) were not significantly involved in the growth of the five species key species. However, species growth was always inferior on non-soil microsites (Figures 3.3a-b).

Browsing had a significantly negative influence on the growth of yellow birch seedlings and saplings and white birch seedlings (Table 3.2, Figures 3.5a-b). Mountain maple seedling growth was not significantly affected by browsing (Figure 3.5a). Such prolific growth on the part of mountain maple seedlings has been documented and is due to its ability to produce basal sprouts (Jobidon, 1995). This characteristic may provide mountain maple with a competitive advantage over other species such as yellow birch. Yellow birch and mountain maple are well known victims of browsing events (Godman and Krefting, 1960, Jobidon, 1995). In addition, a negative response of yellow birch growth toward browsing has already been documented (Bouffard et al. 2004). Browsing was almost significantly more present in heterogeneous sites (Figure 3.5c). Dense understories and heavy timber harvests have been shown to increase the rate of seed and seedling predation (George and Bazzaz, 1999, Bouffard et al. 2004).

Species growth was generally reduced by increasing competition (Figures 3.6a-b). The growth of seedlings and saplings of balsam fir and mountain maple were significantly and negatively affected by competition (Table 3.3).

3.4.3 Response of height, competition and microtopography position to spatial heterogeneity and gap size

Although the height of species did not differ significantly within the different heterogeneity levels, biologically important differences were observed (Figures 3.7a-b). The average height of yellow birch and white birch seedlings was > 30cm and > 80cm less in heterogeneous landscapes when compared to homogenous ones. Although this gives us some indication of growth difficulties encountered by the two species, variability in height growth may be due to species age and plant strategy. The microtopography position did not differ in a significant manner within the gap sizes or spatial heterogeneity levels.

There is no consensus regarding the best way to measure the effects of competition on tree growth (Biging and Dobbertin, 1995). In fact, some evidence suggests, although counter-intuitively, that distance-independent indices that used tree crown measurements were as effective as distance-dependent indices (Biging and Dobbertin, 1995). The authors suggest that this is because the distance-independent measures take into account a larger area of potential interactions (the plot size was 0.08ha), suggesting that an expanded consideration of the neighbourhood and not tree spatial locations are needed for analysis (Biging and Dobbertin, 1995). Typically, competition indices are designed to measure competition under forest cover and not in canopy openings (Biging and Dobbertin, 1995), it is for this reason that we chose to use a simple visual evaluation of the percent competition above the sampled individual within a human conceived cylinder (radius of 1.26m, height of 6m) similar to the measure applied in Archambault et al. (1998). Our work did not establish a direct link between shrub competition and different spatial heterogeneity levels or gap sizes (Table 3.5). This would have provided a verifiable mechanism for the reduced tree density observed in heterogeneous landscapes (Chapter 2, Markgraf, 2012). It is possible that our sampling layout was flawed in two ways regarding our competition measure, even though it was significantly shown to reduce the growth of species (Figures 3.6a-b). Firstly, it is feasible to suggest that we should have included a method to separate shrub and tree regeneration competition (we only measured total competition). Secondly, the experimental disposition only permitted us to take the growth measurements of the largest individual of each species in each microquadrat. Because the competition measure was only used for the tallest stems of each species, smaller stems were not measured and because of this the competition values were under-estimated.

3.4.4 Conclusion

Our growth results suggest that heterogeneity of landscape spatial structures has a weak impact on the growth of tree and shrub species in the understory forest layer. We observed that the seedlings of white spruce had significantly lower growth in heterogeneous systems. This may be due to an increase in shrub density in heterogeneous landscapes (Chapter 2, Markgraf, 2012) and the understory competition and shading that would result. Interestingly, the saplings of balsam fir demonstrated superior growth in heterogeneous landscapes, when compared to the other two categories. This suggests that seedlings are more affected by a recalcitrant understory layer and that saplings are able to pierce through the competition. Our data therefore offers weak support for the notion that in heterogeneous systems there is increased competition specifically at the seedling life stage of regeneration and that saplings may experience reduced competition. This theory is in part supported by the inferior, although not significant, height of seedlings from all five measured species in heterogeneous landscapes, and specifically regarding the birches, reductions that were considered biologically important.

