Succession in the Understory of Red Pine Plantations in Southern Ontario

by

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ABSTRACT

Thousands of hectares of red pine (*Pinus resinosa* Ait.) plantations were established during the early 20th century to restore abandoned agricultural lands and increase forest cover. Concern over the ecological integrity [*i.e.* the degree to which a community is determined to be characteristic of its natural region, including abiotic and biotic components, likely to persist and maintain the rates of change and supporting processes (Canada National Parks Act (S.C. 2000, c. 32) 2011) of these plantations and a desire to increase native forest cover has prompted a more thorough understanding of the understory succession of these plantations. This study addresses the question, *how does the understory vegetation composition and diversity in managed red pine plantations compare to the understory of a reference deciduous forest?*.

I examined the understory diversity in a chronosequence of managed red pine plantations owned by Simcoe County. Biophysical characteristics including diffuse non-interceptance (DIFN), tree regeneration, litter depth, and soil physical and chemical properties were gathered from three replicates of each of four age groups and from a reference deciduous forest group in order to determine how each variable changed and influenced the succession of the understory diversity. Field investigations were completed during the spring, summer, and fall of 2009 in order to examine seasonal differences in diversity.

A two-way analysis of variance with a Tukey's post hoc test was used to determine if the forest groups were significantly different from each other for each variable measured. Species diversity (measured by the Shannon-Wiener Index) generally increased with plantation age and seasonal differences were apparent. A lack of significant difference between the oldest plantation group (est. 1927-1932) and the reference forest group indicates diversity is increasing; this is intriguing because, in contrast, species composition is only 30% similar. This may indicate either not enough time has passed for the understory to regenerate or the understory in the plantations is succeeding in a different trajectory. Furthermore, spring ephemeral species were lacking in the understory of the plantation forests indicating this phenological group is not regenerating in the plantations. Tree density is generally increasing in the plantation groups and the dominant tree species regenerating in the oldest plantation group includes a similar suite of species to that found in the reference forest groups. This indicates that the canopy is succeeding towards a native forest community.

Pearson correlation analysis revealed that litter depth is significantly negatively correlated to diversity in the summer and fall ($p<0.01$). Litter depth was also the primary predictor variable produced by the forward stepwise regression in the summer and fall indicating that litter depth is a major driver of diversity. From comparative studies, a deeper litter layer often inhibits the germination and emergence of herbaceous species; from my study, this may explain the lack of spring ephemerals in the plantation groups observed. DIFN was significantly negatively correlated to diversity in the spring ($p<0.01$) and was the predictor variable for spring diversity indicating that light characteristics in the spring are a major variable influencing spring diversity. With increasing age of plantation group the DIFN followed a similar pattern to the reference forest group indicating that the thinning regime and regeneration is shifting the light characteristics to that found in a natural forest stand.

I conclude that the thinning regime in red pine plantation is promoting the regeneration of trees and increasing the diversity of understory vegetation. However, in order to direct the successional trajectory of the understory vegetation of red pine plantations to a composition similar to the native woodlands of that area, a modified management program should be considered and active restoration should be implemented.

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Table of Contents

List of Tables

List of Figures

1.0 CHAPTER 1 - INTRODUCTION AND LITERATURE REVIEW

About 8,000 years ago, forests covered an estimated 6.2 billion ha of the planet; this was approximately 47% of Earth's land surface (Billington *et al.* 1996). Since that time, it has been estimated that the planet has lost about 40% of its original forest cover, and the remaining forests have suffered varying degrees of degradation and fragmentation (Matthews *et al.* 2000; Ball 2001). As of 2005, the Food and Agriculture Organization (FAO) (2006) estimate the global forest area at about four billion hectares of land including 36.4% of primary (original) forest, 52.7% modified natural forest, 7.1% semi-natural forest, and 3.8% plantation forests. Plantations now make up an estimated 140 million hectares globally and are mainly established for wood and fiber production (FAO 2006). These forests typically consist of even aged stands of one or few types of trees known as plantation forests that are often comprised of introduced species planted in regularly spaced rows.

North American native forest cover has decreased by approximately 20% over the past century primarily because of land clearing for agriculture, other resource extraction uses, transportation corridors, and expansion of urban areas (Bryant *et al.* 1997). Whatever the reason for deforestation, the outcome is generally the same: the acquisition of natural resources and land area at the expense of degrading natural environmental conditions (Foley *et al.* 2005).

Vast areas of forest, approximately264 million hectares, have since been replanted for many purposes (*e.g.* store carbon, reduce soil erosion, improve water quality, and increase biodiversity) and at increasing rates (Rudel *et al.* 2005). According to the FAO (2006), forest cover in North America is now relatively stable (*i.e.* the rate of deforestation is equal to the rate of reforestation). However, in most of the lower 48 states and southern Canada, remaining forests are fragmented, often isolated, and disturbed by surrounding land uses, therefore having a reduced degree of ecological integrity compared with the original forest community (Noguerón 2002). A community has ecological integrity when "it is determined to be characteristic of its natural region and likely to persist, including abiotic components and the composition and abundance of native species and biological communities, rates of change and supporting processes" [Canada National Parks Act (S.C. 2000, c. 32) 2011].

Forest cover and composition in southern Ontario has been transformed time and again by humans, initially by First Nations peoples and then European and other 'old world' settlers (Elliot, 1998). Prior to European settlement, forests covered about 90% of southern Ontario, but by 1978 less than 20% of forest cover remained (Larson *et al.* 1999). The remaining primary and secondary forests in southern Ontario are considered to have moderate ecological integrity, meaning they are less resistant to diseases and pests and are generally less resilient following a disturbance (Parker and Craig 2005). However, due to human pressure these forests continue to be subject to a wide variety of stressors including fragmentation, the still cumulative effects of past timber and fuel wood extraction, high loadings of ground-level ozone, and long term impacts from excessive acid deposition levels (Parker and Craig 2005). Southern Ontario is the most densely populated area in Canada and is expected to continue to intensify (Statistics Canada 2011) further threatening the size and ecological integrity of remaining forest areas.

Few of the remaining forests in southern Ontario comprise their original characteristics as a result of historical land use. Prior to European settlement forests in southern Ontario contained the same species found in today's southern boreal forest, Great Lakes - St. Lawrence forest (transitional zone) and, deciduous forests, however with a different composition and dominant species (Pinto *et al.* 2008). According to Pinto *et al.* (2008) red (*Pinus resinosa* Ait.) and white pines (*Pinus strobus* L.) were once abundant but decreased significantly following European settlement whereas maples (*Acer spp.*) and poplars (*Populus spp.*) increased. The preference for harvesting conifers for use as building materials, suppressing forest fires (*i.e.* fire is required by some conifers such as Jack pine (*Pinus banksiana* Lamb.) to regenerate), and exotic insect and disease infestations have been cited as reasons for the decline of the conifers (Pinto *et al.* 2008; Maloy 1997). With the lack of regeneration of these conifers hardwoods became dominant (Pinto *et al.* 2008). Early settlers also saw forests as obstacles to roads and agriculture which led to felling and burning to make way for desired uses (Schoch and Rowsell 2004). This attitude towards forests was imposed by the government on farmers who were given grants for land; *i.e.* if they did not clear 4.86 ha of land within five years they risked losing title to their land (Schoch and Rowsell 2004). The disregard for the importance of forests changed by the early 20th century as the effects of land abandonment of unproductive and unprofitable land resulted in erosion of top soil by wind and rain leaving behind the sandy substrate (Carman 1941; Wood 1991).

By the early 20th century the Ontario government recognized the extent and impact of land degradation prompting a series of legislative efforts to encourage reforestation of these areas in order to control soil erosion and protect watersheds (Borczon 1986). One such measure was the Agreement Forest program, a long-term agreement where the Ministry of Natural Resources (formerly the Ontario Department of Lands and Forests) would manage the lands of the owner for forestry purposes (MNR 2001). Made possible through the Reforestation Act of 1921, the main focus of the program was to reforest waste lands and protect soil from further erosion. Due to the severity of the problems associated with land abandonment Simcoe County was the first to take advantage of this program with the first trees being planted in 1922 (Simcoe County 2009). The sandy droughty nature of the soils was suitable to conifers, primarily red pine, and hundreds of hectares were planted across southern Ontario eventually stabilizing the eroding sandy soil and beginning the process of restoration of these lands. The establishment of these plantations provided many benefits: restoration of wastelands and abandoned farm land; prevention of soil erosion; protection of water resources from sedimentation; improvement of wildlife habitat; increase in recreational areas; and a source of income for the land owners (both private and county) (Simcoe County 2009). The success of this program led to the introduction of the Department of Lands and Forests' "Woodlands Improvement Act" in 1966. Financial assistance from the Province allowed for over 40 million trees to be planted on private and county owned land. As a result of the financial assistance offered through these programs, plantation forests consisting of one or few species of trees planted in straight rows were established throughout southern Ontario.

Conifer plantations are planted and managed in such a way as to maximize yield for commercial harvest. They are typically planted in rows about 1.8-2.4 meters apart with seedlings planted every 1.8 meters (OMNR 1999). The spacing of the trees is selected in order to control the growth and development of the crown (Prince Edward Island Forestry Division 1997). During the first several years of growth surrounding vegetation is either mown or suppressed with the use of herbicides in order to reduce competition with the saplings (OMNR 1999). With time, the competition for resources moves from interspecific to intraspecific. In order to control the density of the stand and maximize growth a thinning regime is prescribed. Generally, a conventional thinning typically involves a first thinning between the ages of 30 to 40 years followed by thinning approximately every 10 years (County of Simcoe 2009). The first thinning involves the removal of one of every four rows (County of Simcoe 2009). The initial thinning provides future access to the trees by machinery in addition to reducing the stand density and increasing light penetration to the understory. Each thinning alters the light dynamics and microclimate in the understory. Older plantations having at least one thinning typically begin to increase in understory plant diversity including the regeneration of hardwoods as can be seen in the understory of plantations established in the 1920's and 30's (Watt 1996). Stands are typically harvested for sixty years beginning with the first row removal (Prince Edward Island Forestry Division 1997). Management of these plantations, particularly the thinning of trees, results in a disturbance that directly changes the understory light and microclimate conditions. Consequently, these changes drive succession in the understory vegetation.

From an economic perspective, establishing plantations provides large quantities of fiber from relatively small land areas (Sedjo 1999) and they sequester large amounts of carbon (Newmaster *et al.* 2006). Forest plantations also have a potentially high productivity. In optimal growing conditions mean annual increments for *Pinus spp.*, *Picea spp.*, and *Larix spp.* plantations in temperate and southern boreal zones can reach 12-15 m^3/ha per year (Millennium Ecosystem Assessment 2011). Alternatively, environmentalists, ecologists, and wildlife biologists argue that the intensive management of forest plantations are a major contributor to the establishment of exotic species, loss of native species from forest communities, and create single-layered monocultures, or "biological deserts" (Conde *et al.* 1983; Mosquin *et al.* 1995) consisting of simplified communities low in biodiversity compared with native forests (Smith *et al.* 1997; Brockerhoff *et al.*2008). Particularly, diversity of understory flora and abundance of native species is often low compared with native forests (Gilliam 2003; Roberts 2002; Newmaster *et al.* 2006). The effects of forest communities low in biodiversity may include reductions in resilience, declines in ecological services provided to humans, and a reduced resistance to competition by invasive exotic species [*i.e.* species introduced by human action outside their natural past or present distribution whose introduction or spread threatens the environment, economy, or society including human health (Environment Canada 2004)] (Hansen *et al.* 2001). In a comprehensive survey of invasive exotic species across Ontario, Newmaster and Ragupathy (2005) provide empirical data to support the position that there are more invasive exotic species in plantations (12%-25%) than in native forests (1%-3%). There is additional research providing further evidence that invasive exotic species may displace or reduce populations of native species, significantly hindering the goal of preserving native biodiversity (Hobbs and Huenneke 1992).

The lack of diversity and abundance of native species in the understory of conifer plantations compared with native forests has been a concern for ecologists (Gilliam 2002; Roberts 2002; Newmaster *et al.* 2006) particularly because the important role the understory has in the ecological functioning and integrity of forests (Wingham 2004). Ecological integrity is often evaluated using a multitude of attributes including species richness, biodiversity, indicator taxa, abundance, biomass or measures of ecological processes (Schmidt *et al.* 2002). Because of the role the understory community has in the ecological functioning of forests studies investigating the ecological integrity of forests often examine the composition and diversity of the herbaceous layer as these are good indicators of forest ecological integrity (Meier *et al.* 1995). Therefore, having an understanding of the processes influencing understory vegetation dynamics and their role in the ecological function of forests ecosystems can provide insight into what is driving the succession and diversity of the understory in conifer plantations and how this may contribute to the ecological integrity of conifer plantations.

Compared to conifer plantations, native forests, particularly deciduous forests in eastern North American are comprised of a highly diverse layer of vascular and non-vascular plants (Newmaster *et al.* 2006). Factors affecting understory vegetation include the interaction between plants, wildlife, soil, light, and precipitation, all of which are affected by seasonal variation and successional change (Wingham 2004). Seasonal variation in light and precipitation, particularly in the understory of deciduous forests, play a role in the dynamics of the understory vegetation. Deciduous forests see notable changes in light availability in the understory over a season (Anderson 1964) partly contributing to the diversity in the understory. Guilds of plants have become specifically adapted to thrive under different light regimes and during different seasons including early emerging species, early summer species, and late summer species.

Deciduous forests, specifically relatively undisturbed deciduous forests, have a high diversity of early emerging and flowering herbs or spring ephemerals (Duffy and Meier 1992; Burke *et al.* 2008). Spring ephemerals tend to display foliage between 5-15 cm above the ground on basal leaves or short umbrellas which is presumed to provide efficient temperature regulation, permitting efficient use of light during the short period between emergence and development of the tree canopy (Givnish 1987). They also have high saturation points and maximum photosynthetic rates (Taylor and Pearcy 1976), and an inability to adapt to low-light environments (Hicks and Chabot 1985). These differ from early summer species that have determinate growth with leaves higher above the ground shaped to minimize shading while maximizing light capture, and also from late summer species that have indeterminate growth also with leaves high above the ground (Givnish 1987).

Woodland herbs account for a large portion of the vascular plant diversity (Wingham, 2004). Gilliam (2007) estimated that the herbaceous layer made up on average 80% of the plant diversity of a forest. The role of the understory, specifically, the herbaceous layer in cycling nutrients is a vital component of the functioning of forest ecosystems (Muller and Bormann 1976; MacLean and Wein 1977; Blank *et al.* 1980; Anderson and Eickmeier, 2000; Mabry *et al.* 2008). Forest herbs disproportionately cycle essential plant nutrients (*e.g.*, N, P, K) relative to their biomass in forest ecosystems (Muller 2003; Welch *et al.* 2007). They also function to rapidly take up, retain, and recycle nutrients in the early spring at a time when uptake by trees is minimal. This was documented by Muller and Borman (1976) who found that uptake of essential nutrients, especially nitrogen, by spring ephemerals before the canopy develops helps to reduce the loss of nutrients in the soil, which they termed the 'vernal dam theory'.

The understory is also the most sensitive vegetative component of forest ecosystems to natural and anthropogenic disturbance, particularly changes in micro-environmental at the community level (MacLean and Wein 1977; McCarthy and Facelli 1990; Meier *et al.* 1995). Because understory vegetation is specifically adapted to lower light conditions, changes in light penetration through the canopy has a significant impact on species composition and dominance (Fahey and Puettmann 2008; Smith et. al. 2008; Ares *et al.* 2009). These changes come in the form of canopy gap creation, whether natural or man-made (*e.g.* harvesting of trees). The increase in light subsequently causes changes in temperature, nutrient cycling, and soil moisture

(Meier *et al.*, 1995), all of which may favour r-selected plants (i.e. species that produce a high number of seeds that tend to have a high rate of germination, fast growth, and are short lived). This will ultimately result in a change in the composition of the species where the environmental conditions have changed. As is generally the case, the larger the disturbance, the larger the change in the species composition. Depending on the degree of disturbance, the understory may never return to pre-disturbance species composition (Noble and Slatyer 1980; Duffy and Meier 1992). In southern Ontario clearing of forests to make way for agriculture and subsequent reforestation of monospecific conifer plantations is an example of a large disturbance.

The establishment of conifer plantations in Ontario was the first step in restoring disturbed and degrading landscapes that remained after deforestation and exploitative agriculture. It can be argued that since plantation forests do serve a role in restoring ecosystem services and provide habitat for some species of wildlife, they could continue to be managed to both generate revenue in addition to increasing understory diversity. However, if the goal is eventual conversion of these plantations to natural forests with a similar composition of species to relatively undisturbed native forests, the management of these plantations should include measures to meet this. A lack of management and understanding of successional trajectory and restoration goals can suppress the increase in native floral diversity and can take hundreds rather than tens of years to achieve (Goldblum 1998). For example, Goldblum (1998) found that naturalizing conifer plantations had no hardwood tree regeneration in a stand of 55-65 year old white spruce for nearly 30 years and regeneration to a mixed forest would likely take 100-150 years if unmanaged. Understory plant communities and insect communities would take even longer, potentially never fully regenerating to represent primary forests of the region (Peterken and Game 1984; Duffy and Meier 1992; Robinson *et al.* 1994). Also, regeneration of plantations may be impeded as exotic species might become persistent members of the plant community, and may even prevent successional change, as has been observed in other plant communities (Kellman 1980; Jumpponen *et al.* 1998).

There has been recent interest by the Ministry of Natural Resources, County foresters, and Conservation Authorities in continuing the restoration of these plantations by converting these monocultures into a more native mixed (*i.e.* neither the deciduous nor the coniferous composition of the community is less than 25%.) or deciduous-dominated forest with the long term goal of increasing diversity and native forest cover in southern Ontario (Parker 2008). This is becoming more of an issue as the increase of root diseases (*e.g. Armillaria* sp.) threatens the health of red pine plantations around the Great Lakes Region of North America (McLaughlin 2001; Erbilgin and Raffa 2002). Ecological restoration of conifer plantations into a more diverse vegetative forest type may prevent the spread of diseases (Morrison and Mallett 1996; Morrison *et al.* 2000) that are more likely to spread in monospecific densely established plantations. Furthermore, increasing diversity can improve the ecological integrity, including resilience, of these forests by ensuring that in the event diseases, pests, or disturbances alter the community, the ecological functioning of the community will not be greatly affected by the loss or reduction of one species (Drever *et al.* 2006). Furthermore, restoration of conifer plantations into a more native forest type has been suggested as a means of controlling the introduction and spread of exotic invasive species, and can increase habitat for native flora and fauna, improve the ecological integrity of these forests, and increase native forest cover in southern Ontario (Parker *et al.* 2008).

Ecological restoration can be described as an intentional activity that "initiates or accelerates the recovery of an ecosystem with respect to its health, integrity and sustainability" (SER 2004). Restoration ecology integrates the studies of ecology, environmental science, economics, sociology, and politics and can be seen as the study of how to repair anthropogenic damage in order to recover the integrity of ecological systems (Cairns and Heckman 1996). Applying the theories of restoration ecology and learning from other studies of ecological restoration of forests can aid in restoring conifer plantations.

In a sense, ecological theories provides some explanation of the dynamics affecting the understory in conifer plantations. Table 1 includes theories that were considered when examining the dynamics of the understory in conifer plantations.

Table 1. Theories/concepts relevant to understanding understory dynamics in forests.

Theory/ Concept	**Definition**	**Relevance to understanding dynamics of Conifer Plantation Understory**
Ecological Succession	- The change in plant communities over time	- The suite of species colonizing a site depends on the stage of succession (*i.e.* primary, or secondary) and the nutrients and resources available to these species. - Through their phenological attributes species that first colonizing the understory can improve site conditions for later colonizing species (*e.g.* nitrogen fixers) - Conversely, some early dominants can persist indefinitely and inhibit the establishment of other species (*e.g.* allelopathic species) - Over time the community will 'mature' and succeed towards a climax community
Island Biogeography Theory	- The number of species established in an isolated community represents a dynamic equilibrium between the immigration of new colonizing species and the extirpation of previously established ones	- The understory of conifer plantations in close proximity to a natural forest stand should increase in diversity more quickly than more isolated plantations. - Larger conifer plantations will take longer to increase in diversity and resemble natural forests in part due to the rate of spread and establishment of colonizing species.
Disturbance	- A temporary change in environmental conditions resulting from natural processes or anthropogenic influences	- A disturbance will set the community back to an earlier stage of succession and will affect biotic and abiotic components of the community - The degree of disturbance will affect the environmental conditions and species suitable to these conditions - Thinning in conifer plantations is a type of disturbance that will alter the understory abiotic conditions

Theory/ Concept	**Definition**	**Relevance to understanding dynamics of Conifer Plantation Understory**
Assembly Rules and Ecological Filters	- The objective of understanding assembly rules is to predict what species might occur in a community based on a set of environmental conditions (i.e. light, available nutrients, moisture).	- The successive assembly of species will influence the ability of later species to become established - If the goal of management of conifer plantations is to increase diversity the thinning regime should be designed to develop the conditions that will encourage the establishment of native species. - Ecological filters can be established to operate on species traits and remove those individuals or populations whose sets of traits are undesirable (Fattorini & Halle 2004). Conversely, ecological filters can be removed to encourage the establishment of desirable species.

The theories behind restoration ecology are primarily based on ecological principles from the genome level to the landscape level. Ecological restoration is "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SERO 2004). The premise of ecological restoration is largely based on the process of ecological succession. Understanding successional processes offers both a short-term and long-term perspective on species dynamics and provides a reference system for restoration that can predict likely outcomes following management actions (van Andel and Aronson 2006).

Examining the change in the understory of red pine plantations over time is in fact examining understory succession. That is, examining the biotic and abiotic changes in the community, driven from biotic interactions, that direct change in ecosystem structure and function beginning with species colonization to interactions and competition among species for resources (Chapin *et al.* 2002). Changes in community composition are a result of species interaction, changes in environmental conditions, and the interactions between the biotic and abiotic components. Environmental change due to physical structures in the community are considered allogenic and environmental changes due to biotic interactions are autogenic changes (Smith and Smith, 2006). The commercial harvesting of trees and thinning of the canopy in conifer plantations are allogenic changes. Autogenic changes are then influenced by the thinning operations and are the basis for successional theories such as facilitation and inhibition. The allogenic changes in conifer plantations come as a result of the thinning operations. These thinning operations result in a disturbance to the canopy and understory that plays an important role in succession, specifically because it results in some change in the abiotic environmental conditions (*i.e*. light, moisture, nutrients) which in turn affects the biotic environment. In a sense, a disturbance such as thinning resets succession in the community to an earlier stage (Hobbs *et al.* 2007).

Early stages of secondary succession can have variable levels of nutrients in the soil depending on the type of disturbance. The type of disturbance resulting from thinning operations directly affects the amount of light penetrating the canopy and increases the amount of organic debris on the forest floor. Following these types of disturbance there is often a pulse of available nutrients and a more rapid mineralization of dead organic matter with an increase in light and temperature (Vitousek *et al.* 1989; Boerner *et al.* 2000; Knoepp *et al.* 2009). High nutrient availability typically supports earlier successional species with high relative growth rates facilitated by high rates of photosynthesis and nutrient uptake (Tilman 1985). In contrast to primary succession, secondary succession is not usually nutrient limited following a natural disturbance and there are typically adequate amounts of nutrients available to support higher rates of photosynthesis and growth (Scatena *et al*. 1996). Anthropogenic disturbances can have a wider range of initial nutrient availability in secondary succession. For example, abandoned agricultural lands may have low nutrients and organic matter due to higher rates of mineralization and organic matter breakdown resulting from tillage practices, leaching of nutrients due to watering regimes, and erosion of top soil from wind and water (Hussain *et al.* 1999). Alternatively, the abandonment of rich agricultural lands or clearing of productive forests will leave conditions with high soil nutrient content (Matson *et al.* 1987).

The pattern of species colonization is also largely shaped by disturbance and life history traits of species. Immediately following a disturbance, including the harvesting of trees during a commercial thinning operation, the species richness may be reduced (Roberts 2002). The reduction in species may be a result of changes to the microclimate following canopy thinning, increased inputs of nutrients to the soil following a fire, or even flooding (Roberts 2004). Those species that are not able to adapt to these changes will no longer persist. A disturbance will allow early successional species, often referred to as pioneer species, to colonize these areas. Pioneer species take advantage of the often higher light levels and available nutrients. Over time shade tolerant species begin to dominate shifting the species composition from fast growing shorter stature species, to longer living slower growing species (Tilman 1985). The processes of species colonization and replacement are the main factors that determine species composition following a disturbance. With no disturbance in the community, early ecologists often assumed it would mature towards a 'climax community', *i.e.* in a steady state with resource demand by vegetation being balanced by the rate of resource supply(Clements 1916). Perhaps this vision is still held by some citizens or even professionals, but this is rarely achieved as eventually some form of disturbance will reset the stage of succession in the community (Gibson 1996).

Initial colonization of vegetation to a site following a disturbance depends on several factors including the degree and type of disturbance, the soil seed bank, proximity to seed source, size and number of seeds, and insect and animal transport of seeds (Mayer *et al*. 2004). For example, disturbances that result in a reduction of live or dead organic matter allows plants to colonize that eventually reduce the available light at the soil surface and the amount of nutrients and water available to other plants (Tilman, 1985). Some disturbance is required for the success of plants requiring a change in environmental conditions in order for dormant seeds in the soil to germinate (*i.e.* Jack pine requiring forest fire to allow seeds to be released from fruit) (Sousa, 1984). Most early succession species grow quickly, require fewer nutrients, are relatively short lived and statured compared with later successional species that tend to allocate fewer resources to dispersal and rapid growth, are able to grow in shade and can achieve greater heights and ages (Noble and Slatyer 1980; McCook 1994).

The pattern of succession varies between communities and it involves a number of species interactions and characteristics (*e.g.* competition, inhibition, differences in life traits and tolerance limits to environmental factors). However, over the short term succession in all communities like managed conifer plantations, is driven temporally by allogenic change. The interaction over time between species results in changes of dominance and species richness that in turn affect the diversity and abundance of species in the community overall. Depending on the stage of succession and the degree of disturbance these changes can take as little as a few days to millennia to occur (Burgess, 1960). In plant communities undergoing secondary succession these changes are often on the scale of years to decades, and sometimes centuries (Goldblum, 1998). Due to the lengthy time required to observe the changes in these communities, studies are often designed to compare sites within an area that are in different stages of succession. In these instances, the researcher is able to substitute space for time (Pickett, 1989) allowing for sequential snap shots of succession over different sites; these sites are referred to as chronoseres or chronosequences. The chronosequence approach of studying vegetation dynamics has allowed significant insights into the patterns and mechanisms that drive plant succession (Picket 1989; Roberts and Vankat, 1991; Garnier et al. 2004). This approach has been used in the design of this study and will be explained in detail in the methods section.

For my study, the red pine plantations are in a stage of secondary succession since the soil still has nutrients and a seed bank that will allow understory regeneration. Studies of ecological succession have led to the paradigm that ecosystems are open systems described by the second law of thermodynamics that are evolving toward a temporarily stationary state in its surroundings by consuming free energy through internal and external processes (Wurtz and Annila 2010). Hobbs and Norton (1996) describe ecosystems as dynamic and nondeterministic, and as such restoration of conifer plantations can be examined in relation to a range of potential outcomes. These outcomes can be influenced by many factors including previous land use history, the size of the plantation, and adjacent vegetation communities. Conifer plantations are found in a matrix of agricultural lands, and urban setting, and are fragmented by roads, natural forest stands, and other land uses (*e.g.* hydro corridors, railways, etc.). Therefore, the spatial dynamics influencing conifer plantations play a major role in the succession of the understory. The spatial dynamics and the processes driving colonization of the understory of conifer plantations can be explained in part by the Island Biogeography Theory described by MacArthur and Wilson (1963). This theory states that the number of species established on an island (or in the case of this study, a regenerating forest community) represents a dynamic equilibrium between the immigration of new colonizing species and the extirpation of previously established ones (MacArthur and Wilson 1963). Therefore understory succession is not only influenced by changes at the community scale, but is influenced by surrounding land uses and vegetative communities.

The natural turnover of species communities over time, that is the succession of the communities, provides the model that restoration ecologists attempt to mimic and accelerate (Cairns and Heckman 1996). Therefore, comparing the understory species composition in conifer plantation to a reference ecosystem model such as a natural forest, will help determine if the understory in conifer plantations is succeeding towards an understory composition of the reference system. A reference system is modeled based on knowledge of the site previous to alteration or on a nearby ecosystem of similar characteristics (SER 2004). The restored system is ultimately expected to replicate the attributes of the reference, and project goals and strategies are developed considering that expectation (Higgs 1997). Restoration ecology works to assist the process of succession usually with this end ecosystem model as the goal. The success of a project is not only based on the completion of the plan, but the ability of a site to sustain itself structurally and functionally without human intervention (SER 2004). It may take a site a few years to even centuries to reach this point, depending on the reference ecosystem being used and the degree of degradation to the site. Restoration of conifer plantations can speed up the increase of native diversity in the understory and more closely resemble the features and functions found in natural woodlands in Ontario.

In order to have a full understanding of how different restoration strategies in red pine plantations may progress and to have a better chance at achieving the goals of the restoration more information is needed on the long term succession of the understory in these communities. Studies have been established to examine the effects of various thinning regimes on the understory of conifer plantations (Ramovs and Roberts 2003; Zhu *et al.* 2003; Utsugi *et al.* 2006) and the use of these thinning regimes to achieve characteristics of a more natural forest (Parker *et al.* 2001; Aubin *et al.* 2008; Parker *et al.*, 2008). However, these are short term studies (< 20 years) and less is known on the long term (50-100 year) trajectory of conifer plantation restoration (Goldblum 1998; Parker *et al.* 2008). Studying the effects of conventional thinning regimes in conifer plantations on the understory vegetation and soil characteristics over decades to centuries can provide restoration ecologists with the information necessary to determine how to best manage these forests.

In place of a long term study of restoration of the understory of red pine plantations, my study examined the understory diversity in a chronosequence, including four age groups, of managed red pine plantations under the same management regime in forests owned by Simcoe County. Biophysical characteristics including light, woody regeneration, litter depth, and soil nutrients were gathered from replicates of each age group and from reference forests in order to determine how each variable changed and contributed to the succession of the understory diversity. Understory diversity was the main focus of the study since it is often used as an indicator of ecological integrity (Gilliam and Roberts 2003; Nilsson and Wardle 2005). This data was collected, analyzed and interpreted for plantation forest groups and the reference forests. The study elucidates how current management of the plantations can influence the succession of the understory and how the understory and the abiotic variables studied compare to reference forests.

The management and thinning regime of the red pine plantations in my study have resulted in an increase in understory diversity and tree regeneration. With each additional thinning cycle the density and regeneration of hardwood trees and the light regime in the understory more closely resembles that of a natural forest stand. Understory diversity and tree density are both increasing in the plantation groups. The composition of regenerating trees in the oldest plantation group is also similar to the reference group indicating the management of these red pine plantations will result in a community dominated by tree species found in natural forests of that area. However, understory species composition is still quite different between the plantations and the reference forest group. This indicates the understory is either slow to develop, is being inhibited by the abiotic conditions of the site, or the successional trajectory of the composition of understory species is moving in a difference direction. Soil characteristics in the plantation groups are also generally different than the reference forest group (*e.g.* the plantations have lower concentrations of nutrients in the upper 10cm of soil and the soils lack a defined profile). Previous land use and current management practices have resulted in soil conditions that differ in the plantations from the reference forest group. Whether there is an autogenic or allogenic influence on the succession of the understory, it is clear that the composition of the soil and particularly the understory vegetation in the oldest plantation groups remains notably different than that of the reference forest group.

