OLD-GROWTH NORTHERN WHITE-CEDAR (*THUJA OCCIDENTALIS* L.) STANDS IN THE MID-BOREAL LOWLANDS OF MANITOBA.

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Abstract

Old-growth Northern white-cedar (*Thuja occidentalis* L.) stands were examined in the mid-boreal Manitoba lowlands, the north-western limit of distribution of this species. Objectives involved the characterization of the structure and old-growth attributes of these stands. In this area old-growth *T. occidentalis* occurs in three vegetation communities which are here compared and contrasted. Environmental and biological variables were explored with redundancy analysis (RDA), cluster analysis and analysis of variance (ANOVA). Stands where jack pine (*Pinus banksiana* Lamb.) was a co-dominant were positively associated with increases in elevation, silt/clay and openness. Stands containing balsam fir (*Abies balsamea* (L.) Mill.) as a co-dominant were positively associated with slope and rock/cobble, and negatively with openness. Stands with tamarack (*Larix laircina* (Du Roi) K. Koch) as a co-dominant were positively associated with increases in moisture, pH and openness. Results suggest that old-growth *T. occidentalis* occurs in three successional pathways in the region and that they vary in associated old-growth characteristics. These stands display characteristics typical of old-growth forests yet differ from each other in composition, density, amounts and sizes of coarse woody debris and snags. These stands reflect the need for revising traditional old-growth definitions to better reflect variation dependent upon region and site type.

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1.0 Introduction

1.1 Political History

Old-growth forests have historically been exploited and described as decadent or over-mature by foresters who favour their replacement with young, productive plantations (Arsenault 2003). These forests are targeted by the forest industry and governments are reluctant to set aside land for conservation (Kneeshaw and Gauthier 2003). This being the case, much of the world's remaining old, unmanaged forest being under the threat of conversion to younger forests, or another land use (Kimmins 1997, 2003).

In the past few decades consideration of old-growth forests has increased in both scientific and political realms. Public pressure to conserve these forests has been rising as they become increasingly rare, leading numerous governments around the world to work towards their identification and protection (Villeneuve and Brisson 2003). Despite its pledge in the International Convention on Biological Diversity, Canada has been criticized for not preserving sufficient old forest (Mosseler *et al*. 2003a) to complete representative networks of terrestrial protected areas (Hendrickson 2003). Collectively about 9% of Canada is designated as "protected" including over 90% of some ecoregions and none in others. This leaves about one third of the land occupied overall by these ecoregions with no protection (NRC 2004). The ultimate goal is to have every ecoregion represented in protected areas. Focus on old-growth publicly, politically and scientifically has created the need for research documenting the characteristics of these forests. Policy makers need to know how much there is, was, where it is, how fast it is disappearing and if more is being created (Hendrickson 2003). To understand, restore and manage old-

growth there must be understanding of the defining characteristics of old-growth and their development at both stand and landscape levels (Kneeshaw and Gauthier 2003).

1.2 Old Growth – Significance

1.2.1 Old-Growth as Essential Habitat

Old-growth forests support elements of biodiversity due to presence of old trees, dead trees in various stages of decay, and undisturbed soil (Villeneuve and Brisson 2003). Old forests have ecological characteristics that differ from those of younger forests (Kimmins 2003). Old forests are more structurally complex due to variation in diameters and a high density of large trees (Zenner 2004) also differing from post-fire secondary forests in having more shade tolerant trees, a lower density of small stems and larger coarse woody debris (CWD) (Ziegler 2004). In northern coniferous forests few if any vertebrate species absolutely depend on old-growth. However, many such as the spotted owl (*Strix occidentalis* Merriam) in the Pacific northwest (Kimmins 1997) and the pine marten (*Martes americana* Turton) (Wilbert *et al.* 2000) have a preference for these ecosystems or components of them (Mosseler *et al.* 2003b) such as large snags and CWD. Because old-growth forests provide essential habitats, environmentalists and scientists insist they be protected (Hendrickson 2003).

1.2.2Old-Growth Ecological Significance

Old-growth forests were historically valued for lumber and more recently as habitat for wildlife with an increasing consideration of other associated values (Mosseler *et al*. 2003a). Old-growth forests are recognized as basic components of ecosystem diversity with essential roles in the functioning of ecological cycles (Villeneuve and Brisson 2003).

Some examples include roles in carbon sequestration, nutrient cycling, water and soil protection and ecological stability (Mosseler *et al.* 2003a).

1.2.3 Old-Growth-Value to Science

Old-growth forests have potential for scientific research in various realms. Some examples include research in genetics, human disturbance, dendroclimatology and disturbance reconstruction. These forests are desirable for research of adaptive evolution having survived decades of stress (Mosseler *et al.* 2003a,b). They can also function as control plots to understand human influence on the natural landscape (Villeneuve and Brisson 2003) by being used as benchmarks to compare the effects of management on forest form and function (Kimmins 1997). Many applications of dendrochronology, which researches past environmental events by examining variation in tree ring patterns, also depend largely on old trees. Tree ring data is used for climatic reconstruction or dating disturbances, information sometimes impossible to obtain other ways (Sheppard and Cook 1988).

1.3 Old-Growth Definitions and Descriptions

As researchers collect information about the physiognomy (which classifies forests based on their overall physical structure or developmental stage) and processes of old-growth forests, problems arise due to the lack of field procedures to identify old-growth stands (DeLong *et al*. 2004). The need for tools to identify these stands has caused researchers to work towards refining definitions (Thompson *et al.* 2003).

Definitions of old-growth forests in the literature are variable; though there is agreement that old-growth pertains to successionally advanced forests (Spies and Franklin 1988). Minimums of age and size of trees have been used to define old-growth though these concepts remain ambiguous. Old-age is a relative term and age does not necessarily provide any information on factors that wildlife depends on such as structure or composition. Tree size has been used as a proxy for age but is not necessarily indicative of age. The inability to form a precise definition has prompted investigations to define the unique characteristics of old-growth forests (Spies and Franklin 1988).

The major structural attributes of old-growth forests researched include abundance/size of CWD and snags, tree size (Mosseler *et al.* 2003a; Stewart *et al.* 2003; DeLong *et al*. 2004) and age structure of the forest (Mosseler *et al*. 2003a; Stewart *et al* 2003). Process based attributes associated with these forests includes the cessation of density dependent mortality of canopy trees (Carleton 2003; Mosseler *et al*. 2003a,b) and compositional attributes associated have included the presence and importance of shade tolerant species (Mosseler *et al*. 2003a,b; Villeneuve and Brisson 2003).

Researchers have found certain species or plant assemblages to be useful indicators old-growth forests such as lichens, fungi (Selva 2003) and various bryophyte assemblages (Newmaster *et al.* 2003). Selva (2003) examined species dependent on mature forests for specific microhabitats (which are expected to increase with increasing forest age). The presence or absence of old-growth specialists can be used to determine if the forest is as old as it appears. Newmaster *et al.* (2003) examined stands of various ages and

determined how age influenced the occurrence of certain species allowing for the formation lists of species associated with old-growth forests.

Old-growth boreal forests sometimes are reported as having characteristics differing from common conceptions of old-growth such as large trees or abundant CWD (Harper *et al.* 2003; Thompson *et al*. 2003). For example, old black spruce (*Picea mariana* Mill.) forests lack large trees, snags and CWD. These forests are still unique in compositional and structural features when compared to their younger counterparts being more structurally complex, with greater diversity of *Sphagnum*, epiphytic lichens and ericaceous species. Old-growth *P. mariana* forests can be distinguished in terms of functional attributes such as single tree replacement (Harper *et al.* 2003). Old balsam fir (*Abies balsamea* (L.) Mill.) forests described by Thompson *et al.* (2003) were found to have few large trees yet still have old trees, multiple gaps, abundant CWD and snags. These old-growth forests demonstrate that not all of the criteria associated with old-growth forests need to be met to be unique.

Examination of the main attributes of old-growth forests allows for development of quantitative definitions and criteria to identify them (Villeneuve and Brisson 2003). Recent studies have documented the ecological characteristics of old-growth forests in terms of age, species composition, structure, CWD, and snags (Stewart *et al.* 2003; Thompson *et al.* 2003; Angers *et al.* 2005). Old-growth attributes show considerable geographic variation making criteria best established for each region (Thompson *et al.* 2003; DeLong *et al.* 2004). Criteria must also be based on the natural range of variation within an ecological zone and site type (Kimmins 2003). Not all forests are alike resulting

from unique combinations of processes in a specific area. unproductive sites might not ever have trees that achieve the same structure, stature, composition or dynamic phases as a productive site (Carleton 2003) but they may get as old or even older (Loehle 1988).

Some researchers have advocated the use of old-growth indices as an identification method for these forests (Spies and Franklin 1988; Kimmins 2003; Kneeshaw and Gauthier 2003; Mosseler *et al.* 2003a). Characteristics associated with old-growth are given a weight of importance and the stand evaluated with a result ranging from one to 100, 100 representing the forest with the most old-growth attributes. Zenner (2004) used the number of large trees (>100 cm diameter at breast height (dbh=1.3 m), number of dominant shade tolerant species, density of all trees and standard deviation of dbh hectare as inputs into this model. Forests in a given area are then given scores relative to forests with the highest amounts of these characteristics. The rating can be based on characteristics specific to region and site type allowing for consideration of the natural range of variation.

1.4 Ecology of Northern white-cedar (*Thuja occidentalis* L.)

The distribution of *T. occidentalis* encompasses south-eastern Canada and the northern United States, the north-west limit occurring in the disjunt stands in west-central Manitoba (Johnston 1990a). It grows in a relatively humid climate with annual precipitation commonly ranging from 710 to 1170 mm. It is found on a variety of organic and mineral soils though it does not develop well on extremely wet or dry sites. Its growth is greatly affected by site productivity with the maximum stand basal area (BA) around 69 m^2/ha (Johnston 1990a). This species grows best on neutral or alkaline soils

(Sims *et al.* 1990) and is often associated with cool, moist, nutrient-rich sites, particularly on organic soils near water-ways, or on calcareous mineral soils with pH values commonly ranging from 5.5 to 7.2 (Johnston 1990a). *Thuja occidentalis* is a monoecious conifer commonly reaching sizes of 12 to 15 m tall, 30 to 60 cm dbh at maturity (Johnston 1990a). *Thuja occidentalis* is usually a subcanopy tree compared to white spruce (*Picea glauca* (Moench) Voss) and *A. balsamea.* (Bergeron and Charron 1994).

