

INFLUENCE OF OVERSTORY COMPOSITION ON UNDERSTORY VEGETATION
AND RESOURCE ENVIRONMENT IN THE BOREAL FORESTS OF CANADA

BY

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ABSTRACT

The forest canopy is a major determinant of microclimate within the forest ecosystem, as it intercepts, absorbs and modifies light environment in the understory. The availability of resources in the understory has implications on the growth and establishment of understory plants. The objectives of this thesis were to: (1) determine by means of literature synthesis whether understory plant species diversity is driven by resource quantity and/or resource heterogeneity, and (2) examine the influence of overstory composition on understory vegetation, and on the understory light resource environment in mature boreal forest stands of central and eastern Canada.

A database of studies that investigated the effects of resources on understory plant diversity was compiled and analyzed using log-linear models. Whether resource quantity or resource heterogeneity is the determinant of understory plant diversity in individual studies was dependent on stand successional stage(s), presence or absence of intermediate disturbance, and forest biome within which the studies were conducted. Resource quantity was found to govern species diversity in both young and mature stands, whereas resource heterogeneity dominated in old-growth stands. Resource quantity remained the important driver in both disturbed and undisturbed forests, but resource heterogeneity played an important role in disturbed forests. The results suggested that neither resource quantity nor heterogeneity alone structures species diversity in forest ecosystems, but rather their influence on understory plant diversity vary with stand development and disturbances in forest ecosystems.

Patterns of species richness, abundance, and composition of three understory vegetation layers (shrub, herbaceous, and bryoid layers) were examined along an overstory broadleaf compositional gradient in the boreal mixedwood forests of central

Canada. Shrub cover, as well as herbaceous species richness and cover, increased with increasing proportions of broadleaves in the overstory, whereas bryoid richness and cover declined. Among vegetation layers, herbaceous richness increased with increasing shrub richness, and bryoid cover decreased with increasing shrub and herbaceous cover. Species richness, cover, and composition of the three vegetation layers studied showed different patterns of association with measured environmental variables. Shrub and herbaceous richness and cover peaked along the broadleaf compositional gradient, while bryoid richness and cover peaked in conifer and less often in mixedwood ranges. On the basis of resource homogeneity and heterogeneity in pure and mixed species stands, these results suggest that resource quantity may be the important driver of herbaceous richness, shrub cover, and bryoid cover, whereas both resource quantity and resource heterogeneity may drive bryoid richness and herbaceous cover. Therefore, maintaining a diverse overstory in the boreal forests will ensure diversity of various life forms, because each overstory type, through modification of resources, may favor the establishment of different understory plant communities.

Instantaneous measurements of photosynthetic photon flux density (PPFD) were taken at 1.3 m above the forest floor in the understories of pure and mixed, closed-canopy boreal stands, dominated by *Populus tremuloides* (trembling aspen), *Pinus banksiana* (jack pine), and *Picea mariana* (black spruce), in eastern and central regions of the boreal mixedwood forests. Light quantity, calculated as percent PPFD, was higher under trembling aspen canopy ($14.9 \pm 0.8\%$) than mixedwood ($10.4 \pm 0.7\%$), and black spruce ($12.9 \pm 0.6\%$) stands in the eastern boreal region, but least under aspen canopy ($7.6 \pm 1.3\%$), and highest in mixedwood stands ($12.6 \pm 0.6\%$) in the central boreal region. Light

heterogeneity, calculated as spatial variation of %PPFD within a stand, was higher in mixedwoods than single species stands. Light transmission was generally higher under overcast than under clear sky conditions. Overstory tree composition, as well as tall shrubs affects understory light quantity and heterogeneity. In closed-canopy stands, light measurements taken on both clear and overcast sky conditions are required to adequately quantify total light resource quantity and heterogeneity, available to understory plants over a growing season.

In summary, overstory composition influences resource availability in the understory and consequently on the richness, cover and composition of understory plants. Understory resource conditions may be fairly homogeneous in broadleaf and conifer stands, and heterogeneous in mixed stands. Patterns of species diversity in the resource limited understory may be governed by both the average supply (resource quantity) and spatial variability (resource heterogeneity) of available resources.

Keywords: Understory vegetation; resource availability; resource heterogeneity; plant diversity; boreal forest; photosynthetic photon flux density; broadleaf forests; bryoid.

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NOTE

Much care and effort was put into the write-up of this thesis to integrate chapters two, three, and four. These chapters were written as separate chapters to suit submission requirements of selected peer-review journals. As such, writing and styles of referencing may differ among these chapters. Chapter two has been accepted for publication in *Ecology*, chapter four has been submitted to *Forest Science*, while chapter three awaits submission.

Chapter two:

Bartels, S.F. and Chen, H.Y.H. 2009. Is understory plant species diversity driven by resource quantity or resource heterogeneity? *Ecology* (in press), DOI: 10.1890/09-1376

Chapter four:

Bartels, S.F. and Chen, H.Y.H. 2009. Overstory composition and weather conditions influence light quantity and heterogeneity in the understory of boreal forests. (Submitted).

CHAPTER ONE: GENERAL INTRODUCTION

Overstory composition and structure influence the growth and establishment of understory plants (Berger and Puettmann 2000; Barbier *et al.* 2008; Hart and Chen 2008), through modification of resources including light, moisture, nutrients, and substrate conditions (Messier *et al.* 1998; Prescott 2002; Bartemucci *et al.* 2006; Brassard and Chen 2008). However, what maintains plant species diversity in the resource-limited understory remains unknown. Theoretically, species diversity in resource-limited environments are regulated by the average supply (resource quantity) and/or spatial variability of resources (resource heterogeneity) as predicted by the resource quantity (Stevens and Carson 2002; Chen *et al.* 2004; Hart and Chen 2008) and resource heterogeneity (Ricklefs 1977; Huston 1979) hypotheses. In the forest understory where light energy is filtered and water and nutrients are asymmetrically prioritized by more competitive overstory trees, patterns of understory plant diversity may be related to resource limitations induced by overstory-understory interactions.

However, the influence of the forest canopy, as a major determinant of microclimate is not well investigated for its potential effects on the understory resource environment and on understory vegetation. Examining the influence of overstory composition on resource conditions and patterns of species diversity, abundance, and composition in the understory is necessary for addressing concerns regarding biodiversity conservation and forest management. The objectives of this thesis were to: (1) determine by means of literature synthesis, whether understory plant species diversity is driven by resource quantity and/or resource heterogeneity, and (2) examine the influence of

overstory composition on understory vegetation and on the understory light resource environment in mature boreal forest stands of central and eastern Canada.

Chapter two presents a synthesis of the role of resource quantity and resource heterogeneity as drivers of understory plant species with respect to stand successional stage, presence or absence of intermediate disturbance, relating the review to the forest biome within which studies were conducted. Chapter three presents an empirical study of the influence of overstory composition on the patterns of species richness, cover, and composition of understory vegetation in the boreal forests of northwestern Ontario, Canada. The study examines patterns of understory vegetation of three understory layers: shrub, herbaceous, and bryoid layers, along an overstory broadleaf compositional gradient. The study also examines the interrelationships among understory layers and their responses to the same suite of environmental variables. Patterns of species richness and cover were used to establish the role of resource quantity and heterogeneity as drivers of understory richness and cover. Chapter four also presents an empirical study of the effect of overstory composition and weather conditions on light quantity and heterogeneity in the understory of eastern-central boreal forests of Canada.

CHAPTER TWO: IS UNDERSTORY PLANT SPECIES DIVERSITY DRIVEN BY RESOURCE QUANTITY OR RESOURCE HETEROGENEITY?

INTRODUCTION

Understory vegetation in forest ecosystems plays a crucial role in regulating succession (Royo and Carson 2006), accounts for the majority of floristic diversity (Halpern and Spies 1995, Gilliam and Roberts 2003), and facilitates nutrient cycling and energy flow as ecosystem drivers (Nilsson and Wardle 2005). Understanding the mechanisms that maintain understory vegetation is thus essential for forest management. Accordingly, ecologists have developed several conceptual models to explain the patterns of plant diversity in natural ecosystems (MacArthur 1968, Ricklefs 1977, Huston 1979, Waide *et al.* 1999, Hubbell 2001). Among these models are the resource heterogeneity and resource quantity hypotheses. While there is no doubt that availability of resources, including light, soil nutrients, and soil moisture influence plant establishment and community succession, there is no general consensus among authors concerning the directional effect of resource availability, i.e., whether resource quantity or resource heterogeneity maintains plant diversity, as the influence of resource availability on species diversity is least investigated or overlooked in many studies.

In forest ecosystems where understory plants grow under overstory tree canopy, a crucial question is whether understory species diversity is driven by resource heterogeneity (spatial and temporal variability in light and soil resources), or resource quantity (the average supply of light and soil resources). The resource heterogeneity hypothesis proposes that species diversity is a function of habitats or heterogeneity in resources as plants specialize in variable light and soil resource environments (Ricklefs

1977, Huston 1979), while the resource quantity hypothesis suggests that the average supply rate of the limiting resources maintains species diversity in the understory (Stevens and Carson 2002, Chen *et al.* 2004, Hart and Chen 2008). These contrasting views among authors have hampered our ability to draw general conclusions regarding mechanisms that maintain understory plant diversity patterns in forest ecosystems.

This study therefore seeks to reconcile the two hypotheses by addressing whether understory plant diversity in forest ecosystems is driven by resource quantity or resource heterogeneity. In order to draw a generalized conclusion concerning the importance of these drivers in structuring understory plant diversity, a literature search of published studies was conducted. The aim was to establish whether resource quantity or resource heterogeneity alone explains understory plant species diversity patterns, or whether they are interactive and collectively explain understory species diversity.

The supply of resources including light, soil nutrients, and moisture in forest ecosystems are regulated by the nature and severity of disturbance (Stone and Wolfe 1996, Clinton 2003), and dominant overstory canopy trees and shrubs at different maturity stages (Légaré *et al.* 2002, Bartemucci *et al.* 2006, Barbier *et al.* 2008). While stand replacing disturbances initiate new stands (Chen and Popadiouk 2002, Franklin *et al.* 2002), intermediate disturbances, such as thinning, partial harvesting, disease, insect outbreak, or windthrow that remove partial overstory canopy, generally create more growing space and release more resources, and therefore influence understory plant diversity. Both average supply and variations in available resources as affected by these factors have consequent effects on understory vegetation. We therefore discuss understory plant diversity with regards to studies that were conducted at different stand

development stages, and in systems experiencing intermediate disturbance in boreal, temperate and tropical forests.

METHODS

Definition of terms

Understory vegetation as used in this study refers to all vascular and nonvascular plants ≤ 1.3 m high (Chen *et al.* 2004, Hart and Chen 2008). Understory vegetation may be classified into various life forms including woody plants (shrubs and tree seedlings), herbaceous plants (forbs, graminoids and ferns), and terrestrial non-vascular plants (Chen *et al.* 2004). We defined resource heterogeneity as the spatial variation or patchy distribution of available resources: variability in light, soil moisture, and nutrients, as well as the relative abundance of microhabitats or heterogeneous substrates associated with coarse woody debris, microtopographic pits and mounds, and leaf litter. Resource quantity is defined as the average supply of key resources such as light, soil moisture, and soil nutrients (*sensu* Stevens and Carson 2002).

Literature search and selection criteria

We compiled a database of empirical studies that report the influence of resource availability on understory plants. Literature searches were carried out using the online database search engine, ISI Web of Knowledge (version 4.6), and covered all available years. We used subject heading terms and keywords such as “understory plant diversity OR understory plant richness,” “understorey plant diversity OR understorey plant richness,” “understory species diversity OR understory species richness,” and “understorey species diversity OR understorey species richness.” In addition, we

reviewed the reference lists of the retrieved papers to search for additional papers on the same subjects.

For the purpose of this study, we considered only peer-reviewed articles that report original empirical findings in a particular forest ecosystem and avoided literature syntheses or reviews. Since this study relates plant diversity to resource availability, studies eligible for analysis were those that investigated understory plant diversity patterns in response to resource availability, i.e., environmental factors including light, soil moisture, nutrients, and/or substrate conditions such as leaf litter depth, coarse woody debris, and microtopographic pits and mounds. Experiments that were conducted in greenhouses to mimic forest understory conditions, as well as studies in grasslands or prairies where there exist no overstory canopies were not considered. The search encompassed studies conducted in both managed and unmanaged stands at various successional stages and with various management or disturbance histories. The study did not target a particular forest type or overstory type; however, most of the studies included in our database represent upland forest ecosystems, as there were few studies of understory diversity in peat-land, swampy, and riparian forests which prevented meaningful conclusions for these ecosystem types.

The search yielded over 500 papers, but most of them concerned insects, small mammals, or bird communities. Of the studies that attempted to understand the mechanisms that affect understory plant communities, 130 studies sought to establish a relationship between understory plant diversity and resource availability according to our working definition (Appendices A).

Classification of hypotheses and study parameters

We carefully examined how individual studies attributed the observed plant diversity patterns to either resource quantity, resource heterogeneity, or both. Classification was based on original author's interpretation of the observed diversity patterns. Studies were classified as having support for the resource quantity hypothesis when the observed understory diversity patterns in those studies were attributed to the effects of average supply of light, water, and/or soil nutrients. Alternatively, studies that attributed the observed diversity patterns to the influence of patchy distribution of resources such as heterogeneity or variation in light and soil resources, or to specific substrates or microsites characterized by diverse coarse woody debris, leaf litter, pit and mound microtopography, and litter depth were classified as having support for the resource heterogeneity hypothesis. Studies that reported the combined effects of both resource quantity and heterogeneity were also classified.

In order to determine whether support for a particular hypothesis was attributed to forest stand condition(s) in a given study, we determined stand successional/development stage(s) and presence or absence of intermediate disturbance for each study. Stand development stage was classified on the basis of stand overstory canopy structure into "young/mature," "old-growth," and "multi-stage". The first two categories applied when all study stands were in one stage of stand development, while "multi-stage" represents a study that includes stands of both young/mature and old-growth stages. The young/mature stage included stands in both the stem-exclusion and canopy transition stages with closed or nearly closed canopies, whereas old-growth stage referred to stands

in the gap dynamics stages with sparse canopies due to frequent treefalls (Chen and Popadiouk 2002, Franklin *et al.* 2002).

Disturbances reported in this study refer to intermediate disturbances that occur at one point in time during stand development; natural and anthropogenic interventions were categorized into ‘absence’, ‘presence’, and ‘both’. Since all stands regardless of age originated from stand replacing disturbances (natural or anthropogenic), we classified a study into absence of disturbance where none of the study stands showed evidence of intermediate scale disturbance, such as silvicultural thinning, partial harvesting, disease, insect outbreak, or windthrow that partially removes the overstory canopy, and ‘both’ where a study involved both disturbed and undisturbed stands. Forest biome was categorized into boreal, temperate, and tropical. Support for resource heterogeneity hypotheses was denoted by ‘H’, resource quantity by ‘Q’, and by ‘HQ’ where both hypotheses were supported in one particular study (*see* Appendices A and B).