If the goal is simply to increase diversity in the understory and encourage tree regeneration without consideration of understory composition, the current management regime is achieving that goal. However with a more recent focus on converting plantations to native forests and the need to improve ecological integrity of plantation forest stands through increasing diversity, there is more of a need to understand the variables driving the succession of the understory in conifer plantations. Considering the goal of ecological restoration is typically “to return an ecosystem to its historic trajectory” (SER 2004), the current management of these red pine plantations is not meeting this end. Therefore further considerations for ecological restoration would be required to achieve an understory composition similar to reference forest groups.

The purpose of the present study was to determine the effects of conventional thinning regimes on the succession of understory vegetation and soil characteristics in red pine plantations in southern Ontario over time. This outcome was motivated by the following research questions: *How do conventional thinning regimes for red pine plantations in southern Ontario affect the diversity of the understory vegetation and the regeneration of trees? What variables drive the change in understory vegetation in red pine plantations over time and how do they compare to native deciduous reference forests? And, how does the understory vegetation composition and diversity in managed red pine plantations compare to the understory of a reference forest?* Through answering these questions the aim is to 1) quantify and compare the understory vegetation diversity and composition among and between plantations and the reference deciduous forest group, and 2) determine if and how diversity is related to site variables such as light, substrate, and soil characteristics. This information will be used to build on previous studies in order to provide forest managers with more knowledge about the ecology of red pine plantations thereby facilitating more informed decisions regarding the future management of these forests and restoration of native floral diversity.

The scope of the present study was limited to forests of southern Ontario in Simcoe County, situated in the Great Lakes- St. Lawrence Forest region. Moreover, the plantations were focused on various ages of red pine stands that had been managed using the same thinning technique and regime. The reference forests were limited to relatively undisturbed native stands of deciduous forest that likely comprise the species composition of pre-settlement deciduous forests in the immediate area. The fieldwork methods were limited to understory (<1.5 m in height) plant diversity, woody regeneration, and light and soil characteristics. Finally, the scope of this project was limited to floral diversity and did not take into account diversity of fauna.

1.1 Summary

In considering the mechanisms driving understory succession in red pine plantations, several ideas have been discussed. Initial site conditions can differ depending on the previous land use history, including available nutrients and seed bank. Proximity to a local seed source and the size of the forest fragment will determine the colonization and richness of species. Disturbance as a result of thinning operations also impacts site environmental characteristics which will in turn influence the regeneration of species in the understory. Understanding the mechanisms of community change through time in the understory of red pine plantations requires knowledge of the nature and interaction of the plant populations, and the factors which influence those interactions. Once these mechanisms are better understood, management of red pine plantations whether for timber production or to increase biodiversity and native forest cover will be more successful.

2.0 CHAPTER 2 METHODS

2.1 Introduction to Fieldwork Methods

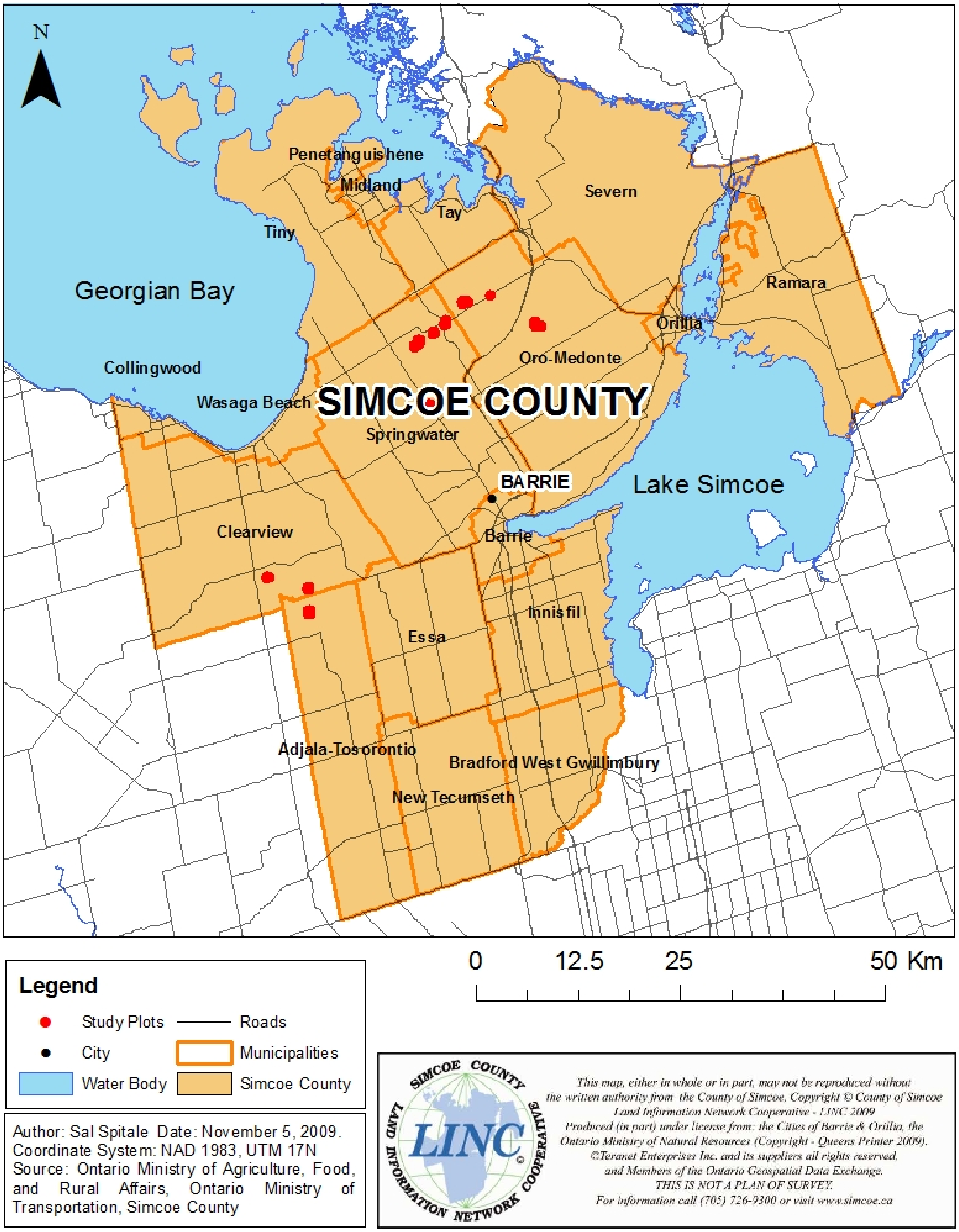
The goal of the field work was to collect biophysical data from the understory of managed red pine plantations in southern Ontario in order to explain, 1) how the understory vegetation changes over time; 2) what variables drive changes in understory diversity and composition; and 3) how the understory vegetation composition and diversity in managed red pine plantations compares to the understory of a reference forest. In place of a long term study sites of various ages (also known as a chronosequence) of plantations were selected essentially swapping space for time (Pickett 1989). Interest in increasing understory biodiversity and conversion to more 'natural forest' requires a comparison of the understory species composition with a reference forest. Natural forests (also referred to as reference forests) are described as being complex adaptive systems composed primarily of naturally regenerating native tree species (Aubin 2008). These forests exhibit a complex connectivity among their components, and are self-organized into hierarchies and cycles (Levin 1998; Holling 2001), that are expressed at three levels of diversity: structural, compositional, and functional (Noss 1990). Multiple reference sites were selected in this study in order adequately express the potentially wide range of variables expressed in these communities (Halpern 1989; Pickett & Parker 1994; Ruiz-Jaén & Aide 2005). Reference forests were chosen based on composition of vegetation, size, shape, known land-use history, and level of disturbance. Forests selected were those that contained mainly deciduous trees in the overstory such as red oak (*Quercus rubra* L.), sugar maple (*Acer saccharum* Marshall *var. saccharum*) American beech (*Fagus grandifolia* Ehrh.), and hop-hornbeam (*Ostrya virginiana* (Miller) K. Koch). The forests appeared unmanaged, had not been recently selectively harvested and had a diverse understory. These forests were also large enough to sustain interior forest habitat (at least 100 meters from the edge).

Evaluating impacts of silviculture treatments and thinning regimes on understory vegetation is most often achieved by using the chronosequence technique of sampling vegetation in stands that are in varying stages of management (Smith *et al.* 2008). Some considerations to this approach for site selection were that sites have comparable initial conditions (*e.g.* soil type, moisture regime), similar land-use history, and have been managed using the same silviculture method and thinning regime (Halpern 1989).

2.2 Boundaries and Study Scope

The scope of this study primarily concentrated on the understory vegetation and abiotic variables influencing the growth of plants in the understory of the plantations and to further compare these variables with those of the reference forests. The variables measured include diffuse non-interceptance (DIFN), tree relative importance and density, and soil moisture, bulk density, pH, and macronutrient content. This study primarily focused on the temporal changes in understory diversity and avoided spatial changes in vegetation and climate throughout the forest. By collecting data from the central hectare of each study plot, located no closer than 100m to the edge of the forest, edge effects and spatial variation could be minimized. Edge effects occur where there is a sharp boundary between forest edges and a neighbouring community. The sharp boundary of forest to open habitat affects air temperature, vapour pressure deficit, soil moisture, light intensity and levels of photosynthetically active radiation (PAR) at forest edges (Forman 1995). Although edge effects may penetrate deeper into the forest, due to the sizes of the forests available for study 100m was deemed appropriate as this distance is often considered far enough to minimize edge effects (Austen *et al.* 2001; Devlaeminck *et al.* 2005; De Schrijver *et al.* 2007; Wuyts *et al.* 2008). Also, by focusing on the interior of the forest germination and regeneration of wind dispersed seeds would be minimized therefore minimizing the spatial variation in understory plant regeneration. The spatial component was not studied due to the increased complexity and time that would be necessary to fully examine understory vegetation regeneration and the variables driving succession.

The red pine plantations and reference forests examined are located within a 30 km radius of Midhurst, Ontario, in Simcoe County (Figure 1), and are all managed and owned by Simcoe County. The study was carried out during the spring (late April – early May), summer (late June – early July), and fall (early October) of 2009 in order to account for seasonal differences in plant diversity. A background discussion of the fieldwork methods used in this study is presented in this chapter, as well a description of each field site and the reference ecosystem.



Author: Sal Spitale Date: November 5, 2009.
Coordinate System: NAD 1983, UTM 17N
Source: Ontario Ministry of Agriculture, Food, and Rural Affairs, Ontario Ministry of Transportation, Simcoe County

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Figure 1. Study plots located within Simcoe County, Ontario. A total of 15 study plots, illustrated in red, are located within a 30 km radius of Midhurst, Ontario.

2.3 Study Design

In order to capture the change in the dynamics of the understory in managed red pine plantations over time four age groups were selected based primarily on the thinning regime and time since plantation establishment. Each age group consisted of three replicates from a different location all surveyed in 2009. The first plantation group consisted of stands that were established during 1978-1981 (surveyed 28-31 years since planted) and had not been thinned. The second group was planted during 1967-1971 (surveyed 38-42 years since planted) and had undergone one thinning. The third group consisted of plantations established between 1949 and 1961 (48-60 years since planted) and had been thinned two to three times. And the fourth group contained stands that were established between 1927 and 1932 (77-82 years since planted) and had received four or more thinning treatments and were nearing the end of their thinning cycle. Therefore there were a total of 12 plantations examined - three replicates for each of the four age groups. These plantations were compared to three replicates of a reference deciduous forest group. In total there were five forest groups, each consisting of three replicates (Table 2).

The vegetation in the understory was examined three times over the course of the growing season in order to record plant species that are found only during one of those times of year (Tremblay and Larocque 2001). Understory differences in light were also measured during each season for each forest. Soil samples and measurements were taken only once as examining seasonal variation in soil physical properties and nutrient levels would have been beyond the scope of this study which was to look at changes in the understory in plantations over the decades of management.

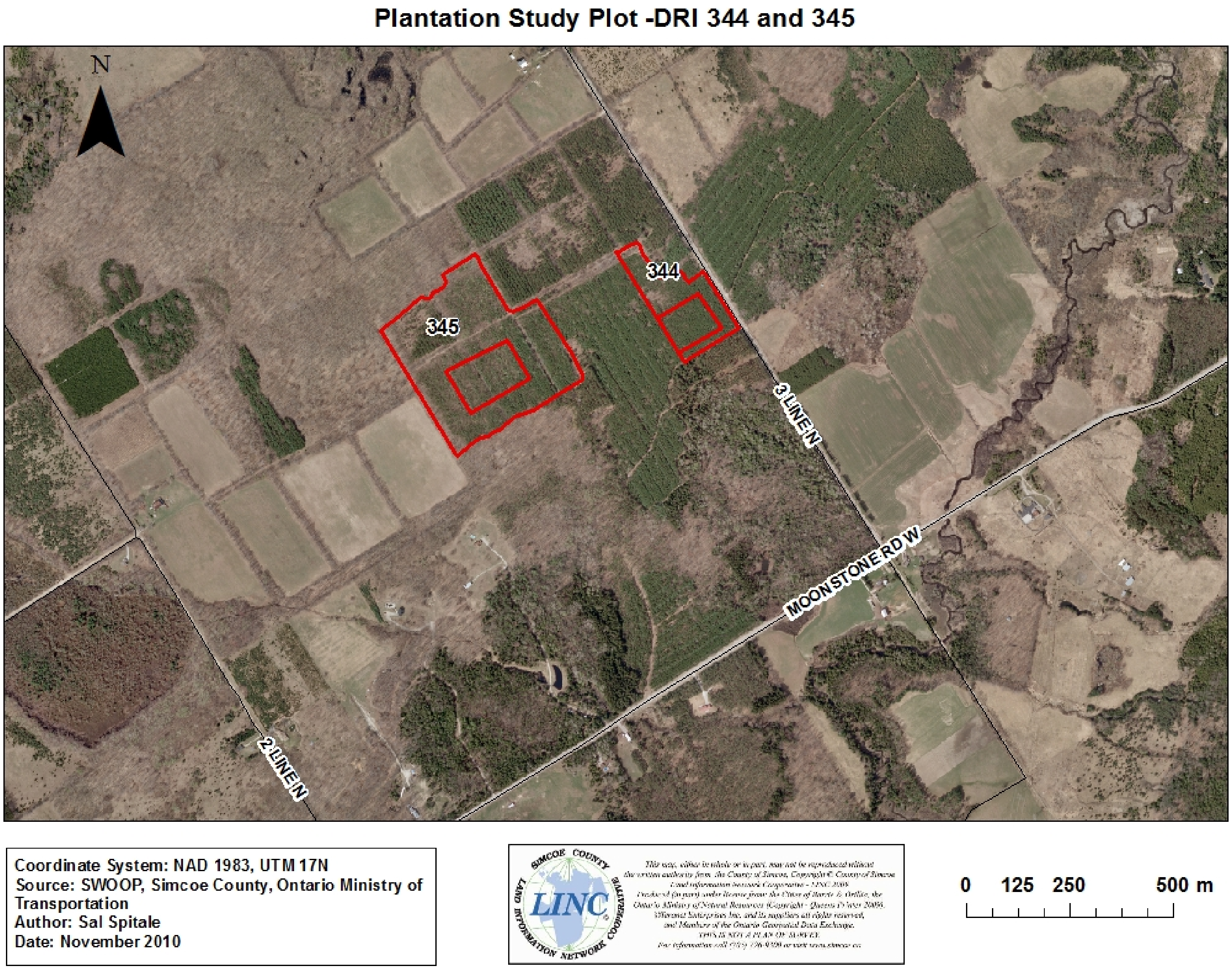
2.4 Site Selection

Simcoe County was chosen as a study area partly because it is in the central portion of southern Ontario and the results from this study can be compared to other areas within southern Ontario. Simcoe County is located in southern Ontario, with Georgian Bay bordering the northwest corner and Lake Simcoe along the eastern boundary. Simcoe County covers an area of

4,840.56 km^2 (Statistics Canada 2001) and includes 16 towns and townships. The plantations and forests managed by Simcoe County are also ideal to study because they have been well documented, have been tended using the same thinning regime, and include a large number and sizes of red pine stands. The earliest plantations in Simcoe County were established in 1922 and became the first 'Agreement Forest', formally managed by the Ontario Ministry of Natural Resources up until 1996, when they were taken over by the County (Simcoe County 2011). Simcoe County has approximately 6, 070 ha of conifer plantations, many of which are red pine (Simcoe County 2011). The close proximity of a large number of sites at various stages of management allowed for a more accurate comparison between sites and a higher likelihood of abiotic and biotic components to be similar across sites. The forest plots studied in Simcoe County are summarized in Table 2 including information on the location (lat/long), size (ha), age, dominant tree types, reference or plantation forest, and soil series and type. The aerial image of each study forest and the central hectare study plot are shown in Figures 2-11

Table 2. Information on study site locations.

Tract Name	**Forest Type**	**Year Planted**	**Size (Ha)**	**Dominant Tree Species**	**Longitude**	**Latitude**	**Soil Series**	**Soil Type**
Douglas 100b	Reference	1892	8.2	sugar maple, oak	79°37'59.745"W	44°36'4.385"N	Tioga	Loamy Sand
Moon 309	Reference	1895	20.1	sugar maple, basswood	79°34'46.116"W	44°41'5.688"N	Osprey	Loam
Orr Lake Main 76a	Reference	1897	7.2	sugar maple, red oak	79°47'49.174"W	44°35'45.182"N	Tioga	Sandy Loam
Orr Lake 61a	Plantation	1927	14.5	red pine	79°46'40.49"W	44°36'21.736"N	Tioga	Sandy Loam
Stony 82b	Plantation	1932	11.3	red pine	79°49'31.542"W	44°34'58.414"N	Tioga	Sandy Loam
Stony 81b	Plantation	1932	10.1	red pine	79°49'21.586"W	44°35'2.7"N	Tioga	Sandy Loam
Douglas 98a	Plantation	1949	18.4	red pine	79°38'25.675"W	44°36'12.242"N	Tioga	Loamy Sand
Cummings 161e	Plantation	1951	11.2	red pine	79°48'18.988"W	44°30'58.852"N	Wyevale	Gravelly Sandy Loam
Brentwood 336d	Plantation	1961	9.3	red pine	79°59'42.544"W	44°19'1.139"N	Tioga	Loamy Sand
Modrits 343b	Plantation	1967	12.9	red pine	79°59'39.761"W	44°17'18.831"N	Alliston	Sandy Loam
Lawden 359b	Plantation	1968	12.5	red pine	80°3'24.35"W	44°19'43.517"N	Tioga	Loamy Sand
Stoney 339a	Plantation	1971	14.5	red pine	79°49'7.7"W	44°35'10.966"N	Tioga	Sandy Loam
Barr 410c	Plantation	1978	2	red pine	79°42'31.294"W	44°38'9.638"N	Vasey	Sandy Loam
DRI 344h	Plantation	1981	3.5	red pine	79°44'37.919"W	44°37'45.781"N	Tioga	Sandy Loam
DRI 345i	Plantation	1981	12.6	red pine	79°45'0.338"W	44°37'41.892"N	Tioga	Sandy Loam



Coordinate System: NAD 1983, UTM 17N
Source: SWOOP, Simcoe County, Ontario Ministry of Transportation
Author: Sal Spitale
Date: November 2010

Figure 2. Plantation study plot at DRI tract (est. 1981) in Simcoe County. The outer red line delineates the tract boundary and inner red line delineates the 1 ha study plot.

Coordinate System: NAD 1983, UTM 17N
Source: SWOOP, Simcoe County, Ontario Ministry of Transportation
Author: Sal Spitale
Date: November 2010

Figure 3. Plantation study plot at Lawden tract (est. 1968) in Simcoe County. The outer red line delineates the tract boundary and inner red line delineates the 1 ha study plot.

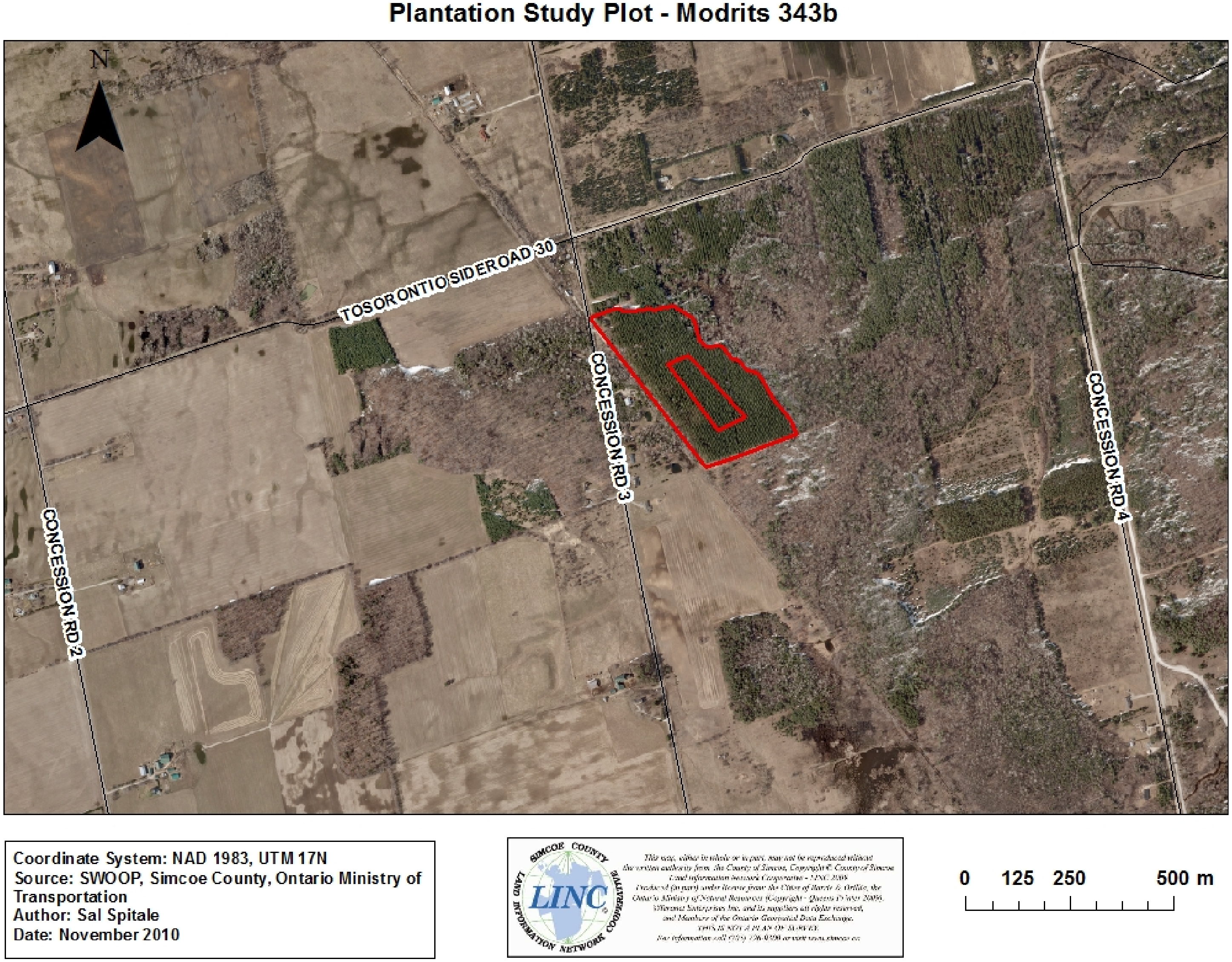


Figure 4. Plantation study plot at Modrits tract (est. 1967) in Simcoe County. The outer red line delineates the tract boundary and inner red line delineates the 1 ha study plot.

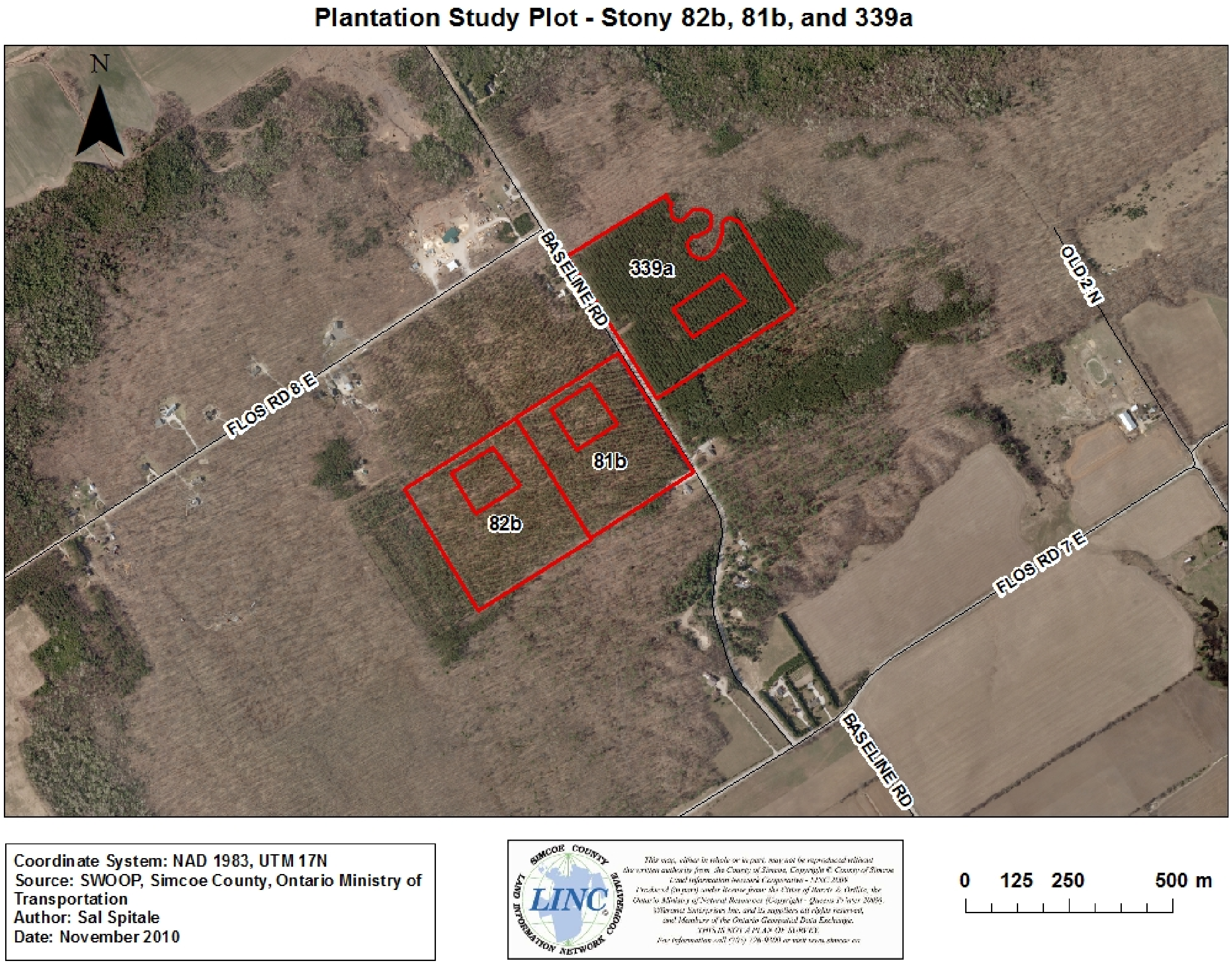


Figure 5. Plantation study plot at Stony tract (82b and 81b est. 1932; 339a est. 1971) in Simcoe County. The outer red line delineates the tract boundary and inner red line delineates the 1 ha study plot.

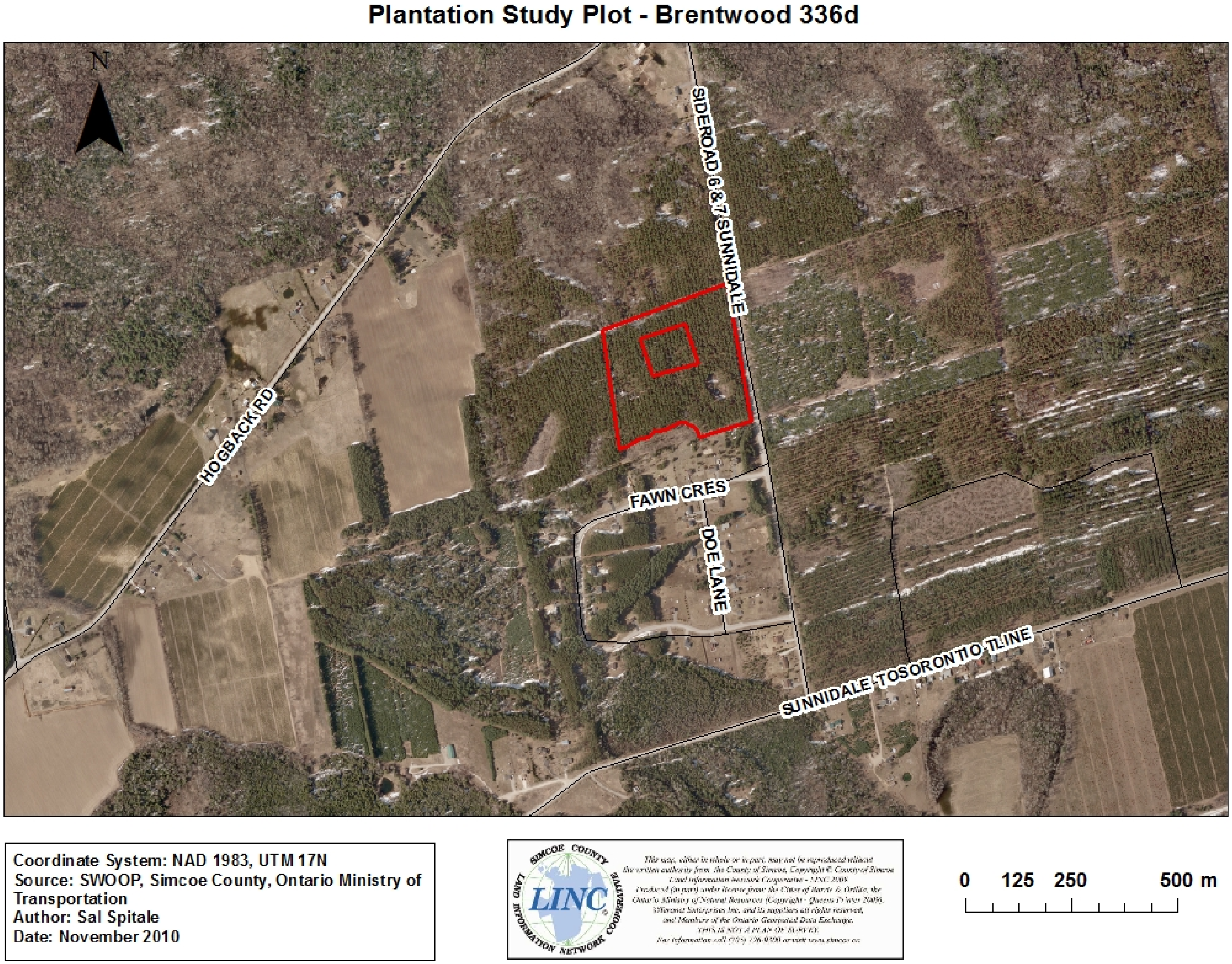


Figure 6. Plantation study plot at Brentwood tract (est. 1961) in Simcoe County. The outer red line delineates the tract boundary and inner red line delineates the 1 ha study plot.