Thuja occidentalis can occur in multi-aged forests where gap-phase replacement dominates disturbance (Frelich and Reich 2003). Stands with components of *T. occidentalis* can develop within the boreal forest in patches that have been skipped by fire and surrounded by even aged, jack pine (*Pinus banksiana* Lamb.) dominated forests (Frelich and Reich 2003). In the boreal forest lake landscapes can have a more variable fire regime compared to the surrounding forest resulting in *T. occidentalis* stands on sites ranging from bedrock to bogs (Bergeron 1991). *Thuja occidentalis* trees are susceptible to fire due to the high oil content of leaves and bark and its shallow root system (Curtis 1946). Due to its susceptibility to fire and shade tolerance, the dominance of *T. occidentalis* increases with time after a fire (Bergeron and Dubuc 1989) and it is generally considered a late successional species (Musselman *et al*. 1975; Bergeron and Charron 1994; Asselin *et al.* 2001).

Thuja occidentalis is often a co-dominant with *P. mariana* with occurrences of tamarack (*Larix laircina* (Du Roi) K. Koch) on organic soils. On moist to dry sites co-dominants may include *A. balsamea,* paper birch (*Betula papyrifera* Marsh.)*,* quaking aspen (*Populus tremuloides* Michx.)*,* and *P. glauca* (Johnston 1990a; Sims *et al.* 1990). *Thuja*

occidentalis stands provide a habitat for rare species around the upper Great Lakes including the regionally rare calypso orchid (*Calypso bulbosa* L.), showy lady's slipper (*Cypripedium reginae* Walt.), large round leaf orchid (*Platanthera orbiculata* (Pursh) Lindley) and the globally threatened ram's head lady's slipper (*Cypripedium arietinum* R. Brown) (Epstein *et al*. 1999 in Rooney *et al*. 2002). The northern pileated woodpecker (*Dryocopus pileatus* L.) makes use of *T. occidentalis* stands where it bores holes in the lower boles of live trees (Curtis 1946).

The late-successional status of *T. occidentalis* and potential for old age make it an old-growth candidate. Ages of these trees have been found to surpass 1032 years of age (Larson and Kelly 1991). Old specimens are often described as stunted, gnarled in appearance, with frequent apical mortality, and sparse foliage (Archambault and Bergeron 1992 a, b). *Thuja occidentalis* trees are thought not to reach as extreme age when of large stature as they do when stunted by poor growing conditions (Johnston 1990a) being found to live longer when in smaller form and in the range of 200-400 when of large stature (Frelich and Reich 2003). The value of *T. occidentalis* to dendrochronology has been pointed out by Sheppard and Cook (1988), Larson and Kelly (1991) and Archambault and Bergeron (1992b) who emphasize the value of its long lived nature and the relationship between its tree-ring chronologies and drought indices during the growing season.

1.5 *Thuja occidentalis* in Manitoba

Thuja occidentalis in west-central Manitoba occurs on beach ridges with mixed hardwoods and in bogs with *P. mariana* (Tardif and Stevenson 2001). Weber and Bell (1990) reported *T. occidentalis* trees approximately 179 years occurring with the common

co-dominant species and *P. banksiana* prior to a fire in 1988. Living *T. occidentalis* trees were found to be present after light or partial burnings (Weber and Bell 1990). The maximum age of *T. occidentalis* stands in this area have been dated to nearly 400 years (F. Conciatori pers. Comm. 2007). Forests of this age are unique in Manitoba and little is known about them in terms of old-growth qualities and composition. *Thuja occidentalis* is found at a variety of site types in this area with a variety of co-dominants (Tardif and Stevenson 2001) providing the opportunity to study the old-growth characteristics of these stands across the natural variation in this area.

The radial growth-climate association of *T. occidentalis* trees has been studied in this area. Results indicated that climatic conditions in late summer prior to, and those in June and July the year of ring formation, influence radial growth of *T. occidentalis* (Tardif and Stevenson 2001). They also found that climate does not strongly affect radial growth and suggested that forest fires or habitat availability may limit the range of this species.

1.6 Objectives

The objectives of this study were to determine the old-growth nature and characteristics of several stands of *T. occidentalis* located at the north-western limit of distribution of this species. Sites were selected along three moisture regimes (xeric, mesic, and hydric) to encompass the habitat range of old-growth stands in the area. It was suspected that these stands would stray from old-growth characteristics such as in the occurrence and abundance of large trees, snags and CWD. The hypothesis was that mesic sites would have more larger trees and larger and more CWD. Biotic and abiotic factors were examined to determine what causes the observed differences among stand types.

2.0 Methods

2.1 Study area

The study area is located in west-central Manitoba near Grand Rapids (53°09'N, 99°17'W) in between Lakes Winnipeg, Cedar, and Winnipegosis (Appendix 1). This is in the area of a proposed Manitoba lowlands park (CPAWS 2006). It also corresponds to the north-western limit of the distribution of *T. occidentalis* which is disjunct from the continuous zone of the population (Johnston 1990a; Tardif and Stevenson 2001).

The study area is underlain by the glacial till of The Pas end moraine which extends from The Pas south and east into Lake Winnipeg as Long Point (Teller 1975). End moraines are composed of till that was pushed to the edge of past glaciers. Till contains a mix of particles from gravel to clay. Till derived soils in the Interlake are high in calcareous Palaeozoic limestone and dolomite fragments. There is an apparent relationship between vegetation communities and geographic variations caused by glacial deposition as different stand types occur at different points on the end moraine. The abrupt 30.5 m high edge of the moraine that forms the northern shore of Lake Winnipegosis is where the mesic study sites; the gentle slopes to the northeast the hydric study sites (Teller 1975) and an area of higher elevation to the north-west the xeric study sites.

Mean annual temperature reported from the Grand Rapids Hydro station (53°09'N, 99°17'W; figure 1) was 0.8°C for the reference period 1971 to 2000. Mean temperatures reach a high of 18.6°C in July and a minimum of -19.7°C in January. For this same period total mean annual precipitation was 473.7 mm with approximately 76% of total annual precipitation occurring as rainfall (Environment Canada 2004).

The vegetation zone of this region has been classified as mixed-woods boreal forest and occurs in the midboreal subhumid ecoclimatic zone with the dominant soil type being a eutric brunisol (Scott 1996). In this ecozone there are extensive areas of *P. glauca* and P. *mariana*, with *P. banksiana* on sandy and rock outcrops and *L. laricina* in fens (Scott 1996).

2.2 Site selection

To characterise old-growth stands of *T. occidentalis* in this area, site selection was partly done using information collected during preliminary dendroecological analysis (Tardif and Stevenson 2001; Ko-Heinrichs and Tardif in prep.). These studies indicated of several *T. occidentalis* stands of advanced age in a variety of moisture conditions with different co-dominant species. The two sites suspected to be the oldest were sampled for each moisture regime (hydric, mesic, and xeric). An additional site was sampled to test the efficacy of the sampling scheme. This gave a total of seven sites sampled (Appendix 1).

2.3 Field sampling - Point center quarter

A modified version of the point-center quarter (PCQ; Cottam and Curtis 1956) was employed to characterize the structure of the selected stands. This provided an estimation of density, basal area and frequency of occurrence by species for a given area. This method was relatively easy to apply in the field and statistically robust (Cottam and Curtis 1956; Krebs 1998; Mitchell 2006). There has been evidence of increasing bias when distributions begin to stray from complete spatial randomness (Byrant *et al.* 2004) but there has been found no significant bias related to the species distribution of basal area results. Other authors have also drawn attention to the problem of this method and its

reliance on random distributions (Cottam and Curtis 1956; Engeman 1994). Density results obtained with the PCQ method should be viewed with caution for this reason.

Fifteen points were laid out in three parallel transects in areas representing of each stand. In each transect five points, 10 m apart, were sampled forming a three by five grid. The exception was a site (xeric site #3) that had 20 points. This was used to determine if a sufficient number of points had been taken. Increased sampling intensity increases the precision of density and BA measurements (Byant *et al.* 2004), up to a certain point. The first point was placed in a semi-random fashion by throwing a weighted stick into the stand of the specified parameters (i.e. old, with a significant component of *T. occidentalis*, in area lacking obvious human disturbance). A cardinal compass bearing heading into the stand was selected as the direction to the next point. Each point was divided into four 90° quarters and the closest individual in each quarter was measured (Cottam and Curtis 1956; Mitchell 2006).

2.3.2 Tree Characterization

The following measurements were taken at each PCQ; identity of living trees closest to the point in each quarter; its distance to the point (maximum of 10 m), diameter at breast height (dbh), defect class and total height. A tree was defined as ≥ 5 cm dbh and height ≥1.3 m. Defect classes consisted of five categories (Appendix 1). In addition to the standard measurement for trees, similar information was also collected from seedlings, sapling and snags. Measurements taken for small saplings (>30 cm but <130 cm in height), large saplings (≥1.3 m in height, < 5 cm dbh) and snags (dead > 5 cm dbh) included species determination, height and distance. Origins (seed or layering) were

recorded for seedlings and saplings when determinable. Saplings were placed into one centimetre diameter classes (1-5). The decay class (Appendix 2) of each snag was determined. The maximum distance of inclusion for all PCQ sampling was 10 m, assuming this is a sufficient distance to capture variability and prevent re-sampling.

