Anatomy of white rings in trembling aspen and reconstruction of forest tent caterpillar outbreaks in the Duck Mountain region, Manitoba.

By

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A thesis submitted to

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Abstract

   Insect outbreaks in forest ecosystems are an important natural disturbance, and the
source of much timber loss. The forest tent caterpillar (*Malacosoma disstria* Hubner) is a
major defoliator throughout the distribution of trembling aspen (*Populus tremuloides*
Michx.), its preferred host. Forest tent caterpillar outbreaks have been shown to cause
reduced growth and even mortality in the past, and recently, the presence of 'white' rings
in trembling aspen have been linked to severe early season defoliation. While a good
correspondence between the formation of white rings and severe defoliation has been
found, white rings are, as yet, not described anatomically. In addition, white rings are
presumed to be useful in the reconstruction of past forest tent caterpillar outbreaks. A
study was undertaken to determine the difference between white rings and 'normal' rings
in trembling aspen. White rings were also used in the spatiotemporal reconstruction of
forest tent caterpillar outbreaks in the Duck Mountain Provincial Forest. To assess the
difference in white ring formation and other forest tent caterpillar characteristics among
vegetation and age classes, sites were sampled within four vegetation types and two age
classes.

   White ring development in the tree stem was found to occur uniformly around the
stem from the base, up to approximately 70% of the stem height at the time of white ring
formation. White rings were also found to be narrower and less dense than normal rings
and to have thinner fiber cell walls, smaller fiber diameter and a higher proportion of
fiber lumen than normal rings. It is speculated that the growth hormones within the stem,

and the re-allocation of reserves for re-foliation are affected by severe defoliation, causing a structural sacrifice.

White rings were associated with all major forest tent caterpillar outbreaks in the Duck Mountain Provincial Forest, as well as many of the smaller, suspected outbreaks. Major outbreaks in the Duck Mountain Provincial Forest occurred between 1939 and 1948, 1961 and 1965 and 1982 and 1985, with another suspected major outbreak occurring during the 1870s. Smaller possible outbreaks were also observed in the 1950s, 1970s and the 1990s. These outbreaks were also recorded in the balsam poplar (*Populus balsamifera* L.) and paper birch (*Betula papyrifera* Marsh.) chronologies, and white rings observed in these two species also corresponded with these periods of forest tent caterpillar outbreaks. The 1960s outbreak was different than all other outbreaks, occurring directly after a year of extreme drought, and spreading to the entire Duck Mountain Provincial Forest within a single year. The other major outbreaks were not associated with extreme drought events, and did not cause growth suppression in trembling aspen as severe as that produced during the 1960s outbreaks. In addition, during the 1960s outbreak, sites which were composed of trembling aspen and jack pine (*Pinus banksiana* Lamb.) recorded more severe growth suppression and white ring formation than any other stand type. The increased severity of forest tent caterpillar outbreaks in dry sites may become more important in a warmer climate, as has already been predicted. White rings, while being useful in the reconstruction of forest tent caterpillar outbreaks, must be used cautiously and in addition to other markers like

growth suppression, as they were not always present in trees from the same sites, nor did they occur in all sites in the Duck Mountain Provincial Forest.

Acknowledgements

Dedication

I dedicate this work to all the strong women in my life, especially my grandmothers, Elsie Edgar and Velma Sutton. I miss you both.

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1.0 General Introduction

1.1. Literature Review

1.1.1. Insect disturbances

Insect outbreaks are important natural disturbances in forest ecosystems. Timber loss in the boreal zone of Canada due to insect outbreaks is estimated to be 1.3 to 2.0 times greater per year than wildfire loss (Volney and Fleming 2000). From 1988 to 1992, timber loss to insect and disease in west-central Canada was 16.2 million m^3/year (Brandt 1995). In eastern Canada, the spruce budworm (*Choristoneura fumiferana* Clem.), which defoliated 69 million hectares between 1980 and 1996 (Simpson and Coy 1999), has been shown to negatively affect growth and survival of balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss) (Blais 1958; Zarnovican 1982; Ferguson 1985; Morin and Laprise 1990; Morin *et al.* 1993; Morin 1994). Studies done on the western spruce budworm (*Choristoneura occidentalis* Freeman), a related species in western Canada and the USA, have shown the negative impact of defoliation on Douglas fir (*Pseudotsuga menziesii* (Mirb.) growth (Alfaro 1985; Swetnam and Lynch 1993; Weber and Schweingruber 1995). Other important defoliating insects, which have caused reduced growth in North American trees, include the gypsy moth (*Lymantria dispar* L.) (Muzika and Liebhold 1999; Naidoo and Lechowicz 2001), the red pine shoot moth (*Dioryctria resinosella* Mutuura) (Hainze and Benjamin 1984); the balsam fir sawfly (*Neodiprion abietis* (Harr.)) (Piene *et al.* 2001), the larch sawfly (*Pristiphora erichsonii* (Htg.)) (Arquillière *et al.* 1990; Tailleux and Cloutier 1993; Girardin *et al.* 2001), and the western false hemlock looper (*Nepytia freemanii* Munroe) (Alfaro and Macdonald 1988).

In the prairie provinces of Canada (Alberta, Saskatchewan, Manitoba) and the Northwest Territories, major defoliators, other than the spruce budworm; include the jack pine budworm (*Choristoneura pinus pinus* Freeman), the larch sawfly, the large aspen tortrix (*Choristoneura conflictana* (F. Walker)) and the forest tent caterpillar (Malacosoma disstria Hubner) among others (Simpson and Coy 1999). According to Brandt (1995), the forest tent caterpillar, which caused 25% of the total timber loss, was among the top three groups of organisms causing the largest impacts in the prairie provinces from 1988 to 1992. Forest tent caterpillar defoliation covered 80.6 million hectares in central Canada between 1980 and 1996 (Simpson and Coy 1999). In the north-central United States, the forest tent caterpillar also ranks high when it comes to impact on forest productivity (see Witter 1979). Other insects affecting trembling aspen (*Populus tremuloides* Michx.) in the prairie provinces include the large aspen tortrix, a species which does not usually reach the same outbreak extent as the forest tent caterpillar (Ives and Wong 1988), the bruce spanworm (*Operophtera bruceata* (Hulst), more important in the western portion of the prairies, and the aspen serpentine leaf miner (*Phyllocnistis populiella* Chambers), which is not known to cause major adverse effects in host stands (Ives and Wong 1988; Perala 1990; Peterson and Peterson 1992).

1.1.2. Forest tent caterpillar life cycle

The forest tent caterpillar is a common leaf eater in the forests of Canada, especially the mixedwood boreal and the hardwood forests (Martineau 1984) and is found throughout the United States and Canada. Its distribution corresponds almost entirely

with the range of trembling aspen, its preferred host (Hanec 1966; Sippell and Ewan 1967; Witter 1979). Forest tent caterpillar defoliation provides a major stress for trembling aspen, and affects many other species such as sugar maple (*Acer saccharum* Marsh.), basswood (*Tilia americana* L.), red oak (*Quercus rubra* L.), bur oak (*Quercus macrocarpa* Michx.), paper birch (*Betula papyrifera* Marsh.), American elm (*Ulmus americanus* L.) and balsam poplar (Populus balsamifera L.) with little or no effects on the red maple (*Acer rubrum* L.) (Hodson 1941; Sippell and Ewan 1967; Hildahl and Campbell 1975; Ives and Wong 1988).

One generation of the forest tent caterpillar occurs per year, with the emergence of larvae occurring in synchronization with the bud break of the host plant (Hodson 1941; Rose 1958; Sippell and Ewan 1967; Ives and Wong 1988; Volney and Fleming 2000). The larvae experiences five larval instars within one generation. During each successive stage the size of the larvae increases and the amount of feeding necessary increases (Hodson 1941; Rose 1958; Hildahl and Campbell 1975). Young larvae feed on expanding buds and account for very little of the total defoliation, which occurs during the last larval stage (Sippell and Ewan 1967; Hildahl and Campbell 1975). Larvae begin to wander and forage for food during the 4th and 5th larval instar when food sources become depleted (Hodson 1941). Fitzgerald and Costa (1986) have shown that young colonies can wander extensively and that they can leave pheromone based trails, which aid in guiding siblings to new food sources. Approximately 5-6 weeks elapse between emergence of the larvae until the appearance of the first "tent' cocoons (Hodson 1941). By mid-June (in most areas), larvae have matured enough to begin forming their silk

cocoons among the leaves and twigs of trees, shrubs and other vegetation, or occasionally on buildings or other man-made structures (Hodson 1941; Rose 1958; Sippell and Ewan 1967; Ives and Wong 1988). The pupa stays in the cocoon for 8-12 days; the beige/brown moth then emerges which in turn lays an egg band around young host twigs (Rose 1958; Sippell and Ewan 1967; Martineau 1984). The adult forest tent caterpillars are active fliers and can cause rapid expansion of the infested areas within a year or two. Hodson (1941) observed forest tent caterpillar moths which had been attracted to building lights located 3 km away from the outbreak area. Though the forest tent caterpillar occurs throughout North America, reproductive characteristics have been shown to vary from north to south. Parry *et al.* (2001) have shown that populations in the Southern United States have much smaller clutch sizes than populations in Manitoba. However, offspring of the Manitoban populations have been found to be significantly bigger than those from the southern United States.

Forest tent caterpillar outbreaks generally occur on a regular basis every 10-12 years (with a range of 6-16 years) in any one area and can last in the same area for 3 to 6 years (Duncan and Hodson 1958; Hildahl and Campbell 1975; Martineau 1984; Ives and Wong 1988). The causes of initiation and cessation of outbreaks of the forest tent caterpillar are not well understood, but it is thought that these events are most likely related to temperature and weather fluctuations (Hodson 1941; Blais *et al.* 1955; Hildahl and Campbell 1975; Daniel and Myers 1995). Forest fragmentation (heterogeneity) has also been found to be a good predictor of outbreak duration along with elevation (Roland 1993; Cooke and Roland 2000). Results suggest that some unidentified variable could be

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driving the spatial control on outbreak duration and forest fragmentation may affect the

spatial nature of this unidentified factor (Cooke and Roland 2000). Parasitism by other

organisms may also lead to the decline of forest tent caterpillar outbreaks (Parry 1995).

Forest fragmentation may also affect the ability of parasitic organisms to disperse (Cooke

and Roland 2000). It has also been suggested that intrinsic factors such as larval

gregariousness and adult feeding capacity play a role in all Lepidoptera population

behaviors (Miller 1996).

During an outbreak, large populations of forest tent caterpillars are able to

completely strip trembling aspen of their leaves before foliation is complete, as the first

larvae appear while leaves are beginning to unfold (Hodson 1941; Sippell and Ewan

1967). Although refoliation by trembling aspen occurs after the initial defoliation and

mortality is rare, repeated attacks by the forest tent caterpillar can make host trees

susceptible to other diseases or stresses (Duncan and Hodson 1958; Sippell and Ewan

1967; Hildahl and Campbell 1975), such as drought (Hogg and Schwarz 1999; Hogg *et

al.* 2002a). It is generally acknowledged that direct mortality due to forest tent caterpillar

defoliation is rare (Sippell and Ewan, 1967; Hildahl and Campbell, 1975; Ives and Wong,

1988; Hall *et al.*, 1998). However, it has been shown that repeated defoliation of

increasing severity can lead to mortality (Hildahl and Reeks 1960; Churchill *et al.* 1964).

Growth loss due to forest tent caterpillar defoliation is well documented (Churchill *et al.*

1964; Hildahl and Campbell 1975; Hogg and Schwarz 1999), as well as branch and twig

mortality (Ives and Wong 1988). Radial growth reduction has been found to be

dependent on the severity of defoliation. Reduced growth in trembling aspen has also

been observed after artificial defoliation (Jones *et al.* 2004). In fact, Rose (1958) reported in one study that radial growth in completely defoliated trees ceased at defoliation and did not restart during the same year, even after refoliation. However, Hildahl and Reeks (1960) and Churchill *et al.* (1964) found that one year of severe defoliation only depressed radial growth during the year of defoliation. Trees which experienced one year of light and two years of severe defoliation, required one or two extra years to recover radial growth.

1.1.3. Forest tent caterpillar outbreaks and climate

Insects may be partly responsible for declining host stands at the southern margins of host species ranges (Volney and Fleming 2000), a factor which may become important with increasing global temperatures and climate change. Hogg and Schwarz (1999) found that defoliation was the most important factor in reducing basal area growth of trembling aspen in declining stands in Saskatchewan. They also found that changes in moisture played a significant role in basal area growth reduction. Forest tent caterpillar activity was also found to be involved in dieback of aspen stands in northwestern Alberta (Hogg *et al.* 2002a) and sugar maple stands in southern Québec (Payette *et al.* 1996). Trembling aspen may show only a limited compensatory response after defoliation, as responses to 50% and 98% defoliation showed similar response levels (Hart *et al.* 2000). Trembling aspen productivity may be negatively affected if increased severity and frequency of forest tent caterpillar defoliation occurs due to increasing temperatures (Hart *et al.* 2000). Hogg and Hurdle (1995) have speculated that increased temperatures would

reduce the extent of the forested zone due to drier conditions. An increase in temperature due to climate warming may also lead to increased mortality due to drought and defoliation in many boreal forest stands and aspen parkland areas (Hogg 2001).

1.1.4. Trembling aspen and white spruce autecology

Trembling aspen is a deciduous member of the family *Salicaceae*. The distribution of trembling aspen is transcontinental from the Atlantic to the Pacific Ocean and from the northern tree limit to the northeastern United States (Perala 1990; Sims *et al.* 1990). Trembling aspen grows across Canada on a variety of soils, from shallow and rocky to deep and loamy (Perala 1990; Sims *et al.* 1990; Peterson and Peterson 1992). Trembling aspen can reproduce sexually, but is best known for vegetative reproduction through root suckers (rhizomes), forming large clones. Its ability to reproduce vegetatively allows it to quickly revegetate sites which have been disturbed, such as in the case of a fire or even harvesting, and where the soil has become bare (Perala 1990; Sims *et al.* 1990). Seedlings are quick to take over a disturbed area and growth is very rapid, especially during the first 20 years (Perala 1990; Sims *et al.* 1990). Trembling aspen as a whole is a medium sized, fast-growing species and typically grows in large, genetically identical clones, which may reach a hectare or more in size. (Perala 1990; Sims *et al.* 1990; Peterson and Peterson 1992). Trembling aspen provides habitat for wildlife such as deer, elk and black bears, which require young forests, as well as providing aesthetical values for camping and other recreational activities (Perala 1990;

Peterson and Peterson 1992). Trembling aspen is also valued as a firewall because of its low flammability (Perala 1990).

White spruce is a member of the coniferous family *Pinaceae*. The distribution of white spruce is transcontinental, occurring from Newfoundland across Canada to the Yukon (Nienstaedt and Zasada 1990; Sims *et al.* 1990). It is found as far north as the northern tree line, where it grows with black spruce reaching almost to the Arctic Ocean, and as far south as northern Minnesota and Wisconsin (Nienstaedt and Zasada 1990; Sims *et al.* 1990). White spruce can be found growing in highly variable climatic conditions on a variety of soils such as those with glacial, lacustrine, marine or alluvial origin (Nienstaedt and Zasada 1990; Sims *et al.* 1990). Sexual reproduction occurs via small winged seeds, which develop in cones and in the north, vegetative reproduction may also occur (Nienstaedt and Zasada 1990; Sims *et al.* 1990). White spruce is a shade tolerant species and is often found growing under pioneer species such as trembling aspen, where it grows slowly until a disturbance opens the canopy and the availability of light and other resources increases (Nienstaedt and Zasada 1990; Sims *et al.* 1990).

1.1.5. Basic plant anatomy and physiology

The three major tissue types in vascular plants, the dermal, the vascular and the fundamental tissue, develop from the apical meristem, a localized region of growth present from germination (Esau 1953; Mauseth 1988). One of the three tissues, the vascular tissue, is composed of phloem and xylem and in some plants includes a

secondary meristem called the vascular cambium. In woody plants, the vascular cambium region is a continuous ring-shaped cylinder that includes the active cambial cells and several derivatives on both the inside and outside of the cambium (Esau 1953; Morey 1973). The vascular cambium itself is composed of two types of cells, elongated fusiform initials and ray initials (Mauseth 1988). Fusiform initials give rise to the axial secondary xylem cells (woody part of the stem), such as parenchyma, tracheids, fibers and vessels and to the axial secondary phloem cells (part of the bark), such as companion cells in Angiosperms and sieve albuminous cells in Gymnosperms (Esau 1953; Morey 1973). Ray initials may produce uniseriate or multiseriate rays in the secondary xylem and secondary phloem. Rays provide a horizontal connection so that the conduction of resources between the phloem and the xylem cells may occur; they also provide storage for carbohydrates and nutrients.

Due to the seasonal variation in climate, vascular cambium activity does not remain constant throughout the year. In general, much activity occurs for a few weeks after initiation in the spring, followed by a slowing of cambium activity for the rest of the growing season, until dormancy occurs in the late fall (Schweingruber 1996). Cambial activity is controlled by the production of hormones, such as the production of auxins in the developing leaves (Kozlowski and Pallardy 1997). Cambial growth therefore begins below leaf buds and occurs for a longer period in the upper portions of the stem, due to the proximity to the hormone source. Other hormones, such as gibberellins and cytokinins are also involved in the regulation of cambial activity and the relative concentration of each hormone changes throughout the growth season (Kozlowski and

Pallardy 1997). Because of this seasonality, earlywood xylem cells, which develop early in the growing season, are large and have relatively thin cell walls and latewood cells, which develop later in the season, become progressively smaller, finally developing very thick cell walls. The difference in size and cell wall thickness of these cells provide distinct delimitations between years of xylem growth, known as annual growth rings (Mauseth 1988; Schweingruber 1996). Several annual rings may remain functional during the growing season and are involved in the transport of water, this portion of the stem is known as the sapwood. The older portion of the xylem, near the center of the stem becomes non-functional and is termed the heartwood. All stores of food are removed from the sapwood as it becomes non-functional, as the primary function of the heartwood is mechanical support (Esau 1960; Mauseth 1988).

Cell development in the plant is divided into three distinct, but integrated processes; cell division, cell enlargement and cell differentiation (Esau 1953, Wardrop and Bland 1959; Wardrop 1965). Cell division, which occurs at the meristem, increases the number of cells in the plant body and may be genetically controlled (Greulach 1973). Cell enlargement is required after division for plant growth to occur. Enlargement requires great flexibility in the cell walls and the increase in cell length and width requires a steady supply of growth hormones, such as auxins, gibberellins and cytokinins and resources, such as cellulose, to be assimilated into the growing cell wall. These basic cells begin to specialize during the cell differentiation phase, which involves the deposition of secondary cell walls, a change in shape and other specializations. During the last phase of differentiation in woody plant cells, the cell wall is often cemented by

lignin, a stable rigid polymer, which provides added strength to the wood (Wardrop and Bland 1959; Mark 1967; Morey 1973).

Plant growth hormones (phytohormones) play an important role in plant growth and development (Morey 1973; Aloni 1991). These hormones may be produced in one portion of the plant, but affect cells in another. The synthesis of auxin, the most widely studied hormone, occurs mostly in areas of active meristematic activity such as in leaf buds and can be synthesized in expanding tissues, such as young leaves (Leopold 1955; Morey 1973). The hormone is translocated basipetally, from the crown towards the base, and the concentration of auxin in the stem decreases from the top to the bottom and is much lower in the root (Roberts *et al.* 1988; Aloni and Zimmerman 1983; Aloni 1991). Auxin is responsible for cell differentiation and enlargement and is probably involved in the incorporation of resources into the growing cell wall (Morey 1973). Other phytohormones, such as ethylene, gibberellins and cytokinins, are also present in the plant body and affect different processes within the plant (Greulach 1973; Little and Savidge 1987; Roberts *et al.* 1988; Aloni 1991). For instance, ethylene was often found to work as an inhibitor of some processes stimulated by auxin (Greulach 1973). Gibberellins are responsible for the breaking of dormancy in the apical meristems, increased cell division and have some small effect on cell enlargement, but very little effect on differentiation (Morey 1973). Cytokinins have been found to be very important in cell division. They may also play a small role in cell enlargement and differentiation (Morey 1973; Little and Savidge 1987). Although plant hormones affect many processes within the plant, the relative concentration and the interaction of one hormone with

another is thought to be more important than the actual concentration of one hormone on any one process (Kozlowski and Pallardy 1997).

1.1.6. Trembling aspen wood anatomy

Although the arrangement of tissues is the same in both softwoods and hardwoods, the cellular composition of the xylem is quite different. The axial system of cells in the xylem of conifers, also referred to as softwoods, produced by fusiform initials, is comprised entirely of tracheid cells (Morey 1973; Mauseth 1988). Tracheids in general are much longer, between 3 and 4 mm in length (Morey 1973), than conducting cells in hardwood xylem. In hardwood species, vessel elements form long tube-like vessels to provide water conductance and fibers provide structural support (Esau 1960; Mauseth 1988). The axial systems of hardwood species are also composed of tracheids and axial parenchyma (Esau 1960; Mauseth 1988; Wheeler *et al.* 1989). In hardwood species, different types of wood are formed, depending on the type and pattern of cells, which form (Esau 1953; Morey 1973; Schweingruber 1996). Ring porous wood forms when much larger vessels are formed in the earlywood than in the latewood, forming a well-defined ring (Wheeler *et al.* 1989). Diffuse porous wood is characterized by vessels, which remain equal in size throughout the annual growth ring (Wheeler *et al.* 1989). Trembling aspen, a diffuse porous species, is characterized by numerous (more than 76 vessels/ mm^2) small vessels (less than 100 microns in diameter), which can be solitary or in multiples. This species is also characterized by indistinct terminal parenchyma cells, which delimit the transition from one ring to the next and very fine, uniseriate rays

(Panshin and de Zeeuw 1970). Fibers in trembling aspen are generally thin to medium thick walled cells, which reach sizes of 16 to 25 microns.

1.2 Introduction to Thesis

1.2.1. Introduction

Although trembling aspen is the most important deciduous species in the boreal forest zone, it has only recently been recognized as a commercially important species (Peterson and Peterson 1992) and there is limited information about the effects of forest tent caterpillars on trembling aspen. Trembling aspen is a major resource in the Duck Mountain Provincial Forest (DMPF), where it is harvested for use in the production of Oriented Strand Board (OSB) by Louisiana Pacific Inc. (Manitoba Conservation Forestry Branch 2004). Although many insects and diseases affect white spruce, the forest tent caterpillar does not defoliate this species. Since trembling aspen and white spruce grow in mixed stands, and a good correlation has been found between trembling aspen and spruce chronologies (Cooke 2001; Girardin and Tardif 2005), white spruce can be used as a non-host species comparison to trembling aspen.

1.2.2. White rings and outbreak reconstruction

Light rings in conifers have been well documented. They were defined as rings with reduced latewood cell wall thickness compared to normal rings and have been observed in many coniferous species such as larch (*Larix laricina* (Du Roi) K.Koch)

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(Liang *et al.* 1997; Girardin *et al.* 2001; Case and MacDonald 2003), jack pine (Pinus banksiana Lamb.)(Gill 1930; Volney and Mallet 1992; Tardif *et al.* 2004), black spruce (*Picea mariana* (Mill.) B.S.P.) (Arseneault and Payette 1998; Wang *et al.* 2000), white spruce (Szeicz 1996) and timberline spruce (*Picea abies* (L.) Karst.) (Gindl 1999). The term 'white ring' has been used to describe white bands found in ring porous species such as white (*Fraxinus americana* L.) and green ash (Fraxinus pennsylvanica Marsh.) (Yanosky 1984). Yanosky (1984) showed that small bands of large, thin walled cells in the latewood of ring-porous species formed after a late season growth increase due to late season root flooding. Recently, 'white rings' have been observed in trembling aspen (Hogg and Schwarz 1999). These white rings have only been reported in a few cases in Saskatchewan (Hogg and Schwarz 1999) and Alberta (Cooke 2001; Hogg *et al.* 2002a). White rings have also been observed in Manitoba and Québec in trembling aspen, balsam poplar and white birch (F. Conciatori, pers. communication). White rings are unlike light rings found in conifers and ring porous species, and differ from normal growth rings in that both early and latewood xylem appear to be white (Hogg and Schwarz 1999; Cooke 2001). Cooke (2001) concluded that this was fair evidence that white rings were caused early in the year, most likely by forest tent caterpillars and not by drought, which usually occurs near the end of the growing season. Hogg and Schwarz (1999) and Hogg *et al.* (2002a) found that there was a good correspondence between the presence of white rings and the recorded history of forest tent caterpillar defoliation. Hogg *et al.* (2002b) were able to experimentally produce white rings in trembling aspen clones by severe artificial defoliation (98-100%) early in the growing season, closely representing damage done by severe forest tent caterpillar larvae defoliation. It has been suggested that white rings

may be used in the reconstruction of past forest tent caterpillar outbreaks (Hogg and Schwarz 1999; Cooke 2001; Hogg *et al.* 2002b).

1.2.3. Objectives and hypotheses

The purpose of this study was to add to the growing knowledge of the impact of forest insects on tree growth. The first objective was to characterize the distribution of white rings within the stem of trembling aspen trees and to determine which anatomical characteristics distinguish them from normal growth rings. A comparison of white rings formed near the base of the tree and near the crown of the tree was also performed, to determine if there is a change in white ring anatomy within the tree. This study will provide a quantitative definition of white rings in trembling aspen. It is hypothesized that white rings will be well distributed throughout the stem of trembling aspen and that there will be no difference in white ring distribution among the trees. It is hypothesized that the cells found in the white rings will have reduced cell wall thickness as compared to 'normal' growth rings. The second objective was to document the spatial and temporal extent of forest tent caterpillar activity in the DMPF from the late 19th century to the present, using tree ring analysis. Using methods similar to those described in Swetnam *et al.* (1985), host and non-host chronologies will be compared to identify specific periods of reduced growth in the host species, which could be related to defoliation events. The presence of white rings in the trembling aspen chronology will also be used in combination with the host, non-host comparison. Tree ring chronologies will also be constructed throughout the DMPF for different stand types and age classes. This will

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allow us to determine if the susceptibility to insect outbreaks varies with stand

composition or age. It is hypothesized that older stands will be more severely affected by

FTC outbreaks and that pure trembling aspen stands will be affected more frequently than

mixed stands, therefore, affecting the spatial distribution of an outbreak within the forest.