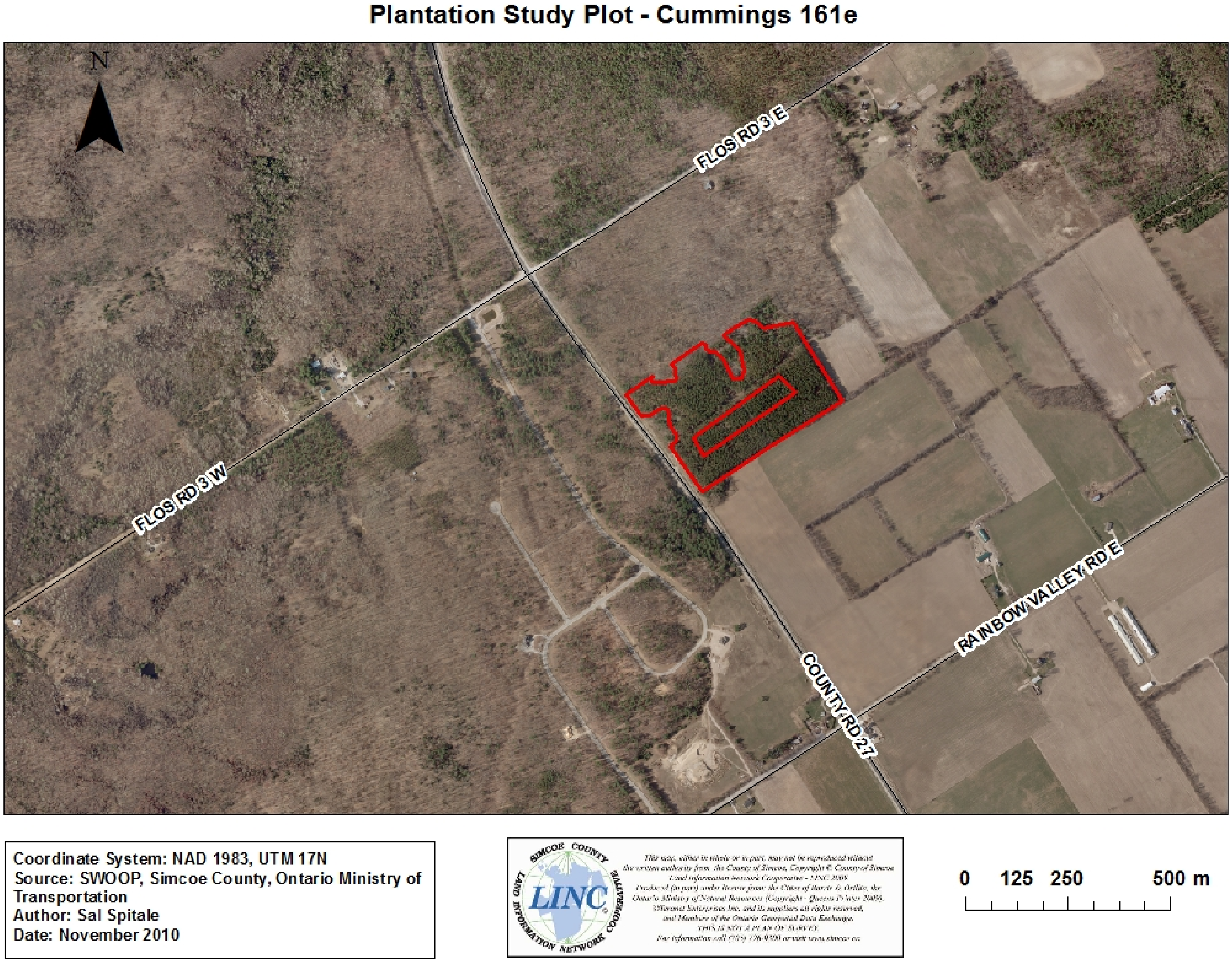
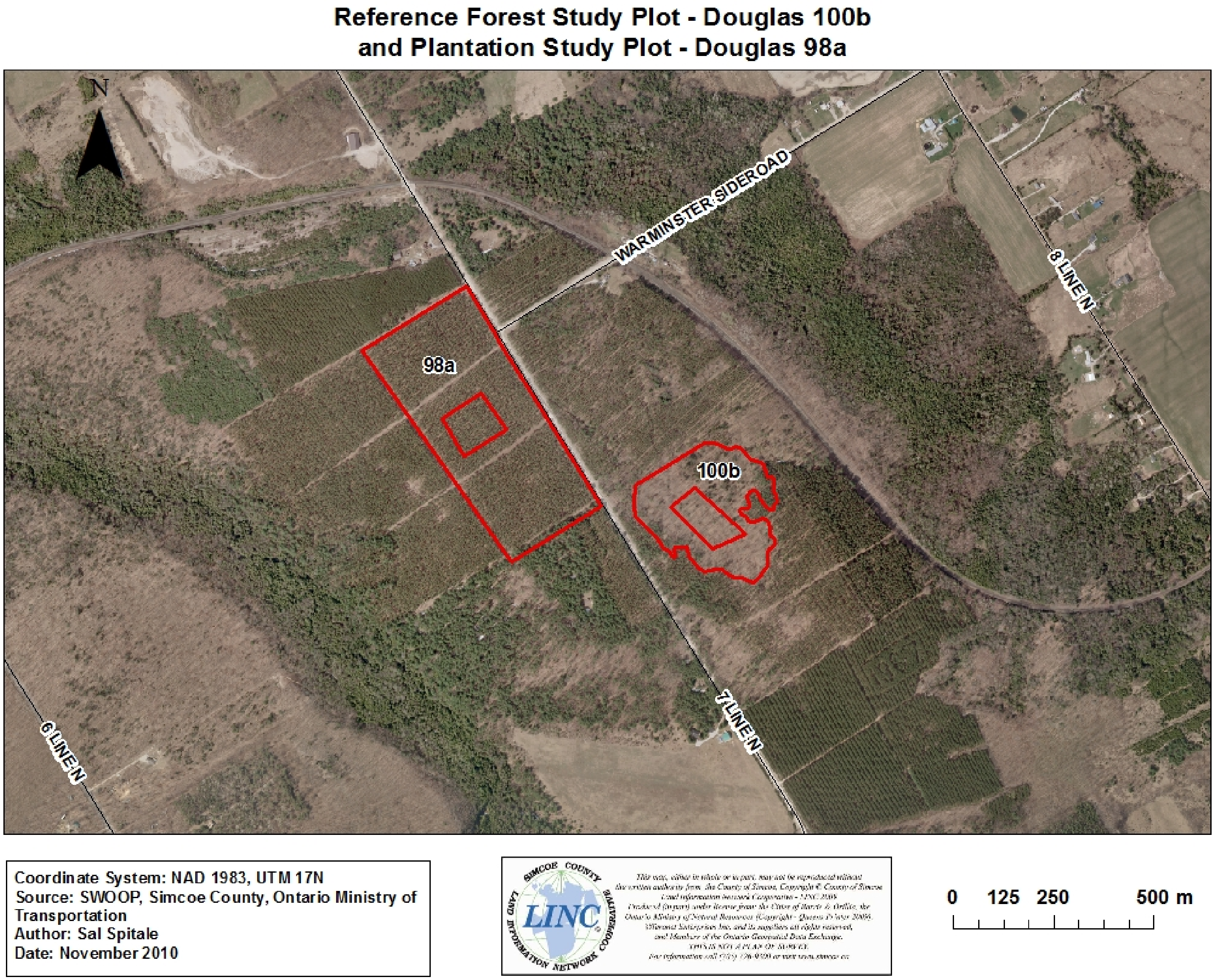


Figure 7. Plantation study plot at Cummings tract (est. 1951) in Simcoe County. The outer red line delineates the tract boundary and inner red line delineates the 1 ha study plot.



Reference Forest Study Plot - Douglas 100b and Plantation Study Plot - Douglas 98a

Coordinate System: NAD 1983, UTM 17N
Source: SWOOP, Simcoe County, Ontario Ministry of Transportation
Author: Sal Spitale
Date: November 2010

Figure 8. Reference forest (100b) and plantation study plot (98a) at Douglas tract (98a est. 1949; 100b est. 1892) in Simcoe County. The outer red line delineates the tract boundary and inner red line delineates the 1 ha study plot.

Figure 9. Plantation study plot at Orr Lake tract (est. 1927) in Simcoe County. The outer red line delineates the tract boundary and inner red line delineates the 1 ha study plot.

Figure 10. Reference forest study plot at Orr Lake Main (est. 1897) tract in Simcoe County. The outer red line delineates the tract boundary and inner red line delineates the 1 ha study plot.

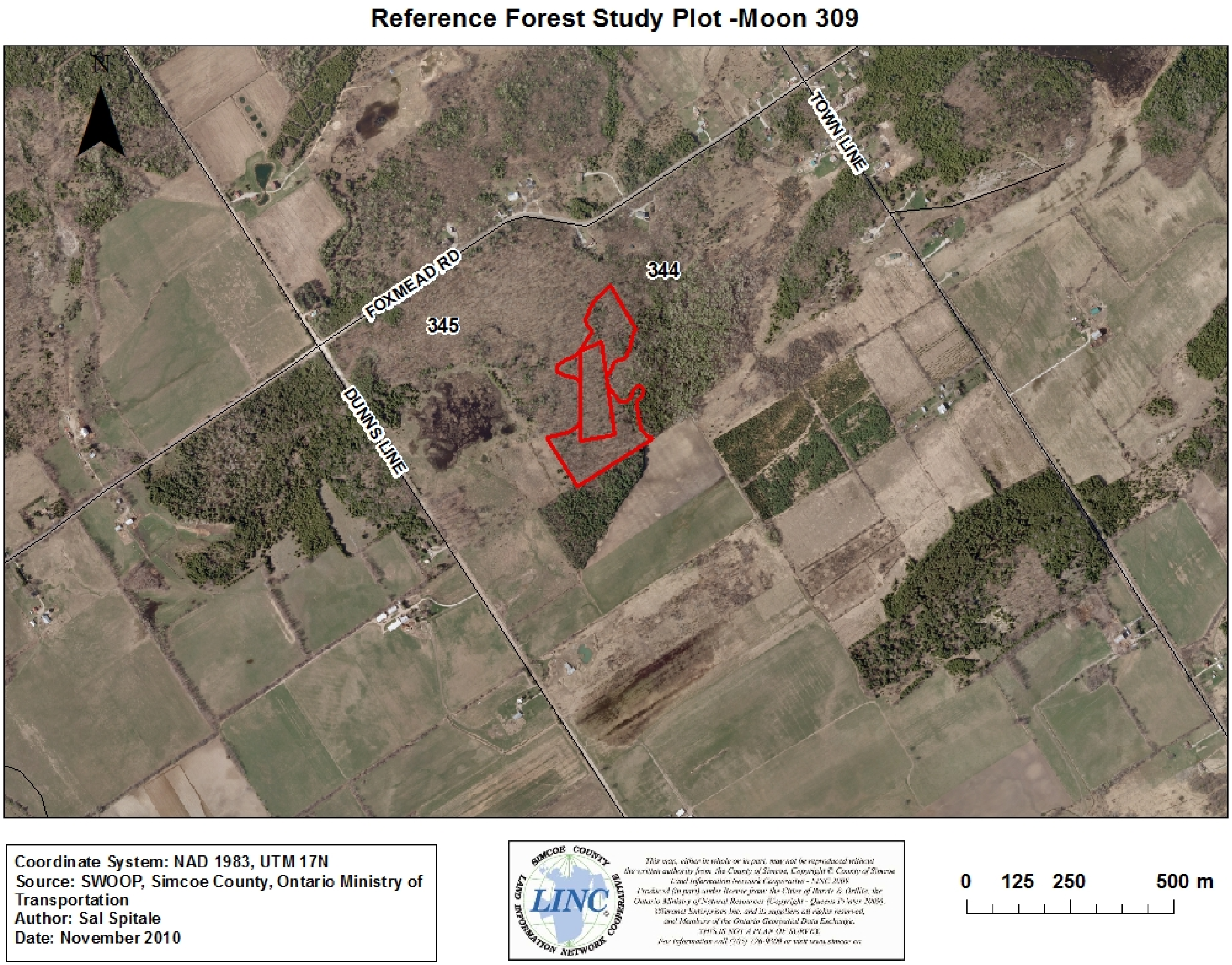


Figure 11. Reference forest study plot at Moon tract (est. 1895) tract in Simcoe County. The outer red line delineates the tract boundary and inner red line delineates the 1 ha study plot.

2.4.1 Simcoe County Physiography

Simcoe County has a varied landscape that is mainly undulating but includes rugged Niagara Escarpment in the west, and rolling hills in the east with changes in elevation from about 485 to 180 meters above sea level (Hoffman *et al.* 1990). The underlying geology of the County includes rocks of the Ordivician, Silurian, and Precambrian ages that are primarily composed of limestones of the Black River, Trenton, Medina, Cataract, and Lockport formations, with layers of shales of the Utica, Queenston, and Richmond formations (Hoffman *et al.* 1990). Surficial geological deposits are primarily composed of glacial materials that have developed the overlying soils that are found to be coarse textured, consisting of a mixture of boulders, cobbles, gravel, sand, silt and clay (Hoffman *et al.* 1990). The soils underlying the study sites are listed in Table 2.

The forests managed by Simcoe County cover an area of over 11,700 ha of which approximately half are naturally regenerated deciduous forests and half are coniferous plantations (Simcoe County 2011). Trees grown in plantations are mainly red, white, and jack pine,and white (*Picea glauca* Moench (Voss)) and Norway spruce (*Picea abies* (L.) Karsten), while natural forests mainly consist of sugar maple, red oak, American beech, largetoothed aspen (*Populus grandidentata* Michx.), white ash (*Fraxinus americana* L.), black cherry (*Prunus serotina* Ehrh.), white cedar (*Thuja occidentalis* L.), eastern hemlock (*Tsuga canadensis* L. Carriere*)*, and balsam fir (*Abies balsamea* L. Miller) (Simcoe County 2011). The plantations are planted in rows about 1.8-2.4 apart with seedlings planted every 1.8 meters. Some of the oldest tracts of deciduous forest managed by Simcoe County were planted in 1862 (Simcoe County 2009).

Thirty year climate normals derived from Environment Canada (2010) from 1971-2000 give a daily mean temperature of 6.6°C (SD ± 1.5°C), ranging from -7.8°C in January to 20°C in July. There is an annual precipitation of 888.3mm, of which 675 mm/year is rain and 212 cm is snow. The weather was recorded at the Essa Ontario Hydro Transformer Station (44° 21.000' N, 79° 49.200' W) in Barrie, central to the study sites, and includes data from 1971 to 2000, less one year (due to missing data).

2.5 Field Work

2.5.1 Assessing Understory Vegetation

A three season inventory of vascular plants (herbs, grasses, ferns, shrubs, trees) up to 1.5 meters in height was conducted. Stratified random sampling of twenty $1m^2$ quadrats were examined within each of the twelve plantations and three reference forests in order to determine understory plant diversity. This method of sampling allows for faster sampling of an area and captures a random sample of the species present. A disadvantage to this method is that when low sampling intensities are produced, the results may be subject to local clustering and provide biased results (Smartt and Grainger 1974). However, if the number of sample points are high enough or the area studied is smaller, random sampling estimates will be more accurate than systematic sampling (Smartt and Grainger 1974). Random sampling of vegetation is also necessary in order to meet the assumptions of independence imposed by statistical analysis (Miandonald and Braun 2010). This was achieved by assigning a distance in meters between each of four transects for each plot using a random number generating program. Randomly generated numbers were then used to determine five sampling points along each of the transects for a total of 20 randomly selected sampling locations. This procedure was used for each site during each season to ensure each location was randomly selected. At each sampling location a one square meter quadrat was established. In each quadrat twenty points were located using a random drop of a pencil to record the species or ‘0’ if no species was found at that point. Therefore, for each site, 400 points of data were collected including the species name or a ‘0’ if no species was present.

The materials used in this analysis of the understory vegetation included the following: a compass to delineate transects, a GPS unit to orient within forest plots, flagging tape, re-sealable plastic bags to collect and store unidentified plant species, a $1m^2$ wooden quadrat, a plant field guide to aid in the identification of unknown species, and datasheets for recording observations.

2.5.2 Assessing Regeneration of Woody Vegetation

Understory tree regeneration was assessed by using a point-centred quarter technique as described by Mitchell (2007) in order to determine the diversity, relative importance, and density. Along four transects, each 20 meters apart, five sampling points were established, also twenty meters apart, for a total of twenty sampling points. At each point a quadrant was established with the axes laid parallel and perpendicular to the transect direction. Within each quarter of the quadrant the closest tree to the centre of the quadrant within a 10 meter radius was identified. The distance of that tree to the centre of the quadrant was recorded as was the diameter at breast height (d.b.h.) (1.34 m). In addition, the nearest sapling to the centre was identified. A tree was characterized as a woody plant having greater or equal to a d.b.h of 10 cm and a sapling measuring greater than or equal to 4 cm but less than 10 cm. Where a tree or sapling overlapped between sampling points, that tree was only included in the results of one of those sampling points. If a tree was found to have more than one trunk, the average distance to the centre of the quadrant and the average d.b.h. of those trunks was recorded.

The materials used in the analysis of the regeneration woody vegetation included the following: 30m measuring tape, d.b.h. tape, a calliper, and datasheets for recording measurements.

2.5.3 Assessing Understory Light Characteristics

Understory light characteristics were measured using a Li-Cor LAI 2000 hand held device. The LAI 2000 is capable of measuring leaf area index (LAI), and diffuse non-interceptance (DIFN). LAI is measured as the projected one-sided leaf surface area per unit ground surface (Deblonde *et al.*1994), and DIFN is a measure of the fraction of the sky visible to the sensor. Hanan and Begue (1995) found that photosynthetically active radiation (PAR), *i.e.* solar radiation between 400 and 700 nm, estimated from DIFN values closely simulate daily temporal variations of light. The value produced for DIFN ranges between zero (no sky visible to the sensor) and one (no foliage visible to the sensor) (Li-Cor Inc. 2000) and is presented as the percentage (%) of sky visible to the sensor. In essence, the DIFN is an indicator of "canopy light absorption" or conversely, the amount of light able to penetrate the canopy. Therefore, the higher the DIFN, the more light is available for understory vegetation.

At every other quadrat location (used for plant identification) a Li-Cor LAI 2000 hand held device was used to measure LAI. This device works by measuring the attenuation of diffuse sky radiation at five zenith angles simultaneously through the lenses of the sensor (Li-Cor Inc. 1992). The device determines the mean tilt angle (MTA) in degrees and measures LAI. Canopy transmittance values are then calculated, which are used to determine the amount of foliage impeding the penetration of light to the forest floor. The calculations of foliage include several assumptions:

1. The foliage is black – that is, it is assumed the below canopy readings do not include radiation or transmittance that has been reflected by the foliage;
2. The foliage is randomly distributed;
3. The foliage elements are small in relation to the non-foliated space; and
4. The foliage is azimuthally randomly oriented (Li-Cor Inc. 1992).

DIFN is in effect a representation of canopy structure because it combines LAI and MTA into one number (Li-Cor Inc. 1992). In terms of canopy-absorption DIFN is an indicator of the absorption of diffuse, short-wave (<490 nm) radiation.

The methods followed were those described in the instruction manual (Li-Cor Inc, 1992) included with the device. The device was programmed to take the first reading in an open area, ten readings under the canopy, and one final reading in the open. This was done to compare open canopy to the mean of ten readings under the canopy, which are all used to calculate DIFN.

Although ideal conditions for recording DIFN using the LAI 2000 are days with a solid cloud cover (LI-COR Inc. 1992; Messier and Puttonen 1995; Gendron *et al.* 1998), the measurements recorded during this study were recorded on days with a variety of cloud cover conditions, including clear, partly cloudy, and complete cloudy. In order to adjust for the amount of cloud cover, a lens view cap was used that shades a portion of the lens depending on the amount of cloud cover. When the sky was clear a 270° view cap was used with all readings being taken with the sun to the back and the resulting shadow being cast over the lens. On partially cloudy days a 180° lens cap was used following the same method.

The materials used in the analysis include the following: an LAI 2000 Plant Canopy Analyzer consisting of the control unit (computer component) and optical sensor, lens caps, compass and GPS unit for orienting within forest plots.

2.5.4 Assessing Soil Characteristics

Soil was sampled from three random locations within the study area of each plantation and reference forest. An 80-100 cm pit was hand shovelled at each location. Within the pit a sample was taken at 0-10 cm, 10-20 cm, 20-40 cm, and 40-60 cm depths with special care not to cross-contaminate samples. Sampling by depths rather than horizons is useful for chronosequence studies where sites vary in age and include reference sites (Carter and Gregorich 2007; Walker *et al* 2010). Each sample was placed in a re-sealable plastic bag and clearly labelled. A 10% hydrochloric acid (HCl) solution was used to test for the presence of carbonates in the soil by placing a drop of the solution a various depths in order to determine the depth at which free carbonates were detectable. Where effervescence (*i.e.* the bubbling; hissing or foaming resulting from the reaction of the acidic HCl solution with basic carbonates) was observed the depth was recorded.

The number of pits sampled at each site was chosen based on the time required to dig each pit and take samples and the large expense to analyze the soil. Ideally, a larger number of pits would have been selected in order to capture the true variability of soil characteristics within sites and detect statistical differences between sites. For example, 1 to 12 samples per site were found to provide a 10% margin of error for mean pH and moisture in mountain soils studied by Ike and Clutter (1968); however, for the same margin of error 15 to 32 samples were required for available P and exchangeable K concentrations, 14 to 76 samples for exchangeable Mg concentrations, and 507 for exchangeable Ca concentrations. Similar variations in sample sizes were found by Quesnel and Lavkulich (1980), Arp and Krause (1984), Van Wesemael and Veer (1992) in their studies. Recognizing the limitations in sample size, the previous land use of plantations forests may have resulted in homogenizing of the soil through tillage practices

(Robertson *et al.* 1993, Paz-Gonzalez and Taboada 2000, Paz-Gonzalez *et al.* 2000). Similarly, there will likely be a high variability between samples in the reference forests due to previous land use history (*e.g.* selective logging) and differences due to location, composition of vegetation, and parent material. Therefore, the results of this study are expected to provide a general picture of the soil physical and chemical properties that can be used to help explain the changes in plant diversity over time in the understory.

The materials used to collect soil samples included the following: a spade for digging soil pits, measuring tape, a small trowel for scraping the soil profile and collecting samples, an aluminum corer of known dimensions for collecting a sample to determine bulk density, a rubber mallet for hammering the corer into the soil profile, re-sealable plastic bags to store samples, an Acculab VIC -612 (610g capacity x 0.01g readability) portable field scale, and datasheets to record the wet field weight of each sample.

2.5.5 Soil pH

The pH of forest soils plays an important role in the availability of nutrients to plants. Soil pH, or the measure of acidity of soil in a water suspension, is an empirical index of the amount of free H^+ in solution (Binkley and Richter 1987). Soil pH can affect the concentration of available nutrients and is directly related to the cation exchange capacity (CEC) - the measure of the amount of base cations (*e.g.* Ca^{2+}, K^+, and Mg^{2+}) that may be adsorbed to the surface of soil particles (Reed and Mroz 1997). Typically, a decrease is soil pH will result in a loss of CEC leading to a loss of base cations (Lukac and Godbold 2011). As much as pH affects the vegetation by limiting available nutrients, the vegetation affects the pH whether by the addition of acidic leaf litter, or by the buffering capacity of an increase in organic matter also through addition of leaf litter (Finzi *et al.* 1998). Therefore measuring pH provides insight into the interaction between the soil and vegetation and the impact the soil has on the regeneration of the understory plants.

The pH of the soil samples was measured potentiometrically using a VWR symphony SB80PC pH and conductivity meter following the Methods Manual for Forest Soil and Plant Analysis (Kalra and Maynard 1991). The pH meter was calibrated using a buffer solution of pH

4, 7, and 10. Ten grams of 2mm sieved air-dried soil was mixed with 40 ml of distilled water (1:2 soil-to-water ratio) into a beaker. The solution was stirred four to five times over a thirty minute period. The suspension was left to settle for another 30 minutes. The electrode of the pH meter was placed in the supernatant solution. Once the meter had stabilized, the reading was recorded.

2.5.6 Soil Bulk Density

Bulk density, the weight of soil per unit volume, is an important measure of soil quality since it affects plant root penetration, water- and air-filled pore space, and biological activity (Karlen *et al.* 1997). Bulk density in forest soils can vary depending on soil type, amount of organic matter content, and compaction due previous land uses (machinery in tillage of farmed areas) or current silvicultural practices. Soil compaction is a major concern to the quality and structure of soil where conventional farming practices take place (Soane and van Ouwerkerk 1994). In addition, soil compaction can be caused by logging or site preparation practices (Aust *et al.* 1995). Therefore it is conceivable to postulate that previous farming practices and current silviculture techniques may influence the bulk density of the soil.

The methods to determine bulk density were adapted from the General Preparation of Forest Mineral Soil Samples for Physical and Chemical Analysis (OFRILS 2009). In order to determine bulk density (BD) a sample of soil was extracted at each depth using a hollow aluminum core with a diameter of 44.2 mm and a height of 50 mm. The core was carefully pressed into the vertical face of the soil from within the soil pit. Care was taken to remove the core with the contained soil intact. The sample was scraped from the core into a re-sealable bag of known weight. The weight of the sample was taken immediately in the field using an Acculab scale VIC 612, accurate to two decimal places. The weight of the re-sealable bag was subtracted from the total weight giving the wet weight of the soil. The samples were later transferred to an aluminum dish of known weight and placed in a drying oven at 105°C for 48 hours. The samples were then weighed and the results recorded and subtracted from the weight of the aluminum dish. Bulk density was calculated as:

$$\text{BD} = \frac{\text{mass of dry soil (g)}}{\text{Volume of the core (ml)}}$$

2.5.7 Soil Moisture

Soil moisture, often measured as percent moisture, is an important indicator of soil quality since it directly affects the growth of plants through water uptake, as well as the rate of microbial activity and related cycling of nutrients (Pastor and Post 1986).

The methods to determine percent soil moisture were adapted from the General Preparation of Forest Mineral Soil Samples for Physical and Chemical Analysis (OFRILS 2009). Field soil moisture was measured as a percent of the soil mass recorded during the procedures for collecting samples for bulk density. The field wet-weight of the soil was recorded previously for the bulk density samples. The dry weight of those samples was also recorded during the bulk density analysis. The values of percent soil moisture content were calculated as:

$$\%\ \text{soil moisture content} = \frac{\text{wet weight (g)} - \text{dry weight (g)}}{\text{Dry weight (g)}} \times 100$$

2.5.8 Litter Depth

The depth of the forest floor litter layer, characterized as the ‘L’ layer within the ‘O’ (organic) horizon according to the Canadian System of Soil Classification (Soil Classification Working Group 1988), was measured by carefully extending a ruler into the litter layer adjacent to the pits where soil was sampled. The reading was recorded as part of the data collected for each soil pit. Litter depth was recorded for each soil pit for a total of three litter depth measurements per forest plot.

2.5.9 Soil Nutrient Analysis

Soil nutrient analysis was conducted by the Ontario Forestry Research Institute Laboratory Services (OFRILS) in Sault-Ste. Marie, Ontario. The soil was analyzed for total carbon (%), total nitrogen (%), calcium (mg/Kg), potassium (mg/Kg), magnesium (mg/Kg), and phosphorus (mg/Kg). Prior to shipment of the samples to OFRILS the soil was air dried for 28 days in a climate controlled room at ~21°C and sieved to 2 mm. At least 80 g of each sample was placed in a transparent snap cap vile. The procedures used for each of the soil analyses are listed in Table 3.

Table 3. Soil analysis procedures, apparatus, and source of methods used by OFRILS in the analysis of the soil nutrient content.

Soil Analysis	**Procedure**	**Apparatus**	**Source**
Total Nitrogen/Carbon (%)	Simultaneous analysis of total carbon and total nitrogen in soils by dry combustion and thermal conductivity detection method	Elementar - VarioMax CNS Analyzer	OFRILS 2010.
Calcium, Potassium, and Magnesium (mg/Kg)	Ammonium Acetate-Extractable Elements (pH 7)	SPECTRO Genesis OES with XYZ Autosampler	Carter and Gregorich 2007.
Phosphorus (mg/Kg)	Easily Extractable Phosphorus by Bray and Kurtz No. 1 Method (Bray P-1)	Technicon TRAACS 800 Autoanalyzer with linear autosampler	Kalra, and Maynard 1991.

2.6 Issues Encountered During Field Work

Unexpected thinning took place in two plantations after the spring inventory was completed. In Waverly, the plantation was selectively thinned following the spring inventory. This resulted in the trampling and damage to understory vegetation by the machinery. This plantation was substituted by Stoney 82b, which was in close proximity and age (79 vs 77 years since planted). The understory vegetation and characteristics also appeared very similar. The second unexpected thinning took place in Stoney 339. Heavy snow fall from the previous winter resulted in broken tops to individual trees throughout the plantation. Following the spring survey the plantation was thinned in order to remove the damaged trees resulting in small scattered openings in the canopy. Sampling of vegetation, LAI, and soil in Stoney 339 occurred from randomly selected areas where no thinning had occurred.

At each site three soil pits were dug for collection of soil samples, however digging soil pits at Moon309 proved to be quite challenging due to the high content of stones and coarse unconsolidated parent material in the soil. The effort and time required to dig soil pits at this site resulted in samples being collected from only two soil pits.

2.7 Procedures used to record and manage data

The varying types of data and methods used required several procedures to record and organize the data. Data was recorded on specifically designed datasheets to ensure information was recorded accurately. Following each field visit the data was transferred into a database in Microsoft Excel^{TM}. Separate files were created for each site, type of analysis, and where applicable, separate worksheets created for each season. This allowed for later manipulation and analysis of the data. Where identification of plant species was not possible due to a lack of distinguishable parts (*i.e.* only basal leaves visible of immature herbaceous plants in the spring), the species was still recorded (*e.g.* unidentified sp. #1) in the species list for that site.