Data analysis

We used log-linear models to test the following hypotheses: whether understory plant diversity is regulated by either resource quantity, resource heterogeneity, or both is independent of the successional stage(s), presence or absence of intermediate disturbance, and forest biome within which the studies were conducted. Log-linear models analyze the relationship between two or more discrete, categorical variables (Zar 1999). The variables included the resource hypotheses, successional stage, disturbance, and forest biome. We used the likelihood-ratio test, which is considered best suitable for making decisions between hypotheses (Vu and Maller 1996), to test the significance at $\alpha = 0.05$ probability level. We did not attempt to develop a model with all variables and their

possible interactions. Instead, we used log-linear models of three separate 3 x 3 contingency tables to test the hypotheses that understory plant diversity is regulated by resource quantity, resource heterogeneity, or both in each of stand successional stage(s) (young/mature, old-growth, multi-stage), intermediate disturbance (presence, absence, both), and forest biome (boreal, temperate, tropical) respectively. All statistical analyses were conducted using SYSTAT[®] version 12 (Systat Software Inc., San Jose, CA, USA).

RESULTS AND DISCUSSION

Stand successional stage(s)

Whether a study supported resource quantity or heterogeneity as the driver for understory plant diversity was significantly dependent on the successional stage of stands in the study ($P < 0.001$, Table 2-1). The resource quantity hypothesis was more often supported in studies that investigated stands at young/mature stages of development, whereas the resource heterogeneity hypothesis was more often supported in studies that investigated old-growth stands (Fig. 2-1). Studies comparing plant diversity along successional stages also found resource quantity to be a more important driver (Fig. 2-1).

Table 2-1. Likelihood ratio chi-square tests of the influence of resource quantity and resource heterogeneity on understory species diversity in relation to stand successional stage(s), intermediate disturbance, and forest biome.

Factor	LR Chi-square	df	<i>P</i>
Succession	47.954	6	<0.001
Disturbance	32.883	6	<0.001
Forest biome	31.445	6	<0.001

These results could best be explained by the shift from resource limitation to within-stand heterogeneity during stand development and succession in forest ecosystems (Chen and Popadiouk 2002). Overstory species composition and plant diversity in forest ecosystems are known to vary as a function of stand development (Halpern and Spies 1995, Chen and Popadiouk 2002, Bartemucci *et al.* 2006), and may thus explain the fundamental roles of resource quantity and heterogeneity on species diversity at different stages of stand development.

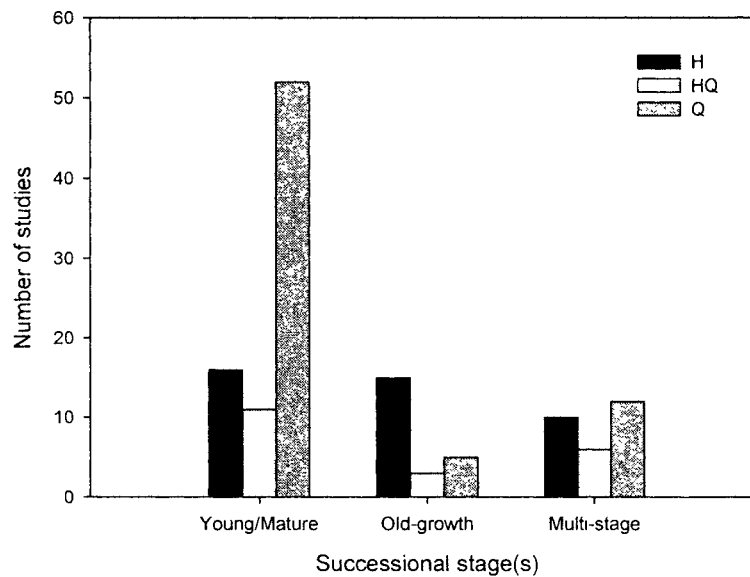


FIGURE 2-1 Number of studies that attributed resource quantity (Q), resource heterogeneity (H), or both resource quantity and heterogeneity (HQ) as the key driver of understory species diversity in relation to stand successional stage(s).

Understory plants are limited by light availability under closed and stratified canopies in young/mature stages of stand development. The limited light availability with forest canopy closure may result in declines in species richness and cover, and limitations in growth and survival of many species that established during the stand initiation stage

(Alaback 1982, Klinka *et al.* 1996, Lezberg *et al.* 1999, Hart and Chen 2006). Others suggest limitations in nutrient availability play a vital role in herb layer development (Gilliam and Turrill 1993, Chipman and Johnson 2002, Chen 2004). Given these resource limitations, resource quantity was supported as the driver in studies in which understory plant diversity was related to a gradient of average light availability (e.g., Klinka *et al.* 1996) or a range of average water and nutrient supply (e.g., Chipman and Johnson 2002, Chen *et al.* 2004). The effects of light as a limiting resource usually lessen later in stand development when tree mortality increases, providing new sources of light in the understory, as well as the addition of coarse woody debris. Coarse woody debris levels usually peak during transitional stages when even-aged stands transition into a more uneven-aged structure (Sturtevant *et al.* 1997, Hély *et al.* 2000, Brassard and Chen 2006, Brassard and Chen 2008).

Resource heterogeneity being the main driver of understory plant diversity in old-growth stages is attributable to stand structure and spatial distribution of resources in old-growth forests. Old-growth forests are characterized by within-stand heterogeneity (Denslow 1987, Guariguata *et al.* 1997), primarily as a result of frequent treefalls, which create light gaps and abundant substrates in the form of microtopographic pits and mounds, and associated coarse woody debris (Beatty 1984, Canham *et al.* 1990, Chen and Popadiouk 2002). These small openings in canopies are common, but important sources of spatial heterogeneity in forest ecosystems (Clinton 2003). Treefalls due to senescence in old-growth result in subsequent increases in forest floor vegetation and shrub cover (Fredericksen *et al.* 1999). As well, forest floor characteristics and surface horizons in old-growth forests vary both in microelevation and chemical properties

(Beatty and Stone 1986), giving old-growth stands distinct features that support a higher species richness and diversity (D'Amato *et al.* 2009).

Intermediate disturbance

The support for resource quantity or resource heterogeneity as the driver of understory plant diversity also differed significantly with presence or absence of intermediate disturbance ($P < 0.001$) (Table 2-1). Resource quantity tended to be the important driver of species diversity in both disturbed and undisturbed forests, while resource heterogeneity dominated in studies comparing conditions in disturbed and undisturbed stands (Fig. 2-2). Forests experience a wide range of disturbances at various spatial and temporal scales that create growing space and facilitate regeneration, and consequently increase diversity of understory plants (Roberts and Gilliam 2003, Roberts 2004). Although disturbances in the short-term are associated with mortality, the more important effects are generally the long-term consequences for resource availability (Huston 1994, Gundale *et al.* 2006). While disturbance through its effect on resource availability is key to plant diversity in managed forests (Jonsson and Esseen 1990, Decocq *et al.* 2004), others also lament the difficulty in making generalized conclusions of the effects of disturbances on plant diversity (Tárrega *et al.* 2006).

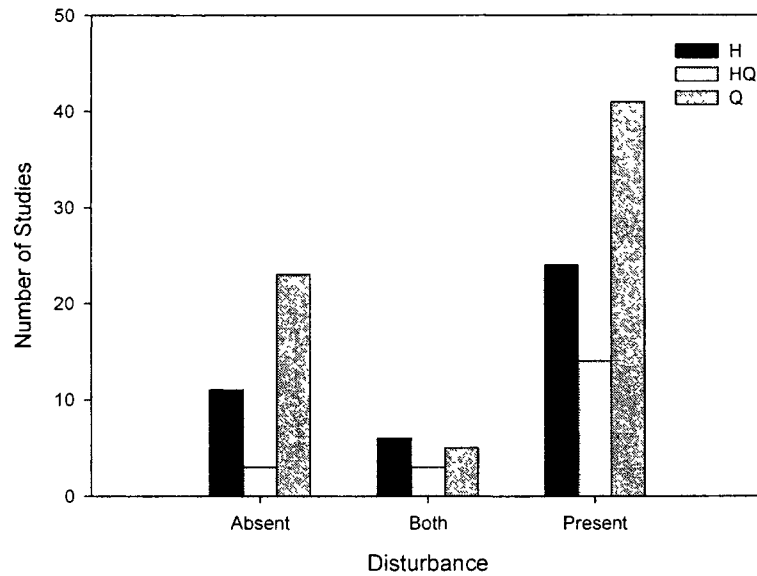


FIGURE 2-2 Number of studies that attributed resource quantity (Q), resource heterogeneity (H), or both resource quantity and heterogeneity (HQ) as the key driver of understory species diversity in relation to presence or absence of intermediate forest disturbance.

Intermediate disturbance typically causes changes in local microclimate by opening up space in the canopy, resulting in the release of resources that would otherwise not be accessible to understory plants (Schaetzl *et al.* 1989, Roberts and Gilliam 2003). This release of resources following disturbances may explain the importance of resource quantity in structuring species diversity in disturbed forests; however, the contribution of resource heterogeneity in disturbed forests cannot be underestimated. Intermediate disturbances such as thinning, partial harvesting, disease, insect outbreak, or windthrow are also important sources of spatial heterogeneity (Bradshaw *et al.* 1996, Denslow *et al.* 1998, Clinton 2003). Resource heterogeneity is also of appreciable importance in disturbed forests (Fig. 2-2), underlying the role of both resource quantity and

heterogeneity created by intermediate disturbances in structuring species diversity. Given the range of intermediate scale disturbance type and its severity, we infer that both resource quantity and heterogeneity may be key factors in structuring understory species diversity in stands that experience intermediate disturbances.

Forest biome

Resource quantity appeared to be the dominant driver of understory plant diversity in all three forest biomes studied (Table 2-1, Fig. 2-3). This observation confirms the profound influence of the physical environment on the patterns and distributions of plant species in natural ecosystems (Stevens and Carson 2002). The resource quantity dominance is perhaps due to the fact that most studies, i.e., 78 of 130 studies, focused on young and mature stands where average light and nutrient supply are the key drivers of understory diversity. Furthermore, because 116 of 130 studies were conducted in boreal and temperate biomes where nitrogen is known to be limiting to plants (Magnani *et al.* 2007), positive relationships found between understory plant diversity and soil nutrients in these studies supported the quantity hypothesis (e.g., Chipman and Johnson 2002, Chen *et al.* 2004). Tropical forests usually maintain a tall and multi-layered canopy and subcanopy; hence, understory light becomes highly limited, often as low as 1% of full sunlight. In turn, abundant treefalls in these forests create light gaps of different ages and sizes, resulting in increased light quantity and heterogeneity, and consequently increased plant diversity (Brandani *et al.* 1988, Chazdon 1996, Nicotra *et al.* 1999, Montgomery and Chazdon 2001).

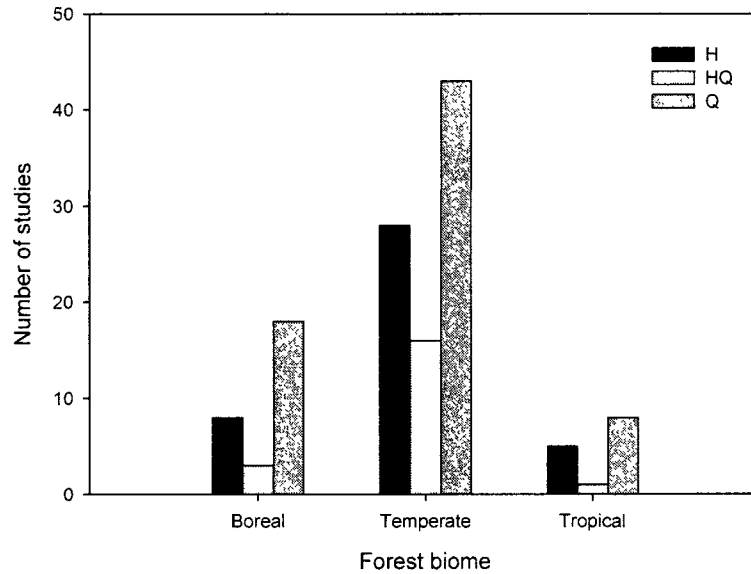


FIGURE 2-3 Proportions of studies that attributed resource quantity (Q), resource heterogeneity (H), or both resource quantity and heterogeneity (HQ) as the key driver of understory species diversity in (a) boreal ($n = 29$), (b) temperate ($n = 87$), and (c) tropical ($n = 14$) forest ecosystems.

Tentative hypotheses for the effects of forest management, overstory type, and spatial scale

Although our study did not directly examine the effects of forest management and dominant overstory composition on understory vegetation, we find a close link between these two factors in shaping diversity patterns in relation to resource quantity or resource heterogeneity. Management mediates forest development processes and usually results in younger forests that are more uniform in structure and composition compared to old-growth stands. Management may help reduce the occurrence of natural treefalls and other minor disturbances and as a result lower environmental and habitat heterogeneity (Crow *et al.* 2002). Natural stands, on the other hand, are more heterogeneous in tree species

composition and structure, and may, therefore, have heterogeneous resource conditions. Thus, resource quantity may be paramount in structuring understory diversity in managed stands, whereas resource heterogeneity may dominate in unmanaged stands.

In forest ecosystems, overstory composition and structure influence understory plant communities through modification of resources including light and soil resources (Klinka *et al.* 1996, Messier *et al.* 1998, Légaré *et al.* 2001) with some species having special affinities for a particular overstory type. The loss of a particular forest cover type could result in the loss of some understory species (Légaré *et al.* 2001, Hart and Chen 2008). Broadleaf or deciduous stands generally transmit more light and have higher nutrient levels in the understory than conifer stands due to their nutrient rich litter (Paré and Van Cleve 1993, Messier *et al.* 1998, Prescott *et al.* 2000). Resource conditions in pure stands may be more homogeneous in space and time. Mixed stands of broadleaves and conifers tend to be structurally and compositionally intermediate between pure stands of broadleaves or conifers and appear to exhibit greater spatial and temporal variations in understory light and soil nutrients (Brown and Parker 1994, Bartemucci *et al.* 2006, Macdonald and Fenniak 2007). On the basis of resource homogeneity and heterogeneity in the various stand types, resource quantity may be the important driver in pure stands of broadleaves and conifers, whereas resource heterogeneity may be important in driving species diversity in mixedwood stands.

Local site conditions influence species presence. At a regional or landscape level, patterns of species richness have often been related to climate, as well as to local site conditions (Gross *et al.* 2000, Cornwell and Grubb 2003). Hillslope hydrology and surficial geology, as well as topographical variations in moisture, N mineralization, and

soil pH and texture, have been related to understory species composition (Hutchinson *et al.* 1999, Chipman and Johnson 2002). Resources may act to influence species diversity at variable scales, as species richness is known to vary as a function of spatial scale (Whittaker *et al.* 2001, Rahbek 2004). Resource quantity may be paramount in structuring understory species diversity at the stand level where overstory composition is relatively uniform, whereas resource heterogeneity may be the dominant species diversity driver at broader scales or at the landscape level.

