Ecology of northern white-cedar (*Thuja occidentalis* L.) stands at their northwestern

limit of distribution in Manitoba, Canada

By

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A thesis submitted to

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THE UNIVERSITY OF MANITOBA

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ABSTRACT

Studies examining disjunct populations of tree species have been infrequent. The objective of this study was to characterize and compare the composition, structure, and environment of disjunct populations of northern white-cedar (*Thuja occidentalis* L.) to populations from its contiguous and peripheral distributions in Manitoba, Canada. *Thuja occidentalis* reaches its northwesterly contiguous distribution limit in southeastern Manitoba, but disjunct populations can be found approximately 300 km northwest, in the Grand Rapids/Cedar Lake area of west-central Manitoba. Forty-two stands were sampled to characterize the *T. occidentalis* populations and five community types were identified by *K*-means clustering. The first hypothesis stated that the disjunct populations of *T. occidentalis* would be restricted to locations with specific environmental conditions/habitat, such as wet locations protected from fire. However, in the disjunct range this species was present in sites with xeric, mesic, and hydric moisture conditions. Stands of the disjunct range were mostly conifer dominated, as represented by the xeric and hydric community types, but there were also three stands of a mesic mixedwood community. In contrast, *T. occidentalis* in southeastern Manitoba only occurred in mesic and hydric moisture regimes. There was support for the second hypothesis that *T. occidentalis* associations would differ geographically, even though there was compositional overlap between three of the five community types. Third, it was hypothesized that the growth vigour of *T. occidentalis* would be reduced in the disjunct populations compared to that of the populations found in the contiguous distribution. The productivity of the three mesic mixedwood stands observed in the disjunct range contrasted with the restricted growth of the common xeric and hydric community types.

In these three stands however, growth vigor was slightly lower than their contiguous counterparts. Lastly, it was hypothesized that regeneration success would be lower in the disjunct populations than the contiguous distribution, however, *T. occidentalis* recruitment was common in all community types, and in fact more abundant in the disjunct range than in the contiguous distribution.

ACKNOWLEDGMENTS

DEDICATION

I dedicate this work to my wife Catherine, and our son, Desmond. Thank you both for your support, love, and patience.

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1.1 Background on the Geographic Distribution of Tree Species

1.1.1 Distribution of a Species

Numerous boreal tree species have been thoroughly studied at various locations within their geographic distributions, but few studies have compared trees growing at their range boundaries with those in the main part of their range (Kavanagh and Kellman 1986). Such studies can shed light on the potential factors limiting a species' distribution, such as climate, habitat availability, disturbance regimes, or time (Kavanagh and Kellman 1986). Additionally, comparative studies on distributions can reveal variability in the realized niche of a species, i.e. where and under what conditions it actually persists (Brown et al. 1996). This is compared to the fundamental niche, which is where and under what conditions it could persist in the absence of competition, other biotic interactions, or disturbance (Chuine and Beaubien 2001). These types of studies generally fall under the discipline of biogeography, the study of the dynamics and determinants of the geographical distribution of a species, especially the size, shape, boundaries, and internal structure of a distribution (Brown et al. 1996).

Disjunct populations that have been included on distribution maps usually cover particularly large areas or are distant from the contiguous distribution (Brown et al. 1996). These populations, as well as smaller, less isolated disjunctions, may be relict populations from a historically larger distribution that has contracted, isolated populations by the formation of a new barrier, or populations that have been established by long-distance dispersal events (Wood 1972; Brown et al. 1996). The internal structure

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of a species distribution, i.e. the spatial patterns of abundance, can fluctuate enormously, for example, species abundances can vary by multiple orders of magnitude across the geographic distribution (Brown et al. 1996). The variability in abundance and degree of fragmentation within the distribution limits (the internal structure) is a component of the distribution that is often ignored (Brown et al. 1996). Studies of the boundaries of geographic distributions are common however, as exemplified by the abundance of latitudinal and altitudinal tree line research for various tree species (e.g., Black and Bliss 1980; Elliott-Fisk 1983; Korner and Paulsen 2004; Wieser and Tausz 2007 and references within). In general, while there is a wide array of abiotic and biotic factors which may limit distributions, it is the limiting factors in effect at the local scale that determine the edge of a range (Brown et al. 1996).

Another general characteristic of a species' geographic distribution is low abundance at the boundary, except when physical boundaries are present (e.g. coastlines), and highly variable abundance at/near the distribution centre (Brown et al. 1996). In a study analyzing the abundance of 134 eastern North American tree species throughout their entire geographic distributions, Murphy et al. (2006) demonstrated that most tree species do not conform to an 'abundant-centre distribution', i.e. highest abundance was not found at the centre of the distribution. They noted that an 'abundant-core', or a peak in abundance that is non-central in the distribution, could be found somewhere within the distribution of the majority of species examined. However, high densities were least likely at the margins of a species' distribution (Murphy et al. 2006). Recently, efforts have been made to provide effective methods for the quantification of i) a species

distribution boundary, ii) the uniformity of abundance within a distribution, and iii) changes in the structure of the distribution over time (Fortin et al. 2005). These authors discussed the methods to analyze and accurately map the above distributional characteristics. They pointed out the importance of accurate boundary delineation for distributions to monitor change and identify appropriate management needs (Fortin et al. 2005).

The distribution of vegetation at the global scale has long been considered controlled by climate (Ritchie 1987; Woodward 1987). This is illustrated by worldwide vegetation cover classification systems, such as vegetation formations, zonobiomes, or ecoclimates, which draw heavily upon the climate of a region (Scott 1995). While these are useful classification systems, Loehle and LeBlanc (1996) noted that most of the forest simulation models define current tree species distribution based on climate (i.e., unfavourable climate at and beyond a species distribution limit would result in 100% mortality, and conversely, maximal growth and survival is achieved at the distribution centre, where climate is assumed optimal). These assumptions of a climate control over tree species distribution result in improbable modeled forest responses to projections of climate change (Loehle and LeBlanc 1996). Johnstone and Chapin (2003) noted that the northern distribution boundary of lodgepole pine (*Pinus contorta* Douglas ex Louden var. *latifolia* Engelm. ex S. Watson) in the Yukon Territory was expanding and not in equilibrium with climate, i.e., the current northern distribution limits were not directly controlled by climate. They highlight the inadequacies of modelling distribution limits for climate change without realizing or understanding species-specific, non-climatic

distribution limits (Johnstone and Chapin 2003). It has been argued that if distribution projections for tree species as responses to climatic change are to be accurate, then climatic and non-climatic factors controlling species at their limit of distribution must all be taken into account (Loehle and LeBlanc 1996; Meilleur et al. 1997; Grace et al. 2002; Johnstone and Chapin 2003; Tardif et al. 2006). Increasing baseline information on population and community dynamics across a geographical distribution, and especially at its boundaries, constitutes an important step required to achieve this objective.

1.1.2 Distribution Boundaries: The Tree Line

Tree lines are often considered dynamic, both historically and currently, having moved over the post-glacial millennia and in recent times due to warmer temperatures (e.g. Grace et al. 2002). Numerous authors consider cold temperatures to be the controlling influence of the northern tree line (e.g. Mitchell 1973; Korner and Paulsen 2004). Mitchell (1973) suggested that it was the mean summer position of the front that was critical. Mitchell (1973) noted that the arctic front dictated the tree line in central Canada for black spruce (*Picea mariana* (Mill.) B.S.P.), and possibly white spruce (*Picea glauca* (Moench) Voss.), and jack pine (*Pinus banksiana* Lamb.). Korner and Paulsen (2004) stated that at a global scale, the alpine tree line would be associated with a mean ground/soil temperature of 6.7°C, ±0.8°C, in the absence of disturbances. Korner and Hoch (2006) suggested that temperature has a greater impact on roots than shoots in limiting a tree's growth. Warmer temperatures should thus result in improved growth form, and an advancement of the tree line, as it has been suggested by some authors (e.g. Goldblum and Rigg 2005; Handa et al. 2006). Due to the challenge of colonizing the sub-

arctic tundra or the more obvious physical barriers of alpine conditions (e.g. steep rock walls, slope debris), tree line dynamics involve temporal fluctuations in population density with occasional small advances or retreats as determined by prevailing conditions. Population densities of *P. glauca* have risen at the tree line since the end of the Little Ice Age in western Canada (Szeicz and MacDonald 1995), central Canada (Scott et al. 1987; MacDonald et al. 1998), and eastern Canada (Payette and Filion 1985; Caccianiga and Payette 2006), in synchrony to a warmer climate. However, tree line movement in these regions has slowed and become minimal (Payette et al. 1985; Scott et al. 1987; Szeicz and MacDonald 1995; MacDonald et al. 1998), and over the last 3000 years it has even been considered static in northern Quebec (Payette et al. 1985; Lavoie and Payette 1996). The influence of recent warming was more favourable for *P. glauca* at the alpine tree line along the northern Labrador coast, where population ranges have advanced a few tens of metres over the last 50 years (Payette 2007). The opposite trend was seen on the nearby Labrador plateau where the latitudinal tree line of *P. glauca* has not recovered from a recession during the Little Ice Age (Payette 2007).

Sexual regeneration at the tree line can be restricted by increasingly harsh conditions, a shortening of the growing season, and a reduction of energy requirements needed to produce pollen, cones and viable seed (Elliott-Fisk 1983; Sirois 2000). In northern Quebec, Lescop-Sinclair and Payette (1995) noted the absence of *P. mariana* trees that had originated from seed (as opposed to asexual origins) at the tree line, and Gamache and Payette (2005) revealed that the abundance of *P. mariana* trees from sexual origins decreased exponentially towards the tree line. Furthermore, observations of

krummholz *P. mariana* in northern Quebec demonstrated increased radial growth coincidental with recent climatic warming, but a continued lack of tree growth form (i.e. trees remained stunted) minimizes the potential for sexual reproduction and colonization of hilltops (Asselin and Payette 2006). However, Elliot-Fisk (1983) noted both sexual and vegetative regeneration in *P. mariana*, *P. glauca*, and tamarack (*Larix laricina* (Du Roi) K. Koch) at the tree line along the nearby Labrador-Ungava Peninsula. Similarly, both reproductive strategies have been observed at the tree line in *P. glauca* in central (Scott et al. 1987; MacDonald et al. 1998) and eastern Canada (Caccianiga and Payette 2006). In the North West Territories, sexual regeneration (seed production and germination) in *P. mariana* was found within about 40 km of the tree line (Black and Bliss 1980), but vegetative reproduction within this species maintained populations at and below the tree line (Black and Bliss 1980; Elliot-Fisk 1983; Lescop-Sinclair and Payette 1995). Under favourable conditions, slow continual seed release from semi-serotinous cones can provide additional recruitment for this species (Black and Bliss 1980). Vegetative reproduction in *P. glauca* and *L. laricina* is isolated to the stressful conditions at the tree line, and appears to be their main method of population maintenance at the tree line in western Canada (Elliott 1979; Elliot-Fisk 1983).

Wind, especially when combined with temperature, also plays an important role in tree line dynamics by altering tree growth form, i.e. flagged krummholz trees (Wieser and Tausz 2007), damaging and killing needles (Hadley and Smith 1986), as well as inducing cambial mortality (Schauer et al. 2001). Wind and snow abrasion can remove needle cuticles and dehydrate them, resulting in their death (Hadley and Smith 1986).

Longevity and population maintenance in *P. mariana* through vegetative reproduction confers stability to the tree line. Arseneault and Payette (1992) observed that a stand of krummholz trees was unable to regenerate after fire, and was subsequently converted to lichen-tundra; however, in other locations tree line *P. mariana* has been noted to maintain itself in the presence of fire (Black and Bliss 1980; Gamache and Payette 2005).

1.1.3 Distribution Boundaries: Northern Distribution Limit

Evidence suggests that temperature limits regeneration success of numerous tree species at their northern distribution limit in temperate and boreal North America (Houle and Filion 1993; Asselin et al. 2003; Morin et al. 2007). Morin et al. (2007) used a process-based model (PHENOFIT) that quite precisely reproduced the distribution of 17 North American temperate tree species. They found that at the northern distribution limit, either the flowering or fruit maturation processes were limited by cold temperature, depending on the species. For *P. banksiana* in particular, Houle and Filion (1993) indicated that variation in cone and seed performance was closely linked to climate, while Asselin et al. (2003) suggested that seed viability or germination was limited by the low number of degree-days above 5°C.

In contrast, at the northern distribution limit of red pine (*Pinus resinosa* Ait.) the number of cones, seed production and viability were not adversely affected by low temperatures (Flannigan and Bergeron 1998; Sutton et al. 2002). Morin et al. (2007) noted that cold temperature did not affect survival of 17 temperate tree species at their northern distribution limit. Studies of the radial growth-climate association also suggests

that climate was not limiting the growth of a variety of species at their northern

distributions, e.g. *P. banksiana* in northern Quebec (Asselin et al. 2003), pitch pine

(*Pinus rigida* Mill.) in Maine (Greenwood et al. 2002), white oak (*Quercus alba* L.) in

southern Quebec (Tardif et al. 2006), or northern white-cedar (*Thuja occidentalis* L.) in

west-central Manitoba (Tardif and Stevenson 2001).

Lack of suitable sites for the establishment of a species can also limit expansion at

its northern distributional boundary, as was noted for balsam fir (*Abies balsamea* (L.)

Mill.) (Messaoud et al. 2007), and a disjunct population of *P. rigida* (Meilleur et al. 1997)

in Quebec. Plants of *P. rigida* occurred with patches of ideal habitat, but were excluded

by competition outside of such settings (Meilleur et al. 1997). Kavanagh and Kellman

(1986) compared growth rates, site preferences, and recruitment rates of eastern hemlock

(*Tsuga canadensis* (L.) Carr.) at the distribution centre to the northern distribution limit.

They found no differences in long term growth rates, but they did observe unlikely site

preferences and less recruitment at the margin of the northern distribution. At this

margin, plants of *T. canadensis* were relegated to steeper, drier slopes, while ideal mesic

sites were occupied by more competitive hardwoods (Kavanagh and Kellman 1986).

While seed predation typically reduces regenerative potential, interestingly, it has been

suggested that the acorn predation and caches can assist the expansion of northern red

oak (*Quercus rubra* L.) at its northern distribution limit (Garcia et al. 2002). These

authors found that blue jays would cache acorns along the edge of forest clearings or in

gaps; conditions that meet regenerative site requirements for this species.

Fire is the dominant disturbance across the boreal forest. Fire frequency and intensity vary regionally within the Canadian boreal forest (Bergeron and Flannigan 1995; Bergeron et al. 2004). Fire can prevent the establishment of some species while maintaining the distribution of others (Bergeron and Dubuc 1989). *Pinus banksiana* and other species such as *P. mariana* that produce serotinous cones will typically perpetuate under an adequate fire cycle (Desponts and Payette 1992). However, a low fire frequency or small fire sizes have both been noted to prevent migration of *P. banksiana* in northern Quebec (Desponts and Payette 1992, 1993; Bergeron et al. 1997; Asselin et al. 2003). In the Yukon Territory, the northern distribution limit of *P. contorta* was found to be in non-equilibrium with the climate, and expanding northwards (Johnstone and Chapin 2003). The slow migration rate of this species was speculated to be limited because of low fire frequency, in addition to low habitat availability.

The presence of frequent or intense fires on the landscape, ideal for the above mentioned species, can limit the range expansion of those species that are not adapted. The fire regime, specifically large intense fires, has been considered to limit the distribution of both *P. resinosa* (Bergeron and Gagnon 1987; Bergeron and Brisson 1990; Bergeron et al. 1997; Flannigan and Bergeron 1998) and eastern white pine (*Pinus strobus* L.) (Bergeron et al. 1997; Engelmark et al. 2000). *Pinus resinosa* is best adapted to recurring, moderate-intensity surface fires, but is unable to survive larger more intense fires (Bergeron and Gagnon 1987; Flannigan and Bergeron 1998). Butson et al. (1987) suggested that a low fire hazard was among the factors that allowed the persistence of disjunct *P. resinosa* populations in Ontario. A few other species that have their northern

distribution limited by fire frequency and/or intensity include *A. balsamea* (Messaoud et al. 2007), *P. glauca* (Parisien and Sirois 2003), and *T. canadensis* (Kavanagh and Kellman 1986).

1.1.4 Disjunct populations

A disjunct population, may occur as a result of long distance dispersal, vicariance (the formation of a barrier cutting it off from the contiguous geographic distribution), or contraction of the distribution range (Brown et al. 1996). Over time, these populations may experience changes and pressures, resulting in the need to adapt to new conditions and associations, or persist in relict habitat if available, or become extirpated (Wood 1972). Comparison of the genetic diversity between disjunct populations and those at the distribution core may help to determine the population's origins as either a relict or a newly established founder population (Mosseler et al. 2004). High levels of inbreeding would point to a small number of founding members, while genetic diversity similar to the rest of the range would suggest a past range contraction leaving the disjunct population isolated (Lamy et al. 1999; Mosseler et al. 2004). By this means, Mosseler et al. (2004) suggested that a disjunct population of *P. rigida* in Ontario may be remnant from a previously larger distribution. Isolated populations beyond the tree line (MacDonald et al. 1998) or beyond the northern distribution limit (Parshall 2002) can act as locations for expansion, and through convergence with the contiguous distribution increase the rate of boundary advance, although this process could still take centuries.

Since species distributions are not uniform, models based on characteristics common to a species distribution centre could not be expected to be applicable to distribution boundaries and disjunct populations (Conkey et al. 1995). Brown et al. (1996) noted that the abundance of a species throughout its geographic distribution is highly variable, but generally decreases towards distribution boundaries. In Ontario, Butson et al. (1987) observed certain characteristics of marginal and disjunct populations of *P. resinosa* that were deemed 'typical' of these types of boundary stands. These included continuous recruitment, longevity, wide age-class distribution, and high survivorship. They also noted that reduced fire frequency at lake boundaries, low competition, and an amenable microclimate were likely to allow for the maintenance of these disjunct stands of *P. resinosa* (Butson et al. 1987). Suitable habitat appears to play an important role in the persistence of disjunct populations, e.g. *P. rigida* in Quebec (Meilleur et al. 1997) and *T. occidentalis* throughout its distribution (Fernald 1919; Kangas 1989; Tardif and Stevenson 2001). Studies that have examined these isolated populations and compared them to other parts of their distribution have been infrequent.

1.2 Objective

The current study will examine both the disjunct and the northwestern distribution limit of *T. occidentalis* in Manitoba, Canada. The objective of this study was:

> to characterize and compare the composition, structure, and environment of disjunct populations of *T. occidentalis* to those from its contiguous and peripheral distributions in southeastern Manitoba.

There are four specific hypotheses related to the objective.

1. First, with regard to stand environmental conditions, it was hypothesized that the disjunct populations would be restricted to locations with specific environmental conditions/habitat, such as those which are wet locations and thus protected from fire.

2. Second, it was expected that the composition and importance of associated tree and understory species would differ between the disjunct and contiguous populations.

3. Third, it was hypothesized that the growth vigour would be reduced in the disjunct populations compared to those of the contiguous distribution.

4. Finally, it was hypothesized that the regenerative success would be less in the disjunct populations than in those of the contiguous distribution.

This study will contribute to the overall knowledge of the ecology of *T. occidentalis*, an important late successional boreal species (Grigal and Ohmann 1975; Bergeron and Dubuc 1989; Bergeron 2000), at its northwestern distribution limit in Manitoba, and highlight differences and similarities between the regions in which it is found. Furthermore, as the ecology of a tree species at its limit of distribution is better understood better modeling of forest dynamics with respect to climate change can result (Meilleur et al. 1997; Tardif et al. 2006).

1.3 Distribution of Thuja occidentalis

1.3.1 Geographic Distribution: Contiguous Distribution and Disjunctions

     Thuja occidentalis (family *Cupressaceae*) is a widespread conifer of eastern North America (Johnston 1990; Sims et al. 1990). The common name of this species is northern white-cedar, but it is also known as eastern white-cedar, arborvitae, or swamp cedar (Johnston 1990). From southeastern Manitoba, the species northern distribution limit (Figure 1) ranges east-north-east to James Bay in Ontario, then through Quebec and the maritime provinces, excluding Newfoundland (Johnston 1990). From southeastern Manitoba, the southern range boundary can be found south-east through Minnesota and Wisconsin, nearly surrounding all of Lake Michigan, and east throughout the northern states to Maine (Johnston 1990). Disjunct populations of *T. occidentalis* can be found beyond the north-western contiguous distribution in west-central Manitoba, the central distribution in northern Ontario, the eastern portion of the distribution in Nova Scotia, and all along the southern boundary of the contiguous distribution, and south following the Appalachian Mountains (Johnston 1990).

     Thuja occidentalis is most often found in cool and humid environments, with annual precipitation extremes between 510 mm and 1400 mm, but typically ranging from 710 mm to 1170 mm (Johnston 1990). Average January temperatures across the range of *T. occidentalis* can be as low as -12°C to -4°C, and summer (July) average temperatures range from 16° to 22°C (Johnston 1990). Populations of *T. occidentalis* experiences frost-free periods of between 90 and 180 days, depending on location (Johnston 1990).
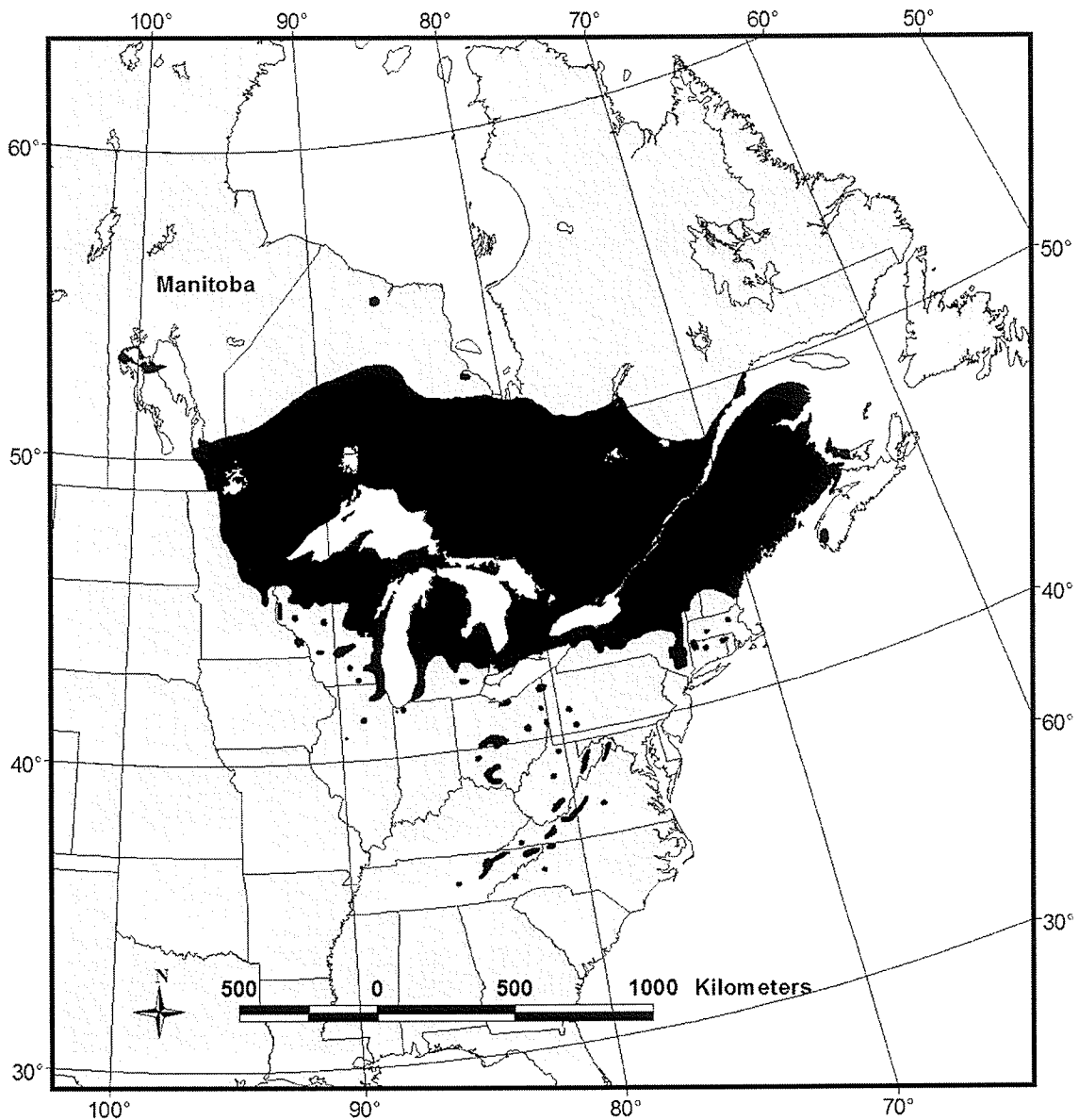
Figure 1. Distribution of *Thuja occidentalis* in North America (in black). Source of distribution map: U.S. Geological Survey 1999. [Available from http://esp.cr.usgs.gov/info/veg-clim/ accessed 17 April 2008]. Note that the location of the disjunct population in Manitoba was incorrect and has been changed to reflect the known distribution of the species.

Thuja occidentalis may form pure stands, but it is more commonly mixed with *P. mariana, L. laricina,* black ash (*Fraxinus nigra* Marsh.), balsam poplar (*Populus balsamifera* L.), and *A. balsamea* in lowland sites of the western portion of the distribution (Johnston 1990; Zoladeski et al. 1995; Walker et al. 2002). Upland stands of *T. occidentalis* in the western part of the range can host *A. balsamea,* paper birch (*Betula papyrifera* Marsh.), *F. nigra, L. laricina, P. glauca, P. mariana, P. balsamifera, P. strobus* and trembling aspen (*Populus tremuloides* Michx.) (Johnston 1990; Zoladeski et al. 1995; Walker et al. 2002). More easterly portions of the distribution may also include red spruce (*Picea rubens* Sarg.), red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britton), bigtooth aspen (*Populus grandidentata* Michx.), and *T. canadensis.*

The paleoecological history of *T. occidentalis* in North America is limited, as its pollen is not readily distinguishable from that of other *Cupressaceae.* Macrofossils are usually necessary to accurately determine its presence, but *Cupressaceae* pollen has been assigned to *Thuja* or *Juniperus* species based on typical associations with other species present (Ritchie 1987; Yu 1997). Recently, the use of conifer stomata as a macrofossil proxy, in combination with pollen, has proved useful to discriminate between *T. occidentalis* and *Juniperus* species (Yu 1997). Furthermore, for *T. occidentalis* and some other conifers, the abundance of stomata at sample locations correlated well with the stem basal area within 20 m of these sites (Parshall 1999). In southern Ontario, the earliest record of post-glacial macrofossils of *T. occidentalis* dates back approximately 8200 years before present (BP), in the form of submerged stumps (Larson and Melville 1996).