The two largest trees that had been identified from the PCQ were cored with an increment borer in each stand and for each species. This was done to determine ages and provide the possibility of reconstructing past forest disturbance history for each stand using multi-century tree-ring chronologies. Tree cores can also be used to determine the relation between age, height, and DBH. For each tree selected, two cores were taken at a minimum 90° from each other 20-50 cm from the tree base to determine age. The next largest tree of that species was sampled whenever a tree was found to be too rotten to obtain an intact core.

2.3.3 *Understory Vegetation*

A 1 m^2 square plot was established at each point to estimate vegetation cover. Percent cover was estimated using the following classes: 1= 0–1%, 2= >1–5%, 3= >5–25%, 4= >25–50%, 5= >50–75%, 6= >75–100%, 7= 100% (Girardin *et al.* 2001). This was carried out for mosses, lichens (classified into leaf, club or shrub forms), graminoids (grass, rush or sedge), and other vascular plants. Percent cover of bare ground, water, CWD, litter, trees and saplings were also recorded in these plots. Litter was further characterized by an estimation of ranked dominance (one through four denoting the relative presence) and classified as coniferous, deciduous, ericaceous or graminoid., Small seedlings (<30 cm) were counted for each tree species within these 1 m^2 plots.

2.3.4 *Abiotic Variables*

Abiotic variables were measured to determine what environmental variables influence the nature of the stands. A soil pit was dug at each point to determine soil type, texture, depth (to mineral horizons), and drainage class. The pit was placed in a representative location within the sampling area of the point. Texture and drainage were determined in the field. Moisture and drainage conditions were classified as xeric-1 (dry soil/rapid drainage), mesic-2 (fresh soil/well drained), mesic-3 (moist soil/imperfect drainage), or hydric-4 (wet soil/very poor drainage) modified from the Ontario Institute of Pedology (OIP 1985). These classes are based on soil depth, degree of mottling/gleying, and texture. Soil samples were collected and frozen in air/water tight bags for later pH determination. Texture was determined by feel and clarified in the lab when needed (Scott 2003). Digital hemispheric photos were taken at each PCQ using a Nikon E8400 digital camera to be analyzed with computer software WinSCANOPY pro 2005 (Regent Instruments 2005) providing percent canopy openness. Slope, elevation, and any evidence of disturbance were also recorded.

2.4 Field Sampling – Site Level

2.4.1 Coarse Woody Debris

Coarse woody debris is defined here as woody material that is discernable from the surrounding substrate, above the soil, not self supporting (as trees and stumps are) with a diameter ≥5 cm (Meidinger *et al.* 1998). The 5 cm minimum diameter must be maintained for at least one meter in length to be considered CWD. The protocol followed that of the Government of British Columbia's CWD sampling procedure (Meidinger *et al.* 1998).

This protocol was modified in that minimum diameter was lowered from 7.5 cm to 5 cm to better reflect the smaller range of tree diameters in Manitoba compared to those in B.C.

Coarse woody debris was measured in each stand using the line intercept method. Three 50 m transects were laid out in an equilateral triangle (chosen for reductions in directional bias; Feller 2003; Stewart *et al.* 2003) totalling 150 m per site. Pieces of CWD were included if the horizontal center of the piece intersected the transect line, met CWD definitions, and was ≥ 5 cm diameter at interception. Length was measured, diameter taken at the small end (to min of 5 cm), large end and point of interception for each piece that met these requirements. The length was measured for the portion of the wood that exceeded 5 cm. The decay class was noted according to a five class system (Meidinger *et al.* 1998; Appendix 4). Cause of death was recorded as natural or due to cutting.

2.4.2 Regeneration

Tree seedlings (≤30 cm height) were surveyed along three 50 m transects in one randomly selected replicate for each stand type to further evaluate regeneration. Origin (vegetative, sexual), seedling substrate and seedling identity were recorded. Seedlings were included to a maximum distance of 0.5 m along each side of the transect. Substrate was classified as moss/litter or logs/stumps and regeneration as seed, vegetative or unknown.

2.5 Laboratory Analyses

Laboratory analysis included the of soil pH, soil texture, analysis of hemispheric photos and dating/crossdating of tree cores. The pH was tested with a pH meter by the calcium chloride method (Scott 2003). Remaining questions regarding texture and organic matter

content were explored following the methods of Scott (2003). In some instances organic matter was burned off to determine if any mineral component was present that would aid in the identification of soil type.

Canopy openness was determined by analysis of hemispheric photos using WinSCANOPY pro 2005 (Regent Instruments 2005). Openness was either determined using one of two devised colour schemes or a grey scale for analysis depending on light conditions at the time photos were taken. Colour schemes were based on the dominant shades found in the photos. Photo analysis was visually verified for each photo.

The ages of the largest trees at each site were determined to provide information on the age of the forest/cohort. Age was determined based on crossdating of annual growth rings. Rings are formed by the process of small thick walled cells being formed in the late summer and large thin walled cells in the early summer. This pattern can be compared among trees from the same area and a crossdated age determined (Stokes and Smiley 1968). Several steps were taken in the preparation and dating of tree cores. They were allowed to dry and then glued to wood mounts. Cores were then sanded using a progression from coarse (50) to fine grits to a level of 600. Tree rings were examined with the aid of a dissecting microscope. This visual technique of crossdating was then verified by an experienced dendrochonology technician; F. Conciatori. Tree ring patterns can further be compared by measuring ring width and crossdating validated with the program COFECHA (Holmes 1992).

2.6 Data preparation

Vegetation and environmental data were summarized for each PCQ to analyse variation among sites. This process involved summarizing tree data to a single value per PCQ, calculating relative frequency understory species occurrence from the 1 m^2 vegetation plots and the logarithmic transformation of the species data.

2.6.1 Vegetation - PCQ

Vegetation data were prepared for ordination and cluster analysis by developing an importance value for each species encountered at each PCQ using the information (species, dbh, height and distance) collected. First relative density of tree species was calculated for each point. For example if a PCQ was composed of four *T. occidentalis*, this species had 100% for relative density at that specific point. Second, the BA of each species at each point was calculated and relativized according to the largest tree BA in all points. For example if a maximum BA of 250cm^2 was found then a tree with 200cm^2 would get a value of 200cm^2 /250cm^2 *100% giving a final value of 80% for its relative BA. The same procedure was used with height. Distance calculations were slightly different as the relationship was inversed so a higher number represented a higher density and thus being a measure of abundance. This was done by subtracting the above equation from one. Importance value was then calculated by adding these resulting percentages together and dividing by four. This was calculated for each point giving a relative weight to species abundance, DBH, distance and height.

Both importance value and vegetation cover data were logarithmically transformed to avoid removal or down weighting of outlier species (Kenkel 2006). Logarithmic

transformation of species data can linearize the species abundance relationship. Biological measurements are usually distributed log-normally with frequency distributions being positively skewed. They often have few large values, more intermediate values and many small values. However the small sample size of biotic surveys often yields many zeros due to the occurrence of many rare species. Multivariate analysis is sensitive to zeros in the data set and often rare species are down weighted or eliminated. This follows the logic discussed in Kenkel (2006).

2.6.2 Environmental PCQ Data

Environmental (active and passive) variables were summarized for each point. Missing values in the environmental matrix were accounted for by using the mean value for the site. This was necessary as missing values in the matrix cause problems with the ordination analyses being recognised as zeros by CANOCO, which the analysis is sensitive to (ter Braak and Smilauer 1998). The quantitative variables included in the environmental matrix were longitude, latitude, elevation, slope, pH of the LFH, bare ground cover, water ground cover, CWD ground cover, litter ground cover, LFH depth, tree species richness, understory richness, overall species richness, and openness. Variables that were semi-quantitative include: drainage class and the dominance of ericaceous, deciduous, coniferous, graminoid litter. Organic, rock/cobble, gravel, sand, silt/clay, and undetermined substrates were recorded as binary variables as were wind throw, fire, and trails disturbance events).

2.7 Statistical analysis

2.7.1 Analysis of the PCQ vegetation data (ordination and cluster)

Redundancy analysis (RDA) was carried out using CANOCO program version 4.52 (ter Braak and Smilauer 2003) to determine what environmental variables explain variance of species data and if the grouping sites into stand types was appropriate. These analyses were chosen based on sampling intensity and gradient length (calculated using detrended correspondence analysis (DCA)). RDA direct gradient analysis of inter-species correlation was used environmental data is used to extract patterns from the explained variation. In RDA the sample units are restricted to be linear combinations of predictor and environmental variables (Legendre and Legendre 1998). Forward selection of environmental variables was done ($P < 0.05$) with significant ones included in the final RDA model (999 permutations generated).

The variance inflation factor values of explanatory variables were examined to determine the level of co-linearity, the maximum threshold allowed 3.5 (a value of ≥ 20 is considered almost perfectly collinear, zero absolutely) (ter Braak and Smilauer 2003). One of the collinear variables was removed either arbitrarily (e.g. latitude and longitude, sites were not far from each other) or based on the suspected quality of measurement (e.g. undetermined soil substrate vs. organic substrate as it is not informative). Variables removed due to co-linearity included: latitude, gleysol, longitude, site, folisol, soil type, and organic soil. Binary variables with rare occurrences were removed, as were descriptive variables (i.e. vegetation type, litter type, species richness, variables pertaining to ground cover etc.). Significance was tested using forward selection and permutation (Monte Carlo 999 $P< 0.05$).

K-means partioning cluster analysis was performed on the species data using SYSTAT 11 (SYSTAT 2004) to determine the similarity of variation. This analysis and program were chosen as it allows the option of using Euclidean distance, the same distance measure as in RDA. Sites clustered best into four groups (the mesic sites fit more or less into one of two clusters), referred to hereon as stand type.

2.7.2 ANOVA - Environmental and Biological Variables

Based on the ordination and cluster analysis, PCQ were deemed suitably similar to be grouped into stand types for summary calculations. This allowed for one-way ANOVAs using the PCQ as replicates of the stand type for explanatory variables and passive variables thought to be of interest. Post hoc Freeman-Tukey tests were performed to test between groups' differences. This was carried out using SYSTAT 11 (SYSTAT 2004).