These resource hypotheses find close linkages to the niche (MacArthur 1968, Chase and Leibold 2003) and neutral (Bell 2001, Hubbell 2001) theories. The niche theory predicts a positive relationship between species richness and habitat heterogeneity, implying that increasing habitat heterogeneity increases the number of species that may exist in a habitat. In contrast, neutral theory assumes that all individuals of all species in a trophically similar community are ecologically equivalent. This assumption of neutrality implies that resource quantity is the driver of plant diversity. In heterogeneous habitats, heterogeneous resources allow species with different niche requirements to meet their habitat requirements, which leads to higher species diversity. Resource quantity in relatively uniform niches, however, tends to determine the number of species that can occupy a particular niche. Hence, the effects of resource heterogeneity on plant diversity may be paramount when studies are conducted in heterogeneous habitats or across niches, whereas resource quantity becomes important when dealing with one particular niche.

CONCLUSIONS

The results of this study show the influence of resources on understory species diversity in forest ecosystems to vary as a function of stand developmental stage, intermediate disturbance, and forest biome. We argue that neither resource quantity nor resource heterogeneity alone structures understory species diversity in forest ecosystems, but rather they express dominance at some point in time during stand development. Resource quantity may drive species diversity during stem exclusion and mature stages of stand development where resource quantity is fairly low, while resource heterogeneity may act to structure species diversity in old-growth stages. Intermediate disturbances, whether man-made or natural, create an avenue for increased resources, and in turn increase the dominance of resource quantity as a key driver of understory plant diversity. However, our results also show that the contribution of resource heterogeneity in disturbed forests cannot be underestimated. Studies in all three biomes found consistent support for resource quantity as the key driver of understory diversity. However, this pattern may reflect sampling effects because most studies were conducted in stands at young and mature stages and in boreal and temperate biomes where light and soil nutrients tend to be limited.

This review throws light on a concept that has not been rigorously investigated or has been overlooked in many empirical studies. We meticulously searched the literature to develop a database of studies for analysis; however, we acknowledge original authors' purported interpretation and inferences other than our classification. It is our recommendation that ecologists pay attention to the dynamics of understory plant diversity in relation to the parameters enumerated in this study. We encourage research to

test these hypotheses in the various forest biomes to form a basis for comparison and meaningful conclusions.

CHAPTER THREE: OVERSTORY COMPOSITION INFLUENCES THE
PATTERNS OF SPECIES RICHNESS, COVER AND COMPOSITION OF
UNDERSTORY VEGETATION IN THE BOREAL FORESTS

INTRODUCTION

The forest understory is an important component of the forest ecosystem, supporting a vast majority of floristic diversity (Gilliam and Roberts 2003; Halpern and Spies 1995; Gilliam 2007). As ecological filters, understory vegetation plays a deterministic role in future forest composition (George and Bazzaz 1999; Nilsson and Wardle 2005; Royo and Carson 2006), and serves as an important driver of nutrient cycling and soil fertility (Chastain *et al.* 2006; Moore *et al.* 2007). Understory plant communities are dynamic, and as such, they change with the mechanisms and processes that take place in the forest ecosystem (Hart and Chen 2006).

Although species diversity exhibits gradient-like changes or more complex scale-dependent patterns in response to variations in biotic (competition, predation, mutualism) and abiotic (resources, habitat, environment) factors, mechanistic understanding is rather poor as to which of the biodiversity theories such as niche differentiation and competitive exclusion (MacArthur 1968; Tilman and Pacala 1993; Waide *et al.* 1999; Abrams 2001; Clark 2010) can explain understory plant coexistence. A dominant pattern is that species diversity at variable scales has been shown to vary as a function of energy availability (Currie 1991; Hall *et al.* 1992). In the forest understory where light energy is filtered and water and nutrients are asymmetrically prioritized by more competitive overstory trees, patterns of understory plant diversity may be related to resource limitations induced by overstory-understory interactions.

Overstory composition and structure influence the availability of resources in the understory including light, moisture, nutrients, and substrate conditions (Messier *et al.* 1998; Prescott 2002; Bartemucci *et al.* 2006; Brassard and Chen 2008), and consequently the growth and establishment of understory plants (Berger and Puettmann 2000; Barbier *et al.* 2008b; Hart and Chen 2008). Theoretically, species diversity in resource-limited environments is regulated by the availability (resource quantity) and/or spatial variability of resources (resource heterogeneity) as predicted by resource quantity (Stevens and Carson 2002; Chen *et al.* 2004; Hart and Chen 2008) and resource heterogeneity (Ricklefs 1977; Huston 1979) hypotheses (Chapter 2).

Mature forest stands exhibit structural complexity and stratification whereby the upper layers (overstory trees) exert a strong influence on the lower layers through resource competition or facilitation (Maestre *et al.* 2009). As such, it may be possible for a community of plants growing on the same site within the understory to experience different growing environments, due to resource partitioning or filtering, especially light, not only from the overstory, but also among layers of understory vegetation (Bartemucci *et al.* 2006). It follows therefore that, compositional changes in one layer may have similar, but undesirable effects on another (Dunn and Stearns 1987). However, few efforts have been dedicated to fully describe the patterns of diversity and composition among forest layers. Unfortunately, many plant community studies pay little attention to species interactions or interrelationships of these layers. Such instances have limited our ability to draw a generalized conclusion regarding ecological processes responsible for plant community structure in the forest ecosystem.

On similar site conditions, in particular, on most productive mesic sites, boreal forests can initiate with a diverse combination of overstory types from single species evergreen conifers, deciduous broadleaved, to variable species mixtures following disturbance, depending on propagule availability (Chen *et al.* 2009; Ilisson and Chen 2009a; Ilisson and Chen 2009b). The resulting overstory composition at any given stage of stand development is known to be dependent on several factors including propagule availability during stand establishment, nature of stand initiating disturbance, site condition, and presence of intermediate disturbance (Chen and Popadiouk 2002; Bouchard *et al.* 2006; Johnstone *et al.* 2009; Chen *et al.* 2009; Ilisson and Chen 2009a; Ilisson and Chen 2009b). The changing overstory composition affects light availability, soil nutrient availability, forest floor substrate conditions, and soil acidity, in particular, humus and surface mineral layers where understory vegetation roots (Brais *et al.* 1995; Paré and Bergeron 1996; Cote *et al.* 2000; Prescott 2002).

Several studies in the boreal forests have found particularly high light and soil resource availability in the understory of deciduous broadleaf dominated stands (Constabel and Lieffers 1996; Paré and Bergeron 1996; Messier *et al.* 1998; Prescott 2002), and higher vascular plants cover and richness in broadleaf dominated stands (Reich *et al.* 2001; Macdonald and Fenniak 2007; Hart and Chen 2008; Chavez and Macdonald 2009). Mixed species stands on the other hand exhibit spatial and temporal variations in understory light and soil nutrients due to within-stand heterogeneity (Brown and Parker 1994; Bartemucci *et al.* 2006; Macdonald and Fenniak 2007). Generally, resource conditions may be more homogeneous in single-species stands of broadleaves and conifers compared to mixed species stands, which are structurally and compositional

intermediate between the two (Brassard *et al.* 2008b). The variation in resource availability (resource quantity and heterogeneity) in single- and mixed-species stands may have consequent implications on the patterns of understory species diversity (Chapter 2).

The study focussed on the patterns of species richness, abundance, and composition of three understory vegetation layers (shrub, herbaceous, and bryoid layers) in the boreal mixedwood forests of central Canada. Our objectives were to: (1) examine the patterns of understory vegetation along an overstory broadleaf compositional gradient; (2) examine the interrelationships among understory layers, and their responses to the same suite of environmental variables, including soil physical and chemical variables, light availability, and forest floor substrate conditions, and (3) test the role of resource quantity and resource heterogeneity in driving species richness and cover of each layer.

METHODS

Study area, stands and site selection

The study was conducted in the central boreal forests of Canada, located approximately 100 km north of Thunder Bay in north-western Ontario (49°23'N to 49°36'N, 89°31'W to 89°44'W). The area records a mean annual temperature of 2.6°C and annual precipitation of 704.7 mm (Environment Canada 2007). The area is upland with deep glacial tills belonging to the Brunisolic order of soil classification (Soil Classification Working Group 1996), with sites varying from hydric to xeric. Dominant tree species found here are jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), black spruce (*Picea mariana* [Mill] B.S.P.), and white birch (*Betula*

papyrifera Marsh.), with significant components of white spruce (*Picea glauca* [Moench] Voss) and balsam fir (*Abies balsamea* L. Mill) in the subcanopy.

We sampled mature, even-aged closed-canopy stands (90 years old) on mesic sites of relatively flat topography (slope < 5%). Mesic sites are presumably the most productive and competitive sites, and so allowed us to test specifically overstory effects on plant communities, with minimum variation in site conditions. We purposefully sampled three overstory composition types ranging from dominance of broadleaves, conifers, and various levels of mixtures, following their natural occurrence in the boreal forests. A total of 29 stands were sampled across an area of approximately 250 km². The selected stands naturally established after fire.

Vegetation sampling

In each stand, a 400 m² circular plot was located at least 50 m from forest edges and cut areas, within which all sampling was done. Within the plots, all trees were tallied by species and the diameters at breast height (dbh) and heights of trees present were measured and recorded. Trees were defined as species with a single woody trunk and usually > 5 m tall at maturity. Understory vegetation were sampled according to three *a priori* vegetation layers: shrub, herbaceous, and bryoid layers. Species with multiple stems or shorter single woody stems usually < 5 m at maturity were classified as shrubs. Herbaceous plants included all rooted low-growing vascular plants < 1.3 m high, while bryoids consisted of all non-rooted ground surface vegetation including bryophytes and lichens.

For the shrub layer, we established three 25-m² subplots which were located randomly within the plots, and the percent cover of all shrub species present was visually

estimated using the count-plot method (Mueller-Dumbois and Ellenberg 1974). The herbaceous and bryoid layers were sampled using twenty 1-m² subplots, which were located at random distances from the plot centre, and the percent cover of all herbs and bryoids by species were visually estimated. All species sampled were identified to the species level. The entire plot was surveyed to ensure that sampling captured all available species.

Understory light measurements

Instantaneous measurements of photosynthetic photon flux density (PPFD) were taken at 1.3 m above the forest floor in the understory, under completely overcast sky conditions, using hand-held LP-80 ceptometers (AccuPAR LP 80, Decagon Devices Inc. Pullman, WA, USA). One ceptometer was used to manually record instantaneous light measurements in the understory while another was time-synchronized and set in the adjacent opening to record incoming radiation at one minute intervals. This technique allowed us to quantify light availability (percentage of incident light) in the understory of the stands. 40 instantaneous light measurements were taken in each of the plots.

Soil characteristics and substrate sampling

Soil characteristics were determined in each stand by excavating four randomly located volumetric forest floor samples (465 cm³). Depending on the thickness of the soil which was stratified by layers, mineral soil samples were taken at 9 to 15 cm from soil surface. This depth was typically within the rooting zone of most shrubs and herbs. Soil carbon (C) and nitrogen (N), and total phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) (mg/g) were determined using the methods described in Laganière *et al* (2009). Soil pH was determined in both 0.5 M CaCl₂ using a PHM82 pH meter

(Radiometer Copenhagen) and in water (Carter 1993). Exchangeable K, sodium (Na), Ca, and Mg (Mg/kg) were determined following extraction with 0.1 M BaCl₂ and atomic absorption spectro-photometry. The values were then summed to give the cation exchange capacity (CEC) (cmol(+)/kg) of each sample (Carter 1993). Soil textural analyses, i.e., calculation of percent sand, silt, and clay was carried out using granulometric analysis (McKeague 1976). Soil moisture content of air-dried soil samples was determined by calculating the differences in sample weights before and after drying to constant mass at 65 C. The averages of soil characteristics analyzed by soil layer (organic and mineral soil) at each site was then calculated and used in analysis. Depth of the organic layer was measured in the center of each subplot, and the percent cover of coarse woody debris (CWD, all twigs and debris > 10 cm) was visually estimated.

Data analyses

Attributes of the tree layer were characterized using tree basal areas and the proportion of broadleaves in the canopy. Basal area by tree species was calculated and summed up to the plot level to obtain total basal area of each stand. The proportion of broadleaf species by basal area in each stand was calculated and expressed as a percentage. Species richness (number of species recorded in each plot) was used to represent diversity of each understory vegetation layer. Species abundance, measured as percent cover, was calculated as the mean percent cover of a species from all subplots within a stand.

Whether there were interactive relationships of species richness, cover, or diversity among understory vegetation layers was examined using Pearson's product-moment correlations. We identified important environmental variables related to species richness,

and cover of each layer using multiple regression analyses. Environmental variables described in the methods section above were transformed, when necessary to meet the assumptions of normality. Trends in species composition of each layer were examined using nonmetric multidimensional scaling (NMDS) ordination. NMDS is a nonparametric ordination technique well suited to data that are non-normal or on discontinuous scales (McCune and Grace 2002). Environmental variables were superimposed on the NMDS ordination to determine important variables closely related to species composition of each understory layer. The significance of fitted vectors was assessed using permutations ($n = 999$) of environmental variables. Sørensen's (Bray-Curtis) index was used as the distance measure in the NMDS ordinations. Multi-response permutation procedures (MRPP) were used to test for significant differences in species composition of each understory layer among stand types. MRPP is a non-parametric multivariate procedure for testing the hypothesis of no difference between two or more groups of entities (McCune & Grace 2002). Average within-group distances in MRPP were calculated using the Euclidean distance measure.

The possible influence of the two resource hypotheses on the richness and cover of species in each understory layer was examined using the gradient of broadleaf composition by basal area as a surrogate measure of resource availability within a stand. We tested these hypotheses against the premises that a higher the proportion of broadleaf component in the overstory was associated with greater availability of resources, including light and soil nutrients, in the understory. We used second-order polynomial regression to examine whether species richness or species cover is linearly or quadratically related to percent broadleaf composition. The underlying assumptions are

that a linear or monotonic curve of species richness or cover along the broadleaf compositional gradient would indicate a role for resource quantity in driving species richness or cover patterns, whereas a unimodal or quadratic curve peaking within the range of mixedwood dominance would indicate a role for resource heterogeneity in driving species richness or cover patterns. We presented only the significant quadratic curves when both quadratic and linear curves were significant. Data analyses were conducted using R statistical package (R Development Core Team, 2009). Goodness-of-fit and significance of regression curves were judged by p -values, and coefficients of determination values (R^2).

RESULTS

We identified 111 species in the understory of stands across the study area: 12 shrub species in the shrub layer, 71 herbaceous species, and 28 bryoids. The herbaceous layer comprised 42 forbs, 22 dwarf shrubs, 2 graminoids, and 5 tree species. The bryoid layer comprised 23 bryophytes and 5 lichen species.

Species richness and cover along an overstory broadleaf compositional gradient

While species richness of the shrub layer had no significant relationship to overstory broadleaf composition (Fig 3-1A), species richness of the herbaceous layer was positively related to overstory broadleaf composition (Fig. 3-1A), while species richness of the bryoid layer had a unimodal relationship (Fig. 3-1C). Shrub cover had a positive linear relationship with overstory broadleaf composition, herbaceous cover had a unimodal relationship, while bryoid cover was negatively related to overstory broadleaf composition (Figs. 3-1D-F).