2.8 Methods for analyzing data

2.8.1 Shannon-Wiener Diversity Index

The analysis of the understory vegetation diversity was calculated using the Shannon-Wiener Index ($H' = - \Sigma\, p\mathrm{i} \log p\mathrm{i}$), also known as the Shannon's Diversity Index. Although the richness of species in a community does provide a true value of diversity, it does not take into consideration the evenness and dominance or abundance of some species. Shannon's Diversity Index does take into consideration evenness and abundance in its calculation. However, values calculated from the formula typically range from 1.5 to 3.5 making it difficult to interpret and assess differences in diversity between sites (Magurran 1988). For example, when comparing a diversity index of 1 in community *A* to a diversity index of 2 in community *B* it is not accurate to say that the diversity in community *A* is twice as high as community *B* since Shannon's diversity index uses a nonlinear scale. In order to provide a more intuitively meaningful measure of diversity this value was further raised to the exponent ($e^{H'}$) which considers all species as equally common (Whittaker 1972). By raising the Shannon's Diversity Index to the exponent the diversity index is converted to the effective number of species, thereby providing a more accurate representation of diversity that can be used to compare diversity across communities (Jost, 2006). Shannon's index assumes that all individuals are randomly sampled, the population is indefinitely large or infinite, and all species in the community are represented (Magurran 1988). These assumptions were met by recording 20 randomly located points within each of 20 randomly located quadrats thereby having a high number of sampling points that were randomly located within the study plot.

2.8.2 Percent similarity of the Understory

Percent similarity of the understory for all forest groups was determined. A resemblance measure such as percent similarity is used to compare community relationships, in this case understory species richness, where percent similarity can be considered an index or distance calculated for every species. Percent similarly was calculated by determining the relative abundance of each species within each forest group and taking the sum of the lower relative abundance value where there were similar species between each group of plantation and the reference forest group. Percent similarity (PS) is calculated as follows:

$$PS_{jl} = \sum_{i} \min (p_{ij}, p_{il})$$

where sample units *j* and *l*, over all attributes *i*. Percent similarity is one of the most robust quantitative measures of similarity available since it is not greatly affected by sample size or by species diversity (Wolda, 1981).

2.8.3 Tree density and importance values

Regenerating tree and sapling density and important values were calculated for each forest plot. Absolute tree density, λ, is defined as the number of trees per hectare, which is calculated by first determining the mean distance, ř, to each tree. The mean distance is the sum of the distances of all trees recorded, divided by the number of quadrants where a tree was recorded and measured. Absolute density was then calculated as:

$$\text{Absolute Density} = \quad \lambda = \frac{1}{\check{r}^2}$$

This value is expressed as the number of trees per meter squared, which is multiplied by 1000 to provide an estimate of the number of trees per hectare. However, due to the lack of regeneration of trees in young plantations, there were instances where a vacant quarter was encountered. In these instances the calculation of the absolute density can be greatly overestimated in these plots and a density calculated from only those quarters containing observations will overestimate the true density. In order to account for vacant quarters Warde and Petranka (1981) provide a derivation of a correction factor (CF). The formula to determine absolute density using the correction factor is,

$$\text{Absolute Density (corrected)} = \frac{1}{(r')} \times \text{CF}$$

where r' is the density of the non-vacant quarters, and CF is the correction factor derived from Warde and Petranka (1981).

Importance value for a species is defined as the sum of three relative measures:
Importance Value = Relative Dominance (%) + Relative Density (%) + Relative Frequency (%)

where,

$$\text{Relative Dominance} = \frac{\sum \text{Basal Area of Species 'A'}}{\sum \text{Basal Area of all species}} \times 100\ ;$$

$$\text{Relative Density} = \frac{\text{\# Trees of Species 'A'}}{\text{Total \# of Quadrants where a tree was observed}} \times 100;$$

$$\text{Relative Frequency} = \frac{\text{Absolute Frequency of Species 'A'}}{\sum \text{Absolute Frequency of all species}} \times 100; \text{ and}$$

$$\text{Absolute Frequency} = \frac{\text{\# of quadrats where Species 'A' was observed}}{\text{total \# of quadrats sampled}} \times 100$$

The importance value of a species can range from 0 to 100 and will not necessarily reflect the species with the highest basal area or highest number of individual trees recorded. This value also may not provide an accurate representation of regenerating trees in the understory, especially in forests where regeneration in the understory is low or in younger plantations (Warde and Petranka 1981). Importance values can be calculated for the older plantation group (et. 1927-1932) and the reference deciduous forest group. When importance values are greater than 25% for a given species, the species with the highest importance value will be considered the dominant tree species. For example if species *x* had an importance value of 42% and species *y* had an importance value of 29%, the dominant species would be species *x* and the subdominant species would be species *y* with the forest referred to as a *x* - *y* forest.

2.8.4 Understory Light Characteristics

The calculation of diffuse non-interceptance (DIFN) consists of a combination of the leaf area index (LAI) and mean tilt angle (MTA). The sensor takes five zenith angle readings at each location and divides the below to above canopy transmittance values for each zenith angle. At each forest study site two above canopy (*i.e.* taken in the open) readings were recorded (one before and one after understory readings) and 10 below canopy readings. The number of readings for each site was programmed into the device, which also calculates mean and standard deviation at each site based on the number of locations where a reading was recorded.

2.9 Statistical Analysis

2.9.1 Analysis of Variance (ANOVA)

Prior to conducting a statistical procedure, checks for normality of data were conducted. With respect to the distribution of data all variables were plotted in a histogram to determine if the data followed a bell curve. By examining the distribution of data, any variables that were not distributed normally were log transformed. The results from magnesium at 0-10 cm depth, phosphorus at 20-40 cm depth, and potassium at 40-60 cm depth were log transformed in order to ensure the data followed a normal distribution. After these variables were transformed, all of the data was normally distributed justifying the use of a parametric Analysis of Variance (ANOVA). The stratified random sampling design also ensured that the assumption of independence was met. A two-way analysis of variance (ANOVA), with $\alpha = 0.1$, was combined with Tukey's post hoc test using SPSS 15 (SPSS, Inc, Chicago, IL) software to test for significant differences between means of all variables between each forest group. The ANOVA compared the sample mean from each of the five forest groups from the overall mean when all forests are grouped together.

2.9.2 Correlation Analysis

A linear correlation analysis including all variables was performed using SPSS 15 (SPSS, Inc, Chicago, IL) software to examine the relationship between each variable. Pearson's correlation was used as a measure of dependence between each variable where a positive value indicates a positive relationship between variables and negative value indicates a negative relationship. The closer the Pearson value approaches 1 or -1, the stronger the relationship is between the variables. Whereas the closer the value is to 0, the less correlated are the variables.

2.9.3 Forward Stepwise Regression

A forward stepwise regression was performed using SPSS 15 (SPSS, Inc, Chicago, IL) software in order to try and determine what variables best explain the variance in the dependent variable. Since the study aims to explain what variables are influencing understory diversity in plantation forests, diversity was the dependent variable used in the analysis. A forward stepwise regression produces a model by successively adding or removing variables based entirely on the *t-statistic* of their estimated coefficients and stops including variables when further addition of variables does not further explain the variance of the dependent variable (Albright *et al.* 2008). The forward stepwise regression method was chosen as opposed to a backward regression because this study included a large set of independent variables from which the forward stepwise would extract a small number of variables. The advantage of using the forward regression as opposed to the backward method is that the forward regression is more restrictive and would be less prone to show an erroneous relationship between variables (Menard 2009). Conversely, this argument can be used in support of using the backward method and forms one of the arguments over the use of forward or backward stepwise regressions (Menard 2009).

There has been criticism over the use of stepwise regressions because the stepwise procedures produce significance tests that can greatly inflate Type I error rates (*i.e.*, the probability of erroneously rejecting a null-hypothesis) (Mundry and Nunn 2009). It is recognized that the stepwise regression is an explanatory procedure used to elucidate the variables that are likely driving the understory succession in the red pine plantations observed.

3.0 CHAPTER 3 RESULTS

3.1 Introduction to Results

The study of the understory dynamics in red pine plantations focused on four groups of plantations each with three replicates including stands established (est.) in 1978-1981, 1967-1971, 1949-1961, and 1927-1932. The variables measured were compared between plantation groups and also to the reference deciduous forest group also containing three replicates. The results of the field work and subsequent analysis are described herein.

3.2 Understory Vegetation

3.2.1 Summary Statistics

Species richness in the understory layer for each forest group was tabulated for each season (Table 4). The species richness for each forest group was broken into the number of native and non-native species in Ontario, further broken down into the number of spring ephemerals per forest group. The mean abundance (Table 5) of the understory for each forest group generally increased with the age of the plantation. In the spring there were no significant differences between plantation groups, whereas in the summer and fall the oldest plantation group (est. 1927-1932) had a significantly higher abundance of species than the two youngest plantation groups (est. 1978-1981 and 1967-1971). The reference deciduous forest group had a significantly higher abundance of species in the understory than the two youngest plantation groups for all seasons, but was not significantly different than the mid-aged (est. 1949-1961) and oldest plantation group.

There were only six spring ephemeral individuals recorded of one species (trout lily (*Erythronium americanum* Ker Gawl. *ssp. americanum*)), in one plantation study plot while there were seven species (total of 313 individuals) recorded in the quadrats of the reference deciduous forest group including downy-yellow violet (*Viola pubescens* Aiton), foam flower (*Tiarella cordifolia* L.), Selkirk's violet (*Viola selkirkii* Pursh ex Goldie), sharp-lobed hepatica (*Anemone acutiloba* (DC.) G. Lawson), squirrel corn (*Dicentra Canadensis* (Goldie) Walp.), *E. americanum*, and white trillium (*Trillium grandiflorum (Michx.) Salisb.*).

Table 4. Number of native, non-native, and total species richness of understory species from each forest group for each season. Percent of non-native species are represented in brackets next to the number of non-native species for each forest group.

Season	**Forest Group**				
	1978-1981	**1967-1971**	**1949-1961**	**1927-1932**	**Reference Forest**
Spring					
Native	4	2	6	7	21
Non-Native	0 (0%)	2 (50%)	4(40%)	2 (22%)	1 (5%)
Total	4	4	10	9	22
Summer					
Native	11	7	10	14	31
Non-Native	3 (21%)	5 (42%)	3 (23%)	3 (18%)	3 (9%)
Total	14	12	13	17	34
Fall					
Native	8	8	16	20	35
Non-Native	2 (20%)	1 (11%)	3 (16%)	1 (8%)	3 (8%)
Total	10	9	19	21	38
All Seasons					
Native	16	11	19	22	57

Season	Forest Group				
	1978-1981	1967-1971	1949-1961	1927-1932	Reference Forest
Non-Native	3 (16%)	6 (35%)	7 (27%)	4 (15%)	4 (7%)
Total	19	17	26	26	61
Spring Ephemerals	1	0	0	0	7

Table 5. Mean abundance of understory species for each forest group in each season. Standard errors are given in parentheses (*n* = 3).

	Spring	Summer	Fall
Forest Group	**Mean Abundance**	**Mean Abundance**	**Mean Abundance**
1978-1981	11 (7)^{a}	53 (26.95)^{a}	22.33 (15.45)^{a}
1967-1971	13.33 (13.33)^{a}	44.33 (17.81)^{a}	47.66 (9.83)^{a}
1949-1961	84 (51.96)^{ab}	159 (60.30)^{ab}	90.66 (25.95)^{ab}
1927-1932	33 (14.74)^{ab}	218 (44.41)^{b}	158.66 (36.81)^{b}
Reference	167 (54.07)^{b}	214.66 (17.70)^{b}	211 (29.02)^{b}

Values followed by the same lowercase letter are not statistically different ($p<0.1$) between forest groups compared within each season.

3.2.2 Percent Similarity of the Understory

Percent similarity of the understory was calculated in order to determine how species richness in the understory for each age group of red pine plantation compared with each other and the reference forest group (Table 6). Generally, the percent similarity was highest when each plantation is compared to an older plantation for all seasons. The lowest percent similarity occurred between plantations established in 1978-1981 and 1967-1971 for all seasons. Seasonal differences were apparent where the percent similarity for all forest groups was lowest in the spring and increased in the summer and slightly more in the fall. One exception to these general trends is the youngest plantation (est. 1978-1981) which had the highest percent similarity (28.56%) to the reference deciduous forest in the spring compared with the other three plantation groups that had a percent similarity of 7.7% (est. 1967-1971), 12.92 % (est. 1949-1961), and 15.57% (est. 1927-1932).

Table 6. Percent similarity matrix of species richness in the understory layer in each forest group for each season. Each number represents the percent (%) of understory species similar between the groups compared.

Spring

Group	**1978-1981**	**1967-1971**	**1949-1961**	**1927-1932**	**Reference Forest**
1978-1981		7.5	7.5	18.2	28.6
1967-1971			8.7	12.6	7.7
1949-1961				52.1	12.9
1927-1932					15.6

Summer

Group	**1978-1981**	**1967-1971**	**1949-1961**	**1927-1932**	**Reference Forest**
1978-1981		19.6	25.6	27.7	13.6
1967-1971			5.2	25.2	13.1
1949-1961				60.4	11.9
1927-1932					29.4

Fall					
Group	**1978-1981**	**1967-1971**	**1949-1961**	**1927-1932**	**Reference Forest**
1978-1981		15.2	25.9	30.8	14.6
1967-1971			26.7	33.1	15.6
1949-1961				30.6	18.4
1927-1940					30.8

3.2.3 Shannon-Wiener Diversity Index

Mean Shannon-Wiener diversity indices ± SEM were reported for each forest group for each season. There is a general increase in mean diversity with increasing age of the plantation (Figure 12). Diversity was highest in the reference forest group for all seasons. The results revealed that the reference forest group was had a significantly higher diversity of understory species in the spring compared with all plantation groups but the mid-aged group ($p<0.1$). There were no significant differences between any of the plantation groups in the spring. During the summer the oldest plantation group (est. 1927-1932) and the reference forest group had a significantly higher diversity than the plantation groups established in 1978-1981 and 1967-1971 but were not significantly different from each other or the mid-aged plantation group (est. 1949-1961). Results of the ANOVA comparing diversity in the fall revealed that the first three plantation groups were not significantly different from each other (est. 1978-1981, 1967-1971, and 1949-1961). Fall diversity in the oldest plantation group (est. 1927-1932) and the reference forest group were not significantly different from each other but both had a significantly higher diversity of understory species compared with the youngest plantation group.

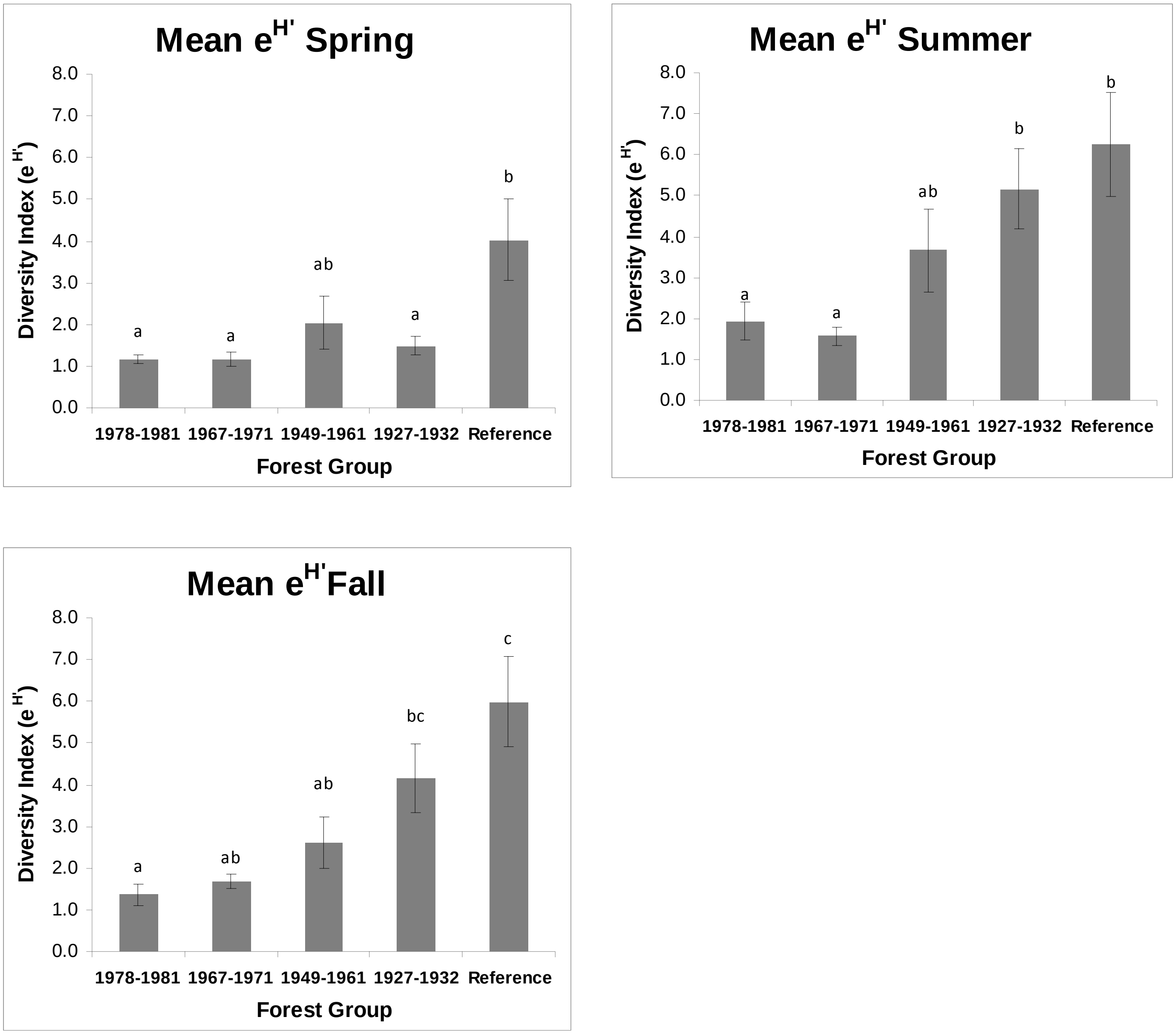


Figure 12. Mean Shannon-Wiener Diversity Indices ± SEM for understory species in each forest group for each season. Letters above bars illustrate significant differences ($p < 0.1$) among groups after Tukey's post hoc test where completely different letters indicate a significant difference.

Table 7. Mean Shannon-Wiener Diversity Indices of understory species for each forest group in each season. Standard errors are given in parentheses (*n* = 3).

	Spring	**Summer**	**Fall**
Group	**Mean $e^{H'}$**	**Mean $e^{H'}$**	**Mean $e^{H'}$**
1978-1981	1.16 (0.10)[a]	1.94 (0.47)[a]	1.36 (0.25)[a]
1967-1971	1.17 (0.17)[a]	1.56 (0.22)[a]	1.67 (0.17)[ab]
1949-1961	2.04 (0.64)[ab]	3.67 (1.01)[ab]	2.61 (0.62)[ab]
1927-1932	1.49 (0.23)[a]	5.16 (0.98)[b]	4.17 (0.83)[bc]
Reference Forest	4.03 (0.98)[b]	6.25 (1.28)[b]	5.99 (1.08)[c]

Values followed by the same lowercase letter are not statistically different ($p<0.1$) between forest groups compared within each season.

3.2.4 Regeneration of Woody Vegetation

The understory regeneration of woody vegetation, specifically trees, was assessed. Tree density generally increased with the age of the plantation (Figure 13). However, two of the replicates in the youngest plantation group (est. 1978-1981) had a tree density of 49 and 232 trees/ha respectively which increased the mean tree density and standard error of the mean (SEM) in that group. The tree density for all plantation groups was significantly lower than the reference forest group. There were no significant differences for tree density between any of the plantation groups.

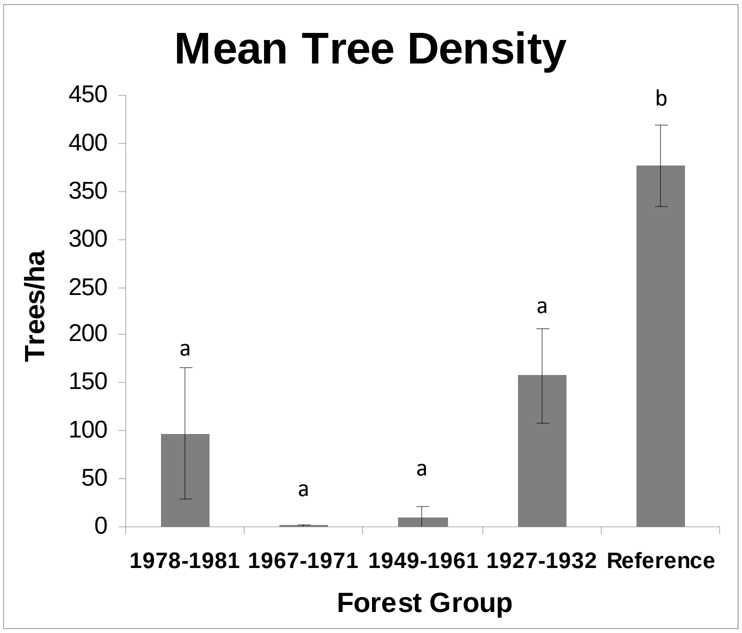


Figure 13. Mean tree density/hectare ± SEM in each forest group. Letters above bars illustrate significant differences (p <0.1) among groups after Tukey's post hoc test where completely different letters indicate a significant difference.

Table 8. Mean tree density/hectare in each forest group. Standard errors are given in parentheses (*n* = 3).

Forest Group	**Mean Tree Density (trees/hectare)**
1978-1981	96.8 (68.8)^{a}
1967-1971	1.5 (1.1)^{a}
1949-1961	10.6 (9.7)^{a}
1927-1932	157.5 (49.3)^{a}
Reference Forest	376.2 (42.5)^{b}

Values followed by the same lowercase letter are not statistically different (p<0.1) between forest groups compared within each season.

There were an average of seven species in both the oldest plantation group (est. 1927-1932) and the reference forest group. The tree species found in both groups includes American beech, white ash, sugar maple, red oak, white birch, and hop hornbeam. Species found exclusively in the oldest plantation group include red maple (*Acer rubrum* L.), balsam fir, white pine, and black cherry. Species found exclusively in the reference forest group include basswood (*Tilia americana* L.), yellow birch (*Betula alleghaniensis* Britton), eastern hemlock, large-toothed aspen and American elm (*Ulmus americana* L.). Importance values were calculated for the oldest plantation group and the reference forest group. The importance values indicate that the dominant tree species in the reference forest group was mainly sugar maple, while the dominant tree species in the oldest plantation group were sugar maple and red oak.

3.2.5 Light Characteristics

There was a general increase in mean diffuse non-interceptance (DIFN) with increasing age of the plantation (Figure 14) in the spring. The DIFN in the spring was highest in the reference forest group indicating the reference deciduous forest group experienced the least amount of shading. During the summer and fall DIFN was generally highest in the second youngest and mid-aged plantation groups (est. 1967-1971 and 1949-1961) which were also significantly higher than the youngest plantation group (est. 1978-1981) and the reference forest group. In the fall the DIFN in the youngest plantation group was significantly lower than the mid-aged plantation group.

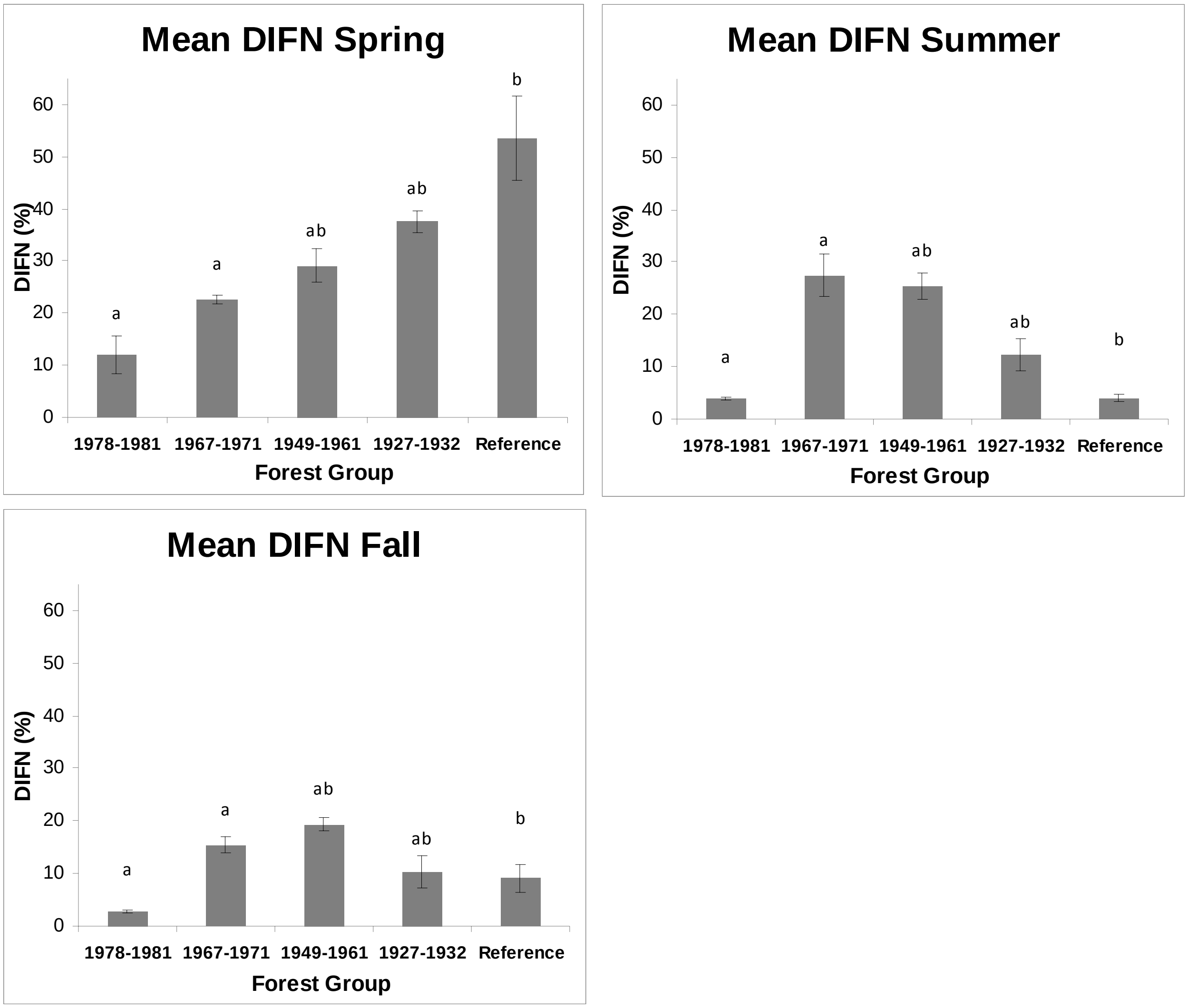


Figure 14. Mean diffuse non-interceptance (DIFN) (%) ± SEM in forest group for each season. Letters above bars illustrate significant differences ($p < 0.1$) among groups after Tukey's post hoc test where completely different letters indicate a significant difference.

Table 9. Mean diffuse non-interceptance (DIFN) for each forest group during each season. Standard errors are given in parentheses (n = 3).

	Spring	Summer	Fall
Group	**DIFN (%)**	**DIFN (%)**	**DIFN (%)**
1978-1981	12.0 (3.6) ^{a}	3.9 (0.3)^{b}	2.8 (0.2)^{b}
1967-1971	22.5 (0.9)^{a}	27.4 (4.1)^{a}	15.5 (1.5)^{ab}
1949-1961	29.1 (3.2)^{ab}	25.4 (2.5)^{a}	19.3 (1.3)^{a}
1927-1932	37.5 (2.0)^{ab}	12.3 (3.2)^{ab}	10.3 (3.0)^{ab}
Reference Forest	53.5 (8.1)^{b}	4.0 (0.6)^{b}	9.1 (2.7)^{ab}

Values followed by the same lowercase letter are not statistically different ($p<0.1$) between forest groups compared within each season.

3.3 Soil Analysis

3.3.1 Soil pH

The pH of the soils appears to follow a similar trend at all depths (Figure 15). The pH increases (becomes less acidic) from the youngest plantation (est. 1978-1981) to the second youngest plantation group (est. 1967-1971). The pH was most acidic in the plantation group established in 1949-1961, and appears to increase slightly again in the oldest plantation group (est. 1927-1932). There are no significant differences between plantation groups in all but the deepest layer sampled (40-60 cm), where the only significant difference was between the plantations established in 1967-1971 and 1949-1961 and the oldest plantation group (est. 1927-1932) (Table 10). The reference forest group soil pH was not significantly different than any plantation at any age for all depths.

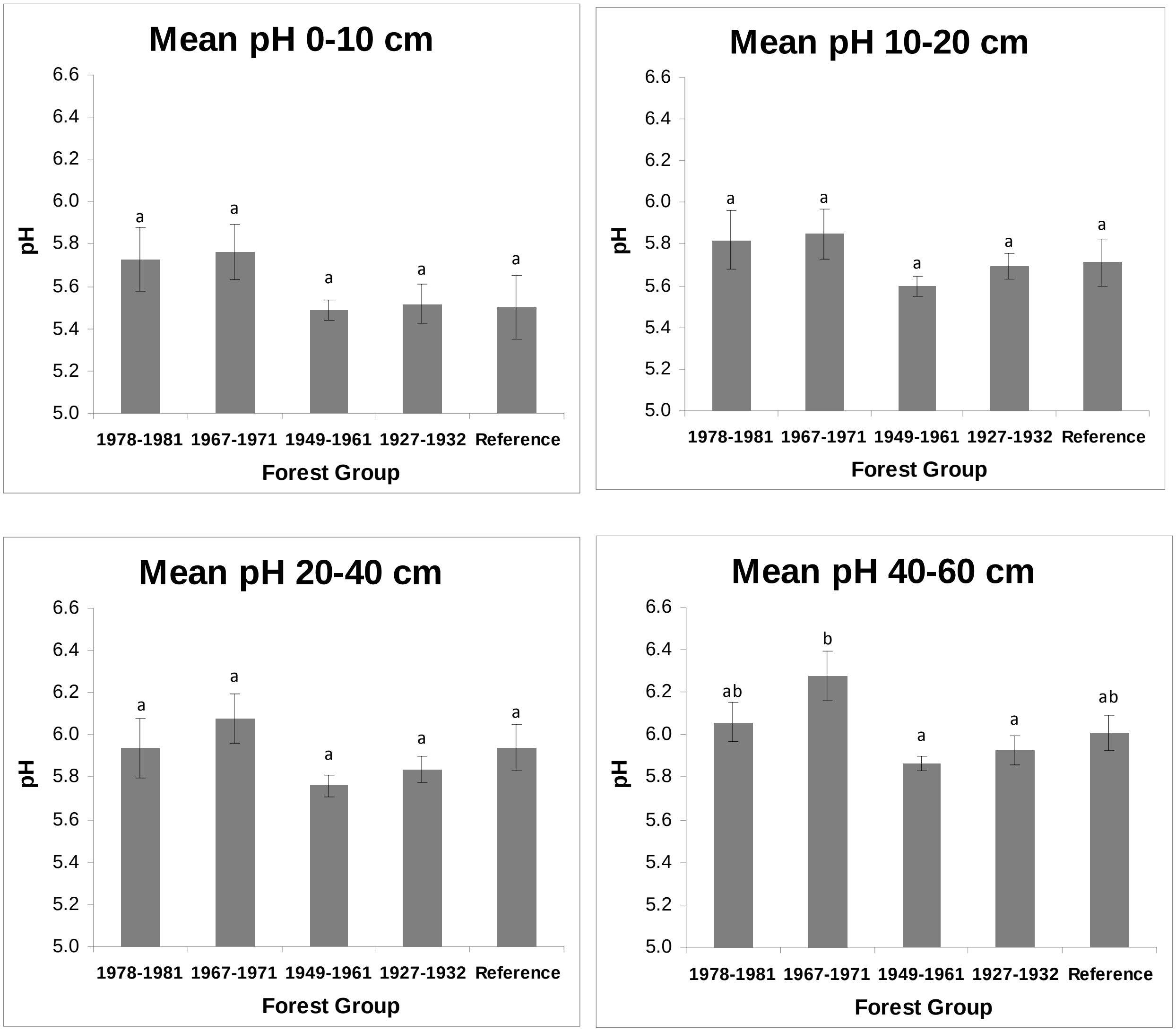


Figure 15. Mean pH ± SEM in forest group for each depth sampled. Letters above bars illustrate significant differences (p <0.1) among groups after Tukey's post hoc test where completely different letters indicate a significant difference.