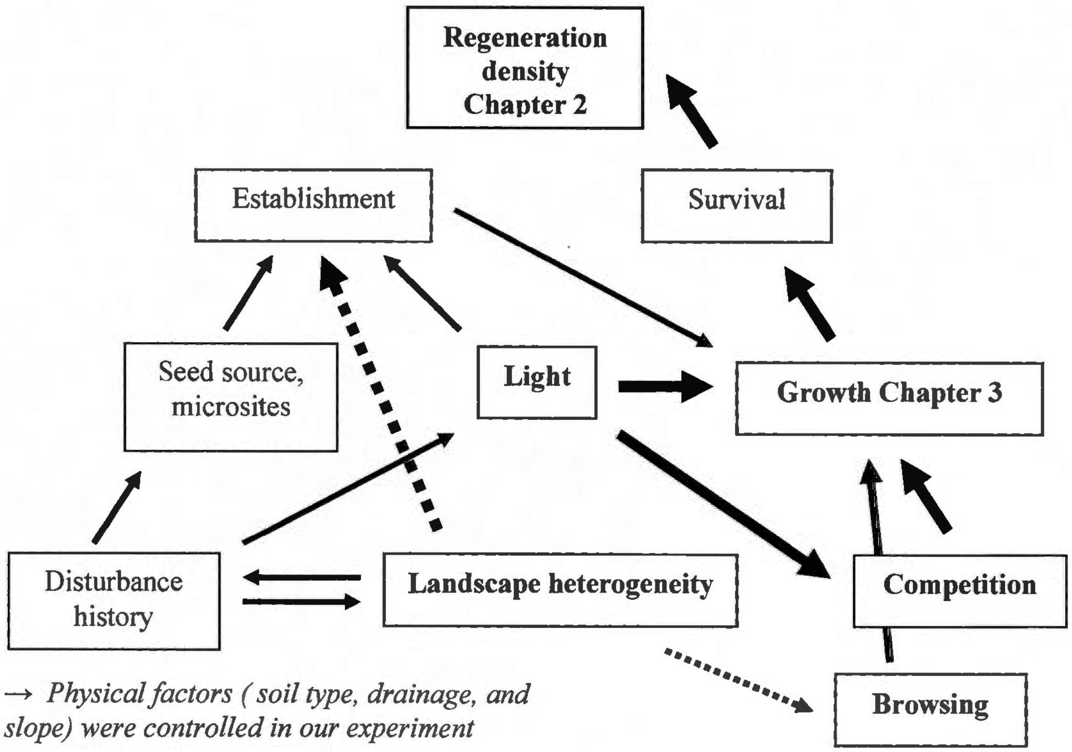
Measurements of the microtopography position, the establishment site, browsing and competition were undertaken to confirm whether these factors affected growth, and whether these factors were significantly different in the different gap size and spatial heterogeneity categories. If the factors significantly affected the growth of species, and were different in the treatments, than we could use them as a control to see what percent of the variability regarding species growth could be attributed to spatial heterogeneity alone. We found that browsing and competition significantly reduced species growth, however, these factors were not different within the different spatial heterogeneity levels. It must be noted that the observed browsing values were almost more frequent in heterogeneous landscapes when compared to expected values (P(f) = 0.0512, ChiSquare = 5.95), thus explaining our change to the conceptual model that would potentially link increased browsing to reduced growth in heterogeneous landscapes (Figure 3.8). Although the presence of non-soil microsites reduced growth in all the examined instances, albeit in a non-significant manner, the establishment site and the microtopography position were not significantly different in the spatial heterogeneity levels.

4.0 General conclusion

Our innovative work provides proof that the accumulation of disturbances at the landscape level, affects the distribution of local populations of shrubs and trees. We demonstrate that multiple tree species densities respond negatively to heterogeneous landscapes and that shrubs are able to dominate in the same situations. The interaction of the two factors, landscape heterogeneity and gap size, confirms that within the same gap size, the effects of landscape heterogeneity remain negative for various tree species. Theoretical implications include the identification of metapopulation processes similar to the colonizer - competitor theory, that regulate the persistence of shrub populations. Our work provides evidence that spatial heterogeneity can be useful for identifying stands that have large shrub populations with remotely sensed data.

