LONG-TERM STAND DYNAMICS OF THE BOREAL MIXED-WOOD

FORESTS OF WEST-CENTRAL MANITOBA

by

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ABSTRACT

To understand the temporal dynamics of a forest, long-term direct observations are required. My study examined the long-term persistence of trembling aspen (*Populus tremuloides* Michx) and white spruce (*Picea glauca* (Moench) Voss) in the boreal mixed-wood forests of Riding Mountain National Park. A set of 266, disturbance-free, permanent sample plots were established in 1947 (stand age = 120 years) and followed through time for 55 years. My results indicate that although the density and basal areas of aspen do decline over the 55-year period, a successful regeneration and establishment occurs around 140 years. The long-term persistence of aspen is a result of clonal reproduction following the canopy breakup beginning around 130 years or earlier. This implies that the long-term persistence of both aspen and spruce occur and the expected succession to softwood dominance does not occur.

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DEDICATION

To my Friends – *Your distractions helped me get through*.

To Hannah – *For providing me support*.

To Sara – *Your friendship and patience are all I need*.

To Dad and Mom – *You provided me with the love to learn*.

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INTRODUCTION

"… conventional theories of population dynamics and evolution, originally developed for unitary organisms, are not readily applied to clonal organisms".

Sackville-Hamilton *et al.* (1987)

1.1 BOREAL MIXED-WOOD FOREST

When compared to tropical and warm temperate ecosystems, the boreal forest has been described as ecologically simple and floristically depauperate (Larsen 1980). This is somewhat misleading, however, since the boreal forest is a disturbance-driven ecosystem the complexity of which derives from forest stands being "reset" following catastrophic fires (Kenkel *et al.* 1997; Weir *et al.* 2000; Chen and Popadiouk 2002). Stand-destroying fires often result in the direct regeneration of stands, such that the established post-fire stand is compositionally similar and proportional to pre-fire conditions (Ilisson and Chen 2009). Over time, boreal mixed-wood stands progress through one of many possible successional pathways, resulting in stands of varying hardwood and softwood abundance (Cattelino *et al.* 1979). Many researchers have proposed that these multiple successional stages eventually converge on a "climax" forest type, characterized by complete softwood dominance (Taylor and Chen 2011). In such models, multiple successional pathways are considered transitional states along a deterministic continuum from deciduous to coniferous dominance (Peters *et al.* 2006). In this view, boreal mixed-wood stands that contain both softwoods and hardwoods are in a "transitional" rather than "climax" stage. This is a curious conclusion given that boreal mixed-wood stands by definition contain both deciduous and coniferous tree species.

Boreal "transition state" succession models were derived directly (and uncritically) from species life history models that were originally developed for the temperate deciduous forests in eastern North America (e.g. Pickett *et al.* 1987). The specific life history traits of boreal tree species are fundamentally different from those of temperate species, however, calling into serious question the relevance and utility of temperate-based models to boreal ecosystems. Our current view of long-term boreal mixed-wood forest dynamics has a strong "temperate bias" that can result in inaccurate or erroneous boreal succession models.

In Western Canada, boreal mixed-wood forest stands are dominated by two tree species, trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) (Rowe 1972). Although trembling aspen produces a prodigious amount of seed, its predominant mode of re-establishment following a stand-replacing fire is prolific clonal root suckering (Peterson and Peterson 1992; Mock *et al.* 2008). Historical succession models hypothesized that canopy break-up of the initial aspen cohort (starting at about age 60-80) allows white spruce seedlings to establish, inevitably leading to white spruce replacing aspen as the dominant canopy species (Rowe 1956, 1961). More recently developed stand dynamic models have perpetuated the notion of mono-dominant replacement of aspen by white spruce, although many authors acknowledge that trembling aspen can occasionally persist in older stands (e.g. multiple successive pathways, three cohort model; Cattelino *et al.* 1979; Bergeron *et al.* 1999; Bergeron 2000; Chen and Popadiouk 2002; Purdy *et al.* 2002). Nonetheless, current boreal forest succession models remain strongly deterministic, advocating the eventual development of a "climax" forest dominated by a single superior competitor (e.g. white spruce). The proposed replacement of trembling aspen by white spruce follows the classic competitive exclusion principle, in which a superior competitor dominates in the absence of disturbance (Kondoh

2001). It is of course impossible to obtain a completely disturbance-free system. In forested ecosystems, disturbances occur at all spatial scales and provide critical mechanisms for species recruitment and persistence (Abrams and Orwig 1996).

The most common and pervasive natural disturbance in the boreal mixed-wood forest is catastrophic, stand-replacing fire (Johnson 1992). Such fires create a spatial mosaic of forest stand ages on the landscape (Weir *et al.* 2000), which become increasingly structurally and compositionally heterogeneous over time. In boreal mixed-wood stands, the loss of trembling aspen apical dominance following a stand-destroying fire initiates root suckering (Frey *et al.* 2003), resulting in a deciduous-dominated forest canopy at the early stages of stand development. Regular, recurrent and frequent fires in mesic forest stands result in a compositional increase in trembling aspen, and over time this can result in stands that are completely deciduous-dominated (Gagnon 1989; Johnson 1992). More commonly, coniferous tree species increase in importance as post-fire mixed-wood stands age. In older stands (> 100 years in age), the coniferous component may predominate with only a minor deciduous component (Paré and Bergeron 1995; Bergeron 2000; Chen and Popadiouk 2002; Brassard *et al.* 2008). Many researchers and land managers view the boreal mixed-wood forest as a quantifiable (i.e. < 80% basal area of any one species) transitional phase between deciduous and eventual coniferous dominance (MacDonald 1995). With increasing fire regulation (i.e. suppression), adaptive management can be used to control the proportion of deciduous versus coniferous species in these forests (*sensu* Luken 1990; Hobbs and Norton 1996; Holling and Meffer 1996).

A "climax" successional community is defined as the stable endpoint reached following a series of changes in species dominance over time (Krebs 2009). When an ecosystem is subjected to recurrent natural disturbances, this

theoretical "climax" endpoint is never reached since disturbances are unpredictable, non-cyclic occurrences that do not coincide with tree species longevity (Weir *et al*. 2000; McIntire *et al*. 2005). Hypothetically, the uncoupling of a boreal mixed-wood forest stand from its natural disturbance regime will result in dominance by shade tolerant species (Dix and Swan 1971; Bergeron 2000; Taylor and Chen 2011).

This classic Clementisian approach to boreal mixed-wood succession implies linear determinism (Cattelino *et al*. 1979; Viereck 1983). However, empirical studies are not consistent with such a model. Specifically, neither inhibition (wherein early colonizing species inhibit the establishment of late-successional species) nor facilitation (in which arrival of late-successional species is facilitated by the presence of early-successional ones) has been demonstrated to play an important role in boreal mixed-wood stand dynamics (Dix and Swan 1971; Fastie 1995; Taylor and Chen 2011). Even so, boreal succession models continue to subscribe to the notion of a predominant and characteristic climax community dominated by coniferous species (Kneeshaw and Bergeron 1998; Bergeron 2000; Taylor and Chen 2011). While the deterministic view of forest succession has been questioned and criticized (Kenkel *et al*. 1997; Pickett *et al*. 2009), boreal succession models continue to emphasize notions of species turnover and canopy replacement that were first inferred from casual observation of the composition and canopy structure of "mature" (typically 100 year old) stands (e.g. Rowe 1956, 1961).

The historic preoccupation with boreal succession models that hypothesize a conifer-dominated "climax" community likely reflects the lack of long-term permanent sample plot data. In the absence of reliable long-term data on forest change (particularly for stands > 100 years old), the chronosequence approach (also known as "space for time substitution", Pickett 1989) has been used to infer

trends in compositional and structural change (Frelich and Reich 1995; Paré and Bergeron 1995; Taylor and Chen 2011). The direct interpretation of chronosequence data almost inevitably leads to a deterministic view of forest change over time (Krebs 2009). Furthermore, little consideration is given to the reliability of chronosequence data, nor of the analytical techniques used to obtain model results (Johnson 1979; Johnson and Miyanishi 2008). Another criticism of contemporary boreal forest succession models is that they fail to consider trembling aspen and balsam poplar clonality (e.g. Bergeron *et al.* 1999; Bergeron 2000; Taylor and Chen 2011). Clonal growth in the poplars (i.e. root suckering) is a critically important mechanism promoting long-term persistence of these species on the landscape. In addition, the spatial scale of an individual poplar clone (i.e. the spatial extent of a genet) is much greater than that of non-clonal coniferous species such as white spruce (Baret and desRochers 2011). Trembling aspen and balsam poplar clonality therefore has important implications to our understanding of mixed-wood stand dynamics.

Early models of plant succession were developed by Clements and colleagues in the early 20th century. Clements (1916, 1936) formulated the basic principles of plant succession, particularly the idea that vegetation change follows a deterministic course leading to a specific "climax" community. Watt (1947) incorporated disturbance into the basic Clementian model, advancing our understanding of vegetation colonization and perpetuation. Egler (1954) proposed two "floristics" models of vegetation dynamics. "Relay floristics" is a linearly deterministic model, in which the early-colonizing species facilitate invasion by later-successional species. Conversely, the "initial floristics" model incorporates the individualistic viewpoint advocated by Gleason (1917), emphasizing the role of "who gets there first" in determining colonization and subsequent stand development.