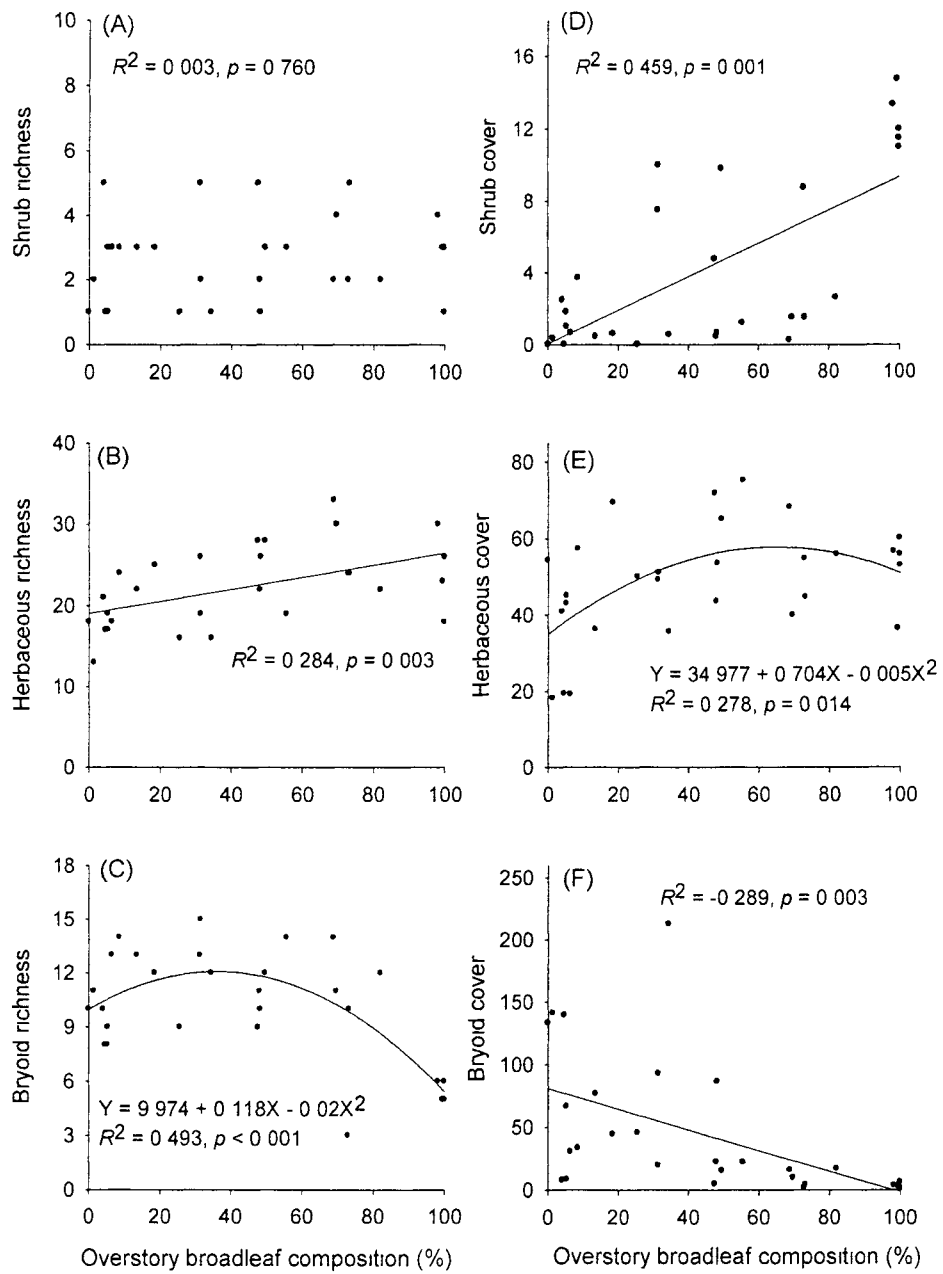


Figure 3-1 Relationships between overstory broadleaf composition (% basal area) and (A) species richness of the shrub layer, (B) species richness of the herbaceous layer, (C) species richness of the bryoid layer, (D) cover of shrub layer, (E) cover of herbaceous layer, and (F) cover of bryoid layers

Interrelationships of species richness and cover of understory vegetation layers

Species richness of the herb layer was positively correlated, while species richness of the bryoid was negatively correlated with that of shrub layer. The richness of bryoid layer was not significantly correlated with species richness of the herb layer (Fig. 3-2). Herb cover did not differ with shrub cover, but bryoid cover was lower with higher cover of shrubs and herbs (Fig. 3-2).

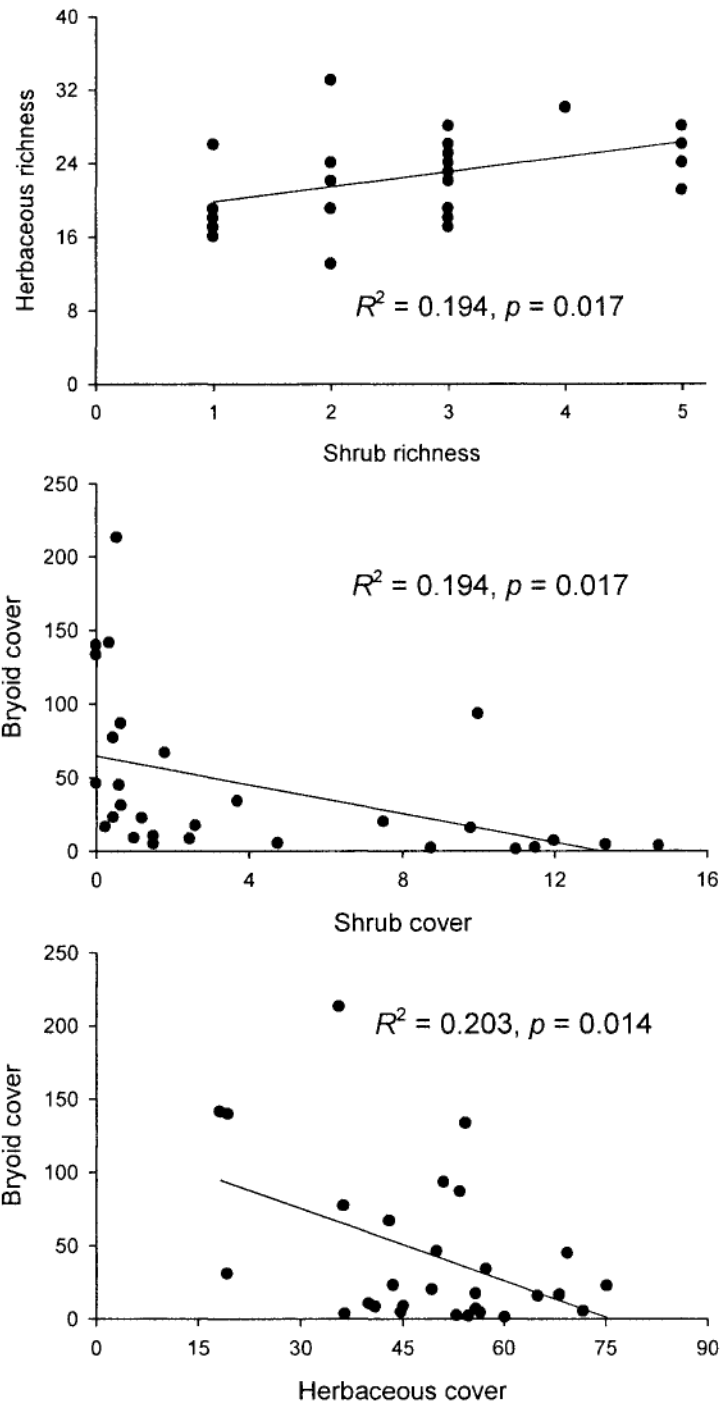


Figure 3-2 Interrelationship between species richness and cover among understory vegetation layers for which significant models could be fit.

Relationships between richness, cover, and composition and environmental variables

Species richness of the shrub layer was negatively related to P concentrations in the soil organic layer and positively related to mineral soil P and nitrogen content of the organic layer ($R^2 = 0.639$, Table 3-1). Species richness of the herbaceous layer was positively related to mineral soil bulk density (BD), CEC of both organic and mineral soils, and negatively related to organic P concentration ($R^2 = 0.671$, Table 3-1). Richness of the bryoid layer was positively related to duff depth and CWD, and negatively related to mineral soil BD ($R^2 = 0.767$, Table 3-1).

Shrub cover was positively related to N content of the organic layer and mineral soil CEC, and negatively related to duff depth, moisture content of the organic layer, and P concentrations of the organic and mineral soils ($R^2 = 0.902$, Table 3-2). Herbaceous cover was positively related to the cover of LF soil horizon ($R^2 = 0.499$, Table 3-2). The cover of bryoids was negatively related to the cover LF soil horizon and positively to organic soil pH ($R^2 = 0.677$, Table 3-2).

Table 3-1 Relationships between species richness and environmental variables for understory vegetation layers (Shrub layer: $F_{6,22} = 6.478$, $p < 0.001$, $R^2 = 0.639$; herbaceous layer: $F_{8,20} = 5.108$, $p = 0.001$, $R^2 = 0.671$; and bryoid layer: $F_{10,18} = 5.921$, $p = 0.001$, $R^2 = 0.767$).

Understory layer	Environmental variable	Sign	Estimate	<i>P</i> -value
Shrub layer				
	Organic layer N	+	4.471	0.003
	Organic layer P	-	5.241	<0.001
	Mineral soil P	+	70.482	0.003
Herbaceous layer				
	Organic layer P	-	20.405	0.004
	Organic layer CEC	+	0.315	0.012
	Mineral soil CEC	+	0.141	0.041
	Mineral soil BD	+	18.709	0.023
Bryoid layer				
	Mineral soil BD	-	11.430	0.023
	% cover of LF horizon	+	0.154	0.002
	% cover of CWD	+	0.271	0.016
	Light availability	+	0.335	0.042

Table 3-2 Relationships between species cover (abundance) and environmental variables for understory vegetation layers (Shrub layer: $F_{9,44} = 19.440$, $p < 0.001$, $R^2 = 0.902$; herbaceous layer: $F_{7,21} = 2.993$, $p = 0.024$, $R^2 = 0.499$; and bryoid layer: $F_{6,22} = 7.687$, $p = 0.0002$, $R^2 = 0.677$).

Understory layer	Environmental variable	Sign	Estimate	P-value
Shrub layer				
	Organic layer N	+	5.823	0.020
	Organic layer P	-	9.321	0.016
	Duff depth	-	2.572	< 0.001
	% cover of CWD	-	0.505	< 0.001
	Mineral soil CEC	+	0.175	< 0.001
	Organic layer moisture content	-	0.157	0.041
Herbaceous layer				
	% cover of LF horizon	+	0.658	0.021
Bryoid layer				
	% cover of LF horizon	-	2.538	< 0.001
	Organic layer pH	+	54.911	0.032

MRPP results showed that the different stand types differed significantly in understory species composition, but showed no apparent segregation from one another (Table 3-3, Fig. 3-3). Stand types appeared to arrange themselves in a continuum, where broadleaf and conifer dominated stands occupied distinctly different positions in ordination space, with mixedwood occupying the intermediate ordination space (Fig. 3-3). The relatively high chance-corrected within-group agreement (A) of species composition of the shrub layer ($A = 0.2211$), indicated more within-group homogeneity among stand types, compared to that of herbaceous ($A = 0.09523$) and bryoid layers ($A = 0.1026$) (Table 3-3, Fig. 3-3). The agreement statistic A describes within-group homogeneity within groups, compared to the random expectation (McCune and Grace 2002).

Several environmental variables were found to have a significant correlation with understory species composition (Table 3-4). Species composition of the shrub layer was correlated significantly to only two variables: soil acidity and forest floor duff depth, while herbaceous and bryoid compositions correlated similarly to a number of variables, including soil acidity, exchangeable cations, nutrients, and forest floor substrate conditions. In all cases, environmental variables correlated strongly with the first axes and weakly with the second axes (Table 3-4).

Table 3-3 Results of multi-response permutation procedures (MRPP) to test for differences in species composition of shrub, herbaceous and bryoid layers among stand types (broadleaf, mixedwoods, and conifer stands).

Understory layer	Stand type	Mean distance	<i>N</i>
Shrub layer			
	Conifer	1.13	10
	Mixedwood	4.41	13
	Broadleaf	7.96	6
Herbaceous layer			
	Conifer	15.76	10
	Mixedwood	18.49	13
	Broadleaf	23.12	6
Bryoid layer			
	Conifer	62.86	10
	Mixedwood	44.79	13
	Broadleaf	5.23	6

Notes: Distance measure used is the Euclidean distance. *N* = number of stands sampled within each stand type. MRPP statistic for the shrub layer: observed delta = 4.013, expected delta = 5.153, *A* = 0.2211, *P* = 0.003; herbaceous layer: observed delta = 18.51, expected delta = 20.45, *A* = 0.09523, *P* < 0.001; and bryoid layer: observed delta = 18.51, expected delta = 20.45, *A* = 0.1056, *P* = 0.008. The observed delta is derived from the data, while expected delta is derived from the null distribution. *A* is the chance-corrected within-group agreement.

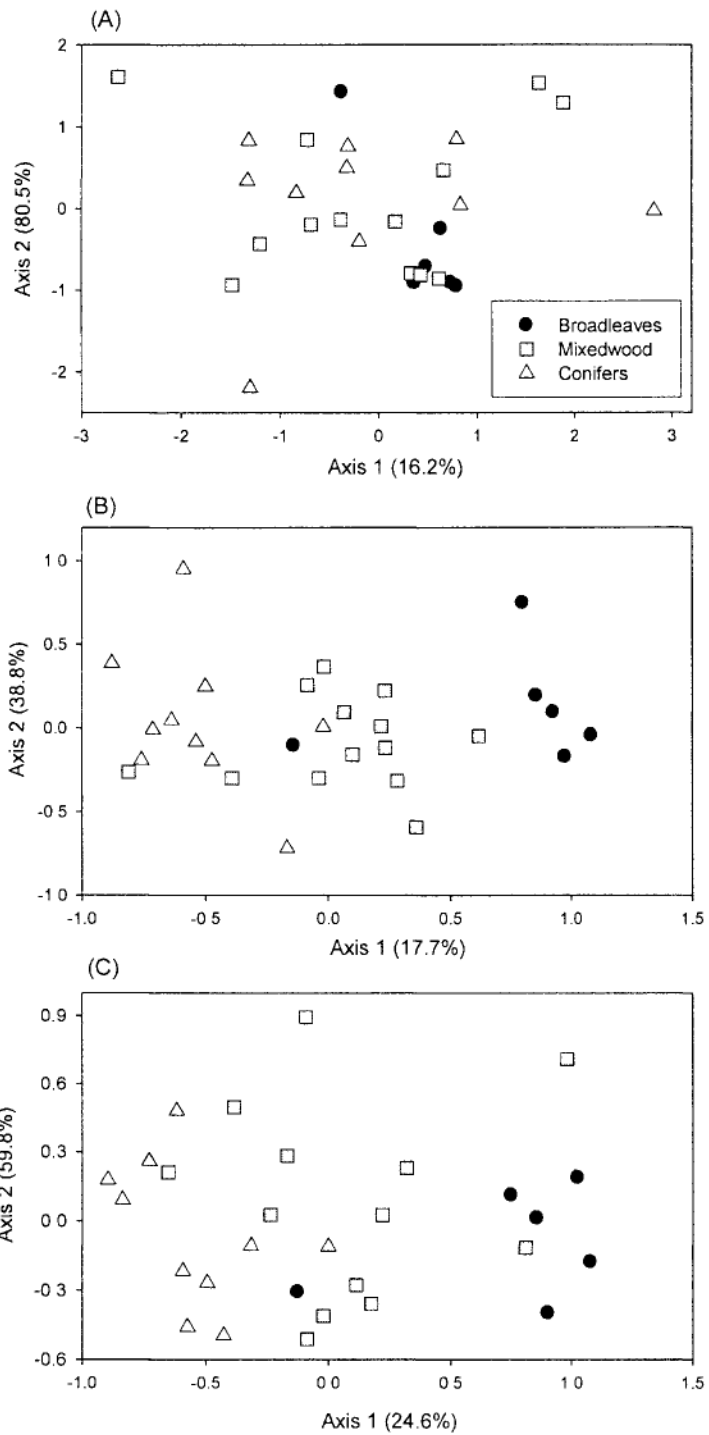


Figure 3-3 Ordination (nonmetric multidimensional scaling) showing the trends in species composition of (A) the shrub layer (final stress = 17.141, after 4 iterations); (B) the herbaceous layer (final stress = 16.802, after 20 iterations); and (3) the bryoid layer

(final stress = 16.741, after 6 iterations), among three stand types. Stands located nearest to one another on each graph plane have the most similar species assemblages, while those located farthest away are the least similar. Species of the shrub, herbaceous and bryoid layers segregate into different communities based on stand type.