We discovered significant plant density response to landscape heterogeneity, but only limited evidence of reduced tree seedling growth in heterogeneous landscapes. Our data showed that balsam fir sapling growth improved in heterogeneous landscapes at the sapling life history stage. This may specifically be due to the ability of tree saplings to pierce through the understory shrub layer in canopy openings, although the evidence is limited. Our work shows that browsing and competition were also factors in plant growth. The conceptual model explaining both our second and third chapters included the cascading response we proposed wherein landscape heterogeneity would affect local competition, which would in turn affect plant growth, then affecting plant survival and finally plant density. Although our work provides a direct link between spatial heterogeneity and tree and shrub regeneration density, we failed to identify the mechanism. Furthermore, we found no evidence that competition was dependent on spatial heterogeneity. There is thus no support for the model that was proposed, our data does not suggest that competition and subsequent growth suppression in heterogeneous landscapes reduce tree density. This leads us to believe that heterogeneous landscapes directly influence species density by impeding species establishment by seed (Figure 3.8).

Our research supplies convincing results that show that landscapes that constitute an indicator of previous disturbances are implicated in the expression of local phenomena. These results should be tested in other regions and in other forest types before the experimental evidence can confirm the universal applicability of our research. Forestry rarely takes into account landscape level factors when analyzing local variables, although seed dispersal of tree species can travel over large distances and therefore large scale interactions can occur. To account for this, metapopulation theories (MacArthur and Wilson, 1967, Hanski and Gilpin, 1991, Tilman, 1994) have attempted to incorporate large scale considerations. The idea that the forest landscape can have an impact on local factors is widespread in wildlife management, largely because animals are mobile. Basic questions about the home range of certain animal species requires an intricate knowledge of landscape factors. In light of our work, forest managers should realize that their management at the landscape level can impact the abundance of plant species throughout the landscape. Landscapes that accumulate high levels of disturbances, result in heterogeneous stand structures, large shrub populations and fragmentation of the forest patch dynamics, to the detriment of interesting forestry species such as yellow birch and white spruce.



→ *Physical factors (soil type, drainage, and slope) were controlled in our experiment*

Figure 3.8. Correction to the conceptual model of the forest dynamics in our system

APPENDIX AA – Results from density of species regeneration as a function of gap size

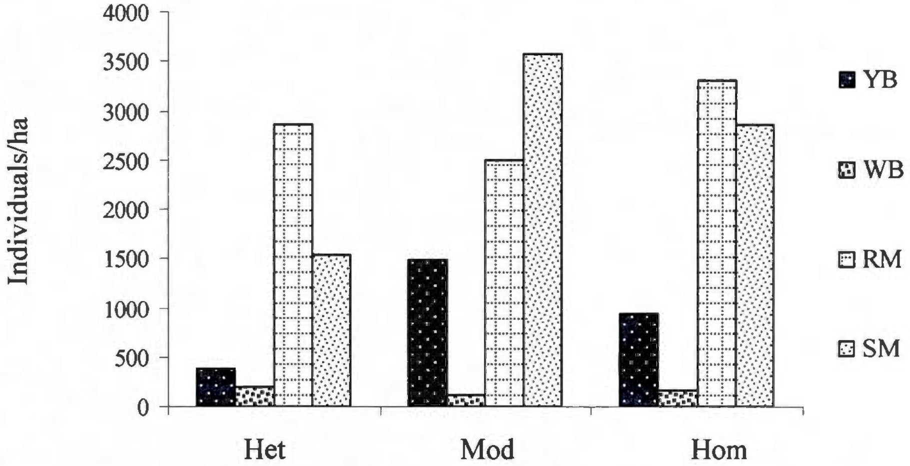


Figure AA.1. Four hardwood tree species [yellow birch (YB), white birch (WB), red maple (RM) and sugar maple (SM)] seedling regeneration density as a function of the spatial heterogeneity levels [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom), actual values]

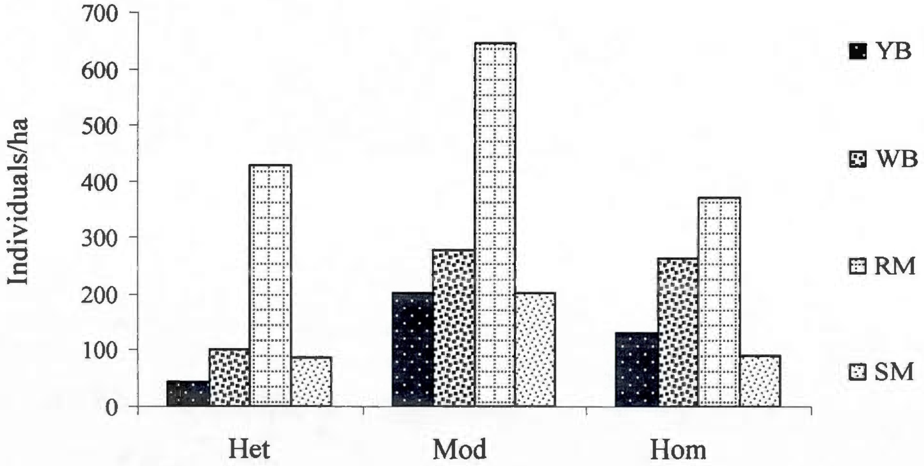


Figure AA.2. Four hardwood tree species [yellow birch (YB), white birch (WB), red maple (RM) and sugar maple (SM)] sapling regeneration density as a function of the spatial heterogeneity levels [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom), actual values]