Radiocarbon dating of a leafy twig of *T. occidentalis* in this region dating back to 10 000 yr BP (Warner 1982) has, however, been questioned by Yu (1997), who suggested that the sample was likely contaminated. Evidence suggests an expansion of possibly pre-existing populations of *T. occidentalis* about 6500 to 6000 yr BP in the Clay Belt of northeastern Ontario (Liu 1990). In north-western Ontario, *T. occidentalis* (*Cupressaceae* pollen) was abundant 9900 – 8600 yr BP at Rattle Lake, and 7000 – 6900 yr BP at Cristal Lake further north (Bjorck 1985). In northeastern Minnesota, pollen of *Cupressaceae* was abundant between 10 300 and 9200 yr BP, but not until about 3000 yr BP could any be assigned to *T. occidentalis* with confidence, based on the presence of commonly associated species (Craig 1972). However, Amundson and Wright (1979) re-examined the samples and considered the abundant pollen of *Cupressaceae* from around 10 000 yr BP to be that of *T. occidentalis*. Also in Minnesota, Janssen (1968) considered *T. occidentalis* a component of the landscape as far back as about 8000 yr BP, even though there is an abundance of *Cupressaceae* pollen earlier. Given the difficulty discriminating between *Thuja* and *Juniperus* pollen, and the subjective assignment of *Cupressaceae* pollen to one or the other genus (e.g. Craig 1972; Amundson and Wright 1979), it is difficult to establish a clear and reliable picture of the historical distribution of *T. occidentalis* in North America.

1.4 Autecology of Thuja occidentalis

1.4.1 General Description

Thuja occidentalis* is a medium sized tree ranging in height from 12 – 15 m and 30 – 60 cm in diameter at 1.3 m (DBH), but able to reach heights up to 24 m and DBH up

to 150 cm (Johnston 1990). *Thuja occidentalis* commonly has a dense conical crown and highly tapered trunk, with grey to brown to reddish-brown fibrous bark that often spirals along with the grain either clockwise or counter-clockwise (Curtis 1946; Sims et al. 1990). This species has layered, arching branches and small scale-like leaves instead of needles (Sims et al. 1990). A shallow widespread root system is typical of *T. occidentalis*, but it may form a long tap root when growing on certain unsaturated upland soils (Johnston 1990).

A monoecious conifer, cones of *T. occidentalis* develop and ripen within the summer, while seed dispersal usually begins in September and is finished by winter (Johnston 1990). Although 30 year-old trees may produce seeds abundantly, they are most productive after approximately 75 years of age (Johnston 1990). Good seed crops are typically produced from every other year to every fifth year (Johnston 1990). The winged, wind-dispersed seeds have a range of 45 – 60 m from their host tree. Germination is most successful on a seedbed of either exposed mineral soil (upland sites), or mossy decaying coarse woody debris and stumps on lowland sites (Scott and Murphy 1987; Johnston 1990). Some light, provided mostly by large gaps, appears to be required for seedlings to reach the sapling stage (Scott and Murphy 1987). Simard et al. (1998) also noted the necessity of logs and an increase in available light for the successful establishment of *T. occidentalis*. These authors found seedlings of *T. occidentalis* under 7.13% full light, which was significantly greater than under random points (2.22% full light). Within moist swamps, reproduction in *T. occidentalis* is predominantly vegetative from branches or the stem by layering (Curtis 1946; Johnston 1990; Sims et al. 1990).

Genetic variation is known across the distribution of *T. occidentalis*, and there are more than 120 ornamental cultivars (Johnston 1990). While levels of inbreeding by populations *of T. occidentalis* have been found to be comparatively high when compared to that of other conifers, this appears not to have a negative impact on fitness at the seed stage (Perry and Knowles 1990; Lamy et al. 1999). A study of small isolated populations of *T. occidentalis* in an agricultural landscape in southwestern Quebec also revealed high levels of inbreeding after their recent establishment (Lamy et al. 1999). These populations had few founding members and relied heavily on vegetative reproduction (Lamy et al. 1999). These authors' results confirmed the expectation of high levels of inbreeding, low gene exchange with other populations, and higher genetic differentiation compared to the more natural forest-bound *T. occidentalis* populations examined by Perry and Knowles (1990) in northwestern Ontario.

1.4.2 Habitat and Growth

Thuja occidentalis has long been known as an occupant of wet lowlands (bogs, fens and swamps) and also of dry uplands (well drained soils, rock outcrops and cliffs) (Fernald 1919; Harlow 1927; Curtis 1946). The recognition of two ecotypes has been reported as a result of these contrasting habitats (Potzger 1941; Habeck 1958; Musselman et al. 1975). However, subsequent evidence has not supported this claim: Collier and Boyer (1989) collected seed from lowland and upland populations of *T. occidentalis* and found that the tissue water relations of seedlings grown in xeric or saturated soil moisture conditions did not differ within each treatment. Briand et al. (1991) found that

architectural variation, i.e. numerous measures of structure and growth form, did not differ between lowland and upland populations. In addition, Matthes-Sears and Larson (1991) found that lowland and upland populations of *T. occidentalis* did not differ in their productivity, photosynthetic light response, foliar nutrient levels, or canopy shading. It was suggested that the species has a broad physiological tolerance and is efficient at acclimatizing to these two moisture extremes (Collier and Boyer 1989).

The most common upland substrates supporting *T. occidentalis* are moist, well drained, limestone-derived mineral soils, including limestone bedrock and cliffs, rock outcrops, shallow loams on limestone, deep coarse loams, fine sands, and calcareous clays (Johnston 1990; Pregitzer 1990; Sims et al. 1990). Disjunct populations along the southern distribution (Kangas 1989) and throughout its range (Fernald 1919) are limited to locations where soils are limestone based. Soil pH values on upland *T. occidentalis* sites are generally high, and often neutral, while lowland values are more variable: acidic conditions are typically found in poorly-drained bogs, but the usual range is between 6.0 – 8.0 (Pregitzer 1990). The most productive lowland sites are eutrophic swamps and fens with good water movement, that is rich in minerals and oxygen (Johnston 1990; Pregitzer 1990). Lowland substrates are shallow to deep (0.3 – 1.8 m) organic peat material that is moderately to well decomposed, with frequent inclusions of rotten wood (Johnston 1990; Pregitzer 1990; Sims et al. 1990).

Growth is commonly better in well drained upland sites (Curtis 1946). In wet locations growth is reduced and height at 50 years of age can be as low as 5 m (Johnston

1990). At the extremes of these two site types (i.e., an excess or lack of moisture), height and diameter growth in *T. occidentalis* can be limited, despite its wide ecological amplitude (Matthes-Sears and Larson 1991). Additionally, these authors echo Fernald (1919) when they state that *T. occidentalis* when growing in mesic conditions would likely have maximum growth, but that populations are rarely found on such sites. The most severe growth restrictions to *T. occidentalis* appear to be under xeric conditions: slow growing individuals reaching 500 to 1000 years or more in age occur along both the limestone cliffs of the Niagara Escarpment in Ontario (Larson et al. 1989; Matthes-Sears and Larson 1991; Larson and Kelly 1991; Matthes-Sears and Larson 1995) and on rock outcrops of the shores and islands of Lake Duparquet, Quebec (Archambault and Bergeron 1992a, 1992b). Cliff face plants in particular had an average height and diameter of 2 m and 20 cm, respectively, a normal lifespan of 500 years, and a maximum age of 1890 years (Larson 2001). The longevity of these trees has been credited to their extremely slow rates of growth which has resulted in increased mechanical strength, decay resistance, and the ability of this species to partition itself into multiple hydraulic clone-like sectors (Larson 2001).

Nutrient deficiency has been considered a factor influencing growth of the cliff-face trees of *T. occidentalis* (Matthes-Sears et al. 1992). The roots of trees from both the cliff-face and an adjacent swamp, where nutrient supply was expected to be deficient and restrictive to growth, were observed to be colonized by a greater than normal abundance of mycorrhizal fungi (Matthes-Sears et al. 1992). Matthes-Sears et al. (1995) identified a small, but significant, nutrient-induced increase in shoot elongation, leaf area, and radial

growth after the addition of water and nutrients to cliff-face *T. occidentalis* saplings. Despite a large amount of fertilizer and more mycorrhizal fungi than normal, uptake efficiency was low and phosphorous concentrations remained deficient (Matthes-Sears et al. 1995). These authors suggested that this was the result of limited root space, but that other factors also restricted growth along the cliff faces.

The shade tolerance of *T. occidentalis* varies according to regeneration type (seedling or layering). The species is, however, generally considered shade tolerant (Curtis 1946; Johnston 1990; Sims et al. 1990). Vegetative propagules were found to be more tolerant of shade than seedlings since they are connected to larger root systems which provide the necessary water and nutrients (Curtis 1946). Seedling germination was good under shade, but mortality was high and few reached the sapling stage (Curtis 1946; Scott and Murphy 1987; Rooney et al. 2002). Scott and Murphy (1987) found that survival of trees beyond ten years of age were associated with canopy gaps at an old-growth site in Michigan. Similarly, Simard et al. (1998) noted *T. occidentalis* seedlings were found in locations with more than average amounts of full light. Lack of light may be a developmental drawback for seedlings of *T. occidentalis* under a mature canopy, but summer desiccation may be the most direct cause of mortality. In some areas, deer browse is one of the greatest threats to regeneration establishment in *T. occidentalis* (Johnston 1990; Rooney et al. 2002). Inouye et al. (1994) observed that invasion of *T. occidentalis* in old fields in Minnesota was greatly delayed through stem herbivory by deer and root herbivory by rodents combined with poor seed dispersal, drought stress, and a shortage of soil nutrients. Deer populations in Michigan, and presumably other

parts of North America, have become many times greater than a century ago, and commonly prevent the regeneration of managed stands of *T. occidentalis* (Heitzman et al. 1997).

1.4.3 Fire

Trees of *T. occidentalis* are susceptible to fire as they have shallow roots, and the leaves and thin bark have a high oil content making them flammable (Curtis 1946; Johnston 1990). Heinselman (1973) indicated that *T. occidentalis* in northeastern Minnesota was predominantly found on lake shores or areas that infrequently experience fire. Bergeron and Dubuc (1989) noted a similar phenomenon in the lake landscape of northwestern Quebec, where abundant fire breaks have allowed this species to maintain nearby seed sources after fire, and subsequently dominate later stages of succession in this landscape. Conversely, the poor representation of *T. occidentalis* on the nearby mainland was a result of unavailable seed sources due to large fires and monospecific forests (Bergeron and Bouchard 1984; Bergeron and Dubuc 1989). Furthermore, compared to today, a longer fire-return cycle in western Quebec during the mid-Holocene coincided with greater abundance of *T. occidentalis* (Bergeron et al. 1998). As pointed out by these authors, as a late successional species, *T. occidentalis* increases in importance with time-since-fire.

1.4.4 Successional and Old-Growth Status

Occasionally, *T. occidentalis* forms dense, even-aged, pure stands in swamps after the occurrence of disturbances such as fire or clearcutting, as long as a nearby seed

source is available (Johnston 1990; Sims et al. 1990). Conversely, uneven-aged stands represent the late-successional stage where gap dynamics are important in perpetuating this long lived species in the absence of fire (Johnston 1990). Bergeron (2000) noted both *T. occidentalis* and *A. balsamea* to be late-successional species, with the former peaking in recruitment 70–130 years after a stand-replacing fire, and the latter continually self replacing. In north-western Quebec, Bergeron and Dubuc (1989) found that on mesic and hydric sites, the forest compositions converged to a dominance of *T. occidentalis* and *A. balsamea*, while xeric sites were dominated by *T. occidentalis* and *P. mariana*. Commonly, trees of these late successional species (*T. occidentalis* and *A. balsamea*) were within 50 years of the age of the initial dominant species. Through senescence and gap creation in the initial overstory, *T. occidentalis* and *A. balsamea* gained in dominance (Bergeron and Dubuc 1989). Grigal and Ohmann (1975) considered *T. occidentalis* to be a member of a climax community on upland sites in Minnesota. This is achieved by its high shade tolerance, ability to reproduce vegetatively, and longevity (Bergeron 2000). In the absence of fire, forests of *P. banksiana* in northeastern Minnesota proceeded to stands dominated by *A. balsamea, B. papyrifera, T. occidentalis, P. glauca,* and some *P. mariana* (Heinselman 1973). Extensive non-fire disturbances, including extensive browsing by deer, resulted in a shift toward other shade tolerant species, such as *A. balsamea* and/or swamp hardwoods (e.g. *F. nigra*) (Johnston 1990). Spruce budworm outbreaks, however, can favour dominance of *T. occidentalis* over *A. balsamea* since only the latter is susceptible (Bergeron 2000).

Under extreme conditions, *T. occidentalis* can be an extremely long-lived species. The oldest individual noted along the Niagara escarpment had 1890 annual rings (Larson 2001). The maximum lifespan of this species in other parts of its distribution has been cited as about 400 years (Johnston 1990). In the deciduous forest region of southern Ontario, *T. occidentalis* trees are considered old-growth by the age of 110 years, and this stage may be expected to last 1000 or more years (Uhlig et al. 2001). In the boreal-east forest region of Ontario, old-growth status for *T. occidentalis* is reached by the ages of 140 and 100 for lowland and upland sites, respectively, and these trees may live another 210 or more years, or another 30 to 70 years, respectively (Uhlig et al. 2001). *Thuja occidentalis* of the boreal-west forest region of Ontario reaches old-growth status by the ages of 140 and 100 for lowland and upland sites, respectively, and this stage may last for another 210 or more years, or another 100 years, respectively (Uhlig et al. 2001).

1.5 Thuja occidentalis in Manitoba

The contiguous distribution of *T. occidentalis* reaches its northwestern limit in southeastern Manitoba, and a disjunct population occurs about 300 km farther northwest (Figure 1). The contiguous distribution of this species reaches the southeastern corner of the province, near the boundary of the Lake of the Woods ecoregion, which is comprised of five ecodistricts (Smith et al. 1998). The disjunct population is found in the Cedar Lake area of west-central Manitoba, along The Pas Moraine ecodistrict of the Mid-Boreal Lowlands ecoregion (Smith et al. 1998). Here this population is nested between three large lakes and occurs on a landscape with scattered wetlands.

The historical distribution of *T. occidentalis* in Manitoba is not known. Pollen of *Cupressaceae* has been noted in Clearwater Bog and Lynn Lake in Manitoba (Nichols 1967, 1969), but was assigned to *Juniperus* species, and no mention was made to the likelihood that it could have been that of *T. occidentalis*. This pollen dates from < 250 years BP and 6500 years BP, respectively (Nichols 1967, 1969). Both of these locations are beyond the current range of *T. occidentalis* but not that of *Juniperus* species.

The presence and maintenance of the population of *T. occidentalis* in the disjunct range may have been the outcome of a favourable fire regime. However, First Nations people in the area may have also played a role. Bell (1897) pointed out that the First Nations often lined the bottom of their canoes with boughs of *T. occidentalis*, suggesting a plausible means of long-distance seed dispersal to a location of suitable habitat in the Cedar Lake area. Furthermore, products from *T. occidentalis* were valuable for both canoe construction and repair. Scoggan (1957) noted that the abundance of *T. occidentalis* around Cedar Lake was important during the fur trade, as the bark was useful in repairing canoes. Wood from *T. occidentalis* has been used to make canoe frames (Podruchny 2006) and ropes of twisted *T. occidentalis* bark were used for tracking canoes over rapids or pulling through marsh waters (Hind 1860). At this point one can only speculate as to whether the usefulness of *T. occidentalis* to the First Nation peoples of the area led to the intended or inadvertent establishment of *T. occidentalis* around Cedar Lake. Future research on the history of *T. occidentalis* distribution in Manitoba could reveal whether this species had arrived in the Cedar Lake area through long-

distance dispersal, human or otherwise, or if it remains as a relic of a once larger distribution.

Regardless of origin of the disjunct population of *T. occidentalis*, isolation, genetic drift, and natural selection act on peripheral and disjunct populations, which lead to genetic divergence from more central populations (Lesica and Allendorf 1995). Such populations are of value for the genetic diversity, the species evolutionary future, and their potential for speciation events (Lesica and Allendorf 1995). The genetic diversity or possible divergence of the disjunct population of *T. occidentalis* in comparison to the contiguous distribution is unknown, but is a commendable future study subject for this species. If the levels of inbreeding in the disjunct population of *T. occidentalis* are high and asexual regeneration is predominant, as in the small disjunct population of *T. occidentalis* studied by Lamy et al. (1999), the genetic diversity would be low, resulting in a higher susceptibility to exploitation by diseases and pests. Channell and Lomolino (2000) noted the importance of the periphery of distributions. They observed that historically, range contractions of endangered species were commonly toward the periphery as opposed to the core of the distribution. This would confer a high conservation value on the disjunct and peripheral stands of *T. occidentalis* compared to the contiguous distribution, especially in light of changing climate.

Forests of *T. occidentalis* in Manitoba have been recognized as floristically rich communities. The latest of three protected areas hosting this species is the Brokenhead Wetlands Ecological Reserve, near the southeastern tip of Lake Winnipeg and at the

periphery of the contiguous distribution. Here, protection is provided to 23 provincially rare or uncommon plants, 28 of the province's 36 orchids, and 8 of Manitoba's 10 carnivorous plants (Manitoba Conservation 2005b; Ames et al. 2005). *Thuja occidentalis* is also represented in the Pocock Ecological Reserve in the contiguous distribution near Marchand, and also in the Long Point Ecological Reserve, the very easterly extent of the disjunct population. However, the Long Point Ecological Reserve burned in 1988 (Weber and Bell 1990). In north-central Minnesota, swampy forests dominated by *T. occidentalis* contained high orchid diversity and abundance (Smith 1993). Furthermore, the proposed Manitoba Lowlands National Park in the Cedar Lake – Grand Rapids area would include a large portion of the disjunct population of *T. occidentalis*, and highlight an area rich and unique in geology, geography, flora, fauna, and cultural heritage (CPAWS 2006).

A number of dendrochronological studies have been conducted on *T. occidentalis* in Manitoba. Within its contiguous distribution, St. George and Nielsen (2001) developed a *T. occidentalis* chronology, dating back more than 300 years, to determine the usefulness of this species in Manitoba for paleoclimatic studies. Case (2000) examined the dendroclimatalogical potential of *T. occidentalis* in the disjunct range. A chronology was constructed, dating back to 1504, and used to successfully reconstruct total annual precipitation for Dauphin, Manitoba (Case 2000). Tardif and Stevenson (2001) also conducted dendroclimatological research on the disjunct population of west-central Manitoba, producing a chronology dating back to 1713. Their results identified positive correlations between radial growth and previous late summer temperatures and current early summer precipitation, but negative correlations were found for current early

summer temperatures. Tardif and Stevenson (2001) suggested that the distribution limit of this species in Manitoba may be controlled by the fire regime and/or habitat availability. Grotte (2007) examined a subset of stands from the current study, all found within the disjunct range, and described the characteristics of old-growth *T. occidentalis* forests in three different vegetation communities.

2. METHODS

2.1 Study Areas

Three regions of Manitoba were considered for this study of *T. occidentalis*: 1) the southeastern corner of the province at the north-western limit of the contiguous distribution, 2) the Belair Provincial Forest and the Grand Beach Provincial Park areas, peripheral to the contiguous distribution, and 3) the Cedar Lake area in west-central Manitoba (Figure 2). *Thuja occidentalis* of the latter area is disjunct from the contiguous distribution, and is approximately 300 kilometres northwest of the peripheral distribution (Figure 2).

The portion of the contiguous distribution found in southeastern Manitoba is part of the Boreal Shield ecozone, and more specifically, it is within the western portion of the Lake of the Woods ecoregion, where *T. occidentalis* is commonly found in three of five ecodistricts (Whitemouth, Piney, and Stead) (Smith et al. 1998). The Lake of the Woods ecoregion covers approximately 13 700 km^2 in the southeastern portion of Manitoba (Marshall et al. 1999). This ecoregion is somewhat wetter and warmer than the more northerly boreal regions. It receives a mean annual precipitation of 610 mm with 20% falling as snow. This data was recorded at the Sprague Weather Station for the reference period 1971-2000 (Environment Canada 2004). The annual mean temperature was 2.4°C, while mean January and July temperatures were -17.4°C and 18.7°C respectively (Environment Canada 2004). The granite bedrock is acidic and is part of the boreal shield. It is undulating in its topography, and there are frequent rock outcrops (Ecological
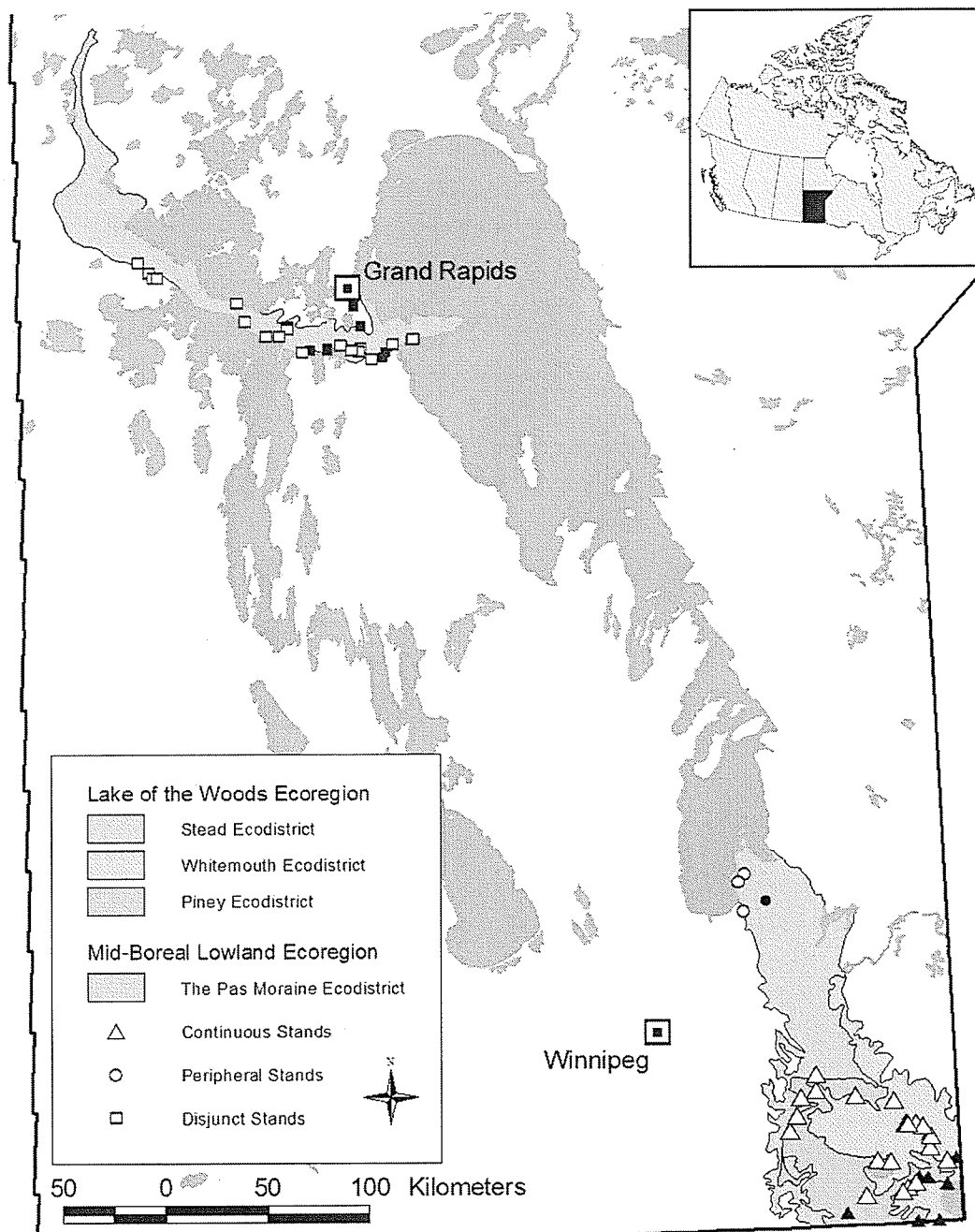
Figure 2. Map of study area showing both preliminary and final stands of *Thuja occidentalis* sampled in Manitoba. Stands that were revisited for the current study are represented by empty symbols, while black symbols were from preliminary sampling only. Three of five ecodistricts within Lake of the Woods Ecoregion are also noted in the legend. Ecoregion and ecodistrict data source: Manitoba Lands Initiative, Government of Manitoba, Online at http://web2.gov.mb.ca/mli (© 2001 Her Majesty the Queen in Right of Manitoba, as represented by the Minister of Conservation. All rights reserved.).

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Stratification Working Group 1995). In addition to the granitic bedrock, substrate materials including glacial till, Lake Agassiz sediment, and limestone make up portions of the region (Smith et al. 1998). The soils are subsequently variable, and include Organics, Brunisols, and Luvisols, and occasional inclusions of Gleysols and Chernozems (Smith et al. 1998). This region is a part of the northwestern end of the Great Lakes-St. Lawrence Forest Region (Rowe 1972). There is a greater diversity of tree species present in the Lake of the Woods ecoregion than in the adjacent Interlake Plain and Lac Seul Upland ecoregions. *Picea mariana* and *L. laricina* can be found in wet locations, but otherwise, common species include *P. tremuloides*, *B. papyrifera*, *P. banksiana*, *P. glauca* and *P. mariana* and *A. balsamea* on more or less mesic soils or rocky outcrops (Smith et al. 1998). Furthermore, *P. resinosa* and *P. strobus* reach their northwestern contiguous distribution limits in the Lake of the Woods ecoregion (Smith et al. 1998), as does *T. occidentalis*. The natural resources of the area serve a number of purposes, including timber harvesting, peat extraction, agriculture, recreation, fishing and hunting, and habitation (Smith et al. 1998).

The peripheral sites (Figure 2) are found in the north-western quarter of the Lake of the Woods ecoregion, and more particularly, in the Stead ecodistrict (Smith et al. 1998). The Pinawa WNRE weather station, for the reference period 1971-2000, recorded an annual mean temperature of 2.3°C, with mean January and July temperatures of -18.1°C and 18.9°C respectively (Environment Canada 2004). Mean annual precipitation over this period was 565 mm, of which 21% was snowfall (Environment Canada 2004). This portion of the Lake of the Woods ecoregion has minimal representation of shield

landscape, but is predominated by peaty lowland areas and substrates of loamy, sandy, and gravelly calcareous glacial till on the uplands (Smith et al. 1998). Vegetation was noted as similar to the Lake of the Woods ecoregion in general, but the Stead ecodistrict did not include the species *P. resinosa* and *P. strobus* (Smith et al. 1998).