These ideas were later synthesized into three general succession models (Connell and Slatyer 1977):

(1) Inhibition: early-colonizing species usurp the available space, inhibiting the establishment of late-sucessional species.

(2) Facilitation: early-successional species facilitate the establishment of later-successional species.

(3) Tolerance: species replacement during succession is dictated by their relative tolerance to resource (nutrients, light, etc.) limitation.

These three general models, which are not mutually exclusive (Kenkel *et al*. 1997; Pickett *et al*. 2009), have provided the essential features for subsequent forest succession models (Catellino *et al*. 1979; Tilman 1985; Frelich and Reich 1995). In the absence of long-term permanent sample plot data, these models have been widely used to interpret chronosequence results, and in the development of boreal mixed-wood forest succession models (Kneeshaw and Bergeron 1998; Bergeron 2000; Chen and Popadiouk 2002; Ilison and Chen 2009; Taylor and Chen 2011).

Succession models developed for the temperate forests in North America and Europe (Clements 1936; Egler 1954) are the basis for all vegetation succession models (Taylor *et al*. 2009). Fundamentally, these models maintain that long-term persistence is directly related to high shade tolerance (Connell and Slatyer 1977; Bazzaz 1979; Huston and Smith 1987). An example of classic temperate succession occurs in the oak – hickory eastern deciduous forests of eastern North America (Thomspon and Dessecker 1997; Aldrich *et al*. 2003). In this community, the early successional shade-intolerant oaks (*Quercus* spp.) are

replaced by the more shade-tolerant maples (*Acer spp.*), which are in turn replaced by the very shade-tolerant hickories (*Carya spp.*).

Gleason (1917) critiqued the early work of Clements (1916), and was heavily criticized for it (see recorded dialogue at the end of Gleason 1939). As a result, Gleason's emphasis on the importance of the individual (as opposed to the "super-organism" or community) in vegetation dynamics was ignored for many years. Egler (1954) implicitly recognized the importance of individual variation in his "initial floristics" model, incorporating Gleason's concepts into a broader succession theory. This insight resulted in a paradigm shift in our conceptualization and understanding of forest stand dynamics (Clark 2007). A focus on individual responses to stochastic events allows for the development of vegetation dynamic models such as the "lottery" model of re-colonization of unoccupied spaces or "gaps" (Sale 1977). In such models, successful tree re-colonization during succession is determined by species life history traits as well as stochastic factors (Huston and Smith 1987; Tilman 1988).

1.2 ECOLOGICAL IMPLICATIONS OF CLONALITY VERSUS SEED PRODUCTION

Clonality is the asexual reproduction of an organism through the production of rhizomes, stolons, or root and basal stem suckers. Physiological integration of the ramets that make up an individual genet is beneficial, since it maximizes the individual's presence on the landscape and thereby maximizes resource acquisition (Stuefer *et al.* 2004). By contrast, non-clonal plants are locally constrained in their acquisition of resources, and must develop adaptive strategies such as root foraging to maximize resource intake (Tilman 1988).

The degree to which a plant species propagates clonally, and is successful within an environment varies. Clonal tree species that reproduce asexually exhibit minimal genetic variation among ramets (Namroud *et al.* 2005; Mock *et al.* 2008). In sexually reproducing tree species, sexual recombination increases overall fitness. Furthermore, sexual tree species tend to exhibit greater genetic variation due to recombination and the accumulation of minor genetic mutations that occur during meiosis (Kondrashov 1982; Li *et al.* 1997). Understanding the role of mutations on species fitness may help to explain why clonal organisms maintain the ability to reproduce sexually. Clonal plants can integrate mutations into their genome through sexual reproduction in order to increase resistance to diseases and/or pathogens. Exclusive clonal reproduction would result in the proliferation of deleterious genes (Klekowski 1997) that would be selected against in a non-clonal species (Antonovics and Ellstrand 1984; Barton and Charlesworth 1998). Lastly, a clonal tree that establishes and reproduces exclusively through asexual reproduction is restricted to local expansion; it may become locally abundant, and will slowly colonize further afield. If a clonal species reproduces sexually (that is, by seed), it will be less dominant at the local scale but more common on the greater landscape. A comparable situation occurs with non-clonal plants; they maintain a (comparatively) rare presence at the local scale, but have the ability to disperse to and colonize the broader landscape. It follows that both asexual (clonality) and sexual (seed production) strategies are suitable adaptations for long-term persistence on the landscape, but they occur on different scales. As a result, long-term persistence is not so much a competition as a "race" to acquire and usurp space ("who gets there first") that is ultimately determined by stochastic mortality and migration (Hubbell 2001).

The two dominant and persistent species of the western boreal mixed-wood forest are trembling aspen, a clonal species, and white spruce, a non-clonal

species. A thorough review of the life history of these two species follows. The review highlights the need to recognize aspen clonality as an important life-history trait that ensures the long-term persistence of the species on the landscape.

1.3 TREMBLING ASPEN

Trembling aspen (*Populus tremuloides* Michx.) is a deciduous tree in the Salicaceae family. It has smooth bark with scaly, resinous buds, simple alternate leaves and precocious, dioecious flowers in drooping catkins (Maini and Cayford 1968). Abundant seed crops are produced every 4 – 5 years, starting as early as 10 years of age (Perala 1990). The seeds remain viable for only 2 – 4 weeks (Mitton and Grant 1996). Although aspen produces prodigious amounts of seed (Perala 1990), clonality is the predominant form of reproduction (Peterson and Peterson 1992; but see Romme *et al.* 1997). The largest known trembling aspen clone is 43 hectares in size and of unknown age (Grant *et al.* 1992).

The mean height of a mature aspen tree (age 70) is 21 m, with an average diameter at breast height (DBH) of 30 cm (Peterson and Peterson 1992). The maximum age of an individual bole (ramet) is greater than 120 years, and such trees may attain a height of 31 m and a diameter of 80 cm (Bonnor and Nietmann 1987). Female clones are typically larger than male clones; females average 200 ramets per clone, versus 150 ramets for males (Sakai and Burris 1985).

Aspen is a wide-ranging species with broad habitat tolerances. Climate conditions over the range of the species vary from an average low of -25ºC (January) in central Alaska to an average high (July) of 23ºC in Indiana. Annual precipitation over the species' range varies from about 150 cm in eastern North America to only 30-35 cm along the eastern slopes of the Rocky Mountains in the

west (Strothmann and Zasada 1965). Aspen occurs on a wide variety of soil types, but best growth occurs on well-drained, loamy, nutrient-rich soils that are high in organic matter (Perala 1990). Hydric (water-logged) or xeric (excessively drained) edaphic conditions result in poor growth, and extreme drought or poor drainage will eventually lead to ramet mortality. Aspen is morphologically and physiologically plastic, adapting to harsh environments (e.g. windy and cold high elevation habitats in the Rocky Mountains; dry aspen parkland habitat in western Canada) by becoming "scrubby" (i.e. numerous small, short ramets with reduced leaves). Conversely, under optimal growing conditions (e.g. rich loamy soils of the lower Manitoba Escarpment) aspen is a dominant forest tree species (Perala 1990). The climate, soil and physiography at the landscape scale dictate species and ecosystem diversity (Lapin and Barnes 1995), and these variables are important predictors of variation in the growth and abundance of trembling aspen across the landscape (Peterson and Peterson 1992).

Root suckering is a vigorous form of vegetative reproduction in aspen. Following a stand-destroying disturbance (e.g. fire, logging), ramet densities typically range from 20,000 – 400,000 stems/ha (Bella 1975), with the amount of root suckering being determined by both pre- and post-disturbance factors. These factors include the type and severity of disturbance, pre-and post-disturbance stand structure and floristic composition, root abundance and distribution, and specific environmental conditions (Quintilio et *al.* 1991; Wang 2003; Frey *et al.* 2003; Mundell *et al.* 2007). While these factors result in variable stand densities, densities in excess of 20,000 stems/ha immediately following a catastrophic fire are not uncommon (Peterson and Peterson 1992).

Regenerating aspen stands undergo considerable self-thinning (density dependent mortality) during the early stages of stand development (Peterson and Peterson 1992). In six regenerating aspen stands in boreal Alberta and

Saskatchewan, mean ramet density declined from 64,583 stems/ha (range 40,903 – 83,958) at 3 years of age to only 33,189 stems/ha (range 22,604 – 46,285) at 6 years of age; i.e. ramet mortality was about 50% over three years (Bella 1975). Regardless of the initial stand density, young aspen stands thin themselves to a density of about 5,000 stems/ha (mean stem diameter = 3 cm) by 10 years of age (Krasny and Johnson 1992). Incremental growth of individual aspen ramets is variable (Gustafson *et al*. 2003), and faster-growing ramets are strongly favoured during the resource-driven, density dependent mortality phase of stand development (Pothier *et al*. 2004; Powell and Bork 2004). Density-dependent aspen mortality (i.e. intraspecific competition) continues until stands are approximately 60-80 years old (Pothier *et al*. 2004). Beyond about 60-80 years of age, aspen stand dynamics shifts from density dependent to density independent mortality. During the density independent stage, mortality is attributable to stochastic factors such as wind damage, drought, pathogenic fungi, and insect pests attack (Peterson and Peterson 1992). Density independent mortality creates "gaps" in the previously closed canopy, creating opportunities for pulse recruitment of aspen root suckers (and other tree species). This results in size-age inequality among ramets within the stand, i.e. an uneven-aged stand (Cumming *et al*. 2000).