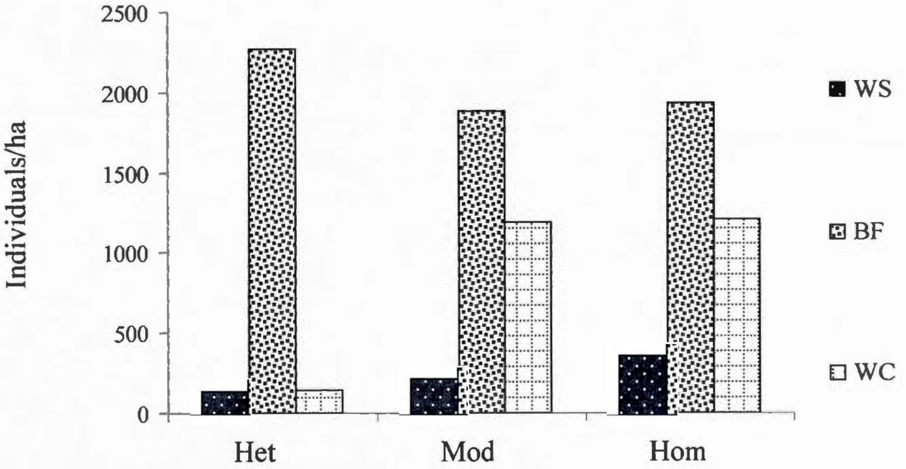


Figure AA.3. Three conifer tree species [white spruce (WS), balsam fir (BF) and white cedar (WC)] seedling regeneration density as a function of the spatial heterogeneity levels [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom), actual values]

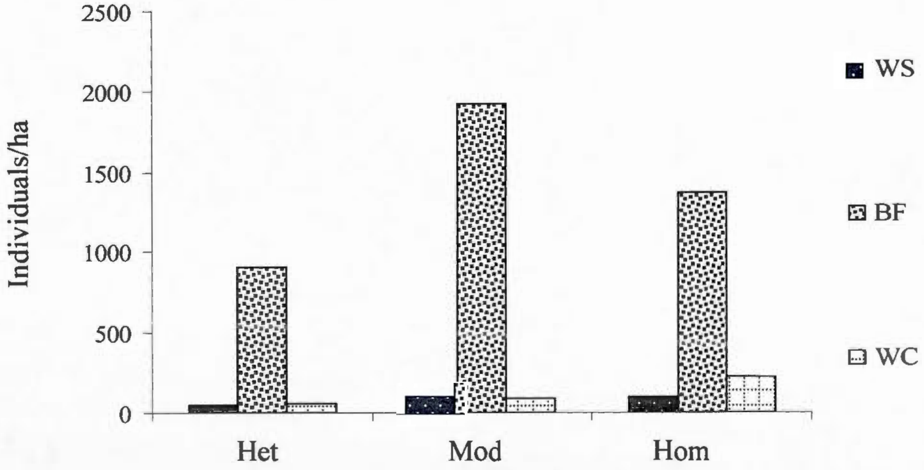


Figure AA.4. Three conifer tree species [white spruce (WS), balsam fir (BF) and white cedar (WC)] sapling regeneration density as a function of the spatial heterogeneity levels [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom), actual values]