The third region of study (Figure 2) was the Cedar Lake area in west-central Manitoba. It is a part of the Mid-Boreal Lowlands ecoregion within the Boreal Plains ecozone (Smith et al. 1998). This ecoregion covers over 34 300 km^2 from Flin Flon in the north, south to the Porcupine Mountains, and encompasses much of the northern Interlake area (Smith et al. 1998; Marshall et al. 1999). More specifically, 14 of the 18 study sites were within The Pas Moraine ecodistrict, while the other 4 were within 3 km south of this ecodistrict boundary, in the Overflowing River and Chitek Lake ecodistricts. The Pas Moraine ecodistrict arches west-northwest from Long Point at Lake Winnipeg to The Pas (Figure 2), and is characterized by a long, narrow moraine composed of thick calcareous till that had been deposited during the Wisconsinian glacial period, which ended between 8000 and 13000 years ago (Teller 1975; Smith et al. 1998). The soils are commonly Mesisolic Organic on glacial Lake Agassiz sediment, or Gray Luvisols and Eutric Brunisols on till and beach gravel (Smith et al. 1998). Bogs and fens are widespread and boreal tree species, including *T. occidentalis,* can be found within this ecodistrict (Smith et al. 1998). *Picea mariana* and *L. laricina* dominate the extensive bogs and fens, while elsewhere, combinations of *P. mariana, P. tremuloides, P. balsamifera,* and *P. banksiana* are typical, but stands of *P. mariana, P. glauca, A. balsamea,* and *P. tremuloides* are also present (Smith et al. 1998). This region received a mean of 474 mm of precipitation

annually, 24% as snowfall, and had an annual mean temperature of 0.8°C, and January

and July temperatures of -19.7°C and 18.6°C, respectively, as recorded at the Grand

Rapids Weather Station during the reference period 1971-2000 (Environment Canada

2004). In 1962, Manitoba Hydro completed a dam on the Saskatchewan River at Grand

Rapids, and flooded approximately 2200 km². This greatly increased the size of Cedar

and Moose Lakes, and significantly influenced both the local environment and the

socioeconomic situation of at least two First Nations communities in negative ways,

resulting from community relocation and a decline in hunting, trapping, and fishing

(Loney 1987).

2.2 Stand Selection and Sampling Layout

In 2005, a preliminary field search for *T. occidentalis* was conducted in the Cedar

Lake and southeastern Manitoba regions with the aid of Forest Resource Inventory data

to identify potential habitat (Manitoba Conservation 2005a) (Figure 2). The Forest

Resource Inventory for the Cedar Lake area identified very few polygons with *T.*

occidentalis. Therefore, in addition to looking for known associated forest types, stands

with *T. occidentalis* were also identified from the roadside. All stands identified in the

three studied regions were thus within a few hundred meters of road or trail access. It

should also be noted that the preliminary sampled stands were mature stands, since they

also served another project. During the 2005 preliminary sampling, the visually estimated

relative abundance of *T. occidentalis* had to be above 10-15% to be considered a '*T.*

occidentalis stand'. Thirty-two stands within the contiguous distribution zone were thus

identified and selected, along with 5 peripheral and 29 disjunct stands. These 66 stands

represented a mixture of xeric, mesic, and hydric moisture regimes. Wood core samples were taken in each stand for stand age determination (see section *2.4* below for more detail). The 66 preliminary stands were stratified by region and moisture regime, and from these, the 42 were randomly selected for this tudy. Of the 42 stands resampled in 2006, 21 were within the contiguous distribution, 3 peripheral to the contiguous distribution, and 18 located in the area of disjunction (Figure 2).

The point-centered quarter method (PCQ; Cottam and Curtis 1956), a plotless sampling design, was employed to capture the compositional and structural heterogeneity within each stand. This allowed the assessment of a larger area than a fixed area plot for the same sampling effort. Fifteen sample points (10 m apart) were located in each of the 42 stands, along three adjacent transects, which formed a three point by five point grid. For consistency, the location of the first point was established as close as possible to the UTM coordinates of the preliminary sampling, i.e. roughly central to the initial sampling area. From there, a cardinal or intermediate direction (i.e. NE, SE, SW, or NW) was chosen for the first transect. The direction was selected in order to capture what appeared to be the most representative characteristics (compositionally and structurally) of the stand. Occasionally, one or more of the transects were moved off the grid to avoid a man-made trail. If an obvious gradient was present (e.g. slope) the transects were run in a parallel direction to this gradient.

2.3 Vegetation Data Collection

The point-centered quarter (PCQ) method enabled the calculation of an importance value (IV) for each tree species at each point (Cottam and Curtis 1956). At each of the 15 sample points, the PCQ method was modified to sample not only the nearest tree (diameter at 1.3 m (DBH) ≥ 5 cm) in each quarter, but sapling/pole stage tree (DBH < 5cm and height > 1.3 m), small sapling (height 0.3 m to 1.3 m), and standing dead stem (snag) as well, for a maximum of 16 stems in four strata. Each of these stems was identified to species and the distance from the point was measured along with DBH, except for small saplings. The diameters were recorded in 1 cm classes for the larger sapling category (sapling/pole stage), but no further information was taken for the small saplings. Snags that were less than 1.3 m in height were not considered. An absence was recorded for any quarter that had no trees, saplings, or snags within a designated distance of 10 m. Since this resulted in an overlap between adjacent points, there was occasional double counting of trees when stand densities were very low. A correction factor (see Table 1 in Warde and Petranka 1981) was applied to each calculated stand density (described in section 2.5 below) wherever quarter data was missing. This avoided an overestimation of density.

A 1 m x 1 m vegetation plot was also established in the right-front quarter at each of the 15 PCQ points. The point was used as the lower left corner of this $1m^2$ vegetation plot. Vascular and non-vascular species were identified and assigned a cover value in all vegetation plots using the following classes: 1= 0–1%, 2= >1–5%, 3= >5–25%, 4= >25–50%, 5= >50–75%, 6= >75–100%, 7= 100% as in Girardin et al. (2001). Plant samples

were collected for later identification when necessary. The assessed vegetation consisted of trees, shrubs, forbs, graminoids, lichens and mosses. Cover values for tree species cover within the 1 m^2 vegetation plots were broken down into trees (diameter at 1.3 m (DBH) $\geq$ 5 cm), saplings (DBH < 5cm and >30 cm in height), and seedlings (< 30 cm in height). Note that the sapling size definition in the vegetation plots encompasses both the small and large sapling sizes identified in the PCQ data collection. Three graminoid families were recognized: *Cyperaceae* (sedges), *Juncaceae* (rushes), and *Poaceae* (grasses). Lichens were classified by form following Johnson et al. (1995), and included crust (crustose), scale (squamulose), leaf (foliose), club/cup (Genera *Cladonia*), and shrub (fruticose), while hair (filamentous) was not included as these are typically arboreal in the area of study. Mosses were placed into one of three categories (*Sphagnum* spp., feather mosses, or other mosses), unless identifiable to one of the following more common species: *Climacium dendroides, Dicranum polysetum, Hylocomium splendens, Pleurozium schreberi,* or *Ptilium crista-castrensis*. The shrubs and forbs were identified to species unless otherwise noted (e.g. *Aster* spp.). The full species list, including scientific names and abbreviations can be found in Appendix A. To avoid seasonal differences in understory vegetation development between the northern (disjunct distribution) and southern (contiguous and peripheral distribution) stands, the sampling periods were alternated among these regions throughout the summer of 2006, between May 30 and September 9, and the duration of each sampling period was kept to a maximum of 10 days.

2.4 Environmental Data Collection

The environmental variables measured at each of the 15 PCQ per stand were grouped into abiotic, biotic (species derived), and historical (disturbance/health) conditions (Appendix B). Abiotic information included the point coordinates (UTM), elevation (metres above sea level), slope (degrees and aspect), and soil variables obtained from a soil profile at each point: pH, depth to mineral soil (up to 60 cm), moisture/drainage (4 classes), and substrate texture (5 classes). Both the UTM coordinates and the elevation data were acquired with a handheld GPS unit. Only single samples were taken where soil profiles consisted of shallow soil on rock or cobble, otherwise entire soil horizons were sampled (e.g. LFH, A, B, and C). For consistency, only the pH of the LFH or organic material was used—typically taken at approximately 15 cm. The pH values were determined in the soils laboratory at the University of Winnipeg with a digital pH meter, using the 0.01 M $CaCl_2$ method (Scott 2004). The percent cover values for water and bare ground were estimated in each 1 m^2 vegetation plot and included as abiotic variables.

Depth to mineral soil, substrate apparent texture and moisture/drainage were measured on semi-quantitative scales. The depth to mineral soil was measured with a ruler to a maximum of 60 cm and each value was placed in five 15 cm depth classes: 1) 0-14 cm, 2) 15-29 cm, 3) 30-44 cm, 4) 45-59 cm, and 5) ≥60 cm. Substrate apparent textures were determined in the field following the Manitoba Forest Ecosystem Classification manual (Zoladeski et al. 1995) and then ranked from 1-5, representing the predominant texture type: 1) organic (described further below), 2) silt/clay (including

silty clay loam, clay loam, sandy clay, sandy clay loam, and loam), 3) sand (including sand, loamy sand, silty sand, sandy loam), 4) gravel, and 5) cobble/rock. Additionally, each substrate texture category was noted as present or absent (0/1) to simply account for the variety of substrate textures present. Moisture and drainage conditions were classified in the field 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). This scale was modified from the Ontario Institute of Pedology classification system (Ontario Institute of Pedology 1985). Soil depth, degree of mottling and/or gleying, and texture were used to establish the moisture/drainage classification. As another approach to the soils data, soils were further classified into three coarse categories: non-organic (i.e. mineral soils (0/1)), lowland organic (i.e. typically wet and deep (0/1)), or upland organic (i.e. typically dry and shallow (0/1)). Soils were considered lowland organic if they had either 40-60 cm of mesic or humic organic material (Om/Oh), or ≥60 cm of fibric, mesic, or humic organic material (Of/Om/Oh) (Soil Classification Working Group 1998). Soils were considered upland organic when the organic material (Of/Om/Oh) or litter layer (L, F, or H) was between 10 and 40 cm on rock or cobble substrate (Soil Classification Working Group 1998).

The biotic information was determined at each point and included canopy openness, amount of coarse woody debris (CWD) and amount of litter cover (both from the 1 m^2 vegetation plot), maximum tree height, and maximum *T. occidentalis* height. The maximum stand ages and maximum age for *T. occidentalis* variables were established at the stand level only. Canopy openness was included as a biotic variable, as

it is a function of canopy and stand dynamics, e.g. gap creation and regeneration (Valverde and Silvertown 1997). Canopy openness (%) was measured by means of a hemispheric image (180°) captured at the centre of each point, from about 1 m above the ground with a Nikon E8400 digital camera (equipped with the FC-E9 fisheye converter) and analyzed using the computer program WinSCANOPY Pro 2005 (Régent Instruments, Inc. 2005). Tree heights were measured with an Impulse® 200 laser rangefinder. For this variable, only one specimen of each tree species present at each PCQ was measured for a maximum of four tree height values per PCQ. The specimen with the greatest DBH had its height recorded if a species had more than one representative at a point (e.g. *T. occidentalis* at two or more of the four quarters would only have one specimen measured for height).

Stand age was determined from core samples taken during the preliminary sampling conducted in 2005. Between two and ten trees of *T. occidentalis* were cored at each stand using an increment borer. At least two trees of any other tree species present at the site were also cored for age comparison. The wood samples collected in 2005 were dried thoroughly for several weeks prior to sanding. Samples were then carefully sanded in six stages using progressively finer grit, ending at the 600 grit level. The cores were cross-dated in the Dendroecology Laboratory at the University of Winnipeg by France Conciatori using standard equipment and visual cross-dating techniques. Pointer years were noted using a modified version of the skeleton plot to avoid dating errors (Yamaguchi 1991). The crossdating was validated with the computer program

COFECHA after the tree-rings were measured to a precision of 0.001 mm using a Velmex measuring system (Holmes 1992).

The presence of any historical variables related to site disturbance were also noted within a 5 m radius of each point. These variables included evidence of damage related to fire (e.g., fire scars on trees, carbonized stems or branches), windthrow, insects, diseases, animal browsing, or parasitism by dwarf mistletoe (Appendix B). The presence of human-made trails and the degree of cutting, i.e. tree harvesting, were also noted. These variables were recorded as present/absent (0/1) except for the degree of cutting, which was semi-quantitative, where 1 = absent, 2 = uncommon, 3 = common, and 4 = abundant.

2.5 Calculation of Importance Value

An importance value (IV) was calculated for each tree species at each stand and for each stratum of the overstory (tree, snag, large and small saplings) by combining relative density (i.e. abundance) and relative dominance (i.e. basal area or percent cover) (Mueller-Dombois and Ellenberg 1974). Although relative frequency was not used in the present study, it is commonly included in the calculation of importance values. However, there is not a standard configuration for the calculation of importance values, and examples can be found in literature where various combinations of two variables, or all three have been used. The first of three steps was the calculation of stand density and stand basal area. Stand density (stems/ha) for PCQ data was calculated using the mean point-to-tree distance as shown in equation 1 (Cottam and Curtis 1956). A correction factor was applied to the stand density of any given stand if there had been any quarters

with missing data (Warde and Petranka 1981; Girardin et al. 2001). It should be noted that Pollard (1971) provided an unbiased estimate of population density for use with PCQ data (equation 2 as found in Krebs (1999)), since the application of equation 1 to a non-random distribution of trees will bias the density (Krebs 1999). Engeman et al. (1994) pointed out however, that while the density calculated from PCQ data was biased when tree distributions were aggregated, this bias did not differ greatly from the distance methods they advocated (Krebs 1999). A comparison of equations 1 and 2 using the tree stratum of the 42 stands revealed a slightly higher estimation of stand density with equation 1 (i.e., mean stand densities were 3% greater than with equation 2). This difference was deemed minor, and thus the use of equation 1 was considered acceptable.

[1] Stand Density (stems/ha) = $\dfrac{10000\ (\text{m}^2\ /\ \text{ha})}{(\text{mean point-to-tree distance (m)})^2}$

[2] Stand Density (stems/m) = $\dfrac{4(4n-1)}{\pi \sum (r_{ij}^2)}$, where r equals the point-to-tree distance.

Stand basal area (m²/ha) was calculated using equation 3 (Cottam and Curtis 1956). The basal area (m²) of individual trees (for use in equation 3) was calculated with equation 4, where d is tree diameter in meters. Then the absolute density of each species in each stand was calculated with equation 5, which distributed stand density to each species present according to its proportion. Likewise, the absolute basal area of each species in each stand was calculated with equation 6.

[3] Stand Basal Area (m² /ha) = mean Basal Area in stand (m²) × Stand Density (stems/ha)

[4] Basal Area (m²) = $\pi d^2 / 4$

[5]

$$\text{Abs.D}_{AB} = \frac{\text{no. of individuals of species A (stems) in stand B}}{\text{no. of individuals of all species (stems) in stand B}} \times \text{Density of stand B (stems/ha)}$$

[6]

$$\text{Abs.BA}_{AB} = \frac{\text{no. of individuals of species A (stems) in stand B}}{\text{no. of individuals of all species (stems) in stand B}} \times \text{Basal Area of stand B (m}^2\text{)}$$

The second step was the calculation of relative density and relative dominance (i.e. basal area). These equations were modified from Cottam and Curtis (1956) to allow for more detailed comparisons among the stands. Instead of simply relativising the density and basal area within each stand, they were relativised against all the stands. The relative density and relative basal area of species A in stand B was calculated with equations 7 and 8, respectively. In effect, the maximum stand density and maximum stand basal area were used to rank species absolute densities and absolute basal areas. This procedure allowed for better comparisons among the 42 stands by repositioning them according to these maximum values. Third and finally, these two variables were averaged to achieve an importance value (maximum 100%) for species A at stand B (equation 9).

$$[7] \quad \text{RD}_{AB} = \frac{\text{Abs.D}_{AB}}{\text{max Stand Density (from all stands)}} \times 100$$

$$[8] \quad \text{RDom}_{AB} = \frac{\text{Abs.BA}_{AB}}{\text{max Stand Basal Area (from all stands)}} \times 100$$

$$[9] \quad \text{IV}_{AB} = (\text{RD}_{AB} + \text{RDom}_{AB})/2$$

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2.6 Statistical Procedures

2.6.1 Data Transformations and Commensurability

The vegetation data set consisted of both the vegetation percent cover (1 m^2 vegetation plot) and tree importance values (IV). Each vegetation cover class was replaced with its midpoint value (1 = 0.5%, 2 = 3%, 3 = 15%, 4 = 37.5%, 5 = 62.5%, 6 = 87.5%, 7 = 100%). The mean percent cover (n = 15 points) of each species for each stand was then calculated. Prior to analyses, both the vegetation cover values (0-100) and the tree IV values (0-100) were log transformed (since the log of 0 is undefined, 1 was added to each value) to normalize the data, minimize the influence of outliers, and make the two data types commensurable (Kenkel 2006). Additionally, species that occurred in only one of the 42 stands (2.4%) were removed from the vegetation matrix to reduce the influence of outliers and rare species. By this means, the vegetation cover species list was reduced to 163 of the original 235 species. Seven entries pertaining to the PCQ tree, snag, large, or small sapling species were also removed from the IV component of the vegetation data set using the same criteria, e.g. *Picea spp.* was listed as a tree species in only one stand and was therefore removed. This reduced the number from 44 to 37.

The environmental data set consisted of the abiotic, biotic, and historical variables listed in Section *2.4* and Appendix B. The quantitative variables, noted in Appendix B, were also log transformed to normalize the data and minimize the influence of outliers (Kenkel 2006).

2.6.2 Clustering Stands of Thuja occidentalis into Plant Communities

K-means clustering analysis was applied to the vegetation matrix to identify community types. This was run on a χ^2 distance matrix in the computer program SYSTAT 11 (SYSTAT 2004). The χ^2 distance matrix was chosen even though various distance metrics can be applied, because this matrix excludes mutual absences that are common in biotic survey data sets, and which could suggest a false similarity among stands (Legendre and Legendre 1998; Kenkel 2006). *K*-means clustering is a non-hierarchical method of combining objects (e.g. forest stands) into a pre-determined number of groups (*k*). The objects are repeatedly relocated until a minimum within-group variance and maximum among-group variance is achieved (Legendre and Legendre 1998; Leps and Smilauer 2003). Dufrêne and Legendre (1997) point out that if a hierarchy results from *K*-means clustering, it would be inherent to the data, since this hierarchical structure was not imposed by the technique. The hierarchical structure of the *K*-means clustering results was examined by sequentially conducting cluster analysis, beginning with two groups, then three, etc. From these data a dendrogram was created. The final number of groups was decided upon based on a combination of observable ecological differences and a minimum group size to allow reasonable characterizations.

2.6.3 Indicator Species of Plant Communities

Indicator species analysis was conducted using PC-ORD v. 4.25 (McCune and Mefford 1999) in order to identify the key species that typify each of the community types grouped by *K*-means clustering (Dufrêne and Legendre 1997). A good indicator species would demonstrate high fidelity to a group, and would be ubiquitous within that

group, but should not be rare (Dufrêne and Legendre 1997). Indicator species are useful for quickly identifying community types, associated habitat, moisture or nutrient regimes, disturbances, or old-growth forests. The calculation combines relative abundance and relative frequency into a value, and then indexes this so that a maximum value of 100 percent is attained when the individuals of species x are observed in all stands of only one group (Dufrêne and Legendre 1997). Additionally, in order to evaluate the significance of these indicator values, a Monte Carlo simulation test (1000 replications) was automatically run that estimates the probability of type I error (Dufrêne and Legendre 1997). The indicator species analysis was applied to the results of the two-, and subsequent three-, four-, and five-group K-means clustering.

2.6.4 Ordination of Stands of Thuja occidentalis

Ordination analyses reveal the relationships among samples (stands) and among species, and can expose underlying gradients such as moisture or nutrients that influence species composition (Legendre and Legendre 1998; Leps and Smilauer 2003). Indirect gradient analyses such as correspondence analysis (CA), detrended correspondence analysis (DCA), or principal components analysis (PCA) can be used when working with only sample and species data. Direct gradient analyses are used with the inclusion of environmental variables, such as the constrained versions of CA, DCA, and PCA: respectively, canonical correspondence analysis (CCA), detrended canonical correspondence analysis (DCCA), and redundancy analysis (RDA) (Leps and Smilauer 2003). However, data structure must be considered since linear data is best handled by PCA or RDA, while CA, CCA, DCA, and DCCA operate best on non-linear or unimodal

data (Legendre and Legendre 1998; Leps and Smilauer 2003; Kenkel 2006). DCA is particularly useful in determining gradient lengths, or compositional turnover, an indicator of the linearity of the data (Leps and Smilauer 2003). The sample scores in a DCA are standard deviations of species turnover, therefore an axis length represents the amount of turnover (ter Braak and Smilauer 1998). Linear ordination methods (e.g. PCA, RDA) are recommended when gradient lengths are less than 3 standard deviations, and unimodal methods (e.g. CA, CCA) are recommended when the gradient length is 4 or greater; however, between 3 and 4 either method is acceptable (Leps and Smilauer 2003). Conducting a DCA on the vegetation matrix revealed a gradient length of 3.168 for the first axis, which indicated some species turnover in the data set. Either method would have been valid, but the unimodal ordination methods (CA and CCA) were preferred because they utilize χ^2 distance, thereby excluding mutual absences, while PCA and RDA preserve Euclidean distance which does not handle frequent double-zeros well (Legendre and Legendre 1998). All ordinations were run using CANOCO 4.52 (ter Braak and Smilauer 1998).

First, a CA was run on the vegetation matrix to examine the relationships among stands based on species composition only. After selecting CA within CANOCO, default settings were maintained. These settings included scaling focused on inter-species distances using biplot scaling and leaving the data untransformed (data was already transformed). A CCA was then conducted to elucidate vegetation – environmental (including abiotic, biotic, and historical variables) relationships within the stands (ter Braak and Smilauer 1998). Initially, 26 environmental variables were subjected to the

CCA analysis (Appendix B). Default settings were maintained initially (see above), without forward selection or the Monte Carlo permutation test. Then the output log file was examined after the first run to identify environmental variables that could be outliers, highlighting those samples (stands) with environmental variable values greater than 3 standard deviations from the mean (ter Braak and Smilauer 1998). After examining these environmental variables for errors, the outliers with the most extreme values were removed. The CCA was run again and the log file was then inspected for highly correlated, or co-linear variables, identified by variance inflation factors (VIF) ≥ 10. A large VIF value for a given variable, i.e. it is highly correlated with one or more other variables, indicates there is no new information being introduced to the analysis by the given variable, and also results in an unstable canonical coefficient (ter Braak and Smilauer 1998). Co-linear variables were removed one at a time, with the CCA being carried out between each removal. When all VIF values were less than 10, there were 20 environmental variables remaining that were then submitted to manual forward selection. During forward selection the environmental variables were subjected to the Monte-Carlo permutation test (999 randomizations) to judge their statistical significance (ter Braak and Smilauer 1998). Environmental variables significant at $P < 0.05$ were kept for a final run of the CCA. Forward selection was turned off, but the significance of the first ordination and of canonical axes together was tested with the Monte-Carlo permutation test (999 randomizations were used) (ter Braak and Smilauer 1998).

Two steps were taken to verify the commensurability of the vegetation cover and tree importance values data sets prior to running all cluster and ordination analyses.

These procedures were carried out to ensure that the two data types (percent cover of understory vegetation and importance values of tree species) could be combined as one vegetation matrix for use in further statistical analyses. First, correlation between CA axes of the vegetation cover and tree IV were calculated. Two additional CAs were run, one of the vegetation cover only and another of only the tree IV values. The first CA axes of the two data sets were strongly correlated ($r = 0.901$, P < 0.01, n = 42), indicating that the data sets shared a high degree of information. The correlation of the second axes was not as strong ($r = 0.562$, P < 0.01, n = 42), but after temporary removal of the four most outlying stands, it improved ($r = 0.723$, P < 0.01, n = 38). These stands were temporarily removal to simply verify if the lower correlation was the result of only a few stands. Secondly, to check that the understory vegetation cover and tree IV values could be combined as one, a congruency test was run between the two data types using the program CADM, which is short for congruence among distance matrices (Legendre 2001; Legendre and Lapointe 2004). The test is run on distance matrices, i.e. the associations (pairwise differences) between objects (stands) (Legendre and Legendre 1998). Therefore, both the vegetation cover and tree IV data sets were converted to chi-squared distance matrices using SPSS 10.1.0 (SPSS Inc. 2000). Described as a generalized Mantel test, CADM tests the null hypothesis that two or more matrices are incongruent (Legendre and Lapointe 2004). The null hypothesis that the vegetation cover and tree IV matrices were incongruent was rejected (P = 0.0002). Both steps demonstrated that the two data types could be used together, as one vegetation matrix, as they reveal the same general relationship among stands.

2.6.5 Other Analyses

Environmental variables including abiotic, biotic, and historical were summarized for each community type and then compared using the Kruskal-Wallis one-way analysis of variance, the non-parametric equivalent of one-way analysis of variance (Sheskin 1997). If significant, this was followed by the Mann-Whitney U post hoc test for pairwise comparisons (Sheskin 1997). The tree height-diameter relationship was modeled in order to evaluate productivity and site quality, as well as the structural heterogeneity. An exponential rise to the maximum regression was used to model the tree height-diameter relationship by species and community type in the computer program SigmaPlot 9.01 (SYSTAT 2004).

3. RESULTS

3.1.1 Clustering

The *K*-means clustering analysis of the 42 stands revealed the existence of five community types (Figure 3 and 4, Appendix C): 1) *T. occidentalis - P. mariana - P. banksiana* (*TOC-PMA-PBA, n = 8*), 2) *T. occidentalis - P. mariana - L. laricina - Heath* (*TOC-PMA-LLA-Heath, n = 7*), 3) *T. occidentalis - P. mariana - L. laricina – Alnus rugosa* (*TOC-PMA-LLA-ARU, n = 10*), 4) *T. occidentalis - A. balsamea - P. mariana - P. glauca* (*TOC-ABA-PMA-PGL, n = 9*), and 5) *T. occidentalis - A. balsamea - P. glauca - P. tremuloides* (*TOC-ABA-PGL-PTR, n = 8*). There was a hierarchical structure to the clustering of stands up to five groups, with one exception (Figure 3). The exception occurred at the second division where there was a migration of three stands (two peripheral and one disjunct) away from their initial cluster.