   Clonal regeneration of aspen is dependent on both physiological and environmental conditions (Frey *et al*. 2003). Light is considered a limiting resource in young, dense aspen stands since very little photosynthetically active radiation penetrates to the ground during the growing season (Constabel and Lieffers 1996). In older stands, increased light and soil temperatures following the death of a canopy tree creates a "regeneration gap" that provides potential space for aspen pulse recruitment (Lee 1998; Cumming *et al*. 2000). Pulse recruitment is uncommon in closed, dense stands, but becomes increasingly important in older stands that show greater heterogeneity in stem sizes and canopy

complexity and greater light penetration through the canopy (Lee *et al.* 1997; Lieffers *et al.* 1999).

Insect defoliation from forest tent caterpillars (*Malacosoma disstria* Hübner) and aspen tortrix (*Choristoneura conflictana* Walker), combined with severe drought conditions, result in a decrease in photosynthesis and water uptake by aspen, slowing and stunting growth (Hogg *et al.* 2002). Warmer, drier conditions also increase the susceptibility of aspen to wood boring insects (*Saperda calcarata* Say), fungal pathogens (the genera *Hypoxylon* and *Agrilus*, which gain access through insect bored holes), and xylem cavitation (Peterson and Peterson 1992; Logan *et al.* 2003; Maherali *et al.* 2004). These factors are severe stressors to aspen, and often result in local dieback (Hogg *et al.* 2002) that creates canopy gaps and promotes local root suckering.

Aspen dieback is a natural phenomenon that typically occurs in aspen parkland communities (Hogg and Wein 2005), although it may also occur in boreal mixed-wood and pure aspen forests. Dieback is most prevalent in older stands (density independent growth phase), and appears to be the result of temporal variability in local climatic conditions (Frey *et al.* 2004; Hogg *et al.* 2008). Specifically, global warming is thought to have increased El Niño events, resulting in drought conditions over much of the western portion of species' geographic range (Cox *et al.* 2000). Increased incidence of drought conditions is a major stressor of aspen stands in drier regions, resulting in a decline in aspen abundance and vigour on the landscape (Hogg *et al.* 2008; Rehfeldt *et al.* 2009). This decline in aspen is compounded when environmental conditions, stand structure and genetic variation are incorporated into the long-term survivorship models of the species (Frey *et al.* 2004). These factors are incited at the local scale by herbivory, defoliation and xylem cavitation, which together increase the susceptibility of aspen to pathogens, insect pests, and structural wind-throw damage (Bailey *et*

al. 2004; Frey *et al.* 2004; Donaldson *et al.* 2006).

Aspen dieback can result two different regeneration scenarios. Most commonly, a flush of root suckers is recruited, maintaining the clone on the landscape. Alternatively, aspen and other tree species may recruit from dispersed seed (Romme *et al.* 1997; Mock *et al.* 2008; Martin-DeMoor *et al.* 2010). Regardless of the recruitment mechanism following aspen dieback or decline, the species will maintain its presence on the landscape.

1.4 WHITE SPRUCE

White spruce (*Picea glauca* (Moench) Voss) is a coniferous tree species and a member of the Pinaceae family. The species has rough scaly bark, non-resinous buds, and short straight stiff needles. White spruce is monoecious, producing separate male and female cones on the same tree. The young female cones are small and erect, but they droop once fertilized (Farrar 2000). White spruce is considered a non-clonal species, although on rare occasions low-lying branches may be weighted down by leaf litter, produce adventitious roots, and develop into upright shoots in a manner similar to black spruce (Nienstaedt and Zasada 1990). However, sexual reproduction from seed is normally the sole method of reproduction. Seed production is prolific: in Riding Mountain, 3,680,300 seeds/ha (about 70% of which were viable) were shed from a mature white spruce stand in 1961 (Waldron 1961), and nearly 15 million (about 60% viability) during the very heavy seed crop of 1960 (Waldron 1965). Seed ripens by mid to late August, and most is dispersed in late August and September (Rowe 1955; Waldron 1961).

Seed masting, defined as the synchronous production of large seed crops in some years and little or no seed production in intervening years, is characteristic of white spruce. Over a ten-year period (1954 – 1963) in Riding Mountain

National Park, a heavy white spruce seed crop was produced only once, moderate seed crops were produced four times, small seed crops three times, and in three of the ten years no seeds were produced at all (Waldron 1965). Between 1940-1950, moderate to heavy seed crops were produced three times, with a particularly heavy crop in 1948 (Rowe 1955). Historical records suggest that, on average, moderate to heavy seed crops are produced for two to three successive years, followed by three or four successive years of little to no seed production (Waldron 1965). For the period 1940-1963, very heavy seed crops occurred in 1948 and 1960, i.e. about once every 10 to 12 years.

White spruce is indigenous to North America. The species occurs throughout the boreal forest ecosystem, from Newfoundland to Alaska and north to the tree line. While primarily a boreal species, white spruce also occurs in Minnesota, Michigan and the upper New England states, with a disjunct varietal population (Black Hills spruce, *P. glauca* var. *densata*) in southwestern South Dakota (Farrar 2000). Climatic conditions range from a mean January temperature of - 27°C (northern Manitoba) to a mean July temperature of 21°C (southern Michigan). Annual precipitation ranges from 30 – 35 cm in northern Alberta to about 150 cm in the Maritime Provinces. White spruce tolerates a wide range of edaphic conditions, and will grow on acidic soils (pH range 4.7 – 7.0) of low nutrient status. White spruce is flood-intolerant, and growth is slow on poorly drained clay soils. Best growth occurs on moderately to well-drained, loamy, nutrient-rich soils that are high in organic matter (Nienstadt and Zasada 1990).

The mean height of a 70-year old white spruce is about 26 m, with mean DBH ranging from 60 – 90 cm depending on stand density (Jameson 1963). Under exceptional conditions white spruce trees can achieve a height of 55 m and a DBH of 120 cm. A typical 70-year-old pure white spruce stand contains between 800 and 1000 trees/ha. White spruce is a long-lived species; the mean lifespan is

100 – 250 years, although some individuals may survive for 1000 years or more (Nienstadt and Zasada 1990).

The timing and success of white spruce recruitment following a stand-destroying fire is dependent on a number of factors. White spruce colonization is seed dispersal limited (Albani *et al.* 2005), and rapid initial recruitment (i.e. within the first 3 – 5 years following a fire) requires a proximal seed source (generally < 100 m, Greene and Johnson 2000). The timing of a fire (spring versus fall burn), and sub-optimal environmental conditions following a burn, can result in delayed post-fire recruitment of white spruce. Recruitment is also delayed if the fire occurs during a period of low seed production (i.e. a non-masting year), or when seed depredation is high (Stewart *et al.* 1998; Purdy *et al.* 2002; Peters *et al.* 2003; Peters *et al.* 2005). In addition, poor seedbed conditions (particularly seedbed desiccation during periods of low precipitation) can strongly limit seedling recruitment. Suitable seedbeds for white spruce germination and establishment include rotten logs, organic substrates (e.g. mosses), and exposed mineral soil mounds (Zasada and Lovig 1983; DeLong *et al.* 1997; Peters *et al.* 2005). At Riding Mountain, white spruce seed germination begins in late June (from seed released the previous fall), and peaks in the first two weeks of July (Rowe 1955).

The early "window of opportunity" for initial white spruce recruitment into mixed-wood stands closes within 3 – 5 years, once a dense closed canopy is formed by the rapidly growing aspen root suckers (ramets). While white spruce germination and establishment rarely occurs after about five years post-fire (Bokalo *et al.* 2007), already established white spruce seedlings will persist beneath the dense aspen canopy provided that light conditions remain above the photosynthetic compensation point of 60 μmol/m^{2}s (Constabel and Lieffers 1996). These early-recruited white spruce saplings grow slowly, remaining in the understory until a

canopy space is vacated and a release event initiated (Gutsell and Johnson 2002).

A second "window of opportunity" for white spruce recruitment does not occur until approximately 60-80 years post-fire, when density independent mortality of mature canopy trees begins and the closed aspen canopy starts to break apart (Lieffers *et al.*1996; Peters *et al.* 2006). White spruce established during this "delayed recruitment" phase of stand development may grow rapidly (particularly if stand density is low), and soon obtain a sub-canopy position (Lieffers *et al.* 1996; Groot 1999).

Topographic features of the landscape, such as channels and concave slopes, restrict seed dispersal and seedling recruitment of white spruce (Albani *et al.* 2005). Moist exposed mineral soils and decaying logs provide optimal germination sites for "delayed" white spruce recruitment (Tucker *et al.* 1968; Lieffers *et al.* 1996). A moist substrate promotes germination, and root mycorrhizal associations develop quickly (Delong *et al.* 1997; Lumley *et al.* 2001). Suboptimal edaphic conditions (particularly dry substrates), together with smothering by deciduous leaf litter, result in high seedling mortality (85 – 98%) within the first year (Gregory 1966; Charron and Greene 2002; Wang and Kemball 2005). If a seedling survives the first growing season its probability of long-term survival greatly increases, and by the third year survival probability approaches 100% (Charron and Greene 2002; Feng *et al.* 2006; Kemball *et al.* 2006). The growth rate of spruce seedlings is highly light dependent. Seedling growth rates are greatest under full light conditions provided there is sufficient soil moisture, but seedlings are able to survive (although they grow very slowly) under low-light conditions (Lieffers and Stadt 1994).