2.0. Distribution and anatomical characteristics of white rings in *Populus tremuloides* Michx. [1]

2.1 Abstract

'White rings' have been reported to occur within trembling aspen (*Populus tremuloides* Michx.) during years of intense early defoliation by the forest tent caterpillar (*Malacosoma disstria* Hbn.). This study was undertaken to 1) assess the distribution of white rings within trembling aspen stems and 2) to quantify the anatomical differences between white rings and the 'normal' rings formed in the previous year. Both stem analysis and image analysis were used. Several cross sections from six trees were dated and the presence of white rings on each disc was recorded. The development of white rings from the base up to about 70% of stem height was found to be uniform. Results from the comparison of eleven white and normal rings indicated that white rings were narrower and less dense than normal rings. The anatomical variable with the most discriminating power was found to be the average fiber cell wall thickness. White rings have smaller fiber diameter with little secondary cell wall thickening resulting in a higher proportion of fiber lumen. Possible mechanisms involved in the formation of white rings are discussed. It is speculated that defoliation affects the growth hormone complex inducing earlier cessation of xylem growth and reallocation of reserves to the production of new foliage. The occurrence of white rings in many diffuse-porous species stresses the

potential for identification of periods of intense defoliation episodes and increased interest in the dendroecology of diffuse-porous species may confirm their widespread occurrence.

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2.2 Introduction

Forest pests are able to interfere with physiological processes involved in tree growth (Kozlowski 1969). They can alter cell development by regulating hormone activity, resource availability, water relations or by modifying a metabolic pathway (Roberts 1983). Physiological interruptions caused by severe defoliation have been known to cause reduction in radial growth (e.g.; Rose 1958; Leininger & Solomon 1994; Naidoo & Lechowicz 2001), height growth (Hainze & Benjamin 1984), volume growth (e.g.; Piene *et al.* 2001) and aerial tree biomass growth (e.g.; Tailleux & Cloutier 1993).

Although defoliating pests feed on the crown, effects of such an attack can be felt in other parts of the tree (Kozlowski 1969). Defoliation can cause a reduction in the quality and quantity of food constituents of the tree (Parker & Houston 1971). Reduced availability of carbohydrates and decreasing light intensity has been shown to affect stem xylem density (cell wall thickness) (Richardson & Dinwoodie 1960; Dinwoodie & Richardson 1961; Richardson 1964). Richardson (1964) also found that defoliation in the apical zone of sitka spruce (*Picea sitchensis* (Bong.) Carr.) seedlings almost entirely interrupted xylem formation. Increased defoliation intensity in the lower part of the crown reduced tracheid cell wall thickness and lumen diameter over the whole length of the seedling stem (Richardson 1964). Harper (1913) found that defoliation by the larch sawfly (*Pristiphora erichsonii* (Htg.) affected latewood formation in European larch (*Larix decidua* Mill.) and in some cases caused xylem growth to cease especially at the base of the stem. *Light rings* with poorly developed latewood and reduced cell wall thickening were also reported in tamarack (*Larix laricina* (DuRoi) K. Koch) following defoliation (Liang *et al.* 1997). Hildahl & Reeks (1960) and Churchill *et al.* (1964) found

that one year of severe defoliation of trembling aspen by the forest tent caterpillar depressed radial growth only in the year of defoliation. Jones *et al.* (2004) found that trembling aspen that were artificially defoliated ceased radial growth earlier than non-defoliated trees.

The forest tent caterpillar is an important forest pest in the Canadian boreal forest and its host, trembling aspen, is the most abundant and widely distributed deciduous species in Canada (Peterson & Peterson 1992). Recently, white (light coloured) rings (Fig. 2.1a, b) have been observed in trembling aspen from Saskatchewan (Hogg & Schwarz 1999) and Alberta (Cooke 2001; Hogg *et al.* 2002a). They have also been noted in balsam poplar (*Populus balsamifera* L.) (Fig. 2.1c) (Hogg & Schwarz 1999; Hogg *et al.* 2002b). They have been observed in Manitoba and North-western Quebec in trembling aspen and in paper birch (*Betula papyrifera* Marsh.) (Fig. 2.1d) (F. Conciatori, pers. comm., 2003). In trembling aspen, the occurrence of white rings has been associated with local written forest tent caterpillar defoliation records (Hogg & Schwarz 1999). White rings have also been experimentally induced in trembling aspen by artificial defoliation early in the growing season (Hogg *et al.* 2002b). X-ray densitometry results presented by Hogg *et al.* (2002b) indicated a lower density in white rings as compared to normal growth rings and a reduction in ring width to 20% of the previous years growth. It should be noted that the term 'white ring' was also used by Ritter *et al.* (1993) when describing the appearance of gelatinous fibers in the tension wood of balsam poplar and should be regarded as a distinct phenomena. *In ring porous species, white coloured bands of large, thin walled cells in the latewood have also been referred to as*

white rings (Yanosky 1984). These 'white rings' have been associated with late season

root flooding and should also be regarded as a separate phenomena.

Although much is known about the physiological impact of defoliation on wood

formation in conifer species, relatively little is known about the effects of defoliation on

wood formation in hardwood species and especially in trembling aspen. The objectives

of this study were 1) to determine the distribution of white rings within the stem of

trembling aspen and 2) to quantify the anatomical differences between the wood formed

during normal growth years and during white ring years. Possible physiological

processes related to white ring formation will be reviewed. We hypothesized that along

with ring width, cell wall thickness of fibers in the white rings will be reduced and that

vessel characteristics will remain constant. We also hypothesized that white rings would

appear consistently throughout the tree stem.

2.3 Materials and Methods

2.3.1 Study area

Study samples were taken from the Porcupine Hills and the Duck Mountain

Provincial Forest, which form part of the mountain park system in west-central Manitoba,

Canada (Corkery 1996). The study area is located in the subhumid mid-boreal ecoregion

(Zoladeski *et al.* 1998) and provides a transition zone between the boreal forest to the

north and the aspen parkland and prairie to the south. Eight tree species dominate the

landscape; trembling aspen, white spruce (*Picea glauca* (Moench) Voss), balsam poplar,

black spruce (*Picea mariana* (Mill.) BSP), paper birch, jack pine (*Pinus banksiana*

Lamb.), balsam fir (*Abies balsamea* (L.) Mill.) and tamarack (Rowe 1956). The landscape includes many small lakes and streams as well as black spruce and tamarack dominated wetlands.

2.3.2 Sample collection and preparation

Dominant and co-dominant trembling aspen trees were felled by Louisiana Pacific Inc. during the winter of 2001-2002. After a preliminary sanding, six trees containing white rings were chosen for stem analysis. White rings were identified as rings with an obvious lighter xylem colouring than the surrounding rings. This whitish colour may be *partially caused by the* accumulation of wood dust in the pores during sanding because white rings were difficult, if not impossible, to see in unprocessed samples.

Cross-sectional discs were cut at the base, 0.33m, 0.67 m, 1.0m, 1.3m, 2.6m and every 1.3m, generally to a height of 18.2 or 20.8m. After drying, the discs were carefully sanded at the 80, 180, 220, 320, 400 and 600 sandpaper grit levels. The age of each disc was determined along four radii (north, east, south, west) using a binocular microscope. A modified version of the skeleton plot described in Yamaguchi (1991) was used to identify pointer years and to reduce potential dating errors. The presence of white rings on each of the discs and in each of the 4 radii was recorded. In addition, the height of the stem at the time of white ring formation was estimated by interpolating between the known disc heights and ages.

From the 19 white ring years identified among the six trees, eleven were chosen for anatomical analysis. The growth rings formed in the year previous to each white ring were also selected for analysis. These rings served as controls and were assumed to be unaffected by the factors responsible for white ring formation, although total lack of defoliation effects during formation of these normal rings cannot be guaranteed. Each white ring was thus paired with the previous year ring for comparison purposes and each of the eleven ring pairs were analyzed at both breast height (1.3m) and at 3.9m or 11.7m depending on the height of the tree at the time of white ring formation. Samples taken at 1.3m were labelled as low and samples taken higher along the stem were labelled as high. Both heights were studied to evaluate differences in white ring anatomy that could be related to an aging cambium or the proximity to the stem apex. In total, 44 rings (11 ring years from 2 ring types at 2 heights) were selected for anatomical analysis.

2.3.3 Microtome sectioning

Sectioning and staining were done using techniques modified from Ruzin (1999) and Chaffey (1982). Small wood blocks, approximately 0.5 cm^3 in size, were cut from the west radius of each disc using a saw and chisel. Each block contained a ring pair and several surrounding rings. Thin cross-sections (15-17μm) were cut using a rotary microtome with disposable blades adjusted to an angle of approximately 15 degrees. An 0.05% astrablue stain was applied to each sample for 1 minute as a cellulose and hemicellulose stain and counterstain to the 1% safranin stain (Chaffey 1982), which was applied for 15 minutes. All thin sections were then washed in successive ethanol baths

(50, 95 and 100%) until all trace of excess stain (and water) was gone. Thin sections were further dehydrated using clearing solvent (Limonene), before being permanently mounted on microscope slides with cover slips using permount®. The finished slides were placed on an electric warming plate at approximately 50°C and were firmly secured using a small magnet to prevent bubble formation under the cover slip. The samples were left for several weeks to ensure proper drying of the permount®.

2.3.4 Image analysis

Each sample ring image was captured separately using a Nikon compound microscope equipped with a Polaroid digital camera linked to a computer. Images were captured (.tiff format) in black and white at a 1200X1500 resolution, using a green filter for maximum contrast. The photographic area was maximized by capturing an image area between two parallel rays located as close as possible to the upper and lower boundary of the photographic field of the camera (maximum 297 µm height). Photographs were taken at 400X magnification and care was taken to avoid capturing areas with broken or largely distorted cells. When multiple photographs were taken, they were merged to reconstitute the entire ring from earlywood to latewood. A total of 44 rings were analyzed.

The WinCELL Pro 2001a program (Régents instruments Inc., 2001) was used to measure several anatomical features within each captured image. Total fiber lumen area (TFLA), total vessel lumen area (TVLA), average fiber lumen area (AFLA), average

vessel lumen area (AVLA), the number of fibers (NF) and vessel elements (NV) were measured using the image analysis software. Grouped vessels, instead of being considered as a 'pore multiple' (Panshin & de Zeeuw 1970), were considered individually as solitary vessels. In addition, average fiber cell wall thickness (AFWT) and average fiber diameter (AFD) were determined along two radial files. One radial file was randomly selected in both the upper and lower portion of the image area. When the radial file was not continuously composed of fibers, due to the presence of numerous vessels or distorted cells, the next radial file was chosen using a predetermined pattern. *Average fiber diameter (AFD) was the average diameter of the fiber lumen plus the respective two-sided cell wall.* On each image, ten vessels were randomly chosen without replacement for measurement. Average vessel cell wall thickness (AVWT) and average vessel diameter (AVD) were calculated similarly to AFWT and AFD. Total ray area (TRA) was also calculated by summing the area of each ray, determined by multiplying the length of each ray by the average of 3 ray width measurements. Ring width (RW) was calculated using the average of three ring-width measurements. Image area (IA) was then calculated by multiplying ring-width and the average of three image heights measured between the upper and lower ray boundaries. This calculation yielded a rectangular approximation of the image area. Image area (IA) was thus considered as the area of the image bounded by the upper and lower parallel rays and by the ring boundaries on the right and left side of the image. Image area dimension varied from sample to sample (mean 0.163 mm^2 ± 0.120 standard deviation) depending on ring width and distance between parallel rays.

Cell wall area percentage (CW%) was estimated using a formula modified from

Park *et al.* (1992) as follows:

$$CW\% = [1 - (TFLA + TVLA) / (IA - TRA)] * 100,$$

which is the inverse of the area of the image through which light may pass. Total ray area

(TRA) was subtracted from the image area because each image did not necessarily have

the same number of rays. Cell wall area percentage has been shown to have a high

correlation with wood density (Park *et al.* 1992). In addition, five variables were

standardized by dividing their values by IA to account for the significant difference in

ring width between the normal and white rings. The following variables were

standardized: TFLA*, TVLA*, NF*, NV* and TRA*. It should be noted that these

standardized values were not calculated per square mm of wood tissue but per unit

surface area (mm^2) minimizing the importance of the ray tissue (see above). In total, 12

anatomical variables were kept for analysis (AFWT, AFD, TFLA*, AFLA, NF*, AVWT,

AVD, TVLA*, AVLA, NV*, TRA*, CW%) along with 2 'ring' variables (RW, IA).

2.3.5 Statistical analysis

Principal component analysis (PCA) was conducted using CANOCO 4.02 for

Windows (Ter Braak & Smilauer 1997). The input matrix included 14 descriptors and 44

objects. PCA was calculated using a correlation matrix so that all descriptors contributed

equally to the separation of the objects in the PCA space, regardless of scale (Legendre &

Legendre 1998). Discriminant analysis, which is a method of linear modeling (Legendre

& Legendre 1998), was used to determine the subset of anatomical descriptors that best

discriminate among the four ring type- height combinations. The four groups were

defined as low white ring (LW), high white ring (HW), low normal ring (LN) and high normal ring (HN). An interactive backward stepwise procedure was used to eliminate discriminators under an f-to-remove and an f-to-enter value of 4.00. Two-way analysis of variance (ANOVA) was also performed for each of the 14 variables to determine the effects of ring type (white or normal), height (low or high) and the interaction term (ring type versus height). Both discriminant analysis and ANOVA were performed using SYSTAT 9.01 for Windows (SPSS 1998).

2.4 Results

2.4.1 White ring distribution

White rings occurred mainly in single years, with a few instances of multiple white rings appearing in 2 or 3 successive years (Fig. 2.2). Tree 3 had successive white ring formation in 1957 and 1958, while tree number 6 had successive years of white ring formation from 1938 to 1940. Two or more white rings were found in most sample trees, with the exception of tree 1 and 2. White ring formation is present both in the oldest part of the tree (near the pith) and in the youngest portion of the tree (near the cambium). All trees recorded white ring formation in either 1962, 1963 or 1965. On average, white ring width reached 30% of the width of the previous years growth. A recovery within one or two years was noticeable in most cases. White ring development varied with stem height in the 6 trees (Fig. 2.3). White ring development near the base of the tree was more uniform than near the apex of the tree. The occurrence of white rings around the circumference became more variable after reaching 70% of total tree height at the date of individual white ring formation.

2.4.2 PCA

The result from the PCA indicated that the first four principal components represented respectively 33.8%, 29.6%, 10.1% and 8.5% of the total variance for a cumulative total of 82.0% (Fig. 2.4). Only the first two principal components are presented. The PCA correlation biplot showed that the 22 white rings and the 22 normal rings were clearly separated, with the former occupying primarily the positive portion of PC-2 (Fig. 2.4). Ring-width (RW), image area (IA), cell wall percentage (CW%), average fiber cell wall thickness (AFWT) and, to some extent, average vessel cell wall thickness (AVWT) were positively inter-correlated as indicated by the narrow angle among their vectors. The projection of the 44 objects along the axis created by these vectors indicates that white rings have lower values than normal rings for these variables. Although no clear distinction was observed between low and high rings within either ring-type (Fig. 2.4), a slight separation is visible with the high samples occupying primarily the positive portion of the axis created by the total vessel lumen area (TVLA*) and number of vessels (NV*) vectors. This indicates that ring and anatomical characteristics were similar within each ring-type regardless of height, with the exception of the tendency for a higher number of vessels and a larger proportion of vessel lumen area in high samples.

The PCA biplot also indicated that the average vessel diameter (AVD) and the average vessel lumen area (AVLA) were positively correlated and were both negatively associated with total vessel lumen area (TVLA*) and number of vessels (NV*) (Fig. 2.4).

Images with a large vessel density and proportion of vessel lumen area had proportionally lower average values for vessel diameter and vessel lumen area. In addition, total fiber lumen area (TFLA*), average fiber lumen area (AFLA) and average fiber diameter (AFD) were also negatively correlated with the number of vessels (NV*) and total vessel lumen area (TVLA*). A larger number of vessels, with proportionally larger lumen area was associated with smaller fibers and a lower proportion of fiber lumen area.

2.4.3 Discriminant analysis

The discriminant analysis of the four predetermined groups (LN, HN, LW, HW) resulted in a highly significant model (F = 10.567, p< 0.0001). The significant discriminating variables, following backward stepwise analysis were AFWT (F-to-remove = 23.84), AVD (F-to-remove = 7.37), NV* (F-to-remove = 6.15) and AFD (F-to-remove = 4.30). However, jacknife classification of the 44 rings using *all four* discriminating variables only led to the correct classification of 64% of the rings (Table 2.1a). The anatomical variables measured were not able to discriminate between heights within the two ring types. From Table 2.1a it can be observed that correct classification of normal and white ring-types still occurred in most cases regardless of height. A second discriminant analysis was thus conducted using only the 2 ring-types. The new discriminant model was also highly significant (F = 34.080, p< 0.0001). The significant variables following backward stepwise analysis were AFWT (F-to-remove = 40.37), AVD (F-to-remove = 11.17), NV* (F-to-remove = 10.45), AFLA (F-to-remove = 9.71), CW% (F-to-remove = 5.95) and AFD (F-to-remove = 5.01). Jacknife classification of the samples into the two groups using the discriminating variables led to correct classification

100% of the time (Table 2.1b). The anatomical variable found to have the most discriminating power between ring-types was average fiber wall thickness (AFWT).

2.4.4 Two-way Anova

The two-way ANOVA results showed no significant interaction between ring-type and height for any of the 14 variables and allowed individual testing of our two factors. The results revealed that white rings had significantly lower average fiber wall thickness (AFWT) and average fiber diameter (AFD) compared to normal rings (Table 2.2). White ring images were also characterized by a higher fiber lumen ratio (TFLA*). The lack of cell wall thickening in fibers and the higher fiber lumen ratio was further illustrated by significantly lower cell wall percentage (CW%) (Table 2.2). In addition, ring-width (RW) and image area (IA) were significantly smaller in white rings. No significant differences at $p<0.05$ were observed between the two ring-types when comparing vessel characteristics.

Fiber characteristics were also shown to significantly differ with respect to height (Table 2.2). Rings sampled at 1.3m had a significantly higher average fiber diameter (AFD) and average fiber lumen area (AFLA), which resulted in a higher fiber lumen ratio (TFLA*). This indicates that larger fibers were found at 1.3m independent of cell wall thickness or number of fibers. Samples taken at 1.3m were also found to have a significantly lower vessel density (NV*) vessel lumen ratio (TVLA*) and total ray area (TRA*) than those taken from higher in the stem. No other significant ($p<0.05$) differences were found between heights for the vessel and ring characteristics.

2.5 Discussion

2.5.1 White ring persistence, distribution and ring-width

Our results indicated that white ring formation can occur in consecutive years, but this was less common than single-year occurrences. The two major periods of white ring formation identified in our sampled trees (1938-1941 and 1962-1963) corresponded with known records of forest tent caterpillar outbreaks in the region (E.H. Hogg, per. comm. 2003). As shown by Hogg *et al.* (2002b), white ring formation occurs in trembling aspen trees undergoing severe defoliation early in the growing season. Forest tent caterpillar defoliation often occurs for 3 to 6 successive years (Hildahl & Campbell 1975; Ives & Wong 1988) and successive years of severe defoliation could be at the origin of repeated white ring years. Defoliation severity in successive years and among trees may also be variable and trees in the same stand may not necessarily form white rings in the same year. Our results showed that white ring development was generally uniform around the stem circumference and up to approximately 70% of the height of the tree at the time of white ring formation. This contrasts with the restricted development of the "white rings", described by Ritter *et al.* (1993), to one side of the tree and associated with tension wood in balsam poplar. It is not clear if white rings are formed in branches or twigs (E.H. Hogg, pers. com., 2002), but the lack of white rings near the crown apex suggests that they may not occur in branches. During defoliation events, the portion of the stem within the crown may receive sufficient amounts of hormones throughout the growing season to ensure proper cell development because of its proximity to the source of auxin i.e., the

rapidly expanding tissue, such as the apical meristem and the new leaves (Leopold 1955; Aloni 1991).

A significant decrease in radial growth was found during the year of white ring formation when compared to the ring formed in the previous year. This was also observed by Hogg *et al.* (2002b) in trembling aspen trees submitted to 98% defoliation. Others have also observed reduced radial growth due to forest tent caterpillar defoliation (e.g.; Rose 1958; Churchill *et al.* 1964; Leininger & Solomon 1994). However, growth usually recovered within a few years (e.g.; Churchill *et al.* 1964), a pattern also visible in our data.

In our study, the average vessel and fiber diameter values were comparable to those reported for *Populus* spp. (Panshin & de Zeeuw 1970; Richter & Dallwitz 2000). However, we reported average vessel density values (above 200 vessels/mm^2) that are much higher than those reported for *Populus* spp. (Panshin & de Zeeuw 1970; Richter & Dallwitz 2000). This overestimation of vessel density is believed to be the result of the small ring area analyzed, the high magnification used (400X) and an area selection method that minimized the importance of rays. Our method was quite different than the one currently accepted to estimate vessel and fiber density *in hardwood identification* (see Wheeler *et al.* 1989) and comparison should thus be avoided with literature data on both vessel and fibre frequency *unless the methodology is comparable.*

2.5.2 Ring type

Normal cell development in the xylem occurs in several 'phases' (Wardrop 1965). During white ring development, xylem mother cell division seems to occur normally as indicated by the absence of a significant difference in the density of vessels and fibers produced in both ring-types. However, the fiber *enlargement*, secondary wall thickening and lignification, which occur after cell division (Wardrop & Bland 1959; Wardrop 1965), appear to be affected during severe defoliation. Although lignin content was not directly measured in this study, safranin staining in some white rings was lighter than in the normal rings. This apparent difference may be due to staining procedures, however, with its affinity for lignin, the lighter safranin colour in the white ring may indicate reduced lignification as hypothesized by Hogg *et al.* (2002b). Fibers in white rings had a smaller diameter, less cell wall thickening and a higher fiber lumen ratio, which leads to a decreased cell wall percentage. A decrease of cell wall percentage in white rings is comparable to the decrease in white ring density observed by Hogg *et al.* (2002b). They also found a drop in density of 29% in the white rings when compared to the rings formed in non-defoliated trees the same year. Two main processes, growth hormone production and reserve allocation, may be affected by defoliation and may be conducive to white ring formation.

Growth hormones such as auxin play an important role in cambial activity and cell maturation (Aloni 1991; Savidge 2000). Differing concentrations of gibberellins and cytokinins may stimulate cell division (Morey 1973; Little & Savidge 1987; Roberts *et al.* 1988), or may negatively affect differentiation of vessels and secondary cell wall deposition (Einspahr & van Buijtenen 1961; Little & Savidge 1987). Some

concentrations may inhibit lignification and may have a negative effect on secondary cell wall deposition in developing xylem (Little & Savidge 1987). Forest tent caterpillar defoliation normally occurs at a time when the new foliage is still expanding and growth hormone production is high (Leopold 1955). Severe defoliation during this time has been shown to induce the formation of white rings (Hogg *et al.* 2002b). This leads us to speculate that a change in the growth hormone balance following severe defoliation may prevent normal fiber development.

Timing of the insect attack early in the growing season may also influence the allocation of reserves. Normally, hormone stimulation of the cambial area causes cell *enlargement* and secondary cell wall thickening to occur (Morey 1973; Little & Savidge 1987; Roberts *et al.* 1988; Savidge 2000). These processes are, in turn, fueled by the integration of cellulose, hemicellulose and other pectic materials (e.g.; Wardrop & Bland 1959; Esau 1965; Panshin & de Zeeuw 1970). The spring foliage flush of a tree utilizes large amounts of reserves accumulated during the previous growing season and there can be a 10-fold drop in the amount of reserves from the fall to the end of the spring flush (Landhausser & Lieffers 2002). Late season growth depends on reserves accumulated during the current growing season (Morey 1973). Severe defoliation occurring during the initial spring foliage flush may force the tree into making a structural sacrifice because of the higher demand for reserves and the loss of the source of any replacement photosynthate. This hypothesis is supported by Jones *et al.* (2004), who observed earlier cessation of radial growth in artificially defoliated trembling aspen trees, when compared to undefoliated controls. An early interruption of cell *enlargement* and maturation could result in decreased fiber diameter and fiber cell wall thickening. Leininger and Solomon

(1994) hypothesized that defoliated trees needed to concentrate on refoliation and reaccumulation of reserves.