Despite four exceptions, the disjunct range was represented by the first two community types: 1) *TOC-PMA-PBA* and *2) TOC-PMA-LLA-Heath* (Figure 3 and 4, Appendix C). With the exception of one stand, these two community types were unique to and widespread across the disjunct range. They represented 14 out of 18 stands located within the Cedar Lake area (Figure 4). Community type-2 was also host to the stand sampled within the Long Point Ecological Reserve (Figure 4, Appendix C). The remaining three community types were mainly represented in the contiguous and peripheral ranges of *T. occidentalis*. Community type-3 (*TOC-PMA-LLA-ARU*) was widespread in southeastern Manitoba and stands of the peripheral distribution were exclusive to this community type. Also, there was one stand of this community type
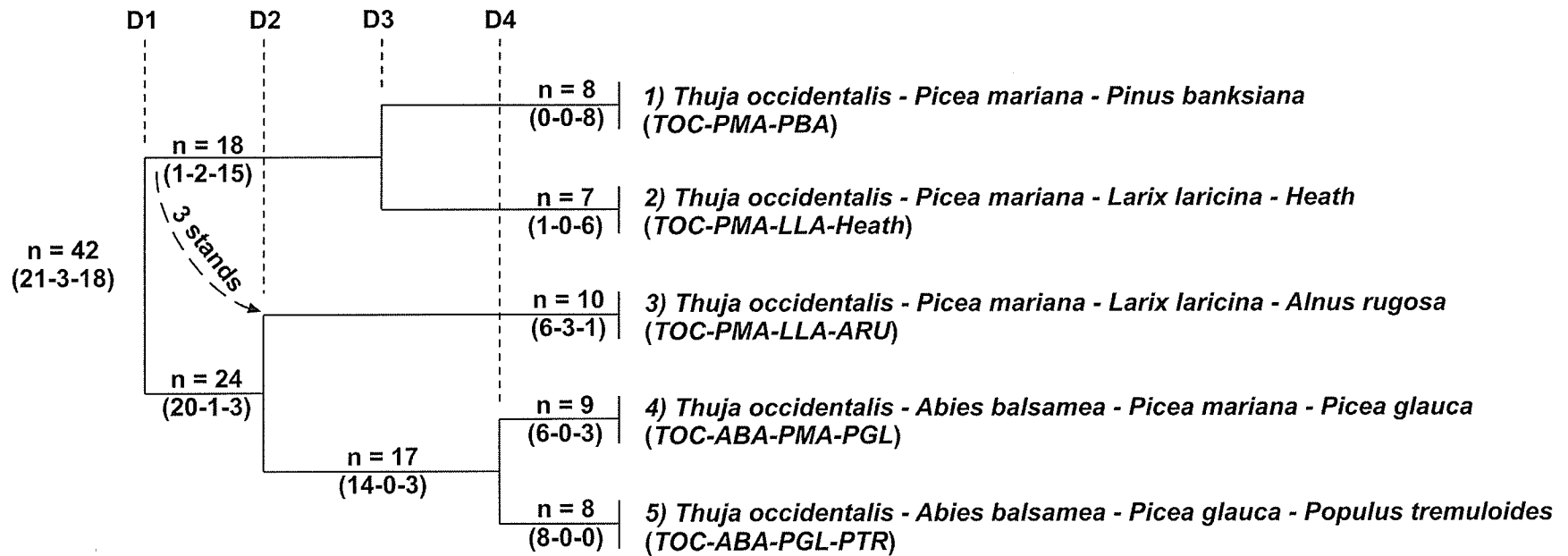
Figure 3. Constructed dendrogram from *K*-means clustering, showing the four "divisions" (D1 to D4) and the near-hierarchical nature of the grouping. The migration of three stands away from their initial cluster is indicated by the arrow. Community type number, names and abbreviations are shown, with number of stand members (*n*) and regional distribution of stands in brackets (contiguous – peripheral – disjunct).
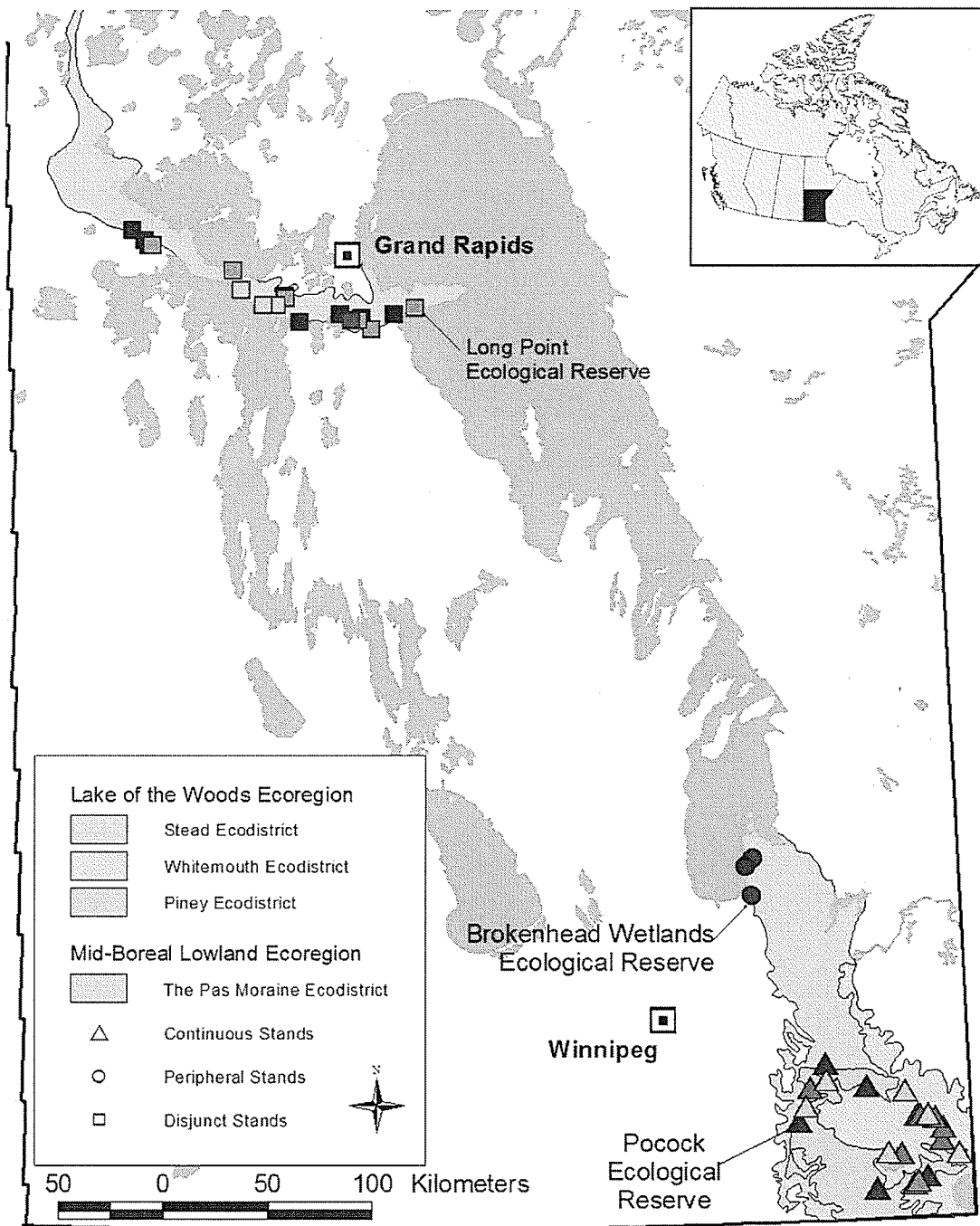
Figure 4. Map of the study area showing the distribution of community memberships amongst stands as established by *K*-means clustering analysis: 1) *TOC-PMA-PBA* (black), 2) *TOC-PMA-LLA-Heath* (green), 3) *TOC-PMA-LLA-ARU* (blue), 4) *TOC-ABA-PMA-PGL* (orange), 5) *TOC-ABA-PGL-PTR* (grey); see Figure 3 for community type definitions. Three of five ecodistricts within Lake of the Woods Ecoregion are also noted in the legend. See Appendix C for individual community type maps.

in the disjunct range. Community type-3 was also the only community type in the Stead

ecodistrict, but was represented by only one stand within the Whitemouth ecodistrict.

Furthermore, both the Brokenhead Wetlands (peripheral distribution) and Pocock

Ecological Reserves (contiguous distribution) were located within community type-3

(Figure 4, Appendix C). Community type-4 (*TOC-ABA-PMA-PGL*) was mainly

distributed in the contiguous range (both Piney and Whitemouth ecodistricts) but three

stands, compositionally similar, were observed in the disjunct range (Figure 3 and 4).

Community type-5 (*TOC-ABA-PGL-PTR*) was mostly restricted to the southeast corner

of the contiguous distribution of *T. occidentalis* in Manitoba and was principally

associated with the Whitemouth ecodistrict (Figure 4, Appendix C). Of the five

community types identified, only types 2 and 3 were found in Ecological Reserves.

3.1.2 Community Type-1: Thuja occidentalis-Picea mariana-Pinus banksiana

      In the *TOC-PMA-PBA* community, *P. mariana* was co-dominant with *T.*

occidentalis in density and basal area, while *P. banksiana* had the next highest values

(Table 1 and 2). Snag species were predominantly *P. mariana* and *P. banksiana*, while

regeneration mainly consisted of *P. mariana* and *T. occidentalis* (Table 1). Some of the

shrub species that were most common were also indicator species; these included

Arctostaphylos uva-ursi, Juniperus communis, J. horizontalis, Potentilla fruticosa,

Rhododendron groenlandicum, Salix myrtillifolia, Vaccinium myrtilloides, and *V. vitis-*

idaea (Table 3). Shrub-form lichens dominated the ground stratum, as did a number of

mosses, especially *Pleurozium schreberi* and *Hylocomium splendens* (Table 3). The rare

Table 1. Mean density (stems/ha) and standard deviation (SD) of trees, snags, large saplings (height >1.3, DBH < 5cm) and small saplings (height 0.3 m to 1.3 m) by community type and species. Values derived from point-centered quarter sampling. See Figure 3 for community type definitions.

	1		2		3		4		5	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Tree species										
Abies balsamea	-	-	-	-	17	45.1	578	498.3	725	635.4
Betula papyrifera	10	21.3	-	-	32	63.3	57	59.5	51	29.1
Fraxinus nigra	-	-	-	-	-	-	1	3.6	-	-
Larix laricina	163	215.1	169	76.8	223	354.0	-	-	-	-
Pinus banksiana	206	235.9	-	-	-	-	17	50.7	-	-
Picea glauca	-	-	-	-	-	-	98	180.2	192	162.5
Picea mariana	792	405.9	555	343.6	258	228.8	131	226.6	44	95.8
Picea spp.	-	-	-	-	-	-	-	-	42	118.1
Populus balsamifera	5	14.5	-	-	5	16.7	39	72.4	32	50.0
Populus tremuloides	-	-	-	-	3	10.2	6	16.9	208	190.7
Thuja occidentalis	620	326.5	477	427.4	1325	645.0	822	422.7	1444	1072.8
Total	**1797**		**1201**		**1863**		**1748**		**2737**	
Snag species										
Abies balsamea	-	-	-	-	37	89.5	97	74.5	117	93.3
Betula papyrifera	2	6.1	-	-	4	9.6	25	24.0	38	40.4
Conifer	3	3.1	10	13.5	11	14.0	4	6.6	17	37.2
Fraxinus nigra	-	-	-	-	-	-	-	-	1	2.0
Larix laricina	<1	1.1	12	15.3	41	97.0	-	-	-	-
Pinus banksiana	85	144.5	-	-	-	-	1	2.8	-	-
Picea glauca	-	-	-	-	-	-	2	4.0	16	28.8
Picea mariana	121	56.9	145	101.1	113	111.9	14	23.8	1	4.0
Populus balsamifera	-	-	-	-	1	3.9	12	28.5	23	21.5
Populus tremuloides	-	-	-	-	<1	1.1	8	24.8	94	90.7
Thuja occidentalis	45	98.9	45	38.4	48	56.4	92	91.2	143	221.3
Total	**256**		**212**		**254**		**256**		**449**	
Sapling (Large, >1.3m ht) species										
Abies balsamea	-	-	-	-	40	75.0	923	900.6	406	322.7
Betula papyrifera	10	23.9	13	21.6	3	7.0	15	21.3	3	8.3
Fraxinus nigra	-	-	-	-	6	20.3	-	-	13	25.7
Larix laricina	100	151.3	398	401.1	48	66.2	-	-	-	-
Pinus banksiana	10	28.6	-	-	-	-	-	-	-	-
Picea glauca	-	-	-	-	-	-	11	19.8	6	12.7
Picea mariana	1646	2779.5	1494	1331.6	41	42.2	7	20.7	-	-
Picea spp.	-	-	-	-	-	-	-	-	6	16.6
Populus balsamifera	-	-	-	-	-	-	17	23.3	5	10.7
Populus tremuloides	-	-	9	24.4	-	-	-	-	10	27.0
Thuja occidentalis	787	517.4	960	645.3	1039	724.1	245	250.1	502	674.0
Total	**2553**		**2873**		**1178**		**1218**		**950**	
Sapling (Small, <1.3m ht) species										
Abies balsamea	-	-	-	-	100	149.6	734	619.4	398	467.2
Betula papyrifera	-	-	-	-	-	-	5	11.5	4	7.8
Fraxinus nigra	-	-	-	-	28	87.7	4	10.6	63	126.6
Larix laricina	23	64.3	770	868.0	4	13.2	-	-	-	-
Pinus banksiana	11	32.1	-	-	-	-	-	-	-	-
Picea glauca	-	-	-	-	-	-	13	20.2	-	-
Picea mariana	2207	1113.8	4036	2605.7	95	187.9	13	26.3	10	27.7
Populus balsamifera	47	133.1	21	55.4	2	6.5	155	254.2	237	148.5
Populus tremuloides	-	-	21	55.6	-	-	35	73.1	151	211.0
Thuja occidentalis	2788	2393.5	3715	2958.1	1793	1643.0	276	235.1	437	635.0
Total	**5076**		**8563**		**2022**		**1235**		**1299**	

Table 2. Basal area (m^2/ha) and standard deviation (SD) of trees, snags, large saplings (height > 1.3, DBH < 5cm) and small saplings (height 0.3 m to 1.3 m) by community type and species. Values derived from point-centered quarter sampling. See Figure 3 for community type definitions.

	1 Mean	1 SD	2 Mean	2 SD	3 Mean	3 SD	4 Mean	4 SD	5 Mean	5 SD
Tree species										
Abies balsamea	-	-	-	-	0.07	0.197	5.21	5.355	8.42	7.339
Betula papyrifera	0.06	0.136	-	-	0.23	0.524	2.18	3.049	1.18	1.429
Fraxinus nigra	-	-	-	-	-	-	0.01	0.032	-	-
Larix laricina	1.49	1.568	1.24	0.663	4.13	3.208	-	-	-	-
Pinus banksiana	4.66	4.178	-	-	-	-	0.62	1.854	-	-
Picea glauca	-	-	-	-	-	-	2.69	3.710	7.70	9.085
Picea mariana	5.06	2.687	2.58	1.620	4.47	4.994	2.80	4.984	0.45	0.983
Picea spp.	-	-	-	-	-	-	-	-	0.29	0.821
Populus balsamifera	0.16	0.460	-	-	0.07	0.225	1.97	3.427	0.47	0.971
Populus tremuloides	-	-	-	-	0.01	0.032	0.15	0.440	4.46	4.321
Thuja occidentalis	6.55	4.936	5.12	5.179	21.98	9.486	39.66	21.941	33.91	19.500
Total	**17.97**		**8.94**		**30.96**		**55.30**		**56.88**	
Snag species										
Abies balsamea	-	-	-	-	0.261	0.5369	1.927	2.1674	1.399	1.5938
Betula papyrifera	0.016	0.0453	-	-	0.035	0.0927	1.186	1.1416	1.263	1.0800
Conifer	0.015	0.0138	0.037	0.0481	0.133	0.2045	0.057	0.1058	0.136	0.2196
Fraxinus nigra	-	-	-	-	-	-	-	-	0.002	0.0070
Larix laricina	0.002	0.0056	0.082	0.1002	0.471	0.8051	-	-	-	-
Pinus banksiana	0.914	1.1833	-	-	-	-	0.090	0.1991	-	-
Picea glauca	-	-	-	-	-	-	0.080	0.1975	0.409	0.7628
Picea mariana	0.924	0.6971	0.667	0.4406	1.212	1.0180	0.392	0.4876	0.028	0.0779
Populus balsamifera	-	-	-	-	0.032	0.1002	1.600	4.2134	1.502	1.4862
Populus tremuloides	-	-	-	-	<1	0.0074	0.684	2.0518	2.439	2.2109
Thuja occidentalis	0.413	0.9920	0.344	0.4193	0.444	0.6628	2.743	2.0542	1.855	3.0324
Total	**2.28**		**1.13**		**2.59**		**8.76**		**9.03**	
Sapling (Large, >1.3m ht) species										
Abies balsamea	-	-	-	-	0.022	0.0450	0.732	0.6913	0.335	0.2662
Betula papyrifera	0.012	0.0246	0.015	0.0336	0.005	0.0116	0.019	0.0297	0.006	0.0163
Fraxinus nigra	-	-	-	-	0.002	0.0072	-	-	0.011	0.0263
Larix laricina	0.068	0.1102	0.238	0.2760	0.046	0.0720	-	-	-	-
Pinus banksiana	0.013	0.0360	-	-	-	-	-	-	-	-
Picea glauca	-	-	-	-	-	-	0.008	0.0173	0.006	0.0128
Picea mariana	1.109	1.9220	1.069	1.0523	0.046	0.0589	0.005	0.0149	-	-
Picea spp.	-	-	-	-	-	-	-	-	0.012	0.0326
Populus balsamifera	-	-	-	-	-	-	0.009	0.0253	0.003	0.0087
Populus tremuloides	-	-	0.001	0.0019	-	-	-	-	0.019	0.0531
Thuja occidentalis	0.484	0.4491	0.563	0.4108	0.776	0.5916	0.246	0.2517	0.410	0.4858
Total	**1.69**		**1.89**		**0.90**		**1.02**		**0.80**	

Table 3. Species frequencies (F%), percent cover (C%, from vegetation plot) or Importance Value (IV, from point-centered quarter sampling) with standard deviation (SD), and Indicator Value (Ind-Val) by community type. See Figure 3 for community type definitions. Indicator values were also tested for significance: * is significant at P ≤ 0.05, ** at P ≤ 0.01, and *** at P ≤ 0.001. To simplify presentation, species shown had ≥ 50% frequency in at least one community type, unless the indicator value was significant.

	1) TOC-PMA-PBA				2) TOC-PMA-LLA-Heath				3) TOC-PMA-LLA-ARU				4) TOC-ABA-PMA-PGL				5) TOC-ABA-PGL-PTR			
	F% (n=8)	C% or IV	SD	Ind-Val	F% (n=7)	C% or IV	SD	Ind-Value	F% (n=10)	C% or IV	SD	Ind-Value	F% (n=9)	C% or IV	SD	Ind-Value	F% (n=8)	C% or IV	SD	Ind-Value
PCQ IMPORTANCE VALUES																				
PCQ - Trees																				
Abies balsamea	0	0.00	0.00	-	0	0.00	0.00	-	20.0	0.22	0.59	-	100.0	8.81	7.60	45.9 **	87.5	11.94	10.11	-
Betula papyrifera	25.0	0.14	0.30	-	0	0.00	0.00	-	40.0	0.47	0.95	-	66.7	1.67	2.04	-	87.5	1.12	0.92	33
Larix laricina	75.0	2.54	3.01	-	100.0	2.44	0.93	-	90.0	4.40	5.07	34.7 *	0	0.00	0.00	-	0	0.00	0.00	-
Pinus banksiana	75.0	4.48	4.38	65.8 ***	0	0.00	0.00	-	0	0.00	0.00	-	11.1	0.48	1.44	-	0	0.00	0.00	-
Picea glauca	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-	66.7	2.35	3.69	-	75.0	5.76	5.75	48 **
Picea mariana	100.0	11.04	5.56	35 **	100.0	7.30	4.50	-	90.0	4.92	4.81	-	33.3	2.77	4.74	-	37.5	0.70	1.51	-
Populus tremuloides	0	0.00	0.00	-	0	0.00	0.00	-	10.0	0.04	0.13	-	11.1	0.13	0.39	-	75.0	4.40	3.76	69 ***
Thuja occidentalis	87.5	9.89	5.18	-	100.0	7.66	7.12	-	100.0	24.98	9.57	-	100.0	27.87	13.95	-	100.0	31.94	18.86	24 *
PCQ Snags																				
Abies balsamea	0	0.00	0.00	-	0	0.00	0.00	-	40.0	3.14	7.31	-	88.9	11.71	9.96	-	100.0	11.54	8.79	45 **
Betula papyrifera	12.5	0.14	0.39	-	0	0.00	0.00	-	30.0	0.35	0.88	-	77.8	4.93	4.68	-	75.0	6.04	5.21	36 *
Conifer	62.5	0.26	0.25	-	57.1	0.78	1.01	-	70.0	1.07	1.48	18.8	33.3	0.45	0.68	-	62.5	1.47	3.01	-
Larix laricina	12.5	0.03	0.09	-	57.1	1.00	1.24	-	80.0	3.95	8.56	50.2 **	0	0.00	0.00	-	0	0.00	0.00	-
Pinus banksiana	62.5	8.08	12.40	54.5 ***	0	0.00	0.00	-	0	0.00	0.00	-	22.2	0.34	0.71	-	0	0.00	0.00	-
Picea glauca	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-	22.2	0.36	0.80	-	37.5	2.19	3.96	29 *
Picea mariana	100.0	10.41	5.36	31.5 *	85.7	11.30	7.73	-	100.0	10.70	10.08	-	44.4	2.03	2.56	-	12.5	0.17	0.48	-
Populus balsamifera	0	0.00	0.00	-	0	0.00	0.00	-	10.0	0.17	0.53	-	55.6	5.30	13.70	-	75.0	5.69	5.51	47 **
Populus tremuloides	0	0.00	0.00	-	0	0.00	0.00	-	10.0	0.03	0.09	-	11.1	2.46	7.38	-	87.5	12.94	9.23	75 ***
Thuja occidentalis	87.5	4.10	9.21	-	100.0	3.89	3.65	-	70.0	4.42	5.36	-	100.0	13.70	10.03	30.6 *	87.5	14.50	18.70	-
PCQ - Large Saplings (>1.3m ht)																				
Abies balsamea	0	0.00	0.00	-	0	0.00	0.00	-	40.0	0.53	1.04	-	100.0	14.74	14.10	52.2 **	87.5	6.63	5.08	-
Betula papyrifera	25.0	0.21	0.44	-	28.6	0.25	0.50	-	20.0	0.08	0.18	-	55.6	0.31	0.48	18.6	12.5	0.08	0.24	-
Larix laricina	62.5	1.46	2.31	-	100.0	5.52	5.88	58.9 ***	70.0	0.85	1.23	-	0	0.00	0.00	-	0	0.00	0.00	-
Picea mariana	100.0	21.00	32.36	-	100.0	22.60	21.08	48.2 **	70.0	0.79	0.93	-	11.1	0.10	0.31	-	0	0.00	0.00	-
Populus balsamifera	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-	44.4	0.22	0.43	31.6 *	25.0	0.08	0.14	-
Thuja occidentalis	100.0	10.97	8.49	-	100.0	13.16	8.90	-	100.0	16.05	11.47	24.4	100.0	4.48	4.57	-	100.0	8.14	10.20	-
PCQ - Small Saplings (<1.3m ht)																				
Abies balsamea	0	0.00	0.00	-	0	0.00	0.00	-	50.0	0.66	1.00	-	100.0	4.90	4.13	51.9 ***	87.5	2.66	3.12	-
Larix laricina	12.5	0.15	0.43	-	100.0	5.14	5.79	92.6 ***	10.0	0.03	0.09	-	0	0.00	0.00	-	0	0.00	0.00	-
Picea glauca	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-	44.4	0.08	0.13	44.4 **	0	0.00	0.00	-
Picea mariana	100.0	14.91	7.41	-	100.0	26.93	17.39	50.4 ***	40.0	0.63	1.25	-	22.2	0.09	0.18	-	12.5	0.07	0.18	-
Populus balsamifera	12.5	0.31	0.89	-	14.3	0.14	0.37	-	10.0	0.01	0.04	-	66.7	1.03	1.70	-	87.5	1.58	0.99	47 **
Populus tremuloides	0	0.00	0.00	-	14.3	0.14	0.37	-	0	0.00	0.00	-	33.3	0.24	0.49	-	75.0	1.06	1.37	51 **
Thuja occidentalis	100.0	18.42	16.17	-	100.0	24.79	19.74	30.4 *	100.0	11.96	10.96	-	100.0	1.84	1.57	-	87.5	2.86	4.27	-

Table 3 continued.