The physiological and morphological adaptations of white spruce that promote high shade tolerance are critical to the long-term persistence of the species, both within stands and on the broader landscape (Walker and Kenkel 2000; Voicu and Comeau 2006). White spruce is capable of germinating and establishing beneath an existing trembling aspen canopy, given its ability to efficiently capture the little solar radiation that manages to reach the forest floor (Constabel and Lieffers 1996). The ability of white spruce saplings to "lie-in-wait" beneath the aspen canopy allows for rapid canopy transition (sapling "release") once a canopy space is vacated (Gutsell and Johnson 2002).

Mature white spruce trees have a shallow root system and are therefore susceptible to wind-throw (Rich *et al*. 2007). During the early stages of mixed-wood stand development, the dominant aspen canopy acts as a wind buffer protecting sub-canopy white spruce from wind-throw (Feng *et al*. 2006). When the canopy of the initial aspen cohort begins to "break-up" (ages 60 – 80), the maturing white spruce grow into the upper canopy and are much more susceptible to wind damage and insect defoliation (Taylor and MacLean 2005; Rich *et al*. 2007). The break-up of the aspen canopy also results in increased light penetration to the forest floor, promoting both aspen root suckering and white spruce establishment (Frey *et al*. 2003). A second aspen cohort quickly attains sub-canopy (and later canopy) position, once again buffering subordinate white spruce against wind-throw damage (Rich *et al*. 2007).

1.5 BOREAL MIXED-WOOD COMMUNITY DYNAMICS

Following a stand-replacing catastrophic fire, the initial 80 to 100 years of forest development (i.e. the composition and structural properties of a stand) are largely predetermined by the first few years of recruitment (Johnstone *et al*. 2004). This predictability, known as "recruitment memory", declines as stands age. As a

result, the relationship between pre- and post-disturbance forest composition-structure becomes uncoupled in the later stages of stand development (Greene 2000). This in turn makes it difficult to predict long-term (> 100 years) stand dynamics using a chronosequencing approach, particularly since older stands are uncommon on the landscape and often occur in atypical habitats (e.g. islands and narrow peninsulas protected from catastrophic fire). Long-term permanent plot studies of forest stand development in older (> 100 year old) stands are therefore required to validate boreal succession models that were developed using the "space-for-time substitution" approach (Pickett 1989; Bergeron 2000).

Untangling pattern and scale in ecology is a major challenge (Levin 1992), but an acknowledgment of species-specific life history traits can help explain long-term species persistence at all spatial and temporal scales (Huston and Smith 1987). The ability of aspen to reproduce both sexually and clonally allows for rapid regeneration following a catastrophic disturbance, thus promoting its long-term persistence on the landscape (Frey *et al.* 2003). White spruce has an entirely different strategy for long-term persistence: it forgoes clonal growth, but has higher sapling shade tolerance. High shade tolerance promotes a "lie-in-wait" strategy, wherein saplings persist in the understory until a canopy space becomes available and they are released (Gutsell and Johnson 2002). Trembling aspen and white spruce persist (and therefore coexist) on the landscape as a result of these highly divergent life-history strategies. Both strategies are well adapted to the dynamic environment that characterizes forest stand development. These two divergent life-history strategies also result in an efficient partitioning of the regeneration niche (Grubb 1977; Collins and Good 1987).

The long-term persistence and coexistence of trembling aspen and white spruce is very much at odds with most long-term succession models proposed in the boreal forest literature (e.g. Bergeron 2000; Taylor and Chen 2011). In the

absence of a catastrophic fire, boreal mixed-wood succession is most often viewed as a linearly deterministic, deciduous-to-coniferous pathway (**Figure 1a**). However, the life history characteristics of trembling aspen and white spruce are inconsistent with this simple deterministic model. This standard model of boreal mixed-wood succession may need to be modified, to incorporate species-specific life-history characteristics and the dynamic complexity of forest stand development (**Figure 1b**).

20
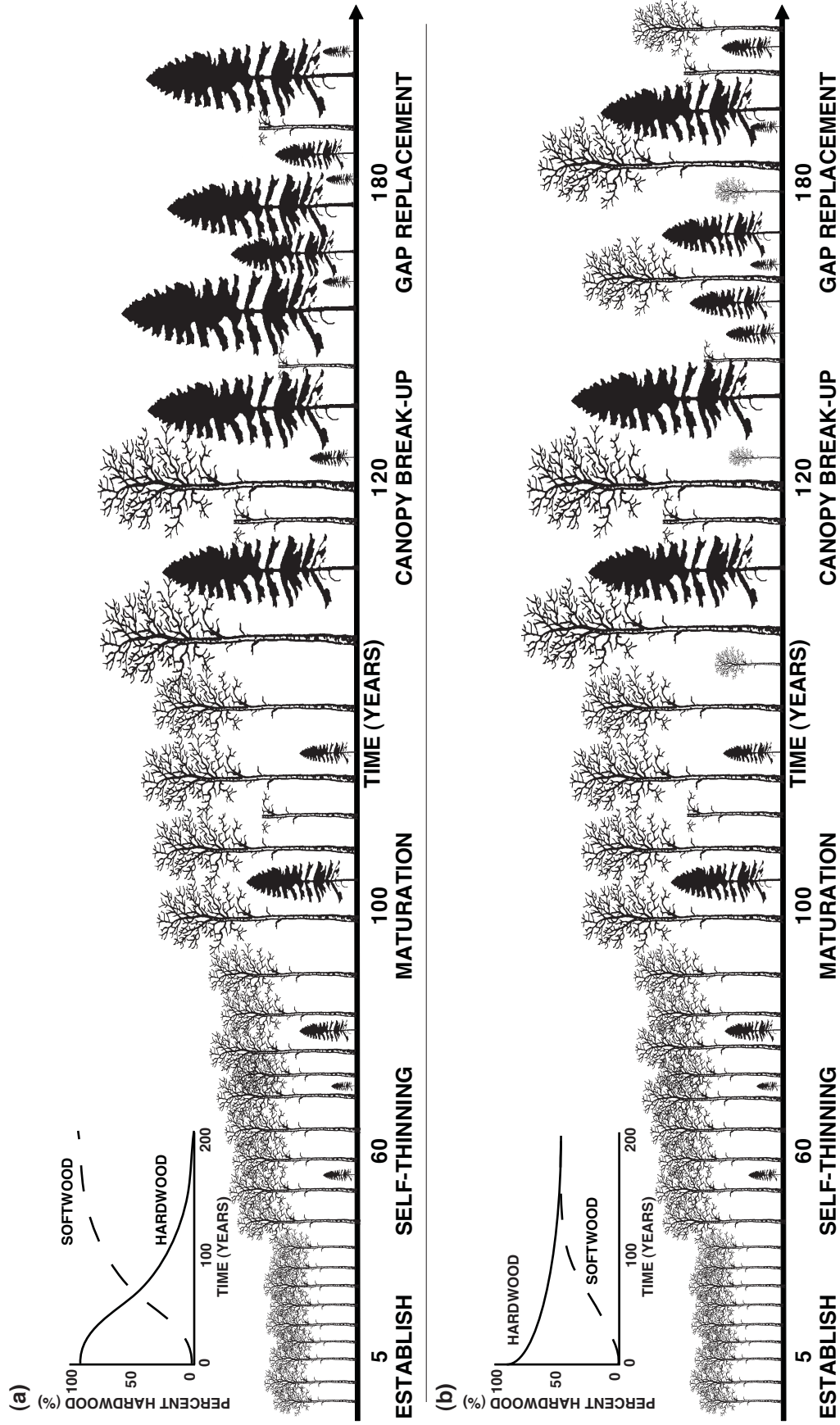
Figure 1.1: (a) - Hypothesized hardwood to softwood successional pathway proposed in earlier boreal mixedwood ecology literature. **(b)** - A hypothetical model of hardwood/softwood coexistence (i.e. hardwood persistence) in the boreal mixedwood forest, incoporating successful clonal reproduction of hardwood species.

CHAPTER 2

THE BOREAL MIXED-WOOD FOREST

2.1 BOREAL MIXED-WOOD FORESTS OF CANADA

The boreal forest is a circumpolar biome occupying *ca.* 8% of the world's landmass. In North America, the boreal forest is the largest forested region containing over 600 million hectares of land (Brandt 2009). The high latitude of the boreal forest results in a short growing season, often <100 days, that is characteristically cool (mean annual temperature of negative 0.85°C) and moderately moist (mean annual precipitation = 591mm; Rowe 1972).

The physiography of the boreal region is a result of the most recent glacial retreat, *ca.* 10000 years before present (i.e. Wisconsinan Glacial Retreat), and provides the foundation for soil formation. Although the boreal flora is considered low in species diversity (< 300 plant species), this ecosystem is a complex temporal mosaic of composition and structure that is altered by disturbances at all scales (La Roi 1967; Larsen 1980; Walker and Kenkel 2001).