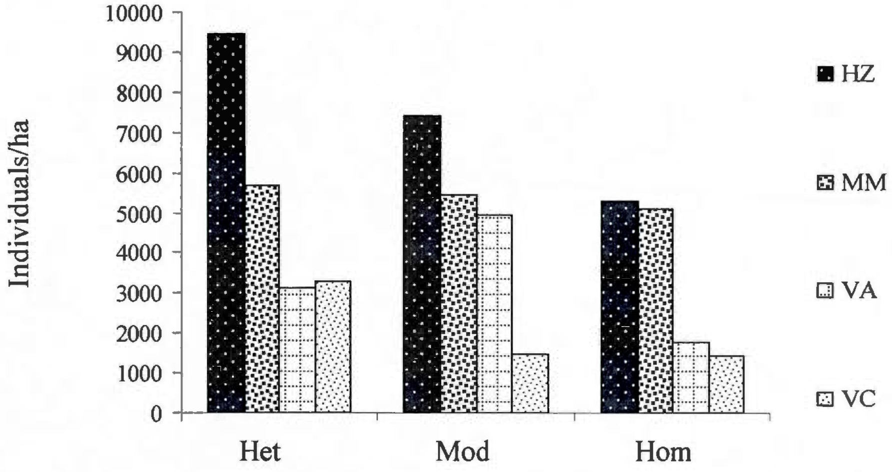


Figure AA.5. Four shrub species [Hazelnut (HZ), mountain maple (MM), *Viburnum alnifolium* (VA) and *Viburnum cassinoides* (VC)] seedling regeneration density as a function of the spatial heterogeneity levels [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom), actual values]

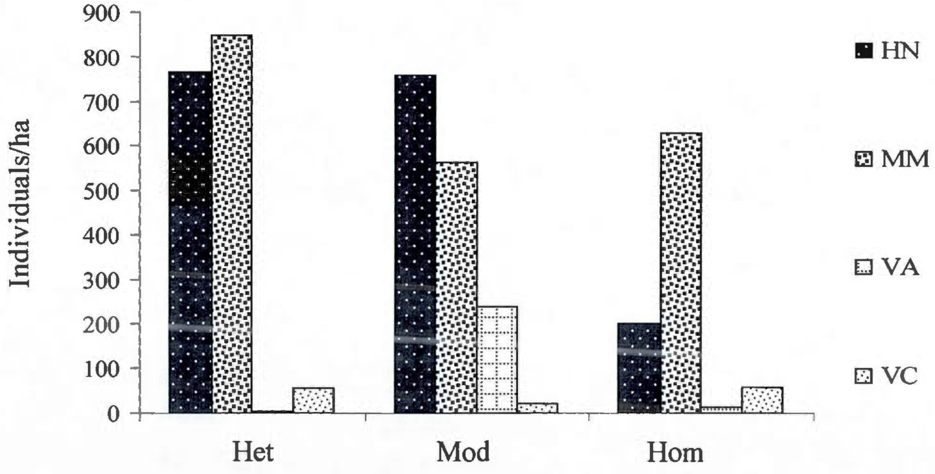


Figure AA.6. Four shrub species [Hazelnut (HZ), mountain maple (MM), *Viburnum alnifolium* (VA) and *Viburnum cassinoides* (VC)] sapling regeneration density as a function of the spatial heterogeneity levels [heterogeneous (Het), moderate heterogeneity (Mod) and homogenous (Hom), actual values]

APPENDIX AB – Results from density of species regeneration as a function of spatial heterogeneity

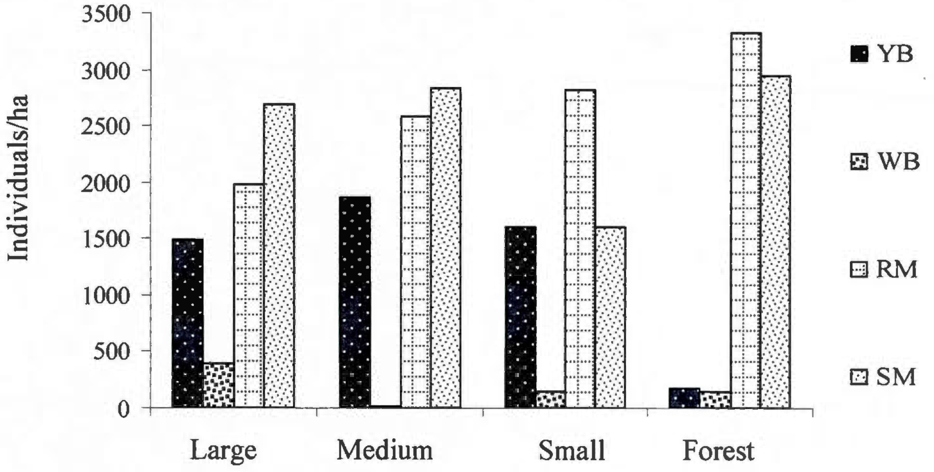


Figure AB.1. Four hardwood tree species [yellow birch (YB), white birch (WB), red maple (RM) and sugar maple (SM)] seedling regeneration density as a function of gap size [actual values]