	1) TOC-PMA-PBA				2) TOC-PMA-LLA-Heath				3) TOC-PMA-LLA-ARU				4) TOC-ABA-PMA-PGL				5) TOC-ABA-PGL-PTR			
	F% (n=8)	C% or IV	SD	Ind-Val	F% (n=7)	C% or IV	SD	Ind-Value	F% (n=10)	C% or IV	SD	Ind-Value	F% (n=9)	C% or IV	SD	Ind-Value	F% (n=8)	C% or IV	SD	Ind-Value
VEGETATION PLOT COVER VALUES (%)																				
Trees within Vegetation Plots																				
Abies balsamea	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-	55.6	0.27	0.45	-	87.5	0.65	0.66	60 **
Picea mariana	75.0	0.63	0.91	-	85.7	1.29	1.03	46.2 **	30.0	0.24	0.46	-	0	0.00	0.00	-	25.0	0.08	0.15	-
Populus tremuloides	12.5	0.00	0.01	-	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-	37.5	0.20	0.35	37 *
Thuja occidentalis	62.5	1.21	2.55	-	85.7	3.00	3.79	-	100.0	2.29	1.59	25	77.8	2.15	1.60	-	87.5	1.35	1.09	-
Saplings within Vegetation Plots (>0.3m ht)																				
Abies balsamea	0	0.00	0.00	-	0	0.00	0.00	-	20.0	0.20	0.42	-	77.8	2.11	2.80	59.2 ***	37.5	0.21	0.49	-
Picea mariana	75.0	9.36	9.14	48.4 ***	42.9	4.83	7.93	-	10.0	0.00	0.01	-	11.1	0.00	0.01	-	0	0.00	0.00	-
Thuja occidentalis	75.0	14.08	12.92	24.5	57.1	9.68	14.57	-	80.0	8.69	8.12	-	77.8	3.43	5.53	-	62.5	0.53	0.54	-
Seedlings within Vegetation Plots (<0.3m ht)																				
Abies balsamea	0	0.00	0.00	-	0	0.00	0.00	-	90.0	0.16	0.21	-	100.0	1.30	2.05	51.8 **	87.5	0.79	1.41	-
Betula papyrifera	0	0.00	0.00	-	0	0.00	0.00	-	20.0	0.01	0.02	-	55.6	0.05	0.06	-	50.0	0.06	0.11	26
Fraxinus pennsylvanica	0	0.00	0.00	-	0	0.00	0.00	-	10.0	0.00	0.01	-	11.1	0.00	0.01	-	37.5	0.02	0.03	28 *
Larix laricina	12.5	0.00	0.01	-	100.0	1.19	2.10	94.3 ***	20.0	0.03	0.07	-	0	0.00	0.00	-	0	0.00	0.00	-
Picea mariana	100.0	2.40	4.25	-	100.0	3.98	5.70	60.3 **	20.0	0.01	0.01	-	33.3	0.01	0.01	-	0	0.00	0.00	-
Populus balsamifera	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-	44.4	0.08	0.16	-	100.0	0.27	0.34	75 **
Populus tremuloides	0	0.00	0.00	-	14.3	0.01	0.02	-	0	0.00	0.00	-	22.2	0.01	0.01	-	37.5	0.04	0.06	27 *
Thuja occidentalis	100.0	2.19	2.49	-	100.0	2.76	3.13	34	100.0	0.42	0.33	-	88.9	0.58	0.45	-	75.0	0.60	1.06	-
Shrubs																				
Acer spicatum	0	0.00	0.00	-	0	0.00	0.00	-	10.0	0.00	0.01	-	55.6	7.08	19.14	45.8 *	50.0	0.22	0.34	-
Alnus rugosa	0	0.00	0.00	-	14.3	0.88	2.34	-	70.0	5.93	10.82	53 **	22.2	0.01	0.02	-	12.5	0.00	0.01	-
Andromeda polifolia	75.0	0.29	0.57	-	85.7	1.63	1.60	64.3 ***	10.0	0.09	0.29	-	0	0.00	0.00	-	0	0.00	0.00	-
Arctostaphylos uva-ursi	100.0	2.17	2.82	95.4 ***	28.6	0.05	0.10	-	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-
Betula pumila	75.0	1.89	3.08	-	85.7	2.05	1.74	42.2 **	10.0	1.89	5.98	-	0	0.00	0.00	-	0	0.00	0.00	-
Chamaedaphne calyculata	25.0	2.85	7.05	-	85.7	4.54	5.13	59.5 **	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-
Cornus stolonifera	12.5	0.00	0.01	-	0	0.00	0.00	-	70.0	0.32	0.50	40.6 *	22.2	0.03	0.07	-	75.0	0.18	0.34	-
Gaultheria hispidula	12.5	0.32	0.91	-	0	0.00	0.00	-	60.0	0.08	0.09	17.9	33.3	0.02	0.03	-	0	0.00	0.00	-
Juniperus communis	75.0	1.98	3.22	74.5 ***	14.3	0.00	0.01	-	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-
Juniperus horizontalis	87.5	3.19	4.06	55 ***	71.4	1.51	2.30	-	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-
Kalmia polifolia	25.0	0.16	0.37	-	85.7	0.13	0.11	43.2 *	10.0	0.00	0.01	-	0	0.00	0.00	-	0	0.00	0.00	-
Lonicera villosa	62.5	0.19	0.38	-	71.4	0.98	1.13	45.5 *	60.0	0.19	0.28	-	22.2	0.03	0.07	-	12.5	0.00	0.01	-
Oxycoccus microcarpus	25.0	0.14	0.36	-	100.0	1.90	2.05	78 ***	50.0	0.19	0.39	-	0	0.00	0.00	-	12.5	0.00	0.01	-
Potentilla fruticosa	87.5	3.35	2.92	65.2 ***	71.4	0.71	0.96	-	10.0	0.00	0.01	-	0	0.00	0.00	-	0	0.00	0.00	-
Rhamnus alnifolius	50.0	0.20	0.44	-	71.4	0.17	0.22	-	70.0	1.98	2.72	49.3 **	11.1	0.00	0.01	-	12.5	0.03	0.08	-
Rhododendron groenlandicum	87.5	16.31	11.75	-	100.0	15.04	13.23	38.2 **	90.0	4.23	5.31	-	66.7	0.82	2.27	-	25.0	0.08	0.16	-
Rosa acicularis	75.0	0.56	0.92	44.2 *	42.9	0.03	0.04	-	30.0	0.03	0.07	-	66.7	0.08	0.10	-	37.5	0.12	0.18	-
Rubus chamaemorus	0	0.00	0.00	-	28.6	0.01	0.02	28.6 *	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-
Salix myrtillifolia	75.0	0.92	1.36	56.6 **	42.9	0.20	0.27	-	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-
Shepherdia canadensis	50.0	0.06	0.09	-	28.6	0.49	0.86	24.1	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-
Vaccinium angustifolium	0	0.00	0.00	-	0	0.00	0.00	-	40.0	0.03	0.06	-	44.4	0.08	0.10	30.9 *	0	0.00	0.00	-
Vaccinium myrtilloides	87.5	2.86	3.91	50.4 **	57.1	1.77	2.68	-	0	0.00	0.00	-	11.1	0.03	0.08	-	0	0.00	0.00	-

Table 3 continued.

	1) TOC-PMA-PBA				2) TOC-PMA-LLA-Heath				3) TOC-PMA-LLA-ARU				4) TOC-ABA-PMA-PGL				5) TOC-ABA-PGL-PTR			
	F% (n=8)	C% or IV	SD	Ind-Val	F% (n=7)	C% or IV	SD	Ind-Value	F% (n=10)	C% or IV	SD	Ind-Value	F% (n=9)	C% or IV	SD	Ind-Value	F% (n=8)	C% or IV	SD	Ind-Value
Shrubs continued																				
Vaccinium vitis-idaea	100.0	2.69	1.75	49.7 ***	100.0	2.22	3.00	-	90.0	0.36	0.36	-	44.4	0.02	0.03	-	0	0.00	0.00	-
Viburnum edule	25.0	0.01	0.02	-	0	0.00	0.00	-	0	0.00	0.00	-	44.4	0.07	0.12	37.2 *	12.5	0.00	0.01	-
Herbs																				
Actaea rubra	12.5	0.00	0.01	-	0	0.00	0.00	-	0	0.00	0.00	-	55.6	0.13	0.34	32	37.5	0.07	0.13	-
Amerorchis rotundifolia	37.5	0.01	0.01	-	57.1	0.10	0.14	51.7 **	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-
Aralia nudicaulis	25.0	0.15	0.38	-	0	0.00	0.00	-	30.0	0.45	0.90	-	100.0	1.50	1.86	52.1 ***	62.5	0.36	0.43	-
Asarum canadense	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-	37.5	0.19	0.38	38 *
Caltha palustris	0	0.00	0.00	-	0	0.00	0.00	-	50.0	0.21	0.33	50 **	0	0.00	0.00	-	0	0.00	0.00	-
Campanula rotundifolia	37.5	0.02	0.02	37.5 *	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-
Clintonia borealis	0	0.00	0.00	-	0	0.00	0.00	-	10.0	0.10	0.32	-	55.6	0.53	1.08	30.9	37.5	0.26	0.72	-
Coptis trifolia	12.5	0.01	0.02	-	0	0.00	0.00	-	60.0	0.13	0.17	-	77.8	0.52	0.39	52.4 **	62.5	0.08	0.15	-
Cornus canadensis	62.5	0.31	0.44	-	57.1	0.08	0.11	-	70.0	0.45	0.58	-	100.0	1.13	0.89	41.2 **	87.5	0.51	0.63	-
Cypripedium calceolus	62.5	0.06	0.09	33.2 *	42.9	0.03	0.04	-	10.0	0.00	0.01	-	22.2	0.01	0.03	-	25.0	0.01	0.02	-
Cypripedium reginae	0	0.00	0.00	-	0	0.00	0.00	-	30.0	0.03	0.09	30 *	0	0.00	0.00	-	0	0.00	0.00	-
Drosera rotundifolia	0	0.00	0.00	-	71.4	0.27	0.24	71.4 ***	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-
Equisetum arvense	25.0	0.02	0.04	-	57.1	0.46	0.49	41.1 *	30.0	0.11	0.19	-	22.2	0.01	0.03	-	25.0	0.01	0.03	-
Equisetum pratense	12.5	0.01	0.03	-	28.6	0.04	0.08	-	40.0	0.06	0.10	-	55.6	0.19	0.40	28	25.0	0.03	0.07	-
Equisetum scirpoides	75.0	0.09	0.09	-	71.4	0.14	0.12	-	40.0	0.06	0.11	-	88.9	0.67	0.69	48.4 **	75.0	0.13	0.15	-
Equisetum variegatum	37.5	0.04	0.08	-	71.4	0.24	0.33	58.5 ***	0	0.00	0.00	-	11.1	0.00	0.01	-	0	0.00	0.00	-
Fragaria virginiana	12.5	0.03	0.08	-	14.3	0.00	0.01	-	40.0	0.04	0.07	-	55.6	0.11	0.15	25.7	50.0	0.05	0.09	-
Galium boreale	62.5	0.03	0.03	24.7	28.6	0.01	0.02	-	10.0	0.01	0.02	-	22.2	0.03	0.07	-	25.0	0.01	0.02	-
Galium trifidum	50.0	0.06	0.08	17.4	14.3	0.01	0.03	-	40.0	0.06	0.12	-	33.3	0.02	0.03	-	25.0	0.02	0.05	-
Galium triflorum	0	0.00	0.00	-	0	0.00	0.00	-	60.0	0.06	0.06	-	88.9	0.15	0.18	52.3 ***	75.0	0.04	0.03	-
Geocaulon lividum	62.5	0.23	0.31	-	85.7	0.32	0.28	48.8 **	10.0	0.00	0.01	-	11.1	0.01	0.02	-	0	0.00	0.00	-
Geocaulon umbellatum	50.0	0.15	0.19	-	42.9	0.23	0.46	23.9	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-
Goodyera repens var. ophioides	37.5	0.03	0.04	-	0	0.00	0.00	-	0	0.00	0.00	-	66.7	0.03	0.03	29.1	12.5	0.02	0.05	-
Grass (Poaceae)	37.5	0.04	0.08	-	42.9	0.04	0.06	-	80.0	0.22	0.28	45.3 *	33.3	0.02	0.05	-	50.0	0.04	0.07	-
Gymnocarpium dryopteris	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-	33.3	0.15	0.35	32.7 *	12.5	0.00	0.01	-
Halenia deflexa	50.0	0.01	0.02	-	0	0.00	0.00	-	10.0	0.01	0.04	-	44.4	0.04	0.09	24.1	12.5	0.00	0.01	-
Lathyrus venosus	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-	33.3	0.01	0.01	33.3 *	0	0.00	0.00	-
Lilium philadelphicum	37.5	0.01	0.01	29.1 *	14.3	0.00	0.01	-	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-
Linnaea borealis	100.0	0.58	0.81	-	57.1	0.14	0.22	-	80.0	0.21	0.16	-	100.0	0.91	1.40	37.6	87.5	0.17	0.23	-
Lysimachia thyrsiflora	0	0.00	0.00	-	14.3	0.05	0.14	-	40.0	0.17	0.32	29.7 *	0	0.00	0.00	-	0	0.00	0.00	-
Maianthemum canadense	37.5	0.10	0.16	-	0	0.00	0.00	-	50.0	0.17	0.27	-	100.0	0.29	0.26	38 *	87.5	0.22	0.31	-
Mitella nuda	50.0	0.04	0.07	-	14.3	0.00	0.01	-	100.0	1.28	1.71	-	100.0	3.13	2.33	46 ***	100.0	1.69	1.83	-
Moneses uniflora	12.5	0.00	0.01	-	0	0.00	0.00	-	50.0	0.02	0.02	-	77.8	0.07	0.06	29.5	37.5	0.10	0.16	-
Parnassia palustris	12.5	0.00	0.01	-	42.9	0.25	0.63	41.7 *	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-
Petasites palmatus	87.5	0.39	0.36	-	57.1	0.15	0.16	-	10.0	0.00	0.01	-	100.0	0.40	0.35	30.4	75.0	0.38	0.47	-
Platanthera obtusata	37.5	0.03	0.05	-	28.6	0.01	0.02	-	30.0	0.01	0.01	-	66.7	0.07	0.07	24.9	50.0	0.08	0.12	-
Polygala paucifolia	87.5	0.12	0.16	-	57.1	0.31	0.50	17.2	30.0	0.60	1.83	-	55.6	0.16	0.18	-	25.0	0.06	0.12	-

Table 3 concluded.

Herbs continued	1) TOC-PMA-PBA				2) TOC-PMA-LLA-Heath				3) TOC-PMA-LLA-ARU				4) TOC-ABA-PMA-PGL				5) TOC-ABA-PGL-PTR			
	F% (n=8)	C% or IV	SD	Ind-Val	F% (n=7)	C% or IV	SD	Ind-Value	F% (n=10)	C% or IV	SD	Ind-Value	F% (n=9)	C% or IV	SD	Ind-Value	F% (n=8)	C% or IV	SD	Ind-Value
Pyrola secunda	37.5	0.03	0.06	-	0	0.00	0.00	-	20.0	0.11	0.33	-	55.6	0.10	0.17	23.7	50.0	0.01	0.02	-
Pyrola virens	50.0	0.03	0.03	-	0	0.00	0.00	-	20.0	0.01	0.01	-	66.7	0.08	0.09	32.4	62.5	0.05	0.06	-
Rubus pubescens	50.0	0.09	0.12	-	14.3	0.10	0.25	-	100.0	2.06	2.18	43.6 *	100.0	1.68	2.82	-	87.5	0.42	0.33	-
Rush (*Juncaceae*)	25.0	0.02	0.04	-	57.1	0.09	0.12	40.9 **	10.0	0.01	0.04	-	0	0.00	0.00	-	0	0.00	0.00	-
Sarracenia purpurea	0	0.00	0.00	-	42.9	0.34	0.56	42.9 **	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-
Sedge (*Cyperaceae*)	100.0	1.78	1.59	-	100.0	3.06	3.55	-	100.0	5.51	5.63	33.9 *	88.9	1.80	3.38	-	75.0	0.24	0.32	-
Smilacina trifolia	12.5	0.00	0.01	-	71.4	2.83	3.59	34.8 *	90.0	1.52	2.84	-	11.1	0.05	0.14	-	37.5	0.62	1.21	-
Solidago hispida var. lanata	50.0	0.03	0.03	50 **	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-
Streptopus roseus	0	0.00	0.00	-	0	0.00	0.00	-	0	0.00	0.00	-	33.3	0.03	0.07	-	50.0	0.08	0.18	35 *
Trientalis borealis	75.0	0.55	0.74	-	57.1	0.20	0.32	-	100.0	0.65	1.32	26.3	100.0	0.46	0.50	-	87.5	0.14	0.18	-
Viola renifolia	50.0	0.08	0.12	-	14.3	0.00	0.01	-	80.0	0.20	0.21	-	100.0	0.36	0.22	43.7 **	87.5	0.17	0.22	-
Mosses																				
Sphagnum spp.	12.5	0.52	1.47	-	71.4	21.58	22.53	41.1 *	90.0	10.05	15.84	-	11.1	0.01	0.02	-	12.5	0.13	0.35	-
Feather mosses	100.0	1.43	1.43	-	100.0	10.61	6.93	-	100.0	16.85	16.32	24.5	100.0	14.57	11.14	-	100.0	12.39	12.09	-
Other mosses	25.0	0.13	0.36	-	14.3	0.18	0.47	-	70.0	1.29	2.10	21.2	55.6	0.89	2.34	-	50.0	3.05	5.12	-
Climacium dendroides	0	0.00	0.00	-	28.6	0.06	0.10	-	60.0	0.51	0.67	29.6	55.6	0.12	0.18	-	37.5	0.26	0.44	-
Dicranum polysetum	100.0	1.15	1.15	65.2 **	14.3	0.07	0.18	-	50.0	0.31	0.66	-	44.4	0.11	0.19	-	12.5	0.00	0.01	-
Hylocomium splendens	100.0	21.87	15.45	36 **	85.7	6.60	5.82	-	80.0	3.78	4.28	-	88.9	9.99	11.17	-	62.5	2.06	3.19	-
Pleurozium schreberi	100.0	26.61	12.89	40.1 **	100.0	6.57	6.61	-	90.0	8.11	11.40	-	100.0	5.07	7.14	-	37.5	0.36	0.87	-
Lichen																				
Lichen-leaf	100.0	0.23	0.16	-	71.4	0.32	0.40	-	90.0	0.26	0.37	-	100.0	0.41	0.26	28.9	75.0	0.20	0.25	-
Lichen-club	100.0	0.38	0.20	-	85.7	2.14	4.87	39.8	80.0	0.23	0.27	-	66.7	0.18	0.27	-	37.5	0.04	0.06	-
Lichen-shrub	100.0	17.87	20.08	65.8 ***	85.7	3.57	5.39	-	50.0	0.06	0.10	-	66.7	0.07	0.09	-	37.5	0.01	0.02	-

Cypridedium arietinum occurred in this community type and in others (Table 4). The combination of *P. banksiana* with *T. occidentalis* was unique to the disjunct range.

The *TOC-PMA-PBA* community type-1 was characterized as the driest of moisture/drainage conditions, an upland dry association, and differed significantly from all but community type-4 (*TOC-ABA-PMA-PGL*; Table 5). The shallowest depth to mineral soil was noted for community type-1; this was significantly different to all communities but community type-5 (*TOC-ABA-PGL-PTR*). The mineral soil texture was most often comprised of gravel, and this differed significantly from that of all other community types. Litter cover was also significantly less than in the other community types, except that of type-2 (*TOC-PMA-LLA-Heath*; Table 5). Community type-1 also showed the most evidence of fire. Fire scars were noted on trees within this site (Table 5); however, very few fire scars were incidentally collected as wood samples and subsequently dated (F. Conciatori, personal communication).

3.1.3 Community Type-2: Thuja occidentalis-Picea mariana-Larix laricina-Heath

Thuja occidentalis and *P. mariana* had similar densities in this community type, but trees of *T. occidentalis* had twice the basal area. *Larix laricina* followed these two species in density and basal area (Table 1 and 2). This community type had the lowest overall basal area as well as tree density of all communities. Snags were mostly of *P. mariana*, while regeneration densities were greatest for *P. mariana* and *T. occidentalis*, followed by *L. laricina* (Table 1). Total regeneration density, especially for small saplings, was much greater here than the other community types (Table 1).

Table 4. Occurrences of provincially rare and uncommon species within stands of *Thuja occidentalis*. Observations here are noted at the stand level, and do not take into account abundance within the stand. See Figure 3 for community type definitions.

Species	Provincial Rank*	Total Occurences	Region Disjunct Range	Region Peripheral Range	Region Contiguous Range	1) TOC-PMA-PBA	2) TOC-PMA-LLA-Hea	3) TOC-PMA-LLA-ARU	4) TOC-ABA-PMA-PGL	5) TOC-ABA-PGL-PTR
Arethusa bulbosa – (Dragon's Mouth)	S2	1	1			1				
Asarum canadense – (Wild Ginger)	S3?	4			4				1	3
Cypripedium arietinum – (Ram's Head Lady's Slipper)	S2?	14	9	1	4	4	5	2	3	
Cypripedium reginae – (Showy Lady's Slipper)	S3?	3	1	1	1				3	
Drosera anglica – (Narrow-leaved Sundew)	S3	1	1					1		
Drosera linearis – (Slender-leaved Sundew)	S2?	1	1					1		
Goodyera tesselata – (Tesselated Rattlesnake Plantain)	S2	2	1	1					2	
Malaxis monophyllos var. *brachypoda* – (White Adder's-mouth)	S2?	3	1		2				1	2
Malaxis unifolia – (Green Adder's-mouth)	S2?	4	2		2	1	1	1	1	
Platanthera hookeri – (Hooker's Rein-orchid)	S2	3			3				2	1
Platanthera orbiculata – (Round-leaved Rein-orchid)	S3	12	3		9	1	1	1	6	3

* Provincial Rank ranges from S1 (very rare) to S5 (demonstrably secure). A rank followed by a "?" indicates uncertainty in the current rank based on the number of reported occurrences. Source of Provincial Rank: http://web2.gov.mb.ca/conservation/cdc/species/reports.php, accessed January 3, 2008.

Table 5. Summary of stand environmental variables used in CCA (abiotic, biotic, and historical) by community type (frequency (F%), mean, and standard deviation (SD)). Table includes P-value from Kruskal-Wallis one-way analysis of variance and different letters indicated significant (P ≤ 0.05) differences among communities for a given variable (Mann-Whitney U post hoc test for pairwise comparisons). See Figure 3 for community type definitions.

	1 TOC-PMA-PBA (n = 8)			2 TOC-PMA-LLA-Heath (n = 7)			3 TOC-PMA-LLA-ARU (n = 10)			4 TOC-ABA-PMA-PGL (n = 9)			5 TOC-ABA-PGL-PTR (n = 8)			
	F%	Mean	SD	F%	Mean	SD	F%	Mean	SD	F%	Mean	SD	F%	Mean	SD	P
Abiotic Misc.																
Elevation (m.a.s.l.)	100	283.4 a	9.45	100	283.0 a	31.83	100	300.8 a	54.91	100	318.3 a	39.14	100	353.3 b	10.49	**0.003**
Water (%)	13	0.03 a	0.07	71	2.38 b	5.35	30	2.93 ab	6.42	0	0.00 a	0.00	13	0.00 a	0.01	**0.013**
Slope (%)	75	1.58 c	1.11	14	0.14 ab	0.38	0	0.00 a	0.00	56	1.64 bc	1.81	38	2.17 bc	4.66	**0.009**
Bare ground (%)	13	0.06	0.16	43	1.07	2.48	10	0.02	0.06	11	0.02	0.07	13	0.52	1.47	0.340
Abiotic Soils																
pH	100	6.12	1.00	100	6.90	1.14	100	6.88	0.64	100	6.48	0.68	100	6.95	0.31	0.345
Moisture/Drainage (1-4)	100	1.87 a	1.04	100	3.84 c	0.37	100	3.75 c	0.41	100	2.65 ab	0.65	100	2.88 b	0.87	**0.000**
Depth to Mineral Soil (1-5)	100	1.65 a	0.49	100	3.59 cd	1.15	100	4.47 d	0.92	100	2.39 b	0.53	100	2.51 abc	1.56	**0.000**
Lowland-Organic (0/1)	25	0.04 a	0.09	100	0.55 bc	0.41	100	0.83 c	0.35	67	0.17 a	0.20	38	0.28 ab	0.40	**0.000**
Upland-Organic (0/1)	63	0.28 c	0.35	43	0.21 bc	0.34	0	0.00 a	0.00	44	0.37 bc	0.47	13	0.03 ab	0.09	**0.037**
Non-Organic (0/1)	100	0.68 c	0.38	43	0.24 ab	0.39	20	0.17 a	0.35	78	0.46 bc	0.37	88	0.69 c	0.38	**0.007**
Subtrate (0-4)	100	1.70 c	0.98	43	0.65 ab	1.07	20	0.33 a	0.69	78	0.90 bc	0.75	88	1.25 bc	0.74	**0.012**
1-SiCL-SCL (0/1)	25	0.12	0.28	14	0.09	0.23	10	0.01	0.02	33	0.03	0.05	50	0.16	0.24	0.355
2-Sand (0/1)	88	0.29	0.26	43	0.10	0.16	30	0.26	0.42	78	0.51	0.42	88	0.54	0.40	0.066
3-Gravel (0/1)	100	0.56 b	0.35	29	0.19 a	0.33	0	0.00 a	0.00	11	0.01 a	0.02	0	0.00 a	0.00	**0.000**
4-Rock/Cobble (0/1)	75	0.49 c	0.37	43	0.26 bc	0.33	0	0.00 a	0.00	33	0.20 abc	0.38	13	0.01 ab	0.02	**0.007**

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Table 5 concluded.

	1 TOC-PMA-PBA (n = 8)			2 TOC-PMA-LLA-Heath (n = 7)			3 TOC-PMA-LLA-ARU (n = 10)			4 TOC-ABA-PMA-PGL (n = 9)			5 TOC-ABA-PGL-PTR (n = 8)			
	F%	Mean	SD	F%	Mean	SD	F%	Mean	SD	F%	Mean	SD	F%	Mean	SD	P
Biotic/Structural																
Max. TOC Age (yrs)	100	140	61.1	100	239	115.8	100	151	61.8	100	180	55.5	100	123	59.9	0.061
Max. Stand Age (yrs)	100	158	56.5	100	287	152.4	100	195	63.6	100	186	47.8	100	142	47.8	0.070
Max. TOC HT (m)	88	6.20 b	1.29	100	4.78 a	1.24	100	9.35 c	2.33	100	13.41 c	2.66	100	12.54 c	1.96	**0.000**
Max. HT sp. *x* (m)	100	9.04 b	1.94	100	6.64 a	0.73	100	12.41 c	2.87	100	13.26 d	3.24	100	14.26 d	2.83	**0.000**
Canopy Openness (%)	100	27.98 c	7.59	100	45.14 d	16.63	100	14.57 b	3.37	100	11.36 a	2.15	100	10.60 a	1.67	**0.000**
CWD (%)	100	7.69 ab	6.37	100	3.66 a	3.43	100	8.27 ab	6.24	100	17.16 c	7.44	100	12.20 bc	6.07	**0.002**
Litter (%)	100	24.02 a	8.42	100	23.03 ab	17.95	100	43.84 bc	20.53	100	59.27 cd	18.31	100	68.60 cd	19.99	**0.000**
Historical																
Windthrow (0/1)	100	0.83	0.32	71	0.47	0.47	100	0.87	0.20	100	0.99	0.03	100	0.92	0.09	0.070
Cutting (1-4)	100	1.19 ab	0.29	100	1.10 a	0.25	100	1.62 bc	0.70	100	1.59 c	0.42	100	1.60 bc	0.57	**0.028**
Scars (0/1)	38	0.10	0.21	43	0.07	0.10	60	0.15	0.24	44	0.17	0.26	75	0.06	0.04	0.918
Insect (0/1)	0	0.00	0.00	14	0.01	0.03	0	0.00	0.00	33	0.02	0.03	0	0.00	0.00	0.071
Fire (0/1)	75	0.24	0.29	43	0.19	0.28	30	0.08	0.21	33	0.14	0.26	25	0.03	0.05	0.262
DMT (0/1)	25	0.09	0.23	43	0.15	0.32	30	0.20	0.39	11	0.01	0.02	13	0.01	0.02	0.474
Trail (0/1)	38	0.09	0.15	14	0.06	0.15	0	0.00	0.00	22	0.02	0.05	25	0.05	0.09	0.357

Community type-2 (*TOC-PMA-LLA-Heath*) had significantly lower tree species richness (3.0 tree species) than all but community type-3 (*TOC-PMA-LLA-ARU*; 3.6 tree species). Some of the most common and abundant indicator shrub species were *Andromeda polifolia, Betula pumila, Chamaedaphne calyculata, Oxycoccus microcarpus,* and *R. groenlandicum* (Table 3). Some significant and common herb species included *Drosera rotundifolia, Equisetum variegatum, Geocaulon lividum, Smilacina trifolia. Sphagnum* spp. dominated the bryophytes along with feather mosses, *Hylocomium splendens, Pleurozium schreberi,* and club- and shrub-lichens (Table 3). Six rare/uncommon species were found in this community type, including two other *Drosera* species and *Arethusa bulbosa.* These species were exclusive to this community (Table 4).