The climatic and topographic variability of the boreal forest regions of Canada results in spatially and temporally variable deciduous and coniferous forests known as boreal mixed-woods (Rowe 1972). The boreal mixed-wood, which extends from coast-to-coast between latitudes 45°N and 65°N, is the most widespread forest type in Canada (Man and Lieffers 1999). This vast area is subjected to a wide variety of disturbances (i.e. fire, insect defoliation, fungal pathogens, wind-throw *etc.*), which affect and alter local and landscape floristic composition and structure (Johnson 1992; Bergeron 2000). The occurrence of

large-scale disturbances, which are influenced by climate, can be used to determine the latitudinal distribution and floristic composition of the boreal mixed-woods (Hogg 1994).

Given the ecological and environmental variation of the boreal mixed-woods, and in the context of the research proposed, a precise definition of the this ecosystem is important to communicate results to researchers and practitioners (Chen and Popadiouk 2002). The boreal mixed-wood forests can be defined as an area of climatic, topographic and edaphic conditions that promotes the cyclic establishment and growth of deciduous and coniferous species in varying densities over time (modified from MacDonald 1995).

Boreal mixed-wood forests are found throughout Canada, including northern British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Quebec, Newfoundland and, the Yukon and Northwest Territories. A number of factors distinguish the boreal mixed-wood forests of the western provinces (Manitoba and west) from those of eastern Canada (Rowe 1972). **Table 2.1** provides a comparison of the boreal mixed-woods of western Manitoba (Mixed-wood section, Rowe 1972) and eastern Quebec (Missinaibi-Cabonga section, Rowe 1972). The boreal mixed-wood region of western Canada is characteristically cooler and drier than its eastern counterpart (**Figure 2.1**). During the winter months (November to February), the eastern region receives twice the amount of snowfall (246 versus 122 cm), which reduces the probability of severe drought and fire in any given year (Bergeron and Archambault 1993).

The boreal mixed-wood is generally considered the most productive and diverse forest stand type within the North American boreal ecosystem (Chen and Popadiouk 2002). In western Canada, the predominant canopy tree species of mixed-wood stands are the deciduous trembling aspen (*Populus tremuloides*

Michx.) and the evergreen conifer white spruce (*Picea glauca* (Moench) Voss); balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh.) are common associates. Other species such as black spruce (*Picea mariana* (Mill.) BSP), balsam fir (*Abies balsamea* (L.) Mill.), jack pine (*Pinus banksiana* Lamb.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and tamarack (*Larix laricina* (Du Roi) K. Koch) are only occasionally found in western mixed-wood stands (Rowe 1972).

The mixed-wood stands of western Canada are dominated by just two tree species, whereas those of eastern Canada show greater compositional diversity. Stands typically contain varying amounts of trembling aspen, white birch, white spruce and balsam fir. In addition, eastern white cedar (*Thuja occidentalis* L.) is often abundant in the oldest stands (Bergeron 2000). In general, coniferous species (particularly balsam fir) are much more abundant in eastern mixed-wood stands compared to those in the west. Minor associates in the eastern mixed-wood boreal include black spruce, jack pine, tamarack, yellow birch (*Betula alleghaniensis* Britt.), eastern white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Ait.), black ash (*Fraxinus nigra* Marsh.), red spruce (*Picea rubens* Sarg.) and eastern hemlock (*Tsuga canadensis* L.).

The tall shrub community of the boreal mixed-wood forest shows a greater east-west dichotomy than the trees (La Roi 1967). The predominant tall shrubs of eastern mixed-wood stands are mountain maple (*Acer spicatum*), pin cherry (*Prunus pensylvanica* L.), and various willow (*Salix* spp.) species (Kneeshaw and Bergeron 1998; Bergeron 2000). In eastern Canada, mountain maple often forms very tall, dense stands that inhibit the establishment and growth of advanced tree regeneration (Aubin *et al.* 2005). In the boreal mixed-wood forests of Manitoba and eastern Saskatchewan, beaked hazelnut (*Corylus cornuta*) can form dense impenetrable thickets that inhibit aspen suckering and white spruce

establishment and growth (Waldron 1959; Kurmis and Sucoff 1989). Tall shrubs are less common in the mixed-wood forests of Alberta. The two most commonly encountered species, buffalo berry (*Shepherdia canadensis* (L.) Nutt. and wild rose (*Rosa acicularis* Lindl.), are relatively low growing and sporadic in occurrence. A number of other shrub species also occur in the boreal mixed-wood forest, but are relatively uncommon and rarely form dense stands that inhibit tree regeneration. These include green alder (*Alnus viridis* (Chaix.) D.C.), various cranberries (*Viburnum* spp.), and mountain-ash (*Sorbus decora* (Sarg.) Schneid.).

As they develop, boreal mixed-wood forests pass through four temporal phases of stand dynamics: stand initiation, stem-exclusion or self-thinning, canopy transition, and gap dynamics. Stand initiation refers to the immediate post-disturbance colonization of a site by fast-growing, shade-intolerant species such as trembling aspen, balsam poplar and white birch and jack pine. This stage, which occurs within the first few years following a catastrophic disturbance (usually fire), is characterized by very dense, even-aged stands of similar-sized trees. The self-thinning stage follows stand initiation. As the colonizing trees grow and begin to compete strongly for space and resources (e.g. light, soil water and nutrients), the stands undergo self-thinning through the differential mortality of smaller, suppressed individuals. Considerable reductions in density can occur during the self-thinning phase; for example, trembling aspen densities may be reduced from 20,000 to only 5,000 stems/ha during the first ten years post-colonization (Peterson and Peterson 1992). This reduction in stand density continues up to about 60-80 years of age, after which stands shift from density dependent mortality (i.e. self-thinning) to density independent mortality (i.e. biotic and environmental causes of death, and natural senescence; Pothier *et al.* 2004). This shift marks the beginning of the canopy transition phase of stand dynamics, defined as the gradual replacement of the shade-intolerant, post-colonization

canopy trees by more shade-tolerant species (e.g. white spruce and balsam fir). The mortality of canopy trees through natural senescence, pathogens or insect pest attack, or stochastic environmental events such as wind-throw increases light penetration to the forest floor, "releasing" shade-tolerant trees previously established beneath the main canopy (Lieffers *et al.* 1996). As a consequence, the canopy becomes a mixture of remnant initial colonizing trees (e.g. trembling aspen) and released shade-tolerant trees (e.g. white spruce). As stands continue to age, they enter the gap dynamic stage. During this stage, mortality of individual or small groups of canopy trees results in the development of "gaps" or openings in the canopy that are colonized by individuals, a phenomenon known as "canopy gap replacement". Although some studies have indicated that the replacement species into canopy gaps are most likely be a shade-tolerant species (Kneeshaw and Bergeron 1998), in larger gaps replacement by shade-intolerant species may occur (Chen and Popadiouk 2002). For example, clonal suckers of trembling aspen are stimulated by the increased light intensity of canopy gaps, and may successfully recruit into the canopy to a much greater extent than previously acknowledged (Cumming *et al.* 2000).

   The complexity of stand development and canopy interactions in boreal mixed-wood forest suggests that proposed deterministic pathways of forest succession do not adequately describe and reflect what is actually occurring in these stands (Johnson 1979). Stand dynamic models based on the direct regeneration and intermediate disturbance hypotheses provide alternative explanations for the variability in stand structure and composition over time. The direct regeneration hypothesis suggests that the density and composition of a given regenerating stand can be predicted based on the composition and abundance of species that were present prior to disturbance (Ilisson and Chen 2009). The intermediate disturbance hypothesis posits that a naturally aging stand is subjected to stochastic small-scale disturbances that alter the temporal trajectories of stands,

resulting in strong variation in stand composition and structure across the landscape. Such stands may appear to be of different ages, but are in fact the same age (Taylor and Chen 2011). Combining the direct regeneration and intermediate disturbance hypotheses results in the multiple pathways hypothesis. This hypothesis proposes that, based on starting conditions that can be coarsely predicted from pre-disturbance conditions (Johnstone *et al.* 2004; Ilisson and Chen 2009), a given stand can follow any of a number of possible pathways toward a "climax" or final steady-state (Taylor and Chen 2011). The specific pathway followed is determined by time since fire, and is continually altered by smaller, intermediate disturbances that are stochastic in both space and time. The concept of multiple successive pathways does not deviate from the overall deterministic view of forest succession, since it proposes that over time all stands succeed irrevocably toward dominance by shade-tolerant species that are considered superior competitors (e.g. white spruce, balsam fir and eastern white cedar).

Frelich and Reich (1995) summarized five pathways that can occur during forest succession. These pathways have been adapted to the boreal mixed-wood forests by Chen and Popadiouk (2002), and are summarized below:

(a) Cyclic Pathway: Here, early colonizing species are replaced over time by later, shade-tolerant species. Such systems are "reset" following a large-scale disturbance, with colonizing species again flourishing until replaced by shade-tolerant species (e.g. Harvey *et al.* 2002).

(b) Convergent Pathway: This is the classic "Clementsian" view of succession, wherein colonizing species prepare the way (i.e. change site conditions) for later-successional species along a pre-specified path of inevitable convergence to a final, deterministic climax state. In the boreal mixed-wood

forest, the proposed deterministic replacement of post-fire deciduous tree species (i.e. trembling aspen) by shade-tolerant conifers (white spruce and/or balsam fir) characterizes this pathway (e.g. Rowe 1956).