Although defoliation may trigger a structural sacrifice, such a sacrifice was not observed in the conductance capacity of white rings. No significant differences in vessel characteristics were observed between normal and white rings except that a trend towards smaller diameter vessels with less developed cell wall was observed. The absence of a significant difference in vessel cell wall thickness may relate to their earlier cell wall lignification compared to the surrounding wood fibers as observed in japanese poplar (*Populus maximowiczii* Henry) (Murakami *et al.* 1999). It may also indicate the importance of the maintenance of conductance capacity for refoliation, because renewed mobilization of reserves to the crown and refoliation are essential for re-building starch reserves in the roots (Landhausser & Lieffers 2002). Mobilization of reserves for refoliation begins in the contact cells of the sapwood rays where phosphatase activity appears to be involved in the metabolic release of sucrose into the vessel sap of trembling aspen (Sauter 1972) and of sugar maple (*Acer saccharum* Marsh.) (Gregory 1978). Sauter (1972) reported that high phosphatase activity was observed in Lombardy poplar (*Populus nigra* L.) during the spring and in summer when starch mobilization had been artificially induced by artificial defoliation. *Parker and Houston (1971) found that re-mobilization of reserves after defoliation may be triggered by decreased growth hormone concentrations. They found an increase in the conversion of reserve starches to sugar immediately following the defoliation of sugar maple. Sauter and Neumann (1994) showed that upon demand, renewed mobilization of protein in the tree stem was possible in Populus hybrid wood.* The reaction by the tree to re-mobilize reserves can result in

overcompensatory effects such as a large increase in leaf size and an increase in CO_2 assimilation (Bassman & Dickmann 1982; Heichel & Turner 1983; Landhausser & Lieffers 2002). This increase in photosythetic activity may also come at the expense of root growth thus creating higher susceptibility to other environmental stresses (Bassman & Dickman 1982; Reichenbacker *et al.* 1996). In trembling aspen, trees undergoing stress from forest tent caterpillar defoliation have been shown to be susceptible to other disease and stress (Duncan & Hodson 1958; Hildahl & Campbell 1975; Hogg & Schwarz 1999).

2.5.3 Height

Fibers in samples taken at 1.3m were found to be of larger diameter and have larger average lumen area than fibers higher in the stem. There was also an increase in the proportion of fiber lumen when compared to the fibers formed closer to the apex of the tree. However, no difference in fiber cell wall thickening was observed. The number of vessels and the vessel lumen area ratio also decrease in lower samples compared to samples from higher in the stem. Although little information is available on fiber development, basipetally decreasing amounts of auxin from the crown to the roots have been associated with larger vessel size, in terms of length and lumen diameter and decreasing vessel density at the base of the stem (Aloni & Zimmermann 1983; Roberts *et al.* 1988; Aloni 1991). Our results showed a decrease in the density of vessels and a reduction in the proportion of vessel lumen in rings from lower in the stem.

2.5.4 Conclusion

White rings were found to be narrower than the rings produced in the year prior to their formation. Their development has been shown to be uniform near the base of the stem and up to approximately 70% of the height of the tree at the date of white ring formation. The lack of white ring development along the entire circumference in the upper portions of the stem may be due to proximity to the source of growth hormones. White rings were also shown to differ anatomically from 'normal' rings in trembling aspen. These narrower rings are composed of smaller diameter fibers, with reduced cell wall thickening and a higher proportion of lumen area. They have a lower density than normal rings. A hormonal trigger caused by defoliation of the rapidly expanding leaves and the consequent re-allocation of reserves to the production of new foliage was hypothesized to be at the origin of this structural deficit. *Our results showed that cell enlargement and cell wall thickening in fibers may be affected by the lack of sufficient reserves. It was speculated that lignification may also be affected but this was not examined.* No sacrifice in the conductance capacity of white rings was observed. Additional investigations into the chemical properties of white rings, as well as the precise physiological processes affecting their formation are needed. Growth hormone processes in trees are not completely understood and interactions between growth hormones and other factors, such as nutrients and other compounds, are complex (Morey 1973; Roberts *et al.* 1988; Aloni 1991; Savidge 2000). With the renewed interest in the dendroecology of diffuse porous species, white rings may prove to be useful in the reconstruction of severe defoliation events. The presence of white rings in balsam poplar and in paper birch indicates that white ring occurrence may be more widespread among diffuse porous tree species than originally imagined.

2.6 Acknowledgements

Fig. 2.1.

Fig. 2.1. White rings in three tree species from the Duck Mountain provincial forest, Manitoba. Growth is towards the left side of each image. a) Trembling aspen white ring earlywood (left) /normal ring latewood (right) boundary at 400X magnification. Scale represents 0.05 mm. b) Entire trembling aspen white (left) and normal ring (right) at 100X magnification. Scale represents 0.1 mm. c) White ring formed in a balsam poplar sample at 40X magnification. Scale represents 0.5 mm. d) White ring formed in a paper birch sample at 40X magnification. Scale represents 0.5 mm.
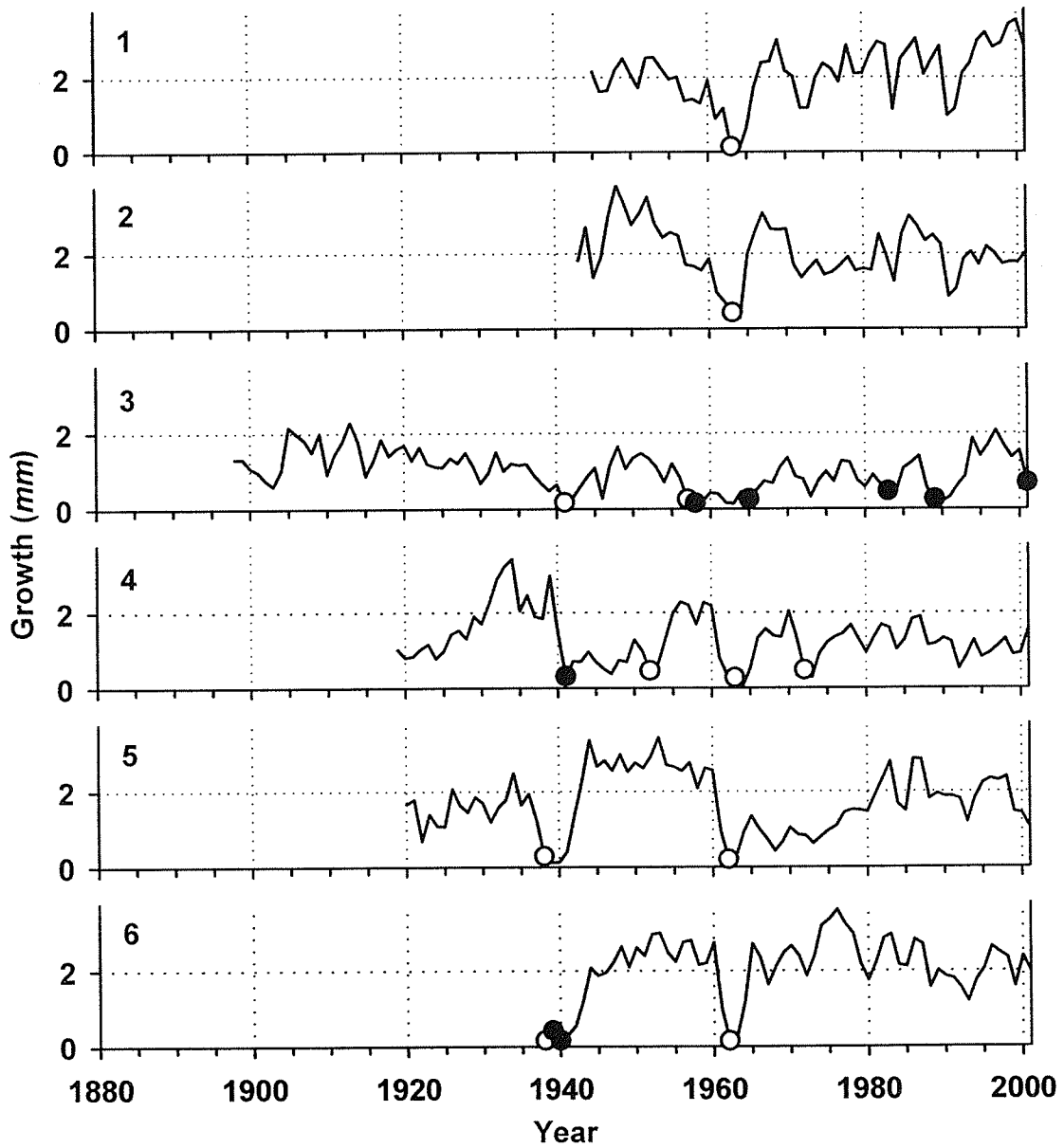
Fig. 2.2. Mean annual radial increment measured at the base of the six sample trees. Circles represent white ring years, with empty circles indicating the white rings chosen for anatomical analysis. Note: tree 6 had a rotten center at the base and only the sound portion of the cross-section was measured.
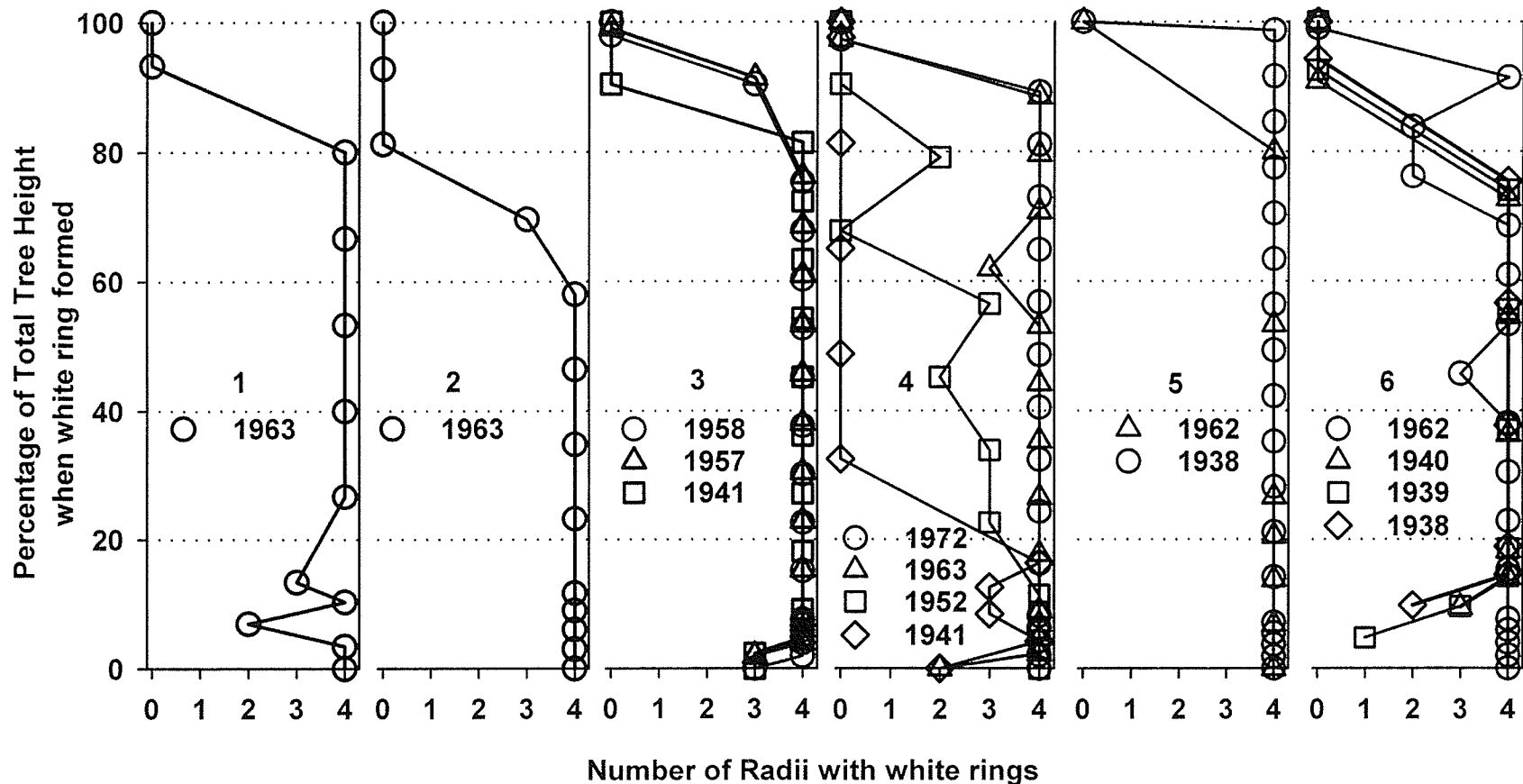
Fig. 2.3. White ring stem uniformity for the 6 sample trees along four radii, represented as the percentage of total height growth at the time of white ring formation. The number of radii indicates the number of radii where white rings have developed. The year of white ring formation is also indicated. Tree height when each of the white rings was formed individually approximated by interpolating the value using the known heights of the cross-sectional disks. The tree heights for each ring are as follows: tree 1 - 9.75m (1963), tree 2 - 11.2m (1963), tree 3 - 14.37m (1941), 17.06m (1957), 17.25m (1958), tree 4 - 7.99m (1941), 11.5m (1952), 14.69m (1963), 16.03m (1972), tree 5 - 4.88m (1938), 18.44m (1962), tree 6 - 6.89m (1938), 7.02m (1939), 7.15m (1940), 17.06m (1962). Note: only 15 of the 19 white rings occurring in the sample trees are represented. Sample discs were not high enough in the stem to determine approximate height during the year of white ring formation for some tree 3 white rings.
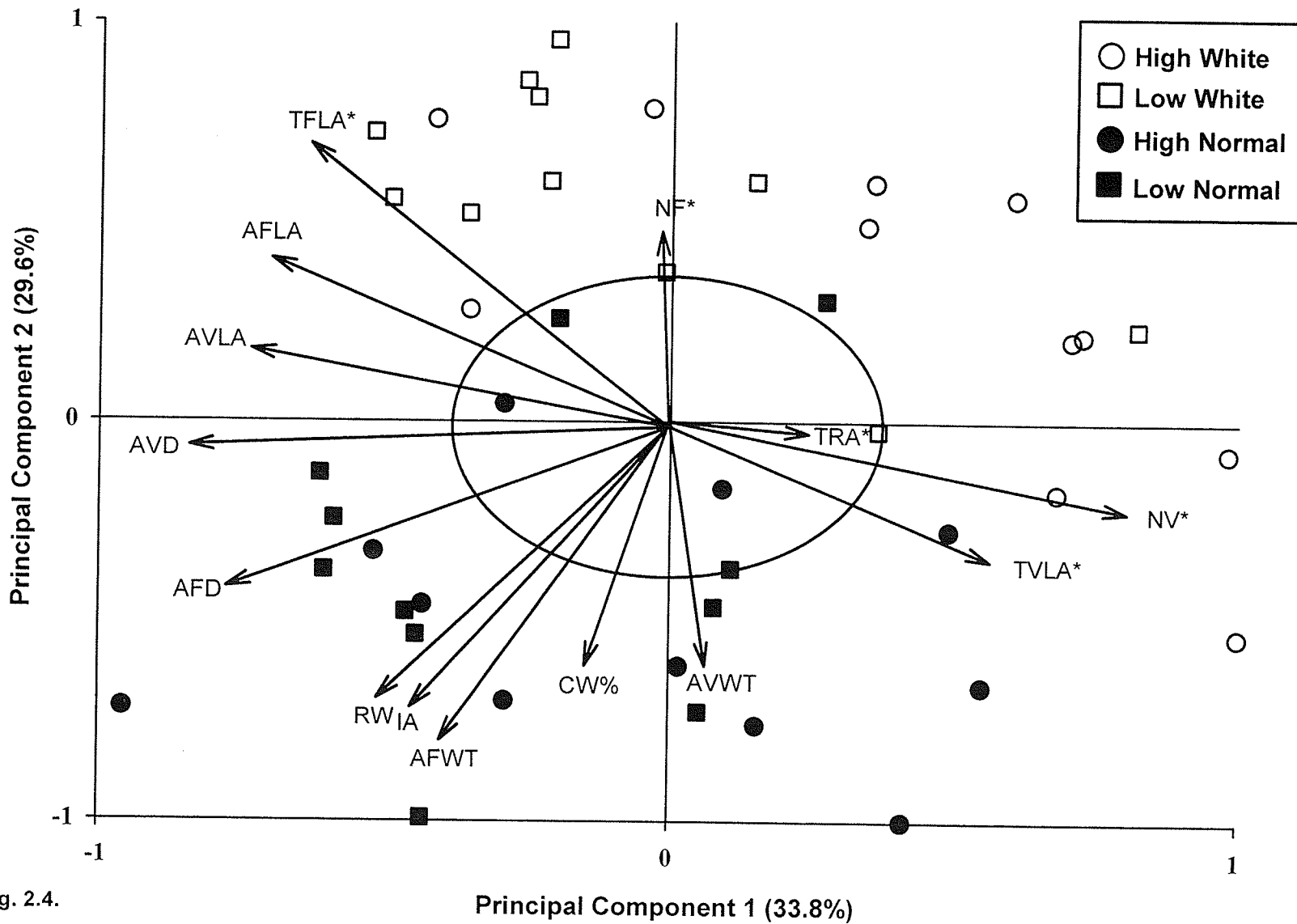
Fig. 2.4.

Fig. 2.4. Principal component correlation biplot of the 14 descriptors axes, represented by arrows, along with the 44 rings, represented by symbols. Descriptor variables included are: average fiber cell wall thickness (AFWT), average fiber diameter (AFD), total fiber lumen area (TFLA*), average fiber lumen area (AFLA), number of fibers (NF*), vessel cell wall thickness (AVWT), average vessel diameter (AVD), total vessel lumen area (TVLA*), average vessel lumen area (AVLA), number of vessels (NV*), total ray area (TRA*), cell wall percentage (CW%), ringwidth (RW), sample area (IA). The 44 rings are divided into their 4 groups: high white rings, low white rings, high normal rings, low normal rings. Equilibrium circle after Legendre & Legendre (1998) shows that all variables, with the exception of TRA* strongly contributed to the formation of both axes. The angle between the vector arrows approximates the correlation between them, with an angle of 0° and 180° representing high positive and negative correlation, respectively, and an angle of 90° representing no correlation (Jongman et al. 1995). In addition, the fitted abundance of each descriptor can be observed by projecting the 44 objects onto the descriptor axis at a perpendicular angle.

Table 2.1. Jacknife classification of the 44 rings following a backwards stepwise discriminant analysis. Table a) high normal ring (HN), low normal ring (LN), high white ring (HW) and low white ring (LW) groups. Classification was done using the discriminating variables: average fiber cell wall thickness (AFWT), average vessel diameter (AVD), number of vessels (NV*) and average fiber diameter (AFD). Table b) normal (N) and white (W) groups. Classification was done using the discriminating variables: average fiber cell wall thickness (AFWT), average vessel diameter (AVD), number of vessel per image area (NV*), average fiber lumen area (AFLA), cell wall percentage (CW%) and average fiber diameter (AFD).

		Discriminant analysis classification				% Correct
		Normal		White		
		High	Low	High	Low	
a)	HN	6	0	4	1	55
	LN	1	9	0	1	82
	HW	6	0	5	0	45
	LW	0	3	0	8	73
	Total	13	12	9	10	64
b)	N	22		0		100
	W	0		22		100
	Total	22		22		100

Table 2.2. Mean, standard deviation (st.dev.), ANOVA r-square (R^2) and p-value (p) for each of the 14 variables: average fiber cell wall thickness (AFWT), average fiber diameter (AFD), total fiber lumen area (TFLA*), average fiber lumen area (AFLA), number of fibers (NF*), vessel cell wall thickness (AVWT), average vessel diameter (AVD), total vessel lumen area (TVLA*), average vessel lumen area (AVLA), number of vessels (NV*), total ray area (TRA*), cell wall percentage (CW%), ringwidth (RW), image area (IA). Interaction term was removed from the ANOVA because of non-significance for all variables. Values of P < 0.05 appear in bold text.

	R^2 (%)	Normal (mean ± st.dev.)	White (mean ± st.dev.)	p	High (mean ± st.dev.)	Low (mean ± st.dev.)	p
AFWT (μm)	77.0	2.80 ± 0.29	1.85 ± 0.25	**<0.001**	2.31 ± 0.55	2.35 ± 0.56	0.696
AFD (μm)	48.0	17.24 ± 1.57	14.60 ± 1.77	**<0.001**	15.30 ± 2.24	16.54 ± 1.84	**0.012**
TFLA* (%)[a]	31.0	19.95 ± 4.04	24.01 ± 6.34	**0.008**	19.66 ± 5.24	24.31 ± 5.13	**0.003**
AFLA (μm^2)	28.0	70.79 ± 14.16	78.50 ± 21.40	0.117	65.90 ± 15.70	83.39 ± 16.82	**0.001**
NF* (mm^{-2})[a]	8.0	2842.34 ± 417.10	3084.46 ± 438.33	0.071	2982.98 ± 386.48	2943.82 ± 496.63	0.766
AVWT (μm)	8.0	2.12 ± 0.22	1.99 ± 0.23	0.068	2.07 ± 0.23	2.05 ± 0.24	0.725
AVD (μm)	8.0	48.64 ± 5.11	45.89 ± 5.35	0.090	46.64 ± 6.01	47.89 ± .65	0.436
TVLA* (%)[a]	18.0	32.42 ± 4.24	32.91 ± 5.25	0.713	34.60 ± 4.62	30.69 ± 4.02	**0.005**
AVLA (μm^2)	5.0	1464.93 ± 297.24	1425.50 ± 521.16	0.756	1350.38 ± 386.59	1540.04 ± 438.73	0.140
NV* (mm^{-2})[a]	14.0	243.58 ± 75.06	275.98 ± 110.53	0.239	291.26 ± 104.74	228.30 ± 73.18	**0.025**
TRA* (%)[a]	12.0	5.47 ± 2.74	5.92 ± 2.69	0.571	6.60 ± 2.95	4.79 ± 2.11	**0.025**
CW% (%)	40.0	44.60 ± 2.88	39.50 ± 3.50	**<0.001**	41.88 ± 4.00	42.22 ± 4.25	0.733
RW (mm)	57.0	1.06 ± 0.46	0.31 ± 0.13	**<0.001**	0.75 ± 0.57	0.62 ± 0.43	0.198
IA (mm^2)	56.0	0.25 ± 0.11	0.08 ± 0.03	**<0.001**	0.18 ± 0.14	0.15 ± 0.10	0.161

[a] values were not calculated per square mm of wood tissue but per unit surface area (sq. mm) minimizing the ray tissue (see methods).

3.0. Tree-ring reconstruction of forest tent caterpillar outbreaks in the Duck Mountain Provincial Forest, Manitoba.

3.1 Abstract

A dendrochronological reconstruction of forest tent caterpillar (*Malacosoma disstria* Hubner) outbreaks was conducted in the Duck Mountain Provincial Forest (DMPF) in western Manitoba. Trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.) and paper birch (*Betula papyrifera* Marsh.) tree-ring chronologies were used to identify periods of forest tent caterpillar outbreaks from approximately 1800 to 2002. In addition, the spatiotemporal dynamics of the major forest tent caterpillar outbreaks were reconstructed and outbreak characteristics were compared among four stand types and two age classes. The presence of white rings, in conjunction with periods of growth suppression was used to identify three important periods of forest tent caterpillar outbreaks, from 1939 to 1948, 1961 to 1965 and 1982 to 1985, with an additional large-scale outbreak suspected during the 1870s. Smaller outbreaks are also suspected prior to 1800, during the 1950s, the 1970s and during the early and late 1990s. A period with no apparent outbreaks lasted from approximately 1906 to 1936. Observations of the spatial dynamics indicate that the major outbreaks of the 20th century started in the north and spread into the DMPF at different rates. The prolonged 1940s outbreak spread slowly whereas the 1960s outbreak spread quickly following a year of extreme drought. The outbreak of the 1980s was also short, but did not reach widespread proportions. Analysis by stand types indicated that during the dry outbreak of the 1960s, mixed trembling aspen/ jack pine (*Pinus banksiana* Lamb.) stands registered stronger

growth suppression and produced more white rings. Younger sites were found to have higher average growth suppression during the 1980 outbreak.

3.2 Introduction

Insect outbreaks are important natural disturbances in the boreal forest. Timber loss in the boreal zone of Canada due to insect outbreaks has been estimated to be greater per year than loss due to wildfire (Volney and Fleming 2000). Between 1988 and 1992, insect and disease loss in west-central Canada was 16.2 million m³/year (Brandt 1995). Reduced radial growth due to insect activity has been well documented for several species such as the eastern spruce budworm (*Choristoneura fumiferana* Clem.) (Blais 1958; Zarnovican 1982; Ferguson 1985; Morin and Laprise 1990; Morin *et al.* 1993; Morin 1994), the larch sawfly (*Pristiphora erichsonii* (Htg.)) (Arquillière *et al.* 1990; Jardon *et al.* 1994; Girardin *et al.* 2001; Case and Macdonald 2003) and the gypsy moth (*Lymantria dispar* L.) (Muzika and Liebhold 1999; Naidoo and Lechowicz 2001) among others. In the prairie provinces (Alberta, Saskatchewan, Manitoba and the Northwest Territories), the forest tent caterpillar, which caused timber losses of 4.1 million m³/ year, was responsible for approximately 25% of the total impacts to forests from 1988 to 1992 (Brandt 1995). An area of 80.6 million hectares was defoliated by the forest tent caterpillar in central Canada between 1980 and 1996 (Simpson and Coy 1999). In general, outbreaks of the forest tent caterpillar occur every 10-12 years (with a range of 6-16 years) and can last 3 to 6 years in the same area (Duncan and Hodson 1958; Hildahl and Campbell 1975; Martineau 1984; Ives and Wong 1988). The forest tent caterpillar is also an important defoliator in the north-central United States (Witter 1979). Several factors, such as temperature and extreme weather events (Hodson 1941; Blais *et al.* 1955; Hildahl and Campbell 1975; Daniel and Myers 1995), forest heterogeneity (fragmentation) (Cooke and Roland 2000), parasitism (Parry 1995; Roland and Kaupp

1995; Rothman and Roland 1998) and genetics (Miller 1996) are thought to control the initiation and cessation of forest tent caterpillar outbreaks.