Table 10. Mean pH in each forest group for each depth (cm). Standard errors are given in parentheses (*n* = 9).

	Mean pH for each depth (cm)			
Group	**0-10**	**10-20**	**20-40**	**40-60**
1978-1981	5.73 (0.15) ^{a}	5.82 (0.14) ^{a}	5.94 (0.12) ^{a}	6.06 (0.09)^{ab}
1967-1971	5.76 (0.13) ^{a}	5.85 (0.12) ^{a}	6.08 (0.11) ^{a}	6.28 (0.12)^{b}
1949-1961	5.49 (0.05) ^{a}	5.60 (0.05) ^{a}	5.76 (0.05) ^{a}	5.86 (0.03)^{a}
1927-1932	5.52 (0.09) ^{a}	5.69 (0.06) ^{a}	5.84 (0.07) ^{a}	5.93 (0.07)^{a}
Reference Forest	5.50 (0.15) ^{a}	5.71 (0.11) ^{a}	5.94 (0.13) ^{a}	6.01 (0.08)^{ab}

Values followed by the same lowercase letter are not statistically different ($p<0.1$) between forest groups compared for each depth.

3.3.2 Soil bulk density

Mean soil bulk density (g/cm^3) ± SEM was reported for each forest group for each depth sampled. There is a slight trend observed in the 0-10 cm layer of soil sampled between groups where bulk density increases with the age of the plantation to the mid-aged plantation group (est. 1949-1961). The soil bulk density then lowers slightly in the oldest plantation group (est. 1927-1932) and the reference forest group (Figure 16). This trend appeared less apparent with increasing depth sampled. The only significant difference occurred between the mid-aged plantation group and the reference forest group at 0-10 cm (Table 11). There were no significant differences in the mean bulk density between any groups at the deeper depths.

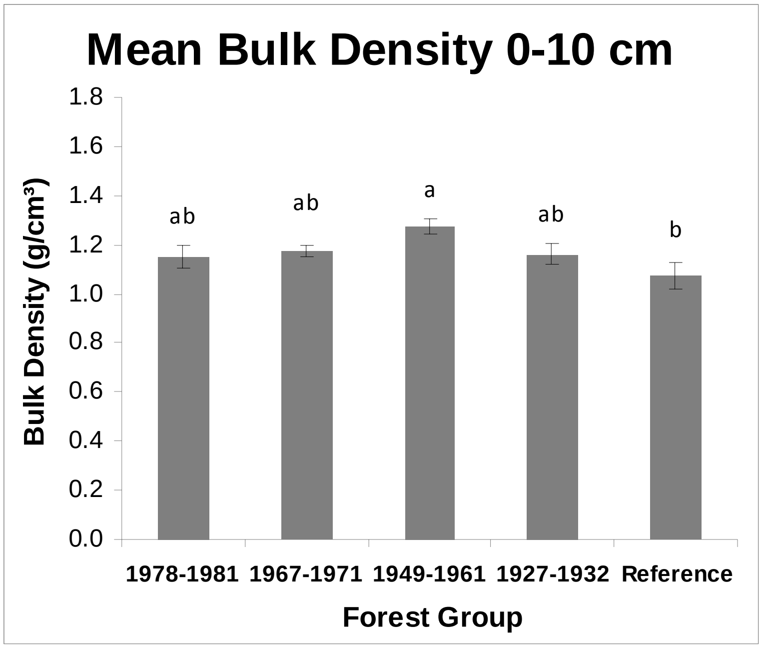


Figure 16. Mean bulk density (g/cm3) ± SEM in each forest group at 0-10 cm sample depth. Letters above bars illustrate significant differences (p <0.1) among groups after Tukey's post hoc test where completely different letters indicate a significant difference.

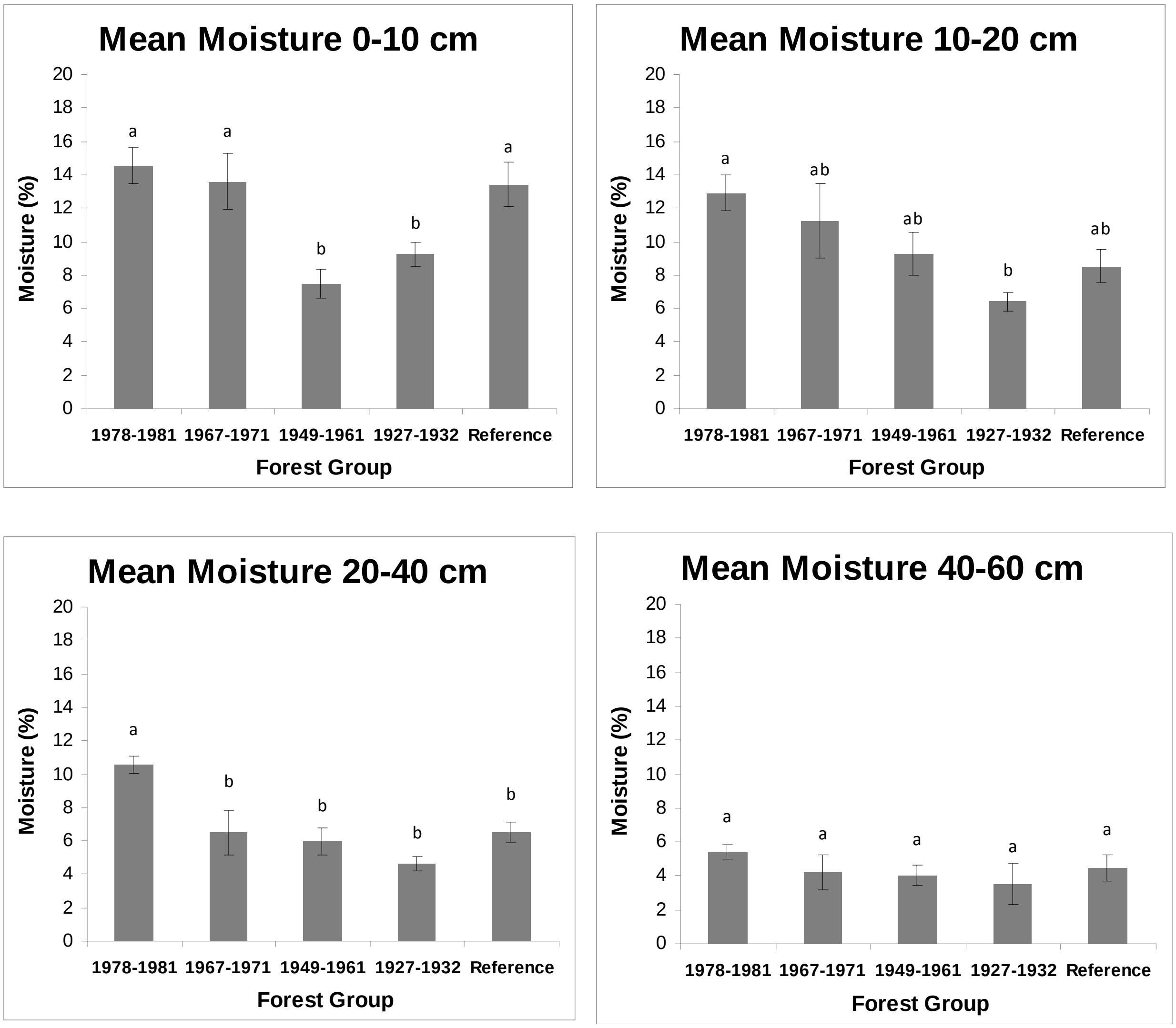
Table 11. Mean bulk density (g/cm3) in each forest group for each depth (cm). Standard errors are given in parentheses (*n* = 9).

	Mean bulk density (g/cm^3) for each depth (cm)			
Group	**0-10**	**10-20**	**20-40**	**40-60**
1978-1981	1.15 (0.05)^{ab}	1.33 (0.04)^{a}	1.39 (0.03)^{a}	1.49 (0.03)^{a}
1967-1971	1.17 (0.02)^{ab}	1.39 (0.05)^{a}	1.46 (0.03)^{a}	1.55 (0.03)^{a}
1949-1961	1.28 (0.03)^{a}	1.40 (0.01)^{a}	1.45 (0.02)^{a}	1.54 (0.01)^{a}
1927-1932	1.16 (0.04)^{ab}	1.32 (0.04)^{a}	1.40 (0.02)^{a}	1.54 (0.03)^{a}
Reference Forest	1.07 (0.05)^{b}	1.30 (0.02)^{a}	1.43 (0.03)^{a}	1.54 (0.06)^{a}

Values followed by the same lowercase letter are not statistically different (p<0.1) between forest groups compared for each depth.

3.3.3 Percent Soil Moisture

Percent soil moisture ± SEM was reported for each forest group for each depth sampled. There is a slight trend observed in the 0-10 cm layer of soil sampled between groups. There is no evident trend overall between groups for all depths (Figure 17). Generally, percent moisture was highest in the youngest plantation group (est. 1978-1981) for all depths and decreases with the age of the plantation except at depth 0-10 cm where it was lowest in the mid-aged plantation group (est. 1949-1961). Percent moisture at 0-10 cm depth in the plantation groups established in 1950-1961 and 1927-1932 were significantly lower than all other groups which were not significantly different from each other. With deeper sampling depths, the differences in percent moisture were less evident and there were no significant differences between moisture at the deepest sample depth (40-60 cm).



Mean Moisture 0-10 cm

Mean Moisture 10-20 cm

Mean Moisture 20-40 cm

Mean Moisture 40-60 cm

Figure 17. Mean moisture (%) ± SEM in each forest group for each depth sampled. Letters above bars illustrate significant differences ($p < 0.1$) among groups after Tukey's post hoc test where completely different letters indicate a significant difference.

Table 12. Mean moisture (%) in each forest group for each depth (cm). Standard errors are given in parentheses (*n* = 9).

	Mean moisture (%) for each depth (cm)			
Group	**0-10**	**10-20**	**20-40**	**40-60**
1978-1981	14.5 (1.1)^{a}	12.9 (1.1)^{a}	10.5 (0.5)^{a}	5.42 (0.45)^{a}
1967-1971	13.6 (1.7)^{a}	11.3 (2.4)^{ab}	6.5 (1.3)^{b}	4.22 (1.02)^{a}
1949-1961	7.4 (0.8)^{b}	9.3 (1.3)^{ab}	6.0 (0.8)^{b}	4.07 (0.61)^{a}
1927-1932	9.2 (0.7)^{b}	6.4 (0.6)^{b}	4.6 (0.4)^{b}	3.54 (1.20)^{a}
Reference Forest	13.4 (1.3)^{a}	8.5 (1.0)^{ab}	6.5 (0.61)^{b}	4.45 (0.77)^{a}

Values followed by the same lowercase letter are not statistically different ($p<0.1$) between forest groups compared for each depth.

3.3.4 Litter depth

Mean litter depth (cm) ± SEM was reported for each forest group for each depth sampled. Generally the litter depth for the plantation groups increased from the youngest plantation group (est. 1978-1981) to the mid-aged group (est. 1949-1961) and was lowest in the oldest plantation group (est. 1927-1932). The litter depth in the reference forest group was lower than all plantation groups. The reference forest group had a significantly lower litter depth than all but the oldest plantation group (est. 1927-1932). There were no significant differences revealed between the first three plantation groups. The oldest plantation group had a significantly lower litter depth than the groups established in 1967-1971 and 1949-1961.

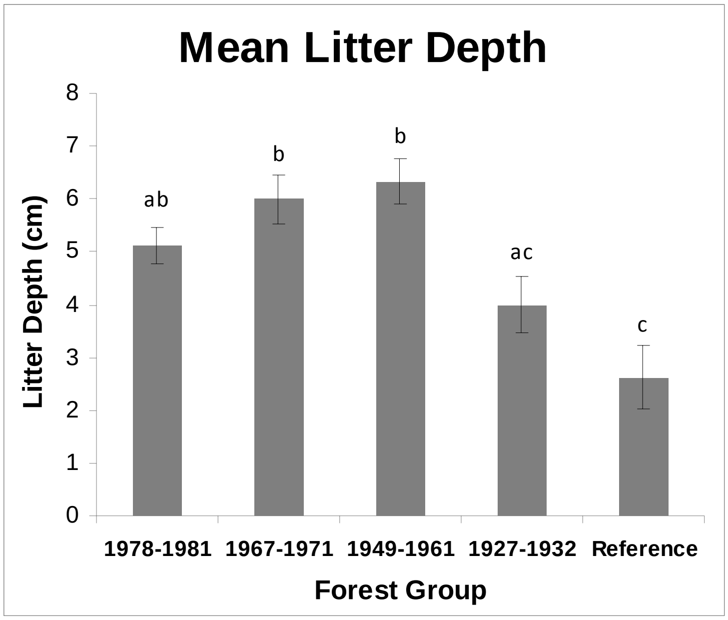


Figure 18. Mean litter depth (cm) ± SEM in each forest group. Letters above bars illustrate significant differences ($p < 0.1$) among groups after Tukey's post hoc test where completely different letters indicate a significant difference.

Table 13. Mean litter depth (cm) in each forest group. Standard errors are given in parentheses ($n = 9$).

Group	**Mean Litter Depth (cm)**
1978-1981	5.11 (0.35)^{ab}
1967-1971	6.0 (0.46)^{b}
1949-1961	6.33 (0.44)^{b}
1927-1932	4.0 (0.53)^{ac}
Reference Forest	2.65 (0.60)^{c}

Values followed by the same lowercase letter are not statistically different ($p<0.1$) between forest groups compared for each depth.

3.3.5 Soil nutrient analysis

Soil nutrient analysis was completed for total carbon (TC) (%), total nitrogen (TN) (%), calcium (Ca) (mg/kg), potassium (K) (mg/kg), magnesium (Mg) (mg/kg), and phosphorus (P) (mg/kg) (Figure 19, Table 14). The mean TC, TN, Ca, K, and Mg followed a similar trend where the amount of each nutrient increased from the youngest plantation group (est. 1978-1981) to the group established in 1967-1971, was lowest in the mid-aged group (est. 1949-1961) and increased again to the oldest plantation group (est. 1927-1932) (Figure 19). The amount of all of these nutrients was consistently highest in the reference forest group and lowest in the mid-aged plantation group. The inverse trend was observed with the amount of phosphorus measured in the plantation groups (Figure 19). Trends were similar across all depths for each nutrient therefore figures were only produced for 0-10 cm depth to illustrate trends across forest groups. The description of statistically significant differences between sites for each nutrient is focused on differences found between sites at 0-10 cm depth.

Total Carbon and Total Nitrogen

The post hoc test revealed that the reference forest group was significantly higher ($p<0.1$) in both percent TC and TN than all plantation groups. There was no significant difference across the plantations groups for TC and TN.

Calcium

The reference forest group had a significantly higher amount of Ca than the youngest group (1978-1981), the mid-aged group (est. 1949-1961), and the oldest plantation group (est. 1927-1932), but was not significantly different from the group established in 1967-1971. There were no significant differences in Ca between any of the plantation groups.

Potassium

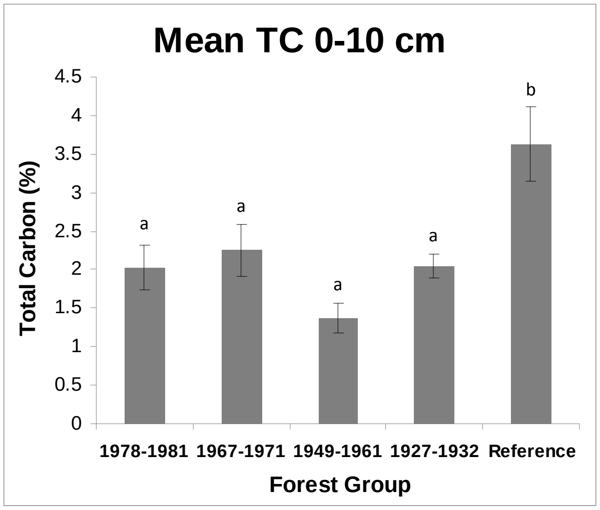
Mean K was significantly higher in the reference forest group and the plantation established in 1965-1975 compared to the mid-aged plantation group (est. 1949-1961). There was no significant difference between the reference forest group and the plantations established in 1978-1981 and 1967-1971, when compared with the oldest plantation group (1927-1932).

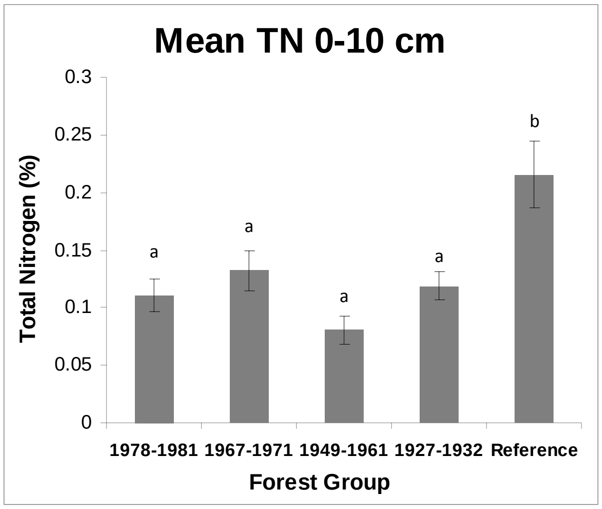
Magnesium

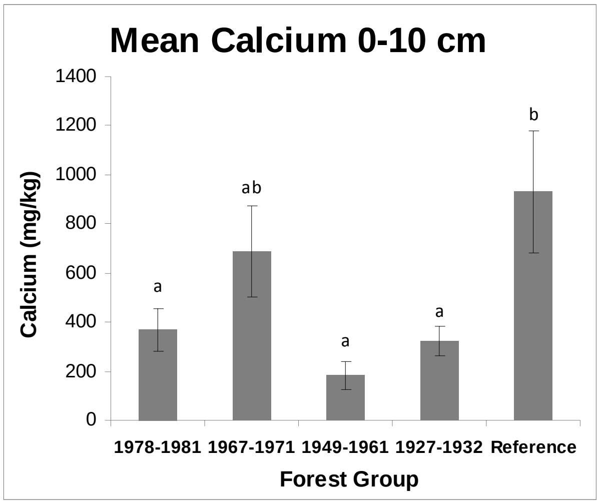
The reference forest group and plantations established in 1927-1932 and 1967-1971, and 1978-1981 were all significantly higher in Mg than the mid-aged plantation group (est. 1949-1961).

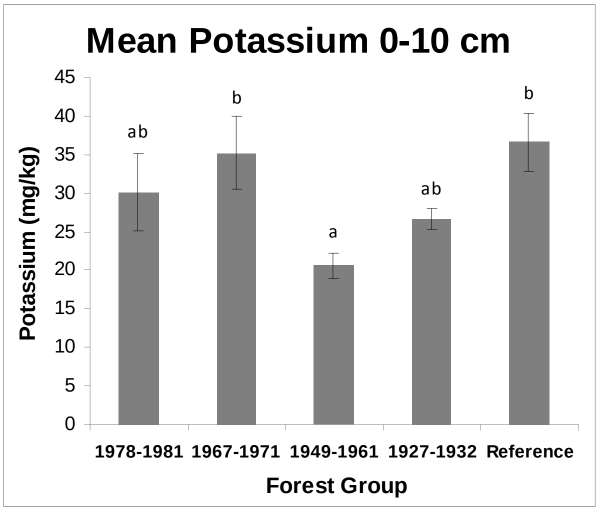
Phosphorus

Mean phosphorus was significantly different between the mid-aged plantation group (est. 1949-1961) and the oldest plantation group (est. 1927-1932) and reference forest group. There were not significant differences in phosphorus between plantations established in 1978-1981, 1967-1971, and 1927-1932. The mid-aged plantation group (est. 1949-1961) was measured as containing the highest amount of phosphorus compared with all other groups.









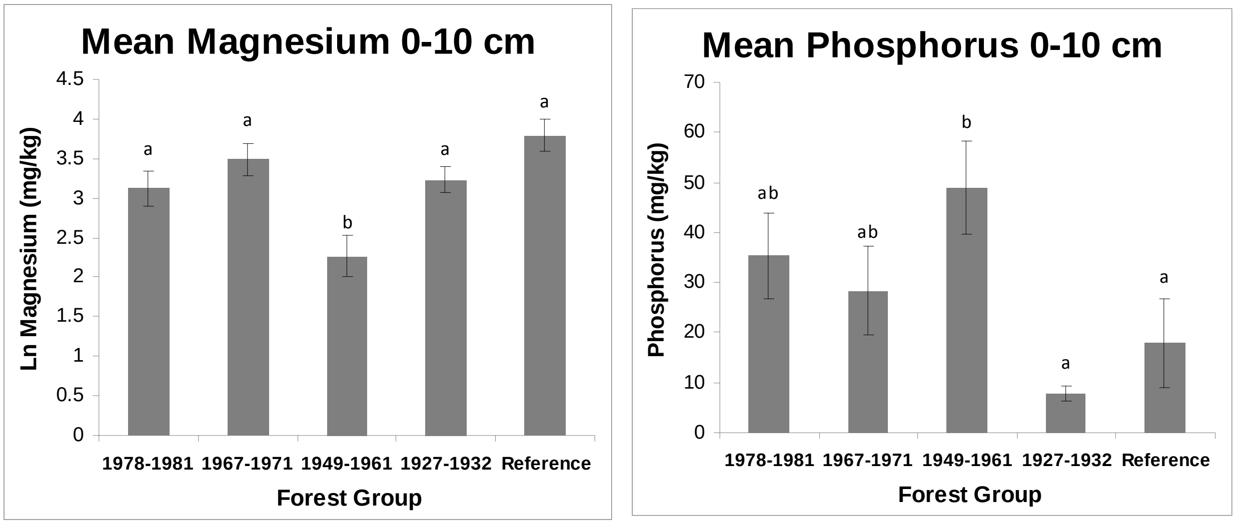


Figure 19. Nutrient analysis illustrating the mean value of total carbon (%), total nitrogen (%), calcium (mg/kg), potassium (mg/kg), magnesium (mg/kg), and phosphorus (mg/kg) ± SEM for each forest group sampled at 0-10 cm. Letters above bars illustrate significant differences ($p < 0.01$) among groups after Tukey's post hoc test where completely different letters indicate a significant difference.

Table 14. Results of nutrient analysis of total carbon (%), total nitrogen (%), calcium (mg/kg), potassium (mg/kg), magnesium (mg/kg), and phosphorus (mg/kg) for each forest group sampled at 0-10 cm. Standard errors are given in parentheses (*n* = 9).

Nutrient	**Depth (cm)**	**Forest Group**				
		1978-1981	**1967-1971**	**1949-1961**	**1927-1932**	**Reference Forest**
		Mean	**Mean**	**Mean**	**Mean**	**Mean**
Total Carbon (%)	**0-10**	2.01 (0.29)^{a}	2.25(0.33)^{a}	1.37 (0.19)^{a}	2.04 (0.16)^{a}	3.63 (0.48)^{b}
	10-20	1.07 (0.17)^{a}	0.97 (0.20)^{a}	0.84 (0.06)^{a}	0.76 (0.08)^{a}	0.91 (0.09)^{a}
	20-40	0.61 (0.07)^{a}	0.95 (0.35)^{a}	0.42 (0.05)^{a}	0.41 (0.06)^{a}	0.52 (0.06)^{a}
	40-60	0.30 (0.03)^{a}	0.87 (0.41)^{a}	0.17 (0.03)^{a}	0.18 (0.02)^{a}	0.77 (0.54)^{a}
Total Nitrogen (%)	**0-10**	0.11 (0.01)^{a}	0.13 (0.02)^{a}	0.08 (0.01)^{a}	0.12 (0.01)^{a}	0.22 (0.03)^{b}
	10-20	0.07 (0.01)^{a}	0.07 (0.01)^{ab}	0.05 (0.01)^{b}	0.05 (0.01)^{b}	0.05 (0.01)^{b}
	20-40	0.05 (0.01)^{a}	0.06 (0.01)^{a}	n.d.	n.d.	n.d.
	40-60	n.d.	n.d.	n.d.	n.d.	n.d.
Calcium (mg/kg)	**0-10**	368.1 (85.9)^{a}	688.9 (185.1)^{ab}	184.0 (55.8)^{a}	325.12 (59.3)^{a}	930.9 (246.7)^{b}
	10-20	303.3 (77.3)^{a}	457.0 (143.2)^{a}	176.1 (29.2)^{a}	170.2 (28.1)^{a}	395.6 (98.1)^{a}
	20-40	282.3 (55.8)^{ab}	1260.2 (737.0)^{a}	162.9 (22.9)^{ab}	125.8 (21.2)^{b}	301.2 (75.2)^{ab}
	40-60	269.4 (72.2)^{a}	1896.8 (939.1)^{a}	120.5 (13.6)^{a}	126.4 (49.5)^{a}	819.0 (651.2)^{a}

Nutrient	Depth (cm)	Forest Group				
		1978-1981	1967-1971	1949-1961	1927-1932	Reference Forest
		Mean	Mean	Mean	Mean	Mean
Potassium (mg/kg)	**0-10**	30.12 (5.05)^{ab}	35.18 (4.72)^{b}	20.59 (1.69)^{a}	26.65 (1.30)^{ab}	36.60 (3.68)^{b}
	10-20	19.90 (2.78)^{a}	19.40 (4.08)^{ab}	12.15 (0.17)^{abc}	10.22 (1.38)^{c}	11.35 (1.13)^{bc}
	20-40	13.93 (2.43)^{a}	14.63 (4.74)^{a}	15.32 (7.25)^{a}	10.34 (4.75)^{a}	6.02 (0.61)^{a}
	40-60*	14.36 (2.61)^{a}	14.05 (3.80)^{a}	7.40 (0.89)^{ab}	7.13 (1.10)^{b}	5.30 (0.72)^{b}
Magnesium (mg/kg)	**0-10***	3.12 (0.23)^{a}	3.49 (0.19)^{a}	2.27 (0.27)^{b}	3.23 (0.16)^{a}	3.79 (0.21)^{a}
	10-20	21.99 (5.11)^{a}	24.73 (11.19)^{a}	10.87 (1.33)^{a}	11.89 (1.87)^{a}	14.59 (0.97)^{a}
	20-40	17.58 (4.86)^{a}	31.21 (17.64)^{a}	5.92 (0.84)^{a}	6.98 (1.43)^{a}	8.80 (1.05)^{a}
	40-60	13.90 (5.24)^{a}	28.72 (15.50)^{a}	3.99 (0.70)^{a}	4.25 (1.13)^{a}	10.36 (4.35)^{a}
Phosphorus (mg/kg)	**0-10**	35.32 (8.59)^{ab}	28.29 (8.88)^{ab}	48.91 (9.29)^{b}	7.75 (1.42)^{a}	17.99 (8.89)^{a}
	10-20	30.04 (6.15)^{ab}	29.83 (8.86)^{ab}	46.13 (7.99)^{a}	11.89 (1.51)^{b}	23.85 (9.39)^{ab}
	20-40*	3.362 (0.19)^{ac}	2.46 (0.45)^{ab}	3.68 (0.20)^{c}	2.36 (0.09)^{b}	2.88 (0.36)^{abc}
	40-60	3.28 (0.13)^{a}	2.95 (0.27)^{a}	3.17 (0.13)^{a}	2.33 (0.13)^{a}	2.41 (0.49)^{a}

Values followed by the same lowercase letter are not statistically different ($p<0.1$) between forest groups compared for each depth.

3.4 Correlation analysis of all variables

A linear correlation analysis was performed for each season examining the correlations between the diversity index of that season, DIFN for that season, and litter depth, bulk density, pH, and nutrients at 0-10 cm depth. This analysis was performed in order to determine how variables might be correlated with each other and point to potential relationships whether causal or correlated. Table 17 shows the results of the correlation analysis between all nutrients.

In the spring diversity was highly positively correlated ($p<0.01$) to DIFN, TN, and Ca, and positively correlated to TC, K, and Mg. In the summer and fall diversity was highly negatively correlated to litter depth ($p<0.01$). TC and TN were negatively correlated to litter depth ($p<0.05$) and highly negatively correlated to bulk density ($p<0.01$). Percent moisture was negatively correlated to BD and DIFN ($p<0.05$). TC and TN were highly positively correlated to each other ($p<0.01$) and were both highly negatively correlated to P ($p<0.01$). K was highly positively correlated to TN, Ca, and Mg ($p<0.01$)

Table 15. Linear correlation analysis with Pearson Correlation of spring diversity and spring DIFN compared to all other variables.

Variable		Diversity	DIFN	Litter Depth	pH	Bulk Density	Moisture (%)	TC (%)	TN (%)	Ca (mg/kg)	K (mg/kg)	Mg (mg/kg)	P (mg/kg)
Diversity	Pearson Correlation	1.00	0.88^{**}	-0.49	-0.20	-0.08	0.33	0.62^{*}	0.74^{**}	0.72^{**}	0.56^{*}	0.63^{*}	-0.44
	Sig. (2-tailed)		0.00	0.07	0.48	0.78	0.24	0.01	0.00	0.00	0.03	0.01	0.10
DIFN	Pearson Correlation	-0.69^{**}	1.00	-0.51	0.10	-0.36	-0.12	0.40	0.47	0.52*	-0.01	0.40	-.03
	Sig. (2-tailed)	0.00		0.05	0.72	0.18	0.68	0.14	0.08	0.05	0.98	0.14	0.27

Significance is reported for a two-tailed analysis. ** Correlation is significant at the 0.01 level (2-tailed). * Correlation is significant at the 0.05 level (2-tailed).

Table 16. Linear correlation analysis with Pearson Correlation of summer diversity and summer DIFN compared to all other variables.

		Diversity	DIFN	Litter Depth	pH	Bulk Density	Moisture (%)	TC (%)	TN (%)	Ca (mg/kg)	K (mg/kg)	Mg (mg/kg)	P (mg/kg)
Diversity	Pearson Correlation	1.00	-0.39	-0.78^{**}	-0.51	-0.18	0.26	0.33	0.25	0.12	0.15	-0.04	-0.20
	Sig. (2-tailed)		0.14	0.00	0.86	0.51	0.34	0.22	0.36	0.68	0.58	0.88	0.47
DIFN	Pearson Correlation	-0.39	1.00	0.64*	0.25	0.42	-0.14	-0.47	-0.44	-0.05	-0.26	-0.13	0.25
	Sig. (2-tailed)	0.15		0.01	0.37	0.12	0.60	0.08	0.10	0.86	0.35	0.65	0.37

Significance is reported for a two-tailed analysis. ** Correlation is significant at the 0.01 level (2-tailed). * Correlation is significant at the 0.05 level (2-tailed).