(c) Divergent Pathway: Here, a given community-type diverges over time to form multiple communities. This temporal divergence is driven by differences in seed source availability, and by differential competitive interactions that reflect species-specific adaptations to resource acquisition. As an example, consider the colonization of aspen suckers over a large area following a catastrophic fire. As these stand age, a nearby seed source may result in colonization by white spruce, white birch or other species. Alternatively, the lack of a seed source for other species may result in aspen persistence, or the senescence of aspen and eventual dominance by tall shrubs (e.g. Caners and Kenkel 2003).

(d) Parallel Pathway: When catastrophic disturbances are regular and sufficiently recurrent, a specific stand composition is replaced by the same stand composition following each disturbance event. In the boreal forest, jack pine and black spruce stands are perpetuated by recurrent catastrophic fire, the species having adapted to such fires by evolving serotinous cones (Dix and Swan 1971; Heinselman 1981).

(e) Individualistic Pathway: This pathway (also called multiple pathway; Cattelino *et al.* 1979) proposes that numerous interacting stochastic factors (e.g. seed masting, disturbances at various scales, climatic fluctuations and weather patterns, insect pest and fungal pathogen attack) will result in a wide range in stand composition at a given location and over time (Frelich and Reich 1995; Chen and Popadiouk 2002). Species that are considered "pioneers" (e.g. trembling aspen, white birch) can occur at all temporal stages of stand

development, provided that stochastic factors create conditions favourable to their establishment. In this view deterministic succession is occurring, but it is interrupted by factors operating at various spatial and temporal scales. As a result, the length of time required to achieve coniferous dominance in boreal mixed-wood stands may be greatly extended.

The complexity of successional pathways is compounded when variability in climatic, edaphic and natural disturbance regimes across the boreal mixed-wood forest region are incorporated (**Table 2.1** and **Figure 2.1**). There are considerable differences in the climate and edaphics (e.g. bedrock geology) of the eastern and western boreal mixed-woods, and these differences have ramifications with respect to severity and relative importance of various natural disturbances. Disturbances such as fire, wind-throw, insect defoliation, fungal pathogens and other gap disturbances are not mutually exclusive and are often synergistic in their effects, further complicating our understanding of stand dynamics (McCullough *et al.* 1998). For example, stands that are heavily defoliated by insect pests such as the spruce budworm (*Choristoneura hebenstreitella* Clem.) accumulate large amounts of coarse woody debris and litter (Martin and Mitchell 1980), which in turn increases the likelihood of a very severe and catastrophic forest fire. Similarly, the compositional and structural development of a forest stand following a stand-replacing fire influences the species composition and abundance of associated insect pest and fungal pathogen communities, and these in turn affect forest stand dynamics. Fire and insect defoliation are often large-scale disturbances that exert their effects at a landscape scale (Blais 1983; Johnson 1992), whereas wind-throw, fungal pathogens and mammalian herbivory are more localized in their effects and are considered gap disturbances (Kneeshaw and Bergeron 1998).

Gap openings, which may arise from small-scale disturbances or the natural senescence of individual trees, promote localized re-colonization of individuals or small groups of trees. Mammalian herbivores such as beaver (*Castor canadensis* Kuhl) and ungulates will consume trembling aspen suckers, and may eliminate the species from a stand and so favour the regeneration of less palatable species such as white spruce (Sinkins 2008). Fungal pathogens also create individual tree gap openings, or larger gaps when a cluster of neighbouring trees are affected (Basham 1981). Canopy gap openings result in greatly increased light penetration to the forest floor, stimulating the growth of the species present. Canopy gap replacement is driven by the composition of suppressed individuals beneath the canopy gap, and to a lesser extent by various stochastic factors (Taylor and Chen 2011). An optimal competitor exists for any given set of environmental conditions within a gap (Tilman 1982), but spatial and temporal variability in environmental conditions, and in the size of gaps, will promote the long-term coexistence of two or more species within a stand (Crawford *et al*. 1998). Upon creation of a canopy gap, already present but suppressed (or advanced regeneration) white spruce trees start to grow quickly and soon replace or "fill" the canopy opening (Lieffers *et al*. 1996; Gutsell and Johnson 2002). Aspen suckers are also stimulated by the higher light levels that occur when a canopy gap is formed, and the species can produce a second cohort that colonizes the gap opening (Cumming *et al*. 2000). Whether white spruce or trembling aspen colonizes a given canopy gap is dependent on species composition and abundance beneath the gap (suppressed white spruce saplings and/or aspen suckers), gap size (which affects light levels), and numerous stochastic factors that are difficult if not impossible to quantify.

Although the boreal forest is compositionally depauperate (Larsen 1980), its spatial and temporal dynamics remain poorly understood (Kenkel *et al*. 1997). As described above, the climate and topography influence the floristic

composition and natural disturbance regime within the region, creating a complex temporal mosaic of forest composition and structure at all spatial scales (Walker and Kenkel 2001). In order to fully understand and appreciate the complexity of the boreal mixed-wood forests of Canada, the following provides a comparison of eastern and western boreal mixed-wood forests. The purpose is to highlight the similarities and differences between eastern and western mixed-wood stands, and to provide a summary of the existing dichotomy in our understanding of stand dynamics (forest succession) in boreal mixed-wood forest.

2.1.1 Boreal Mixed-wood Forests of Western Canada

The boreal mixed-wood forests of western Canada extend from southwestern Manitoba to northeastern British Columbia (**Figure 2.2**). In this region, mixed-wood stands consist of variable mixtures of trembling aspen, balsam poplar, white birch, white spruce and balsam fir that occur on moderately to well-drained upland sites (Rowe 1972). Balsam fir is uncommon in the western boreal mixed-woods (Rowe 1961), being largely restricted to islands, north and east-facing slopes, and other less fire-prone areas on the landscape. The mixed deciduous-coniferous canopy that is characteristic of the western mixed-wood has been described as an intermediate stage of succession, rather than a self-perpetuating system (Rowe 1972). In this view mixed-wood stands will, given the absence of fire, follow an inevitable, deterministic pathway toward conifer dominance (Rowe 1972). However, recent evidence indicates that these systems do not adhere to a simple deterministic temporal sequence from deciduous to coniferous dominance (Gutsell and Johnson 2002).

The dominant tree species of western boreal mixed-wood stands is the deciduous trembling aspen. This is perhaps not surprising given the remarkable

ability of this species to regenerate from root suckers (clonal growth) following a disturbance, which in a disturbance-driven ecosystem promotes its persistence and early dominance through rapid recruitment at high densities. The other major tree species in western boreal mixed-wood forest is the evergreen conifer white spruce, which often occurs with trembling aspen as a co-dominant (Rowe 1956; Jameson 1963). White spruce is a prolific seed producer, and established individuals can persist beneath a closed trembling aspen canopy due to their high degree of shade-tolerance. Balsam poplar often occurs in moister sites, and white birch is also often present in western boreal mixed-wood stands.

The western boreal mixed-wood forest occurs to the north of the temperate grasslands of central North America. The winters are long and cold, and the summers moderately dry and cool. Prevailing winds during the winter months are often from the northwest, bringing cold air from the arctic. The mean temperature during the winter months (November to March) is -13.3°C, and mean snowfall is about 20 cm. In the spring and summer months, winds from the south and west bring warmer temperatures as well as the moist air that provides much of the precipitation. The mean temperature during the spring and summer (April through October) is about 10°C, with a mean monthly precipitation of 5-6 cm. Approximately two-thirds of the total annual precipitation occurs as rainfall between May to August.

Underlying the western boreal mixed-woods is calcareous Cretaceous bedrock, which produces soils that are moderately basic to slightly acidic. Much of the region is a mixture of hummocky moraines, till plains and localized gravel deposits that were deposited during periods of continental glaciation (Ritchie 1964). The soils are a mixture of Brunisolic, Regosolic, Gleysolic, Organic, Crysolic, Podzolic and Luvisolic orders (Acton 1989). These young soils

developed under the influence of glacial and post-glacial sediments and vary in drainage, texture and calcareousness (Ritchie 1964).

Fire is the predominant large-scale disturbance within the western boreal mixed-wood forest, and plays a dominant role in the spatial and temporal dynamics of forest stands in the region (Johnson 1992). Fires are cyclic disturbances that have mean return rates < 80 years in the western Canadian boreal forest (Larsen 1997; Weir *et al.* 2000). During the period of European settlement many fires were human-caused, escaping from settlements areas during the spring and early summer months (Johnson *et al.* 1999). Following the successful implementation of fire suppression practices in the mid-twentieth century, the boreal forests were protected from economic timber loss. However, this period of suppression of a natural disturbance has altered the composition and structural diversity of the western boreal mixed-wood stands (Johnson *et al.* 2001). It has also been suggested that some of the changes that have been attributed to fire suppression may in fact be the results of changes in climate (Kurz *et al.* 2008).

Mammalian herbivores such as moose, elk, white-tailed deer and beaver can adversely affect the regeneration of tree species in boreal mixed-wood stands. These herbivores may heavily browse young aspen trees (Lastra 2011) and balsam fir saplings (Rowe 1955), but white spruce saplings are rarely browsed (Rowe 1955). Beavers are important "ecosystem engineers" that select large-diameter trembling aspen from upland sites adjacent to streams and ponds, thereby releasing the less palatable conifers (Pastor *et al.* 1993). As a result, older stands adjacent to watercourses are often conifer-dominated (Sinkins 2008). Red squirrels and hares forage on white spruce seeds and young shoots (Rowe 1955).