2.7.3 Analysis of the stand types Tree PCQ data

PCQ data were used to calculate density (eq.1, χ = mean distance between trees) and basal area (eq.2, χ = the mean basal area for a species) for trees, snags, saplings, and seedlings for each stand type (Cottam and Curtis 1956; Krebs 1998; Mitchell 2006).

Eq. 1 $$Density/ha = \frac{10{,}000 m^2/ha}{\chi^2/tree}$$

Eq. 2 $$BA/ha = density \times \chi BAsp$$

A correction factor for missing point data was applied using the methods and conversion tables of Warde and Petranka (1981). This is used to correct for the absence of information due to stems (trees, snags, small saplings and large saplings) being farther

from the point than the 10 m limit and is based on the proportion of missing values out of the total quarters sampled. If a blank is recorded and no correction is made this is interpreted as a zeros in the calculation of density leading to an inflated calculated tree density. The correction factor is applied to calculated density and basal area is calculated using the corrected density.

2.7.4 Coarse Woody Debris

Volume of CWD per hectare (Van Wagner 1968; eq.3 d_i = diameter at interception, L = transect length) and per transect (Husch *et al.* 2003; Smalian volume eq.4, h= piece length, A_l=area of the large end and A_s=area of the small) were calculated. The Smalian formula calculates volume per piece based on the diameters of the large end, small end and length of the piece. Van Wagner's method relies solely on diameter at interception and transect length, calculating volume per hectare based on the chances of interception.

Eq. 3 $$V = \frac{\pi^2 \sum d_i^{\,2}}{8L}$$

Eq. 4 $$V = \frac{h}{2}\left(A_l + A_s\right)$$

2.7.5 Diameter-Height Regression Analysis

Diameter-height scatter graphs were made for trees to assess if the relationship between the two variables was maintained among sites and to see if it is indicative of differences in site productivity. An exponential model was fit to the data for *T. occidentalis* and *P. mariana* for each stand type, *L. laricina* for the xeric and hydric stands, *P. banksiana* for the xeric stands and *A. balsamea* and *B. papyrifera* the mesic stands. Height-diameter regressions were carried out using SigmaPlot for Windows version 9.01 (SYSTAT 2004).

3.0 Results

3.1 Ordination and Cluster Analyses

The first two RDA canonical axes explained 44% and 14% of the total variance respectively (Figure 1). Axis-1 most strongly associated to the presence of cobble, steeper slope and closed-canopy conditions which were also associated with the PCQs originating from the mesic sites. Axis-2 mainly distinguished between the xeric and the hydric sites most strongly related to pH and drainage. The PCQs from the hydric stands all shared negative loadings on axis-2 and were found to be associated with higher pH values and impeeded drainage conditions. In contrast, xeric sites were found to be positively correlated to axis-2 as well as elevation and sand (Figure 1b). PCQs from both the xeric and hydric stands were characterized by a more open canopy while the mesic sites were found to have a more closed canopy.

The K-mean cluster analysis differentiated three major *T. occidentalis* stand types (Table 1 and 2). The first cluster (PMA-TOC-PBA) is dominated by *T. occidentalis* followed by *P. mariana*, *P. banksiana*, and *L. laricina* (Table 1). Indicator species for these dry soils include shrubby cinquefoil (*Potentilla fruticosa* L.), sedges and lichens. The second cluster (TOC-PGL-ABA) is characterized by the dominance of *T. occidentalis, P. glauca*, *A. balsamea,* and *B. papyrifera.* Indicators of moist soils include twinflower (*Linnaea borealis* L.) and naked miterwort (*Mitella nuda* L.). The third cluster (TOC-PMA-LLA) is dominated by *T. occidentalis* followed by *P. mariana,* and *L. laricina,* with indicators of wet soil conditions being bog rosemary (*Andromeda polifolia* L.*),* field horsetail (*Equisetum arvense* L.)*,* scouring rush (*Equisetum variegatum* Schleicher ex F.Weber & D.Mohr)*,* and false Solomon's seal (*Smilacina trifolia* (L.) Desf.)

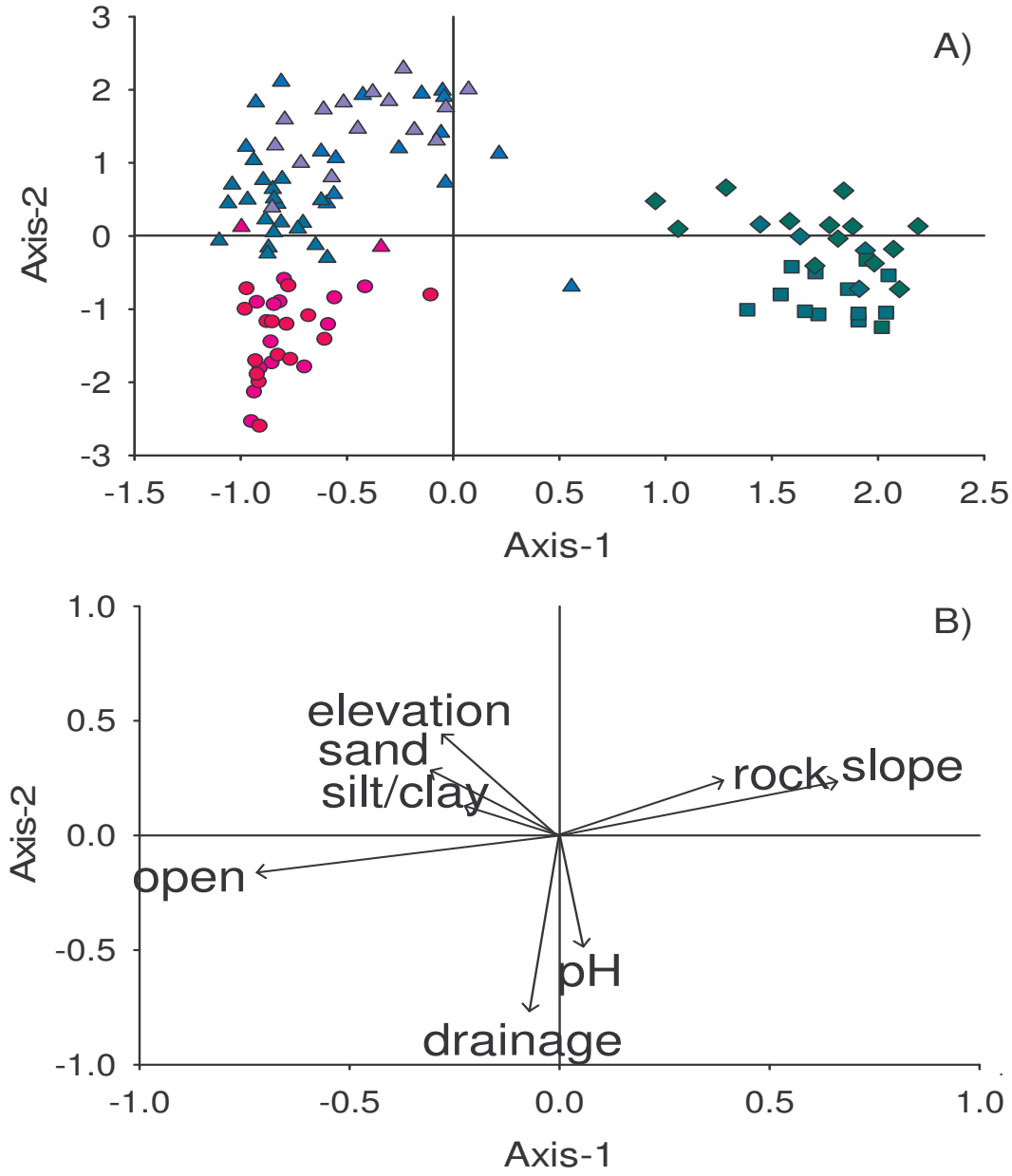

Figure 1. Redundancy Analysis depicting samples and significant environmental variables. The clusters determined by K-Means analysis are represented in sub-figure a, shape depicting cluster; PCQ related to the xeric stands (N=50) are represented by triangles, the hydric stands by circles (N=30), the mesic stands by diamonds and squares (N=30). A different colour represents each stand. Eigenvectors of the redundancy analysis (RDA) conducted on the collected biotic and abiotic variables are displayed in figure b. The descriptors (arrows) are positioned in the biplot based on their correlations with the canonical axes. The angle of the arrows indicates the relationship of variables to each other as well as samples (angles ≤90° indicate a positive correlation, ≥90° a negative one). Only the significant variables are displayed for ease of interpretation.

Table 1. Density and basal area by site type and species for saplings, trees and snags as calculated from the PCQs. SmSap= small saplings, Lgsap=large saplings. Blanks indicated none recorded for that site type. No diameter information was recorded for the small saplings so no basal area (BA) information can be presented. * indicates application of correction factor.