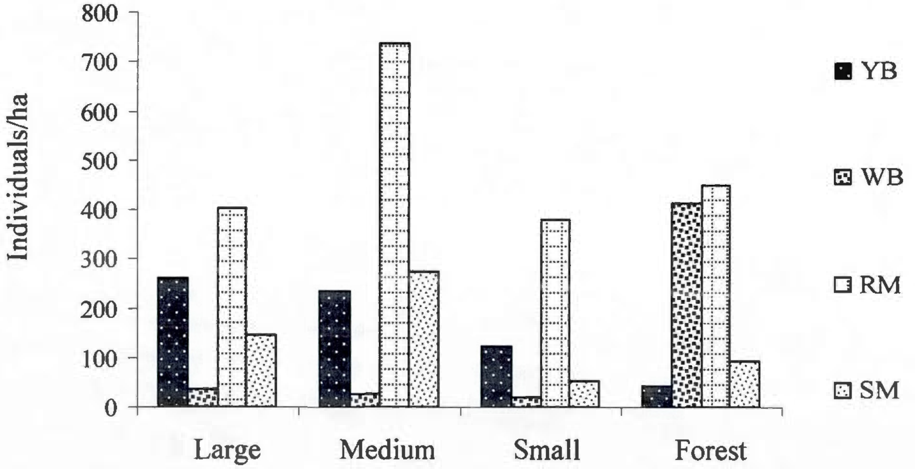


Figure AB.2. Four hardwood tree species [yellow birch (YB), white birch (WB), red maple (RM) and sugar maple (SM)] sapling regeneration density as a function of gap size [actual values]

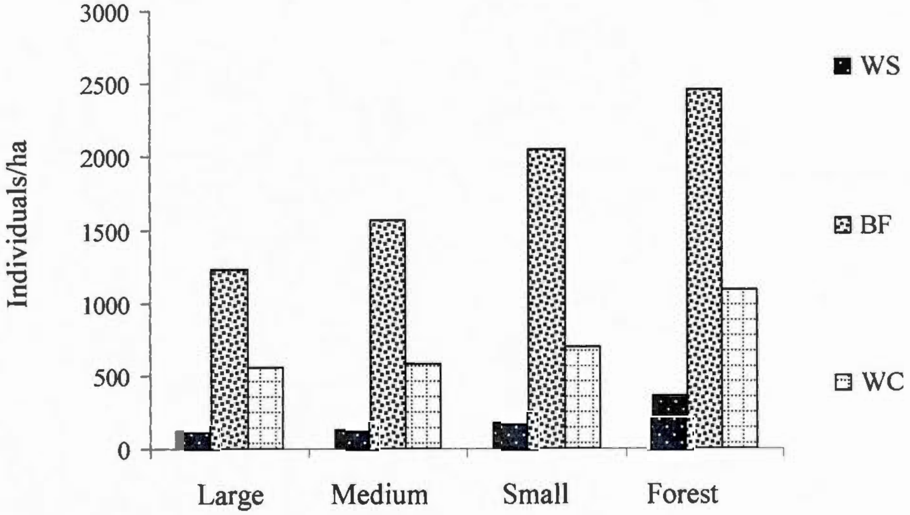


Figure AB.3. Four conifer tree species [white spruce (WS), balsam fir (BF) and white cedar (WC)] seedling regeneration density as a function of gap size [actual values]

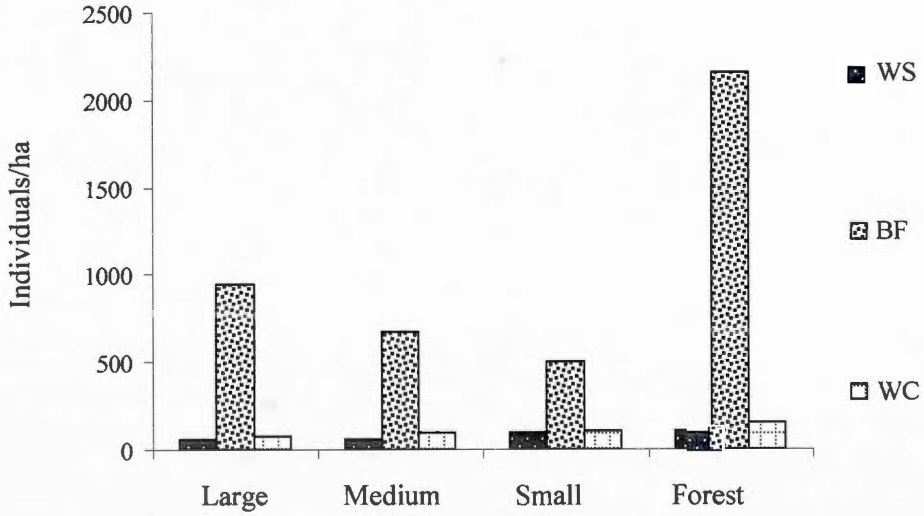


Figure AB.4. Four conifer tree species [white spruce (WS), balsam fir (BF) and white cedar (WC)] sapling regeneration density as a function of gap size [actual values]