Table 3-4. Environmental variables which were significantly related to species composition of understory vegetation layers (shrub, herbaceous, and bryoid layers), as determined when environmental variables were superimposed on nonmetric multidimensional scaling ordination axes.

Variable	Axis 1	Axis 2	Vector length	P-value
Shrub layer				
Mineral soil pH	0.864	-0.503	0.315	0.008
Duff depth	-0.539	0.842	0.232	0.030
Herbaceous layer				
Mineral soil bulk density	-0.682	-0.731	0.522	< 0.001
Mineral soil pH	-0.966	-0.257	0.286	0.018
Organic layer bulk density	-0.693	-0.721	0.270	0.012
Organic layer N	-0.991	0.131	0.467	< 0.001
Organic layer P	-0.967	-0.253	0.443	0.002
Organic layer pH	-0.968	-0.250	0.742	< 0.001
Organic layer CEC	-0.996	-0.084	0.796	< 0.001
Duff depth	0.998	0.070	0.690	< 0.001
LF horizon	-0.958	-0.287	0.745	< 0.001
Bryoid layer				
Mineral soil bulk density	-0.889	0.458	0.439	< 0.001
Mineral soil pH	-0.729	0.684	0.245	0.021
Organic layer N	-0.928	0.373	0.430	< 0.001
Organic layer P	-0.967	0.255	0.426	0.001
Organic layer pH	-0.999	0.054	0.658	< 0.001
Organic layer CEC	-0.970	0.244	0.731	< 0.001
Duff depth	0.991	0.135	0.564	< 0.001
LF horizon	-0.994	-0.108	0.711	< 0.001

Note: Description of environmental variables and how they were determined can be found in the Methods section above.

DISCUSSION

Patterns of species richness and cover along an overstory broadleaf compositional gradient

Herbaceous species richness and cover, as well as shrub cover increased with increasing proportions of broadleaves in the overstory, which suggests that broadleaves may offer a more favorable growing environment for the establishment of herbs and shrubs in the understory. This observation could be attributed to the high resource availability associated with broadleaf dominated stands. Previous studies have found particularly high light transmission/availability (Constabel and Lieffers 1996; Messier *et al.* 1998; Bartemucci *et al.* 2006) and high soil nutrient availability (Paré and Bergeron 1996; Cote *et al.* 2000) in the understory of broadleaf dominated stands. Together, these studies suggest that resource availability plays a crucial role in the growth and establishment of shrubs and herbaceous species, which are presumably the major competitors for available resource in the resource-limited understory. Our result is consistent with several other studies of the boreal forests that found greater herb and shrub richness in deciduous broadleaf forests than in conifer forests (Berger and Puettmann 2000; Macdonald and Fenniak 2007; Hart and Chen 2008).

Unlike herbs and shrubs, the richness and cover of bryoids species declined with increasing broadleaf proportions, and peaked in the ranges of conifer dominance (0 – 39%). This result suggests an affinity of bryoids (bryophytes in particular) for conifers than broadleaves, as reported in other studies (North *et al.* 1996; Ewald 2000). The decline in bryoid richness and cover might be due to the negative effects that deciduous litter has on the development of bryophytes. Deciduous litter limits the growth and

establishment of bryophytes through shading and occasionally allelopathic effects (Légaré *et al.* 2005; Startsev *et al.* 2008; Marialigeti *et al.* 2009). The decline indicates that bryoids, comprising low growing mosses and lichens, are least dependent on high light and soil nutrient availability, since conifer dominated stands are associated with lower nutrients than broadleaf dominated stands (Ste-Marie and Paré 1999; Ste-Marie *et al.* 2007). This supports the findings that bryophyte richness is suppressed at high nutrient levels (Aude and Ejrnaes 2005). Others have also found that bryophytes establish well in microenvironments or substrates (coarse woody debris, pits and mounds) created by dominant trees (Hylander *et al.* 2005; Weibull and Rydin 2005). The trends in species richness and cover suggested that vascular plants (herbs and shrubs) and nonvascular plants (bryophytes and lichens) show contrasting responses to overstory broadleaf composition.

The trend probably highlights the fundamental differences between vascular and nonvascular plants in their morphology and resource capture. Vascular plants differ from nonvascular particularly in their ability to increase in height in response to favorable resource conditions, and as such, vascular plants dominate under favorable growing conditions whereas nonvascular plants dominate under nutrient-poor or adversely dry conditions (Chapin *et al.* 1996). We deduce from our current trend that the establishment of vascular and/or nonvascular plants in the understory is dependent on the proportions of broadleaf component in the overstory. Others also found higher vascular plant diversity under broadleaves than under conifers (Hart and Chen 2008). Trends in species composition of either of the vegetation layers appeared to differ among the three stand types. While broadleaf and conifer dominated stands showed no overlap in the ordination

plane, mixedwood stands appeared to be intermediate between two stand types. This suggests that different stand types may be associated with compositionally distinct plant groups, as implied in other studies (Macdonald and Fenniak 2007; Hart and Chen 2008).

Relationships among understory vegetation layers

The only significant relationship of species richness among vegetation layers was between the shrub and herbaceous layers, in which greater species richness of the shrub layer was associated with greater species richness of the herbaceous layer. The positive relationship between shrubs and herbs presented an interesting result since shrubs compete with herbs for space, light, and soil moisture (Brown *et al.* 1998). Heterogeneity within each plot may have weakened the correlation between richness values. We found no relationship between species richness either of the shrub or the herbaceous layers and species richness of the bryoid layer. Other studies; however, have reported positive correlations between bryophyte and vascular plants richness (Ingerpuu *et al.* 2001), negative relationships between bryophyte richness and vascular plant biomass (Aude and Ejrnaes 2005; Lobel *et al.* 2006), and surrogacy between vascular plant diversity and bryophytes and lichen diversity (Pharo *et al.* 1999). In related studies, poor correlation between forest layers was attributed to the compositional independence of layers (McCune and Antos 1981).

The cover of bryoids was lower where cover of shrubs and herbaceous species was higher, but the relationship between shrub and herbaceous cover was non-significant. These trends suggest an inverse relationship between the cover of vascular and nonvascular plants. Thus, the presence (abundance) of vascular plants in the understory is associated with lower abundance of nonvascular plants. This could be due to the

inhibiting effects shrub litter has on the growth and establishment of bryophytes and lichens (Thompson *et al.* 2005). The inverse relationship between bryoid cover and shrub and herbaceous cover could be attributed to resource limitations, particularly light resource limitations, induced by shrubs and herbs, by virtue of their height, which cast shade on lowing growing mosses. Also, competition between vascular (shrubs and herbs) and nonvascular (bryophytes and lichens) plants, for space and nutrients in the understory might be a factor.

Relationships between species richness, cover, and composition and environmental variables

Generally, species richness, cover, and composition of the three vegetation layers studied differed in their associations with even the same suite of environmental variables. Similar results in related studies led others to conclude that the vegetation layer being studied determine which environmental factor is most important at the scale of that layer (McCune and Antos 1981; Lobel *et al.* 2006). Shrub richness and cover were consistently related to fertility of the organic and mineral soils (N and P concentrations). Nitrogen is perhaps the most limiting nutrient in the boreal forests (Gilliam and Roberts 2003). Species richness and cover of the herbaceous layer were well explained by organic layer P, exchangeable cations, and bulk density, while that of the bryoid layer related to forest floor substrate conditions, soil pH and light availability. The different relationships between species richness and cover and measured environmental variables even in the same layer might be due to the uncorrelated responses of individual life form groups that make up the layer. For instance, the herbaceous layer composed of forbs, graminoids,

ferns, shrubs, and tree species, which individually may have shown different associations with environmental variables.

Shrub species composition was correlated significantly to only two variables: pH and duff depth, unlike herbaceous and bryoid composition which correlated almost similarly to quite a number of variables including soil pH, nutrients and forest floor substrate conditions. Results from the three layers studied, showed no correlation between species composition and light availability and soil moisture content. While patterns of species cover and richness may be related to light availability, to some extent, the same cannot be said for species composition. Similar results of variable and unrelated patterns of species composition and diversity to light transmission in old-growth forests was attributed to the homogenizing effects of upper understory layers (Bartemucci *et al.* 2006). Trends in understory species composition as reported in several studies are related to several factors including stand structural attributes, successional stages, climate, soil nutrients, moisture availability, and disturbance (Légaré *et al.* 2002; Reich *et al.* 2001; Chen *et al.* 2004; D'Amato *et al.* 2009). Our results confirm the relationship between understory species richness, cover and composition and soil physical and chemical variables and forest floor substrate conditions.

The role of resource quantity and heterogeneity on species richness and cover

Our assumption of the role of resource quantity and heterogeneity on species richness and cover was not so evidently supported by the results. We used overstory broadleaf composition by basal area as surrogate measure of resource availability, as opposed to the direct measurement of resource quantity or resource heterogeneity, since our sampling design did not allow us to specifically measure or quantify resource

heterogeneity or spatial variability of resources, particularly, soil resources. The significant, positive linear relationships of herbaceous species richness and shrub cover, and negative linear relationships of bryoid cover indicate a strong dependence of herbaceous species richness, shrub cover, and bryoid cover on resource quantity, whereby herbaceous species richness increases with increasing quantity of resources and bryoid cover decreases with increasing resource quantity. Bryoid richness peaked within the range conifer and mixedwood dominance (~20 – 50%), while herbaceous cover peaked within the range of mixedwood and broadleaf dominance (~50 – 85%). Resource conditions may be more homogeneous in space and time in pure stands (broadleaf or conifer stands) compared to mixed stands, which exhibit greater spatial and temporal variations in understory light, substrate conditions, and soil resources.

On the basis of resource homogeneity and heterogeneity in the various overstory types, our findings support that resource heterogeneity, as well resource quantity, are important drivers of bryoid richness and herbaceous cover. Our results suggest that resource quantity may be the important driver of herbaceous richness, shrub cover, and bryoid cover, and both resource quantity and resource heterogeneity may be the main drivers of bryoid richness and herbaceous cover. It is at least theoretically possible for this divergent pattern of richness and cover to emerge in the resource-limited forest understory. Diversity is often predicted to be highest in habitats with a heterogeneous resource environment, where resource and habitat requirements of most species are likely to be met (Ricklefs 1977; Huston 1979; Pausas and Austin 2001). This idea has led some to predict that diversity is highest in habitats of intermediate resource availability, where species coexist (Tilman 1985; Tilman and Pacala 1993). It is however unknown whether

plant species specialize in different resource environments in the resource-limited understory.

CONCLUSIONS

The results confirm the influence of overstory composition on the patterns of species richness, cover, and composition of understory plant communities. In the forest ecosystem, understory vegetation layers may be interrelated such that changes in species richness and/or cover of one layer may parallel changes in the other. Species richness, cover, and composition of the understory layers studied, showed different patterns of association with soil physical and chemical variables and forest floor substrate conditions. Variations in understory species richness and cover along a gradient of overstory broadleaf composition suggest that resource quantity may be the driver of herbaceous species richness, shrub cover, and bryoid cover whereas both resource quantity and resource heterogeneity may drive bryoid species richness and herbaceous cover. Thus, maintaining a diverse overstory in the boreal forests will ensure diversity of various life forms, because each overstory type, through modification of resources, may favor the establishment of different understory plant communities.

CHAPTER FOUR: OVERSTORY COMPOSITION AND WEATHER
CONDITIONS INFLUENCE LIGHT QUANTITY AND HETEROGENEITY IN
THE UNDERSTORY OF BOREAL FORESTS

INTRODUCTION

Light is an essential resource required by understory plants for growth, survival, and regeneration (Jelaska *et al.* 2006; Petritan *et al.* 2009; Tinya *et al.* 2009). It is the most temporally and spatially variable of all essential plant resources (Bazzaz 1996) and is often limiting to understory plants (Jobidon 1994; Decocq *et al.* 2004). The forest canopy is a major determinant of microclimate within the forest ecosystem, as it intercepts, absorbs and modifies light environment in the understory. In closed canopy forests, only a small fraction of the incident solar radiation is transmitted to the understory because of light attenuation by overstory canopy and subcanopy trees and shrubs (Bartemucci *et al.* 2006; Kabakoff and Chazdon 1996; Montgomery and Chazdon 2001; Shropshire *et al.* 2001). The relatively low light levels reaching the understory have important implications for establishment of tree seedlings and other plants (Denslow *et al.* 1991; George and Bazzaz 1996; Chen and Klinka 1998). Given the profound influence of light on growth and survival of understory trees and other plants (Chen *et al.* 1996; Chen 1997; Kobe 2006; Bartels and Chen 2009), characterizing light transmission and spatial variability of light in the understory of boreal forest stands is imperative for predicting regeneration success and plant diversity at the stand level.

Techniques for measurement of light transmission in forests has not been straightforward, given the wide range of variability in stand and weather conditions. Incoming radiation above forest canopies exhibits a particularly high degree of spatial and temporal

variation due to changes in sun angle and cloud cover (Endler 1993; Pecot *et al.* 2005). The proportion of incident radiation that is transmitted to the understory also differs among forest types as a result of differences in stand conditions such as stand structure, stem density, basal area (Battaglia *et al.* 2002; Valladares and Guzman 2006), phenology (Uemura 1994; Kato and Komiyama 2002), distribution and size of gaps in the canopy (Chazdon and Fetcher 1984; Jennings *et al.* 1999; Capers and Chazdon 2004), and overstory tree species composition (Constabel and Lieffers 1996; Bartemucci *et al.* 2006).