Density	**TOC-PMA-PBA**		N=50		**TOC-PGL-ABA**		N=30		**TOC-PMA-LLA**		N=30	
(trees/ha)	**SmSap**	**LgSap**	**Trees**	**Snags***	**SmSap***	**LgSap**	**Trees**	**Snags***	**SmSap**	**LgSap**	**Trees**	**Snags***
Abies balsamea	-	-	-	-	668	1370	965	285	-	-	-	-
Betula papyrifera	-	-	-	-	-	-	96	-	-	-	-	-
Larix laricina	-	35	75	-	-	-	-	-	1383	969	201	23
Pinus banksiana	-	-	92	32	-	-	-	5	-	-	-	-
Picea glauca	-	-	-	-	29	16	328	90	-	-	-	-
Picea mariana	1295	508	695	209	-	-	96	15	6619	1710	992	305
Populs balsamifera	-	-	-	-	69	16	-	15	-	-	-	-
Thuja occidentalis	1788	849	812	78	373	516	830	105	3853	741	532	30
Unidentified	-	-	-	13	-	-	-	65	-	-	-	3
Total	**3083**	**1393**	**1674**	**333**	**1139**	**1918**	**2315**	**580**	**11856**	**3420**	**1726**	**362**
Basal Area (m^2/ha)												
Abies balsamea	-	-	-	-	-	1.16	7.10	6.1	-	-	-	-
Betula papyrifera	-	-	-	-	-	-	4.98	-	-	-	-	-
Larix laricina	-	0.02	0.64	-	-	-	-	-	-	0.64	1.08	-
Pinus banksiana	-	-	3.24	0.44	-	-	-	0.02	-	-	-	-
Picea glauca	-	-	-	-	-	0.01	11.15	5.78	-	-	-	-
Picea mariana	-	0.38	4.66	2.02	-		1.49	0.62	-	1.33	4.56	1.77
Populs balsamifera	-	-	-	-	-	0.00		1.50	-	-	-	-
Thuja occidentalis	-	0.64	10.03	0.89	-	0.53	20.48	2.47	-	0.49	6.14	0.26
Unidentified	-	-	-	0.09	-			2.12	-	-	-	0.02
Total	-	**1.04**	**18.57**	**3.43**	-	**1.75**	**45.20**	**20.68**	-	**2.47**	**11.79**	**2.05**

Table 2. Mean percent cover (C%) and relative frequency (F%) of vegetation grouped by cluster results. Species shown are those found to have a greater than 20% mean total frequency (exceptions being trees, all are shown and *Cypripedium arietinum* due to its globally threatened status). T=tree, S1=seedlings, S2=sapling, SN=snag.

Species	TOC-PMA-PBA C%	N=50 F%	TOC-PGL-ABA C %	N=30 F %	TOC-PMA-LLA C %	N=30 F %
Abies balsamea T	0	0	37	80	0	0
Betula papyrifera T	0	0	9	17	0	0
Larix laricina T	5	14	0	0	15	40
Pinus banksiana T	8	16	0	0	0	0
Picea glauca T	0	0	21	37	0	0
Picea mariana T	37	84	7	13	42	93
Thuja occidentalis T	41	94	42	77	29	73
A. balsamea S1	0	0	58	90	0	0
L. laricina S1	5	10	0	0	37	70
P. mariana S1	36	68	0	0	50	93
T. occidentalis S1	50	88	33	53	27	53
A. balsamea S2	0	0	51	83	0	0
P. mariana S2	42	68	0	0	57	83
T. occidentalis S2	55	84	31	57	36	57
A. balsamea SN	0	0	37	90	0	0
P. mariana SN	34	92	4	10	41	100
T. occidentalis SN	16	44	16	47	8	27
Andromeda polifolia	0	16	0	0	3	90
Cypripedium arietinum	0	2	0	0	0	3
Equisetum arvense	0	0	0	0	1	80
Equisetum scirpoides	0	12	0	60	0	30
Equisetum variegatum	0	4	0	3	1	73
Juniperus horizontalis	3	62	0	0	2	50
Linnaea borealis	0	16	3	67	0	30
Mitella nuda	0	2	3	93	0	0
Petasites palmatus	0	30	0	27	0	30
Polygala paucifolia	0	14	0	0	1	47
Potentilla fruticosa	5	52	0	0	1	17
Rhododendron groenlandicum	17	84	0	10	12	93
Smilacina trifolia	0	0	0	0	5	77
Trientalis borealis	1	32	1	73	0	7
Vaccinium vitis-idaea	4	96	0	7	1	53
Feather moss	0	20	7	87	15	70
Hylocomium splendens	12	58	14	70	13	53
Pleurozium schreberi	26	82	7	60	8	33
Lichen-leaf	0	32	0	53	0	17
Lichen-club	0	46	0	7	0	57
Lichen-shrub	36	86	0	23	2	43
Sedge	2	94	0	13	7	90

Regeneration in both the TOC-PMA-PBA and the TOC-PMA-LLA stand types were dominated by layering *P. mariana* and *T. occidentalis* (Table 1, Figure 4b). In the case of the TOC-PMA-PBA sites the living trees and snags show a higher component of *P. banksiana* a species not found in the saplings. The TOC-PMA-LLA stands showed a similar proportion of species in the trees, snags and saplings. The TOC-PGL-ABA stands regeneration was dominated by *A. balsamea* (from seed) and *T. occidentalis* (from layering). Large trees and snags show a higher component of hardwoods and *P. glauca.*

3.2 Environmental/Biological Variables

The stand types were found to be significantly different in slope, drainage, LFH depth, openness, pH and the amounts of ericaceous litter (Table 3). The TOC-PMA-PBA stand type occupy xeric soils, at a higher elevation, lower pH, thin LFH and had high dominance of ericaceous litter compared to the other stands. This site type also showed the highest frequency of brunisolic soil, silt/clay and evidence of past fires The TOC-PGL-ABA stand type the highest slope, tree richness, canopy closure, amounts of litter, and overstory diversity with soil that consisted of a thick LFH lying on top of calcareous cobble. TOC-PMA-LLA sites were found to have the highest understory richness, pH and openness and the lowest coverage of CWD on organic soils (Table 3). *Thuja occidentalis* over 200 years of age were found in all three stand types (Table 4). The oldest *P. banksiana* found was 178 years old. In the hydric stands *P. mariana* was 232 years old and *L. larcina* was 186. The oldest tree recorded was a 257 years old *T. occidentalis* tree occurring in the mesic stand. The oldest *A. balsamea* tree was dated to 98 years.

Table 3. Results for ANOVA analysis of selected abiotic and biotic variables, the letters a, b, and c denote grouping and therefore where the significant difference lies (P <0.05) as determined by post hoc Freeman-Tukey test.

	TOC-PMA-PBA	N=50	TOC-PGL-ABA	N=30	TOC-PMA-LLA	N=30			
Variable	Mean	SE	Mean	SE	Mean	SE	F-ratio	P	R2
Tree R	2.6 a	0.1	3.6 b	0.1	2.8 a	0.1	21.48	0.000	0.29
Understory R	12.0 a	0.5	11.1 a	0.7	14.9 b	0.7	9.15	0.000	0.15
Total R	14.6 a	0.5	14.7 a	0.7	17.7 b	0.7	7.40	0.001	0.12
Elevation (m)	286 a	1.3	271 b	1.7	274 b	1.7	29.34	0.000	0.35
Slope	1.47 a	0.2	4.3 b	0.3	0 c	0.3	68.38	0.000	0.56
Drainage	1 a	0.0	2 b	0.0	4 c	0.0	1763.60	0.000	0.97
LFH depth (min)	14.6 a	1.7	25.6 b	2.1	38 c	2.1	37.72	0.000	0.41
% Open	33.9 a	1.2	12.9 b	1.5	44.7 c	1.5	110.17	0.000	0.67
pH	5.3 a	0.2	6.2 b	0.2	7.2 c	0.2	25.37	0.000	0.32
Ericaceous L	1.6 a	0.1	0 b	0.2	0.8 c	0.2	33.27	0.000	0.38
Deciduous L	0.2 a	0.1	1.6 b	0.1	0.2 a	0.1	48.58	0.000	0.48
CWD	5.1 a	1.2	12.4 b	1.5	2.8 a	1.5	10.92	0.000	0.17

N = number of samples, R = species richness, L = litter.

Table 4. Age range of the largest trees sampled at each stand type. tree cores were sampled as low on the stem as possible (20-50 cm from the base) but ages should be considered minimums as samples were not taken at the root collar and in many cases the pith was unobtainable due to heart rot both of which are required to determine exact age.

	Xeric	Mesic	Hydric
Abies balsamea	-	21-98	-
Betula. papyrifera	-	88-126	-
Larix. laricina	55-63	-	48-186
Pinus banksiana	108-178	-	-
Picea glauca	-	64-104	-
Picea mariana	55-195	92-104	98-232
Thuja occidentalis	90-236	59-257	103-216

Table 5. Seedling counts for one by fifty meter plot in each stand type. Displayed variables included origin (sexual or vegetative) and substrate (moss or logs). Seedlings included those ≤30 cm tall. Substrate: M= moss/litter, L=log/stump, v = indicates vegetative reproduction, when absent reproduction is by seed

Seedlings in $50m^2$	Xeric		Mesic		Hydric	
Abies balsamea	-	-	233/23	M/L	-	-
Larix laricina	-	-	-	-	1	M
Picea glauca	-	-	2	L	-	-
Picea mariana	9 v	M	-	-	47	M
Thuja occidentalis	8 v	M	8 v / 2 v	M/L	1/ 2/ 43 v	L/M/M
Total	**17**	**-**	**268**	**-**	**94**	**-**

3.3 Trees

3.3.1 Tree Stature

From now on for simplicity the stand type TOC-PMA-PBA will be referred to as xeric, the TOC-PGL-ABA stand type will be referred to as the mesic stands and the TOC-PMA-LLA as the hydric stands. Maximum tree size varied among the three stand types (Figure 2a). Trees from the mesic stands were found to be represented in more dbh classes and to reach larger diameters than those from the hydric and xeric stands. The same trends were observed with snags and CDW diameter distributions (Figure 2bc). Interestingly, it can also be observed that tree composition changes from the tree layer to the snag and CDW layer in both the xeric and mesic stands whereas it remains constant in the hydric (Figure 2 and 4). For example the proportion of *P. glauca* and hardwoods increases in the snags and CDW of the mesic stands as does *P. banksiana* in the xeric indicating a species-turnover with time.

The results for the tree heights distribution (Figure 2d) are similar to those from the diameter class distribution (Figure 2a). Many large trees were recorded in mesic stands, the largest trees reaching height over 24 m, with a considerable proportion of these larger trees being *P. glauca* and hardwoods (Figure 2d). *Thuja. occidentalis* and *P. mariana* trees in the xeric stands were mostly in the 6 and 8 m height classes with the most *P. mariana* in the 8 m and some in the 10 m class trees larger than this in these stands were *P. banksiana* and *L. laricina*. In the hydric stands *T. occidentalis* were mostly in the 4 to 8 m classes, *P. mariana* 4 to 8 m.