Community type-2, *TOC-PMA-LLA-Heath,* was significantly wetter than all but community type-3 (*TOC-PMA-LLA-ARU*), as represented by soil moisture and drainage conditions and percent water cover (Table 5). Soils of community type-2 were similar to community type-3, i.e. mainly lowland organic. Maximum heights of both *T. occidentalis* and the stand were significantly less than in any other community types. Additionally, the canopy openness was significantly greater than that of the other community types. This reflected low overall basal area and density. Evidence of fire, noted in the field, was the second most frequent among community types (Table 5), and a number of fire scars were dated using the wood samples that had been collected (F. Conciatori, personal communication). Both percent litter cover and amount of noted cutting, i.e. tree harvesting, were least, significantly different from all but community type-1 (*TOC-PMA-*

PBA). The two hydric community types (2 and 3) differed most obviously in basal area, density, and canopy openness.

3.1.4 Community Type-3: Thuja occidentalis-Picea mariana-Larix laricina-Alnus rugosa

Trees and saplings of *T. occidentalis* were dominant in this community type, with densities and basal areas many times greater than other species (Table 1 and 2). *Larix laricina* was a significant indicator of this type, and was similar to *P. mariana* in its IV, density, and basal area (Table 1, 2, and 3). Snags were mostly of *P. mariana*, with *T. occidentalis*, *L. laricina*, and *A. balsamea* components as well. This community type, along with community types 4 (*TOC-ABA-PMA-PGL*) and 5 (*TOC-ABA-PGL-PTR*) had some regeneration of *F. nigra*, a species not found in the disjunct range. A few of the most common shrubs included *Alnus rugosa, Rhamnus alnifolius, R. groenlandicum,* and *Rubus pubescens.* Sedges had a consistent presence, and feather mosses, *Sphagnum* spp., *P. schreberi,* and *H. splendens* were abundant bryophytes (Table 3). *Cypripedium reginae*, ranked as uncommon (with some uncertainty to abundance) by the province, was exclusive to this community type, which also had four other rare/uncommon species (Table 4). Environmental variables characteristic of community type-3 (*TOC-PMA-LLA-ARU*) included the greatest depth to mineral soil and lowland organic soil, both significantly different from those of the other communities except community type-2 (*TOC-PMA-LLA-Heath*; Table 5). There was little evidence of fire (Table 5).

3.1.5 Community Type-4: Thuja occidentalis-Abies balsamea-Picea mariana-Picea glauca

Community type-4 (*TOC-ABA-PMA-PGL*) was dominated by *T. occidentalis*, but *A. balsamea* was a significant indicator of this community type and also had high IV, density, and basal area. Additional recurrent tree species were *B. papyrifera* and *P. glauca* (Table 1, 2, and 3). Overall basal area was among the highest of all community types, after that of community type-5 (*TOC-ABA-PGL-PTR*). In the three disjunct stands of *T. occidentalis* in community type-4, tree density was 1984 stems/ha (663 were *T. occidentalis*), and basal area was 45 m^2/ha (23 for *T. occidentalis*). These values were much greater than those for either community type-1 or type-2 (*TOC-PMA-PBA* or *TOC-PMA-LLA-Heath*) in the disjunct range, but not as high as the two mesic mixedwood types. Snags were most commonly those of *T. occidentalis, A. balsamea,* and *B. papyrifera,* and regeneration was dominated by *A. balsamea,* but there was also *T. occidentalis* and some *P. balsamifera* (Table 1 and 2). Common and abundant shrub species were few, dominated by *Acer spicatum,* while herb species included *Aralia nudicaulis, Coptis trifolia, Cornus canadensis, Equisetum scirpoides, Galium triflorum, Linnaea borealis, Mitella nuda, R. pubescens,* and *Viola renifolia,* all of which were indicator species (Table 3). Dominant bryophytes were the feather mosses, *H. splendens* and *P. schreberi* (Table 3). This community type commonly included *Platanthera orbiculata,* but there were two occurrences each of *P. hookeri* and *Goodyera tesselata,* as well as three other rare/uncommon species (Table 4). The three stands found in the disjunct range had a mixedwood characteristic not usually seen in combination with *T. occidentalis.* The *TOC-ABA-PMA-PGL* community type-4 had significantly greater stand

height, CWD cover, and significantly less canopy openness, than all but community type-5 (Table 5). There were a few fire scars dated from wood samples of this community type (F. Conciatori, personal communication).

3.1.6 Community Type-5: Thuja occidentalis-Abies balsamea-Picea glauca-Populus tremuloides

In community type-5 (*TOC-ABA-PGL-PTR*), *T. occidentalis* once again had the highest density and basal area values, followed by *A. balsamea, P. tremuloides, P. glauca* and *B. papyrifera* (Table 1 and 2). This community type supported the highest density of stems and basal area per hectare. Snag densities and basal areas follow a similar pattern to the tree strata, and regeneration was predominantly *T. occidentalis* and *A. balsamea*, with some *P. balsamifera* and *P. tremuloides* (Table 1 and 2). Community type-5 had significantly higher tree species richness (5.1 tree species) than all but community type-4 (*TOC-ABA-PGL-PMA*; 4.3 tree species). *Populus tremuloides* was nearly exclusive to this community type, and except for a small component of regeneration in the disjunct range, this species was mainly found amongst the stands of *T. occidentalis* within the contiguous distribution. Cover percent of shrubs and herbs was low, but included small amounts of *M. nuda* and a moss layer of feather mosses, other mosses, and *H. splendens* (Table 3). Four rare or uncommon species (Provincial Ranks of S2 or S3) were found within this community, including *Asarum canadense, Malaxis monophyllos* var. *brachypoda,* and *P. hookeri* (Table 4).

Community type-5 (*TOC-ABA-PGL-PTR*) was characterized by its significantly higher elevation than the other community types and lowest maximum tree age (Table 5). Along with community type-4 (*TOC-ABA-PMA-PGL*), maximum stand height was significantly greater and canopy openness was significantly less than the other community types. Field observation of fire evidence was lowest in this community type (Table 5).

3.1.7 Regional Plant Community – Environmental Relationships

Results of the constrained ordination showed that the first two CCA axes were significant ($P \leq 0.001$), and the species-environment correlations for axis 1 and 2 were 0.941 and 0.901, respectively, accounting for 23.3% of the variance in the species data. Correlation between sample scores for CA axis-1 and CCA axis-1 was 0.995, and was 0.962 for both axis-2. These high correlations indicated that the environmental constraint did not alter the ordination of the sample stands along the first two axes and that species distribution reflected the environmental variables shown (Allen and Peet 1990). For this reason, only the CCA will be presented to avoid redundancy (Figure 5). Five significant variables ($P \leq 0.05$) were selected through forward selection, including canopy openness, depth to mineral soil, gravel substrate, windthrow, and pH (Figure 5).

The first axis of the CCA explained 54.2% of the species-environment variance, and the second axis explained 20.0%. Regional separation was observed along the first axis, with the peripheral stands intermediate between the disjunct and contiguous distribution. The five community types identified by *K*-means clustering were also well
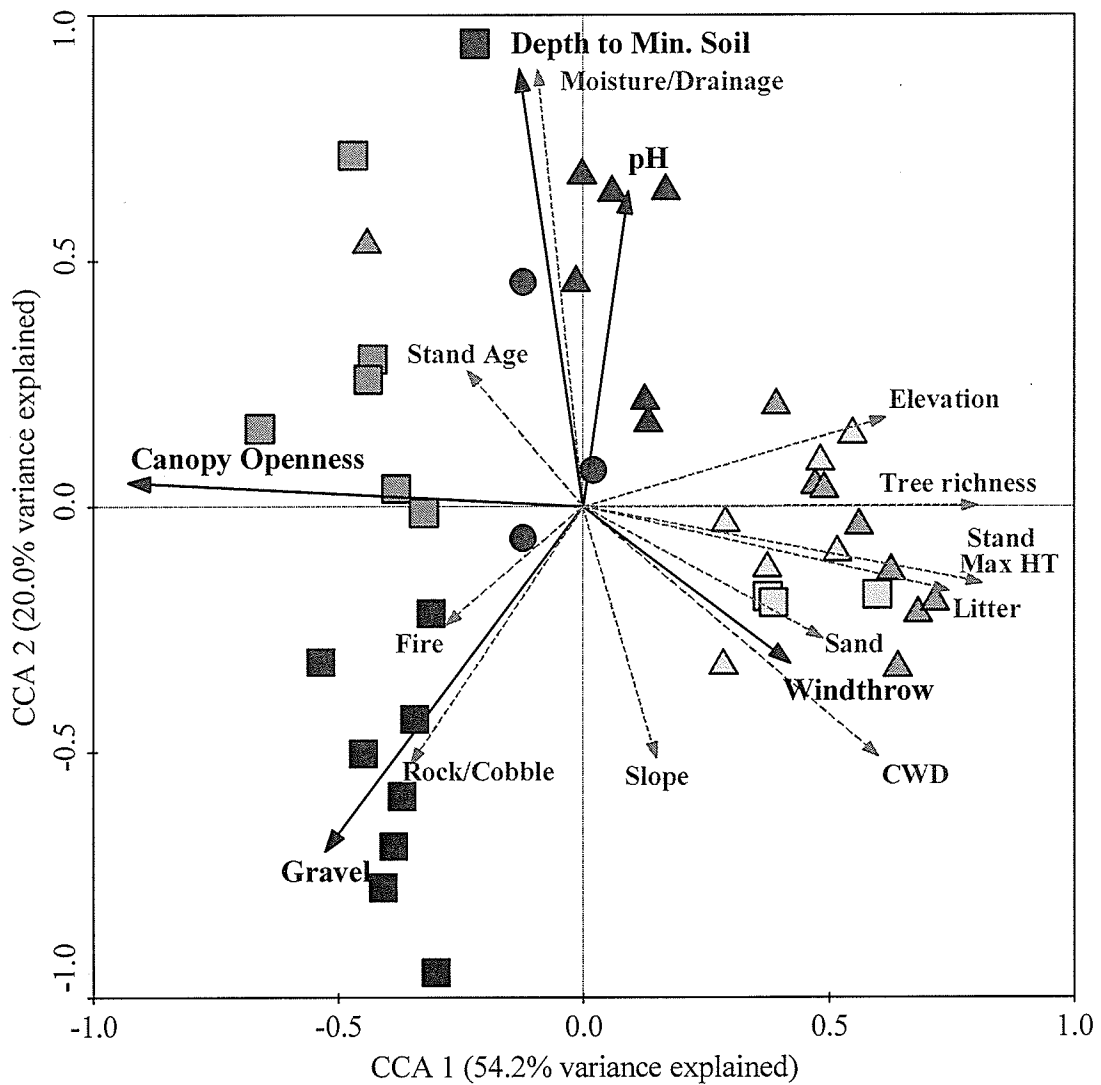
Figure 5. Canonical correspondence analysis (CCA) of 42 stands of *Thuja occidentalis* and both abiotic and biotic environmental variables significant at P < 0.05 (bold arrows) and passive variables (grey arrows). Stands in the disjunct range are represented by squares (n=18) and the contiguous distribution stands by both triangles (n=21 core stands) and circles (n=3 peripheral stands). Stands were also clustered (*K*-means) into five community types: 1) *TOC-PMA-PBA* (black), 2) *TOC-PMA-LLA-Heath* (green), 3) *TOC-PMA-LLA-ARU* (blue), 4) *TOC-ABA-PMA-PGL* (orange), 5) *TOC-ABA-PGL-PTR* (grey); see Figure 3 for community type definitions.

recognized in the ordination space. The xeric community type-1 (*TOC-PMA-PBA*) shared little overlap with the others whereas the hydric community types 2 (*TOC-PMA-LLA-Heath*) and 3 (*TOC-PMA-LLA-ARU*) showed more overlap as did the mesic community types 4 (*TOC-ABA-PMA-PGL*) and 5 (*TOC-ABA-PGL-PTR*) (Figure 5).

The main variable that was associated with compositional changes was canopy openness, which was strongly correlated to the first axis (Figure 5). The two community types (1: *TOC-PMA-PBA* and 2: *TOC-PMA-LLA-Heath*) associated with the disjunct distribution were more open canopied than those found in the contiguous distribution. Community type-1 was associated with a gravel substrate, which was correlated with the second axis. Both the depth to mineral soil and pH variables were also correlated to the second axis, and positively associated with community types 2 and 3 (*TOC-PMA-LLA-ARU*). The main environmental variables associated with community types 4 and 5 (*TOC-ABA-PMA-PGL* and *TOC-ABA-PGL-PTR*, respectively) were closed canopy and more signs of windthrow events. A number of environmental variables were also added passively to the CCA. Those variables associated with the disjunct distribution included greater evidence of fire, greater age, lower tree species richness, and lower tree heights. Further passive variables in the ordination, associated with much of the contiguous distribution, included greater elevation, litter cover, CWD, and sand substrates. The passively added moisture and drainage conditions variable identified a moisture gradient along the second axis, unrelated to the regional separation.

3.2 Stand Structure and Dynamics

3.2.1 Stand Age

Examination of all tree ages revealed that community type-2 (*TOC-PMA-LLA-Heath*) was the oldest (mean maximum age of 287 years) and community type-5 (*TOC-ABA-PGL-PTR*) was the youngest (mean maximum age of 143 years) (Table 6). The mean maximum and oldest individual *T. occidentalis* by community type followed the same pattern. *Thuja occidentalis* trees were the oldest, or were amoung the oldest in all community types. In community type-1 (*TOC-PMA-PBA*), the mean maximum age of *P. banksiana* was 15 years greater than *T. occidentalis*, and likewise, *L. laricina* was only 6 years older than *T. occidentalis* in type-3 (*TOC-PMA-LLA-ARU*).

3.2.2 Diameter distribution

In community type-1 (*TOC-PMA-PBA*), all species except *P. banksiana* visually approximated a negative linear trend for the log transformed densities by diameter class, considered typical of an uneven-aged forest (Husch et al. 2003) (Figure 6). In contrast, the diameter distribution for trees of *P. banksiana* in community type-1 more closely resembled a normal distribution, i.e., with few small and few large diameter trees, suggesting an even-aged cohort without additional recruitment (Figure 6). High frequencies of both large and small saplings for both *P. mariana* and *T. occidentalis* along with a relatively wide distribution, suggested continual recruitment and mortality for individuals of these species. Mortality of the three predominant species (*T. occidentalis, P. mariana,* and *P. banksiana*) of this community type was highest for those

Table 6. Tree maximum age (mean of maximum and standard deviation (SD)) and oldest individual tree by species and community type. No significant differences were noted between community types using the Kruskal-Wallis one-way analysis of variance. See Figure 3 for community type definitions.

Species		Community Types				
		1	2	3	4	5
All	Mean ± SD	158 ± 57	287 ± 152	195 ± 64	186 ± 48	143 ± 48
	Oldest	251	528	309	266	234
	n	*8*	*7*	*10*	*9*	*8*
Abies	Mean ± SD	-	-	65	76 ± 26	73 ± 25
balsamea	Max. age	-	-	65	114	108
	n	-	-	*1*	*6*	*6*
Betula	Mean ± SD	-	-	61	109 ± 45	114 ± 1
papyrifera	Max. age	-	-	61	144	115
	n	-	-	*1*	*5*	*2*
Fraxinus	Mean ± SD	-	-	129	-	-
nigra	Max. age	-	-	129	-	-
	n	-	-	*1*	-	-
Larix	Mean ± SD	89 ± 22	211 ± 172	157 ± 85	-	-
laricina	Max. age	111	528	287	-	-
	n	*5*	*7*	*10*	-	-
Pinus	Mean ± SD	155 ± 46	-	-	129	-
banksiana	Max. age	198	-	-	129	-
	n	*5*	-	-	*1*	-
Picea	Mean ± SD	-	-	-	90 ± 17	104 ± 5
glauca	Max. age	-	-	-	108	109
	n	-	-	-	*3*	*3*
Picea	Mean ± SD	-	-	-	102	-
spp.	Max. age	-	-	-	102	-
	n	-	-	-	*1*	-
Picea	Mean ± SD	147 ± 56	202 ± 78	118 ± 54	115 ± 28	110
mariana	Max. age	240	300	214	159	110
	n	*8*	*7*	*9*	*6*	*1*
Populus	Mean ± SD	-	-	-	108 ± 38	190
balsamifera	Max. age	-	-	-	140	190
	n	-	-	-	*4*	*1*
Populus	Mean ± SD	-	-	-	-	105 ± 14
tremuloides	Max. age	-	-	-	-	116
	n	-	-	-	-	*5*
Thuja	Mean ± SD	140 ± 61	239 ± 116	151 ± 62	180 ± 55	123 ± 60
occidentalis	Max. age	251	392	309	266	234
	n	*8*	*7*	*10*	*9*	*8*
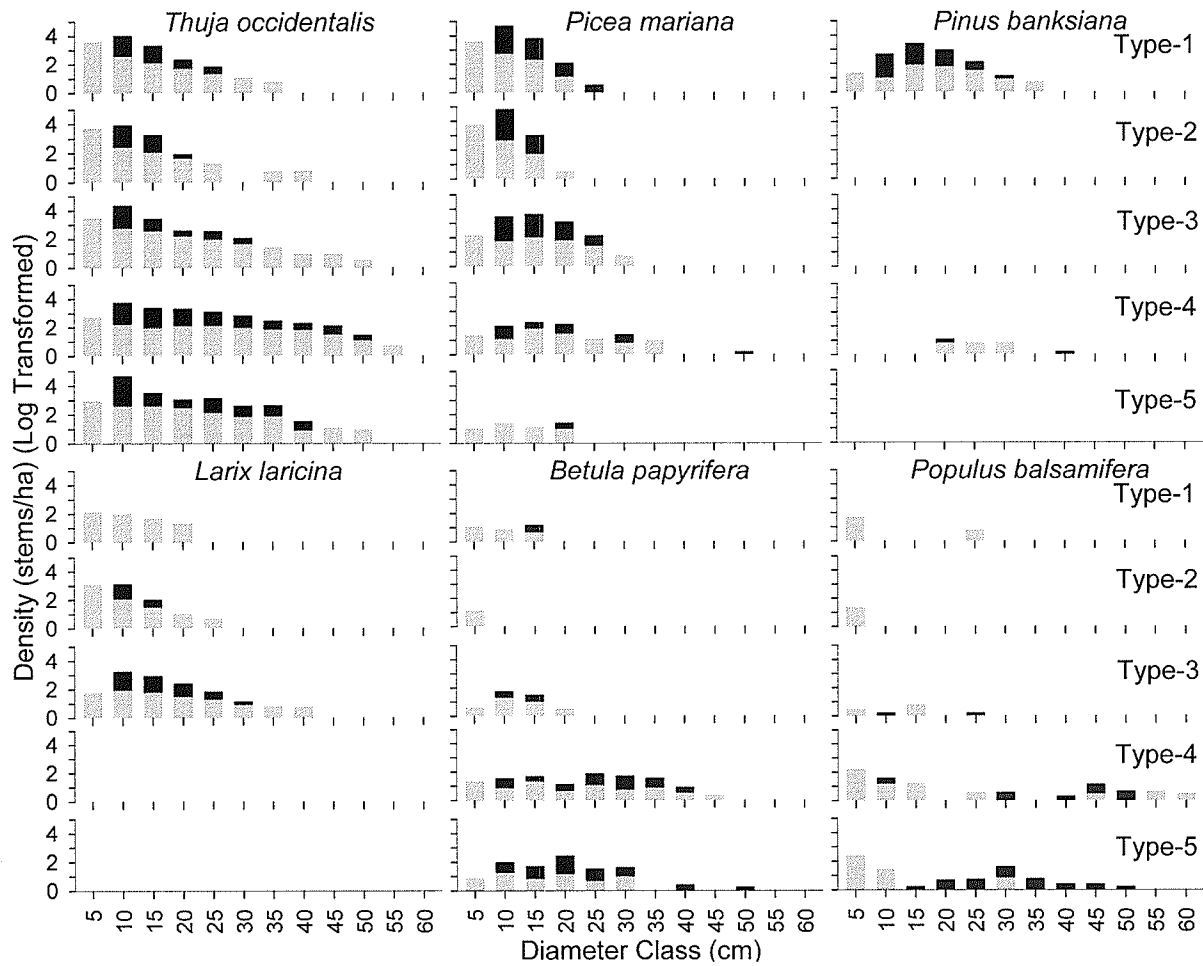
Figure 6. Diameter distribution (stems/ha) of saplings (small and large saplings are represented in the first 5 cm class), trees and snags (>5 cm classes) by community types: 1) *TOC-PMA-PBA*, 2) *TOC-PMA-LLA-Heath*, 3) *TOC-PMA-LLA-ARU*, 4) *TOC-ABA-PMA-PGL*, 5) *TOC-ABA-PGL-PTR*; see Figure 3 for community type definitions. Snags are indicated by black bars whereas both live trees and saplings are grey bars.
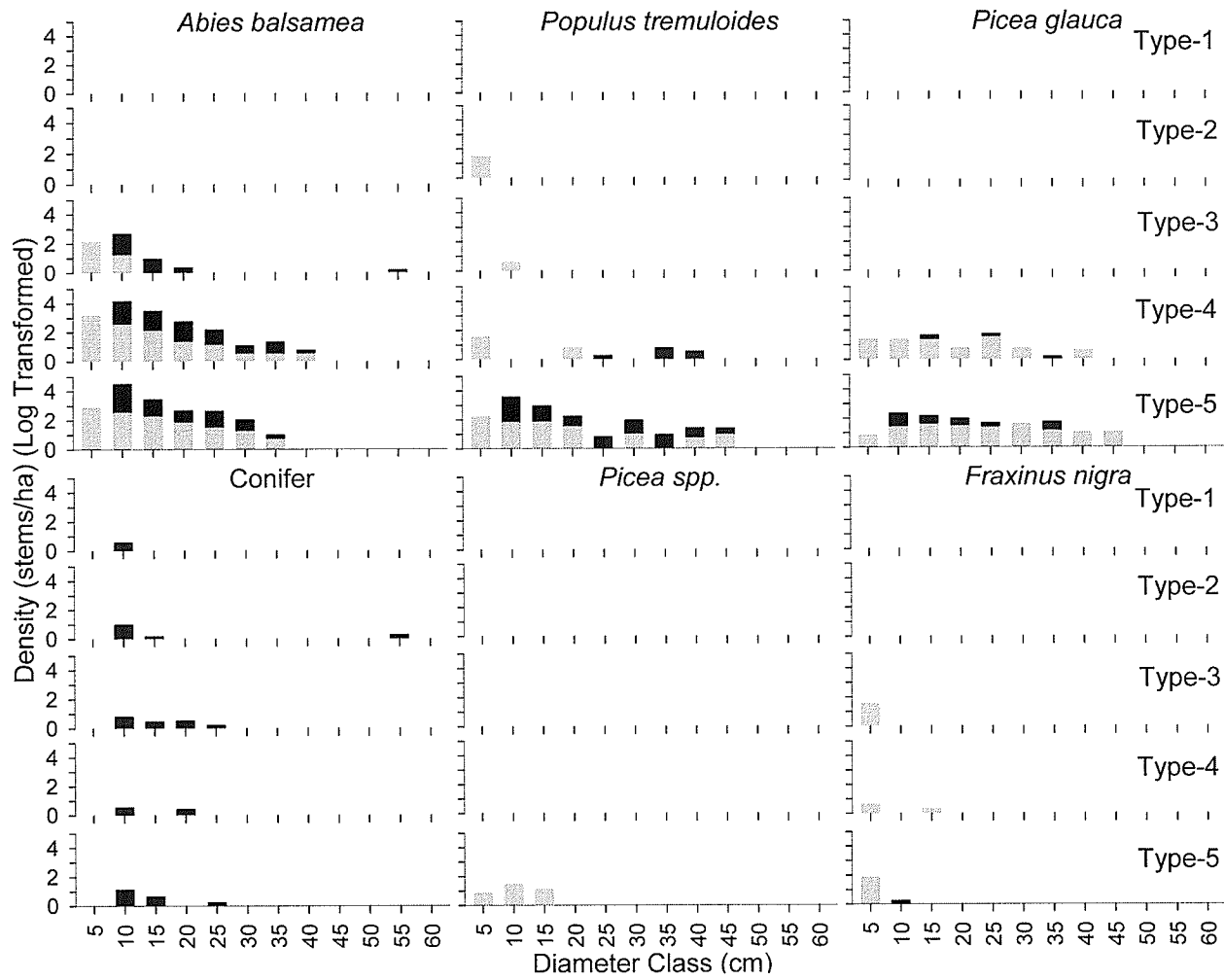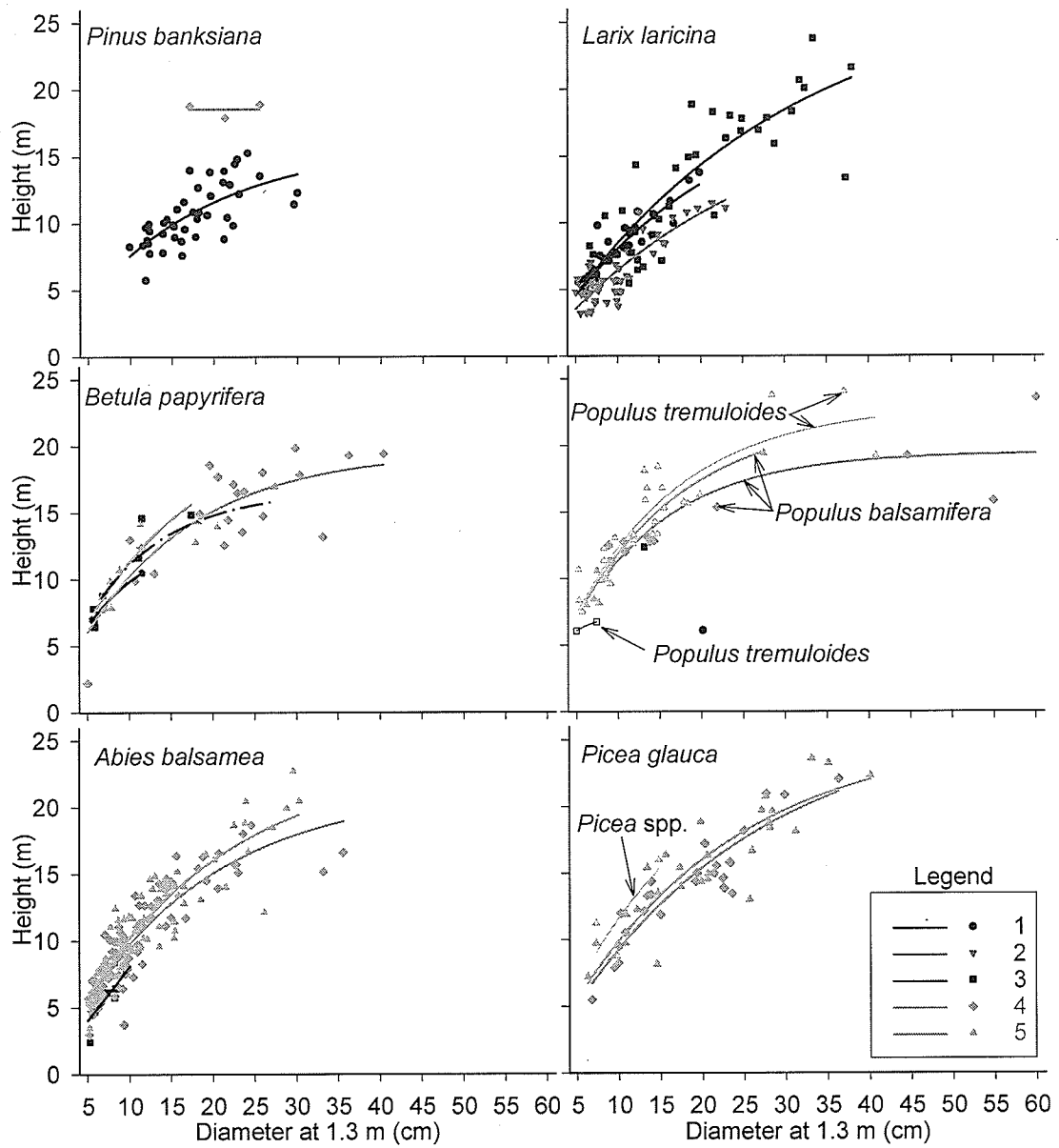
Figure 6 concluded.

with small diameters, and decreased with increasing diameter classes. The diameter distributions of *T. occidentalis*, *P. mariana*, and *L. laricina* in community type-2 (*TOC-PMA-LLA-Heath*) were similar to community type-1 in approximating a negative linear trend and in distribution width. Snag densities were highest for small *P. mariana* and while trees of *T. occidentalis* reached the 36-40 cm diameter class, snags of *T. occidentalis* were not observed larger than the 16-20 cm diameter class.