Although the preferred host of the forest tent caterpillar in west central Canada is trembling aspen (Populus tremuloides Michx.) (Sippell and Ewan 1967; Hildahl and Campbell 1975; Witter 1979; Ives and Wong 1988; Sims *et al.* 1990), secondary hosts include paper birch (Betula papyrifera Marsh.) (Safford *et al.* 1990; Sims *et al.* 1990) and balsam poplar (Populus balsamifera L.) (Zasada and Phipps 1990; Sims *et al.* 1990). Severe defoliation by the forest tent caterpillar has been shown to cause reduced radial growth (Duncan and Hodson 1958; Rose 1958; Hildahl and Reeks 1960; Bergeron and Charron 1994; Hogg and Schwarz 1999; Jones *et al.* 2004; Sutton and Tardif *in press*). Although mortality in trembling aspen stands defoliated by the forest tent caterpillar had previously been reported to be no different than in non-defoliated stands (Duncan and Hodson 1958; Hildahl and Reeks 1960), increased mortality was reported in defoliated stands several years after the defoliation event (Churchill *et al.* 1964; Brandt *et al.* 2003). Forest tent caterpillar defoliation affects trembling aspen growth throughout west-central Canada, (Perala 1990; Sims *et al.* 1990; Peterson and Peterson 1992; Brandt *et al.* 2003) and, in combination with drought, has been associated with trembling aspen stand decline and dieback in northwestern Alberta (Hogg *et al.* 2002a), Saskatchewan (Hogg and Schwarz 1999) and in sugar maple stands (*Acer saccharum* Marsh.) in Québec (Payette *et al.* 1996) as well as in New York (Hibben 1962).

Although defoliation may have a positive effect on leaf size, photosynthesis and stomatal conductance after the event, these effects generally come at the expense of the

root system, increasing the chance of structural damage due to windthrough and susceptibility to pathogens and insects (Bassman and Dickmann 1982; Reichenbacher *et al.* 1996). Hogg *et al.* (2002a) have found that a link existed between defoliation and an increased incidence of wood boring insects and fungal pathogens. Brandt *et al.* (2003) also found that the incidence of *Armillaria* root disease was higher in stands which experienced one or more years of defoliation. Brandt *et al.* (2003) have concluded that the forest tent caterpillar has an important role in the regulation of aspen productivity and can be a factor in crown dieback and mortality.

Recently, 'white' rings have been observed in trembling aspen trees, as well as in balsam poplar and paper birch (Hogg and Schwarz 1999; Cooke 2001; Sutton and Tardif in press). White rings appear completely white and are characterized by small, thin cell walled fibers and an overall decrease in wood density, causing structural weakness (Hogg *et al.* 2002b, Sutton and Tardif in press). White rings have previously been associated with historical surveys of forest tent caterpillar defoliation (Hogg and Schwarz 1999; Hogg 2001; Hogg *et al.* 2002b; Cooke 2001) and have been induced after severe artificial defoliation early in the growing season, simulating a severe forest tent caterpillar outbreak (Hogg *et al.* 2002b). Due to the white appearance throughout the annual ring, it has also been speculated that white rings are induced early in the growing season, such as during an outbreak (Cooke 2001). It has therefore been suggested that white rings may be useful as indicators of past forest tent caterpillar outbreaks in aspen (Hogg *et al.* 2002b; Cooke 2001; Sutton and Tardif *in press*), in a similar way to the use of light rings in the reconstruction of past larch sawfly outbreaks (Jardon *et al.* 1994; Girardin *et al.* 2001; Case and Madonald 2003). White ring presence, along with a dendrochronological

analysis using a host/ non-host comparison can be used to reconstruct past insect outbreaks (Swetnam *et al.* 1985; Cooke 2001; Hogg *et al.* 2002b; Sutton and Tardif *in press*).

Little information is available on the susceptibility of stands of different types and age to insect outbreaks. Older, overmature trees, with reduced physiological activity may become increasingly susceptible to insect attack (Kozlowski 1969). The weakening of trembling aspen trees over time due to repeated forest tent caterpillar outbreaks has been documented (Churchill *et al.* 1964; Brandt *et al.* 2003). This may indicate that older stands are more susceptible to insect outbreak and white ring formation. However, white rings have been artificially induced in young trees (Hogg *et al.* 2002b) and have been identified in natural conditions in the young portions of trembling aspen trees (Sutton and Tardif in press). Hogg and Schwarz (1999) initially hypothesized that the effects of the forest tent caterpillar would be reduced in mixed stands, but found instead that the frequency of white rings in trembling aspen was nearly the same in both pure and mixed stands. It was also found that the less preferred balsam poplar was defoliated as often as trembling aspen by the forest tent caterpillar (Hogg and Schwarz 1999). Roland (1993) found that neither the absolute frequency of trembling aspen within townships or the proportion of trembling aspen in stands had a significant effect on outbreak duration. It is therefore possible that during severe outbreaks, when the available food sources begin to diminish, stand type may not control the pattern of dispersal, especially in the later stages of the insect's development (Hodson 1941; Rose 1958; Sippell and Ewan 1967; Hildahl and Campbell 1975). In Ontario, forest fragmentation, or the amount of forest edge, was the best descriptor of outbreak length, with longer outbreaks occurring in more

fragmented forests (Roland 1993; Roland *et al.* 1998; Cooke and Roland 2000). In addition to forest fragmentation, the dispersal of the insect as well as the parasitic organisms, which control the insect, may be equally important (Smith and Goyer 1986; Roland 1993; Parry 1995; Roland and Kaupp 1995; Rothman and Roland 1998; Maron *et al.* 2001).

The objectives of this study were threefold, 1) to reconstruct the forest tent caterpillar outbreak history in the Duck Mountain Provincial Forest (DMPF) using frequency of white rings and a dendrochronological comparison of the host (trembling aspen, balsam poplar and paper birch) and non-host chronologies, 2) to reconstruct the spatial and temporal dynamics of forest tent caterpillar activity and 3) to determine if the intensity of forest tent caterpillar outbreaks differs among stand type or stand age. It is hypothesized that forest tent caterpillar outbreaks will not differ in time among the three host species. The intensity of outbreaks in the DMPF are not hypothesized to be affected by forest composition or stand age.

3.3 Materials and Methods

3.3.1 Study area

The study area is located in the DMPF, in western Manitoba (51° 15' to 52° 05' North, 100°30' to 101°30' East) (Figure 3.1), which covers approximately 376000 ha (Kenkel *et al.* 2004). The DMPF is situated on the Manitoba escarpment and makes up part of the mountain park system along with the Porcupine Hills to the north, Turtle Mountain Provincial Park and Riding Mountain National Park to the south (Corkery

1996). The escarpment rises to approximately 500 m above the surrounding lowlands and is covered by morainal material (Lang 1974). The study area is located in the subhumid mid-boreal ecoregion (Zoladeski *et al.* 1998) and provides a transition zone between the boreal forest to the north and the aspen parkland and prairie to the south. The highest elevation in the DMPF is located at Baldy Mountain, which rises to 832 m.a.s.l. Mean climate data, taken from the nearest meteorological station at Swan River, located approximately 18km north of the DMPF, shows that mean annual temperature is 1.6°C, with an annual precipitation of 530.3 mm for the period 1971 - 2000 (Environment Canada 2004).

The area is dominated by three hardwood tree species, trembling aspen, balsam poplar and paper birch, and five coniferous species, white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) BSP), jack pine (Pinus banksiana Lamb.), balsam fir (*Abies balsamea* (L.) Mill.) and tamarack (*Larix laricina* (DuRoi) K. Koch). Trembling aspen is a major component of several forest cover types (Zoladeski *et al.* 1995), where it can grow in mostly pure stands with various shrubby understories or in mixed stands with various species (Perala 1990; Sims *et al.* 1990; Peterson and Peterson 1992). The upland sites are predominantly dominated by mixed forest and conifer stands (Sauchyn and Hadwen 2001) and the landscape is marked by many small lakes, streams and wetlands (Tyrrell 1888).

Prior to the 1880s, a short fire cycle in the range of 55 years may have characterized the DMPF with large infrequent fires occurring in conjunction with prolonged periods of drought (Tardif 2004). A lengthening of the fire cycle was observed

in the 20th century and corresponded with European settlement and later fire suppression (Tardif 2004). Notable fires in the DMPF occurred between 1885 and 1895 and it was estimated that about 83% of the forest of the DMPF burned during that period of severe drought (Tardif 2004). The most recent large size fire to occur was in 1961 with about 6% of the forest burned. Lumber production in the DMPF area began as early as the 1890s as settlers began to build homesteads and towns (Manitoba Parks Branch 1973). Since that time, the DMPF has served as an important source of firewood and pulpwood. Louisiana Pacific Inc. was awarded a forest management licence (FML) for the area in 1996 (Hamel and Kenkel 2001) and several smaller operators also continue to harvest softwoods in the DMPF.

3.3.2 Field sampling and data collection

Sampling was initiated in 2000 and 2001 as part of a broader project dealing with fire history in the DMPF (Tardif 2004). Initially the DMPF was divided into 42, 10km by 10km units to ensure adequate spatial coverage of sampling sites throughout the forest. Two hundred and sixty-three sites were initially established in the DMPF as part of the fire history project and at each site, 8 - 10 dominant trees from pioneer species were cored (1 or 2 radii) using an increment borer. Dead woody material was also collected and vegetation composition and abiotic factors were assessed. Ninety-six checkpoint sites were also established where 2 - 3 trees were sampled to assess the continuity of stand age on the landscape. Therefore, 359 sites were sampled in the DMPF and additional details regarding the initial sampling can be found in Tardif (2004).

To reconstuct forest tent caterpillar outbreaks, two strategies were used. First, and at the broadest scale of analysis, the history of the outbreaks within the DMPF was reconstructed using the three host species (trembling aspen, balsam poplar and paper birch). From the original fire study database (359 sites), all cores pertaining to each host species was extracted. A total of 212 sites (155 sites + 57 checkpoint sites) contained trembling aspen samples (Figure 3.1), a total of 104 sites (81 sites + 23 checkpoint sites) contained balsam poplar samples and 118 sites (99 sites + 19 checkpoint sites) contained paper birch. The data from these sites was used to reconstruct forest tent caterpillar activity in each of the 3 species separately.

The second strategy was intended to assess how stands with different tree composition and age differed in their capacity to register outbreaks. To assess the effects of stand age, two age classes were determined based on the fire history study (Tardif 2004): i) old sites, originating before 1930 and usually after the 1880s and ii) young sites, originating after 1930 from several small fires which occurred during the 1930s, the large fire which occurred in 1961 and from regeneration after logging. To assess the effect of stand composition, four general stand types were determined i) nearly pure trembling aspen, ii) mixed trembling aspen - jack pine - black spruce, iii) mixed trembling aspen - balsam poplar - white spruce and iv) mixed trembling aspen - white spruce (Figure 1). For this analysis, a target of 80 sites was fixed (10 sites per stand type and age class). For each stand type/age class, replicate sites were first selected from the fire history database. In cases where less than 10 trembling aspen (1 or 2 radii) trees were previously sampled, sites were revisited in 2002 and 2003 and new sites were added where needed. At each site, ten white spruce trees were also cored (1 or 2 radii) where possible. In total, 67 sites

were sampled to assess the effects of stand composition and age on the history of outbreaks. Difficulty locating young sites resulted in fewer young replicates, particularly in the trembling aspen/ white spruce type. Trembling aspen can suppress white spruce trees up to 10 years (Cayford 1957) and in sites where white spruce were present, they were often not yet 5cm in diameter at breast height (dbh). In total, 1158 trembling aspen series (cores) and 492 white spruce series were kept for dendrochronological analysis. All white spruce series were pooled to produce a common non-host chronology for all host vs. non-host comparisons.

To further assure that each site was attributed the proper stand type, a modified point center quadrat (PCQ) sampling technique from Cottam and Curtis (1956) was used. At each site, ten equally spaced (approximately 5 meters) PCQ were located and the four closest trees to the point were identified and measured for dbh. From the data recorded, an importance value (%) was calculated for the major tree species using relative density, relative basal area and relative frequency, which were summed and divided by 3, and each site was clustered into 4 stands types using k-mean clustering after calculation of an Euclidean distance matrix (SPSS Inc. 1998). The small number of tree species in our data justified the use of Euclidean distance. This resulted in the classification of each of the 67 sites into one of the stand types and an age class (Table 3.1). Each site was also georeferenced using a GPS receiver and soil data, such as texture, drainage type and LFH depth was gathered after the excavation of a soil pit.

3.3.3 Chronology development

All cores and cross-sections used in this study were prepared using standard dendrochronological techniques (Stokes and Smiley 1968; Swetnam *et al.* 1985). Trembling aspen, balsam poplar, paper birch and white spruce wood samples were finely sanded using successive grits up to 600 grit for the hardwoods and 400 grit for the white spruce to ensure that proper tree-ring identification could be performed. The cores were then dated and cross-dated visually using a skeleton plot method, adapted from Yamaguchi (1991). All wood samples were measured using a Velmex Uni Slide micrometer (0.001 mm precision) and the COFECHA program (Holmes 1999) was used to validate the cross-dating and to ensure that measuring errors were eliminated. COFECHA is a statistical program, which calculates the correlation between each individual series and a reference chronology consisting of the remaining series up to a − 10 and +10 year lag to identify the best statistical fit. All potential problems identified with COFECHA were verified and measurement series were corrected when needed. In addition, all incidences of locally missing and white rings were recorded for all hardwood species.

The ARSTAN program (Cook and Holmes 1999) was used to construct the trembling aspen, paper birch, balsam poplar and white spruce residual chronologies. Detrending of all tree-ring series/species into standardized tree-ring indices, with a mean of 1, was done using a 50% spline function of 50 years to remove low frequency trends associated with size/age, or other factors which are site specific (Cook and Peters 1981). Residual chronologies were constructed after the program performed an autoregressive model for each series to remove temporal autocorrelation (Cook and Holmes 1999). The

residual chronologies were then calculated using a robust mean, which reduced the effect of outlier values. In addition to the 4 species residual chronologies, trembling aspen residual chronologies were constructed for each of the 4 stand types separated into the 2 age class categories, resulting in 8 residual chronologies.

3.3.4 Identification of forest tent caterpillar outbreaks

Trembling aspen, balsam poplar and paper birch residual chronologies were used to determine periods of forest tent caterpillar defoliation. The program OUTBREAK (Holmes and Swetnam 1996) was used to compare the host and non-host chronologies. White spruce was used as the non-host species because it has been shown to correlate well with the host species in the DMPF (Girardin and Tardif 2005), a condition that is required for this type of analysis (Swetnam *et al.* 1985). The program removes the common (mostly climatic) signal found in the chronologies, by subtracting the non-host chronology from each of the host series (Holmes and Swetnam 1996). The program then flags all years with negative growth (in standard deviations) in the host series. An outbreak is identified when a minimum number of years in a row produce negative growth, with at least one year below the maximum growth reduction limit. In this case, the default budworm criteria were modified and used to help determine forest tent caterpillar outbreaks. A maximum growth departure of -1.28 standard deviations from the non-host chronology, a growth reduction period of at least 3 years and a fractional power of 0.1 were used as criteria for the identification of forest tent caterpillar outbreaks. The fractional power raises the index value of the non-host chronology to a selected power, to avoid false identification of outbreaks when the non-host species is registering

high growth values (Holmes and Swetnam 1996). Additional trials revealed that similar results were obtained using maximum growth departures between –1.0 and -1.6 standard deviations. A maximum growth departure of -1.7 standard deviations or more identified only the most severe growth suppressions. This program was created for the identification of coniferous pest activity (Holmes and Swetnam 1996) and has not been used to identify forest tent caterpillar outbreaks in trembling aspen to our knowledge, but the procedures could be easily adapted.

In addition to the residual chronology comparison, individual residual series of each of the host species were compared to the non-host residual chronology, using OUTBREAK, in order to determine the number and percentage of series per site affected by the growth suppression. The presence and relative frequency of white and/or locally missing rings were used as an additional indication of outbreak periods. Periods of suspected forest tent caterpillar defoliation were also compared to the available historical survey records of forest tent caterpillar activity. To analyse the effects of stand type and age, the same criteria and methods were used to analyse each of the eight stand type/ age class residual chronologies. The residual chronologies and the individual residual series were also compared to the non-host residual chronology in each case.

3.3.5 Spatiotemporal reconstruction of major outbreaks

To reconstruct the spatial dynamics of outbreaks within the DMPF, the white ring data from all sites containing trembling aspen were used in the construction of outbreak maps. For each site, the relative frequency of white rings per year was calculated, along

with the mean growth suppression in standard deviations. Mean growth suppression was calculated from growth suppression values derived during the OUTBREAK analysis for each series. The Arcview GIS 3.2 program (Environmental Systems Research Institute Inc. 1999) was used to map the mean growth reduction and the relative frequency of white rings for each year of the outbreak. Isolines for mean growth suppression were derived using a 3D surface analyst and a contour interval of 0.5. The spatial progression of white ring abundance and average growth reduction was mapped for three outbreak periods, 1939-1948, 1961-1965 and 1982-1985. For the purposes of mapping, outbreak periods were considered to begin during the first year of white ring formation and to end during the last year of mean growth suppression below the -1.28 standard deviation level.

3.3.6 Outbreak characteristics and stand type/age class

To determine if the forest tent caterpillar outbreak characteristics differed among stand type and age, a total of 38 variables, were calculated from the site residual chronologies (site-level) and the individual residual series (tree-level) for each of the 67 stand type/age class sites. Tree-level variables for each site were calculated as mean values from all series. Twenty-one overall variables describing the period 1900-2002, and 17 variables specific to each of the three major outbreak periods were calculated. To analyse the effect of stand type and age on total white ring, missing ring, growth suppression and the number and length of outbreaks, site-level characteristics were calculated for the period 1900-2002, using the residual chronologies for each site. The site-level variables were: relative frequency of white rings and missing rings (rfwr and rfmr), relative frequency of growth suppression to -1.28 standard deviations and -1.7

standard deviations (s128 and s17) as well as the relative frequency of growth suppression to -1.28 and -1.7 during years flagged as outbreak years by the OUTBREAK program (s128o and s17o), the number of outbreaks determined by the OUTBREAK program (nout), and the mean (xdur), minimum (mindur) and maximum (maxdur) outbreak length, all determined by the OUTBREAK program. Using the mean values from the residual series, for the period between 1900 and 2002, the tree level variables were calculated. Tree-level variables were: average white and missing ring relative frequency (trfwr and trfmr) per series, average relative frequency of growth suppression to -1.28 standard deviations and -1.7 standard deviations (ts128 and ts17) per series, average relative frequency of growth suppression to -1.28 and -1.7 during years flagged as outbreak years by the OUTBREAK program (ts128o and ts17o) per series, the average number of outbreaks (tnout) per series and the average mean (txdur), average minimum (tmindur) and average maximum (tmaxdur) outbreak length per series were also calculated to test tree-level differences. Mean year of origin (xage) of the trees was also calculated for each site.

To determine the effects of stand type and age on the three major outbreaks from the 1940s, 1960s and 1980s outbreaks, 17 site- and tree-level variables were calculated for the periods determined during the spatial reconstruction. Site-level variables for the three specific outbreaks were: relative frequency of white rings and missing rings during the outbreak (wrout and mrout), the number of years of white ring and missing ring formation during the outbreak period (wryr and mryr), number of years of continuous growth reduction below the -1.28 standard deviation level (dur), maximum growth reduction (maxr), average growth reduction (avr). At the tree-level, variables calculated

from the mean individual series for the period 1900 to 2002, for the three outbreak periods were: average relative frequency of white rings and missing rings during the outbreak (twrout and tmrout) per series, average maximum white ring and missing ring relative frequency (twrmax and tmrmax), average relative frequency of white rings/ missing rings during years of white ring/ missing ring formation only (tavwrint and tavmrint) and the average number of years between maximum suppression and maximum white ring abundance (tsupwr), average number of years of continuous growth reduction below the -1.28 standard deviation level (tdur) per series, average maximum growth reduction (tmaxr) per series and average mean growth reduction (tavr).

To determine if these variables differed by stand type or stand age, they were analysed using a one-way Analysis of Variance (ANOVA), using the SPSS 10.1.0 for windows package (Spss Institute Inc. 2000). Variables were tested for homogeneity of variance using the Levene test for equality of variance (p = 0.05). The Levene test is not largely sensitive to departures from normality as is the problem in other homogeneity tests (Sokal and Rohlf 1969; Spss Institute Inc. 2000). If the Levene test was significant (p<0.05), equal variance was not assumed in the ANOVA and a non-equal variance post-hoc test was performed (Tamhane post-hoc test). In the case of equal variance, a Tukey HSD post-hoc test was performed. Mean year of origin (xage) was first tested to ensure that there was no effect within the stand types related to mean tree age. All variables were tested among stand types for the old sites and only the overall and 1980 outbreak variables were tested among stand types for the young sites. To test between the two age groups, all 1980 outbreak variables were tested between the 2 age classes.

3.4 Results

3.4.1 Periods of growth suppression

The residual trembling aspen and white spruce chronologies cover the period between 1806 and 2002, with the majority of the samples occurring from about 1890 to 2002 (Figure 3.2). Eight periods of growth suppression were identified in the trembling aspen residual chronology after comparison to the white spruce residual chronology (Figure 3.2). Regular periods of growth suppression, as determined by OUTBREAK, have occurred in the trembling aspen, with 5 periods of growth suppression between 1806 and 1906 and 3 more between 1937 and 2002. White rings and missing rings were observed in association with one of these periods before 1906 and three times after 1906. The low number of samples before 1890 makes it difficult to be confident before this date, however, white rings were observed in 1876 (Figure 3.2). Between 1900 and 1906, no white or missing rings were produced (Figure 3.2). Between 1907 and 1936, white and missing rings were produced at low frequency (<1%) from 1909 to 1911, 1915 to 1917, 1920, 1924 to 1927, 1929 and 1930.

The first major period of growth suppression was observed from 1937 to 1948 (Figure 3.2). White and/or missing rings were produced in each year except 1937 and 1938 and were most abundant between 1939 and 1942 (Figure 3.2). During this period, 42-72% of all individual series were affected by growth suppression each year. A second period of major growth suppression was observed from 1962 to 1965. White and missing rings were observed throughout the period and in 1961 and were most abundant in 1962 (Figure 3.2). Between 55-61% of individual series were affected by growth suppression

each year of this period. The most recent period of growth suppression was observed from 1982 to 1985. White rings and missing rings were most abundant, yet rare, in 1984 and 51-59% of the individual series were affected by growth suppression each year (Figure 3.2). Other notable periods of white and missing ring formation, not associated with major growth suppression, but with small peaks in the percentage of individual series affected by suppression, occurred between 1952 and 1958, 1967 and 1972 and 1989 and 1994 (Figure 3.2). A small peak of growth suppression in individual series also occurred between 1998 and 2000.

The balsam poplar and paper birch residual chronologies cover the period 1800 - 2001, with a majority of the samples occurring between 1890 and 2001 (Figure 3.3). Periods of growth suppression and white ring formation in these species were similar to those found in trembling aspen (Figure 3.3). White and missing rings appeared in more years in the trembling aspen than the other two species and maximum white ring frequency in trembling aspen (Figure 3.2) was higher than the other two species (Figure 3.3). In addition, the percentage of trees affected by growth suppression in trembling aspen was higher than the other two species, except for a peak between 1920 and 1924 in balsam poplar and between 1998 and 2000, when up to 100% of the trees were affected in both balsam poplar and paper birch (Figure 3.3). Additionally, due to the larger sample size in paper birch prior to 1890, the growth suppression period observed between 1875 and 1880 could indicate a large-scale outbreak during this period. This is supported by synchroneous growth suppression in both trembling aspen and balsam poplar, and also by the production of white rings in 1876 in trembling aspen.

3.4.2 Stand type and age class chronologies

Stand type residual chronologies for old trembling aspen sites cover the period

from approximately 1870 to 2002, with a majority of samples occurring after 1890

(Figure 3.4). Similar periods of growth suppression were found in the 4 stand type

residual chronologies as in the combined trembling aspen residual chronology. The three

major growth suppression periods were observed in all four stand types, along with the

smaller growth suppression periods in the 1950s, the late 1960s and the 1990s (Figure

3.4). During the 1940s, the trembling aspen/ white spruce stand type was affected by

growth suppression earlier than the other stand types, but maximum individual growth

suppression during this period occurred in trembling aspen/ jack pine stands (Figure

3.4b,c). Multiple years of white and missing ring formation occurred in all stand types

between 1939 and 1942, but white ring production in the trembling aspen/ jack pine stand

type occurred later than the other stand types (Figure 3.4a). Trembling aspen/ jack pine

stand type sites recorded the longest overall growth suppression during the 1960s, but

individual series growth reduction was highest in trembling aspen stand type sites (Figure

3.4a,b). In addition, trembling aspen stand type sites recorded white rings in 1961, a year

before the other stand types. Maximum relative frequency of white and missing ring

formation occurred in 1962 in all 4 stand types, with trembling aspen/ jack pine stand

type sites recording the highest frequency of white and missing ring formation observed

for any year (Figure 3.4b). Trembling aspen/ white spruce stand type sites had the lowest

percentage of trees affected by growth suppression during all major outbreaks except for

the 1980s. White and missing rings were recorded in association with all major periods

of growth suppression for each of the stand types, as well as with the smaller growth

suppression periods (Figure 3.4). Overall, the trembling aspen stand type recorded the

highest number of years with white ring production (Figure 3.4).

Young residual chronologies for the 4 stand types cover the period from

approximately 1930 to 2002, with a majority of samples occurring after 1960 (Figure

3.5). Although the small number of samples prevents interpretation of results prior to

1960, all stand types with samples older than 1960 recorded growth suppression during

the 1940s (Figure 3.5). However, very few white and missing rings were observed for

any of the stand types. Growth suppression in individual series was also observed during

the 1960s, but was generally less frequent than in the older sites and was delayed until the

late 1960s. Maximum white and missing ring abundance was observed in 1962 in the

trembling aspen/ balsam poplar stand type (Figure 3.5c). A growth suppression period

during the early 1980s is present in all young stand types and affected residual series most

frequently in the trembling aspen and trembling aspen/ jack pine stand types (Figure 3.5).