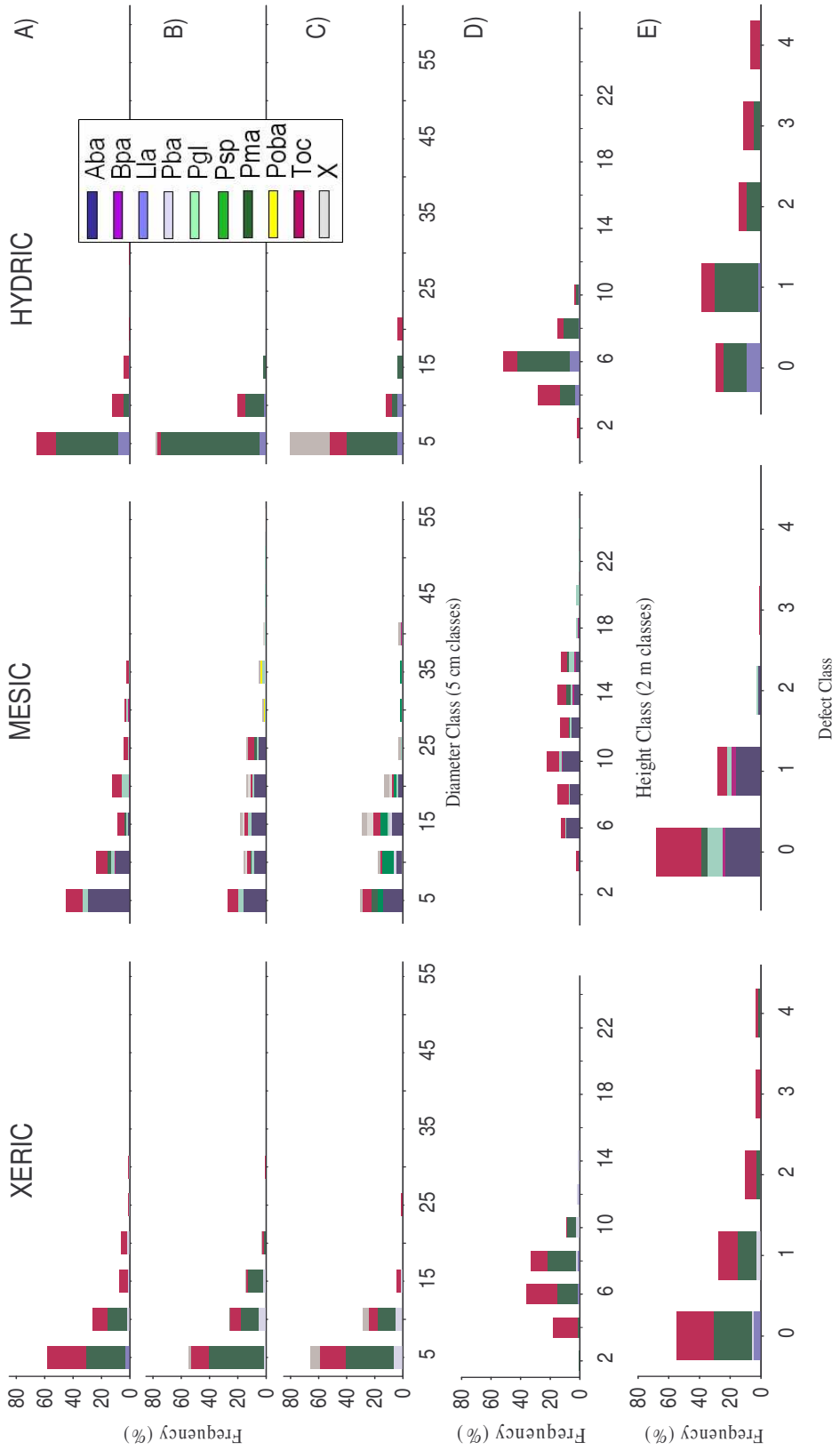

Figure 2. Relative frequency by species of a) tree diameter class, b) snag diameter class, c) CWD diameter class, d) tree height class and e) tree defect class (0 equals no defect while 4 is a nearly senescent tree; Appendix 2. The legend consists of the first three letters of binomial specis names except in the case of Poba which represents *P. balamifera*, Psp which represents unidentifiable *Picea* sp. and X which indicates a species was not identifiable.

3.3.2 Tree diameter-height regression

The mesic stands supported higher growth rates of species present than the other stand types, including *T. occidentalis* (Figure 3a) and *Picea* sp. (Figure 3b). *Thuja occidentalis* was found to reach larger sizes in the mesic stands whereas the *T. occidentalis* trees in the xeric and hydric stands are similarly are not found to attain heights greater than 8 m. *Thuja occidentalis* in all stands shows a levelling off of the curve. The growth curve of *A. balsamea* and *P. glauca* are relatively steep indicating rapid height growth of these species in the mesic stands. *Pinus banksiana* (Figure 3c) shows maximum growth around 12 m high and 30cm diameter. The growth found at these stands relates well to the health of these trees. The majority of trees in all three site types have no to little defect however the mesic stands have the lowest number of living trees with a high defect class number (Figure 2e).

3.3.4 Regeneration

Regeneration in the stands can be seen by the seedling transects results (Table 5) and the sapling information (Table 1). In both instances recruitment into all stands was dominated by shade tolerant species. In the xeric and hydric stands *T. occidentalis* and *P. mariana* dominated regeneration. In the mesic stands there was abundant *A. balsamea* regeneration with a smaller amount of *T. occidentalis*. The mesic stands also showed some balsam poplar (*Populus balsamifera* L.) regeneration in the PCQ results with the highest amounts found as small saplings. The mesic stands show the highest numbers of seedlings per transect, however, the hydric stands showed the highest densities of small and large saplings.

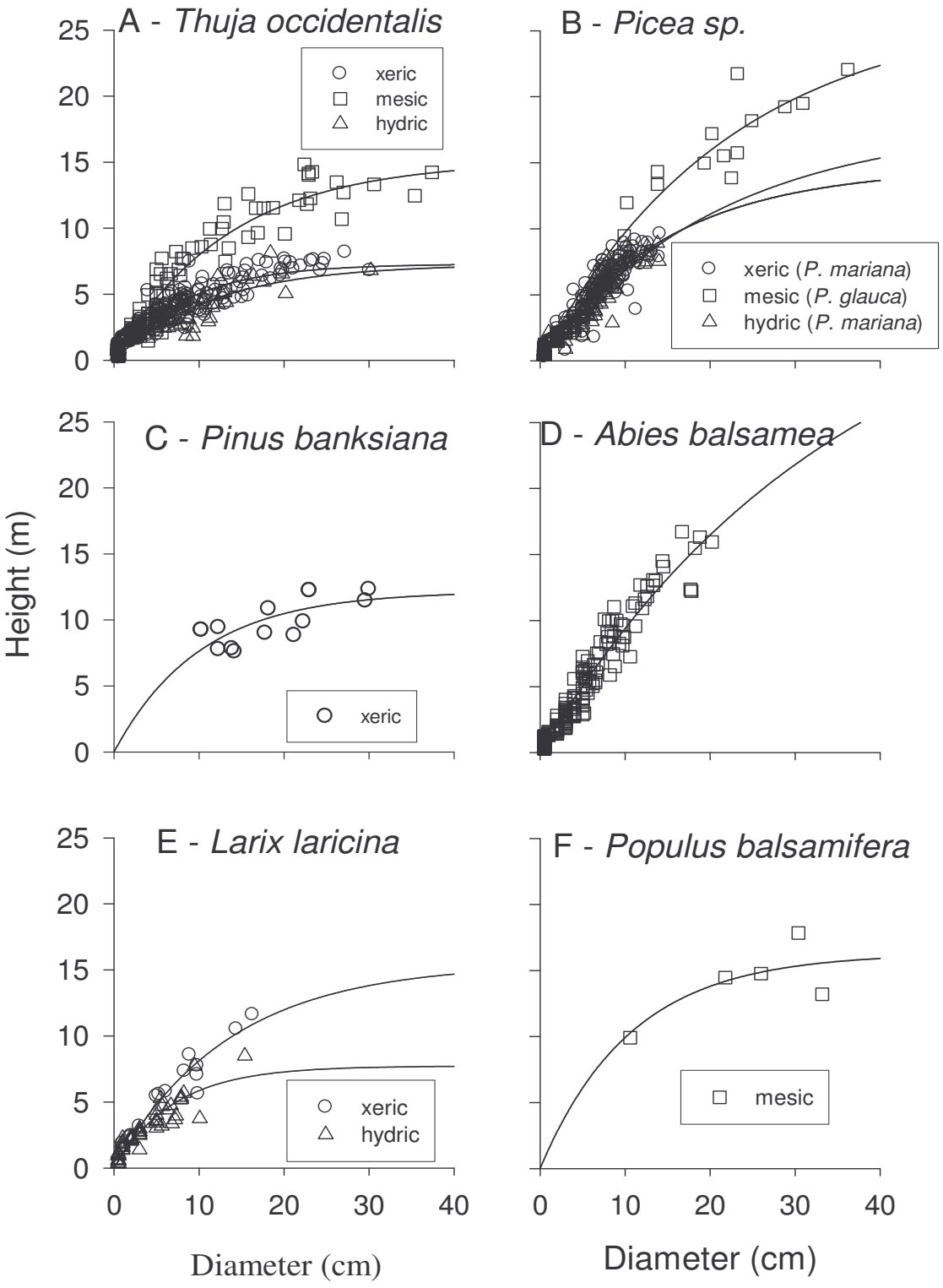

Figure 3. Diameter and height regression for the dominant overstory species by stand type.