The diameter distributions of tree species in community types 1 (*TOC-PMA-PBA*) and 2 (*TOC-PMA-LLA-Heath;* the disjunct range) were narrower than those found in community types 3 to 5 (peripheral and contiguous range predominantly). In community type-3 (*TOC-PMA-LLA-ARU*), *T. occidentalis*, *P. mariana*, and *L. laricina* achieved diameters 10-15 cm greater than in the first two community types (Figure 6). Both *T. occidentalis* and *L. laricina* also maintained the negative linear trend to the diameter distribution, and all species repeated this trend in the snag distribution, exhibiting high frequencies of small live and dead stems.

With exceptions, community type-4 (*TOC-ABA-PMA-PGL*) and type-5 (*TOC-ABA-PGL-PTR*) had similar composition of tree species and stem diameter distributions (Figure 6). Trees of both *T. occidentalis* and *A. balsamea* had wide diameter distributions with a negative linear trend, indicating continual recruitment, high densities of small stems and few large trees. Snags of these two species generally replicated their living counterparts. The remaining species (*B. papyrifera, P. glauca, P. balsamifera,* and *P.*

tremuloides) of the last two community types demonstrated a more sporadic diameter distribution, suggesting episodic recruitment and/or mortality events.

3.2.3 Height-Diameter Relationships

The height-diameter relationship for trees of *T. occidentalis* demonstrated that growth for this species was most restricted in the two disjunct community types (*TOC-PMA-PBA* and *TOC-PMA-LLA-Heath;* Figure 7, Appendix D). Growth of trees of *T. occidentalis* in the wet contiguous distribution community type-3 (*TOC-PMA-LLA-ARU*) was intermediate among the community types, and *T. occidentalis* trees showed their greatest growth in community types 4 and 5 (*TOC-ABA-PMA-PGL* and *TOC-ABA-PGL-PTR,* respectively). Projected height growth of *P. mariana* was low in community type-2. Growth of both *P. mariana* and *L. laricina* was least for this community type. The tallest projected heights for trees of *L. laricina,* at 18.4 m (Appendix D), were found in community type-3. *Pinus banksiana* was found in stands of *T. occidentalis* essentially exclusive to the disjunct range (community type-1). The height-diameter relationship in *A. balsamea* did not vary greatly by community type; however, most representatives were from community types 4 and 5, the latter of which had slightly greater growth, with the highest maximum modeled height (asymptote) (Appendix D). *Betula papyrifera* showed similar growth curves among its community type representatives, and the tallest projected heights were found in community type-3. Both *P. tremuloides* and *P. balsamifera* had similar projected growth in community type-5 (Figure 7).
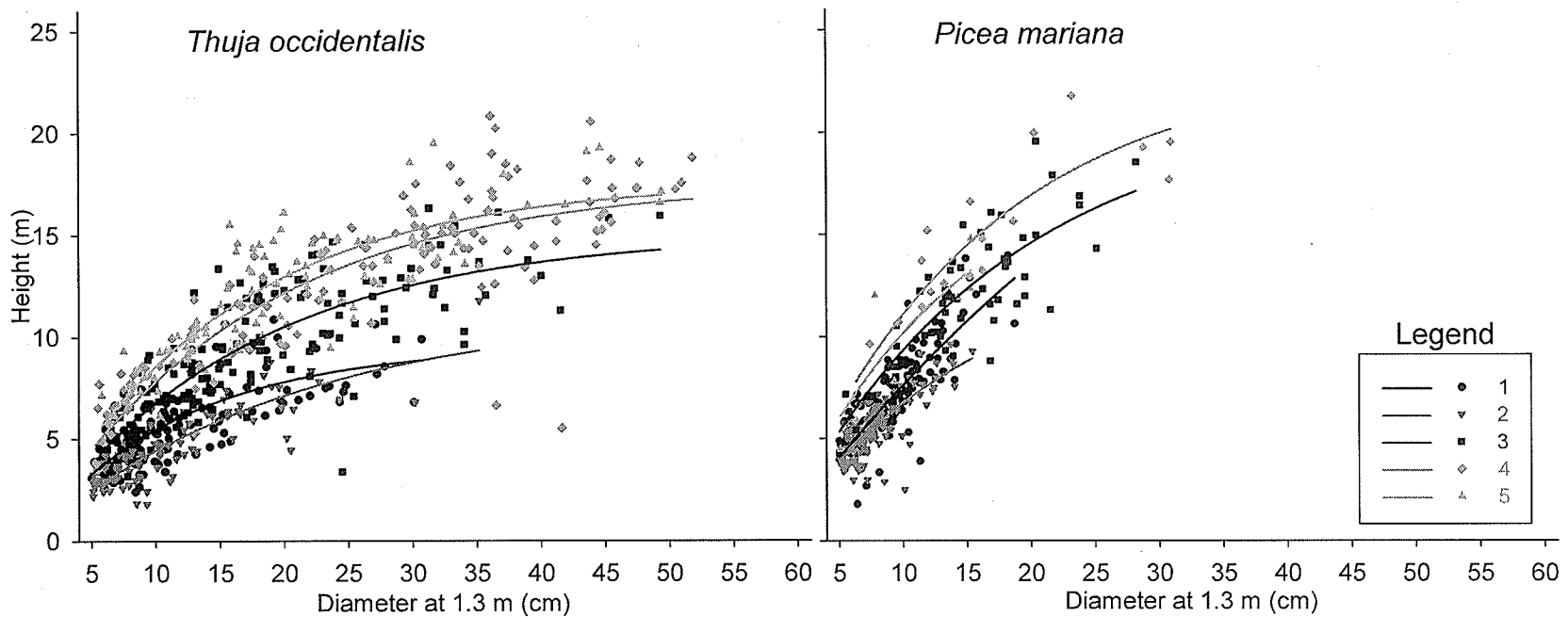
Figure 7. Tree Diameter – Height regressions (exponential rise to the maximum) by species and community types (1-5): 1) *TOC-PMA-PBA*, 2) *TOC-PMA-LLA-Heath*, 3) *TOC-PMA-LLA-ARU*, 4) *TOC-ABA-PMA-PGL*, 5) *TOC-ABA-PGL-PTR*; see Figure 3 for community type definitions.

Figure 7 concluded.

4. DISCUSSION

4.1 Diversity of Communities with Thuja occidentalis in Manitoba

Characterization of *T. occidentalis* populations in Manitoba showed that this species was found in a greater variety of habitat within its disjunct range than within its peripheral or contiguous ranges. *Thuja occidentalis* within the disjunct range appeared to act as a habitat generalist, present in a range of conditions including xeric, mesic, and hydric moisture regimes. This contradicted our first hypothesis that predicted the disjunct population would be restricted to wet locations where it was less susceptible to fire. Some evidences, however, suggested protection from frequent stand replacing fires in this region of Manitoba. For example, the presence of *P. banksiana* with a mean maximum age of 155 years indicated that stand replacing fire is not frequent. The abundance of *T. occidentalis* in the Cedar Lake area may also be a reflection of the occurrence of limestone as a bedrock in that region. This species appears to do well on such substrates (Fernald 1919; Kangas 1989; Johnston 1990). Other tree species at their distribution limit are known to occupy specific habitats, for example *P. resinosa* was restricted to shorelines where competition was low, and there was a low fire hazard and more suitable microclimate (Butson et al. 1987), disjunct populations of *P. rigida* were restricted to sandstone outcrops within open forests (Meilleur et al. 1997), and *Q. alba* was restricted to drought and fire prone south- to southwest facing slopes (Tardif et al. 2006). Kavanagh and Kellman (1986) demonstrated the tolerance of *T. canadensis* at its northern distribution limit in central Ontario, where it was found most commonly on westerly and northerly slopes as opposed to the expected warmer southerly slopes. While the disjunct populations of *T. occidentalis* at their northern distribution limit do not at first seem to be

habitat specific, they do appear to be found in a region that provides safe and suitable habitat, such as a low fire hazard and a limestone base. This species' presence in the Cedar Lake area may suggest that the region's fire frequency/intensity has been sufficiently reduced, compared to the surrounding areas, by the landscape mosaic of wetlands, uplands and lakes. It follows also that in an area where these conditions have allowed *T. occidentalis* to become widespread over time, that the otherwise unexpected co-occurrence of *T. occidentalis* with *P. banksiana* could occur. These results are in agreement with the known broad physiological tolerance of this species (Collier and Boyer 1989; Matthes-Sears and Larson 1991). In contrast to the disjunct range, *T. occidentalis* in southeastern Manitoba only occupied sites with mesic and hydric moisture regimes, although it does occupy xeric sites elsewhere in its contiguous distribution (e.g. Sheppard and Cook 1988; Larson and Kelly 1991; Archambault and Bergeron 1992a).

As noted, there was a slightly higher stand density estimation using the original equation provided by Cottam and Curtis (1956) compared to the unbiased equation (Pollard 1971; Krebs 1999). Through the congruency test and correlation between correspondence analysis axes of the vegetation cover and tree IV data sets, it was shown that these two data types revealed the same relationship among stands. This indicates that the bias in density estimate was inconsequential to the clustering results and was not enough to influence the interpretation of the results.

This study revealed the existence of five community types dominated by *T. occidentalis* populations in Manitoba and these communities occurred under three

moisture regimes. The region of disjunction was represented mostly by conifer dominated

community types, such as the xeric type-1 (*TOC-PMA-PBA*), the hydric type-2 (*TOC-PMA-LLA-Heath*), but also included one stand of type-3 (*TOC-PMA-LLA-ARU*), and a

few stands from the mesic mixedwood community type-4 (*TOC-ABA-PMA-PGL*). The

peripheral region was represented by the conifer dominated hydric community type-3,

which was also common within the contiguous range. The rest of the contiguous range

was made up of the mesic mixedwood communities 4 and 5 (*TOC-ABA-PMA-PGL* and

TOC-ABA-PGL-PTR). This provides some support for our second hypothesis that plant

associations which included *T. occidentalis* would differ among regions, although there is

some overlap in three of the five community types.

Despite the five distinct community types described in this study, the Manitoba

Forest Ecosystem Classification (FEC) guide only recognized one *T. occidentalis*

dominated vegetation type (V19: Cedar Conifer and Mixedwood), which is described as a

wet to moist conifer mixedwood, but based on only five sample sites (Zoladeski et al.

1995). The Manitoba FEC does not adequately cover the variety of stands with *T.*

occidentalis in southeastern Manitoba, or its disjunct populations in west-central

Manitoba. Others have recognized a wider range of habitats for *T. occidentalis* in their

classification systems. The Northwestern Ontario FEC guide (Sims et al. 1997)

recognized the bimodal habitat preference of *T. occidentalis*, as it is most commonly

found in wet lowlands and dry uplands (e.g. Fernald 1919; Curtis 1946; Pregitzer 1990),

and four ecosites described for Manitoba by Walker et al. (2002) are similar to the current

findings. Walker et al. (2002) described three ecosites that corresponded to three of the

community types described here, and the fourth ecosite corresponded to the two

mixedwood types 4 and 5. The three stands protected within Ecological Reserves

represent only two of the community types (Figure 4, Appendix C). Those with existing

protection include community type-2 (*TOC-PMA-LLA-Heath*; Long Point Ecological

Reserve) in the disjunct range, and community type-3 (*TOC-PMA-LLA-ARU*; both

Brokenhead Wetlands and Pocock Ecological Reserves) within the peripheral and

contiguous distribution.

4.2 Thuja occidentalis and Pinus banksiana

Interestingly, the association of *T. occidentalis* with *P. banksiana* was unique to

the region of disjunction, where this combination was common under the xeric moisture

regime and was described as community type-1 (*TOC-PMA-PBA*). This association was

not described by the FEC vegetation types of Manitoba (Zoladeski et al. 1995), but

Walker et al. (2002) noted that *T. occidentalis* was a rare component of ecosite E2 (Jack

pine-black spruce on very shallow soil rugged terrain features), making it somewhat

similar to community type-1. However, the current findings indicate that trees of *T.*

occidentalis were dominant in stands of community type-1 (Table 2). The presence of

this association demonstrated the unexpected success of *T. occidentalis* in occupying

xeric conditions alongside *P. banksiana* and *P. mariana*. This association did have

precedent, although it was little recognized in Manitoba. *Thuja occidentalis* with similar

habitats and associations were noted in northeastern Minnesota (Frelich and Reich 1995).

The presence of *T. occidentalis* in xeric conditions was also reported in Ontario (Larson

and Kelly 1991; Matthes-Sears and Larson 1995) and Quebec (Sheppard and Cook 1988; Archambault and Bergeron 1992a).

The fourth hypothesis stated that regeneration of *T. occidentalis* in the disjunct range would be minimal. Seedling recruitment for *T. occidentalis*, however, was common in all community types, and in fact it was more abundant in the disjunct sites than in the contiguous range. In the xeric community type-1 (*TOC-PMA-PBA*), regeneration was dominated by *P. mariana* and *T. occidentalis*. Not only was *P. banksiana* regeneration nearly absent from this community type, the high frequency of snags of this species indicated a reduced presence and former importance of *P. banksiana*. The decline in this species and lack of regeneration can be attributed to the infrequent stand replacing fires, as supported by the mean maximum age of 155 years. Whether *T. occidentalis* was regenerating predominantly by seed or layering was, unfortunately, not recorded. While both sexual and asexual reproduction were noted, layering was generally common. Grotte (2007) observed that regeneration in *T. occidentalis* (< 30 cm tall) were nearly all vegetative propagules in 7 of the current 18 disjunct stands. Regeneration was recorded as layering in the three xeric stands examined by Grotte (2007). The gravel road along Long Point provided access to one of the community type-1 stands containing *P. banksiana*, which was common there. This road has a mown buffer on either side of approximately 3-5 m, which for many kilometres has seedlings and saplings of *T. occidentalis* growing directly in a xeric gravel substrate with no organic layer (personal observation). This indicated that germination could occur in relative abundance and that

cone development in *T. occidentalis* was not limited by cold temperature, counter to findings of Morin et al. (2007) for many other tree species at their distribution limit.

It had been hypothesized that to be successful in the Cedar Lake area, a population of *T. occidentalis* would be confined to habitats or locations that were wet and protected from fire. Contrary to these expectations, the population was successful in community type-1 (*TOC-PMA-PBA*) under very dry conditions, but in support of the expectations these appear to have been missed by frequent, stand-replacing fires. In community type-1 only a very few fire scars were sampled incidentally (F. Conciatori, personal communication); however, observations in the field showed evidence of frequent fires (e.g. fire scars, carbonized stems or branches). This evidence in combination with the presence of nearly 200 year old trees of *P. banksiana*, and an uneven-aged stand structure, pointed toward occasional surface fires and a long stand-replacing fire return cycle. Specifically, trees of *P. banksiana* in community type-1 had a mean maximum age of about 155 years, which could be considered to approximate the length of the fire return cycle (Bergeron and Dubuc 1989). It appeared that *T. occidentalis* had survived alongside a fire prone species in locations where intense fires are infrequent. This was likely due to the open canopied nature of the forests located in a mosaic of wetlands and gentle ridges and surrounded by three large lakes (Cedar Lake, Lake Winnipegosis, and Lake Winnipeg). Similarly, in the Boundary Waters Canoe Area of northeastern Minnesota, the reduced fire intensity resulting from the many lakes, rivers, bogs, peatlands, and other topographic features had allowed populations of *T. occidentalis* to survive (Heinselman 1973; Frelich and Reich 1995). Historically, even

large, intense fires would not easily remove populations of *T. occidentalis* from the landscape of its disjunct range. The landscape mosaic could provide enough breaks to leave nearby seed sources for reintroduction, as noted in northwestern Quebec (Bergeron and Dubuc 1989).

In stands of community type-1 (*TOC-PMA-PBA*) that continue to elude stand-replacing fires, the population of *P. banksiana* will continue to decline and a successional transition from *P. mariana – P. banksiana* dominated stands to *P. mariana – T. occidentalis* will continue. *Thuja occidentalis* is a long-lived, late successional species that, over time and if undisturbed, will co-dominate with *P. mariana* on xeric sites in Quebec (Bergeron and Dubuc 1989). These authors found that stands of *P. banksiana* were replaced by those of *P. mariana* and *T. occidentalis* over the course of about 200 years. This process reflected a similar situation in northeastern Minnesota, where old senescing stands of *P. banksiana*, for lack of fire, were being invaded by a community of *T. occidentalis*, *A. balsamea*, *P. mariana*, and *B. papyrifera* (Frelich and Reich 1995). The mean maximum age for trees of *P. banksiana* in community type-1, and maximum ages of nearly 200 years, indicated that the trees of *P. banksiana* in these stands may be near the end of an old-growth stage, as defined by Uhlig et al. (2001).

Despite the current associations of *T. occidentalis* and *P. banksiana* in the Cedar Lake area of Manitoba and in northeastern Minnesota (Heinselman 1973), this co-occurrence does not appear successful in southeastern Manitoba. An abundance of fire breaks and low fire intensity have been highlighted as important factors allowing the

maintenance of *T. occidentalis* in association with otherwise fire prone species like *P. banksiana* (Heinselman 1973; Bergeron and Dubuc 1989). This evidence for a low fire hazard requirement implied that the fire regime in southeastern Manitoba may not be conducive to this association. However, the stand ages did not differ significantly between the community types of southeastern Manitoba and those of the disjunct range. Also, *T. occidentalis* may be excluded from xeric sites that host *P. banksiana* in southeastern Manitoba if there is a lack of limestone base. Despite a listed FEC vegetation type of *P. strobus* with a *T. occidentalis* component in the extreme southeastern corner of Manitoba (Zoladeski et al. 1995) and northwestern Ontario (Sims et al. 1997), this association was not observed in this study. However, the reported co-occurrence of *T. occidentalis* with *P. strobus* in the contiguous range suggests that *T. occidentalis* inhabits areas with a longer fire return cycle than are generally found for stands of *P. banksiana* in the region.

4.3 Mixedwood Communities with Thuja occidentalis

While the disjunct population of *T. occidentalis* was present under a wide range of conditions, those of the mesic mixedwood forests were uncommon in the Cedar Lake area, and represented by only three stands (community type-4, *TOC-ABA-PMA-PGL*). Mixed boreal forests, however, were noted in this region at several sites, such as along lake shores (Smith et al. 1998). This corresponded approximately to the location of these three stands, on the well-drained, relatively steep north shore of Lake Winnipegosis, which is in the centre of the disjunct range. The southern aspect, soil moisture and/or soil nutrient regime may play roles in determining the local mixedwood characteristics.

Among the samples collected in these stands, fire scars were rare (F. Conciatori, personal communication) and the protection from fire that is provided by the landscape is likely important in allowing *T. occidentalis* to become a notable part of these stands, not unlike community type-1 (*TOC-PMA-PBA*).

The results provided evidence that growth vigour of *T. occidentalis* in the Cedar Lake area is habitat specific, not universally limited, counter to our third hypothesis which held that diameter and height would be reduced in this region. Despite the wide ecological amplitude of *T. occidentalis* (Matthes-Sears and Larson 1991), growth and productivity in the Cedar Lake sites were greatly restricted in the xeric and hydric community types when compared to these attributes in the three mesic stands of community type-4. These three stands demonstrated the ability of this species to thrive amongst larger trees and a more closed canopy in this region. Density of trees of *T. occidentalis* in these stands was higher and basal area per hectare was much greater than elsewhere at the Cedar Lake site. This corresponded well with the findings by Fernald (1919) and those of Matthes-Sears and Larson (1991) that the growth of trees of this species would be best under mesic conditions. The fire cyle in the Cedar Lake area may have been long enough to allow not only the inclusion of *T. occidentalis* in these mesic stands, but also for succession to occur toward their dominance. This data reinforced the importance of suitable habitat for disjunct populations (e.g. Meilleur et al. 1997), and highlights the need for local, species-specific information when modeling distribution limits for climate change (Loehle and LeBlanc 1996; Johnstone and Chapin 2003; Tardif et al. 2006).

It should also be noted that while density of the disjunct population was greatest at the three mesic-mixedwood stands, it was still lower than that of the rest of the mesic-mixedwood stands in community types 4 and 5 (*TOC-ABA-PMA-PGL* and *TOC-ABA-PGL-PTR*) from the sites within the contiguous range. This provided some support for the observed decrease in abundance towards a distributional boundary that had been highlighted by others (Brown et al. 1996; Murphy et al. 2006). *Abies balsamea* may have increased importance in community type-4, even though *T. occidentalis* was dominant in the overstory. Regeneration was *A. balsamea* dominated, followed by *T. occidentalis*, *P. balsamifera* and a few trees of *P. tremuloides*. However, other species retained a presence by means of invading gaps caused by windthrow events, a prevalent disturbance type. Regeneration of *T. occidentalis* and *A. balsamea* was of equal importance in the other mesic-mixedwood type (community type-5). This suggested that their continued presence was dependant upon the absence of stand replacing disturbances. Regeneration of *P. balsamifera* was disproportionately high compared to that of the overstory component of this species, and individuals of *F. nigra* were only found in the understory. In time there may be a shift in the overstory towards these two species at the expense of *B. papyrifera* and *P. glauca*, which were rare as young plants.

In characterizing the mixedwood community types, the trees of the community type-5 (*TOC-ABA-PGL-PTR*) were found to be the youngest. The young ages of these stands and lack of observed fire scars suggested a stand replacing fire regime and a short fire interval. While it seems counter-intuitive to have a late successional species present

where there is a short fire return interval, Bergeron and Debuc (1989) noted in their study that even the forests less than 50 years old already had late successional species present (both *T. occidentalis* and *A. balsamea*). The relatively rapid introduction of these species after stand replacing fires was possible due to the fire breaks on the landscape and thus the availability of nearby seed sources (Bergeron and Dubuc 1989). The overstory species that were common to community type-5 and community type-4 (*TOC-ABA-PMA-PGL*) had similar mean maximum ages except for those of *T. occidentalis*, which were younger in type-5, and a single *P. balsamifera*, which was younger in type-4. These findings suggested that community type-5 may be an earlier successional stage of community type-4, where the initial cohort was still intact. In time, *T. occidentalis* is likely to survive a die-off of co-dominant species which have continued to maintain themselves as a smaller component of this community. Furthermore, while *T. occidentalis* and *A. balsamea* were the dominant species in these two community types, regeneration of *T. occidentalis* was much less than that of *A. balsamea* in the older community type-4. This may lead to a future shift in overstory dominance in the absence of fire.

This study found that *T. occidentalis* occurs in two distinct ecosystems in the contiguous range and, as such supports findings of Curtis (1946) and Pregitzer (1990). The bimodality of its habitats are also reflected in the Northwestern Ontario FEC guide, which recognized two vegetation types that are dominated by *T. occidentalis*, i.e. an upland community (NW-V21; Cedar (inc. Mixedwood)/Mountain Maple), and a wetter lowland community (NW-V22; Cedar (inc. Mixedwood)/Speckled Alder/Sphagnum)

(Sims et al. 1997). Community types 4 and 5 (*TOC-ABA-PMA-PGL* and *TOC-ABA-PGL-PTR*) are also recognized in Ontario (i.e. NW-V21) and community type-3 (*TOC-PMA-LLA-ARU*) closely resembles NW-V22 of Ontario (Sims et al. 1997). This suggested that a degree of compositional consistency is continued from northwestern Ontario into Manitoba and towards the boundary of the contiguous range.

4.4 Wetland Communities with Old Trees of Thuja occidentalis

Community type-2 (*TOC-PMA-LLA-Heath*) was widespread in the Cedar Lake region and was characterized by trees that were old and stunted, in open canopied wetlands dominated by a *T. occidentalis – P. mariana – L. laricina* community. These findings provide some of the support for the first hypothesis, that *T. occidentalis* in its disjunct range finds safety in wet locations protected from fire. This community appears to be self-replacing and stable, with the overstory species having the same composition as snag and regeneration populations. Trees of these three species were older than their counterparts in other community types. Furthermore, the mean maximum age of each of the trees of the three species in community type-2 easily exceeded the minimum old-growth ages identified for the most similar ecosites in northwestern Ontario (Uhlig et al. 2001). The restricted growth amongst the trees in this community type and their great ages likely resulted from the extreme conditions which also minimized the influence of fire. Stunted trees of community type-2 exhibited a similar cambial dieback (personal observation) that was characteristic for trees growing on cliff faces along the Niagara Escarpment (Kelly et al. 1992) and also on rock outcrops in northwestern Quebec (Archambault and Bergeron 1992b). Kelly et al. (1992) noted that individuals of *T.*

occidentalis experienced 50% cambial dieback between 130 and 280 years of age, and that many trees grew for hundreds of years with less than 20% of potential cambium in a functional state. The old age of trees in community type-2 may suggest low frequency of large intense fires, which in turn could result from the wet conditions, low tree densities, and most openness of canopy (nearly 50%), and the shortest trees. Trees in a few stands within community type-2 showed fire scars (F. Conciatori, personal communication) and evidence of fire in the field was common (Table 4). These factors suggested the occurrence of a surface fire regime. Larson (2001) pointed out that the long-lived individuals of *T. occidentalis* which were found growing on the cliffs of the Niagara Escarpment were extremely slow growing. This age-growth rate relationship appeared to be replicated in the trees of *T. occidentalis* in community type-2. There was one stand within the contiguous range that had the same composition, environment and structure as stands in the Cedar Lake area; however, trees were very young (*c.* 50 years) in that single stand.