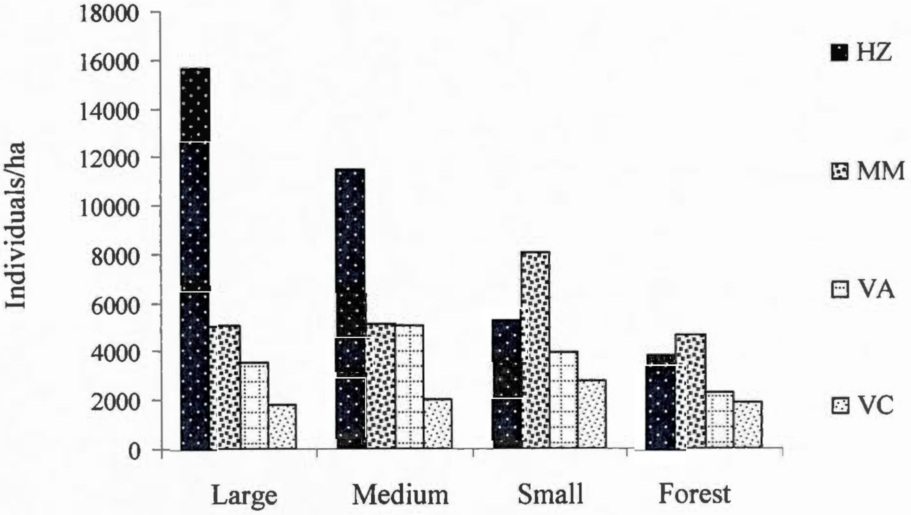


Figure AB.5. Four shrub species [Hazelnut (HZ), mountain maple (MM), *Viburnum alnifolium* (VA) and *Viburnum cassinoides* (VC)] seedling regeneration density as a function of gap size [actual values]

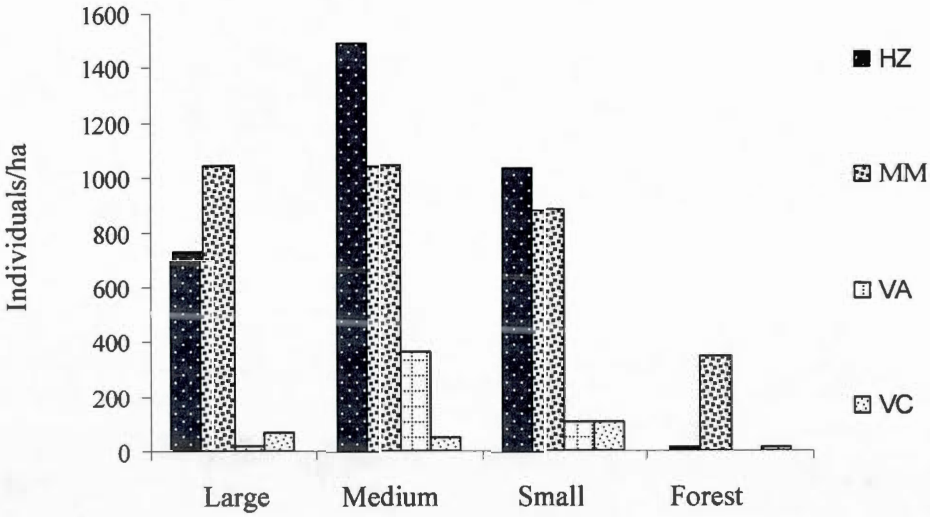


Figure AB.6. Four shrub species [Hazelnut (HZ), mountain maple (MM), *Viburnum alnifolium* (VA) and *Viburnum cassinoides* (VC)] sapling regeneration density as a function of gap size [actual values]

APPENDIX AC – Results for the regression shrub seedling density versus tree seedling density