Insect defoliation can dramatically alter boreal stand dynamics. In eastern Canada, the spruce budworm is an important and major disturbance agent (Blais 1983), but it plays a much lesser role in western Canada. The forest tent caterpillar (*Malacosoma disstrium* Hubner) is the most common forest insect pest in the western region. Trembling aspen is the most common host of the forest tent caterpillar, although balsam poplar and white birch may also be affected (Sutton and Tardif 2007). However, the forest tent caterpillar rarely affects the long-term health of afflicted stands (Peterson and Peterson 1992).

Rowe (1956) was the first to describe succession trends in the western boreal mixed-wood forest. His characterization of mixed-wood forest succession as a simple, predefined deterministic pathway from deciduous to coniferous tree dominance reflected the Clementsian view of succession that prevailed at the time (Johnson 1979). Nevertheless, this rather simplistic view remains the cornerstone of most discussions and models of boreal succession. Dix and Swan (1971) examined the order of post-disturbance recruitment of major tree species in Saskatchewan, classifying the most common western species (aspen, birch, black and white spruce, and balsam fir) into one of three categories: pioneer, chiefly pioneer, and successional. They concluded that balsam fir was the only truly "successional" species. Balsam fir is uncommon in the region, however, and the frequency of fires led the authors to conclude that "succession does not seem to be important" in the region, and that "any attempt to fit the vegetation into the mold of a climax concept would be unreal and, in our opinion, unjustified" (Dix and Swan 1971).

Until recently, succession studies in boreal ecosystems have given little consideration to the regenerative capacity of so-called "early" successional species such as trembling aspen. An important and characteristic adaptation of trembling aspen (and balsam poplar), the ability to reproduce asexually through

root suckering, was all but ignored in the earlier literature except as a strategy for rapid re-colonization following catastrophic fire (Rowe 1956, 1961; Dix and Swan 1971). It was assumed that suckering by trembling aspen and other species (e.g. balsam poplar, white birch) was unimportant as a mechanism of secondary cohort recruitment. Only recently has the importance of clonality, and its implications for the long-term persistence of hardwood species in boreal forest stands, been recognized (Cumming *et al.* 2000; Baret and desRochers 2011; Lastra 2011).

In many western boreal mixed-wood stands, both deciduous, shade-intolerant species (e.g. trembling aspen) and coniferous, shade-tolerant species (e.g. white spruce) establish contemporaneously (Gutsell and Johnson 2002). The clonal deciduous component establishes immediately post-fire at very high density, and grows much more quickly than the seed-established conifer component (Peters *et al.* 2006). As a result, during the early stages of stand development these stands appear to be deciduous-dominated. Over time, the conifer component is more conspicuous and the stands take on a characteristic "mixed-wood" appearance. Few studies have examined succession trajectories beyond this "mixed-wood" stage (i.e. in stands > 100 years in age), although there is some evidence to suggest that trembling aspen (and presumably other clonal deciduous tree species) are able to recruit in second, and potentially third, cohorts once the initial post-disturbance canopy begins to break-up (Cumming *et al.* 2000).

2.1.2 Boreal Mixed-wood Forests of Eastern Canada

The Missinaibi-Cabonga region is a well-studied representative of the eastern boreal mixed-wood forest. It occurs between the Great-Lakes St. Lawrence

decidous forests to the south and the high-boreal forests to the north (Rowe 1972). Forest stands in this region have greater compositional and structural diversity than their western boreal mixed-wood counterparts.

The eastern boreal mixed-wood region is considerably wetter and snowier, and somewhat warmer, than the western region (**Table 2.1; Figure 2.1**). Over two-thirds of the annual precipitation falls as rain between April and October. Mean temperature during the winter months (November to March) is about -12.5°C, with about 45 cm of snow. The spring summer months (April – October) average about 10°C, with mean precipitation of 8.5 cm per month.

The bedrock of the eastern boreal mixed-wood region is Precambrian acidic granite (Canadian Shield), which in places is overlain by deposits of glacial, lacustrine or alluvial origin ranging from coarse to fine-textured (Paré *et al*. 2011). As in the west, the region was entirely covered by glaciers during the late Pleistocene. The major soil types include the Regosolic, Organic, and Ferro-Humic Podzolic orders (CSSC 1998). The large region known as the Clay Belt is characteristically of low topographic relief. Soils in this region are fine silt to silty sands deposited by the pro-glacial Lake Ojibway (Lecomte and Bergeron 2005).

The fire history of the eastern boreal mixed-wood forest is well documented. Dendrochronological techniques and aerial photography have been used to reconstruct landscape patterns of fire frequency and severity (Payette *et al*. 1989). The fire cycle has been estimated at 65-70 years prior to 1870, and > 100 after 1870 (Bergeron 1991; Dansereau and Bergeron 1993). Comparable values for western Canada are about 40 years prior to 1860, and 75 years after 1870 (Larsen 1997). Many stands in the region have not burned for > 250 years (Bergeron 2000), whereas very few mixed-wood stands in western Canada are

more than 100-150 years old (Tardif 2004). This indicates that fire return intervals in eastern Canada are much greater than those in western Canada, which likely reflects the much higher levels of precipitation in the eastern region (90-100 cm annually, versus about 50 cm in western Canada).

Forest stands of the Missinaibi-Cabonga region were mostly initiated by wildfires and large-scale spruce budworm outbreaks (Bergeron 1991; Morin *et al*. 1993). The boreal mixed-wood stands in this region typically occur on moderate to heavy silt deposits, and are generally dominated by trembling aspen, white birch, white spruce, balsam fir and eastern white cedar (Bergeron 2000). Other stand types in the region include black spruce and birch on granite-based morainal deposits, black spruce, jack and/or red pine on well to excessively drained sandy soils, and black spruce, cedar and tamarack in wet lowlands with long fire return intervals (Bergeron and Bouchard 1984)

The Missinaibi-Cabonga forest has been well studied (Bergeron 1991; Kneeshaw and Bergeron 1998; Bergeron 2000; Bergeron *et al*. 2004; Bouchard 2008), and these studies have provided valuable insight into the stand dynamics of eastern boreal mixed-wood forests. These are disturbance-driven ecosystems, the two major large-scale disturbances being fire and massive spruce budworm outbreaks. Stand composition and structure are strongly influenced by both recurrent fires and by the frequency and severity of spruce budworm cycles. Eastern mixed-wood stands have a longer fire cycle (typically > 100 years) than those in the west (typically < 80 years). A longer fire cycle promotes higher species turnover, and a greater predominance of shade-tolerant species such as balsam fir, eastern white cedar, white spruce and black spruce in eastern mixed-wood stands (Bergeron and Dubuc 1989; Viereck 1983). Shade-tolerant (or late successional) species such as balsam fir and eastern white cedar will occasionally establish contemporaneously with shade-intolerant early

successional species (e.g. trembling aspen) following disturbance (Bergeron and Charron 1994), but their recruitment is more often delayed until suitable seedbed and other environmental conditions are met (Bergeron and Dubuc 1989).

   The successional dynamics of the mixed-wood forests of the Missinaibi-Cabonga region have been inferred using the chronosequence approach, supplemented by detailed dendroecological studies (Morin 1990; Payette *et al*. 1990; Paré and Bergeron 1995; Bergeron 2000). Stand-level disturbances such as fire and spruce budworm defoliation events promote the prolific regeneration of trembling aspen and paper birch (Bergeron and Charron 1994; Morin 1994). The dominant species of early post-disturbance stands (< 100 years) are trembling aspen and white birch, with lesser amounts of white spruce and balsam fir (Bergeron 2000). These stands though undergo intense self-thinning until the age of 60-80 years, at which point a shift from density dependent mortality occurs (Pothier *et al*. 2004). Trembling aspen declines in abundance after 150 years: at this stage mixed stands of balsam fir, white birch and white spruce are typical. After 150 years the abundance of white cedar increases considerably, and by 200 years in age stands are dominated by eastern white cedar, paper birch and balsam fir with lesser amounts of white spruce (Bergeron 2000). Most of the trees established in the first 30 years maintain a presence in these stands for up to 250 years (Cogbill 1985). The importance of small-scale disturbances (canopy gap dynamics) increases throughout this temporal sequence, and is the predominant factor determining changes in species and canopy turnover during later successional stages (Kneeshaw and Bergeron 1998). These stands are subject to increased probability of stochastic death through wind-throw, localized insect and pathogen outbreaks, and senescence, creating canopy gaps that promote the recruitment of many boreal species (Kneeshaw and Bergeron 1998; Bergeron *et al*. 2001; Kneeshaw and Gauthier 2003).

As these stands age, they slowly become self-perpetuating as a result of shade-tolerance being the principal characteristic promoting longevity (Kneeshaw *et al.* 2006). Thus, it is purported that the eastern mixed-woods are deterministic in their long-term stand dynamics. Chronosequencing studies in the eastern boreal mixed-wood forests confirm a deterministic temporal replacement model, whereby shade-intolerant, early succession deciduous species are replaced over time by shade-tolerant late-successional coniferous species. However, it has been acknowledged that "small numbers of aspen are present even a long time after fire" (Bergeron 2000). More recent studies in the eastern mixed-woods have recognized that clonality of deciduous boreal tree species (e.g. trembling aspen suckers) may be an important recruitment mechanism, and not merely an anomaly (Baret and DesRocherss 2011).