The hydric community type-2 (*TOC-PMA-LLA-Heath*) of the disjunct range and community type-3 (*TOC-PMA-LLA-ARU*) of the peripheral and contiguous range were somewhat similar in character. However, supporting the third hypothesis, the stand structure of the hydric community at Cedar Lake was much different, because they had more open canopies, shorter trees, lower tree densities, and lower basal areas than the community type-3 sites. One possible reason for this disparity may have been differences in nutrient availability. Indicator species analysis in community type-2 identified species that are usually associated with a poor nutrient regime, i.e. *A. polifolia, C. calyculata, O.*

microcarpus, R. groenlandicum, D. rotundifolia, H. splendens, and *Sphagnum* spp. (Ringius and Sims 1997). The presence of some of the common species that are also indicator species in the more productive community type-3 (*A. rugosa, R. groenlandicum, R. pubescens, H. splendens,* and *Sphagnum* spp.) did not reflect a specific nutrient regime (Ringius and Sims 1997). However, *A. rugosa,* a nitrogen fixing species, was common in community type-3 but nearly absent in community type-2. Structural and productivity differences between the three study areas may have been related to their different climatic conditions. Compared to the contiguous and peripheral distribution, the disjunct population experienced a colder mean January temperature (by roughly 2 °C), and about 100 fewer growing degree days above 10 °C for the year (an 11% - 12% difference) (Environment Canada 2004). There was little evidence of fire scars noted in the field or collected as wood samples in community type-3, suggesting stand replacing fires, and the comparative youth of type-3 versus type-2 implies a much shorter fire return cycle. Regeneration in community type-3 was dominated by *T. occidentalis,* while a number of other conifer and deciduous species were of minor importance. *Thuja occidentalis* can be expected to increase its dominance with time.

The peripheral stands of community type-3 (*TOC-PMA-LLA*) were somewhat intermediate between the contiguous and disjunct ranges. Stands within the peripheral range were similar in composition to stands of community type-2 (*TOC-PMA-LLA-Heath*), perhaps due to a more boreal influence as these three stands were at the very northwestern tip of the Lake of the Woods ecoregion.

4.5 Conservation of Populations of Thuja occidentalis

Forests of *T. occidentalis* in Manitoba are to be valued, due to the longevity of the species within them and their associated scientific usefulness (i.e., forest ecology and dendrochronology), their late successional and old-growth status, as well as the diversity of stand compositions/associations. The diversity of vegetation types associated with *T. occidentalis* has been poorly described by previous forest classification, and in addition, only two of the community types described by the current study are being protected at the moment.

Thuja occidentalis has been compared to bristlecone pine (*Pinus longaeva* D.K. Bailey) in its ability to live remarkably long (Kelly et al. 1992). *Thuja occidentalis* reaching great age have been observed growing on exposed rocky substrates along the Niagara escarpment (e.g. Kelly et al. 1992) and northwestern Quebec (Archambault and Bergeron 1992a, 1992b) and the Gaspé Peninsula, Quebec (Sheppard and Cook 1988). In eastern Canada trees of *T. occidentalis* have provided the longest tree-ring chronology, and these chronologies have proven to be especially useful in the reconstruction of past droughts (e.g., Archambault and Bergeron 1992a, Buckley et al. 2004). A number of dendroclimatic studies using this species have been conducted in Manitoba: chronologies for the disjunct range dated back to 1713 (Tardif and Stevenson 2001) and 1504 (Case 2000), and a chronology in the contiguous range dated back to 1658 (St. George and Nielson 2001). The oldest individual *T. occidentalis* tree in the current study had lived for more than 459 years (a tree that had died in 1997), while the longest lived snag that Case (2000) found had lived for 473 years. Samples used to determine the age of the trees in

this study also extended the *T. occidentalis* tree-ring chronology in the disjunct range back to 1315 A.D., spanning 690 years (F. Conciatori, personal communication). Likewise, the chronology built from samples of the current study for the peripheral region dated back to 1696, and in the contiguous range, dated back to 1669 (F. Conciatori, personal communication). There is excellent potential for extending these tree-ring chronologies further in all regions. Continued dendrochronological research of this species can also increase the sample depth (i.e. replication).

Many of the stands with *T. occidentalis* studied in Manitoba had trees that could be considered old-growth by the age criteria set by Uhlig et al. (2001). As noted in the current study, living trees of *T. occidentalis* were found to be greater than 200, 300, and nearly 400 years of age in the contiguous, peripheral, and disjunct ranges, respectively. Archambault and Bergeron (1992b) have commented that it is impressive for old forests of *T. occidentalis* to persist on extreme sites in eastern Quebec, especially in a boreal landscape regularly visited by fire. This comment is applicable to *T. occidentalis* in Manitoba as well. In the case of *T. occidentalis* in Manitoba, the oldest forests are found commonly under wetter conditions (e.g. very old trees of *L. laricina*, *T. occidentalis*, and *P. mariana* in community type-2, *TOC-PMA-LLA-Heath*), but the xeric stands (i.e. community type-1, *TOC-PMA-PBA*) are also old, typically exceeding the normal life span of the pioneer trees of *P. banksiana*. There are numerous values attached to old-growth forests, including ecological, social, cultural, and economic values (OMNR 1994). As noted earlier, *T. occidentalis* has historically had important uses for First Nations peoples in transportation along the waterways (e.g. Hind 1860; Bell 1897;

Scoggan 1957; Podruchny 2006). This suite of values and the fact that old-growth forests usually occur only on a small percent of the landscape, especially the extreme sites (consider the long tail of the age class distribution), provides further grounds for conservation.

At least three Ecological Reserves provide protection to *T. occidentalis* in Manitoba, one in each of the three regions studied. These three Ecological Reserves were found in different ecodistricts (three out of four noted in the study areas), but the three stands with this protection represent only two of the community types (Figure 4, Appendix C). Those with existing protection include community type-2 (*TOC-PMA-LLA-Heath*; Long Point Ecological Reserve) in the disjunct range, and community type-3 (*TOC-PMA-LLA-ARU*; both Brokenhead Wetlands and Pocock Ecological Reserves) within the peripheral and contiguous distribution. The location of the proposed Manitoba Lowlands National Park (CPAWS 2006) in the disjunct range would provide further protection to community type-2 and the one stand of community type-3, as well as add the unique composition of community type-1 (*TOC-PMA-PBA*) which is exclusive to the area.

Independently from the proposed National Park, the priority for protection of stands of *T. occidentalis* in the disjunct range should be as follows: firstly, the unique composition of community type-1 (*TOC-PMA-PBA*), in particular some of the most westerly stands, thereby highlighting the very edge of the distribution; secondly, one or more of the mesic-mixedwood stands from community type-4 (*TOC-ABA-PMA-PGL*),

which were located in (relatively) close proximity to each other along the northern shore of Lake Winnipegosis, west of Denbeigh Point on relatively uncommon mesic conditions; and thirdly, more stands of the very old community type-2 (*TOC-PMA-LLA-Heath*), perhaps along the Easterville road, central to the disjunct distribution, since the Long Point Ecological Reserve was burned in 1988 (Weber and Bell 1990). Although common in the contiguous distribution, members of the mesic mixedwood community types 4 and 5 (*TOC-ABA-PGL-PTR*) do not have representatives under protection. A number of exemplary stands of these two community types that could be protected can be found along highway 308, between East Braintree and Moose Lake. These two community types had the most evidence of occasional cutting, i.e. tree harvesting, likely because the trees were typically large and they were not wetlands, which made these stands accessible. Since one of the three peripheral stands sampled is already protected through the Brokenhead Wetlands Ecological Reserve, further protection in this region may not be essential.

4.6 Future Research

A few interesting and potentially fruitful areas of future research should be considered. The usefulness of *T. occidentalis* in dendroclimatology, especially drought reconstruction, has been pointed out before (Archambault and Bergeron 1992a; Tardif and Stevenson 2001; Buckley et al. 2004). The ability for future work to increase tree-ring sample depth, i.e. replication, and extend the chronology farther back in all regions seems highly feasible. Further information on the fire regimes and fire histories of the three study areas would be beneficial in determining the role fire has in the distribution of

T. occidentalis as well as provide a baseline for comparison against a change in fire regime. It would also be useful to have clarification on the regenerative ability of *T. occidentalis* across the disjunct range, specifically the seed viability, germination requirements, and establishment success.

Examination of the genetic diversity of *T. occidentalis* across the disjunct range compared to the contiguous range would be able to suggest a possible origin of the species in the Cedar Lake area (Lamy et al. 1999; Mosseler el al. 2004). If the disjunct populations exhibited high levels of inbreeding, this would suggest long-distance dispersal and few founding members, but if the genetic diversity was found to be similar to the contiguous distribution, this would suggest that the contiguous distribution once included the current region of disjunction (Lamy et al. 1999; Mosseler et al. 2004). In support, paleoecological studies looking for macrofossils, especially stomata, would aid in determining range history (Yu 1997; Parshall 1999). Genetic studies of this species would also identify potential divergence from the contiguous distribution and aid in deciding upon conservation efforts (Lesica and Allendorf 1995).

5. CONCLUSION

This study of the habitats for *T. occidentalis* in Manitoba has revealed regional differences in stand composition, structure, and environment. Stands were associated with hydric moisture regimes for disjunct, peripheral and contiguous populations, but xeric habitats were only found for the disjunct population in the Cedar Lake area. Mesic habitats hosting *T. occidentalis* were found within the contiguous range but were uncommon for the disjunct population. These findings were counter to the first hypothesis which predicted the disjunct population would be restricted to wet locations where it would be protected from fire. There was, however, evidence to suggest protection from frequent stand replacing fires in the Cedar Lake area. The disjunct *T. occidentalis* appears to experience a favourable, rather than absent, fire regime and preferred habitat, allowing it to thrive in this region.

The results supported the second hypothesis that regional ecosystem composition differences would characterize the disjunct, peripheral, and contiguous populations. The disjunct range was represented mostly by conifer dominated xeric or hydric community types 1 and 2 (*TOC-PMA-PBA* and *TOC-PMA-LLA-Heath*), but also by three stands from the mesic mixedwood community type-4 (*TOC–ABA–PMA–PGL*). The association between *P. banksiana* and *T. occidentalis* was unique to the Cedar Lake area. The two mesic mixedwood community types 4 and 5 (*TOC-ABA-PMA-PGL* and *TOC-ABA-PGL-PTR*) were common in the contiguous distribution. These two highly productive communities were the only ones described by the single *T. occidentalis* dominated vegetation type in the Manitoba Forest Ecosystem Classification guide. The hydric

community type-3 (*TOC-PMA-LLA-ARU*) was common within the contiguous range of
T. occidentalis of southeastern Manitoba and included all three peripheral stands found in
the Grand Beach/Belair area. Community type-3 had much higher basal area, density,
canopy closure, tree height, and had a small deciduous component, but was otherwise
similar in character to community type-2.

The third hypothesis expected reduced growth vigour of trees of *T. occidentalis* in
the disjunct population compared to the contiguous distribution. The disjunct range was
dominated by community types 1 and 2 (*TOC-PMA-PBA* and *TOC-PMA-LLA-Heath*),
which were much more open canopied stands that had reduced stand heights and tree
diameters when compared to the peripheral and contiguous range. However, the
productivity of the three mesic mixedwood stands observed in the disjunct range
demonstrated that growth vigour of *T. occidentalis* in the Cedar Lake area is habitat
specific, not universally limited. The fourth hypothesis stated an expectation that the
regenerative success of *T. occidentalis* would be lowest in the disjunct populations, but
recruitment was greatest here.

This study demonstrated the need for further conservation of habitat that supports
T. occidentalis and provides some of the baseline information to that end. *Thuja
occidentalis* is an important late successional and old-growth species, can provide an
extremely long chronology for climatic reconstruction, and exhibits uncommon
compositional associations at its range boundary. The creation of the proposed Manitoba
Lowlands National Park would be an important step towards protecting some of the

highlighted characteristics of the disjunct *T. occidentalis* stands, but some additional protection for *T. occidentalis*-mixedwood forests in the contiguous range would be advisable. Future research should focus on extending the chronology and increasing sample replication for dendroclimatological purposes. Also, undertaking genetic and paleoecological studies, involving pollen and macrofossils, could determine the range history, and it would be useful to have a better understanding of the mechanisms behind *T. occidentalis*'s regenerative success at its range boundary in the disjunct range.

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APPENDIX A

Species list, including scientific name and abbreviation.

Scientific Name	Abbreviation
Trees	
Abies balsamea	*ABA*
Betula papyrifera	*BPA*
Conifer spp.	Conifer
Fraxinus nigra	*FNI*
Fraxinus pennsylvanica	*FPE*
Larix laricina	*LLA*
Pinus banksiana	*PBA*
Picea glauca	*PGL*
Picea mariana	*PMA*
Picea spp.	*Picea spp.*
Populus balsamifera	*Poba*
Populus tremuloides	*PTR*
Quercus macrocarpa	*QMA*
Thuja occidentalis	*TOC*
Shrubs	
Acer spicatum	*Ace spi*
Alnus crispa	*Aln cri*
Alnus rugosa	*Aln rug*
Amelanchier alnifolia	*Ame aln*
Andromeda polifolia	*And pol*
Arctostaphylos uva-ursi	*Arc uva*
Betula pumila	*Bet pum*
Chamaedaphne calyculata	*Cha cal*
Cornus stolonifera	*Cor sto*
Empetrum nigrum	*Emp nig*
Gaultheria hispidula	*Gau his*
Gaultheria procumbens	*Gau pro*
Juniperus communis	*Jun com*
Juniperus horizontalis	*Jun hor*
Kalmia polifolia	*Kal pol*
Lonicera oblongifolia	*Lon obl*
Lonicera villosa	*Lon vil*
Oxycoccus microcarpus	*Oxy mic*

Scientific Name	Abbreviation
Potentilla fruticosa	*Pot fru*
Prunus virginiana	*Pru vir*
Rhamnus alnifolius	*Rha aln*
Rhododendron groenlandicum	*Rho gro*
Rhus radicans	*Rhus rad*
Ribes glandulosum	*Rib gla*
Ribes lacustre	*Rib lac*
Ribes oxyacanthoides	*Rib oxy*
Ribes triste	*Rib tri*
Rosa acicularis	*Ros aci*
Rubus idaeus	*Rub ida*
Salix candida	*Sal can*
Salix glauca	*Sal gla*
Salix maccalliana	*Sal mac*
Salix myrtillifolia	*Sal myr*
Salix spp.	*Salix spp*
Shepherdia canadensis	*She can*
Symphoricarpos albus	*Sym alb*
Vaccinium angustifolium	*Vacc ang*
Vaccinium myrtilloides	*Vac myr*
Vaccinium vitis-idaea	*Vac vit*
Viburnum edule	*Vib edu*
Viburnum opulus	*Vib opu*
Viburnum rafinesquianum	*Vib raf*

Herbs

Actaea rubra	*Act rub*
Amerorchis rotundifolia	*Ame rot*
Anemone quinquefolia	*Ane qui*
Aralia nudicaulis	*Ara nud*
Asarum canadense	*Asa can*
Aster borealis	*Ast bor*
Aster ciliolatus	*Ast cil*
Asteraceae	*Ast spp*
Botrychium virginianum	*Bot vir*
Calla palustris	*Call pal*
Caltha palustris	*Caltha pal*
Campanula aparinoides	*Cam apa*
Campanula rotundifolia	*Cam rot*
Chimaphila umbellata	*Chi umb*

Scientific Name	Abbreviation
Circaea alpina	*Cir alp*
Clintonia borealis	*Cli bor*
Coptis trifolia	*Cop tri*
Corallorhiza trifida	*Cor tri*
Cornus canadensis	*Cor can*
Cyperaceae.	Sedge
Cypripedium arietinum	*Cyp ari*
Cypripedium calceolus	*Cyp calc*
Cypripedium reginae	*Cyp reg*
Drosera rotundifolia	*Dros rot*
Epilobium angustifolium	*Epil ang*
Equisetum arvense	*Eq arv*
Equisetum fluviatile	*Eq fluv*
Equisetum pratense	*Eq pra*
Equisetum scirpoides	*Equ scir*
Equisetum sylvaticum	*Eq sylv*
Equisetum variegatum	*Eq var*
Fragaria virginiana	*Fra vir*
Galium boreale	*Gal bor*
Galium trifidum	*Gal trifid*
Galium triflorum	*Gal trifl*
Geocaulon lividum	*Geo liv*
Geocaulon umbellata	*Geo umb*
Goodyera repens	*Goo rep*
Gymnocarpium dryopteris	*Gym dry*
Halenia deflexa	*Hal def*
Impatiens capensis	*Imp cap*
Juncaceae.	Rush
Lathyrus venosus	*Lat ven*
Lilium philadelphicum	*Lil phi*
Linnaea borealis	*Lin bor*
Lycopus uniflorus	*Lyc uni*
Lysimachia thyrsiflora	*Lys thy*
Maianthemum canadense	*Mai can*
Malaxis unifolia	*Mal uni*
Matteuccia struthiopteris	*Mat str*
Menyanthes trifoliata	*Men tri*
Mitella nuda	*Mit nud*
Moneses uniflora	*Mone uni*
Monotropa uniflora	*Mono uni*

Scientific Name	Abbreviation
Parnassia palustris	*Par pal*
Petasites palmatus	*Pet pal*
Petasites sagittatus	*Pet sag*
Platanthera aquilonis	*Pla aqu*
Platanthera obtusata	*Pla obt*
Platanthera orbiculata	*Pla orb*
Poaceae.	Grass
Polygala paucifolia	*Pol pau*
Polygonum amphibium	*Poly amp*
Potentilla palustris	*Pot pal*
Pyrola asarifolia	*Pyr asa*
Pyrola secunda	*Pyr sec*
Pyrola spp.	*Pyr spp*
Pyrola virens	*Pyr vir*
Rubus chamaemorus	*Rub cha*
Rubus pubescens	*Rub pub*
Sanicula marilandica	*San mar*
Sarracenia purpurea	*Sar pur*
Scutellaria galericulata	*Scut gal*
Smilacina stellata	*Smi ste*
Smilacina trifolia	*Smi tri*
Solidago hispida var. lanata	*Sol his*
Spiranthes romanzoffiana	*Spi rom*
Streptopus roseus	*Str ros*
Tofieldia glutinosa	*Tof glu*
Trientalis borealis	*Tri bor*
Viola nephrophylla	*Vio neph*
Viola renifolia	*Vio ren*
Zygadenus elegans	*Zyg ele*

Mosses

Sphagnum spp.	*Sphag*
Feather mosses	Feather
Other mosses	Moss spp
Climacium dendroides	*Clim dend*
Dicranum polysetum	*Dicr poly*
Hylocomium splendens	*Hyl spl*
Pleurozium schreberi	*Ple schr*
Ptilium crista-castrensis	*Ptil cri*

| Scientific Name	Abbreviation
Lichens	
Crust form lichen	Lich-cru
Scale form lichen	Lich-scal
Leaf form lichen	Lich-leaf
Club form lichen	Lich-club
Shrub form lichen	Lich-shrub

APPENDIX B

Environmental variables recorded at each point of each stand. Data type (Quantitative, Semi-Quantitative, or Qualitative) and data transformation (logarithmic) are noted. The variables kept for canonical correspondence analyses (CCA) after variable removal due to collinearity are also noted.

Environmental Variables	CCA	Data	Transformation
Latitude (degrees)		Quantitative	-
Longitude (degrees)		Quantitative	-
Region (1-3)		Qualitative	-
Elevation (m.a.s.l.)		Quantitative	logarithm
Slope (degrees)	●	Quantitative	logarithm
Water cover (%)		Quantitative	logarithm
Bare ground cover (%)		Quantitative	logarithm
Soils			
pH	●	Quantitative	-
Depth to mineral soil (1-5)	●	Semi-Quantitative	-
Moisture/Drainage (1-4)	●	Semi-Quantitative	-
Subtrate texture (0-4)		Semi-Quantitative	-
SiCL-SCL (0 or 1)	●	Qualitative	-
Sand (0 or 1)	●	Qualitative	-
Gravel (0 or 1)	●	Qualitative	-
Rock/Cobble (0 or 1)	●	Qualitative	-
Lowland Organic (0 or 1)		Qualitative	-
Upland Organic (0 or 1)	●	Qualitative	-
Non-Organic (0 or 1)		Qualitative	-
Species derived & descriptive			
Canopy openness (%)	●	Quantitative	logarithm
Coarse woody debris cover (%)	●	Quantitative	logarithm
Litter cover (%)	●	Quantitative	logarithm
NWC max. age (yrs)	●	Quantitative	logarithm
Stand max. age (yrs)	●	Quantitative	logarithm
NWC max. height (m)	●	Quantitative	logarithm
Stand max. height (m)	●	Quantitative	logarithm
Understory species richness		Quantitative	-
Tree species richness		Quantitative	-
Disturbance/Health			
WT (0 or 1)	●	Qualitative	-
Cutting (1-4)	●	Semi-Quantitative	-
Fire (0 or 1)	●	Qualitative	-
Scars (0 or 1)		Qualitative	-
Insect (0 or 1)	●	Qualitative	-
Dwarf mistle toe (0 or 1)	●	Qualitative	-
Trail (0 or 1)	●	Qualitative	-

APPENDIX C

Study area map displaying individual community types: see Figure 3 for names. Three ecodistricts within Lake of the Woods Ecoregion are outlined in the top-left panel: 1) Stead, 2) Piney, and 3) Whitemouth. Ecoregion and ecodistrict source: Manitoba Lands Initiative, Government of Manitoba – online at http://web2.gov.mb.ca/mli (© 2001 Her Majesty the Queen in Right of Manitoba, as represented by the Minister of Conservation. All rights reserved.).
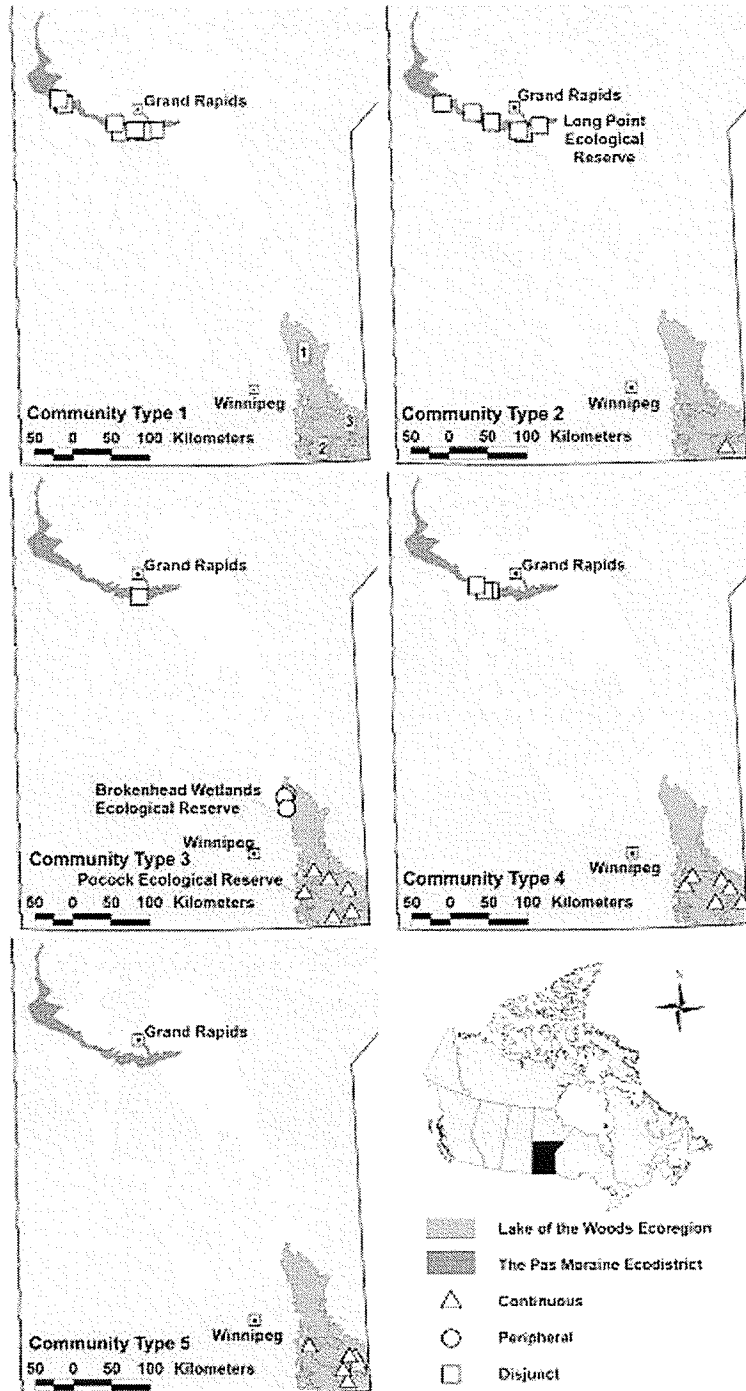
APPENDIX D

Parameters of the exponential rise to maximum regression for diameter-height relationship for tree species by community type (equation: f=a*(1-exp(-b*x))). Parameter a is the asymptote (maximum modeled height), and b is the initial slope. All regressions were significant at $P < 0.05$ except where underlined. See Figure 3 for community type definitions.

	1 TOC-PMA-PBA				2 TOC-PMA-LLA-Heath				3 TOC-PMA-LLA-Alder				4 TOC-ABA-PMA-PGL				5 TOC-ABA-PGL-PTR			
Tree species	Rsqr	a	b	Ht30*	Rsqr	a	b	Ht30*	Rsqr	a	b	Ht30*	Rsqr	a	b	Ht30*	Rsqr	a	b	Ht30*
Abies balsamea									_0.703_	_30878_	_0.000_	_24.2_	0.815	21.4	0.061	18.0	0.806	23.8	0.056	19.4
Betula papyrifera									0.897	21.4	0.076	19.2	0.743	19.6	0.074	17.5	0.821	16.6	0.110	16.0
Fraxinus nigra																				
Larix laricina	0.765	20.4	0.050	15.9	0.736	19.3	0.041	13.6	0.718	27.9	0.036	18.4								
Pinus banksiana	0.504	16.0	0.065	13.7									0.000	18.6	9710	18.6				
Picea glauca													0.842	26.6	0.043	19.4	0.759	25.5	0.050	19.8
Picea mariana	0.693	33.9	0.025	18.1	0.599	14.0	0.066	12.1	0.691	21.2	0.058	17.5	0.824	23.3	0.065	19.9	_0.582_	_88763_	_0.000_	_22.1_
Picea sp.																	_0.543_	_27.1_	_0.056_	_27.5_
Populus balsamifera													0.721	19.5	0.088	18.1	0.924	22.3	0.076	20.0
Populus tremuloides																	0.798	23.0	0.077	20.8
Thuja occidentalis	0.547	9.5	0.085	8.8	0.693	11.3	0.050	8.8	0.662	15.0	0.060	12.6	0.734	17.6	0.059	14.6	0.747	17.6	0.067	15.2

* Modelled tree height (m) at 30 cm dbh