Table 17. Linear correlation analysis with Pearson Correlation of fall diversity and fall DIFN including litter depth, pH, BD, moisture (%), TC (%), TN (%), Ca (mg/kg), K (mg/kg), Mg (mg/kg), and P (mg/kg).

		Diversity	**DIFN**	**Litter Depth**	**pH**	**Bulk Density**	**Moisture (%)**	**TC (%)**	**TN (%)**	**Ca (mg/kg)**	**K (mg/kg)**	**Mg (mg/kg)**	**P (mg/kg)**
Diversity	Pearson Correlation	1	.01	-0.83**	0.07	-0.25	-0.15	0.39	0.36	0.18	-0.07	0.20	-0.20
	Sig. (2-tailed)		0.98	0.00	0.80	0.37	0.60	0.15	0.19	0.51	0.82	0.47	0.48
DIFN	Pearson Correlation	0.01	1	0.26	0.35	0.45	-0.58*	-0.29	-0.34	-0.19	-0.32	-0.34	0.18
	Sig. (2-tailed)	0.97		0.35	0.20	0.09	0.02	0.32	0.21	0.51	0.24	0.22	0.52
Litter Depth	Pearson Correlation	-0.83**	0.23	1	-0.04	.049	-0.03	-0.62*	-0.52*	-0.03	-.010	-0.16	0.37
	Sig. (2-tailed)	0.00	0.35		0.88	0.07	0.91	0.01	0.05	0.90	0.73	0.56	0.18
pH	Pearson Correlation	0.07	0.35	-0.04	1	0.04	0.03	0.21	0.17	0.14	0.28	0.17	-0.25
	Sig. (2-tailed)	0.80	0.20	0.88		0.88	0.93	0.45	0.55	0.63	0.31	0.55	0.36
Bulk Density	Pearson Correlation	-0.25	0.45	0.49	0.04	1	-0.56*	-0.76**	-0.77**	-0.45	-0.36	-0.48	0.57*
	Sig. (2-tailed)	0.37	0.09	0.07	0.88		0.03	0.00	0.00	0.09	0.19	0.07	0.03
Moisture (%)	Pearson Correlation	-0.15	-0.58*	-0.03	0.03	-0.56*	1	0.28	0.33	0.48	0.41	0.54*	-0.14
	Sig. (2-tailed)	0.60	0.02	0.91	0.93	0.03		0.32	0.24	0.07	0.13	0.04	0.63
TC (%)	Pearson Correlation	0.39	-0.28	-0.62*	0.21	-0.76**	0.28	1	0.97**	0.47	0.63*	0.55*	-0.65**

		Diversity	**DIFN**	**Litter Depth**	**pH**	**Bulk Density**	**Moisture (%)**	**TC (%)**	**TN (%)**	**Ca (mg/kg)**	**K (mg/kg)**	**Mg (mg/kg)**	**P (mg/kg)**
	Sig. (2-tailed)	0.15	0.32	0.01	0.45	0.00	0.32		0.00	0.08	0.01	0.03	0.01
TN (%)	Pearson Correlation	0.36	-0.34	-0.52*	0.17	-0.77**	0.33	0.97**	1	0.64*	0.70**	0.70**	-0.68**
	Sig. (2-tailed)	0.19	0.21	0.05	0.55	0.00	0.24	0.00		.001	0.00	0.00	0.01
Ca (mg/kg)	Pearson Correlation	0.18	-0.19	-0.03	0.14	-0.45	0.48	0.47	0.64*	1	0.66**	0.93**	-0.32
	Sig. (2-tailed)	0.51	0.51	0.90	0.63	0.09	0.07	0.08	0.01		0.01	0.00	0.25
K (mg/kg)	Pearson Correlation	-0.07	-0.32	-0.10	0.28	-0.36	0.41	0.63*	0.69**	0.66**	1	0.77**	-0.51
	Sig. (2-tailed)	0.82	0.24	0.73	0.31	0.19	0.13	0.01	0.00	0.01		0.00	0.05
Mg (mg/kg)	Pearson Correlation	0.20	-0.34	-0.16	0.17	-0.48	0.54*	0.55*	0.70**	0.93**	0.77**	1	-0.49
	Sig. (2-tailed)	0.47	0.22	0.56	0.55	0.07	0.04	0.03	0.00	0.00	0.00		0.06
P (mg/kg)	Pearson Correlation	-0.20	0.18	0.37	-0.25	0.57*	-0.14	-0.65**	-0.68**	-0.32	-0.51	-0.49	1
	Sig. (2-tailed)	0.48	0.52	0.18	0.36	0.03	0.63	0.01	0.01	0.25	0.05	0.06	

Significance is reported for a two-tailed analysis. ** Correlation is significant at the 0.01 level (2-tailed). * Correlation is significant at the 0.05 level (2-tailed).

3.5 Forward stepwise regression

The forward stepwise regression was used to develop a model that might explain which variables are driving the diversity the forest groups. The regression was performed for each season where diversity was the dependent variable and the independent variables were DIFN for that season, litter depth, and all other variables sampled at 0-10 cm depth excluding BD. Bulk density was removed from the analysis because the model initially included BD as a predictor variable for spring diversity. As a result of the lack of significant difference between forest groups ($p>0.05$) and low correlation reported between diversity and BD (Pearson Correlation between -0.08 and -0.25; $p >0.1$), BD was not included in the forward stepwise regression for any season.

The results of the analysis revealed that DIFN was the main predictor of the model for diversity in the spring. The R square value was 0.772 therefore DIFN accounts for 77.2% of the variance in the spring diversity

The forward step-wise regression analysis found that litter depth and percent moisture were predictor variables of summer diversity. As the primary predictor variable for the model explaining the variance for summer diversity litter depth had a R square of 0.615 while percent moisture increased the R square value to 0.698. According to the model litter depth would explain 61.5% of the variance of understory diversity in the summer and percent moisture an additional 8.3% of the variance.

The model resulting from the step-wise regression for diversity in the fall found litter depth was the main predicting variable with a R square of 0.686. Therefore the amount of variance for fall diversity that can be explained by litter depth is 68.6% based on the model produced from the analysis.

Table 18. Forward stepwise regression with spring diversity as the dependent variable.

Model Summary – Spring				
Model	**R**	**R Square**	**Adjusted R Square**	**Std. Error of the Estimate**
1	.879[a]	.772	.755	.677
a. Predictors: (Constant), DIFN				

Table 19. Forward stepwise regression with summer diversity as the dependent variable.

Model Summary – Summer				
Model	**R**	**R Square**	**Adjusted R Square**	**Std. Error of the Estimate**
1	.784[a]	.615	.586	1.461
2	.836[b]	.698	.648	1.347
a. Predictors: (Constant), Mean Litter Depth (cm) b. Predictors: (Constant), Mean Litter Depth (cm), Percent Moisture				

Table 20. Forward stepwise regression with fall diversity as the dependent variable.

Model Summary – Fall				
Model	**R**	**R Square**	**Adjusted R Square**	**Std. Error of the Estimate**
1	.829[a]	.686	.662	1.185
a. Predictors: (Constant), Mean Litter Depth (cm)				

3.6 Summary of fieldwork results

In conclusion, the percent similarity for understory species indicates that the oldest plantation group (est. 1927-1932) was most similar to the reference forest group for summer and fall followed by plantations established in 1949-1961, 1967-1971, and 1978-1981. The youngest plantation group (1978-1981) was most similar to the reference forest group in the spring, followed by plantations established in 1927-1932, 1949-1961, and 1967-1971. There was one spring ephemeral species (*E. americanum*)), including six individuals, noted in the quadrats in one plantation forest study plot, compared with seven species (total of 313 recorded in the quadrats) in the reference group.

The Shannon-Wiener Index of Diversity indicates that the reference forest group had the highest diversity of all forest groups and diversity generally increased with plantation age. Tree density was also highest in the reference forest group, and lowest in the plantation group established in 1967-1971.

The results of the soil analysis revealed the reference forest group generally had the lowest bulk density, shallowest litter layer, and highest levels of TN, TC, cations (Ca, Mg, and K) compared with the other forest groups. The opposite is apparent for the mid-aged plantation group (est. 1949-1961) which had the highest bulk density, deepest litter layer, and lowest levels of TN, TC, cations and highest levels of anions (*i.e.* P).

The results of the correlation analysis revealed that diversity was highly negative correlated ($p<0.01$) to DIFN in the spring, and highly negatively correlated to litter depth in the summer and fall. Bulk density was negatively correlated to moisture and nutrients ($p<0.05$).

The models produced by the stepwise regression predicted that DIFN explained 77.2% of the variance of spring diversity, litter depth and percent moisture explained 69.8% of the variance of summer diversity, and litter depth explained 68.6% of the variance of fall diversity.

4.0 CHAPTER 4 DISCUSSION AND CONCLUSIONS

4.1 Introduction to Discussion and Conclusions

The purpose of the present study was to determine the effects of conventional thinning regimes on the succession of understory vegetation and soil characteristics in red pine plantations in southern Ontario over time. This outcome was motivated by the research questions:

- *How do conventional thinning regimes for red pine plantations in southern Ontario affect the diversity of the understory vegetation and the regeneration of trees?*
- *What variables drive the change in understory vegetation in red pine plantations over time* and *how do they compare to native deciduous reference forests?*
- *How does the understory vegetation composition and diversity in managed red pine plantations compare to the understory of a reference forest?*

This study was designed with the overarching purpose of being able to 1) quantify and compare the understory vegetation diversity and composition among and between plantations and the reference deciduous forest group, and 2) determine whether and how diversity is related to site variables such as light, substrate, and soil characteristics. This study included an examination of a chronosequence of four age groups of red pine plantations and a reference forest group. The desired outcome was to build on previous studies in order to provide forest managers with more knowledge about the ecology of red pine plantations thereby facilitating more informed decisions regarding the future management of these forests and restoration of native floral diversity. The discussion is broken down into sections in order to answer the questions posed throughout this thesis. Conclusions are drawn from the interpretation of the results and findings from referenced literature.

4.2 How do conventional thinning regimes for red pine plantations in southern Ontario affect the diversity of the understory vegetation and the regeneration of trees?

The thinning regime in these managed plantations resulted in an increase in the understory diversity with increasing age of the plantation. The results of the Shannon-Weiner Diversity index are consistent with other findings where diversity generally increased with increasing age of plantations (Newmaster *et. al.* 2006; Parker et. al. 2001). Also, tree density (number of trees/ha) is increasing and was highest in the oldest plantation group (est. 1927-1932). An anomaly was observed in the youngest group (est. 1978-1981) which had an unexpectedly high density in two of the replicates (232 and 49 trees/ha). The variation in the tree density between the replicates in this group was higher than all other groups indicating the initial site conditions or the management of the plantations in the youngest group were different than the other plantation groups. The plantation forest groups were selected based on their land use history (cleared for agriculture), age, and stand composition (pure stands of red pine). One of these plantations, known as DRI345, was recorded by the County as being a pure stand of red pines established in 1981. Additional records from Simcoe County show this plantation was likely previously a Scots pine plantation that was cleared using fire and replanted with white pine. The survival of those replanted trees may have been poor requiring later planting in 1981 of red pine resulting in the mislabeling of this plantation in the records. However, the diversity and richness of the understory vegetation (<1.5m in height) did not appear different than that of other stands of that age group.

The increase in both understory diversity and tree density are part influenced by the thinning regime which results in a disturbance that changes the ecology of the plantation specifically because it results in a change in the abiotic environmental conditions (*i.e.* light, moisture, nutrients) which in turn affects the biotic environment. Commercial thinning of conifer plantations typically involves the use of large machinery that cuts trees at the base, removes the slash (*e.g.* branches, tops) which is left to decompose on the forest floor, and takes only straight stems that are commercially desirable. The resulting disturbance immediately opens up the canopy and adds litter/organic matter to the forest floor as can be seen in the results from the DIFN and litter layer measurement in the plantations examined in this study and discussed in the next section. The use of large machinery also disturbs and exposes the soil to various depths which in turn influences plant diversity and community composition by creating conditions suitable for colonizing species from adjacent communities. The level of disturbance, both to the canopy and the soil can affect the type of colonizing species, the abundance and growth response of extant vegetation or seeds in the seed bank, and the resources available to those species (Hauessler *et al.* 2002). Furthermore, the level of disturbance to the soil can influence the type of species colonizing the site where minor disturbances will favour existing species, whereas larger disturbances to the soil will remove extant vegetation and tends to favour r-selected species including exotic invasive species (Haeussler *et al*. 2002). It is these change in the abiotic conditions that initially drive changes in the biotic environment, thereby resulting in the succession of the understory over time.

4.3 What variables drive the change in the composition of understory vegetation in red pine plantations over time and how do they compare to native deciduous reference forests?

4.3.1 Understory Light Characteristics

Stand density and light interception (Goetz and Prince 1996) are considered crucial factors that drive forest stand development and the succession of the understory (Oliver and Larson 1990) and are the variables most often studied when predicting understory regeneration following thinning (Nyland 1996; Smith *et al.* 1997). The effect of the disturbance caused by thinning was apparent in this study where DIFN was always lowest in the youngest plantation group compared with all others. Prior to the first thinning the foliar shading produced in the youngest plantation group (est. 1978-1981) is quite high. The first thinning opens up the canopy allowing more light to penetrate to the forest floor as can be seen in the higher DIFN in all plantation groups that have received at least one thinning. The lower DIFN in all plantation groups compared with the reference forest group in the spring results in cool and dark spring conditions that have been found to inhibit the establishment of light-demanding spring ephemerals (Lapointe 2001; Whigham 2004). In this study only six individuals of one species of spring ephemeral (*E. americanum*) were recorded in a plantation forest group, while 313 individuals comprising seven species were recorded in the reference deciduous forest group. The lack of spring ephemerals in the conifer plantation may be in part a result of the lower light conditions associated with the conifer plantation groups (Lapointe 2001; Whigham 2004).

The model for the step wise regression analysis indicated that DIFN is the primary variable explaining the variation in diversity in the spring. DIFN was also highly negatively correlated to spring diversity. Son *et. al.* (2004) found similar results in their study where plantations subjected to increasing intensities of thinning (*i.e.* increasing light penetration to the understory) had a significantly higher diversity of understory vegetation. In a study conducted by Harrington and Edwards (1999) the main driving factor influencing understory diversity following thinning was increased light. The darker conditions associated with the younger plantation groups are likely a major inhibitor to understory diversity in red pine plantations.

DIFN was also negatively correlated to percent soil moisture indicating that with an increase in understory light conditions, there is a decrease in soil moisture. The thinning operations and resulting overstory removal causes changes to the microclimate at the ground surface including increases in temperature maxima, higher diurnal temperature ranges, and decreases in surface soil moisture (Aude and Lawesson 1998; Ramovs 2003). Therefore the thinning operations also influence the soil moisture by increasing the amount of light which would then have a negative effect on species that are sensitive to changes in soil moisture content (Ramovs and Roberts 2003). This may in turn inhibit the establishment of native understory species and favour r-selected and exotic invasive species (Haeussler *et al.* 2002).

4.3.2 Litter Depth

These results of the correlation and forward stepwise analyses indicates litter depth was likely a major contributing factor influencing the diversity of the understory in the summer and fall. Thinning of the plantations in this study appears to successively increase the depth of the litter layer up to approximately 60 years after plantation establishment (plantation group est. 1949-1961). During this time the plantation would typically have been thinned two to three times. The first thinning occurs around 30 years since plantation establishment and typically involves the removal of every fourth row - about 30% of the stand (MNR 1999). The second thinning would remove trees that are growing slowly, are unhealthy, or impeding the growth of healthy trees in the stand (MNR 1999). It is during these first two thinning cycles that the greatest amount of slash would have been left on the forest floor to decompose adding to the litter layer. The result of more intense thinning and accumulation of litter is observed in the higher litter depth of the second youngest plantation group (est. 1967-1971). The litter depth is at its greatest in the mid-aged plantation group (est. 1949-1961). Although diversity is not lowest in this plantation group the deeper litter layer is likely inhibiting the germination and emergence of plants. Litter depth is considered a major factor controlling the regeneration of the understory in temperate and boreal forests (Barbier *et. al.* 2008). Litter accumulation has been found to inhibit seed germination, particularly for light-demanding species (Seiwa 1997). Sydes and Grime (1981) also found that litter depth is a critical trait affecting the ability of understory herbs to penetrate upward through the litter layer. Facelli and Pickett (1991) report that light penetration below the litter layer is reduced exponentially with increasing amounts of litter. Higher litter depth has also been found to inhibit seedling emergence for small-seeded species, such as spring ephemerals, that cannot penetrate thick layers of litter (Peterson and Facelli, 1992; Lapointe, 2001; Kanno and Seiwa, 2004; Whigham, 2004). The number of species and abundance of spring ephemerals in the conifer plantations was considerably lower than in the reference deciduous forest group which may also be a result of the deeper litter layer..

The litter layer of conifer plantations has also been found to be nutrient-limited and acidic (Hunter, 1990; Augusto *et al.*, 2002) neither of which were favorable conditions for the germination of nutrient- and light-demanding ephemeral species (Lapointe, 2001; Whingham, 2004). Although the pH and nutrient content of the litter layer was not assessed in this study, the quality of the litter may partly explain why there was a lack of spring ephemerals in all but one plantation study plot in this study. In addition to litter depth being negatively correlated to diversity, it was also found to be negatively correlated to TN and TC at 0-10 cm depth. This relationship is further discussed in section 4.3.4.

Following the pre-commercial thinning, the subsequent thinning cycles would be more selective in the removal of commercially valuable trees and less slash would be left on the forest floor. This explains why the oldest plantation group (est. 1927-1932) has a lower litter depth than the youngest group, and a significantly lower litter depth than the second youngest and mid-aged plantation groups. The oldest plantation group also has the highest diversity of species in the understory compared with other plantation groups further indicating that as the litter depth decreases, the establishment of plants is less inhibited by the litter depth.

4.3.3 Soil Bulk Density, Percent Moisture, and pH

Although no direct correlation with diversity was found between BD, percent moisture, pH, these variables are known to be important variables affecting understory vegetation composition (Pastor and Post 1986; Karlen *et al.* 1997.).

The pH in the samples collected from 0-10 cm, 10-20 cm, and 20-40 cm were not significantly different across all forest groups. Because the pH in conifer plantation soil is typically lower than deciduous forests (Eviner and Chapin 2003) one would expect to find significant differences between the plantation groups and the reference deciduous forest group. However, the smaller sample size and natural variability in the soils may partly explain the lack of statistically significant differences between forest groups. Another consideration may be the buffering capacity of the calcareous bedrock underlying the glacial till. However, the A and upper B horizons of the soils in the study areas are considered acidic to strongly acidic (Hoffman, 1990). Furthermore, assessment for the presence of carbonates in the soil using a 10% HCl solution detected carbonates in only five of the 44 soil pits indicating that carbonates were not buffering the pH of the soil at least in the upper 80-100 cm of the soil. Deeper depths of the soils in the study area are found to be closer to neutral as is also described by Hoffman (1990) which is likely a result of the buffering capacity of the underlying calcareous bedrock. That being said, the pH of soils is still an important variable to consider especially because it can affect the uptake and immobilization of exchangeable cations from the soil pool thus the amount of nutrients available to plants (Brand *et. al.* 1986).

There were significant differences detected in BD and soil moisture between the reference deciduous forest group and some of the plantation groups, however, their impact to understory diversity is not directly evident. With an increase in BD, the pore space between the soil particles decrease therefore reducing the amount of pore space that can be filled by water (McNabb *et al.* 2001). Furthermore, the relationships between root growth and BD are well established where a higher BD density may inhibit the rooting capacity of some species and preclude other species all together (Taylor *et al.* 1966; Sands *et al.* 1979). However, compared with a similar study examining changes in soil properties over time in conifer plantations (McPherson and Timmer 2002), the BD in the plantations in this study, even at its highest (1.28 g/cm^3) was similar to the BD measured in the mature plantation from their study (1.24 g/cm^3). Furthermore, these values are considered suitable for the establishment of understory species (Fisher and Binkley 2000; Gale *et al.* 2003) therefore BD would have had little to no effect on differences in diversity between sites. However, BD appears to have a greater influence on percent moisture which is negatively correlated to bulk density. A higher bulk density results in a lower percent soil moisture (McNabb *et al.* 2001) which is evident in the results of this study. The influence of BD on percent soil moisture may be indirectly influencing the diversity in the understory since soil moisture was one of the predictor variables of the variance in the understory diversity in the summer. Understory species are typically sensitive to changes in moisture content of the soil (Ramovs and Roberts 2003).

4.3.4 Soil Nutrients

The inventories of the understory included all plants <1.5 m in height, where forest herbs comprised the vast majority of the species identified. The rooting volume of forest herbs are generally limited to surficial soils (Bauhus and Messier 1999). Therefore the statistical analysis and discussion around soil nutrients and their impact on understory diversity is focused mainly on the samples gathered from a depth of 0-10 cm.

Agricultural practices often result in the loss of soil organic matter (Houghton *et al.* 1983; Schlesinger 1990) and associated declines in nutrients (Rolfe and Boggess 1973; Inouye *et al.* 1987; Nowak *et al.* 1991; Quideau and Bockheim 1996). Therefore the previous agricultural land use of these sites is likely the reason for the lower concentrations of these nutrients in the plantation forests compared with the reference deciduous forest group.

Soil C and N in plantation forests have been of upmost concern to soil scientists because they are the more limiting of the macronutrients considered in soil fertility (Pritchett and Fisher 1987). The lack of difference in TC and TN between plantations may indicate that either not enough time has passed since plantation establishment for a change in the amounts of TC and TN to be detected, or possibly that the sample size was too small considering the natural variation and heterogeneity of soils even within a small area such as the study plots (1 ha). McPherson and Timmer (2002) found that an increase in organic matter contributed to a two fold increase in TN in mature red pine plantations. Neither TN nor TC were measured in newly established sites following agricultural activity, therefore the increase in these nutrients from plantation establishment is not known. Ellert and Gregorich (1996) compared the amounts of soil organic carbon and TN in cultivated soils versus forest soils and found surface layers of the cultivated soils had 34% less carbon and 19% less N than forests. Ellert and Gregorich (1996) attributed the difference in carbon in agricultural soils was due to the reduced organic matter inputs and enhanced rates of plant litter decay while differences in nitrogen were largely dependent on the application of fertilizer in cultivated sites. In this study, even after 82 years, the soil TN and TC in the oldest plantation has not been restored to levels found in the reference deciduous forest group.

One would expect that there would be a more apparent increase in the amount of TC in the soil of plantations with time, especially given the addition of organic material following thinning operations and litterfall. The lower levels of TC in the conifer plantations may be in part due to the chemical properties associated with litter in plantations. Nakane (1995) has suggested that the lower rate of decomposition of the leaf litter in red pine forests, compared to that of oak forests may be due to the chemical properties of the litter layer. Generally, conifer needles have higher amounts of lignin and lower amounts of nitrogen resulting in a slower decomposition rate (Hendricks and Boring, 1992). Since bacteria require large amounts of N to process organic matter (Marshall 2000), organic matter low in N will decompose more slowly. Therefore, the addition of organic matter, and therefore an increase in TC in the soils of conifer plantations may be occurring more slowly, explaining the significantly lower amounts of TC in soils of the plantations compared with the reference deciduous forest groups.

Red pine needles have markedly lower concentration of N compared with deciduous leaves (Aber *et al.* 1990) which likely accounts for the significantly lower concentration of TN in the soils in the red pine plantations compared with the reference forest group. Further contributing to the lower amount of TN in the plantation groups compared with the reference forest group may be the abundance of species in the understory, of plantations compared with the reference forest group. Herbaceous plants make up a relatively high proportion of species in the understory and relative to their biomass, forest herbs disproportionately cycle essential plant nutrients (*e.g.*, N, P, K) in forest ecosystems (Muller 2003; Welch *et al.* 2007). There is a significantly higher abundance of understory plants in the reference forest group compared with the two youngest plantation groups (est. 1978-1981 and 1967-1971). Although not significantly different than the two oldest plantation groups (est. 1949-1961 and 1927-1932), the mean abundance of understory plants in the reference forest group is twice that of any plantation group in the spring. During the spring freshet nutrients may be leached from the upper layers of soil if not retained in the biomass of early emerging plants. This phenomenon has been described by Muller and Borman (1976) who found that uptake of essential nutrients, especially nitrogen, by spring ephemerals before the canopy develops helps to reduce the leaching of nutrients in the soil, which they termed the `vernal dam theory`. This theory and the comparison of the abundance of spring ephemerals in the plantation groups and the reference forest groups is explained further in section 4.4.

The amounts of Ca, Mg, K, and P in the soils of the plantation groups were variable within and among groups and did not differ significantly from the reference deciduous forest group. The management of these plantations may partly explain the variability in these nutrients. During the thinning operation the slash is left behind and foliage and branches contain such disproportionately high nutrient levels that when they are left on site, after logs are removed, most of the total nutrients on that site are conserved (Stanley and Montagnini 1999). The replenishment of soil nutrients in red pine plantations to the surface soils may also occur as a result of a the extensive root systems of red pines (Fayle 1975) acting as a “nutrient pump” (McPherson and Timmer 2002) by taking up nutrients from the deeper soil layers that are later redeposited on the forest floor as litter therefore concentrating nutrients in the surface soil layers (Fisher 1990). However, the role of the “nutrient pump” in affecting the amount of nutrients in the upper layer of soil should result in a gradual increase in the amount of nutrients in the soil. This trend is not evident and indicates other factors are likely influencing the amount of nutrients in the soils of plantations. Furthermore, the amounts of these nutrients at deeper depths are apparently lower and there is more variability in the amounts for all forest groups including the reference forest. The addition of nutrients to the surface soils through uptake by the red pines as well as the practice of leaving the slash on the surface to decompose would likely contribute to the variations in shallow soil nutrients.

The lack of significant difference of pH in the upper 40 cm of the soil and the general lack of a correlation between soil nutrients and pH indicates that pH may not be playing a major role in driving the differences in soil nutrients. Soil pH influences the soil biology and chemistry simultaneously and may not in and of itself provide direct information as to which soil processes are being affected and how pH may in turn affect the capacity of the soil (Schoenholtz *et al.* 2000). In some instances soil pH should more appropriately be considered a surrogate examining the complex influence pH has on limiting nutrients and in some cases may not be a useful parameter in measuring soil quality (Aune and Lal 1997).

4.4 How does the understory vegetation composition and diversity in managed red pine plantations compare to the understory of a reference forest?

The diversity of conifer plantations was consistently lower in all age groups for all seasons than the reference deciduous forest group as was expected and has been found in other studies comparing plantations to mature native forest stands (Goldblum 1998; Scheller and Mladenoff 2002; Newmaster *et al.* 2006; Aubin *et al.* 2008). The trajectory of understory diversity in the plantation groups indicates diversity is increasing with time since plantation establishment. The diversity in the oldest plantation group (est. 1927-1932) was not significantly different than the reference deciduous forest group for any season indicating the level of diversity in the plantations are reaching that of the native forest stands. However, the vegetation assemblages were markedly different between the plantation groups and the reference forest group. This was apparent in the spring, particularly with respect to the low number of spring ephemerals (6 individuals) compared with the reference forest group (313 individuals). Several factors may account for the lack of spring ephemerals in the conifer plantations. The litter depth was significantly higher in all but the oldest plantation compared with the reference forest group. As mentioned previously litter accumulations can inhibit seed germination, particularly for light demanding species such as spring ephemerals (Seiwa 1997). If there is a seed bank of spring ephemeral herbs in the soil, the depth of the litter may also prevent the ability of these species from penetrating upward through the litter layer (Sydes and Grime 1981; Peterson and Facelli 1992; Lapointe 2001; Kanno and Seiwa 2004; Whigham 2004). Facelli and Picket (1991) report that light penetration below the litter layer is reduced exponentially with increasing amounts of litter which may further inhibit the growth of spring ephemerals. Litter has also been found to impede the establishment of understory vegetation, particularly in younger plantations (Halpern 2005). As the model produced by the forward stepwise regression suggests, litter depth is an important variable affecting diversity in the summer and fall. The greater litter depth in the younger plantation groups (est. 1978-1981 and 1967-1971) compared to the oldest plantation group (est. 1927-1932) and the reference forest group partly explains the differences in diversity, composition, and abundance of species found in each forest group.

Spring ephemerals are nutrient demanding (Lapointe 2001; Whigham 2004) and the litter layer of conifer plantations is nutrient-limited and acidic (Hunter 1990; Augusto *et al.* 2002) which are not favourable conditions for the germination of ephemeral species. This phenological group is thought to play a crucial role of retaining and cycling nutrients particularly in the spring when uptake by trees is minimal. This was documented by Muller and Borman (1976) who found that uptake of essential nutrients, especially nitrogen, by spring ephemerals before the canopy develops helps to reduce the leaching of nutrients in the soil, which they termed the `vernal dam theory`. More recent field and laboratory testing of this theory by Rothstein (2000) have found that spring ephemeral uptake of nitrogen was large relative to nitrate leaching in the spring, however, these experiments failed to support the theory that the removal of these spring ephemerals would result in lower amounts of N in the soil during the summer months. Although the soil samples were not taken during the spring surveys, the larger amounts of TN in the soil of the reference forest group may be partly due to the presence of spring ephemerals and generally the larger diversity in reference forests which likely plays a role in reducing the loss of nitrogen from the soil in the spring (Whigham 2004).

The previous agricultural land use history of the site may also influence the presence, or absence, of spring ephemerals in the understory in the plantation groups (Bellemare 2002). Prior to plantation establishment, the plantations would have been agricultural land for some time. Given that the seeds of spring ephemerals are only viable for several years (Baskin and Baskin

1998), the years of farming these areas would have eliminated the presence of a viable spring ephemeral seed bank. Following plantation establishment the understory has been repopulated by seeds dispersed from surrounding vegetation communities. Some plants that have become established in the conifer plantations are dispersed by wind (*e.g. Taraxacum officinale*) and by wildlife (*e.g.* seeds of *R. idaeus* and *M. canadense* by birds and mammals eating their fruit). Spring ephemerals are typically dispersed by ants thereby being considered as having a high conservation value (Keddy and Drummond 1996; McLachlan and Bazely 2001; Aubin *et al.* 2007; Aubin *et al.* 2008). This results in the slower dispersal of the seeds and restricts their spread to communities inhabited by seed dispersing ants. Therefore, in addition to unfavourable site conditions due to the deeper litter layer in conifer plantations, the restricted colonizing capacity of spring ephemerals may explain the lack of this group in the understory of the plantation groups.