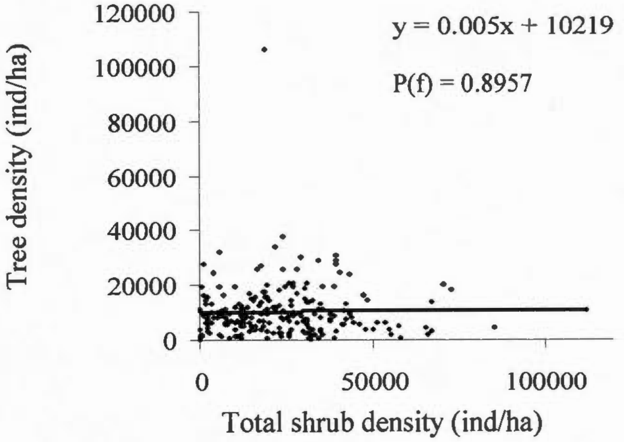


Figure AC.1. Tree seedling regeneration density as a function of total shrub density

APPENDIX B – Results for the growth of species regeneration as a function of gap position

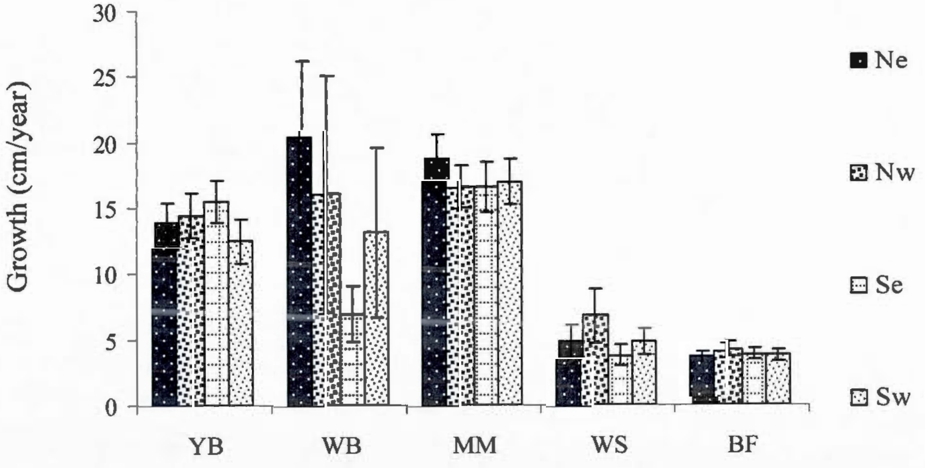


Figure B.1. Seedling growth of 5 species [yellow birch (YB), white birch (WB), mountain maple (MM), white spruce (WS) and balsam fir (BF)] as a function of gap position [north east (Ne), north west (Nw), south east (Se) and south west (Sw), actual values with standard error]

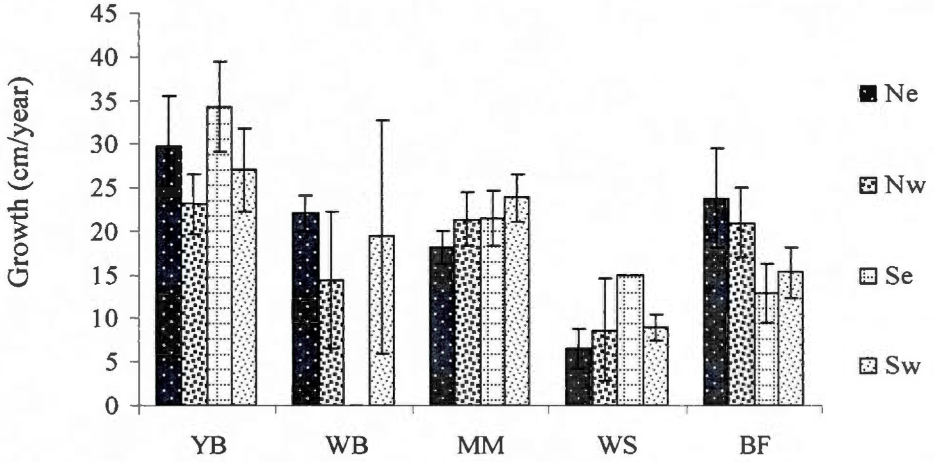


Figure B.2. Sapling growth of 5 species [yellow birch (YB), white birch (WB), mountain maple (MM), white spruce (WS) and balsam fir (BF)] as a function of gap position [north east (Ne), north west (Nw), south east (Se) and south west (Sw), actual values with standard error]

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