White ring formation in the young stands was almost entirely limited to the trembling

aspen/ balsam poplar stand type (Figure 3.5c). No white rings were formed in young

trembling aspen/ white spruce stand type sites.

3.4.3 Spatial outbreak dynamics

Mean growth departure from white spruce (a measure of growth suppression) and

white ring relative frequency were plotted to generate maps for the three major outbreak

periods, which were considered to occur between the first year of white ring formation

and the last year of growth suppression below -1.28 standard deviations (Figures 3.6-3.8).

The first major outbreak was the longest, occurring between 1939 and 1948 (Figure 3.6). White ring and growth suppression occurred gradually starting in the north western portion of the DMPF and spread throughout the DMPF until 1942. A clear pattern of white ring formation was observed, with white rings appearing in the north in 1939, to the northwest in 1940, the northeast in 1941 and the east in 1942 (Figure 3.6). This outbreak may be described as a 'gradual' outbreak, with small areas being infected year after year with a slower dispersal of the insect. Localized areas of white ring and growth suppression formation occurred between 1945 and 1948 (Figure 3.6). Multiple years of growth rings occur in many sites, especially between 1939 and 1942. White rings and growth suppression were closely associated, except in 1941, 1947 and 1948, however, growth suppression was not a major outcome for most of the 1940s outbreak (Figure 3.6).

The second major outbreak studied lasted only a few years between 1961 and 1965 (Figure 3.7). This outbreak appeared as a short, intense, 'pulse' type outbreak. Multiple years of white ring formation occurred in some sites, with one site in the north eastern portion of the park recording white rings each year between 1961 and 1963 (Figure 3.7). Other sites recorded multiple years of white ring formation in 1962 and 1963. White ring formation began in 1961, with 5 trembling aspen sites with over 50% white ring frequency, but was not associated with growth suppression as determined by OUTBREAK. However, a severe drop in growth was present in both the trembling aspen and white spruce chronologies (Figure 3.2) during this year. In 1962, growth suppression and white rings were widespread throughout the DMPF, except in some areas to the south of the DMPF and in the center of the DMPF (Figure 3.7). White rings in the northern half of the DMPF are associated with intense growth suppression in 1962, but white rings

were not observed in the southernmost sites despite strong growth suppression. In 1963 and in 1965, white rings and growth suppression occurred only in small localized patches and were not associated together (Figure 3.7). During the most recent outbreak, from 1982 to 1985, growth suppression and white ring formation predominated in 1984 (Figure 3.8). This outbreak appeared to have developed as a 'multi-foyer' type outbreak, with small, localized outbreaks occurring in many areas of the DMPF. Multiple years of white ring formation did not occur in any of the sites and both white rings and growth suppression were localized (Figure 3.8). Sites where white rings had formed were generally associated with growth suppression, but this was not always the case.

3.4.4 Stand type and age class outbreak characteristics

Mean age (xage) was not found to be significantly different among the stand types in both young and old sites indicating that stand types were comparable (Table 3.2). A trend ($p < 0.1$) was, however, observed in older sites, with trembling aspen/ balsam poplar stand type sites being slightly younger. None of the characteristics calculated for the period 1900 - 2002 were found to differ significantly among the stand types and this for both the old sites (Table 3.2a) and the young sites (Table 3.3b). A trend in the relative frequency of suppression (s128) was observed, with young trembling aspen/ jack pine stand type sites recording more severe suppression at the −1.28 standard deviation level (Table 3.2b).

During the outbreak of the 1940s, one characteristic was found to be significantly different among the stand types. In old sites, trembling aspen/ balsam poplar trees had a

higher maximum growth suppression (tmaxr40) during the 1940 outbreak than trembling aspen/ jack pine site trees, which had the lowest value (Table 3.3a). Despite not being significant at the P<0.05 level, a trend was also observed in site level maximum growth reduction (maxr40) and the duration of severe growth reduction (tdur40), during the 1940 outbreak, with higher values in the trembling aspen/ balsam poplar sites.

During the 1960s outbreak, seven variables were found to be significantly different among the stand types during the 1960s outbreak (Table 3.3b). Average relative frequency of white rings (tavwrint60) was higher in trembling aspen/ jack pine trees than in any of the other site types. Trembling aspen/ jack pine trees were also found to have higher average growth reduction (tavr60) than trembling aspen trees. A higher maximum (twrmax60) and average (twrout60) relative frequency of white rings was recorded in the trembling aspen/ jack pine trees, than the trees in the other 2 mixed site types during the 1960 outbreak (Table 3.3b). The jack pine mixed sites were also found to have a higher occurrence of missing rings (mrout60) and more years with white ring formation (yrmr60) during the 1960 outbreak period than trembling aspen/ white spruce sites (Table 3.3b). Lastly, during the 1960 outbreak, severe growth suppression lasted longer (dur60) in trembling aspen/ jack pine sites than in trembling aspen and trembling aspen/ balsam poplar sites. Trends were also observed in trembling aspen/ jack pine sites, for higher maximum and average growth reduction (maxr60 and avr60), a higher occurrence of white rings (wrout60) and more years with white ring production (wryr60). During the 1980s outbreak, no variables were found to differ significantly among stand types from the old sites (Table 3.4a).

As previously stated, none of the variables calculated for the period 1900 - 2002 (Table 3.2b), nor for the 1980 outbreak period (Table 3.4b) was significantly different among the young stand types. When comparing the 1980s outbreak between the old and the young sites, trees from the young sites registered significantly higher average growth reduction (tavr80) than in old sites (Table 3.5).

3.5 Discussion

3.5.1. Forest tent caterpillar outbreak history

Based on the occurrence of white rings and growth suppression in the trembling aspen chronology, three important periods of forest tent caterpillar outbreaks were identified between 1900 and 2002. Major outbreaks have occurred from 1939 to 1948, 1961 to 1965 and 1982 to 1985 and all have originated in the north. These periods of forest tent caterpillar outbreak are supported by previous reports of forest tent caterpillar activity in the Canadian prairie provinces during these periods (Brown 1940, 1941; Hildahl and Reeks 1960; Elliot and Hildahl 1963, 1964, 1965; Moody and Cerezke 1983, 1984, 1985). Additional outbreaks are suspected in the 1830s, the 1850s, 1870s, the early 1900s, however, it is difficult to validate these periods due to the low number of samples. However, the synchronicity of growth suppression among the three host species and the occurrence of white rings in the trembling aspen indicate a potential large-scale outbreak in the 1870s. Additional suspected outbreak periods in the 1920s, 1950s, the early 1970s and the 1990s correspond to forest tent caterpillar activity and white ring formation in western Saskatchewan and central Alberta (Hogg and Schwarz 1999; Cooke 2001) and to periods of reduced growth in trembling aspen and paper birch in Québec caused by the

forest tent caterpillar (Bergeron and Charron 1994; Bergeron *et al.* 2002). Between 1906 and 1937, no forest tent caterpillar outbreaks were identified in the DMPF, and only small local outbreaks in some western states and provinces were recorded during this time (Hodson 1941). Additionally, much of the DMPF burned between 1885 and 1895 (Gill 1930; Tardif 2004), affecting forest tent caterpillar dynamics during the early parts of the century.

The longest forest tent caterpillar outbreak in the DMPF occurred during the 1940s and was documented in historical survey records (Brown 1940, 1941). Outbreaks of the forest tent caterpillar occurred in Northern Minnesota between 1933 and 1938 and between 1948 and 1959 (Hodson 1941; Duncan and Hodson 1958; Hodson 1977). Extensive defoliation took place in much of Ontario, British Columbia and parts of Saskatchewan until 1938 when outbreaks had been greatly reduced except in parts of Saskatchewan and Manitoba (Brown 1941; Hodson 1941). The forest tent caterpillar, in part, caused growth reduction and white ring formation in trembling aspen from central Alberta between 1936 and 1938 and 1941 and 1943 (Cooke 2001) and growth reduction in trembling aspen and paper birch in 1933 and 1940 in Québec (Bergeron and Charron 1994; Bergeron *et al.* 2002). The outbreak spread into the DMPF via the Porcupine Forest Reserve (PFR) to the north and by 1939/1940, the extensive outbreak occurring in the PFR had invaded the northern portion of the DMPF (Brown 1941). Forest insect and disease survey maps indicate that the outbreak continued to grow steadily in area and intensity until 1942 and 1944 (Brown 1940, 1941; Hildahl and Reeks 1960). However, white ring and suppression data indicate that a peak in forest tent caterpillar activity occurred in 1942 and again in 1946, when white ring formation and growth suppression

were widespread in the DMPF. These peaks in forest tent caterpillars were not detected by aerial surveys despite the large amount of the DMPF that seems to have been affected during this period, however, Hildahl and Reeks (1960) do report the 1942 peak in defoliation.

In the DMPF, the early 1960 'pulse' outbreak was shorter and more intense than the outbreak of the 1940s. Growth suppression was observed throughout the DMPF in 1962 and white rings were formed throughout the northern half, except in the central area, where a large fire had burned in 1961 (Tardif 2004). This outbreak occurred as a part of a larger outbreak, which covered 350000km^2 of the prairie provinces from 1957 to 1965 (Prentice and Hildahl 1961; Elliot and Hildahl 1962, 1963, 1964, 1965; Hildahl and Campbell 1975). White ring formation has also been associated with this outbreak period in western Saskatchewan and central Alberta (Hogg and Schwarz 1999; Cooke 2001). Populations of forest tent caterpillars in the DMPF had been steadily increasing in years previous to 1962 (Prentice and Hildahl 1961; Elliot and Hildahl 1962). In 1961, an extremely dry year occurred along with a large fire, which burned approximately 6% of the DMPF in the summer of 1961 (Tardif 2004). Forest tent caterpillar activity in 1962 was recorded as the most extensive of any year ever recorded in Manitoba and Saskatchewan (Elliot and Hildahl 1963), and white rings were more abundant in both trembling aspen and paper birch in 1962, than in any other year. The population explosion in 1962, observed across the prairie provinces (Elliot and Hildahl 1963) was most likely due to the extreme drought event in 1961.

Forest tent caterpillar activity during the early 1980s was recorded within the province of Manitoba, particularly in the north western region (Moody and Cerezke 1983, 1984, 1985, Grandmaison 1993) and in western Saskatchewan and Alberta, where white ring formation was recorded (Hogg and Schwarz 1999; Cooke 2001). Forest tent caterpillar defoliation covered 6000 km^2 in Manitoba for 1982 and 1983 and 769 km^2 in 1984, with a decrease in insect activity in following years (Grandmaison 1993). During the 1980s, several localized outbreaks occurred, mainly in the northern portion of the DMPF, however, the outbreak never reached the same extent as the 1960 or 1940 outbreaks. It is possible that the rising severity of forest tent caterpillar activity between 1982 and 1984 (Moody and Cerezke 1983, 1984; Grandmaison 1993) marked the beginning of a large slow spreading outbreak similar to the 1940s outbreak. However, severe late spring frosts occurred in 1984 in western Manitoba as reported by Moody and Cerezke (1985), with 20 days with a minimum temperature below 0°C between April 1st and May 10th (Environment Canada 2004). Spring frosts may have reduced forest tent caterpillar populations in 1984, as extreme weather events have been known to control forest tent caterpillar populations, simply by killing off young buds and leaves and causing starvation in the insect populations (Hodson 1941; Blais *et al.* 1955; Hildahl and Campbell 1975). Roland *et al.* (1998) also found that early season cold weather was a factor in forest tent caterpillar outbreak length in Ontario. Although white rings were observed before 1984, it is not known if late spring frosts could have caused the formation of white rings in trembling aspen instead of the forest tent caterpillar in 1984. Although white rings have been linked to forest tent caterpillar defoliation (Hogg and Schwarz 1999; Cooke 2001; Hogg et al. 2002b), other natural processes may also cause the formation of white rings in some cases. It is therefore necessary to consider extreme

events such as severe late season frosts as a possible source of error while reconstructing forest tent caterpillar activity.

Although trembling aspen is the preferred host species for the forest tent caterpillar (Hodson 1941; Sippell and Ewan 1967; Hildahl and Campbell 1975; Ives and Wong 1988; Zasada and Phipps 1990), balsam poplar and paper birch were affected by the same outbreaks as the trembling aspen. The occurrence of growth suppression and white rings in the balsam poplar and paper birch chronologies indicate that the DMPF outbreaks during the 1940s, 1960s and 1980s were intense. Radial growth reduction of paper birch in Québec, after forest tent caterpillar defoliation, was more severe than trembling (Bergeron et al. 2002) similarily, in the DMPF, growth suppression during the 1920s and the late 1990s affected balsam poplar and paper birch more than trembling aspen. White rings were not present in either species during these periods however, and it is unclear if these growth suppression periods were caused by factors other than the forest tent caterpillar. In a study done in Minnesota, paper birch foliage was defoliated only after trembling aspen and both red oak (*Quercus rubra* L.) and bur oak (*Quercus macrocarpa* L.) trees were stripped, because of the inability of young larvae to eat the sticky paper birch leaves (Hodson 1941).

3.5.2. Forest tent caterpillar dynamics

The reconstruction of forest tent caterpillar outbreaks by stand type and age confirmed that the major outbreaks identified for the DMPF overall chronologies occurred in each of the old stands. For the major outbreaks occurring during the 1940s

and the 1980s, which were not associated with severe drought, very little differences were found among the stand types. No differences in outbreak frequency, duration or intensity were observed among the stand types when comparing the period 1900 - 2002. Hogg and Schwarz (1999) also found that similar numbers of white rings were formed in mixed forest stands and in pure trembling aspen stands between 1978 and 1992. In Ontario, the proportion of trembling aspen was not found to affect outbreak duration either (Roland 1993). However, our results clearly indicated significant differences among stand types during the 1960s outbreak. During the 1960s outbreak, trembling aspen/ jack pine sites recorded more growth loss and more white and missing rings. As previously stated, the 1960s outbreak was associated with an extreme drought, which took place during the summer of 1961. The eight major tree species in the DMPF have been found to react negatively to moisture stress caused by high summer temperatures (Girardin and Tardif *in press*). Trees in the trembling aspen/ jack pine site type may be especially susceptible to moisture stress as jack pine sites in the DMPF are typically located on well drained substrates (Hamel and Kenkel 2001). Jack pine in general grows on dry sites throughout its range and is known to grow on rock outcrops in the boreal forest (Rudolph and Laidly 1990).

Drier sites may thus be especially susceptible to the effects of forest tent caterpillar defoliation following extreme drought events. Trembling aspen decline has been associated with the combined effects of drought and forest tent caterpillar outbreaks (Hibben 1962; Payette *et al.* 1994; Hogg and Schwarz 1999; Candau *et al.* 2002; Hogg *et al.* 2002a). Drought stressed trees may be more attractive to insects, due to the changing chemical compositions of their leaves and the concentration of nutrients within the tree

(Mattson and Haack 1987). An increase in foliar nitrogen in sugar maple trees was associated with biological performance of forest tent caterpillars feeding on the more nutritional leaves from forest edge trees (Fortin and Mauffette 2001). Microclimate conditions associated with forest-edge effects have also been shown to affect the spread of viruses and parasitoids within the forest tent caterpillar population (Roland and Kaupp 1995; Rothman and Roland 1998). Differences in forest structure and microsite conditions may also affect the spread of these controlling agents, but this remains untested.

Evidence for forest tent caterpillar outbreaks in the young sites was also present, however, the length and timing of the growth suppression period varied. In addition, white rings were not observed in a large percentage of the young sites, except in the case of the trembling aspen/ balsam poplar site type. Additionally, the period between 1900 and 1936, when very little evidence for forest tent caterpillar outbreaks exists, represents a period of time when young forest stands dominated the DMPF, after fires burned much of the forest during the late 1800s. Although this may suggest that young stands are less reliable for the identification of forest tent caterpillar outbreaks, all young site types, which were old enough, showed evidence of the outbreaks both in the 1940s and 1960s. In addition, white rings have been experimentally induced in young trees (Hogg *et al.* 2002b) and have been observed in the young portion of trembling aspen stems (Sutton and Tardif in press). It is possible that young sites may only record outbreaks of a given intensity, and the 1980s, or those occurring between 1900 and 1936 were not intense enough to be recorded by the younger trees. Although older stands may be more susceptible to insect activity, due to reduced physiological activity (Kozlowski 1969),

especially after repeated defoliation throughout their lives (Duncan and Hodson 1958; Rose 1958; Hildahl and Reeks 1960; Leininger and Solomon 1994; Naidoo and Lechowicz 2001), the evidence for the outbreak during the 1980s was also weak in older sites. During the 1980 outbreak younger sites were found to have higher average growth suppression than the older sites. However, compared to the outbreak of the 1960s, growth suppression during the 1980s was not very intense, and the difference between old and young sites may be due to differences in competition or clonal carbohydrate reserves (Bassman and Dickmann 1982; Landhausser and Lieffers 2002).

3.5.3 White ring occurrence

In general, white rings and growth suppression during the major outbreaks occurred simultaneously in the same sites, but this was not always the case. In some cases, where growth suppression occurred, white ring formation was not recorded and some sites, where white rings formed, did not show growth suppression. White rings were produced several years in a row in some sites but not in other sites and they were not necessarily formed in all trees sampled within a site (data not presented). This is particularly evident during the 1940 outbreak, where white rings were abundant throughout the outbreak period, but not always associated with growth suppression. The same may be said of 1961, however, severe growth suppression during this year occurred in the trembling aspen and white spruce residual chronologies because of the extremely dry year (Girardin and Tardif *in press*) and the OUTBREAK program was not able to distinguish the defoliation signal from the drought signal. The 1940s were not associated with an extreme drought and although forest tent caterpillar activity throughout the

DMPF may have been intense enough to induce white ring formation, it was not as effective at causing severe growth suppression. It is unclear why white rings are formed in some cases and not in others and this requires more study. Cooke (2001) found that some periods of severe growth suppression in trembling aspen in central Alberta occurred in the absence of white rings. Hogg and Schwarz (1999) also found that white rings were not necessarily formed in all stems within a site and were not formed in every site within the same year. White rings were experimentally produced only when 98-100% of the tree was defoliated in early June and were not produced with less defoliation, or when defoliation occurred in late June, July or August (Hogg *et al.* 2002b; Jones *et al.* 2004). In some cases, the absence of white rings may be explained by slight delays in the timing of the insect attack (Kozlowski 1969).

Other factors which may also affect the formation of white rings have been previously discussed (Sutton and Tardif *in press*) and the response to insect attack may also be related to previous reserve accumulation (Morey 1973; Landhausser and Lieffers 2002) or the ability of the trees to rebound after the insect attack with the remobilization of reserves (Parker and Houston 1971; Bassman and Dickman 1982; Heichel and Turner 1983; Sauter and Neumann 1994; Landhausser and Lieffers 2002). In general, white rings have been useful for identifying past forest tent caterpillar outbreaks, but they should be used in combination with other indicators. White ring evidence during the 1940 and the 1960 outbreak indicated that not only are white rings associated with forest tent caterpillar activity in trembling aspen (Hogg and Schwarz 1999; Hogg 2001; Hogg *et al.* 2002b; Cooke2001) but may also be used as an indicator of defoliation in balsam poplar and paper birch.

3.5.4 Conclusion

Three major forest tent caterpillar outbreak periods and three smaller suspected outbreak periods were identified the DMPF between 1900 and 2002, with an additional possible large-scale outbreak occurring during the 1870s. Outbreak periods occurring from 1939 to 1948, 1961 to 1965 and 1982 to 1985 were associated with severe growth suppression and the formation of white and/or missing rings. Additional outbreaks are suspected in the 1870s, 1950s, the early 1970s and the 1990s. Balsam poplar and paper birch chronologies revealed similar periods of forest tent caterpillar outbreaks and were also found to produce white rings during these periods. The major outbreak periods corresponded to large outbreaks in other parts of North America and differed slightly in their intensity. The 1940 outbreak was a prolonged outbreak that spread slowly throughout the DMPF, causing the formation of white rings throughout and in many cases white rings were produced in multiple years in the same site during this outbreak. The 1960 outbreak was a short outbreak that followed an extreme drought year in 1961. Intense white ring formation and growth suppression affected much of the DMPF and spread quickly throughout the forest and dry sites were especially affected. The 1980s outbreak began as small, localized pockets of insect activity and a larger outbreak may have been cut short. Although white rings and growth suppression were produced during each of these outbreaks, they were not always associated and this may be due to differences in the timing and severity of the defoliation and to the ability of individual trees to react to defoliation.

Further research is needed to discover why white rings are not always produced in different sites or even in different trees within the same site, even when defoliation causes severe growth suppression. A small scale study would be useful to investigate the differences in the response to white ring causing defoliation by individual trees/clones and to the effects of clone responses to insect defoliation. Investigations are also needed into the effect that climate warming will have on the trembling aspen population in the DMPF, since climate change may affect moisture regimes in western Canada (Hogg and Hurdle 1995), and drier conditions may favour forest tent caterpillar activity, as warmer temperatures are ideal for the insect (Hodson 1941). In terms of forest management, the susceptibility to disease and mortality of older trees after repeated outbreaks also needs to be better assessed.