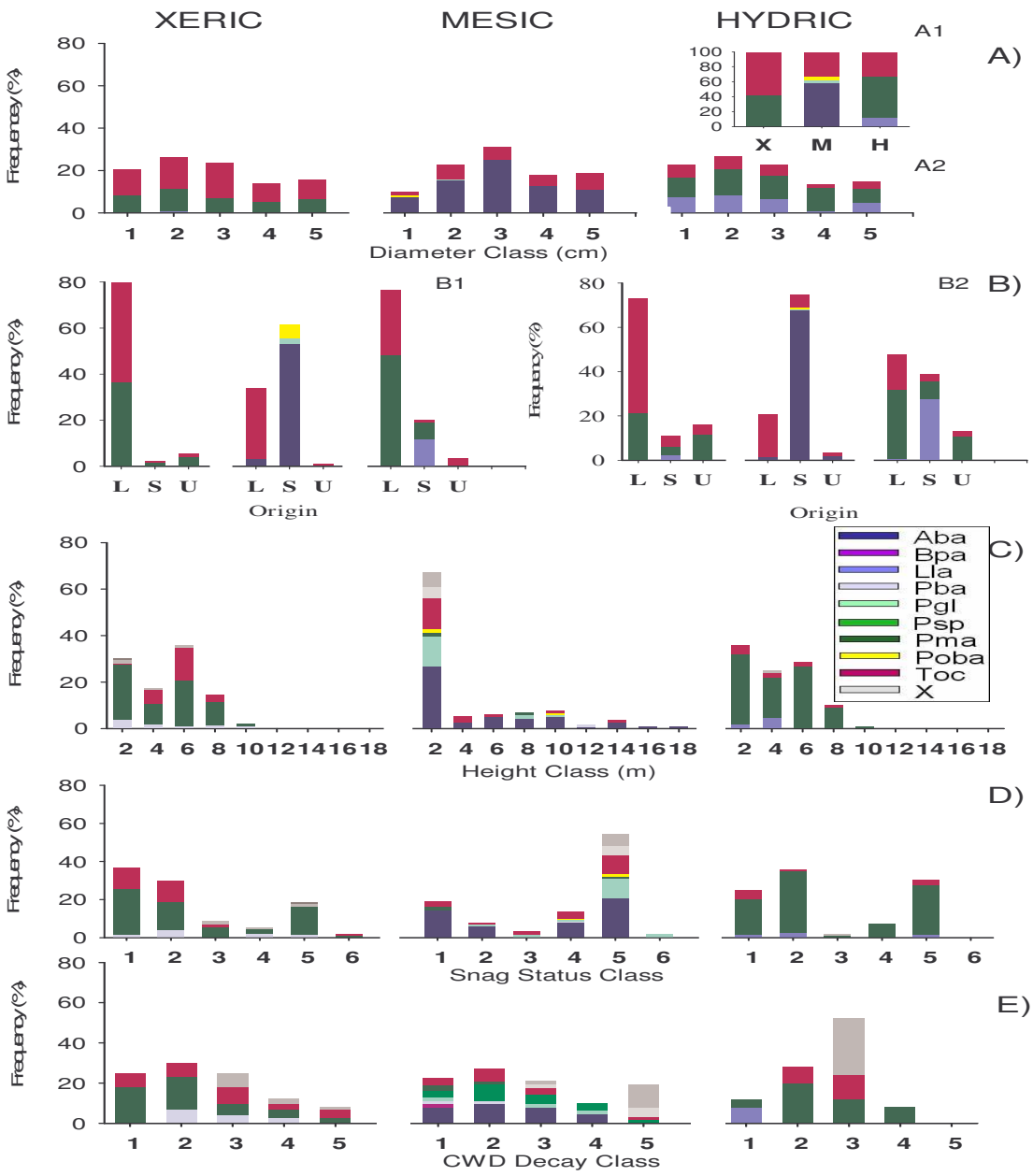

Figure 4. Relative frequency of the distribution of a) large sapling diameter class (inset (A1) showing small sapling frequency), b) sapling origin (L=layering, S=seed, U=unknown) by stand type (X=xeric, M=mesic, H=hydric) for small saplings (B1) and large saplings (B2), c) snag height distribution, d) snag class distribution (1 representing a recently dead tree and 5 a stump; Appendix 3) and e) CWD decay class (1 recently fallen tree and 5 well decayed; Appendix 4). Legend consists of the first three letters of binomial species names except in the case of Poba which represents *P. balsamifera*, Psp which represents an indiscernible *Picea* sp. and X which indicates a species that was completely indiscernible. For saplings and snags the number of individuals sampled was approximately 200 in the xeric stands, and 120 in the mesic and hydric stands (not accounting for blanks).

3.4 Coarse Woody Debris

There overall distribution of decay classes was similar among stands (Figure 4e). Where differences were found was that there was no class five CWD recorded in the hydric stands whereas there was in the other stand types. There was also more class three CWD found in the hydric stands. The mesic stands differ in having more extremely decayed material in class five most of it being of an indiscernible species (Figure 4e). There was variation in the species distribution among stands. *Thuja occidentalis* for example was found evenly throughout classes in the xeric stands, largely as class two in the mesic and with most in the hydric as class two with none more decayed than a class three. *Picea mariana* decay also varied among stands being mostly classes one and two in the xeric and mesic stands with more class two and three in the hydric. *Larix laricina* was only found as a class one, *P. banksiana* mostly as classes two and three. There was found to be a higher volume of CWD at the mesic sites than either the xeric or hydric (Table 6).

Table 6. Coarse woody debris volumes for each stand type as obtained from 150 m transect.

Volume	TOC-PMA-PBA (1,3,7)*	TOC-PGL-ABA (5,6)*	TOC-PMA-LLA (2,4)*
Smalian m3 along 150m	1.1	4.1	0.2
Smalian m3 along 150m	1.0	7.4	0.3
Smalian m3 along 150m	1.0	-	-
Wagner m^3/ha	17.9	68.6	4.8
Wagner m^3/ha	23.3	87.0	14.12
Wagner m^3/ha	17.2	-	-

* indicates site number/s

4.0 Discussion

4.1 Relationship between Stand Type and Dynamics

Stand types were found to differ in species composition, vertical and horizontal structure as well as measured abiotic variables. Evidence suggests that the differences among stands are not due to differences in age but rather in environmental factors that affect the successional pathway, the species present and tree growth.

Results indicated an association between the *T. occidentalis* stand type and substrate. The stands sampled are on a moraine and different stand types are located in areas of differing elevation, superficial deposits, drainage and pH. The range of environmental conditions found results in low elevation, high pH fens (TOC-PMA-LLA), nutrient rich, sloped, moist seepage areas with soil that consists of organic material underlain by calcareous rock and cobble (TOC-PGL-ABA) and dry, thin soiled, higher elevation stands (TOC-PMA-PBA).

This may indicate an association between *T. occidentalis* form and the nature of the substrate. Trees of a more regular form (with little apical mortality) and a larger size were found in the mesic stands. Results indicate that this is related to soil characteristics such as pH and substrate. Johnston (1990a) notes the relationship between *T. occidentalis* growth and soil, growing best on limestone derived soils that are neutral or slightly alkaline and moist but well drained (Johnston 1990a). Curtis (1946) mentions the relationship of the occurrence of this species and basic soils, reaching its maximum development there. Differences in soil aeration may be related to differences found in the tree form in different stands as flowing water positively effects growth (Curtis 1946). It is

likely that the more rigorous growth of *T. occidentalis* trees in the mesic stands is indicative of more optimal soil conditions in relation to pH, aeration and moisture levels.

These *T. occidentalis* stands studied have developed different vegetation communities reflecting variation in environmental conditions. As previously observed old *T. occidentalis* trees occur in three stand types representing the later stages of three successional pathways. Old-growth *T. occidentalis* stands have been researched in other areas. The ancient *T. occidentalis* discussed by Larson and Kelly (1991) and Archambault and Bergeron (1992a) were found to occur in areas that have not burned for extended periods. In the case of Larson and Kelly (1991) these trees are found on cliffs of dolomitic limestone of the Niagara Escarpment. The old *T. occidentalis* discussed by Archambault and Bergeron (1992a) occurs on thin soils or rock outcrops on moraine deposits.

The successional trend found in the mesic stands parallels similar trends found in eastern forests where *A. balsamea, P. glauca* and *T. occidentalis* occurs as late successional species (Asselin *et al.* 2001). *Thuja occidentalis* and *P. mariana* experience suppression early on, dominating stands later after fire compared to other species (Bergeron and Charron 1994). Bergeron (2000) found *P. glauca* to decline in basal area approximately 150 years after the last stand replacing fire, about the same time that *T. occidentalis* increases in stand importance. Park *et al.* (2005) also found the same trend where *T. occidentalis* trees dominated in the oldest stands, increasing in importance with increasing stand age. Another similar finding between Park *et al.* (2005) and this study is the presences of small numbers of large aspen and birch, as remnants of species associations

more dominant in the past. Bergeron (2000) also reported a decrease of trembling aspen (*Populus tremuloides* Michx.) approximately 75 years after fire. This mirrors what we find in these mesic stands with remnants of past cohorts that once were more important in the stand now senescing (*P. glauca* and hardwoods).These mesic stands were found to have a relatively closed canopy showing a trend towards increasing presence of shade tolerant species. In mesic stands the presence *P. glauca* and hardwoods only as larger trees, their increased importance in deadwood and lack of regeneration of these species, indicate they are becoming less important in the stands with time. There is a tendency toward increasing components of late successional *T. occidentalis*, and *P. mariana,* and *A. balsamea* which are all shade tolerant.

The xeric stands contain *T. occidentalis, P. mariana* and *P. banksiana* in relatively open, dry stands on thin soils. There are also evidences of species turnover in this site due to the distribution of *P. banksiana* in the CWD, snags and living trees indicating no new recruitment of this species into the stand. The regeneration and smaller trees were dominated by *T. occidentalis* and *A. balsamea.* Old *T. occidentalis* tress have been noted co-occurring with *P. banksiana* at xeric sites along lake shorelines (Archambault and Bergeron 1992ab), and is also found at dry sites on islands and peninsulas (Archambault and Bergeron 1992a). It has been suggested that the longevity of *T. occidentalis* in xeric sites could be enhanced by the low density of tree and the sparse ground cover (Archambault and Bergeron 1992a). *Pinus banksiana* is a pioneer species intolerant of shade establishing on recent burns or other exposed sites. In the absence of fire it is usually succeeded by more tolerant species, such as a *P. mariana- A. balsamea* association, but may persist as an edaphic climax (Rudolph and Laidly 1990).