Unlike the tropical and temperate forests, where numerous studies of light dynamics are reported (e.g., Percy 1983; Chazdon 1987; Canham *et al.* 1990; Capers and Chazdon 2004), only few studies report on light transmission in the boreal mixedwood forests (e.g., Ross *et al.* 1986; Messier and Puttonen 1995; Lieffers *et al.* 1999). In mature stands of boreal forest, overstory composition varies from dominance of single-species evergreen conifers, to dominance of deciduous broadleaf trees, to various levels of broadleaf-conifer mixtures, depending on propagule availability during stand establishment, nature of stand initiating disturbance, site condition, and presence of intermediate disturbance (Chen and Popadiouk 2002; Bouchard *et al.* 2006; Chen *et al.* 2009; Ilisson and Chen 2009a; Johnstone *et al.* 2009). Previous studies characterizing understory light environment in the boreal forests have established seasonal differences in light regimes in early and late successional forests (Ross *et al.* 1986; Constabel and Lieffers 1996), light interception and attenuation by above canopy and understory vegetation at different heights within the understory (Messier *et al.* 1998; Aubin *et al.*

2000; Bartemucci *et al.* 2006), as well as several predictive models of light transmission (Stadt and Lieffers 2000; Stadt and Lieffers 2005).

However, the dependence of understory light regimes on overstory composition has not been examined in much detail. Mixed-species stands may have distinct understory light regimes during the growing season, due to their distinct stand structural characteristics (Brassard *et al.* 2008a). Given the within-stand heterogeneity of mixedwood stands, understory light conditions in these stands may be expected to exhibit high spatial variability, compared to the fairly homogeneous resource conditions in single-species stands. Furthermore, how understory light regimes may differ in the various zones of the boreal forest also remains unknown. In the boreal forests of Canada, for instance, the eastern boreal zone typically has wetter conditions because of more rainfall and fewer fires compared to the western boreal zone. The diverse landforms of the boreal region also differ in slope positions, Parent material, and soil texture. Given the influence of regional climate and regional-scale geomorphic features on forest productivity and overstory species composition (Host and Pregitzer 1992; Ollinger *et al.* 1998; Koca *et al.* 2006), overstory transmission patterns may differ among the various regions of the boreal forests.

Light availability of a forest microsite is assumed to be best estimated using instantaneous measurements of light taken on completely overcast days (Messier and Puttonen 1995; Parent and Messier 1996). However, others suggest caution in using overcast estimates due to the influence of the variation of the sky view on solar radiation, especially in heterogeneous canopies (Stadt *et al.* 1997). Clear sky estimates may be ideal for estimating the potential contribution of sunflecks to understory light dynamics, and

their importance to understory plants (Chazdon 1988; Chazdon and Pearcy 1991; Mercado *et al.* 2009). However, it is unclear how understory light estimates under these two sampling conditions may be related.

In this study, we sought to quantify and compare light regimes beneath various closed-canopy stand types in eastern-central boreal forests of Canada. We posed the following questions: (i) how do average percent light transmittance and spatial heterogeneity of light differ among stand types in the two regions? (ii) do relative understory light quantity and heterogeneity differ with weather conditions, i.e., overcast and clear sky conditions?

MATERIALS AND METHODS

Study areas

The study was conducted in two zones of the boreal forests of Canada. The first study area was located approximately 100 km north of Thunder Bay in northwestern Ontario (49°23'N to 49°36'N, 89°31'W to 89°44'W). This area records a mean annual temperature of 2.6°C and total average annual precipitation of 704.7 mm (Environment Canada 2007). Sites vary from hydric to xeric, but for the purpose of this study, only mesic sites were selected for sampling. Soils have developed from relatively deep glacial tills, belonging to the Brunisolic order of soil classification (Soil Classification Working Group 1996). Jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), black spruce (*Picea mariana* [Mill] B.S.P.), and white birch (*Betula papyrifera* Marsh.) dominate in this area in varying proportions. White spruce (*Picea glauca* [Moench] Voss) and balsam fir (*Abies balsamea* L. Mill) are minor components, typically in the subcanopy.

The second study area was located in the black spruce–feather moss forest of western Québec (Bergeron 1996), at the border of Abitibi-Témiscamingue and Nord du Québec (49°08'N to 49°11'N, 78°46'W to 78°53'W). This area forms part of the Clay Belt region of Québec and Ontario. The region originated from deposits left by the proglacial lakes Barlow and Ojibway at the time of their maximum expanse during the Wisconsin glacial stage (Vincent and Hardy 1977). It records an average annual temperature of 0.7°C and average annual precipitation of 889.8 mm (Environment Canada 2007). All study sites were located on subhygric Grey Luvisols (Soil Classification Working Group 1996).

Study stands and sampling

Mature, even-aged closed-canopy stands (70-90 years) were sampled in both regions. In each stand, a 400 m² circular plot was established within which all sampling was carried out. Established plots were at least 50 m from forest edges and cut areas. Stands were categorized into compositional types based on relative basal area of dominant species. Pure stands were sampled to comprise > 70% of the dominant broadleaf or conifer species by basal area, whereas mixedwood stands composed of mixtures of both conifers and broadleaves in relatively equal proportions (Table 4-1). In each stand, diameters at breast height and heights of all trees were measured and recorded. Basal area by species was calculated and summed to the plot level, and then scaled to per hectare.

In the Ontario study area, twenty-five sampling plots were established across an area of approximately 250 km². Stand types included jack pine dominated (JP), trembling aspen dominated (TA), and jack pine-trembling aspen mixedwood (MW). However, due

to the significant numbers of late successional species in co-dominance, these three stand types were sampled with black spruce sub-canopy (denoted by JPbs, TAbs, and MWbs, respectively), resulting in six stand types (Table 4-1). In the Québec study area, 22 sampling plots were established across an area of 36 km², dominated by black spruce and patches of aspen. Stands were categorized into three compositional types: black spruce dominated (BS), trembling aspen dominated (TA), and spruce-aspen mixedwood (MW). In both regions, stand types were replicated a minimum of three times (Table 4-1).

Table 4-1 Stand characteristics of the stand types sampled (mean \pm 1 SE)

Stand type	Replicates	Species composition by basal area (%)				Broadleaf (%)	Basal area (m ² /ha)	Height (m)
		Black spruce	Jack pine	Trembling aspen	Other species			
Ontario study								
JP	3	9.4 \pm 0.8	80.2 \pm 0.5	1.8 \pm 1.8	8.6 \pm 2.5	5.1 \pm 2.1	42.7 \pm 3.3	14.0 \pm 1.2
JPbs	4	29.1 \pm 2.7	62.8 \pm 3.2	2.8 \pm 2.0	5.3 \pm 2.5	5.6 \pm 2.8	42.8 \pm 2.8	14.2 \pm 1.2
MW	5	6.7 \pm 2.1	51.6 \pm 8.6	35.7 \pm 7.8	6.0 \pm 1.9	40.8 \pm 9.5	37.3 \pm 2.0	17.4 \pm 1.0
MWbs	4	22.5 \pm 3.9	35.3 \pm 5.7	37.3 \pm 5.7	4.9 \pm 1.6	39.0 \pm 5.5	43.4 \pm 4.7	15.2 \pm 0.6
TA	5	-	-	96.7 \pm 0.8	3.3 \pm 0.8	99.5 \pm 0.4	37.2 \pm 4.1	23.9 \pm 0.9
TAbs	4	18.2 \pm 6.0	2.7 \pm 2.3	68.1 \pm 4.9	11.0 \pm 5.0	70.0 \pm 5.5	40.0 \pm 2.7	15.8 \pm 0.6
Québec study								
BS	7	90.8 \pm 3.9	7.7 \pm 3.4	1.5 \pm 0.7	0.1 \pm 0.1	1.5 \pm 0.7	37.8 \pm 2.9	13.8 \pm 0.9
MW	7	33.7 \pm 4.4	5.4 \pm 1.6	60.7 \pm 4.6	0.2 \pm 0.1	60.7 \pm 4.6	46.0 \pm 2.7	18.7 \pm 0.8
TA	8	9.0 \pm 1.8	-	88.6 \pm 2.5	2.4 \pm 2.4	88.6 \pm 2.5	49.6 \pm 3.5	21.8 \pm 0.8

Note: Other species consists of co-dominant late successional species including balsam fir, white spruce, and white birch.

Light measurements

Light measurements were conducted in August and early September. Photosynthetic photon flux density (PPFD) at 1.3 m above the forest floor was measured using handheld LP-80 ceptometer (AccuPAR LP 80, Decagon Devices Inc. Pullman, WA, USA). The 90 cm-long probe consists of eight active sensors, appropriate for detecting light intensity variations along the probe. One ceptometer was used to manually record instantaneous measurements in the understory, while the other, which was time-synchronized with the ceptometer used for understory measurement, was set in the adjacent opening to record averages of incoming radiation continuously at one-minute intervals. Sensors were calibrated periodically under clear sky conditions to ensure that both devices read equally. Within each 400-m² sample plot, 40 measurements were taken at random positions at 1.3 m height. Measurements were made under both clear and overcast sky conditions, such that sampling at each site included at least one clear and one overcast sky measurements. To minimize the influence of solar angle on incoming radiation, all measurements were conducted between 10 am and 3 pm.

Data analysis

Stand-level estimates of light transmission were calculated as the percentage of PPFD reaching the understory in relation to time synchronized (at one minute) adjacent open measurements. The mean and standard deviation of the 40 PPFD measurements within each sample plot were used to quantify light quantity and light heterogeneity, respectively (Kato and Komiyama 2002; Stevens and Carson 2002). One-way or two-way analysis of variance (ANOVA) was used to test for significant differences in average light quantity and spatial heterogeneity of light among stand types, and between the two

regions. When significant differences were found, Tukey's HSD tests were conducted to compare means. The student's t-test for unequal variances and Pearson's correlation analysis were used to compare light quantity and heterogeneity under the two weather conditions.

RESULTS

The %PPFD received in the understory of the stands in the Ontario study ranged from 3.6% to 6.9% of above-canopy transmission in clear sky conditions, and from 7.6% to 12.6% in overcast conditions (Fig. 4-1A). The %PPFD of the stands in the Québec study ranged from 7.9% to 9.7 % of above-canopy transmission in clear sky conditions, and from 10.4% to 14.9% under overcast conditions (Fig. 4-1B). Light transmission in the various stand types in both regions varied significantly under overcast sky conditions, but not under clear sky conditions (Table 4-2). In the Ontario study, mixedwood stands [$12.56 \pm 0.6\%$ (average \pm SE)] transmitted more light to the understory under overcast conditions, whereas trembling aspen dominated stands ($7.60 \pm 1.3\%$) transmitted the least (Fig. 4-1A). On the contrary, light transmission in the Québec study was highest in trembling aspen dominated stands ($14.9 \pm 0.8\%$) and lowest in mixedwood stands ($10.4 \pm 0.7\%$) (Fig. 4-1B).

Table 4-2 Effects of stand type on understory light quantity and heterogeneity in both overcast and clear sky conditions.

Source	df	Light quantity		Light heterogeneity	
		Mean square	<i>P</i>	Mean square	<i>P</i>
Overcast condition					
<i>Ontario</i>					
Stand type	5	17.68	0.036	3.92	0.018
Error	19	5.87		1.09	
<i>Québec</i>					
Stand type	2	51.12	0.002	2.65	0.050
Error	19	5.54		0.75	
Clear sky conditions					
<i>Ontario</i>					
Stand type	5	5.46	0.395	3.69	0.598
Error	19	4.98		4.94	
<i>Québec</i>					
Stand type	2	8.97	0.681	17.58	0.383
Error	19	22.84		17.42	

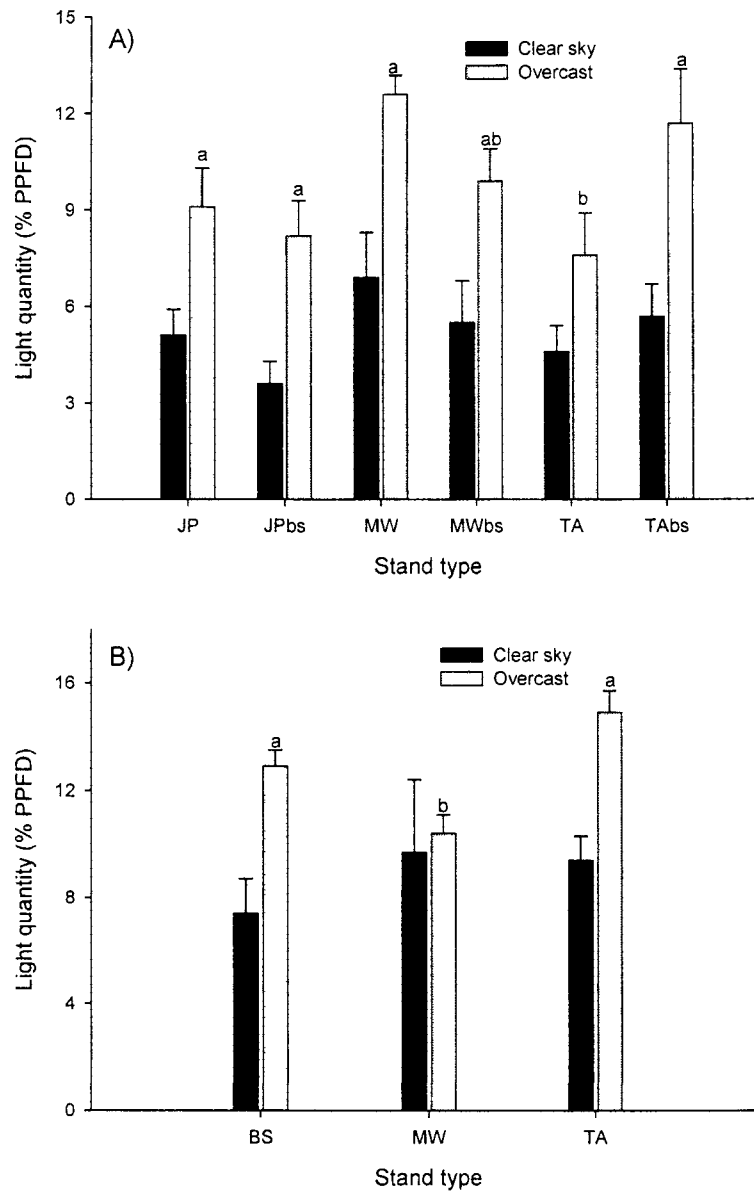


Figure 4-1 Light quantity (% above-canopy PPF transmission received in the understory) (means + 1 SE) in the understory of sampled stands in Ontario (A) and Québec (B) under clear sky clear and overcast sky conditions.

Light heterogeneity in the understory as measured by the standard deviation of %PPFD transmitted varied significantly among stand types only under overcast conditions in both regions (Table 4-2). In the Ontario study, understory light was much more heterogeneous in mixedwood stands ($4.40 \pm 0.3\%$) and less heterogeneous in jack pine with black spruce subcanopy stands ($2.0 \pm 0.1\%$) (Fig. 4-2A). Light heterogeneity in the Québec study was also highest in trembling aspen dominated stands ($3.2 \pm 0.4\%$) and least in black spruce dominated stands ($1.9 \pm 0.2\%$) (Fig. 4-2B).