Another possible explanation for the lack of spring ephemerals in the understory of the plantation groups is the design of this study. Study plots were specifically selected to be no closer than 100 m to the edge of the plantation in order to minimize edge effects, including the presence and abundance of species that may colonize from adjacent communities. The design of the study was meant to focus on variables affecting the succession of the understory on a temporal rather than spatial scale. The rate of colonization and species composition within a community are partly determined by the size of the community being examined (*i.e.* the size of the fragment) and the distance to propagules (*i.e.* source of colonizing species). These factors form the crux of the Island Biogeography Theory proposed by MacArthur and. Wilson (1963) that states that the number of species established on an island (or in the case of this study, a regenerating forest community) represents a dynamic equilibrium between the immigration of new colonizing species and the extirpation of previously established ones. Adjacent communities and surrounding land use would have a major role in determining the succession of the conifer plantations that are essentially starting at an earlier stage of secondary succession. The vegetational composition of the surrounding communities would add another variable that would need to be considered in this study had study plots been closer to the edge of the plantation (Hartley 2002). The transport of seeds to the study plots by wildlife would have occurred given the distance most birds and mammals (*e.g.* deer) travel to find food. This explains the higher abundance of red raspberry (*R. Idaeus* L. ssp. *strigosus*) (dispersed by birds and larger mammals such as deer (Whitney 1986)) and Canada mayflower (*M. canadense* L.) (dispersed mainly by birds (Crowder and Taylor 1984)). However, the seeds of spring ephemerals are mainly ant-dispersed (Lapointe 2001) further explaining why such a low number of this phonological group was observed in the study plots of the plantation forest groups.

The percent similarity of each plantation group to the reference deciduous forest group also provides some insight into the understory dynamics. The increase in percent similarity between plantations with increasing age indicates that the dominant species colonizing the understory varies in younger plantations and is likely a result of initial colonizers from adjacent lands. With time, the dominant species between the plantations become more similar resulting in the higher percent similarity. The species contributing to the high percent similarity in the spring and summer were *M. canadense* and *R. idaeus*. *M. canadense* is a common native herbaceous plant that has a wide ecological amplitude (Gunn 1994). *R. idaeus* is a biennial shrub, typically found in open woodlands, that vigorously reproduces vegetatively (clonally) and by seed (Chourmouzis, *et. al*. 1997). In the fall both of these species did contribute to the percent similarity between the older plantations, however, they were not dominant therefore their contribution to the percent similarity was lower. The abundance of *R. idaeus* did not decrease as this result might suggest. The lower account of this species is due to the sampling method whereby the drop of the pencil would fall below the canopy of *R. idaeus.* The stems of *R. idaeus* are not densely clustered therefore the pencil would not as frequently come into contact with their stem. By autumn the stems of *R. idaeus* are over 1 meter in height with the majority of the foliage around this height, therefore little surface area of the plant takes up space on the forest floor where the pencil would come into contact with other plants.

One of the main limitations of the percent similarity statistic occurs when a low species richness exaggerates the relative abundance of a few species; when those species are similar to the community being compared, the percent similarity between those communities will appear higher. Also, it does not take into account the overall abundance of those species compared with another site (*i.e.* there may be a high total abundance of species in one site compared to another). This is the case in the spring where the youngest plantation group (est. 1978-1981) had a species richness of four with only 33 individual plants recorded in the quadrats, producing a relative abundance of 28.6% for *M. canadense*. The species richness in the oldest plantation group (est. 1927-1932), mid-aged group (est. 1949-1961), and reference forest group are nine, 10, and 22 respectively, while the total number of individuals recorded were 99, 252, and 510 respectively. Although there may be more species similar in the older plantations to the reference forest group, the relative abundance of those species was lower when compared with the youngest plantation group.

After 82 years since being established, the oldest plantation has an understory composition that is as high as 30% similar to reference forest group indicating that the understory diversity in plantation groups is increasing with time. However, the percent similarity is still quite low. Several studies have found that the understory plant community composition and insect communities in plantations would take decades to centuries to regenerate, potentially never fully regenerating to represent primary forests of the region (Peterken and Game 1984; Duffy and Meier 1992; Robinson *et al.* 1994). Since insect communities, particularly ants are responsible for the dispersal of spring ephemeral herbs, the establishment and proliferation of these species in conifer plantations will be a very slow process.

Another factor that has been attributed to slower successional change in the understory of conifer plantations is the presence and often high abundance of non-native species (Kellman 1980; Jumpponen *et al.* 1998). Non-native species are known to out-compete native species for resources and preclude native species from establishing in the understory of conifer plantations (Parker *et al.* 2001; Wingham 2004; Newmaster et al 2006). The relative abundance of non-native species in the plantation forest groups was generally higher than the reference forest group. The plantation groups from youngest to oldest contained 5.8%, 50.1%, 7.3% and 8.2% relative abundance of non-native species while the reference forest group had a relative abundance of 0.8%. With the exception of the mid-aged plantation group (est. 1949-1961), the understory of the plantations in this study generally had a low relative abundance of non-native species indicating the lower diversity in these conifer plantations is likely not due to competition with non-native species.

Tree density for all plantation forests groups was found to be lower than the reference forest group and significantly different. However, the assessment of the regeneration of trees in the understory indicates that the tree density is increasing and becoming more similar in composition to the reference forest group. This indicates that trees in the understory are regenerating towards a similar composition to that of the reference forest group. There is a mosaic of plantations and natural stands of forests in Simcoe County where the plantations are often adjacent to the natural stands. The proximity of natural stands and the ability of these tree species to disperse seeds by wind and animals would contribute to the regeneration of trees in the understory (Hartley 2002).

4.1 Summary of the Research Findings

The management and thinning regime of the red pine plantations in this study have resulted in an increase in understory diversity and tree regeneration due to the changes in the abiotic conditions, mainly DIFN. With increasing age of the plantation the light regime in the understory more closely resembles that of the reference group which is likely influencing the diversity in the understory and promoting tree regeneration. The composition of regenerating trees is similar in the oldest plantation group indicating the management of these red pine plantations will result in a community dominated by trees species found in the reference forest group. However, understory species composition is still quite different between the plantations and reference forest group indicating the understory is either slow to develop, is being inhibited by the abiotic conditions of the site, or the successional trajectory of the composition of understory species is moving in a different direction. There is a notable difference in the number of species identified and abundance of spring ephemerals noted in the quadrats surveyed in the understory of the plantation groups compared with the reference forest group indicating that the spring ephemeral species are not regenerating. Soil characteristics in the plantation groups are also generally different than the reference forest group and are partly due to the previous agricultural land use, and the composition of vegetation in red pine plantations. The combination of previous agricultural land use, the thinning regime favouring r-selected species, deeper litter depths, and the slow recruitment of native understory species, particularly spring ephemerals, are together influencing the composition of the understory in red pine plantations and have resulted in a different composition of understory species compared with the reference forest group.

4.2 Applications of the Research Findings

Red pine plantations can be considered a good first step in restoring the disturbed and degrading landscapes that remained after deforestation and farming following European settlement. Current management of these plantations has played an important role in not only maintaining the health of the commercial timber, but in restoring the soils and understory vegetation. There has been increasing interest understanding the succession of the understory of conifer plantations specifically for the purpose of increasing diversity and converting these stands into native deciduous forests (Parker 2008). The results of this study indicate that the diversity of understory vegetation is increasing over time in managed red pine plantations as is tree density, and the species composition of regenerating trees in these plantations is similar to that of the native deciduous forests in the study area. These results demonstrate that the current management and thinning regime applied to these red pine stands is acting to restore the understory. Therefore, plantations that are properly managed are not ‘biological deserts’ and can successfully restore forest cover and improve soil quality.

Current management of the plantations in this study successfully improves site conditions, increases understory diversity, encourages the regeneration of trees, and effectively accelerates succession of the plant community. The increase in tree density and similar composition of tree species demonstrates that current thinning practices do favor the regeneration of trees in the understory. However, these plantations are currently not managed specifically to restore understory diversity, particularly species composition. The frequency of thinning operations and the resulting disturbance causes changes in understory light regimes which are expected to favor generalist species (Herault *et al.* 2005) and early-successional and exotic species (*e.g.*, Collins and Picket 1998; Parker *et al.* 2001; Newmaster *et al.* 2006). Forest herbs are particularly sensitive to competition with early-successional species following disturbances such as thinning and gap creation (Meier *et al.* 1995). Further, clonal species (*e.g. R. idaeus*) have been found to proliferate rapidly in canopy openings and would be differentially favored by thinning (*e.g.*, Tappeiner *et al.* 1991; Tappeiner and Zasada 1993; Huffman *et al.* 1994; O'Dea *et al.* 1995). Although this study did not look particularly at the plant functional groups or guilds, the species identified in the plantation groups are mainly generalist species compared with those species found in the reference forest plots.

Although conifer plantations may be an artifice, they can be managed in a way that not only maximizes the yield of commercially desirable timber, but mimics natural disturbance, albeit more controlled and more uniform. Red pine plantation establishment and management has been studied and modified since the late 1800s mainly for the purposes of maximizing the yield of commercial timber (Lundgren and Buckman 1998). Initial stand density and thinning regimes affect stand growth, tree diameter, costs, and ultimately profits earned from red pine plantations (Lundgren and Buckman 1998). Management of plantations for commercial yield can still be achieved while increasing understory diversity.

Whether being managed for commercial yield or for restoration to a native woodland, the main variables inhibiting understory development in these plantations appears to be the light characteristics, particularly in younger plantations, and the litter depth. Pre-commercial thinning usually takes place around 30 years after plantation establishment. An earlier thinning can improve understory light conditions and the microclimate of the site, both of which would promote the growth of vegetation in the understory. Earlier thinning has been found to promote a vigorous understory of mid-tolerant species (Parker *et al.* 2008) without compromising timber production objectives (Dickmann *et al.*1987; Bender *et al.* 1997). Also, given that litter accumulates to a maximum depth around 60 years since plantation establishment, thinning of the litter layer or scarification of the surface of the soil prior to this point would reduce the depth of the litter layer and allow the germination and proliferation of understory vegetation including tree regeneration. Precaution should be taken with any measure that in effect increases the disturbance of the soil, not to promote the establishment or proliferation of exotic invasive species. Thinning of the litter layer will improve conditions for the germination of plants in the understory; however, the disturbance associated with thinning may favour generalists including exotic invasive species (Parker *et al.* 2001; Newmaster *et al.* 2006). Therefore if possible, thinning of the litter layer should take place closer to a source of propagules that are desirable, such as from an adjacent native forest. This would improve the success of increasing native species composition in the understory. Whereas, if the adjacent community is comprised of exotic species, particularly exotic invasive species, any disturbance to the soil including thinning of the litter layer may encourage the germination of exotic invasive species. Thinning of the litter layer should follow immediately after the first precommercial thinning operation since there has been very little regeneration of the understory up to this point. The rows created during the first precommercial thinning will be used as access rows for the harvesting machinery in future thinning operations. The use of this machinery been known to disturb extant vegetation (Hunter 1990; Moore and Allen 1999), therefore efforts to promote regeneration of the understory in the access rows is not suggested.

Where plantation management includes restoration of native understory diversity and is designed to promote the regeneration of tree species, a more intensive thinning regime can be applied. Several studies have examined the effect of increased stand thinning and creation of canopy gaps with the purpose of increasing understory diversity and promoting tree regeneration (Parker *et al.* 2001; Parker et al 2008; Ares *et al.* 2009). The results of these studies find that creating canopy gaps of 100-150% the height of the canopy trees can improve light and microclimate conditions and favour the regeneration of understory vegetation. Increased pre-commercial thinning of two of every 5 rows (40%) as opposed to conventional thinning (one of every four rows) can also accelerate the regeneration of understory plants (Parker *et al.* 2008).

Where management of plantations includes restoration of ecological integrity through conversion of these stands to a natural forest comprised of a diverse assemblage of plant species similar to those found in native woodlands, a different management approach needs to be considered. In this study the oldest plantation group, after 82 years since being established, only has a 30% similar species composition in the understory of the reference deciduous forest group indicating either the understory composition is slow to develop into a composition similar to the reference forest group, or the successional trajectory of the understory vegetation is following a different path all together. This is particularly evident with respect to the number of spring ephemeral species found in the plantation forest groups. Current management and harvesting methods may actually prevent the establishment of understory vegetation, particularly herbaceous vegetation, at least up to 82 years since plantation management. Further, without active restoration, the composition of species regenerating in the understory in plantations may remain dissimilar to native forests for decades to centuries (Goldblum 1998; Flinn and Marks 2007). In particular, the conditions in red pine plantations are not suitable for the establishment and proliferation of this phenological group. The slow dispersal mechanism of the seeds from spring ephemerals would also contribute to the lack of regeneration of this group, especially in the interior of plantations. Given the important role spring ephemerals play in nutrient cycling, more attention and active restoration would be required to reintroduce this group into plantation forests.

The restoration of woodland herbs should take place after thinning regimes since the use of heavy machinery and the resulting disturbance to the litter layer and soil (Ramovs and Roberts 2005). Further, current site conditions (*e.g.* light characteristics, soil quality, and composition of vegetation) should be considered before determining the species assemblage that will be used to restore understory diversity. Assembly rules should therefore be considered when determining the order and timing for restoration of vegetation (Keddy 1992; Murphy 2004). Restoration of the understory herbs, including spring ephemerals, in plantations can be accomplished by a number of methods such as planting of nursery grown stock or by borrow pitting. Borrow pitting involves the transplanting of a species including the soil surrounding the plant as not to disturb the roots. This survival of the plant will be higher since the roots are intact and the soil ecosystem (*e.g.* nutrients, mesofauna, microfauna, fungi and microbial community) remains unchanged. An additional benefit to borrow pitting is the inclusion of the seeds from other species. Any transplants should be taken from a community where that species is abundant. Care should also be taken not to transplant unwanted species such as exotic invasive species.

Plantations do play an important role in providing timber and indirectly protect biodiversity by reducing pressure to harvest timber from natural forest stands (Sedjo and Botkin 1997; Rudel 1998; Messier et al 2003). Therefore if the goal of plantation management is primarily to maximize commercial value, not for restoring native woodlands, selecting a diversity of planted trees and promoting understory diversity through management can still earn comparable revenues to monocultures while improving the ecological integrity of the forest stand (Barbour *et al.*, 1997). For example, in Simcoe County, planting a mix of red pine and white pine with a wider spacing to accommodate the later under planting of red oak and sugar maple would provide a diversity of canopy species that are well suited for the types of sandy soils associated with this area. These species are all commercially valuable. The thinning regime in these stands can be used to promote the health of the planted species while increasing the diversity in the understory by improving the variables that normally inhibit understory development (*e.g.* light characteristics and litter depth).

If the goal of forest managers is to simply increase diversity in the understory and encourage tree regeneration without consideration of understory composition, the current management regime is achieving that goal. However with a more recent focus on converting plantations to native forests and the need to improve ecological integrity of forest stands through increasing diversity, there is more of a need to understand the variables driving the succession of the understory of conifer plantations. The ecological integrity of plantation forests, particularly monocultures, can be at risk due to pests (*e.g.* bark beetle predators) and pathogens (*e.g. Armarillia spp.*) that interact with the biotic and abiotic (Erbilgin and Raffa 2002). Compared to a plant community with high biodiversity, a community low in biodiversity (including genetic diversity, species diversity, structural diversity, and functional diversity) is less resistant to pests and disease and is generally less resilient and may not recover following a disturbance (Carnus *et al.* 2006). Therefore, increasing biodiversity, at least in the understory of red pine plantations, should be considered at least to improve the ecological integrity of the forest ecosystem. Furthermore, considering the goal of ecological restoration is typically "to return an ecosystem to its historic trajectory" (SER 2004), the current management of these red pine plantations is not meeting this end. Therefore further considerations in ecological restoration would be required to achieve an understory composition similar reference forest groups.

4.3 Recommendations for Further Research

This study examines the changes in the diversity in the understory of managed red pine plantations and attempts to understand what variables drive this change. In addition to determining understory diversity and regenerating tree density, 11 variables were measured. In total three replicates from each of the four plantation age groups and the reference forest group were studied. Given the amount of variance in values associated with the variables measured, especially soil nutrients and pH, more replicates would have allowed for a more statistically robust analysis. The results of the analysis did however reveal where trends existed and can provide future research endeavours with information necessary to determine an effective sample size.

This study attempted to examine how selected variables may influence seasonal differences in understory diversity. However, when examining the effect of these variables on the diversity for a particular season, these variables should all be sampled in that particular season. This study collected soil samples and measured litter depth only during the early fall. Since there are seasonal differences in both soil nutrients and litter depth and soil samples were only taken in the fall as were litter depth measurements, the higher correlation between diversity and litter depth in the fall may be a result of the timing of sampling.

Through the literature searches and results of this study, there appears to be little attention paid to the spatial dynamics associated with the understory regeneration in managed plantations. This component was not examined in this study due to the additional scope of sampling and time required to examine the spatial dynamics of understory succession. The role of surrounding vegetation communities on the understory succession is critical to understand, especially if one is considering restoring the understory of the plantation and promoting the regeneration of the plantation to a native forest. Adjacent natural forests stands would act as a source for propagules and with active restoration could be used to accelerate the increase in functional, structural, genetic and species diversity of conifer plantations.

The data gathered from this study could be analyzed further to look at the functional group associations found in the plantation groups and reference forest group. Ordinations and cluster analysis would further elucidate how the diversity and composition of species in plantations differs from reference deciduous forests. The results of this analysis could further provide plantation managers with information about what phenological groups may be lacking or underrepresented and how the addition of these groups may improve stand health and even the value of the timber.

4.4 Conclusions of the Study

In place of a long term study of restoration of the understory of red pine plantations, this study examined the understory diversity in four age groups of managed red pine plantations under the same management regime in forests managed by Simcoe County. Biophysical characteristics including light, woody regeneration, litter depth, and soil nutrients were gathered from replicates of each age group and from reference forests in order to determine how each variable changed and contributed to the succession of the understory diversity. Understory diversity was the main focus of the study since it is often used as an indicator of ecological integrity (Gilliam and Roberts 2003; Nilsson and Wardle 2005). Measuring the structure, diversity, and composition of the vegetation provides information on successional pathways, habitat suitability, ecosystem productivity, susceptibility to invasions, ecosystem resilience, and a measure of ecosystem integrity (Anand 2000; Bash & Ryan 2002; McLachlan & Bazely 2003). This data was collected, analyzed and interpreted for each plantation forest group and the reference forest group. The study elucidates how each variable interacts and contributes to the succession of the diversity in the understory and how they compare to reference forests characteristics. The management and thinning regime of the red pine plantations in this study have resulted in an increase in understory diversity and tree regeneration. With each additional thinning cycle and the regeneration of hardwood trees the light regime in the understory more closely resembles that of a natural forest stand. Understory diversity and tree density have increased and are not significantly different than the reference deciduous forest group. The composition of regenerating trees in the oldest plantation group is also similar to the reference group indicating the management of these red pine plantations will result in a community dominated by trees species found in natural forests of that area. However, understory species composition is still quite different between the plantations and the reference forest group. This indicates that the understory is either slow to develop, groups of herbaceous plants are being inhibited by the abiotic conditions of the site (light and leaf litter depth), or the successional trajectory of the composition of understory species is different. Soil characteristics in the plantation groups are also generally different than the reference forest group. Particularly, TN and TC are significantly lower in plantation groups than the reference deciduous forest group.

If the goal is to simply improve soil conditions, increase diversity in the understory and encourage tree regeneration without consideration of understory composition, the current management regime is achieving that goal. However with a more recent focus on converting plantations to native forests and the need to improve ecological integrity of forest stands through increasing diversity, management of these plantations should be modified. This might include changes to the conventional thinning regime such as earlier pre-commercial thinning, thinning of the litter layer, the creation of gaps, and/or an increase in row removal to reduce the density of the stand. These changes in the thinning regime would improve abiotic conditions and promote the establishment of plants in the understory. Active restoration through the planting of native herbs and hardwood plants considering current site conditions and assembly rules can further achieve improve ecological integrity. Whether there is a need to harvest the plantation for commercial timber, or a desire to promote the succession of the understory with the goal of restoring the plantation to a native woodland, current management of the red pine plantations is successful in promoting the regeneration of trees and increasing the diversity of understory vegetation. However, in order to direct the successional trajectory of the understory vegetation of red pine plantations to a composition similar to the native woodlands of that area, active restoration should be considered.

REFERENCES

Aber, J.D., J.M. Melillo, and C.A. McClaugherty. 1990. Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. Canadian Journal of Botany **68**: 2201-2208.

Albright, S. C., W. Winston, C. Zappe. 2008. Data Analysis and Decision Making with Microsoft Excel. South-Western College Publishers, Cincinnati, OH.

Anand, M. 2000. Fundamentals of vegetation change - complexity rules. Acta Biotheorica **48**:1-14.

Anderson, M.C., 1964. Studies of the woodland light climate. 1. The photographic computation of light conditions. Journal of Ecology **52**: 27-41.

Anderson, W.B. and W.G. Eickmeier. 2000. Nutrient resorption in Claytonia virginica L.: implications for deciduous forest nutrient cycling. Canadian Journal of Botany. **78:** 832-839.

Ares, A., S.D. Berryman, and K.J. Puettmann. 2009. Understory vegetation response to thinning disturbance of varying complexity in coniferous stands. Applied Vegetation Science **12**: 472-487.

Arp, P.A. and H.H. Krause. 1984. The forest floor: lateral variability as revealed by systematic sampling. Canada. Canadian Journal of Soil Science **64**: 423-437.

Aubin, I., S. Gachet, C. Messier, and A. Bouchard. 2007. How resilient are northern hardwood forests to human disturbance? An evaluation using a plant functional group approach. Ecoscience **14**: 259-271.

Aubin, I., C. Messier, and A. Bouchard. 2008. Can plantations develop understory biological and physical attributes of naturally regenerated forests? Biological Conservation **141**: 2461-2476.

Aude, E., and J.E. Lawesson. 1998. Vegetation in Danish beech forests: the importance of soil, microclimate and management factors, evaluated by variation partitioning. Plant Ecology **134**: 53–65.

Augusto, L., J. Ranger, D. Binkley, and A. Rothe. 2002. Impact of several common tree species of European temperate forests on soil fertility. Annals of Forest Science **59:** 233-253.

Aune, J.B., and R. Lal. 1997. The tropical soil productivity calculator - a model for assessing effects of soil management on productivity. *In*: Lal, R., Stewart, B.A. (Eds.), Soil Management - Experimental Basis for Sustainability and Environmental Quality. Advances in Soil Science., Lewis Publishers, London, UK, pp. 499-520.

Aust, W.M., M.D. Tippett, J.A. Burger, and W.H. Jr. McKee. 1995. Compaction and rutting during harvesting affect better drained soils more than poorly drained soils on wet pine flats. Southern Journal of Applied Forestry **19**: 72-77.

Austen, M.J.W; C.M. Francis, D.M. Burke, and M.S.W. Bradstreet. 2001. Landscape context and fragmentation effects on forest birds in southern Ontario. The Condor **103**: 701-714.

Ball, J.B. 2001: Global Forest Resources: History and Dynamics. The Forest Handbook. Oxford, Blackwell Science, 3-22 pp.

Barbier, S. F. Gosselin, and P. Balandier. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved - A critical review for temperate and boreal forests
Forest Ecology and Management **254**: 1-15.

Barbour, R.J., S. Johnston, J.P. Hayes, and G.F. Tucker. 1997. Simulated stand characteristics and wood product yields from Douglas-fir plantations managed for ecosystem objectives. Forest Ecology and Management **91**: 205-219.

Bash, J.S., and C.M. Ryan. 2002. Stream restoration and enhancement projects: is anyone monitoring? Environmental Management **29**(6): 877-885.

Baskin, C.C. and J.M. Baskin. 1998**.** Seeds. Academic Press, Inc., San Diego, CA. 665 pp.

Bauhus J. and C. Messier. 1999 Evaluation of fine rot length and diameter measurements obtained using RHIZO image analysis. Agronomy Journal **91**: 142-147.

Bellemare, J., G. Motzkin, and D.R. Foster. 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. Journal of Biogeography **29:** 1401-1420.

Bender, L.C., D.L.Minnis, and J.B.Haufer. 1997.Wildlife response to thinning red pine. Northern Journal of Applied Forestry **14**: 141-146.

Billington C, V. Kapos. M. Edwards, S. Blyth, and S. Iremonger. 1996. Estimated Original Forest Cover Map - A First Attempt. World Conservation Monitoring Centre (WCMC), Cambridge.

Binkley, D. and D. Richter. 1987. Nutrient cycles and H budgets of forest ecosystems. Advances in Ecological Research **6**: 1-51.

Blank, J., Olson, R. & Vitousek, P. 1980. Nutrient uptake by a diverse spring ephemeral community. Oecologia **47**: 96-98.

Boerner, R.E.J., S.J. Morris, E.K. Sutherland, and T.F. Hutchinson. 2000. Spatial variability in soil nitrogen dynamics after prescribed burning in Ohio mixed-oak forests. Landscape Ecology **15**: 425-439.

Borczon, E.I. 1986. Evergreen Challenge: The Agreement Forest Story. Ontario Ministry of Natural Resources, Toronto, Ontario.

Brand, D.G., P. Kehoe, and M. Connons. 1986. Coniferous afforestation leads to soil acidification in central Ontario. Canadian Journal of Forest Research. **16**: 1389-1391.

Brockerhov, E.G., H. Jactel, J.A. Parrotta, C.P Quine, and J. Sayer. 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity and Conservation **17**: 925-951.

Bryant, D., D. Nielsen, and L. Tangley. 1997. The Last Frontier Forests: Ecosystems and Economies on the Edge. 42. Washington, DC : World Resources Institute.

Burgess, A. 1960. Time and size as factors in ecology. Journal of Animal Ecology, **29**(1): 1-14.

Burke, D.M. K.A. Elliott, S.B. Holmes, and D. Bradley. 2008. The effects of partial harvest on the understory vegetation of southern Ontario woodlands. Forest Ecology and Management **255**: 2204–2212.

Cairns, J. Jr., and J.R. Heckman. 1996. Restoration ecology: The state of an emerging field. Annual Review of Energy and Environment **21**(1): 167-189.

Canada National Parks Act (S.C. 2000, c. 32). 2011. Published by the Minister of Justice at the following address: http://laws-lois.justice.gc.ca.

Carman, R. S. 1941. The glacial pot hole area, Durham County, Ontario. The Forestry Chronicle **17**: 110-120.

Carnus, J-M., J. Parrotta, E. Brockerhoff, M. Arbez, H. Jactel, A. Kremer, D. Lamb, K. O'Hara, and B. Walters. 2006. Planted forests and biodiversity. Journal of Forestry, **104**(2): 66-77.

Carter, M.R. and E.G. Gregorich. 2007. Soil Sampling and Methods of Analysis, 2nd ed. Pinawa, Manitoba: Canadian Society of Soil Science; Boca Raton, FL: CRC Press, pp. 1224.

Chapin, F.S., III, P.A. Matson, and H.A. Mooney. 2002. Principles of terrestrial ecosystem ecology. Springer, New York.

Clements, F.E. 1916. Plant succession: Analysis of the development of vegetation. Carnegie Institute of Washington Publication, No. 242. Washington, DC, pp 512.

Collins, B.S. and S.T.A. Picket. 1998. Response of herb layer cover to experimental canopy gaps. American Midland Naturalist **119**(2): 282-290.

Conde, F; Swindel, F; Smith, E. 1983. Plant species cover, frequency, and biomass: Early responses to clearcutting, burning, widrowing, discing, and bedding in *Pinus elliottii* flatwoods. Forest Ecology and Management **6** (3): 319-331.

Crowder, A.A. and G.J. Taylor. 1984. Characteristics of sites occupied by wild lily-of-the-valley, *Maianthemum canadense*, on Hill Island, Ontario. Canadian Field-Naturalist **98**(2): 151-158.

Deblonde, G.M. Penner, and A. Royer, 1994. Measuring leaf area index with the Li-Cor LAI-2000 in pine stands. Ecology **75**(5): 1507-1511.

De Schrijver, A; R. Devlaeminck, J. Mertens, K. Wuyts, M. Hermy, and K. Verheyen. 2007. On the importance of incorporating forest edge deposition for evaluating the exceedance of critical pollutant loads. Applied Vegetation Science **10**, 293-298.

Devlaeminck, R; A. De Schrijver, and M. Hermy. 2005. Variation in throughfall deposition across a deciduous beech (*Fagus sylvatica* L.) forest edge in Flanders. Science of the Total Environment **337:** 241-252.

Dickmann, D.I., W.J. O'Neill, and N. Caveney. 1987. Wide-spaced red pine: a multiple use opportunity. Northern Journal of Applied Forestry **4**: 44-45.

Drever, C.R., G. Peterson, C. Messier, Y. Bergeron, and M. Flannigan. 2006. Can forest management based on natural disturbances maintain ecological resilience? Canadian Journal of Forest Research **36**: 2285-2299.

Duffy, D.C., and A.J. Meier. 1992. Do Appalachian herbaceous understories recover from clear cutting? Conservation Biology **6**: 196-201.

Ellert, B.H. and E.G. Gregorich. 1996. Storage of carbon, nitrogen, and phosphorus in cultivated and adjacent forested soils of Ontario. Soil Science **161**(9): 587-603

Elliot, K.A. 1998. The forests of southern Ontario. The Forestry Chronicle. **74**(6): 850-854.

Environment Canada. 2004. An invasive alien species strategy for Canada. Government of Canada, Environment Canada. 46 pp.

Environment Canada. 2010. National Climate Data and Information Archive. Canadian Climate Normals or Averages 1971-2000. http://climate.weatheroffice.gc.ca/climate_normals/index_e.html, accessed September 2010.

Erbilgin, N. and K.F. Raffa. 2002. Association of declining red pine stands with reduced populations of bark beetle predators, seasonal increases in root colonizing insects, and incidence of root pathogens. Forest Ecology and Management **164**: 221-236.

Eviner V.T. and F.S. Chapin, III. 2003. Biogeochemical interactions and biodiversity. *In*: Melillo, J.M, C.B. Field, and M. Moldan, eds. *Element interactions: rapid assessment project of SCOPE*. Washington: Island Press.

Facelli, J.M. and S.T.A. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. Botany Review **57**: 1-32.

Fahey, R.T. and K.J. Puettmann. 2008. Patterns in spatial extent of gap influence on understory plant communities. Forest Ecology and Management **255**: 2801-2810.

Fattorini, M., and S. Halle. 2004. The dynamic environmental filter model: how do filtering effects change in assembling communities after disturbance? Pages 96-114 in V. M. Temperton, R. J. Hobbs, T. Nuttle, and S. Halle, editors. Assembly Rules and Restoration Ecology: Bridging the Gap between Theory and Practice. Island Press, Washington, D.C.

Fayle, D.C.F. 1975. Extension and longitudinal growth during the development of red pine root systems. Canadian Journal of Forest Research **5**: 109-121.

Finzi, A.C., C.D. Canham, and N. van Breemen. 1998. Canopy tree-soil interactions within temperate forests: Species effects on pH and cations. Ecological Applications **8**(2): 447-454.

Fisher, R. F. 1990. Amelioration of soils by trees. Pages 290-300 *in* S. P. Gessel, D. S. Lacate, G. F. Weetman, and R. F. Powers, eds. Sustained productivity of forest soils: proceedings of the 7th North American forest soils conference. University of British Columbia, Faculty of Forestry, Vancouver, BC.

Fisher, R.F. and D. Binkley. 2000. Ecology and Management of Forest Soils. John Wiley and Sons Inc., New York, New York. 489 pp.

Flinn, K.M., and P.L. Marks, P.L. 2007. Agricultural legacies in forest environments: tree communities, soil properties, and light availability. Ecological Applications **17**: 452-463.

Foley, J.A., R. DeFries, G.P. Asner, C. Barford, G. Bonan, S.R. Carpenter, F.S. Chapin, M.T. Coe, G.C. Daily, H.K. Gibbs, J.H. Helkowski, T. Holloway, E.A. Howard, C.J. Kucharik, C. Monfreda, J.A. Patz, I.C. Prentice, N. Ramankutty, and P.K. Snyder. Science **309**: 570-574.