3.6 Acknowledgements

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and manuscript revision.
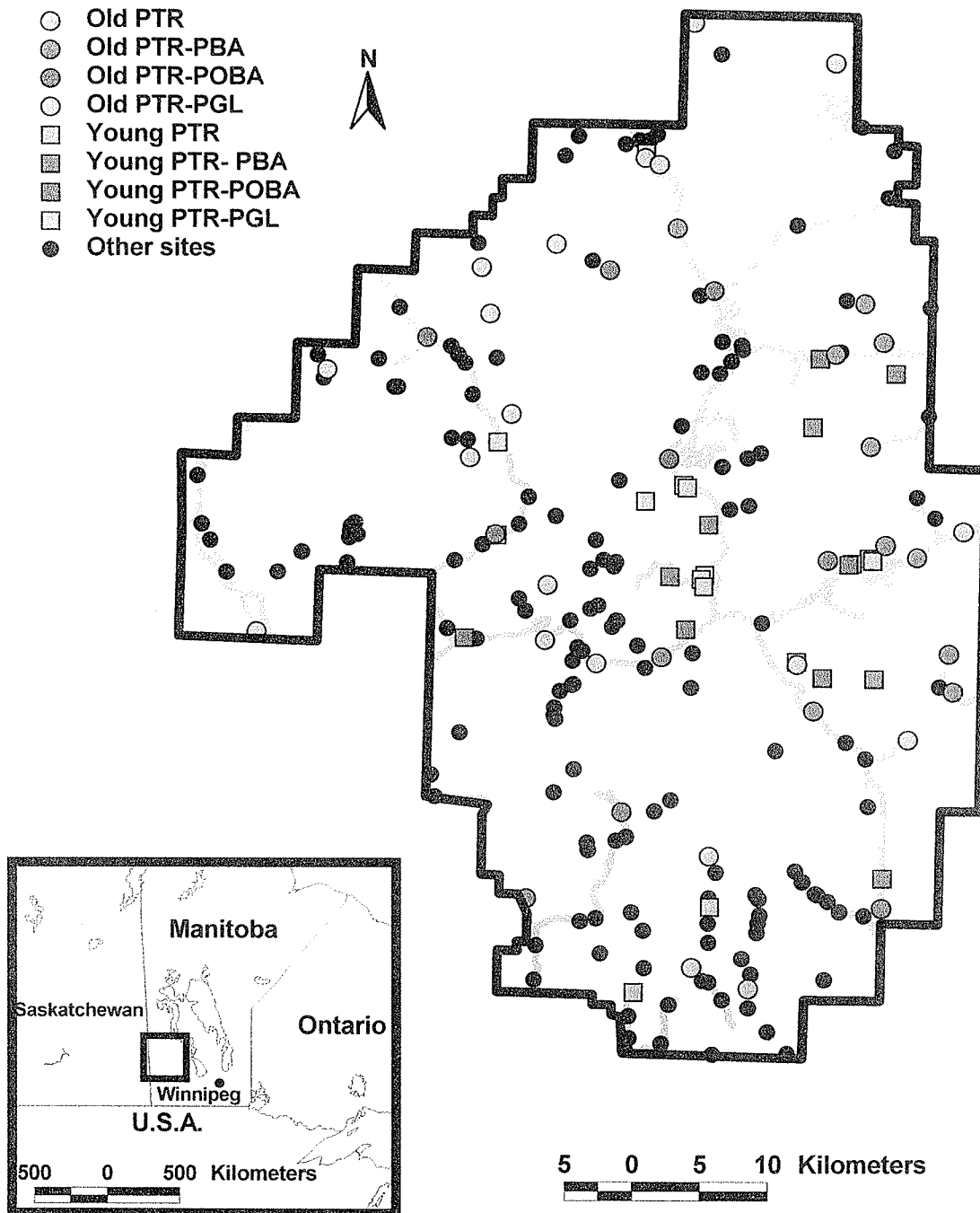
Figure 3.1. Map of the Duck Mountain Provincial Forest, showing the location of the sites containing trembling aspen trees sampled during a forest fire history reconstruction (Tardif 2004) and additional sites added in 2002 and 2003. The 67 vegetation/age class sites are categorized into age class and vegetation type as follows: trembling aspen (PTR), trembling aspen/ jack pine (PTR-PBA), trembling aspen/ balsam poplar (PTR-POBA), trembling aspen/ white spruce (PTR-PGL), all other sites are also included.
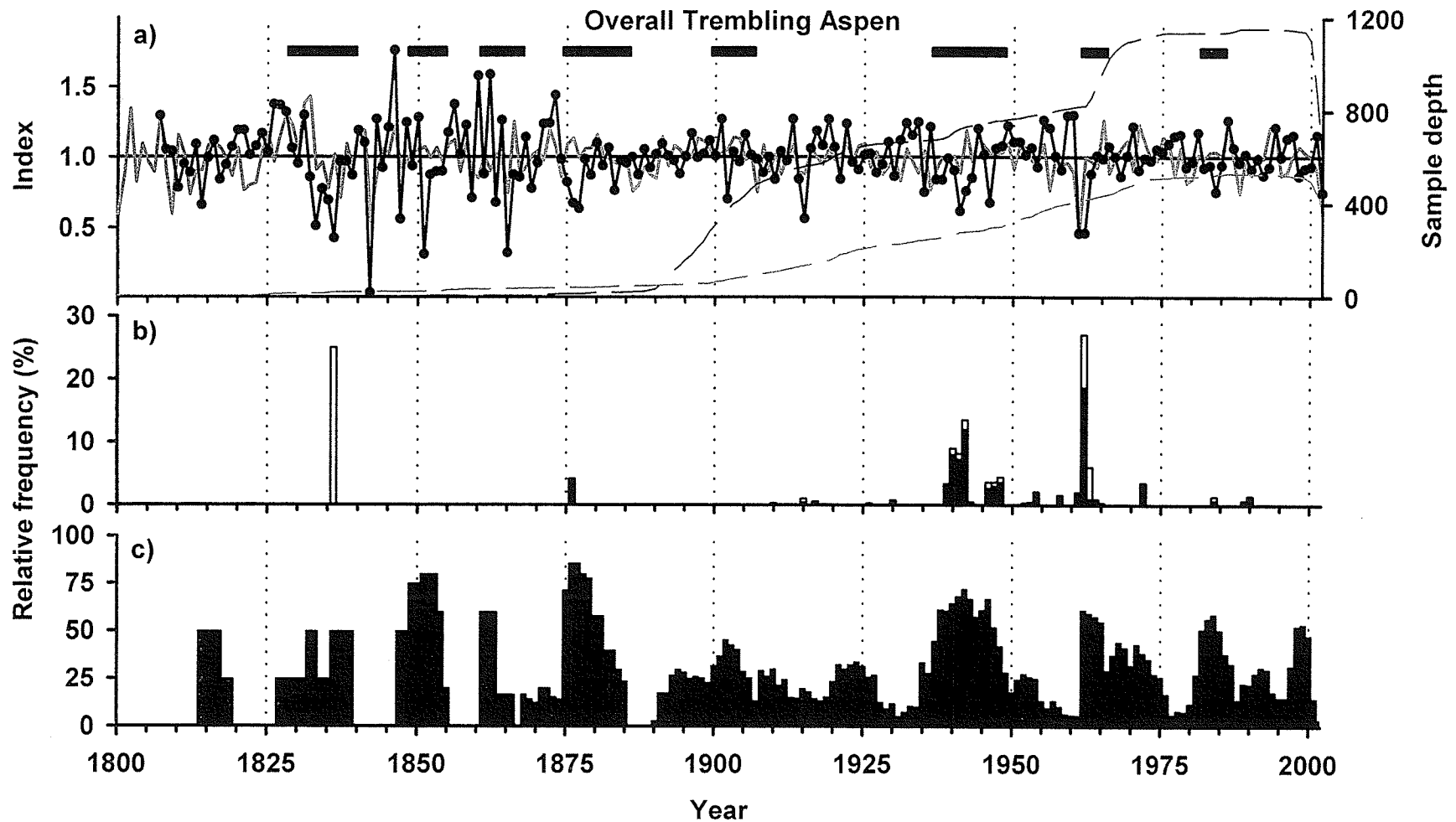
Figure 3.2. Overall trembling aspen residual chronology calculated from all sites with trembling aspen sampled in the Duck Mountain Provincial Forest. a) Residual trembling aspen (black lines) and white spruce (red lines) chronologies (smooth lines) and sample depth (broken lines). Periods of growth suppression, identified as possible forest tent caterpillar outbreaks by the OUTBREAK program, are marked by a solid black bar. b) Stacked bar chart showing the relative frequency of white (black bars) and missing rings (empty bars). c) Bar chart showing the percentage of individual series affected by growth suppression as identified by the OUTBREAK program.
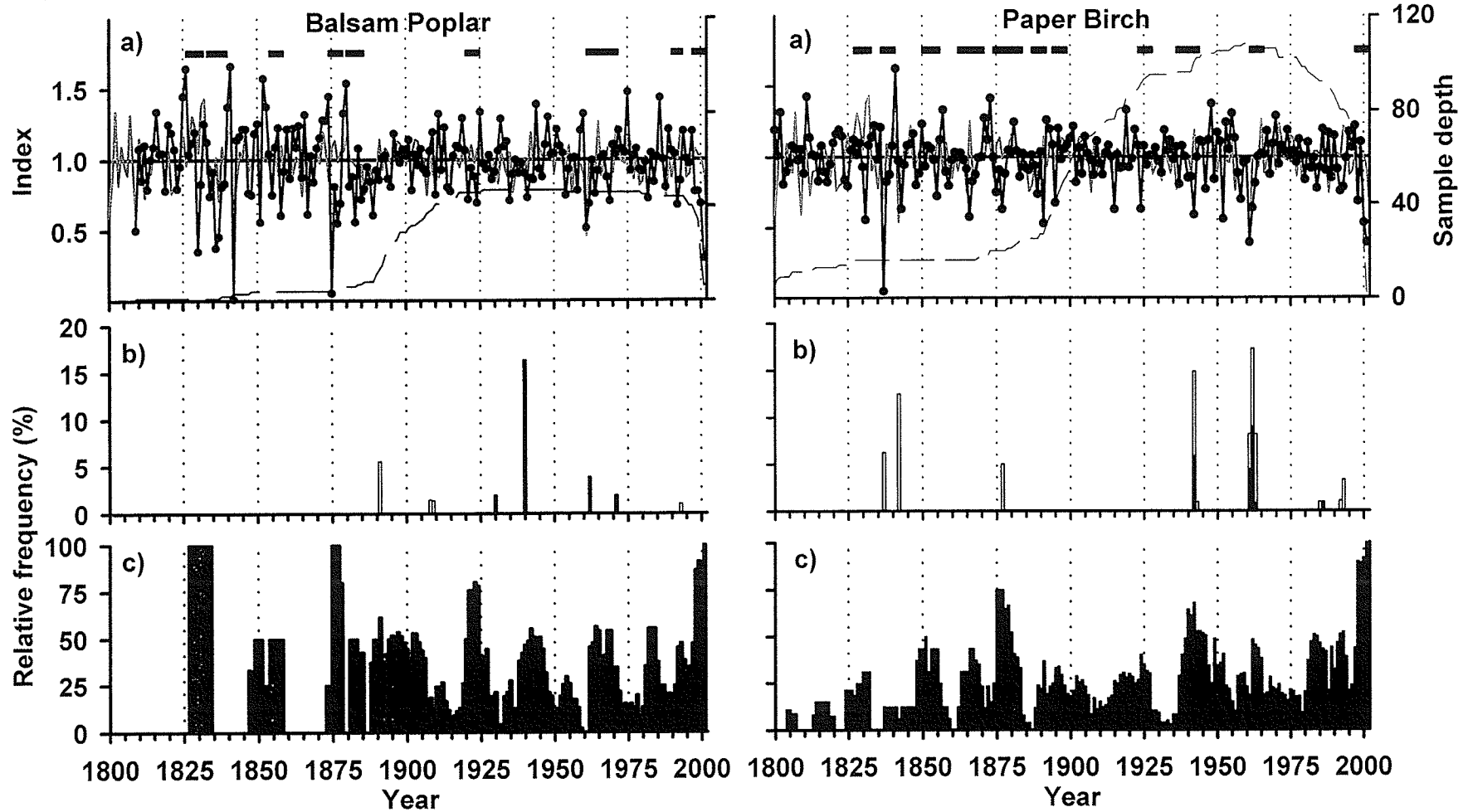
Figure 3.3. Overall balsam poplar and paper birch residual chronologies calculated from all sites with balsam poplar and paper birch (respectively) sampled in the Duck Mountain Provincial Forest. a) Residual trembling aspen (black lines) and white spruce (red line) chronologies (smooth lines) and sample depth (broken lines). Periods of growth suppression, identified as possible forest tent caterpillar outbreaks by the OUTBREAK program, are marked by a solid black bar. b) Stacked bar chart showing the relative frequency of white (black bars) and missing rings (empty bars). c) Bar chart showing the percentage of individual series affected by growth suppression as identified by the OUTBREAK program.
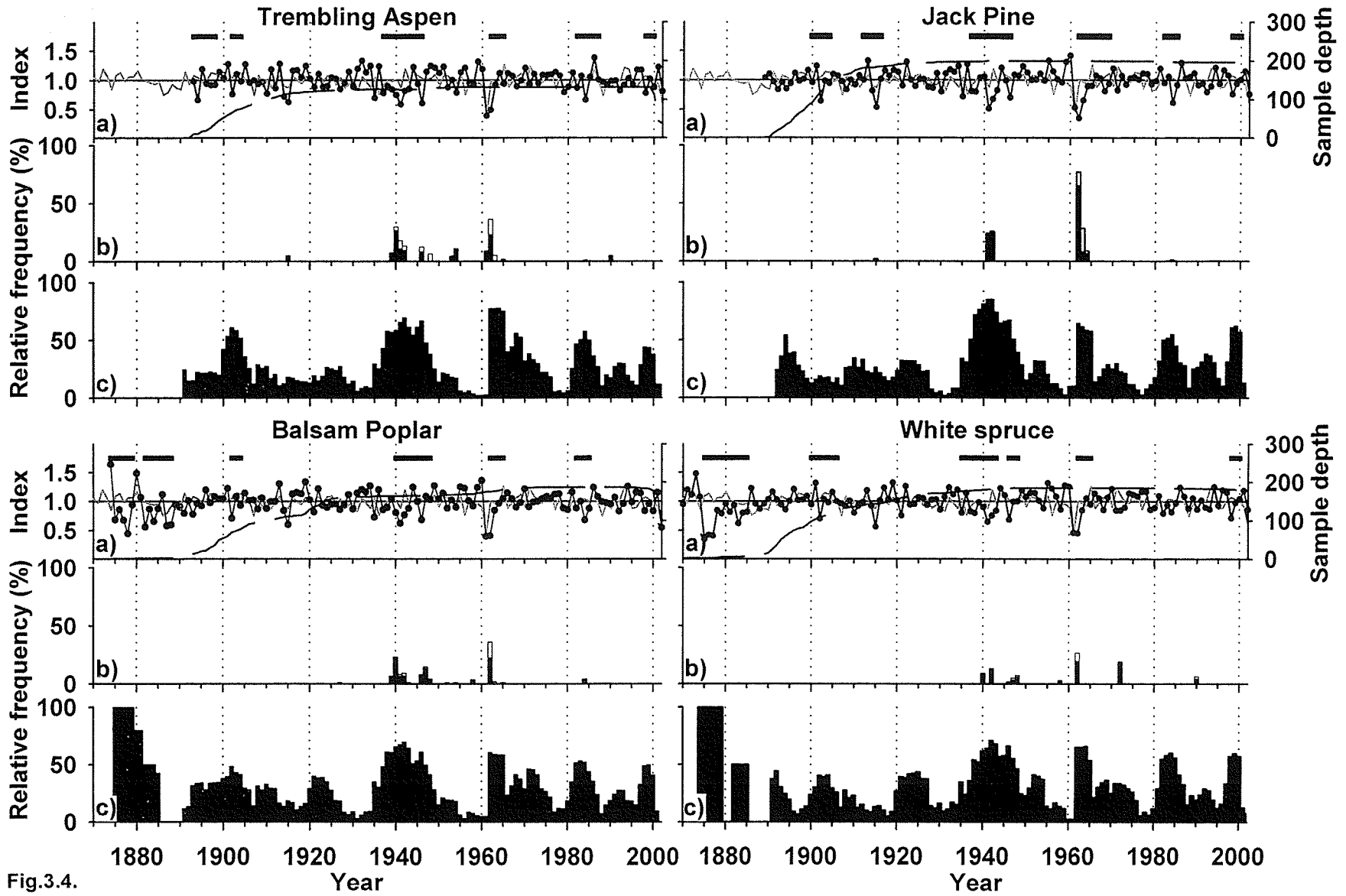
Fig.3.4.

Figure 3.4. Old trembling aspen, trembling aspen/ jack pine, trembling aspen/ balsam poplar and trembling aspen/ white spruce residual chronologies. a) Residual host (black lines) and white spruce (red line) chronologies (smooth lines) and sample depth (broken lines). Sample depth of the white spruce chronology is the same as in figure 3.2. Periods of growth suppression, identified as possible forest tent caterpillar outbreaks by the OUTBREAK program, are marked by a solid black bar. b) Stacked bar chart showing the relative frequency of white (black bars) and missing rings (empty bars). c) Bar chart showing the percentage of series affected by forest tent caterpillar defoliation as identified by the OUTBREAK program.
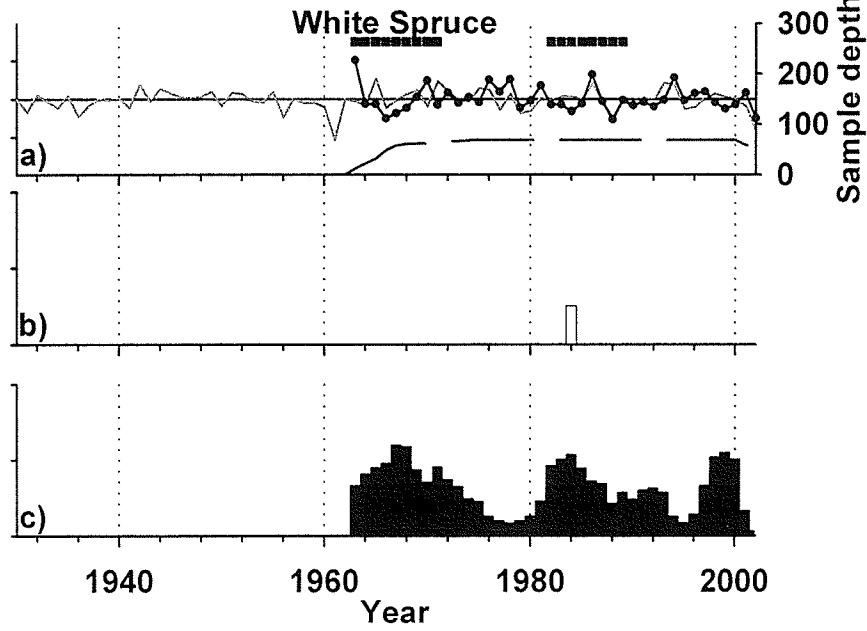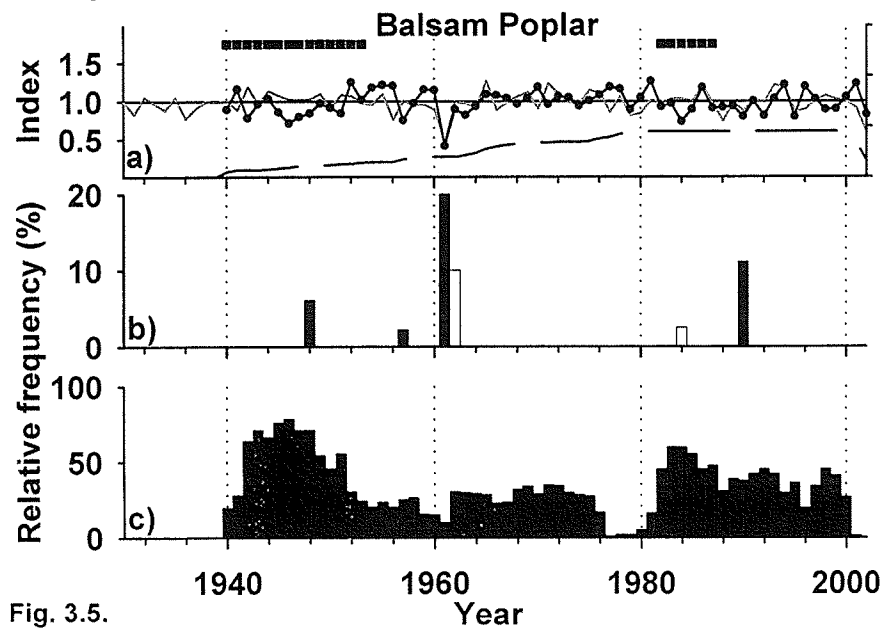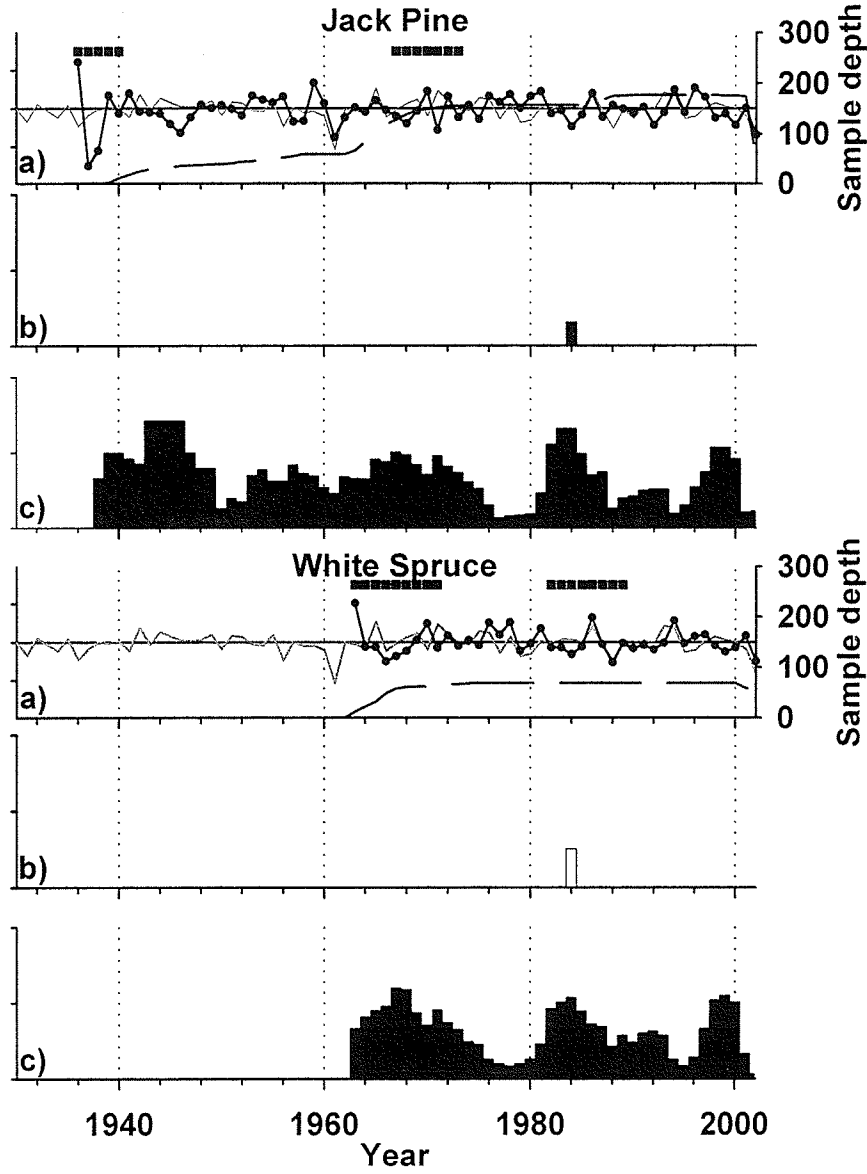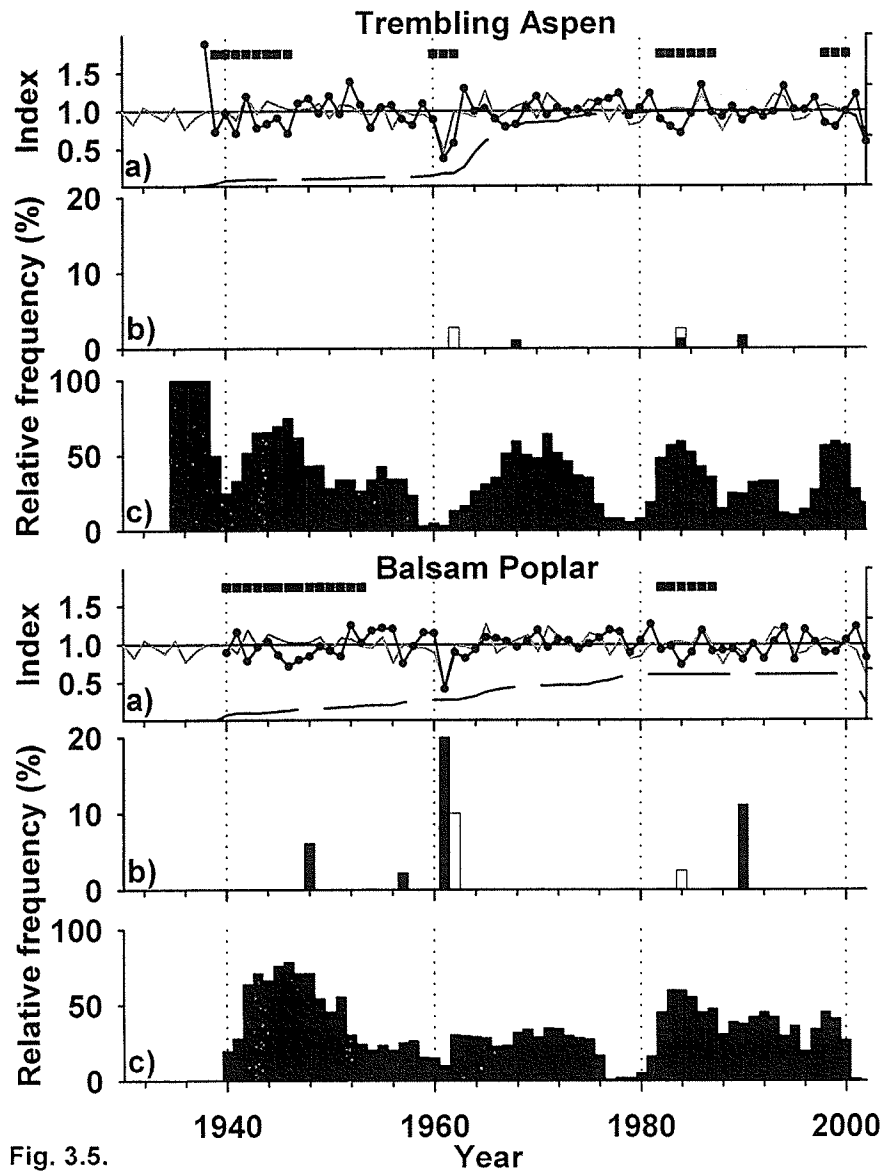
Fig. 3.5.

Figure 3.5. Young trembling aspen, trembling aspen/ jack pine, trembling aspen/ balsam poplar and trembling aspen/ white spruce residual chronologies. a) Residual host (black lines) and white spruce (red line) chronologies (smooth lines) and sample depth (broken line). Sample depth of the white spruce chronology is the same as in figure 3.2. Periods of growth suppression, identified as possible forest tent caterpillar outbreaks by the OUTBREAK program, are marked by a solid black bar. b) Stacked bar chart showing the relative frequency of white (black bars) and missing rings (empty bars). c) Bar chart showing the percentage of series affected by forest tent caterpillar defoliation as identified by the OUTBREAK program.
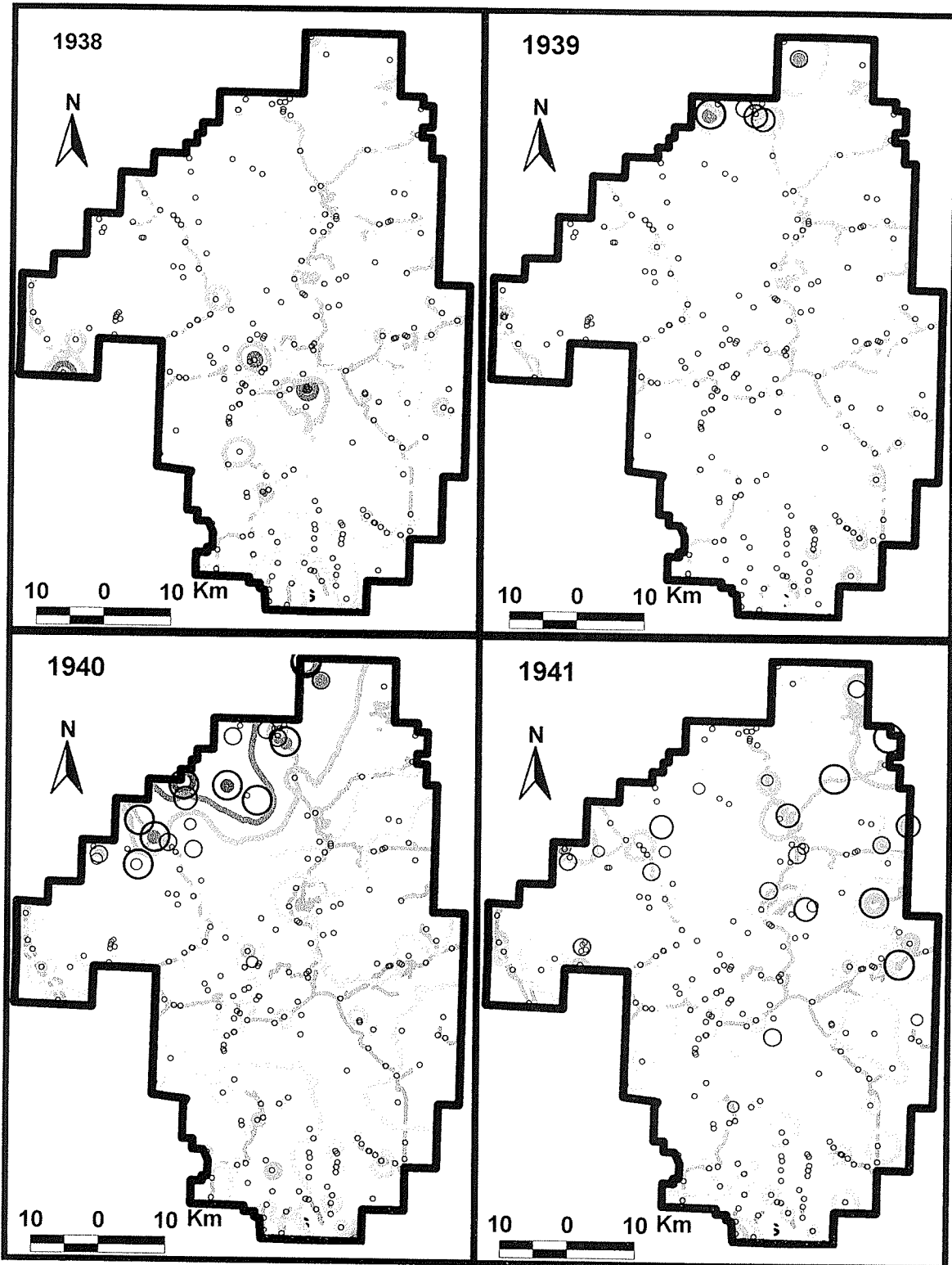
Fig. 3.6. Map of the Duck Mountain Provincial Forest showing the progression of the 1939 to 1948 forest tent caterpillar outbreak (with one year before and after the outbreak period). Mean negative growth deviation from white spruce growth (lines), in standard deviations (s.d.) is presented. The relative frequency of white rings (circles), in percentage (%) is also presented. Data was calculated for all sites with trembling aspen and are presented for each year.