Average %PPFD was consistently higher under overcast than clear sky conditions across all stand types in both regions (Fig. 4-1). In Ontario, mean %PPFD was significantly higher in overcast conditions (mean = 9.88) than clear sky conditions (mean = 5.58, $t = 6.28$, $P < 0.001$, $df = 45$). Likewise, mean %PPFD was significantly higher in overcast conditions (mean = 13.15) than clear sky conditions (mean = 10.10, $t = 2.55$, $P = 0.015$, $df = 37$) in the Québec study. Understory light heterogeneity was, however, significantly higher in clear sky (mean = 4.63) than overcast sky conditions (mean = 3.27, $t = 2.70$, $P = 0.010$, $df = 39$) in Ontario, and significantly higher in clear sky (mean = 8.27) than overcast sky conditions (mean = 2.44 $t = 6.37$, $P < 0.001$, $df = 23$) in Québec.

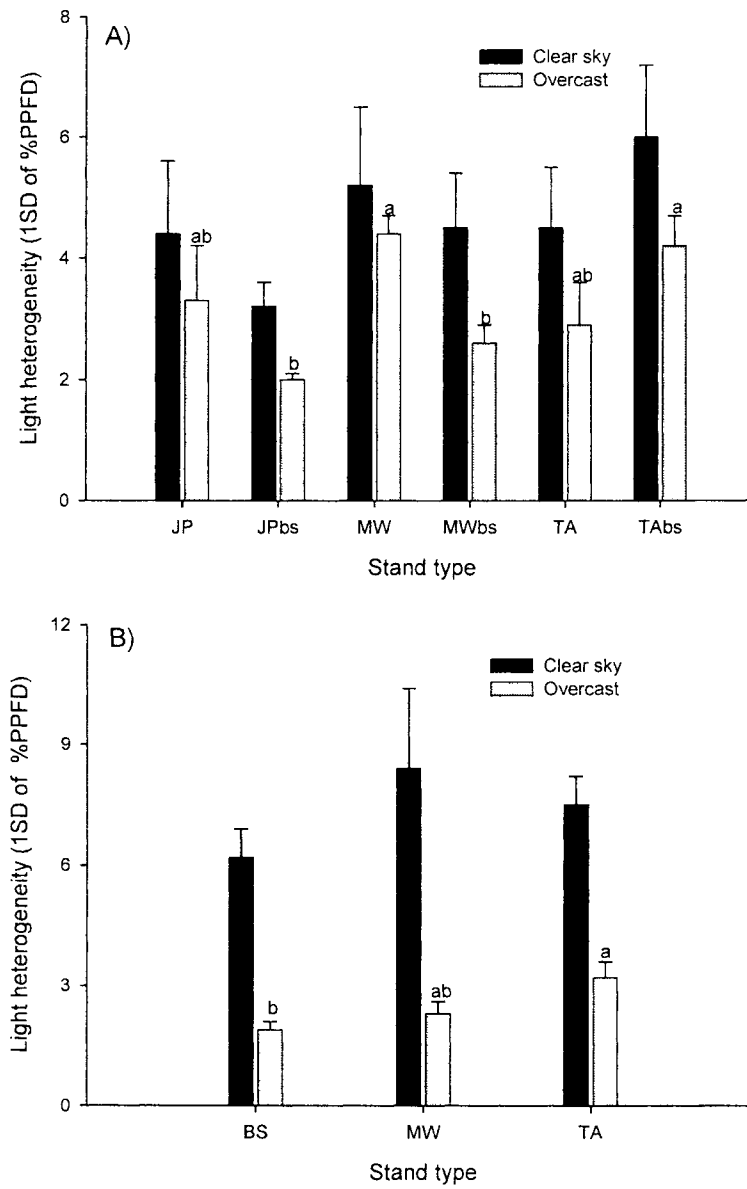


Figure 4-2 Light heterogeneity (means + 1 SE) in the understory of stands in Ontario (A) and Québec (B) under clear and overcast sky conditions.

Light quantity in clear and overcast sky conditions were significantly correlated in Ontario ($r = 0.57$, $P = 0.002$, $df = 23$), but not in Québec ($r = 0.11$, $P = 0.614$, $df = 20$) (Fig. 4-3A). There were, however, no significant correlations between light heterogeneity in clear and overcast sky conditions in either Ontario ($r = 0.34$, $P = 0.096$, $df = 23$) (Fig.4A) or Québec ($r = 0.09$, $P = 0.686$, $df = 20$) (Fig. 4-3B).

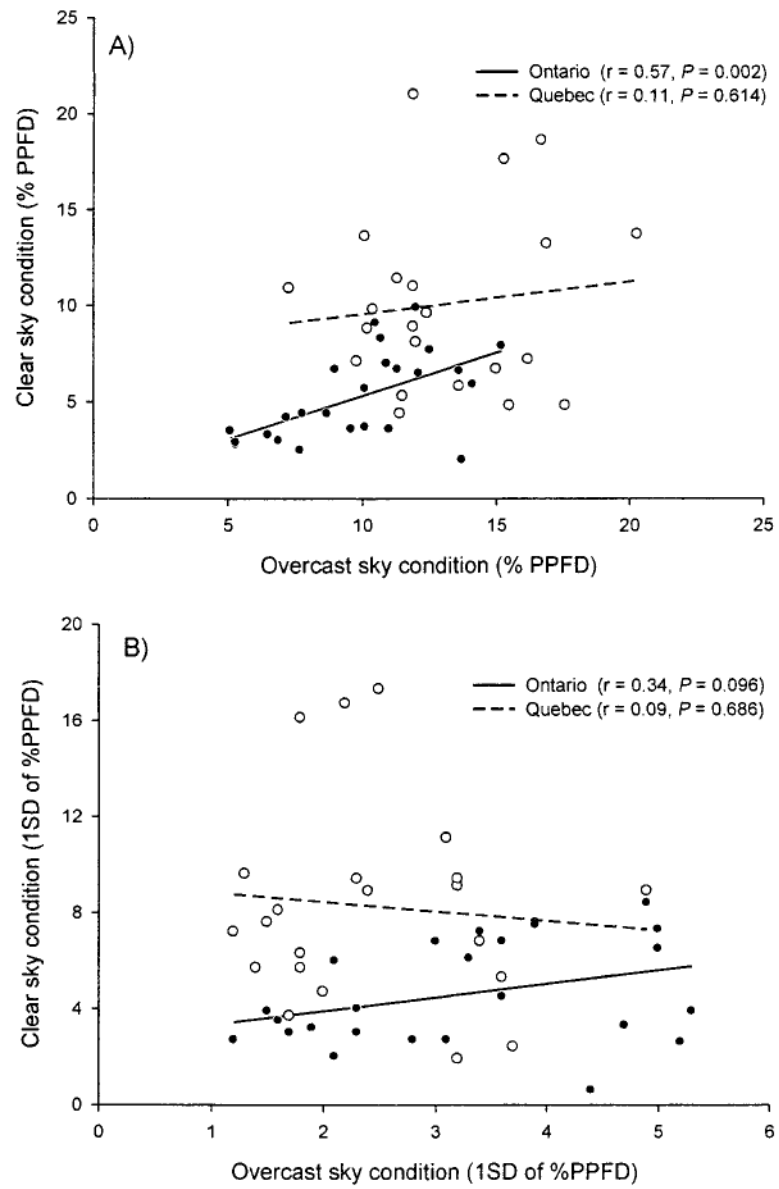


Figure 4-3 Correlation between light quantity (A) and light heterogeneity (B) in clear sky and overcast sky conditions in Ontario and Québec.

DISCUSSION

Light transmission/quantity

Our results suggest that differences in canopy tree composition can have significant effects on light availability in the understory. Mean %PPFD differed among stand types in both regions when measurements were made under overcast conditions. The values we report in this study generally fall within the range of light transmission values reported in similar stand types in the boreal forest (Constabel and Lieffers 1996; Messier *et al.* 1998). However, we observed a contrasting pattern of light transmission among stands in the two regions studied. Mixedwoods in Ontario generally transmitted more light than pine or aspen dominated stands, contrary to the case in Québec, where mixedwood stands transmitted the least. That mixedwood stands transmitted more light than aspen dominated stands presented an interesting result, as it contrasted several empirical findings of light transmission in mixed stands in other parts of the boreal forests (Constabel and Lieffers 1996; Messier *et al.* 1998).

In our case, the significantly lower %PPFD in aspen dominated stands compared to mixedwoods in Ontario is attributable to the occurrence of a dense layer of tall shrubs including *Acer spicatum*, *Corylus cornuta*, and *Alnus spp.*, as tall as 5 m, in the understory of aspen stands. These shrubs likely intercepted the supposedly high light transmission in aspen stands to much reduced levels, significantly lower than that of mixedwoods which largely composed of early successional, shade-intolerant trembling aspen and jack pine. Stands dominated by shade-intolerant species in our study, and like other studies, were found to transmit more light than stands dominated by shade-tolerant trees (Canham *et al.* 1994; Messier *et al.* 1998; Lieffers *et al.* 1999), as a result of less

light interception by shade intolerant tree species because of their thinner, conical crowns and small leaf area indices at the stand level (Kuuluvainen 1992; Canham *et al.* 1999). All conifer-dominated stands in Ontario, regardless of their shade tolerance, had lower %PPFD transmission than those with some broadleaf components in the overstory. This observation confirms other findings of low light transmission in conifer-dominated stands in the boreal forest (Messier *et al.* 1998).

In the case of the Québec study, aspen dominated stands transmitted more light than mixedwood and spruce dominated stands. This finding is consistent with other studies, especially in this part of the boreal region (Messier *et al.* 1998; Bartemucci *et al.* 2006), and other regions that report similar results (Constabel and Lieffers 1996). Mixedwoods in Québec were composed of aspen and shade-tolerant black spruce. Shade-tolerant trees tend to have greater leaf area index, and therefore less light transmission through their canopies. As such, shade-tolerant spruce under aspen, may have contributed to the low light transmissions in the understory of mixedwoods compared to aspen dominated stands. Light transmission in the stands of this region cumulatively ranged between 10% and 15% of above-canopy transmission, slightly higher than that recorded in Ontario. This regional difference is also attributed to the presence of tall shrubs in Ontario, but mostly mosses in Québec.

Light heterogeneity

Like many ecological variables, light availability varied independently among stands in time and space. Though the degree of light variation in the understory was high in clear sky conditions, it did not differ significantly among stand types (Table 3). Light heterogeneity was the highest in mixedwood stands in Ontario, and intermediate in

mixedwood stands in Québec (Fig 2). The higher variation of light in the understory of mixedwood stands could be best explained by the within-stand heterogeneity of mixedwoods, which exhibit structural complexity in spatial distribution of tree crowns and foliage distributions (Brown and Parker 1994; Van Pelt and Franklin 2000). Species-specific differences in canopy and tree architecture likely influence light availability in the understory (Kabakoff and Chazdon 1996; Nicotra *et al.* 1999; Tobin and Reich 2009); therefore, the heterogeneous nature of mixedwood stands potentially caused light to penetrate at various angles and intensities high enough to result in higher spatial variation of light in the understory compared to single species stands.

Of the stand types sampled in Québec, understory light was more heterogeneous in aspen dominated stands. This observation, though not expected, may reflect differences in crown architecture of aspen overstory and spruce subcanopy, as there were significant components of black spruce in the subcanopy of these stands. Patches of spruce in the subcanopy may have intercepted the high light transmission of the aspen overstory, thereby creating spatial variation of light in the understory. The distinction in light heterogeneity among stands according to post hoc test was subtle between mixedwood and aspen dominated stands, but was much higher than black spruce dominated stands.

Our study targeted mature stands with closed canopies and avoided gaps, and as such limited us in characterizing light heterogeneity in the understory in the presence of large and small canopy gaps. Canopy gaps are important sources of light heterogeneity in the understory, as they allow higher light transmission to the forest floor (Brandani *et al.* 1988; Canham *et al.* 1990; Canham *et al.* 1994). We could not account for the potential

contribution of sunflecks to light heterogeneity in the understory, since we focused on stands of full crown closure and used instantaneous rather than continuous measurements (e.g., Chen and Klinka 1997; Chen *et al.* 2004). In other studies, sunflecks and sunfleck duration were identified as sources of variation in transmitted light (Canham *et al.* 1994; Koizumi and Oshima 1993; Valladares and Guzman 2006). Our results, however, suggest that heterogeneity in understory light conditions is dependent on the degree of the mixture effect, in which mixedwoods exhibits greater degree of spatial variation in understory light.

Weather conditions

The percentage of above-canopy transmission received in the understory of the various stand types differed between the two sampling weather conditions considered in this study. In both regions, there were consistently higher light transmissions in overcast than clear sky conditions. A similar result in a closed canopy tropical forest was attributed to the changes in light quality under these conditions (Capers and Chazdon 2004). Clear sky measurements in our study did not result in any significant differences in light transmission of the stand types. This observation also seems to support the hypothesis that light availability of a forest microsite can be better estimated using instantaneous measurements taken on completely overcast conditions (Messier and Puttonen 1995; Parent and Messier 1996). However, others maintain that light estimation using instantaneous overcast measurements may be erroneous for forests with heterogeneous canopies, but efficient for microsite light availability in closed, homogeneous canopies (Stadt *et al.* 1997).

Clear sky measurements, unlike overcast measurements, gave variable results, but did not differ significantly among stand types. Similar findings of highly variable PPF_D measurements on clear days were attributed to the interplay of sun-position and gap location (Messier and Puttonen 1995; Battaglia *et al.* 2003). We found high understory light heterogeneity under clear sky than overcast conditions in both regions, which we attribute to the constant fluctuation in sun angle and intensity, and greater interception of direct radiation by tree crowns under clear sky conditions (Whitehead *et al.* 1990). Others also report high variability of %PPFD during clear days than overcast days in open-canopy stands (Battaglia *et al.* 2003), suggesting the contribution of both diffuse and direct light to total irradiance in the understory (Gendron *et al.* 2001).

There was a significantly weak correlation of light quantity between overcast and clear sky conditions, but no correlation of light heterogeneity between the two weather conditions. This suggests less or no predictive relationship of light environment between overcast and clear sky conditions in the understory of closed-canopy stands. Light conditions beneath a forest canopy are dynamic given the interplay of sky conditions and position of the sun. Overcast sky conditions allow accurate determination of relative amount of diffuse component of the PPF_D that is transmitted through a forest canopy (Messier and Puttonen 1995; Gendron *et al.* 2001). These measurements may approximate understory light availability over a growing season when direct light from the sun represents only a small fraction of the total during the growing season (Comeau *et al.* 1998). However, the total amount of understory light under clear sky conditions typically accounts for a larger share, given the number of sunny days than overcast days during the growing season in continental climate. Although our data show no difference

among stand types in clear sky conditions in the closed-canopy stands which had small variations among stands, instantaneous measurements that consider solar angles under clear sky conditions have been useful in quantifying total amount of solar radiation in the boreal forests (Chen 1997; Stadt *et al.* 1997; Comeau *et al.* 1998)

Regional effect

We found regional differences in light transmission between the two regions of the boreal forest studied. %PPFD values were generally higher in Québec (10% – 15%) than in Ontario (7% - 12%). The lower annual precipitation of Ontario study area (704.7 mm) compared to that of Québec (889.8 mm) may mean lower leaf area index (LAI) with less interception in Ontario, which should have translated into higher overstory light transmission, as was the comparison between aspen dominated stands in northwestern Québec and northern Alberta (Messier *et al.* 1998). The disparity in %PPFD between the regions likely results from the differences in site conditions, which influenced aboveground live biomass in the understory. The understory of stands in Ontario was generally dominated by a dense strata of tall shrubs and tree seedlings, whereas in Québec, the wetter glacial lacustrine clay deposits of the sites favoured the establishment of mosses on the forest floor (Han Chen and Samuel Bartels' personal observation). Dense subcanopy and understory vegetation strongly influence understory light levels (Aubin *et al.* 2000; Bartemucci *et al.* 2006). Thus, there was much light interception by the tall shrubs in Ontario and little to no light interception in Québec.