Food and Agriculture Organization [FAO]of the United Nations. 2006. Global Forest Resources Assessment 2005 - Progress towards sustainable forest management. Food and Agriculture Organization of the United Nations, Rome, 2005. FAO Forestry Paper 147.

Food and Agriculture Organization [FAO] of the United Nations. 2011. Planted Forests. http://www.fao.org/forestry/plantedforests/en/, accessed, November, 2011.

Garnier, E., J. Cortez, G. Billes, M.L. Navas, D. Roumet, M. Debussche, G. Laurent, A. Blanchard, D. Aubry, A. Bellmann, C. Neill, and J.P. Toussaint. 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology **85**: 2630-2637.

Gedron, F., C. Messier, and P.A. Comeau. 1998. Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density in forests. Agricultural and Forest Meteorology **92**: 55-70.

Gibson, D.J. 1996. Textbook misconceptions: The climax concept of succession. The American Biology Teacher **58**(3): 135-140.

Gilliam, S. 2002. Effects of harvesting on herbaceous layer diversity of a central Appalachian hardwood forest. Forest Ecology and Management. **155**: 33-43.

Gilliam F. S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience **57**: 845-858.

Gilliam, F.S., and Roberts, M.R. 2003. The Herbaceous Layer in Forests of Eastern North America. Oxford University Press, New York, New York. pp. 408.

Givnish TJ. 1987. Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. New Phytologist **106**:131-60.

Goetz, S.J., and Prince, S.D. 1996. Remote sensing of net primary productivity in boreal forest stands. Agricultural and Forest Meteorology **78**: 149-179.

Goldblum, D. 1998. Regeneration in unmanaged conifer plantations, upstate New York. Northeastern Naturalist **5** (4): 343-358.

Haeussler, S., L. Bedford, A. Leduc, Y. Bergeron, and J.M. Kranabetter. 2002. Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. Silva Fennica **36**: 307-327.

Halpern, C.B. 1989. Early Successional patterns of forest species: interactions of life history traits and disturbance. Ecology **70**(3): 704-720.

Halpern, Charles B., Donald McKenzie, Shelley A. Evans, and Douglas A. Maguire. 2005. Initial responses of forest understories to varying levels and patterns of green-tree retention. Ecological Applications **15**:175-195.

Hanan, N.P. and A. Begue. 1995. A method to estimate instantaneous and daily intercepted photosynthetically active radiation using a hemispherical sensor. Agricultural and Forest Meteorology **74**: 155-168.

Hansen A.J., R.P. Neilson V.H. Dale, C,H, Flather, L.R. Iverson, D.J. Currie, S. Shafer, R. Cook, and P.J. Bartlein. 2001. Global change in forests: Responses of species, communities, and biomes. BioScience **51**: 765-779.

Harrington, T.B. and M.B. Edwards. 1999. Understory vegetation, resource availability, and litterfall responses to pine thinning and woody vegetation control in longleaf pine plantations. Canadian Journal of Forest Research **29**: 1055-1064.

Hartley, M.J. 2002. Rationale and methods for conserving biodiversity in plantation forests. Forest Ecology and Management **155**: 81-95.

Hendricks, J.J. and L.R. Boring. 1992. Litter quality of native herbaceous legumes in a burned pine forest of the Georgia Piedmont. Canadian Journal of Forest Research **22**: 2007-2010.

Herault, B., O. Honnay, and D. Thoen. 2005. Evaluation of the ecological restoration potential of plant communities in Norway spruce plantations using a life-trait based approach. Journal of Applied Ecology **42**: 536-545.

Hicks, D.J., and B.F. Chabot. 1985. Deciduous forests. Pages 257-277 in B.F. Chabot and H.A. Mooney, editors. Physiological ecology of North American plant communities. Chapman and Hall, London.

Higgs, E.S. 1997. What is good ecological restoration? Conservation Biology **11**(2):338-348.

Hobbs, R.J. and F. Huenneke. 1992. Disturbance, diversity, and invasion: Implications for conservation. Conservation Biology **6**(3): 324-337.

Hobbs, R.J., A. Jentsch, and V.M. Temperton. 2007. Restoration as a process of assembly and succession mediated by disturbance. In *Linking restoration and ecological succession*, ed. L. R. Walker, J. Walker, and R. J. Hobbs, 150-67. New York: Springer.

Hobbs, R.J., and D.A. Norton. 1996. Towards a conceptual framework for restoration ecology. Restoration Ecology **4**:93-110.

Hoffman, D.W., R.E. Wicklund, and N.R. Richards. 1990. Soil survey of Simcoe County, Ontario. Ontario Ministry of Agriculture and Food, Canada Department of Agriculture, Research Branch, Toronto. pp 109.

Holling, C.S. 2001. Understanding the complexity of economic, ecological, and social systems. Ecosystems **4**: 390-405.

Houghton, R.A., J.E. Hobbie, J.M. Melillo, B, Moore, B.J. Peterson, G.R. Shaver, and G.M. Woodwell. 1983. Changes in the Carbon Content of Terrestrial Biota and Soils between 1860 and 1980: A NetRelease of CO"2 to the Atmosphere. Ecological Monographs **53**(3): 235-262.

Huffman, D.W., J.C. Tappeiner, and J.C. Zasada. 1994. Regeneration of salal in the central coast range forests of Oregon. Canadian Journal of Botany **72**: 39-51.

Hunter, M.L. 1990. Wildlife, forests and forestry. Principles of managing forests for biological diversity. Prentice Hall, Englewood Cliffs, NJ.

Hussain I, K.R. Olso, and S.A. Ebelhar. 1999. Long-term tillage effects on soil chemical properties and organic matter fractions. Soil Science Society of American Journal **63**:1335-1341.

Ike, A.F. and J.L. Clutter. 1968. The variability of forest soils of the Georgia Blue Ridge Mountains. Soil Science Society of America Journal **32**: 284-288.

Inouye, R. S., N.J. Huntly, D. Tilman, J.R. Tester, M. Stillwell, and K.C. Zinnel. 1987. Old-field succession on a Minnesota sand plain. Ecology **68**: 12-26.

Jumpponen, A; K. Mattson, J.M. Trappe, R. Ohtonen. 1998. Effects of established willows on primary succession on Lyman Glacier forefront, North Cascade Range, Washington, U.S.A.: Evidence for simultaneous canopy inhibition and soil facilitation. Arctic and Alpine Research **30**: 31-39.

Jost, L. 2006. Entropy and diversity. Oikos **113**(2): 363-375.

Kalra, Y.P. and D.G. Maynard. 1991. Methods manual for forest soil and plant analysis. Forestry Canada, Northwest Region, Northern Forest Centre, Edmonton, Alberta. Information Report NOR-X-319, pp. 116.

Kanno, H. and K. Seiwa. 2004. Sexual vs. vegetative reproduction in relation to forest dynamics in the understorey shrub, *Hydrangea paniculata* (*Saxifragaceae*). Plant Ecology **170:** 43-53.

Karlen, D.L., M.J. Mausbach, J.W. Doran, R.G. Cline, R.F. Harris, and G.E. Schuman. 1997. Soil Quality: A Concept, Definition, and Framework for Evaluation (A Guest Editorial). Soil Science Society of America Journal **61**: 4-10.

Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science **3**(2): 157-164 .

Keddy, P.A., and C.G. Drummond. 1996. Ecological properties for the evaluation, management, and restoration of temperate deciduous forest ecosystems. Ecological Applications **6:** 748-762.

Kellman, M. 1980. Geographic patterning in tropical weed communities and early secondary successions. Biotropica **12**(2): 34-39.

Knoepp, J.D., K.J. Elliot, J.M. Vose, and B.D. Clinton. 2009. Effects of prescribed fire in mixed-oak forests of the southern Appalachians: forest floor, soil, and soil solution nitrogen responses. Journal of the Torrey Botanical Society **136**(3): 380-391.

Lapointe, L. 2001. How phenology influences physiology in deciduous forest spring ephemerals. Physiologia Plantarum **113:** 151157.

Larson, B.M, J.L. Riley, E.A. Snell and H.G. Godschalk. 1999.The woodland heritage of southern Ontario: a study of ecological change, distribution and significance. Federation of Ontario Naturalists, Don Mills, Ontario. 262 p.

Levin, S.A. 1998. Ecosystems and the biosphere as complex adaptive systems. Ecosystems **1:** 431–436.

Li-Cor. 1992. LAI 2000 Plant Canopy Analyzer – Instruction Manual. Li-Cor Inc., Lincoln, Nebraska. pp. 174.

Lukac, M. and D.L. Godbold. 2011. Soil Ecology in Northern Forests: A Belowground View of a Changing World. Cambridge University Press, 268 pp.

Lundgren, A.L, and R.E. Buckman. 1998. Managing Red Pine for Timber Productivity and Sustainability: Lessons Learned Over the Past Century, from the conference proceedings of *Improving Forest Productivity for Timber ... A Key to Sustainability*, December 1-3, 1998. Department of Forest Resources, University of Minnesota.

Mabry, C.M., M.R. Gerken, and J.R, Thompson. 2008. Seasonal storage of nutrients by perennial herbaceous species in undisturbed and disturbed deciduous hardwood forests. Applied Vegetation Science **11**(1): 37-44.

MacArthur, R.H. and E.O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution **17**: 373-387.

MacLean, D.A. and R.W. Wein. 1977. Changes in understory vegetation with increasing stand age in New Brunswick forests: species composition, cover, biomass, and nutrients. Canadian Journal of Botany **55**: 2818-2831.

Magurran, A.E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, New Jersey. pp 1-114.

Maloy, O.C. 1997. White pine blister rust control in North America:a case history. Annual Review of Phytopathology. **35**: 87-109.

Marshall, V.G. 2000. Impacts of forest harvesting on biological processes in northern forest soils. Forest Ecology and Management **133**: 43-60.

Matson, P.A., P.M. Vitousek, J.J. Ewel, and M.J. Mazzarino. 1987. Nitrogen transformations following tropical forest felling and burning on a volcanic soil. Ecology **68**: 491-502.

Matthews, E., R. Payne, M. Rohweder, and S. Murray. 2000. Pilot Analysis of Global Ecosystems: Forest Ecosystems. World Resources Institute, Washington, DC.

Mayer, P., C. Abs, and A. Fischer. 2004. Colonisation by vascular plants after soil disturbance in the Bavarian Forest—key factors and relevance for forest dynamics. Forest Ecology and Management **188**(1-3): 279-289.

McCarthy, B.C. and J.M. Facelli. 1990. Microdisturbances in oldfields and forests: implications for woody seedling establishment. Oikos **58:** 55-60.

McCook, L.J. 1994. Understanding ecological community succession: Causal models and theories, a review. Vegetatio **110**(2): 115-147.

McLachlan, S.M., and D.R. Bazely. 2003. Outcomes of longterm deciduous forest restoration in southwestern Ontario, Canada. Biological Conservation **113**:159-169.

McLaughlin, J.A. 2001. Distribution, hosts, and site relationships of Armillaria spp. In central and southern Ontario. Canadian Journal of Forest Research **31**(9): 1481-1490

McNabb, D.H., A.D. Startsey, and H. Nguyen. 2001. Soil wetness and traffic level effects on bulk density and air-filled porosity of compacted boreal forest soils. Soil Science Society of America Journal **65**(4): 1238-1247.

McPherson, T. S. and V.R. Timmer. 2002. Amelioration of degraded soils under red pine plantations on the Oak Ridges Moraine, Ontario. Canadian Journal of Soil Science **82**: 375-388.

Meier, A.J., Bratton, S.B., Duffy, D.C., 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. Ecological Applications **5**: 935–946.

Menard, S.W. 2009. Logistic Regression: From Introductory to Advanced Concepts and Applications. SAGE Publications Inc., pp. 377.

Messier, C., B. Bigue´, and L. Bernier. 2003. Using fast-growing plantations to promote forest ecosystem protection in Canada. Unasylva **54**: 59-63.

Messier, C. and P. Puttonen. 1995. Spatial and temporal variation in the light environment of developing Scots pine stands: the basis for a quick and efficient method of characterizing light. Canadian Journal of Forest Research **25**: 343-354.

Miandonald, J. and W.J. Braun. 2010. Data Analysis and Graphics Using R: An Example-Based Approach. *Volume 10 of Cambridge Series in Statistical and Probabilistic Mathematics* Edition3, revised, Cambridge University Press, pp. 552

Millennium Ecosystem Assessment (Content Source);Peter Saundry (Topic Editor) "Ecosystems and Human Well-Being: Volume 1: Current State and Trends: Forest and Woodland Systems". In: Encyclopedia of Earth. Eds. Cutler J. Cleveland (Washington, D.C.: Environmental Information Coalition, National Council for Science and the Environment). [First published in the Encyclopedia of Earth August 30, 2011; Last revised Date September 21, 2011; Retrieved November 6, 2011.

Ministry of Natural Resources [MNR]. 2001. Critical Review of Historical and Current Tree Planting Programs On Private Lands in Ontario. Ontario Ministry of Natural Resources, 43 pp.

Mitchell, K. 2007. Quantitative analysis by the point-centered quarter method. Department of Mathematics and Computer Science, Hobart and William Smith Colleges, Geneva, NY. pp. 34

Moore, S.E., Allen, H.L., 1999. Plantation forestry. In: Hunter, M.L. Jr. (Ed.), Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, New York, pp. 400-433.

Morrison, D.J., and K.I. Mallett. 1996. Silvicultural management of armillaria root disease in western Canadian forests. Canadian Journal of Plant Pathology **18**: 194-199.

Morrison, D.J., K.W. Pellow, A.F.L. Nemec, D.J. Norris, and P. Semenoff. 2001. Effects of selective cutting on the epidemiology of armillaria root disease in the southern interior of British Columbia. Canadian Journal of Forest Research. **31**: 59-70.

Mosquin, T; Whitney, P.G; Mcallister, D.E. 1995. Canada's biodiversity. Canadian Museum of Nature, Ottawa, Ontario.

Muller, R.N. 2003. Nutrient relations of the herbaceous layer in deciduous forest ecosystems. Pages 15-37 in Gilliam FS**,** Roberts MR, eds. The Herbaceous Layer in Forests of Eastern North America. New York: Oxford University Press.

Muller, R. & Bormann, F. 1976. Role of *Erythronium americanum* Ker. in energy flow and nutrient dynamics of a northern hardwood forest system. Science **193**: 1126-1128.

Mundry, R. and C. Nunn. 2009. Stepwise model fitting and statistical inference: turning noise into signal pollution. American Naturalist **173**(1): 119-123.

Murphy, S.D. 2004. Assembly methods for ecological restoration of forest communities. 16th Int'l Conference, Society for Ecological Restoration, August 24-26, 2004, Victoria, Canada.

Nakane, K., 1995. Soil carbon cycling in a Japanese cedar (*Cryptomeria japonica*) plantation. Forest Ecology and Management **72**: 185-197.

Newmaster, S.G., Bell, F.W, Roosenboom, C.R., Cole, H.A., and Towill, W.D. 2006 Restoration of floral diversity through plantations on abandoned agricultural land. Canadian Journal of Forest Research **36**: 1218-1235.

Newmaster, S.G; Ragupathy, S. 2005. Flora Ontario — Integrated Botanical Information System (FOIBIS). OAC Herbarium, Biodiversity Institute of Ontario, Guelph. http://www.uoguelph.ca/foibis, accessed on January 30, 2008.

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

Noble, I.R. and R.O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio **43**(1-2): 5-21.

Noguerón, R., D.A. Bryant, J. Strittholt, and J. Kool. 2002. Low-access Forests and Their Level of Protection in North America. Global Forest Watch. World Resources Institute. pp. 31

Norman, J.M. and S.T. Gower. 1990. Rapid estimation of leaf area index in forest using the LI-COR LAI-2000. Submitted to *Ecology*.

Norman, J.M. and P.G. Jarvis. 1975. Photosynthesis in Sitka spruce (*Picea sitchensis* [Bong.] Carr.) V. Radiation penetration theory and a test case. Journal of Applied Ecology. **12**: 839-878.

Noss, R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology **4**: 355-364.

Nowak, C. A., R.B. Downard Jr., and E.H. White. 1991. Potassium trends in red pine plantations at Pack Forest, New York. Soil Science Society of America Journal **55**: 847-850.

Nyland, R.D. 1996. Silviculture: concepts and applications. McGraw-Hill, Inc., New York.

O'Dea, M.E., J.C. Zasada, and J.C. Tappenier. 1995. Vine maple clone growth and reproduction in managed and un- managed coastal Oregon Douglas-fir forests. Ecological Applications **5**: 63-73.

OFRILS [Ontario Forest Research Institute Laboratory Services]. 2009. General Preparation Of Forest Mineral Soil Samples For Physical and Chemical Analysis, Including Moisture Content & Bulk Density Measurements - Standard Operating Procedure for Preparation of Forest Mineral Soil Samples For Physical and Chemical Analysis. Ontario Ministry of Natural Resources, Sault Ste. Marie, Ontario pp. 10.

OFRILS [Ontario Forest Research Institute Laboratory Services]. 2010. Simultaneous Analysis of Total Carbon and Total Nitrogen in Soils by Dry Combustion and Thermal Conductivity Detection Method - Standard Operating Procedure for the Analysis of Total

Carbon And Total Nitrogen In Soil Samples by Dry Combustion and Thermal Conductivity Detection. Ontario Ministry of Natural Resources, Sault Ste. Marie, Ontario pp. 9.

Oker-Blom, P. and S. Kellomaki. 1981. Light regime and photosynthetic production in the canopy of a Scots pine stand during a prolonged period. Agricultural and Forest Meteorology. **29**: 191-206.

Oliver, C.D., and Larson, B.C. 1990. Forest stand dynamics. McGraw-Hill, Inc., New York.

Ontario Ministry of Natural Resources [OMNR]. 1999. Extension Notes: Managing Red Pine Plantations. Queen's Printer for Ontario, Ontario, Canada

Parker, W.C, K.A. Elliot, D.C. Dey, E. Boysen, and S.G. Newmaster. 2001. Managing succession in conifer plantations: converting young red pine (*Pinus resinosa* Ait.) plantations to native forest types by thinning and underplanting. The Forestry Chronicle, **77**(4): 721-734.

Parker, B.H. and B. Craig. 2005. The Status of Forest Health in Southern Ontario: An Assessment using Tree Mortality Rates.Ecological Monitoring Coordinating Office, Environment Canada, Canada Centre for Inland Waters, Burlington, Ontario. 21 pp.

Parker, W.B., K.A. Elliot, D.C. Dey, and E. Boysen. 2008. Restoring southern Ontario forests by managing succession in conifer plantations. The Forestry Chronicle **84**(1): 83-94.

Pastor, J. and W.M. Post. Influence of climate, soil moisture, and succession on forest carbon. Biogeochemistry **2**(1): 3-27.

Paz-Gonzalez, A., and M.T. Taboada. 2000. Nutrient variability from point sampling on 2 meter grid in cultivated and adjacent forest land. Communications in Soil Science and Plant Analysis **31**: 2135-2146.

Paz-Gonzalez, A., S.R. Vieira, and M.T.T. Castro. 2000. The effect of cultivation on the spatial variability of selected properties of an umbric horizon. Geoderma **97**: 273-292.

Peterken, G.F and M. Game. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. Ecology **72**(1): 155-182.

Peterson, C. and J. Facelli. 1992. Contrasting germination and seedling growth of *Betula alleghaniensis* and *Rhus typhina* subjected to various amounts and types of plant litter. American Journal of Botany **79**: 1209-1216.

Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. In: G. E. Likens (ed.). Long-Term Studies in Ecology: Approaches and Alternatives. Springer-Verlag New York, Inc. pp. 110-135.

Pickett, S.T.A. and V.T. Parker. 1994. Avoiding the old pitfalls: opportunities in a new discipline. Restoration Ecology **2**: 75-79.

Pinto, F, S. Romaniuk, and M. Ferguson. 2008. Changes to preindustrial forest tree composition in central and northeastern Ontario, Canada. Canadian Journal of Forest Research. **38**: 1842-1854.

Prince Edward Island Forestry Division. 1997. A Review of Red Pine Management. Silviculture Development Section Forestry Division, Department of Agriculture and Forestry. pp. 21

Pritchett, W.L. and R.F. Fisher. 1987. Properties and Management of Forest Soils, 2nd Edition. Wiley, New York.

Quesnel, H.J. and L.M. Lavkulich. 1980. Nutrient availability of forest floors near Port Hardy, British Columbia, Canada. Canadian Journal of Soil Science **60**: 565-573.

Quideau, S.A. and J.G. Bockheim. 1996**.** Vegetation and cropping effects on pedogenic processes in a sandy prairie soil. Soil Science Society of America Journal **60**: 536-545.

Ramovs, B.V. and M.R. Roberts. 2003. Understory vegetation and environment responses to tillage, forest harvesting, and conifer plantation development. Ecological Applications **13**(6): 1682-1700.

Ramovs, B.V. and M.R. Roberst. 2005. Response of plant functional groups within plantations and naturally regenerated forests in southern New Brunswick, Canada. Canadian Journal of Forest Research **35**: 1261-1276.

Reed, D.D. and G.D. Mroz. 1997. Resource assessment in forested landscapes, 3rd Ed. John Wiley and Sons, pp. 386.

Roberts, M. 2002. Effects of forest plantation management on herbaceous layer composition and diversity. Canadian Journal of Botany. **80**: 378-389.

Roberts, M. 2004. Response of the herbaceous layer to natural disturbance in North American forests. Canadian Journal of Botany **82**: 1273-1283.

Roberts, T.L. and J.L Vankat. 1991. Floristics of a chronosequence corresponding to old field-deciduous forest succession in southerwestern Ohio. II. Seed Banks. Bulletin of the Torrey Botanical Club **118**: 377-384.

Robertson, G.P., J.R. Crum, and B.G. Ellis. 1993. The spatial variability of soil resources following long-term disturbance. Oecologia **96**: 451-456.

Robinson, G.R; M.E. Yurlina, and S.N. Handel. 1994. A century of change in the Staten Island flora: Ecological correlates of species losses and invasions. Bulletin of the Torrey Botanical Club **121**(2): 119-129.

Rolfe, G. L. and W.R. Boggess. 1973. Soil conditions under old field and forest cover in southern Illinois. Soil Science Society of America **37**: 314-318.

Rudel, T.K. 1998. Is there a forest transition? Deforestation, reforestation and development. Rural Sociology **63**: 533-552.

Rudel, T.K., O.T. Coomes, E. Moran, F. Achard, A. Angelsen, J. Xu, and E. Lambin. 2005. Forest transitions: towards a global understanding of land use change. Global Environmental Change **15:** 23-31.

Ruiz-Jaén, M.C., and T.M. Aide. 2005. Vegetation structure, species diversity, and ecosystem processes as measures of restoration success. Forest Ecology and Management **218**: 159-173.

Sands, R., E.L. Greacen, and C.J. Girard. 1979. Compaction of sandy soils in radiata pine forests. I. A penetrometer study. Australian Journal of Forest Research **17**: 101-113.

Scatena, F.N.S., S. Moya, C. Estrada, and J.D. Chinea. 1996. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. Biotropica **28**: 424-440.

Scheller, R.M. and D.J. Mladenoff. 2002. Understory species patterns and diversity in old-growth and managed northern hardwood forests. Ecological Applications **12**: 1329-1343.

Schlesinger W.H. 1990. Evidence from chronosequence studies for a low carbon-storage potential of soils. Nature **348**: 232-234.

Schmidt, R. M.T. Dokulil, R. Psenner, and J. Wanzenbock. 2002. Ecological integrity: Concept, assessment, evaluation: The Traunsee case. Water, Air, and Soil Pollution: Focus **2**(4): 249-261.

Schoch, M and Rowsell, M. 2004. History of Eastern Ontario's Forests. Eastern Ontario Forest Model, Kemptville, Ontario.

Schoenholtz, S.H., H.V. Miegroet, and J.A. Burger. 2000. A review of chemical and physical properties as indicators of forest soil quality: challenges and opportunities. Forest Ecology and Management **138**: 335-356.

Sedjo, R. 1999. The potential of high-yield plantation forestry for meeting timber needs. New Forests **17**(1-3): 339-259.

Sedjo, R.A. and D. Botkin. 1997. Using forest plantations to spare natural forests. Environment **39**: 14-20.

Seiwa, K. 1997. Variable regeneration behaviour of *Ulmus davidiana* var. *japonica* in response to disturbance regime for risk spreading. Seed Science Research **7**: 195-207.

Simcoe County. 2009. County Forests – County Forests From Past to Present. http://www.simcoe.ca/dpt/cf/history/index.htm, accessed March 2009.

Simcoe County. 2011. County Forests – Forest Management. http://www.simcoe.ca/dpt/cf/management/index.htm, accessed March 2011

Smartt, P.F.M. and J.E.A. Grainger. 1974. Sampling for vegetation survey: some aspects of the behaviour of unrestricted, restricted, and stratified techniques. Journal of Biogeography **1**(3): 193-206.

Smith, K.J., W.S. Keeton, M.J. Twery, and D.R.Tobi. 2008. Understory plant responses to uneven-aged forestry alternatives in northern hardwood-conifer forests. Canadian Journal of Forest Research **38**: 1303-1318.

Smith, M; Larson, C; Kelty, J; Ashton, S. 1997. The practice of silviculture: Applied forest ecology. 9th ed. John Wiley and Sons, New York.

Smith, T.M. and R.L. Smith. 2006. Elements of Ecology, 6th ed. Pearson Benjamin Cummings, 658. pp.

Soane, B.D. and C. van Ouwerkerk. 1994. Soil compaction problems in world agriculture. In: Soane, B.D., van Ouwerkerk, C. (Eds.), Soil Compaction and Crop Production, Developments in Agricultural Engineering, vol. 11. Elsevier, Amsterdam, pp. 1-21.

Society for Ecological Restoration International Science & Policy Working Group, 2004. *The SER International Primer on Ecological Restoration*. www.ser.org

Soil Classification Working Group. 1988. The Canadian System of Soil Classification (third edition). Agriculture and Agri-Food Canada Publication 1646, 187 pp

Son, Y., Y.Y. Lee, Y.C. Jun, and Z-S. Kim. 2004. Light availability and understory vegetation four years after thinning in a *Larix leptolepis* plantation of central Korea. Journal of Forest Research **9**: 133-139.

Sousa,W.P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics **15**: 353-391.

Stanley, W.G. and F. Montagnini.1999. Biomass and nutrient accumulation in pure and mixed plantations of indigenous tree species grown on poor soils in the humid tropics of Costa Rica. Forest Ecology and Management **113:** 91-103.

Statistics Canada. 2001. Community Highlights for Simcoe County. http://www12.statcan.ca/english/profil01/CP01/Details/Page.cfm?Lang=E&Geo1=CD&C

ode1=3543&Geo2=PR&Code2=35&Data=Count&SearchText=simcoe county&SearchType=Begins&SearchPR=01&B1=All&Custom=, accessed March 2011.

Statistics Canada. 2011. Canada Yearbook 2011 – Population and Demography. http://www.statcan.gc.ca/pub/11-402-x/2010000/chap/pop/pop-eng.htm, accessed, October 2011.

Sydes, C., and J.P. Grime. 1981. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. II. An experimental investigation. Journal of Ecology **69**: 249-262.

Tappeiner, J. C., and J. C. Zasada. 1993. Establishment of salmonberry, salal, vine maple, and bigleaf maple seedlings in the coast forests of Oregon. Canadian Journal of Forest Research **23**: 1775-1780.

Tappeiner, J.C., J.C. Zasada, P. Ryan, and M. Newton. 1991. Salmonberry clonal and population structure: the basis for a persistent cover. Ecology **72**: 609-618.

Taylor, R.J. and R.W. Pearcy. 1976. Seasonal patterns of CO2 exchange characteristics of understory plants from a deciduous forest. Canadian Journal of Botany **54**: 1094-1103.

Taylor, H.M., Robertson, G.M., Parker Jr., J.J., 1966. Soil strength root penetration relations for medium to coarse-textured soil materials. Soil Science **102**: 18-22.

Tilman, G.D. 1985. The resource-ratio hypothesis of succession. American Naturalist **125**: 827-852.

Tremblay, N.O. and G.R. Larocque. 2001. Seasonal dynamics of understory vegetation in four eastern Canadian forest types. *International Journal of Plant Sciences*. **162**(2): 271-286.

Utsugi, E; H. Kanno, N. Ueno, M. Tomita, T. Saitoh, M.; Kimura, K. Kanou, and K.Seiwa. 2006. Hardwood recruitment into conifer plantations in Japan: Effects of thinning and distance from neighboring hardwood forests. Forest Ecology and Management **237**(1-3): 15-28.

van Andel, J and J. Aronson. 2006. Restoration ecology: The new frontier. Blackwell, Oxford, U.K.

Van Wesemael, B. and M.A.C.Veer. 1992. Soil organic matter accumulation, litter decomposition and humus forms under Mediterranean-type forests in southern Tuscany, Italy. Journal of Soil Science **43**: 133-144.

Vitousek, P.M., Matons, P.A., and Cleve, K. 1989. Nitrogen availability and nitrification during succession: Primary, secondary, and old-field seres. Plant and Soil **115**(2): 229-239

Walker, L.R., D.A. Wardle, R.D. Bardgett, and B.D. Clarkson. 2010. The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology. **98**: 725-736.

Warde, W. and J.W. Petranka. 1981. A correction factor table for missing point-center quarter data. Ecology **62**(2): 491-494.

Watt, J. 1996. From forest to wasteland to forest. Ontario Ministry of Natural Resources, Ontario Forest Research Institute. Insights **1**(2): 1-4.

Welch N.L., J.M. Belmont, and J.C. Randolph. 2007. Summer ground layer biomass and nutrient contribution to aboveground litter in an Indiana temperate deciduous forest. American Midland Naturalist **157**: 11-26.

Whitney, G.G. 1986. A demographic analysis of *Rubus idaeus* and *Rubus pubescens*. Canadian Journal of Botany **64**(12): 2916-2921.

Whittaker, R.H. 1972. Evolution and Measurement of Species Diversity. Taxon **21**(2-3): 213-251.

Wingham, D.F. 2004. Ecology of woodland herbs in temperate deciduous forests. Annual Revue of Ecology, Evolution, and Systematics. **35**: 583-621.

Wolda, H. 198 1. Similarity indices, sample size and diversity. Oecologia **50:** 296-302.

Wood, J.D. 1991. Moraine and metropolis: the Oak Ridges and the Greater Toronto Area. International Journal of Environmental Studies **39** (1-2): 45-53.

Wurtz, P. and A. Annila. 2010. Ecological succession as an energy dispersal process. Biosystems **100**: 70-78.

Wuyts, K; A. De Schrijver, J. Staelens, M. Gielis, G. Geudens, and K. Veheyen, K. 2008. Patterns of throughfall deposition along a transect in forest edges of silver birch and Corsican pine. Canadian Journal of Forest Research **38** (3): 449-461.

Zhu, J; T. Matsuzakib, F. Leea, and Y. Gondab. 2003. Effect of gap size created by thinning on seedling emergency, survival and establishment in a coastal pine forest. Forest Ecology and Management **182** (1-3): 339-354.