90
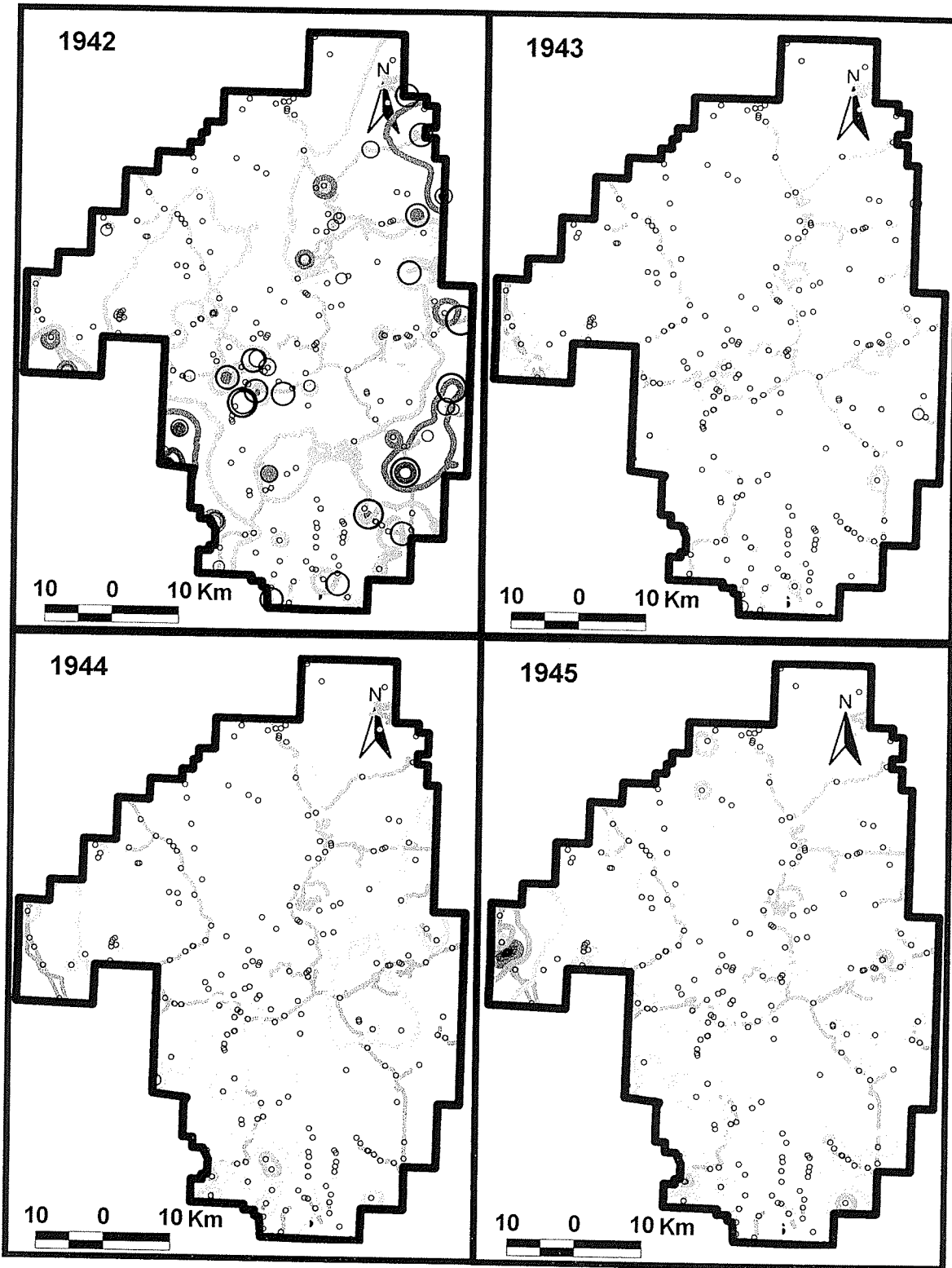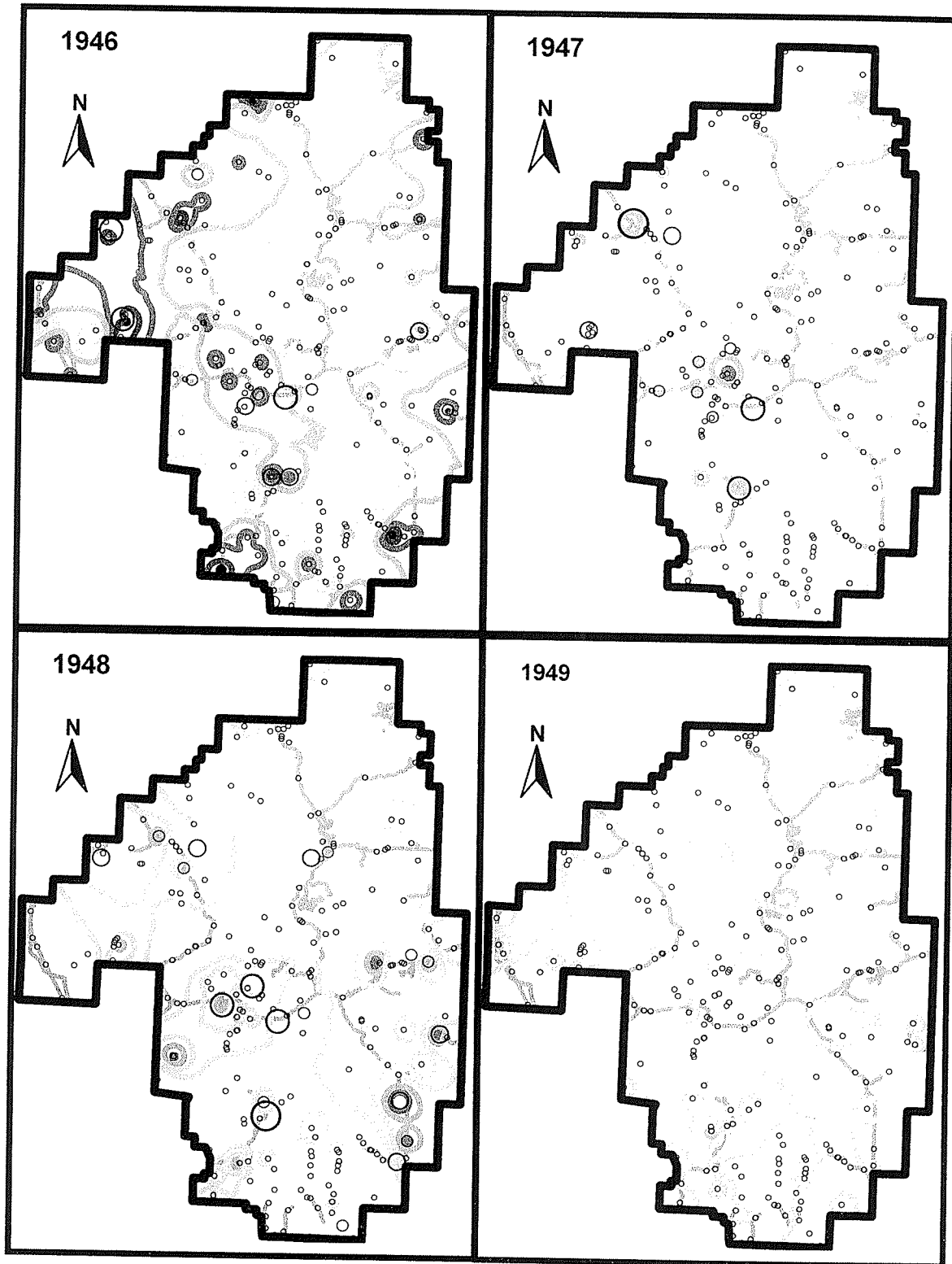
Fig.3.6. (con't)

Fig. 3.6. (con't)

Map legend

White rings
- o   **0%**
- o   **0 - 25%**
- ○   **26 - 50%**
- ○   **51 - 75%**
- ○   **76 - 100%**

Negative growth departure
- **0.00 - -0.50 s.d.**
- **-0.51 - -1.00 s.d.**
- **-1.27 - -1.01 s.d.**
- **-1.28 - -1.50 s.d.**
- **-1.51 - -2.00 s.d.**
- **< -2.00 s.d.**

Fig. 3.6. (con't)
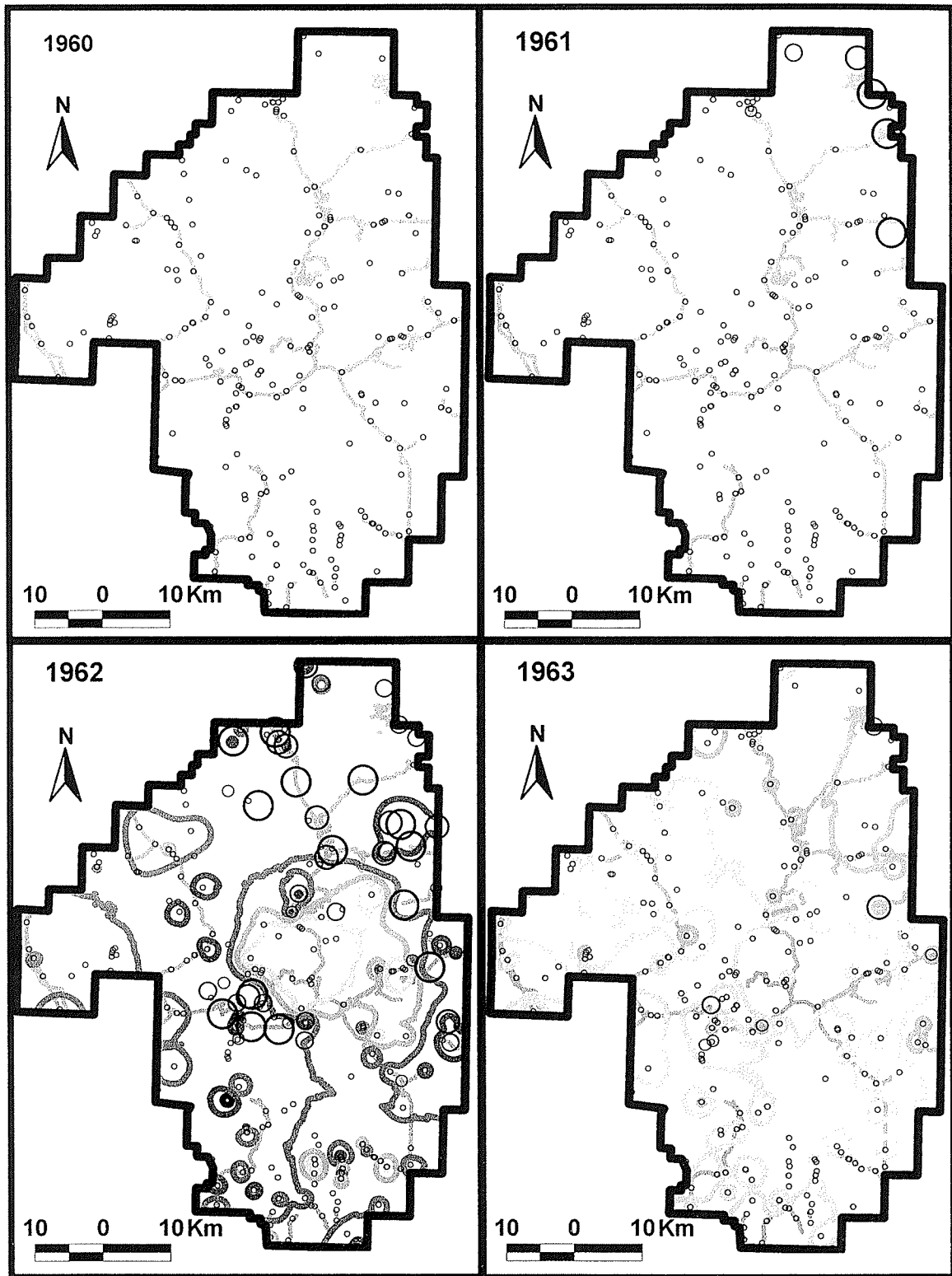
Fig. 3.7. Map of the Duck Mountain Provincial Forest showing the progression of the 1961 to 1965 forest tent caterpillar outbreak (with one year before and after the outbreak period). Mean negative growth deviation from white spruce growth (lines), in standard deviations (s.d.) is presented. The relative frequency of white rings (circles), in percentage (%) is also presented. Data was calculated for all sites with trembling aspen and are presented for each year.
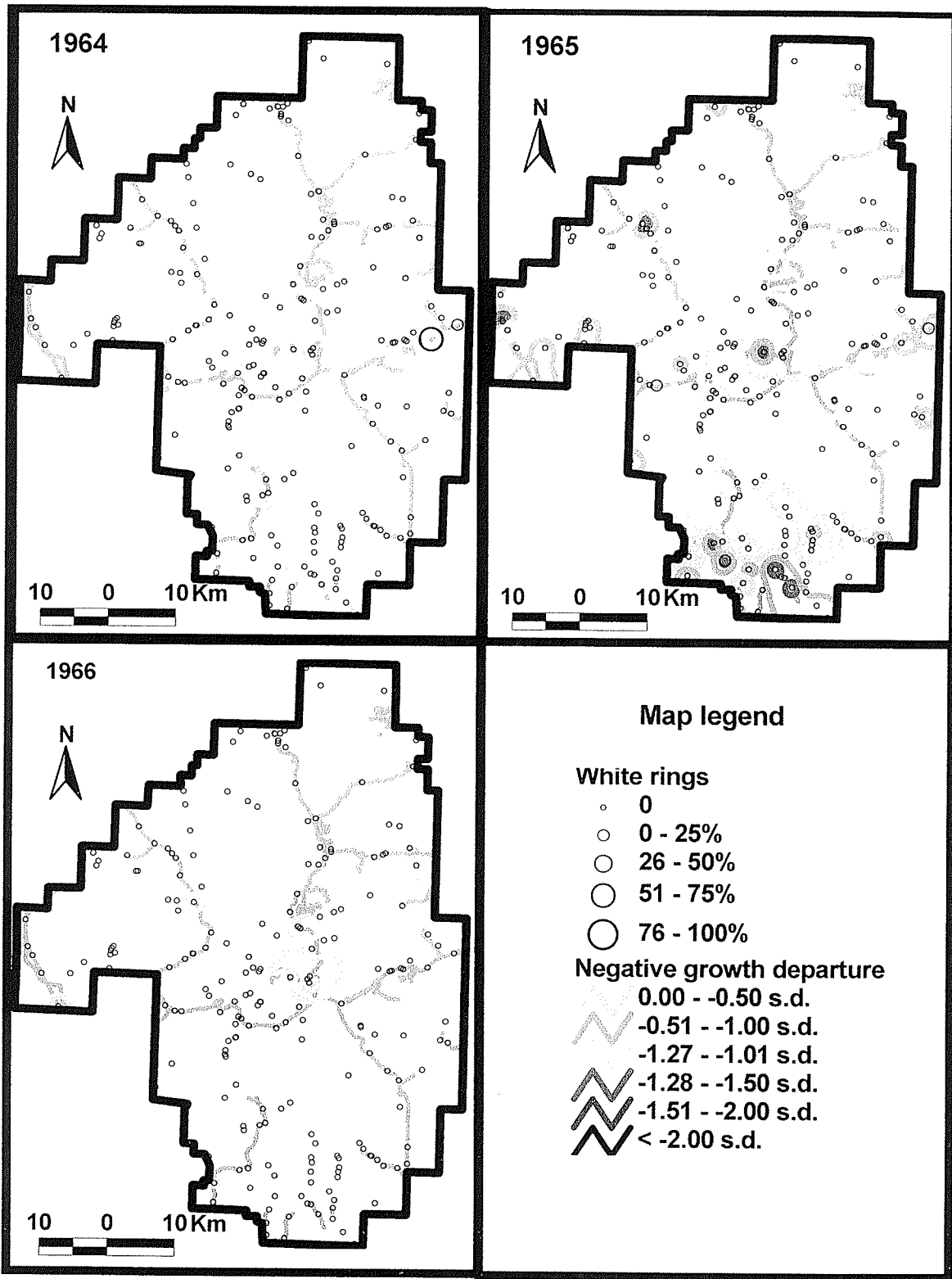
Fig. 3.7. (con't)
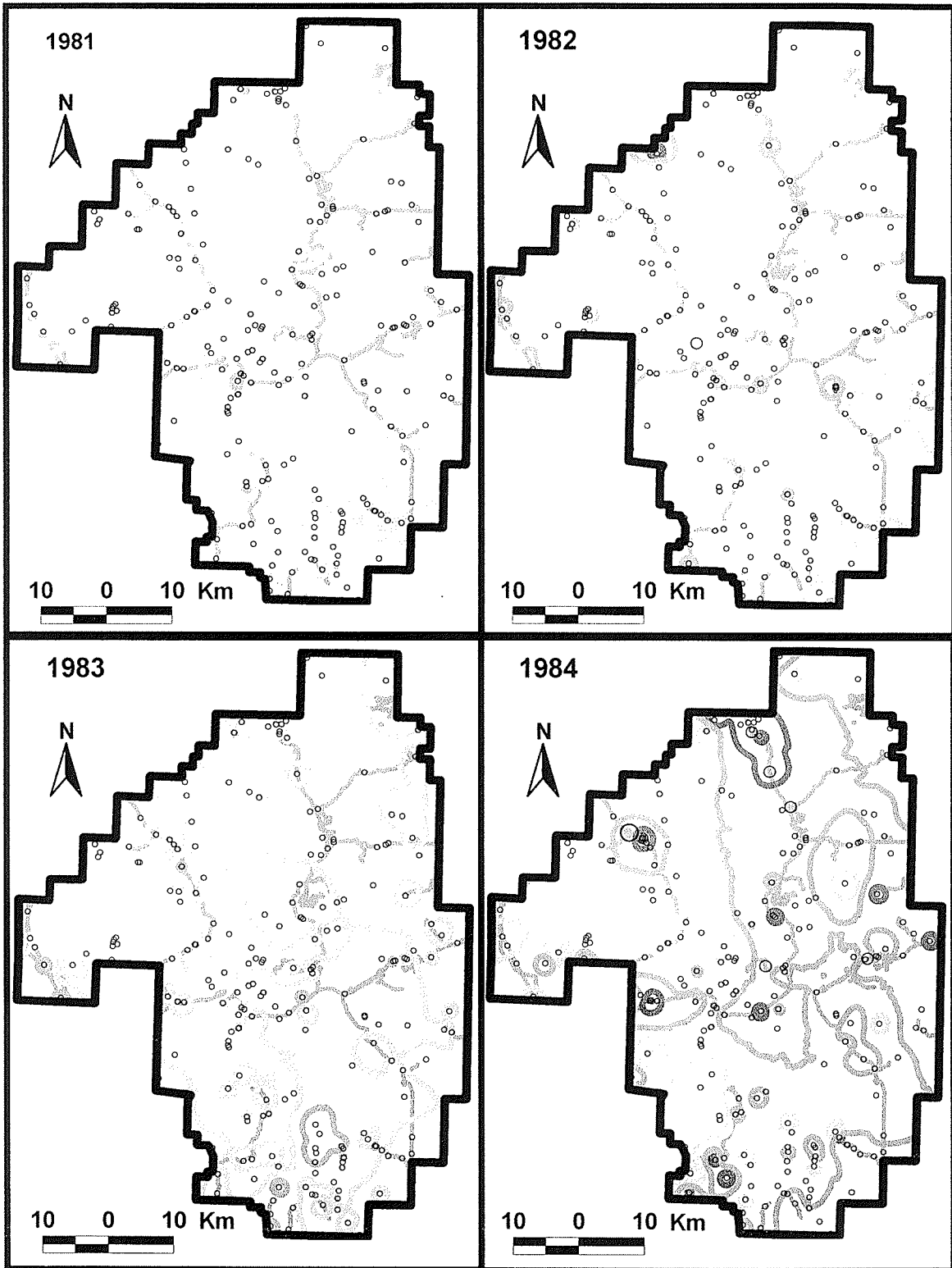
Fig. 3.8. Map of the Duck Mountain Provincial Forest showing the progression of the 1982 to 1985 forest tent caterpillar outbreak (with one year before and after the outbreak period). Mean negative growth deviation from white spruce growth (lines), in standard deviations (s.d.) is presented. The relative frequency of white rings (circles), in percentage (%) is also presented. Data was calculated for all sites with trembling aspen and are presented for each year.

1985

N

10　0　10 Km

1986

N

10　0　10 Km

Map Legend

White rings
- ○ 0%
- ○ 0 - 25%
- ○ 26- 50%
- ○ 51 - 75%
- ○ 76 - 100%

Negative growth departure
- 0.00 - -0.50 s.d.
- -0.51 - -1.00 s.d.
- -1.27 - -1.01 s.d.
- -1.28 - -1.50 s.d.
- -1.51 - 2.00 s.d.
- < -2.00 s.d.
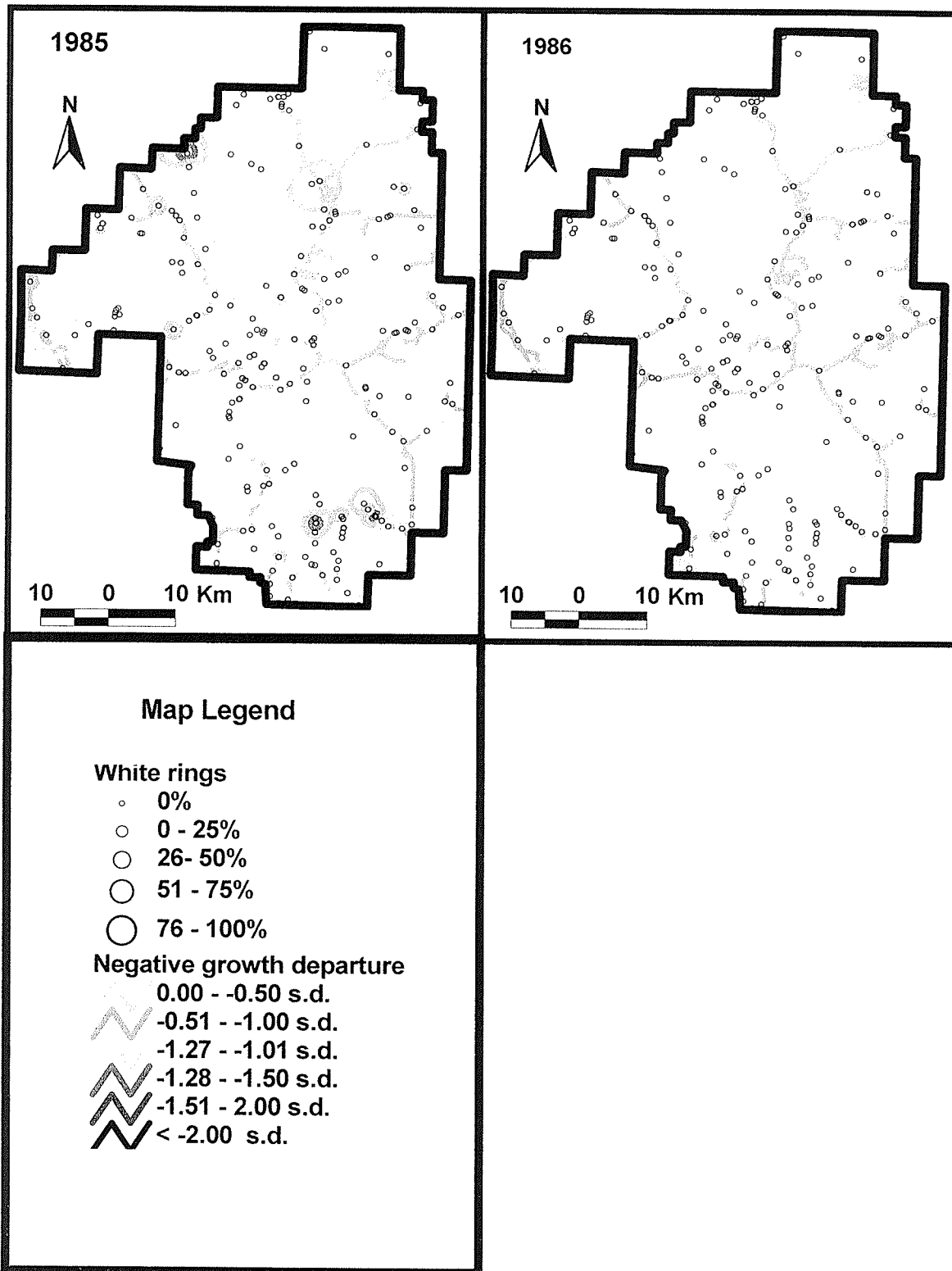
Fig. 3.8. (con't)

Table 3.1. Mean importance value and standard deviation for trembling aspen (PTR), balsam poplar (POBA), paper birch (BPA), white spruce (PGL), jack pine (PBA), black spruce (PMA) and balsam fir (ABA) and number of sites in each of the four stand types; trembling aspen (1-PTR), trembling aspen/ jack pine (2-PTR-PBA), trembling aspen/ balsam poplar (3-PTR-POBA), trembling aspen/ white spruce (4-PTR-PGL).