CONCLUSIONS

Certainly, overstory species composition of a given stand affects the amount of radiation in the understory, particularly at 1.3 m heights in the understory. Generally,

shade-intolerant canopy trees transmit more light to the understory than shade-tolerant trees. Shade-tolerant trees and tall shrubs in the subcanopy of closed forests significantly reduce light transmission to the understory. Understory light conditions tend to be more heterogeneous in mixedwoods stands, which are structurally and compositionally intermediate between pure stands of broadleaves and conifers. Through light attenuation and shading, the composition of species in the understory (trees, shrubs, herbs, bryophytes etc.) in a give forest ecosystem, may determine the amount of light reaching the understory. In accordance with other studies, overcast sky conditions may be ideal for characterizing microsite light availability in closed-canopy forests. However, both clear and overcast sky light measurements may be useful to adequately quantify understory light, available to understory plants, over a growing season.

CHAPTER FIVE: GENERAL CONCLUSION

Evidence of the effects of overstory composition on understory light resource environment, and understory plant community patterns highlighted in this study, leads to the conclusion that overstory-understory interactions are perhaps the most important determinant of understory community structure in the boreal forest. Although other factors such as the effects of stand successional stage and disturbance were not examined in this study, the results generally indicate that maintaining a diverse overstory in the boreal forests will ensure diversity of the various understory life forms. Patterns of plant species diversity in the resource-limited understory may be driven by both the average supply rate, and the spatial variation of key resources such as light, soil moisture, and nutrients. However, whether plant species specialize in different resource environments in the resource-limited understory has yet to be established.

Interrelationships among understory vegetation layers seem to suggest a neighborhood effect among vegetation layers, where compositional changes in one layer may result in changes in the subsequent layer. Particularly, species richness and cover of the shrub and herbaceous layers appear to be inversely related to that of the bryoid layer. It is therefore important to examine the spatial dependence of understory vegetation communities in studies of forest dynamics. Understory vegetation layers show different patterns of association with available soil physical and chemical variables as well as forest floor substrate conditions. The patterns probably reflect differences in resource requirements and resource capture. Understory light and soil moisture appeared to be least related to the dynamics of understory vegetation. Long-term studies as well as

experimental manipulations of resource availability are therefore needed to establish causal relationships between resource availability and understory plant communities.

Understory light availability appear to be higher under shade-intolerant canopy trees than shade-tolerants. It may be possible that dense strata of shade-intolerant trees and tall shrubs in the subcanopy of closed-canopy forests attenuate transmitted light through the upper canopies to much reduced levels in the understory. The spatial distribution of understory light appears to be more heterogeneous in mixedwood stands than single species-stands. Studies of resource distribution in forest ecosystems need to consider not only the average levels of resources, but also the variance, frequency, and spatial distribution of resources. Overcast sky conditions appear to be suitable for sampling light in the understory of closed-canopies than clear sky conditions. However, these two sampling conditions may not be correlated with each other. Light measurements in clear sky conditions may be suitable for characterizing sunflecks and sunflecks duration. Attempts to adequately characterize understory light, available to understory plants over a growing season in closed-canopy forests, should incorporate both overcast and clear sky measurements, in order to make full use of direct and diffuse lights.

APPENDIX A: Database of studies used in analysis. H, Q, and HQ represent studies that attribute the observed understory plant diversity to the influence of resource heterogeneity, quantity or both, respectively.

Author	Hypothesis supported	Forest biome	Intermediate disturbance	Successional stage(s)
Anderson and Leopold (2002)	H	Temperate	Present	Young/Mature
Anderson <i>et al.</i> (1969)	Q	Temperate	Absent	Young/Mature
Atuari <i>et al.</i> (2004)	H	Temperate	Present	Multi-stage
Bailey <i>et al.</i> (1998)	HQ	Temperate	Both	Multi-stage
Barik <i>et al.</i> (1992)	H	Tropical	Absent	Old-growth
Bartemucci <i>et al.</i> (2006)	Q	Boreal	Present	Multi-stage
Bates <i>et al.</i> (1998)	HQ	Temperate	Present	Young/Mature
Beatty (1984)	H	Temperate	Both	Young/Mature
Berger and Puettman (2000)	H	Temperate	Absent	Young/Mature
Brakenhielm and Liu (1998)	H	Boreal	Present	Old-growth
Brockerhoff <i>et al.</i> (2003)	Q	Temperate	Present	Young/Mature
Brososke <i>et al.</i> (2001)	HQ	Temperate	Present	Young/Mature
Brososke <i>et al.</i> (1999)	Q	Temperate	Present	Young/Mature
Brunet <i>et al.</i> (1996)	Q	Temperate	Present	Young/Mature
Burrascano <i>et al.</i> (2009)	H	Temperate	Both	Multi-stage
Chan <i>et al.</i> (2006)	Q	Temperate	Present	Old-growth
Chen <i>et al.</i> (2004)	Q	Boreal	Absent	Young/Mature
Chipman and Johnson (2002)	Q	Boreal	Absent	Multi-stage

Collins <i>et al.</i> (2007)	Q	Temperate	Present	Young/Mature
Cook <i>et al.</i> (2008)	Q	Temperate	Present	Young/Mature
Costa and Magnusson (2002)	Q	Tropical	Present	Young/Mature
Costa and Magnusson (2003)	Q	Tropical	Present	Young/Mature
Crow <i>et al.</i> (2002)	HQ	Boreal	Present	Multi-stage
Crozier and Boerner (1984)	HQ	Temperate	Absent	Young/Mature
Cusack and Montganini (2004)	Q	Tropical	Present	Young/Mature
D'Amato <i>et al.</i> (2009)	HQ	Temperate	Both	Multi-stage
De Grandpré <i>et al.</i> (1993)	Q	Boreal	Present	Multi-stage
De Grandpré and Bergeron (1997)	H	Boreal	Present	Multi-stage
Decocq (2000)	H	Temperate	Present	Young/Mature
Decocq <i>et al.</i> (2004)	Q	Temperate	Present	Young/Mature
del Rio (2006)	H	Temperate	Present	Old-growth
den Ouden and Alaback (1996)	H	Temperate	Present	Old-growth
Dirzo <i>et al.</i> (1992)	H	Tropical	Present	Old-growth
Elliot <i>et al.</i> (2002)	H	Temperate	Both	Young/Mature
Eycott <i>et al.</i> (2006)	Q	Temperate	Present	Young/Mature
Falk <i>et al.</i> (2008)	H	Boreal	Present	Young/Mature
Ferris <i>et al.</i> (2000)	HQ	Temperate	Absent	Multi-stage
Fredericksen <i>et al.</i> (1999)	Q	Temperate	Present	Young/Mature
Frisvoll and Presto (1997)	H	Boreal	Present	Multi-stage
Gálhidy <i>et al.</i> (2007)	H	Temperate	Present	Young/Mature
Gilliam and Turril (1993)	Q	Temperate	Absent	Multi-stage

Graae and Heskjaer (1997)	Q	Temperate	Both	Multi-stage
Griffith <i>et al.</i> (2007)	Q	Tropical	Absent	Young/Mature
Gundale <i>et al.</i> (2006)	H	Temperate	Present	Young/Mature
Halpern and Spies (1995)	H	Temperate	Present	Multi-stage
Halpern <i>et al.</i> (2005)	Q	Temperate	Present	Multi-stage
Härdtle <i>et al.</i> (2003)	Q	Temperate	Absent	Young/Mature
Harms <i>et al.</i> (2004)	Q	Tropical	Absent	Old-growth
Harrington and Edwards (1999)	HQ	Temperate	Present	Young/Mature
Hart and Chen (2008)	Q	Boreal	Present	Multi-stage
He and Barclay (2000)	H	Boreal	Present	Young/Mature
Howard and Lee (2003)	Q	Temperate	Absent	Multi-stage
Huebner <i>et al.</i> (1995)	H	Temperate	Absent	Young/Mature
Huisinga <i>et al.</i> (2005)	HQ	Temperate	Present	Young/Mature
Hutchinson <i>et al.</i> (1999)	Q	Temperate	Present	Young/Mature
Jalonen and Vanha-Majamaa (2001)	Q	Boreal	Present	Young/Mature
Janišová <i>et al.</i> (2007)	HQ	Temperate	Absent	Young/Mature
Jenkins and Parker (1999)	Q	Temperate	Absent	Young/Mature
Kembell <i>et al.</i> (2005)	Q	Boreal	Present	Young/Mature
Kennedy and Quinn (2001)	H	Temperate	Present	Old-growth
Kerns <i>et al.</i> (2006)	H	Temperate	Present	Young/Mature
Klinka <i>et al.</i> (1996)	Q	Boreal	Present	Young/Mature
Krzic <i>et al.</i> (2003)	Q	Boreal	Present	Young/Mature

Laska (1997)	Q	Tropical	Both	Multi-stage
Laughlin and Abella (2007)	Q	Temperate	Present	Young/Mature
Lee and Roi (1979)	Q	Boreal	Absent	Young/Mature
Lee and Sturgess (2001)	H	Boreal	Present	Young/Mature
Légaré <i>et al.</i> (2001)	Q	Boreal	Absent	Young/Mature
Légaré <i>et al.</i> (2002)	Q	Boreal	Absent	Young/Mature
Leuschner and Lenzion (2009)	Q	Temperate	Absent	Young/Mature
Lindgren <i>et al.</i> (2006)	Q	Boreal	Both	Multi-stage
Linière and Houle (2006)	Q	Boreal	Absent	Young/Mature
Lyon and Sagers (1998)	H	Temperate	Absent	Young/Mature
McDonald and Fenniak (2007)	HQ	Boreal	Present	Young/Mature
McGuire <i>et al.</i> (2001)	Q	Temperate	Present	Young/Mature
Metlen and Fiedler (2006)	Q	Temperate	Present	Young/Mature
Miller <i>et al.</i> (2002)	H	Temperate	Absent	Old-growth
Molofsky and Augspurger (1992)	H	Tropical	Absent	Old-growth
Moora <i>et al.</i> (2007)	HQ	Temperate	Present	Multi-stage
Nagaike <i>et al.</i> (2003)	Q	Temperate	Absent	Multi-stage
Newmaster <i>et al.</i> (2007)	H	Boreal	Present	Young/Mature
Nicotra <i>et al.</i> (1999)	H	Tropical	Present	Multi-stage
Nieppola and Carleton (1991)	Q	Boreal	Absent	Young/Mature
North <i>et al.</i> (1996)	HQ	Temperate	Present	Young/Mature
North <i>et al.</i> (2005)	HQ	Temperate	Present	Old-growth
Oberle <i>et al.</i> (2009)	H	Temperate	Absent	Young/Mature

Økland and Eilertsen (1996)	Q	Boreal	Absent	Old-growth
Økland <i>et al.</i> (1999)	HQ	Boreal	Both	Old-growth
Okubo <i>et al.</i> (2005)	Q	Temperate	Present	Young/Mature
Pausas (1994)	Q	Temperate	Absent	Young/Mature
Pausas and Carreras (1995)	Q	Temperate	Absent	Young/Mature
Peltzer <i>et al.</i> (2000)	Q	Boreal	Both	Young/Mature
Peterson and Campbell (1993)	H	Temperate	Absent	Old-growth
Peterson and Pickett (1995)	H	Temperate	Present	Old-growth
Pharo <i>et al.</i> (1999)	Q	Temperate	Present	Young/Mature
Pollock <i>et al.</i> (1998)	H	Temperate	Present	Old-growth
Powers <i>et al.</i> (1997)	HQ	Tropical	Present	Young/Mature
Qian <i>et al.</i> (1997)	Q	Boreal	Absent	Multi-stage
Qian <i>et al.</i> (2003)	Q	Boreal	Absent	Young/Mature
Ramovs and Roberts (2003)	H	Boreal	Present	Multi-stage
Rankin and Tramer (2002)	Q	Temperate	Present	Young/Mature
Riegel <i>et al.</i> (1991)	Q	Temperate	Present	Young/Mature
Riegel <i>et al.</i> (1992)	Q	Temperate	Present	Young/Mature
Riegel <i>et al.</i> (1995)	Q	Temperate	Present	Young/Mature
Rogers <i>et al.</i> (2008)	Q	Temperate	Present	Young/Mature
Scheller and Mladenoff (2002)	HQ	Temperate	Present	Old-growth
Schoonmaker and Mckee (1988)	H	Temperate	Both	Multi-stage
Small and McCarthy (2002)	HQ	Temperate	Present	Multi-stage
Small and McCarthy (2002)	HQ	Temperate	Present	Young/Mature

Son <i>et al.</i> (2004)	Q	Temperate	Present	Young/Mature
Son <i>et al.</i> (2004)	Q	Temperate	Present	Young/Mature
Soo <i>et al.</i> (2009)	Q	Temperate	Present	Young/Mature
Sparks <i>et al.</i> (1998)	Q	Temperate	Present	Young/Mature
Stone and Wolfe (1996)	H	Temperate	Present	Young/Mature
Svenning (2000)	H	Tropical	Absent	Old-growth
Sweeney and Cook (2001)	Q	Temperate	Absent	Young/Mature
Tárrega <i>et al.</i> (2006)	Q	Temperate	Present	Young/Mature
Tárrega <i>et al.</i> (2007)	Q	Temperate	Present	Young/Mature
Thomas <i>et al.</i> (1999)	HQ	Temperate	Present	Young/Mature
Thomsen <i>et al.</i> (2005)	H	Temperate	Absent	Old-growth
Thysell and Carey (2001)	H	Temperate	Both	Multi-stage
Turner and Franz (1986)	H	Temperate	Absent	Old-growth
Uotila and Kuoki (2005)	H	Boreal	Present	Multi-stage
Van Pelt and Franklin (2000)	Q	Temperate	Present	Old-growth
Vazquez and Givnish (1998)	Q	Tropical	Both	Young/Mature
von Oheimb <i>et al.</i> (2007)	H	Temperate	Both	Old-growth
Wayman and North (2007)	Q	Temperate	Absent	Old-growth
Weisberg <i>et al.</i> (2003)	Q	Temperate	Present	Young/Mature
Wetzel and Burgess (2001)	Q	Boreal	Present	Young/Mature
Yager and Smeins (1999)	Q	Tropical	Present	Young/Mature

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