Hydric sites appear to have reached a stable climax community as there is no compositional change evident in the diameter class distribution, legacies of past stands (CWD or snags) or regeneration. These stands are dominated by *T. occidentalis* and *P. mariana. Larix laricina* is generally considered a pioneer species readily establishing on recently burned organic soils, the first to colonize filled-lake bogs and not able to establish in its own shade and is eventually succeeded by *T. occidentalis and A. balsamea* on good sites (Johnston 1990b). It likely remains a significant component of these old-growth stands due to the open canopy resulting from low tree densities.

If one compares these sites to the Forest Ecosystem Classification for Manitoba field guide (Zoladeski 1995) one finds difficulty as a dominance of *T. occidentalis* in the stand leads to only one vegetation type V19 and while this may compare well to the mesic stands it is not appropriate for the xeric and hydric stands. The xeric stands could possibly be compared to V22 and the hydric V31. The fact that these sites do not fit into this classification scheme with ease suggests that *T. occidentalis* stands could be better represented in the guide particularly in reference to the xeric stands which do not compare well to any V-type.

4.1.2 Coarse Woody Debris and Snags

The findings for CWD and snags are likely associated to species composition, density of trees, stand productivity and site conditions. The more productive mesic stands had higher amounts and sizes of CWD and snags which is not surprising as CWD is known to increase with increasing productivity (Feller 2003). The amounts and sizes of CWD present has implications for the ability of stands to provide high quality wildlife habitat

and is one of the factors looked at by those attempting to locate old-growth stands. Results for the mesic stands also displayed more highly decayed snags and CWD. This could be explained in part by the increased presence of relatively soft wooded species. This higher amount of large and abundant dead wood (snags and CWD) could indicate a potential of the mesic stands as high quality wildlife habitat.

There are some parallels to draw between the less typical old-growth stands found here and late successional eastern *P. mariana* and *A. balsamea* forests in relation to the CWD. The amounts of CWD found in the mesic stand type is comparable to those found by Thompson *et al*. (2003) in old *A. balsamea* forests (vol. of logs >10 cm was 55.2 m^3/ha) and the old *P. mariana* on clay and organic sites (vol. 25-50 m^3/ha) by Harper *et al.* (2003). Harper *et al.* (2003) also found relatively low volumes of CWD in the clay and organic sites compared to the coarse sites. The sites in Harper *et al.* (2003) are similar to our xeric, hydric and mesic sites respectively. They also found the highest tree species diversity in the coarse sites, much like these mesic stand types.

4.2 Old-Growth Manitoba *Thuja occidentalis* – Implications for Old-Growth Definitions

The *T. occidentalis* stands in this study and the multiple successional pathways they display reaffirm the need for definitions of old-growth that reflect not solely regional variations but also forest dynamics. Time-since-last-fire is a good indicator of old-growth however it is difficult to determine when the life span of trees is shorter than disturbance frequency. Old-growth forests often do not fit a notion of them determined elsewhere due to differences in species composition and environmental factors such as climate. Differences in site factors such as drainage and superficial substrates can influence the

structure and character of a stand. When seeking definitions for future management one must consider many characteristics of a forest rather than just age or size. If one single characteristic had to be chosen to define a forest as old-growth or not the simplest, most effective way to do that would be age or, for even further reductions in bias, time-since-last-stand replacing disturbance. To better reflect the characteristics of old-growth that are valued due to their benefits to ecosystems and wildlife a wider range of parameters should be considered.

Old-growth indices should be developed for each region. If this were to be done in this area the stand types examined here would be best considered separately. All stand types were found to be of old-age and contain at least one late successional species. Old-growth xeric stands in the area show an increasing trend of shade tolerant species, decreases in the pioneer cohorts, and low densities. Old-growth mesic stands were found to have relatively large trees and abundant woody debris. The hydric stands were found to have species compositions that have reached a steady state and further research could reveal these stands to could contain bryophyte indicators of old-growth. To develop an old-growth index for the region these old-growth forests would have to be compared to younger stands in the area for each stand type to better determine what variables would be used in index for the region. This would require further sampling efforts to characterize the variety of old-growth forests and would enable the quantification of the old-growth value of a stand, based on multiple parameters considered of importance. In this way definitions applicable to the region and site type could be applied to all forests and perhaps be added to the forest inventory providing information on the amount and kind of old growth characteristics these forests have.

5.0 Conclusions

Old-growth *T. occidentalis* occurs in three different vegetation communities in west-central Manitoba corresponding to three different successional pathways. The different successional pathways and resulting vegetation communities result from differences in abiotic factors including substrate and drainage. The stand types found display differences in old-growth characteristics such as amounts and size of CWD, snags and trees, which can have implications for wildlife habitat and adherence to old-growth definitions. The characteristics of these forests indicate the variability found among old-growth forests and therefore the need for methods of defining them that are regional and based on site type. There are similarities to the successional pathways found in these stands and those in the rest of *T. occidentalis's* range. These old-growth *T. occidentalis* stands are unique in composition, age and location offering opportunities for further research on species distribution, dendrochronology and old-growth.

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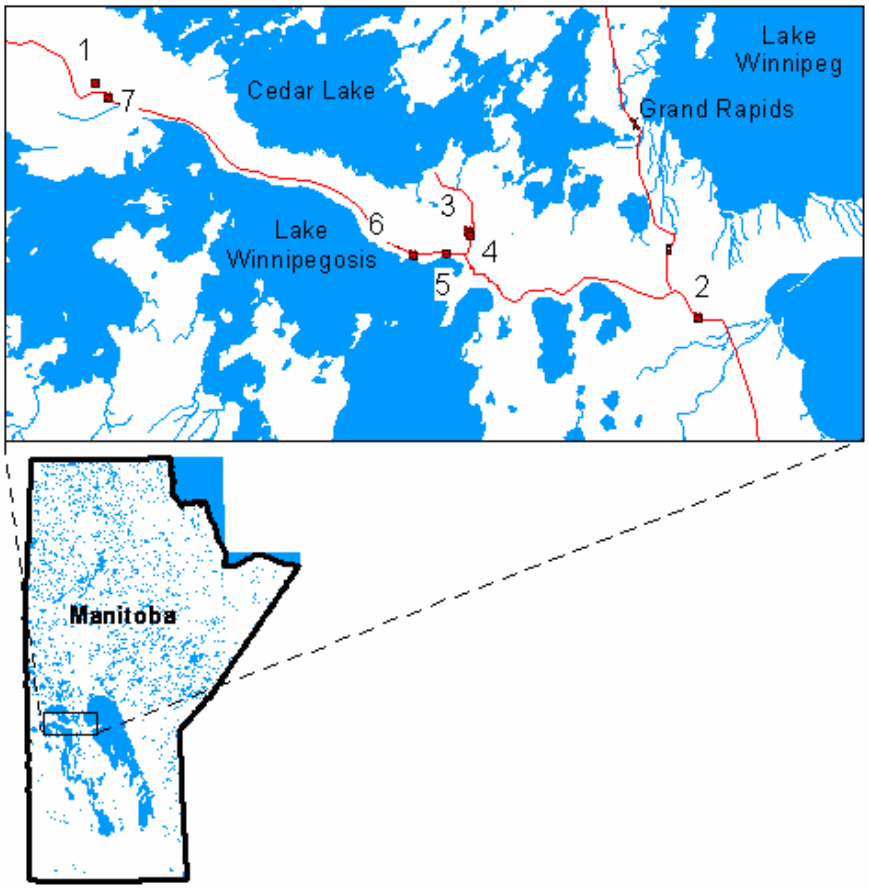
Appendices



Appendix 1. Map of Manitoba with inset detailing study area. Numbers indicate sampling sites the location of which corresponds with The Pas end moraine. These sites are near Grand Rapids in the area of Lakes Winnipeg, Cedar and Winnipegosis.

Appendix 2. Defect class for living trees (adapted from Angers *et al.* 2005).

Class	Description
0	no defect
1	localized, minor: small to medium knot or canker, small lesion with exposed rot, small holes
2	localized, moderate: large knot or canker, small open split, small to medium healed split, medium lesion with exposed rot
3	extensive, spreading: large knot or canker, medium open split, medium cavity, medium to large lesion with exposed rot, presence of fungi
4	hollow or moribund tree: part of the bole visibly hollow and/or part of the crown dead

Appendix 3. Snag Decay/Status classes (adapted from McCleary 2005):

1	intact bark, recently dead, branches and needles may be intact
2	bark missing, trees dead for several years, bark partially deteriorated and fallen off; tops often broken
3	clean snag, tree dead for several years with no bark left. Most of braches gone, tops often broken
4	broken above breast height, tree dead for a long time with no bark and extensive decay
5	broken below breast height
6	cut stump

Appendix 4. Coarse woody debris classification scheme (adapted from Meidinger *et al.*1998)

Vegetation Resource Inventory Ground Sampling Procedures March 1997 Table 8.1					
	CLASS 1	CLASS 2	CLASS 3	CLASS 4	CLASS 5
WOOD TEXTURE	intact, hard	intact, hard to partly decaying	hard, large pieces, partly decaying	small, blocky pieces	many small pieces, soft portions
Other associated characteristics					
PORTION ON GROUND	elevated on support points	elevated but sagging slightly	sagging near ground, or broken	all of log on ground, sinking	all of log on ground, partly sunken
TWIGS < 3 cm (if originally present)	twigs present	no twigs	no twigs	no twigs	no twigs
BARK	bark intact	intact or partly missing	trace bark	no bark	no bark
SHAPE	round	round	round	round to oval	oval
INVADING ROOTS	none	none	in sapwood	in heartwood	in heartwood

From Government of BC Field manual for describing terrestrial ecosystems: Land management handbook 1998