	1-PTR	2-PTR-PBA	3-PTR-POBA	4-PTR-PGL
Sites	17	19	17	14
PTR	81.65±7.81	30.80±18.57	49.49±17.52	51.81±19.43
POBA	13.42±12.06	3.58±6.38	54.01±12.56	6.28±9.71
BPA	9.62±14.47	9.01±13.37	5.54±9.63	6.62±6.90
PGL	15.00±13.91	5.88±10.01	16.24±12.58	59.76±10.00
PBA	0.00±0.00	60.13±17.16	3.24±8.03	2.14±6.74
PMA	0.65±1.45	24.94±19.13	1.75±5.01	0.87±3.26
ABA	1.21±3.41	5.65±10.25	1.50±3.80	5.59±13.29

Table 3.2. Mean and standard deviation for the 21 variables characterizing the forest tent caterpillar outbreaks identified from 1900 to 2002. The variables are calculated for both old (a) and young sites (b), among the 4 stand types; trembling aspen (1-PTR), trembling aspen/ jack pine (2-PTR-PBA), trembling aspen/ balsam poplar (3-PTR-POBA), trembling aspen/ white spruce (4-PTR-PGL). The variables are: number of sites (nsites) and cores (ncores), mean age (xage), relative frequency of years with white rings (rfwr), with missing rings (rfmr), with growth suppression below -1.28 and -1.7 standard deviations for the entire period (s128 and s17, respectively), and for years identified as outbreak years (s128o and s17o, respectively), number of outbreaks (nout), mean (xdur), maximum (maxdur) and minimum (mindur) duration of outbreaks in years. Variables calculated from the site chronology have no added prefix and those calculated from the mean of the individual series (cores), have the added prefix t. The p value for the Levene (LP) and one-way ANOVA (AP) tests are indicated.

a) old	LP	AP	1-PTR	2-PTR-PBA	3-PTR-POBA	4-PTR-PGL
Nsites	--	--	9	10	11	10
Ncores	--	--	135	199	185	186
Xage	0.245	0.060	1905±12.28	1900±5.22	1912±9.83	1903±11.64
Rfwr (%)	0.034	0.608	3.07±1.99	2.23±1.30	2.47±1.57	2.00±2.18
Rfmr (%)	0.155	0.772	1.51±1.33	2.14±1.65	2.08±1.11	1.67±1.88
S128 (%)	0.181	0.344	8.91±1.48	9.92±1.44	8.13±2.09	9.15±3.32
S128o (%)	0.751	0.351	26.55±4.01	27.40±7.73	24.26±5.47	23.03±6.07
S17 (%)	0.620	0.866	4.40±2.10	3.99±1.40	4.48±1.82	3.91±2.05
S17o (%)	0.723	0.391	13.93±6.55	12.63±7.05	13.35±6.40	9.40±4.10
Nout	0.432	0.399	5.44±0.88	5.00±1.15	4.82±1.25	4.50±1.43
Xdur	0.021	0.317	5.57±0.52	6.20±0.97	6.07±1.18	6.70±1.99
Mindur	0.083	0.303	3.22±0.44	5.60±0.52	3.36±0.67	3.80±1.03
Maxdur	0.095	0.710	9.56±1.33	9.10±2.18	8.82±2.40	10.10±3.90
Trfwr (%)	0.326	0.663	1.27±0.64	1.29±1.02	1.02±0.86	0.84±1.10
Trfmr (%)	0.004	0.333	0.42±0.61	0.37±0.40	0.24±0.10	0.14±0.19
Ts128 (%)	0.330	0.405	7.70±1.28	8.02±0.61	7.80±1.11	8.43±0.98
Ts128o (%)	0.558	0.635	13.88±4.49	16.23±7.45	18.09±6.51	17.68±4.95
Ts17 (%)	0.180	0.432	2.89±0.96	3.06±0.57	3.18±0.64	3.42±0.67
Ts17o (%)	0.222	0.782	6.60±4.01	5.63±2.54	7.35±6.76	5.60±3.42
Tnout	0.562	0.085	3.11±1.62	2.90±0.99	4.00±1.41	2.60±0.97
Txdur	0.192	0.452	7.33±3.29	6.47±1.62	6.19±1.53	7.67±2.73
Tmindur	0.024	0.337	5.67±4.09	4.70±1.25	3.73±1.49	5.50±2.99
Tmaxdur	0.516	0.391	9.89±3.30	8.30±2.36	8.64±2.34	10.20±3.49

Table 3.2. (con't).

b) young	LP	AP	1-PTR	2-PTR-PBA	3-PTR-POBA	4-PTR-PGL
Nsites	--	--	8	9	6	4
Ncores	--	--	149	178	93	69
Xage	0.079	0.559	1961±9.98	1960±14.07	1954±13.52	1964±0.45
Rfwr (%)	0.030	0.341	0.78±1.11	0.27±0.81	1.04±1.46	0.00±0.00
Rfmr (%)	<0.001	0.409	0.54±1.02	0.00±0.00	0.71±1.11	0.61±1.22
S128 (%)	0.116	0.087	9.76±3.82	11.28±2.91	9.64±1.69	6.40±2.68
S128o (%)	0.491	0.151	31.20±10.99	29.64±6.60	23.70±9.24	20.15±7.51
S17 (%)	0.229	0.289	3.88±2.90	3.79±1.85	3.72±1.02	1.39±2.77
S17o (%)	0.119	0.593	14.74±16.75	11.45±7.51	11.40±7.55	5.00±10.00
Nout	0.642	0.258	2.13±0.84	3.00±1.00	2.67±1.37	2.00±0.82
Xdur	0.134	0.225	5.94±1.02	5.39±1.01	7.08±2.62	6.50±1.29
Mindur	0.041	0.388	4.88±1.36	3.78±1.09	5.33±2.58	4.25±2.50
Maxdur	0.247	0.285	7.25±2.12	7.22±1.64	9.00±3.46	9.25±2.06
Trfwr (%)	0.005	0.338	0.08±0.12	0.07±0.20	0.57±1.24	0.00±0.00
Trfmr (%)	0.002	0.293	0.07±0.60	0.00±0.00	0.24±0.45	0.12±0.24
Ts128 (%)	0.133	0.761	3.70±0.79	3.74±1.27	3.99±1.48	3.22±0.25
Ts128o (%)	0.502	0.281	13.42±9.24	12.28±8.56	9.10±4.94	4.17±8.33
Ts17 (%)	0.171	0.620	1.45±0.40	1.42±0.56	1.68±0.88	1.19±0.30
Ts17o (%)	0.234	0.880	2.27±4.21	1.55±3.00	0.83±2.04	2.08±4.17
Tnout	0.763	0.170	1.00±0.76	1.00±0.71	1.33±0.82	0.25±0.50
Txdur	0.923	0.247	4.13±2.79	4.83±3.39	6.50±3.74	2.00±4.00
Tmindur	0.793	0.317	3.88±2.70	4.67±3.28	5.83±3.13	2.00±4.00
Tmaxdur	0.980	0.209	4.38±2.97	5.00±3.57	7.17±4.49	2.00±4.00

Table 3.3. Mean and standard deviation for the 17 variables characterizing the individual forest tent caterpillar outbreaks from 1939-1948 (a) and 1961-1965 (b) for the old sites and the 4 stand types: trembling aspen (1-PTR), trembling aspen/ jack pine (2-PTR-PBA), trembling aspen/ balsam poplar (3-PTR-POBA) and trembling aspen/ white spruce (4). The variables are: number of years below -1.28 standard deviation growth reduction (dur), maximum (maxr) and average (avr) growth reduction, relative frequency of white rings during the outbreak period (wrout), number of years with white rings (wryr), relative frequency of missing rings during the outbreak period (mrout), number of years with missing rings (mryr), maximum relative frequency of white rings in one year (wrmax), average white ring relative frequency during years of white ring formation only (avwrint), number of years between the year of maximum growth reduction and the year of maximum white ring relative frequency (supwr), maximum relative frequency of missing rings in one year (mrmax) and average white ring relative frequency during years of white ring formation only (avmrint). Variables calculated from the site chronology have no added prefix and those calculated from the mean of the individual series (cores), have the added prefix t. The p value for the Levene (LP) and one-way ANOVA (AP) are indicated. Significant differences ($P<0.05$) identified by the ANOVA appear in bold. Different letters indicate significant differences ($P<0.05$) among stand types after the Tukey post-hoc test (in cases of equal variance) or Tamhane post-hoc test (in cases of unequal variance).

a) 1939-1948	LP	AP	1-PTR	2-PTR-PBA	3-PTR-POBA	4-PTR-PGL
Dur	0.592	0.659	1.56±0.53	1.40±0.70	1.73±0.65	1.40±0.64
Maxr	0.010	0.054	-2.10±0.23	-1.71±0.35	-2.24±0.53	-1.80±0.66
Avr	0.005	0.727	-0.59±0.19	-0.48±0.17	-0.49±0.29	-0.52±0.24
Wrout (%)	0.192	0.648	12.12±6.43	9.09±8.57	12.40±14.24	7.27±10.32
Wryr	0.192	0.648	1.33±0.71	1.00±0.94	1.36±1.57	0.80±1.14
Mrout (%)	0.240	0.757	6.67±13.22	2.00±4.22	5.45±9.34	5.00±10.80
Mryr	0.240	0.757	0.67±1.32	0.20±0.42	0.55±0.93	0.50±1.08
Tdur	<0.001	0.051	1.25±0.46	1.00±0.00	1.56±0.53	1.00±0.00
Tmaxr	0.230	**0.005**	**-1.59±0.24ab**	**-1.27±0.23a**	**-1.66±0.38b**	**-1.37±0.40ab**
Tavr	0.197	0.572	-0.52±0.16	-0.42±0.11	-0.44±0.22	-0.44±0.16
Twrout (%)	0.130	0.562	6.48±3.87	4.97±5.83	6.94±7.55	3.53±5.47
Twrmax (%)	0.242	0.416	53.66±31.00	38.37±42.11	41.83±37.27	24.79±36.85
Tavwrint (%)	0.619	0.169	45.56±30.62	26.86±28.30	34.78±32.70	16.13±22.54
Tsupwr	0.311	0.333	0.13±1.32	2.67±2.80	-0.14±0.69	-0.75±4.11
Tmrout (%)	0.009	0.271	2.33±5.57	0.10±0.21	0.52±0.93	0.29±0.61
Tmrmax (%)	<0.001	0.135	11.11±20.43	1.00±2.11	3.34±4.90	1.48±3.35
Tavmrint (%)	<0.001	0.110	9.17±15.41	1.00±2.11	3.34±4.90	1.21±2.64

Table 3.3. (con't).

b) 1961-1965	LP	AP	1-PTR	2-PTR-PBA	3-PTR-POBA	4-PTR-PGL
Dur	0.452	**0.015**	**1.11±0.33a**	**1.70±0.48b**	**1.09±0.54a**	**1.20±0.42ab**
Maxr	0.629	0.067	-2.24±0.57	-2.70±0.34	-2.19±0.57	-2.13±0.52
Avr	0.823	0.055	-0.15±0.35	-0.56±0.33	-0.26±0.40	-0.18±0.32
Wrout (%)	0.002	0.062	22.22±29.17	30.00±15.81	11.36±13.06	10.00±12.91
Wryr	0.002	0.062	0.89±1.17	1.20±0.63	0.45±0.52	0.40±0.52
Mrout (%)	0.173	**0.031**	**13.80±18.16ab**	**37.50±27.00a**	**27.27±17.52ab**	**12.50±17.68b**
Mryr	0.173	**0.031**	**0.56±0.73ab**	**1.50±1.08a**	**1.09±0.70ab**	**0.50±0.71b**
Tdur	0.096	0.290	0.00±0.33	1.20±0.42	1.00±0.45	1.00±0.00
Tmaxr	0.734	0.102	-1.76±0.30	-2.00±0.21	-1.72±0.27	-1.74±0.32
Tavr	0.584	**0.039**	**0.09±0.22a**	**-0.20±0.24b**	**-0.00±0.26ab**	**0.04±0.18ab**
Twrout (%)	0.549	**0.010**	**8.70±11.55ab**	**20.62±13.74a**	**5.71±8.94b**	**4.97±9.23b**
Twrmax (%)	0.996	**0.015**	**25.52±34.20ab**	**67.54±35.56b**	**22.86±35.75a**	**19.86±36.90a**
Tavwrint (%)	0.965	**0.017**	**20.57±28.72a**	**63.75±35.05b**	**22.86±35.75a**	**19.86±36.90a**
Tsupwr	0.036	0.299	0.25±0.50	-0.11±0.33	0.00±0.00	0.00±0.00
Tmrout (%)	0.089	0.223	4.21±8.02	8.00±9.19	3.79±2.86	2.03±3.81
Tmrmax (%)	0.242	0.353	12.74±21.50	22.00±24.18	13.43±11.27	7.13±14.31
Tavmrint (%)	0.514	0.635	11.57±18.86	15.17±13.60	12.77±11.31	6.88±14.17

Table 3.4. Mean and standard deviation for the 17 variables characterizing the individual forest tent caterpillar outbreaks from 1982-1985 for the old (a) and young (b) sites and the 4 stand types: trembling aspen (1-PTR), trembling aspen/ jack pine (2-PTR-PBA), trembling aspen/ balsam poplar (3-PTR-POBA) and trembling aspen/ white spruce (4). The variables are: number of years below -1.28 standard deviation growth reduction (dur), maximum (maxr) and average (avr) growth reduction, relative frequency of white rings during the outbreak period (wrout), number of years with white rings (wryr), relative frequency of missing rings during the outbreak period (mrout), number of years with missing rings (mryr), maximum relative frequency of white rings in one year (wrmax), average white ring relative frequency during years of white ring formation only (avwrint), number of years between the year of maximum growth reduction and the year of maximum white ring relative frequency (supwr), maximum relative frequency of missing rings in one year (mrmax) and average white ring relative frequency during years of white ring formation only (avmrint). Variables calculated from the site chronology have no added prefix and those calculated from the mean of the individual series (cores), have the added prefix t. The p value for the Levene (LP) and one-way ANOVA (AP) are indicated.

a)	LP	AP	1-PTR	2-PTR-PBA	3-PTR-POBA	4-PTR-PGL
Dur	0.671	0.256	0.67±0.50	0.90±0.57	1.00±0.77	0.50±0.53
Maxr	0.253	0.332	-1.55±0.59	-1.71±0.40	-1.60±0.47	-1.31±0.36
Avr	0.041	0.673	-0.62±0.15	-0.67±0.38	-0.77±0.34	-0.71±0.19
Wrout (%)	0.671	0.937	2.78±8.33	2.50±7.91	4.55±10.11	2.50±7.91
Wryr	0.671	0.937	0.11±0.33	0.10±0.32	0.18±0.40	0.10±0.32
Mrout (%)	0.001	0.299	0.00±0.00	5.00±10.54	2.27±7.54	0.00±0.00
Mryr	0.001	0.299	0.00±0.00	0.20±0.42	0.09±0.30	0.00±0.00
Tdur	0.171	0.337	0.33±0.50	0.60±0.52	0.36±0.50	0.20±0.12
Tmaxr	0.828	0.591	-1.15±0.42	-1.29±0.37	-1.12±0.35	-1.08±0.32
Tavr	0.123	0.815	-0.52±0.12	-0.57±0.29	-0.59±0.25	-0.61±0.15
Twrout (%)	0.007	0.440	0.29±0.88	0.13±0.42	1.02±2.43	0.21±0.66
Twrmax (%)	0.007	0.440	1.17±3.51	0.53±1.66	4.09±9.70	0.83±2.64
Tavwrint (%)	0.007	0.440	1.17±3.51	0.53±1.66	4.09±9.70	0.83±2.64
Tsupwr*	--	--	--	--	--	--
Tmrout (%)	0.001	0.286	0.00±0.00	0.26±0.56	0.11±0.38	0.00±0.00
Tmrmax (%)	0.001	0.286	0.00±0.00	1.06±2.22	0.45±1.51	0.00±0.00
Tavmrint (%)	0.001	0.286	0.00±0.00	1.06±0.22	0.45±1.51	0.00±0.00

* Tsupwr did not have enough cases for Levene or ANOVA analysis.

Table 3.4. (con't).

b)	LP	AP	1-PTR	2-PTR-PBA	3-PTR-POBA	4-PTR-PGL
Dur	0.563	0.318	1.25±1.04	0.56±0.73	0.83±0.75	0.50±0.58
Maxr	0.447	0.467	-1.59±0.55	-1.40±0.40	-1.72±0.64	-1.25±0.32
Avr	0.123	0.458	-0.87±0.39	-0.68±0.28	-0.93±0.26	-0.80±0.10
Wrout (%)	0.197	0.767	3.13±8.84	2.78±8.33	0.00±0.00	0.00±0.00
Wryr	0.137	0.767	0.13±0.35	0.11±0.33	0.00±0.00	0.00±0.00
Mrout (%)	0.025	0.591	3.13±8.84	0.00±0.00	4.17±10.21	6.25±1.25
Mryr	0.025	0.591	0.13±0.35	0.00±0.00	0.17±0.41	0.25±0.50
Tdur	<0.001	0.258	0.50±0.59	0.22±0.44	0.50±0.55	0.00±0.00
Tmaxr	0.369	0.519	-1.27±0.47	1.12±0.30	-1.32±0.48	-0.98±0.23
Tavr	0.209	0.503	-0.77±0.29	-0.61±0.21	-0.74±0.19	-0.66±0.13
Twrout (%)	0.112	0.739	0.35±0.98	0.69±2.08	0.00±0.00	0.00±0.00
Twrmax (%)	0.112	0.739	1.39±3.93	2.78±8.33	0.00±0.00	0.00±0.00
Tavwrint (%)	0.112	0.739	1.39±3.93	2.78±8.33	0.00±0.00	0.00±0.00
Tsupwr*	--	--	--	--	---	--
Tmrout (%)	0.003	0.411	0.31±0.88	0.00±0.00	0.62±1.53	1.25±2.50
Tmrmax (%)	0.003	0.411	1.25±3.54	0.00±0.00	2.50±6.12	5.00±10.00
Tavmrint (%)	0.003	0.411	1.25±3.54	0.00±0.00	2.50±6.12	5.00±10.00

* Tsupwr did not have enough cases for Levene or ANOVA analysis.

Table 3.5. Mean and standard deviation for the 19variables characterizing the individual forest tent caterpillar outbreaks from 1982-1985 for the old and young sites. The variables are: number of sites (nsites) and cores (ncores), number of years below -1.28 standard deviation growth reduction (dur), maximum (maxr) and average (avr) growth reduction, relative frequency of white rings during the outbreak period (wrout), number of years with white rings (wryr), relative frequency of missing rings during the outbreak period (mrout), number of years with missing rings (mryr), maximum relative frequency of white rings in one year (wrmax), average white ring relative frequency during years of white ring formation only (avwrint), number of years between the year of maximum growth reduction and the year of maximum white ring relative frequency (supwr), maximum relative frequency of missing rings in one year (mrmax) and average white ring relative frequency during years of white ring formation only (avmrint). Variables calculated from the site chronology have no added prefix and those calculated from the mean of the individual series (cores), have the added prefix t. The p value for the Levene (LP) and one-way ANOVA (AP) are indicated. Significant differences (P<0.05) identified by the ANOVA appear in bold. Different letters indicate significant differences (P<0.05) among stand types after the Tukey post-hoc test (in cases of equal variance) or Tamhane post-hoc test (in cases of unequal variance).

	LP	AP	Old Stands	Young Stands
Nsites	--	--	40	27
Ncores	--	--	705	489
Dur	0.123	0.823	0.78±0.62	0.81±0.83
Maxr	0.949	0.959	-1.52±0.48	-1.51±0.50
Avr	0.801	0.105	-0.70±0.28	-0.82±0.30
Wrout (%)	0.181	0.511	3.13±8.37	1.85±6.67
Wryr	0.181	0.511	12.50±33.49	7.41±26.69
Mrout (%)	0.321	0.618	1.88±6.67	2.78±8.01
Mryr (%)	0.321	0.618	7.50±26.68	11.11±32.03
Tdur	0.485	0.732	0.38±0..49	0.33±0.48
Tmaxr	0.638	0.728	-1.16±0.36	-1.19±0.39
Tavr	0.557	**0.036**	**-0.58±0.21**	**-0.70±0.23**
Twrout (%)	0.635	0.773	0.43±1.40	0.33±1.30
Twrmax (%)	0.635	0.773	1.73±5.58	1.34±5.19
Tavwrint (%)	0.635	0.773	1.73±5.58	1.34±5.19
Tsupwr*	--	--	--	--
Tmrout (%)	0.001	0.129	0.10±0.35	0.42±1.25
Tmrmax (%)	0.001	0.129	0.39±1.39	1.67±5.00
Tavmrint (%)	0.001	0.129	0.39±1.39	1.67±5.00

* Tsupwr did not have enough cases for Levene or ANOVA analysis.

4.0 General conclusions

The objectives of this study were to characterize white rings found in trembling aspen. The distribution of white rings in the stem of trembling aspen, as well as the characteristics which differentiate 'white' from 'normal' rings were studied. In addition, both the analysis of white rings and a dendrochronological comparison of trembling aspen growth to non-host white spruce provided an historical reconstruction of forest tent caterpillar outbreaks in the DMPF. A temporal and spatial reconstruction of forest tent caterpillar outbreaks through time in the DMPF and a comparison of outbreak characteristics among 4 different stand types and 2 age classes was done. Results showed that ring width was reduced in white rings, as previously shown (Hogg et al. 2002b), and development around the stem of the tree was uniform from the base, up to approximately 70% of the height of the tree at the date of white ring formation. Smaller diameter fibers, with reduced cell wall thickening and a higher proportion of lumen area were found to occur in white rings than in 'normal' rings. White rings also had a lower density than normal rings.

White rings have been previously shown to occur in association with historical insect surveys in western Canada (Hogg and Schwarz 1999; Cooke 2001; Hogg et al. 2002a), and have been artificially induced in trembling aspen by defoliation simulating forest tent caterpillar activity (Hogg et al. 2002b). In this study, white rings were formed during periods of forest tent caterpillar outbreaks and were associated with the major and minor outbreaks of the 20th century, in the DMPF. White ring production however, did not necessarily occur in all trees within a site, nor did they occur in all sites during any of

the outbreak periods. In addition, white ring production in the southern portion of the DMPF was reduced compared to the northern portion. Differences in nutrition, forest fragmentation, clonal variation and the availability of the natural pathogens of the forest tent caterpillar, as well as the timing of defoliation during the growing season may have contributed to the differences between trees within the individual sites, between different sites and between the northern and southern portion of the DMPF. Further study of individual sites is required to better identify the major factors causing the differences within and between sites.

In the DMPF, three large outbreak periods were identified between 1939 and 1948, 1961 and 1965 as well as between 1982 and 1985, according to the presence of white rings and severe growth suppression. An additional large scale outbreak is suspected in the 1870s. Smaller suspected outbreaks were also observed in the 1830s, 1850s, the early 1900s, 1920s, 1950s, the early 1970s and the 1990s. White rings in trembling aspen corresponded to the 1870s, 1950s, 1970s and 1990s periods. The three major periods of forest tent caterpillar outbreaks were also observed in balsam poplar and paper birch, with the formation of white rings and growth suppression also occurring in these species, which are less preferred hosts compared to trembling aspen (Safford *et al.* 1990; Sims *et al.* 1990; Zasada and Phipps 1990). The occurrence of white rings in these three diffuse-porous species indicates a potential for the identification of intense forest tent caterpillar outbreaks, or outbreaks of other defoliating insects even when trembling aspen is not present.

The increased susceptibility of trembling aspen to white ring production and growth suppression in drier sites stresses the importance that the forest tent caterpillar could have in a warmer, drier climate. The effects that a drier climate will have on the interaction of the forest tent caterpillar and the trembling aspen in the DMPF needs to be assessed. In addition, the effect that continued fragmentation of the forest due to logging will have on forest tent caterpillar populations needs also to be addressed, as forest tent caterpillar outbreaks in fragmented forests in Ontario have been shown to last longer than in continuous forest (Roland 1993; Roland *et al.* 1998; Rothman and Roland 1998; Cooke and Roland 2000). These issues need to be addressed in regards to the management of the DMPF, and forest tent caterpillar outbreaks need to be considered as part of a natural disturbance based management plan.

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