The other important disturbance agent within the Missinaibi-Cabonga forest section is large-scale insect defoliation (Bergeron *et al.* 1995). As with catastrophic fires, the cyclical nature of spruce budworm outbreaks is a function of local climatic conditions (Morin *et al.* 1993). Spruce budworm outbreaks have historically coincided with extended periods of drought, although the severity of insect defoliation is apparently not influenced by climate (Régnière and You 1991). Instead, the important attribute determining the degree of defoliation by spruce budworm is tree size; larger trees are much more susceptible to defoliation, and exhibit increased mortality (Bergeron *et al.* 1995). Despite its name, spruce budworm is most damaging to balsam fir, which is its preferred host. Tree mortality attributable to spruce budworm defoliation is an important mechanism for the creation of canopy gaps of various sizes. The spatial and temporal variability in canopy gap formation is a critical driver of tree recruitment and stand dynamics of eastern boreal mixed-wood stands (Kneeshaw and Bergeron 1998). Another insect defoliator, the forest tent caterpillar, mainly affects trembling aspen. Unlike spruce budworm, the severity of forest tent

caterpillar defoliation is unpredictable and trees are not generally killed (Cooke and Lorenzetti 2006).

Table 2.1: A comparison between the eastern and western boreal mixed-wood forests. All meteorological information was obtained from Environment Canada (2009).

	EASTERN	WESTERN
LOCATION	Duparquet (La Sarre)	Riding Mountain (Wasagaming)
Latitude (DMS)	48°47'00"N	50°39'18"N
Longitude (DMS)	79°13'00"W	99°56'31"W
Elevation (m)	244.1	627.4
CLIMATE		
Total precipitation (mm)	890	521
Rainfall (mm)	644	398
Snowfall (cm)	246	123
Mean Annual Temperature (°C)	0.7	0.1
Warmest Month (mean °C)	July (16.9)	July (16.5)
Coldest Month (mean °C)	January (-18.2)	January (-19.6)
Average wind speed (km/h) and direction	15.8 from SW	9.4 from the NW
GEOLOGY AND EDAPHICS		
Bedrock	Precambrian granite (Canadian Shield), lacustrine and morainic deposities, glacial till, acidic soils	Sedimentary bedrock, glacial till, calcareous soils[a,b]
Soil types	Clay and silt deposits[c]	Clay, silt and sand[d]
pH	3.60 – 5.10[e]	4.83 – 6.23[f]
SOIL NUTRIENTS		
Ca (cmol/kg)	0.79 – 43.44[e]	5.1 – 42.3[g]
K (cmol/kg)	0.11 – 3.80[e]	0.2 – 3.2[g]
Mg (cmol/kg)	0.22 – 5.34[e]	0.4 – 6.5[g]
NH_4-N (mg/kg)	4.50 – 393.56[e]	8.3 – 71.5[g]
NO_3-N (mg/kg)	0.04 – 1.53[e]	0.5 – 5.6[g]
PO_4-P (mg/kg)	4.26 – 61.20[e]	6.7 – 95.8[g]

Table 2.1: CONTINUED

	EASTERN	WESTERN
TREES		
Deciduous	Major: trembling aspen, white birch	Major: trembling aspen. Secondary: balsam poplar, paper birch
Coniferous	Major: balsam fir, white spruce, eastern white cedar. Secondary: black spruce, jack pine.[c]	Major: white spruce. Secondary: black spruce, jack pine, balsam fir.[h]
SHRUBS		
	Major: mountain maple, pin cherry, willows. Secondary: green alder, beaked hazel, cranberries, mountain-ash[e]	Major: beaked hazel (MB), buffalo berry (AL). Secondary: green alder, wild rose, willows[i]
FIRE		
Return rate	pre-1870 – 63 years post-1870 – > 99 years[j]	pre-1860 – ≈37 years post-1860 – ≈74 years[b]
Intensity	Affected by climate; generally less intense than in the west[k]	Affected by climate; generally more intense than in the east[k]
INSECTS AND PATHOGENS		
Insects	Spruce budworm[l,m]	Forest tent caterpillar[n]
Fungal pathogens	*Phellinus igniarius* (L.) Quél., *Armillaria mellea* (Vahl) P. Kumm.[o,p]	*Peniophora polygonia* [Pers.:Fr.] Boud., *Phellinus tremulae* [Bond.] Bond. And Boriss.[q]
HERBIVORY		
Beaver	Common in the waters of areas that have recently burned or been logged[r]	Common throughout region, although may be locally extirpated[s]
White-tailed deer	Extensive browsing of balsam fir and aspen[t,u]	Extensive browsing of balsam fir and aspen suckers[h,v]
Moose	Common in 15 – 30 year old aspen stands[w]	Common in 15 – 30 year old aspen stands[x,y]
Elk	Not present	Extensive browsing of balsam fir and aspen suckers[h]
Small Mammals	High densities of snowshoe hares in 20 – 30 year old aspen stands[z]	Red squirrels cache white spruce cones and hares preferentially forage young aspen[aa, ab]

a – Porter *et al.* 1982; *b* – Larsen 1997, *c* – Bergeron 2000, *d* – Hamel 2002, *e* – Légaré *et al.* 2001, *f* – Ste. Marie and Paré 1999, *g* – Schmidt *et al.* 1996, *h* – Rowe 1955, *i* – Lieffers and Stadt 1994, *j* – Bergeron and Archambault 1993, *k* – Bessie and Johnson 1995, *l* – Blais 1983, *m* – Bergeron *et al.* 1995, *n* – Hogg and Schwarz 1999, *o* – Chen and Popadiouk 2002, *p* – Whitney 1981, *q* – Brandt *et al.* 2003, *r* – Naiman *et al.* 1986, *s* – Sinkins 2008, *t* - Potvin *et al.* 2000, *u* – Potvin *et al.* 2003, *v* – Pike 1955, *w* – Crête *et al.* 1981, *x* – Hundertmark *et al.* 1990, *y* – Loranger *et al.* 1991, *z* – Guay 1994, *aa* – Brink and Dean 1966, *ab* – Oldemeyer 1983.
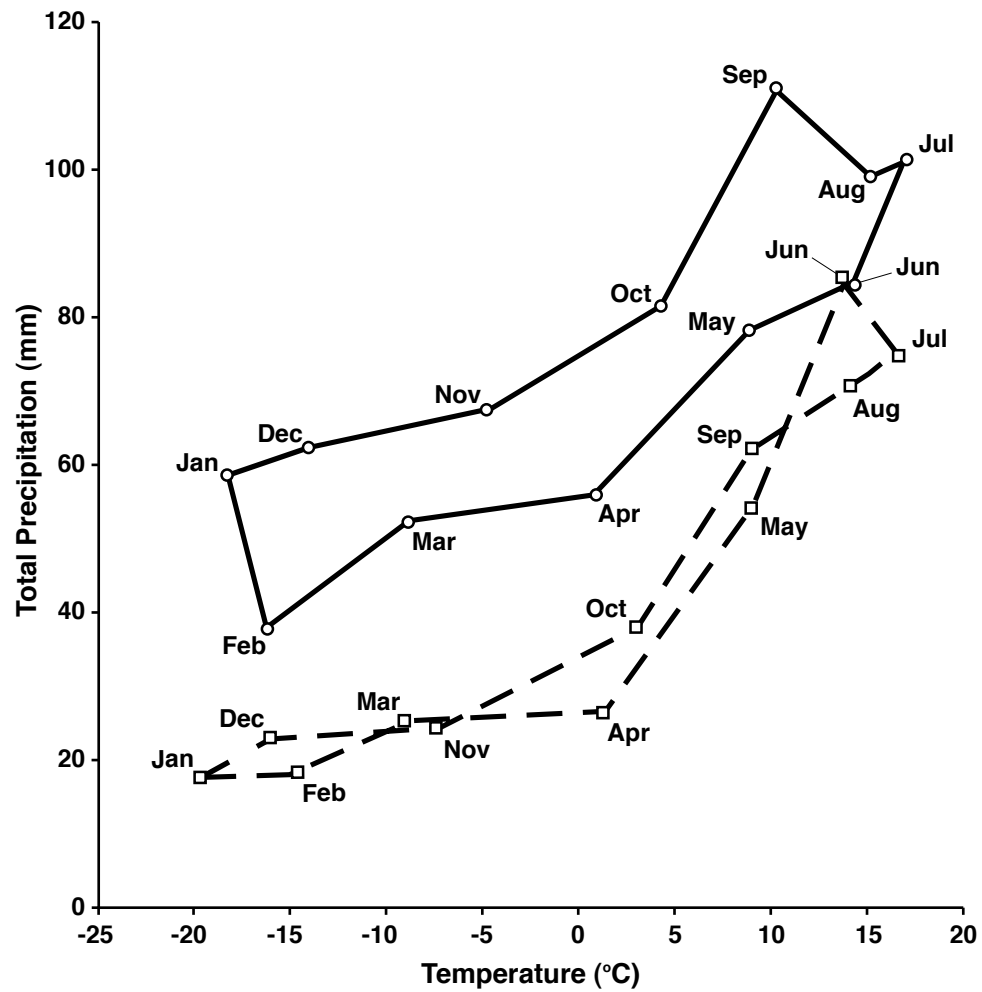
Figure 2.1: 12-month temperature and precipitation plots for La Sarre, Québec (solid line) and Wasagaming, Manitoba (dashed line) (Environment Canada 2009).
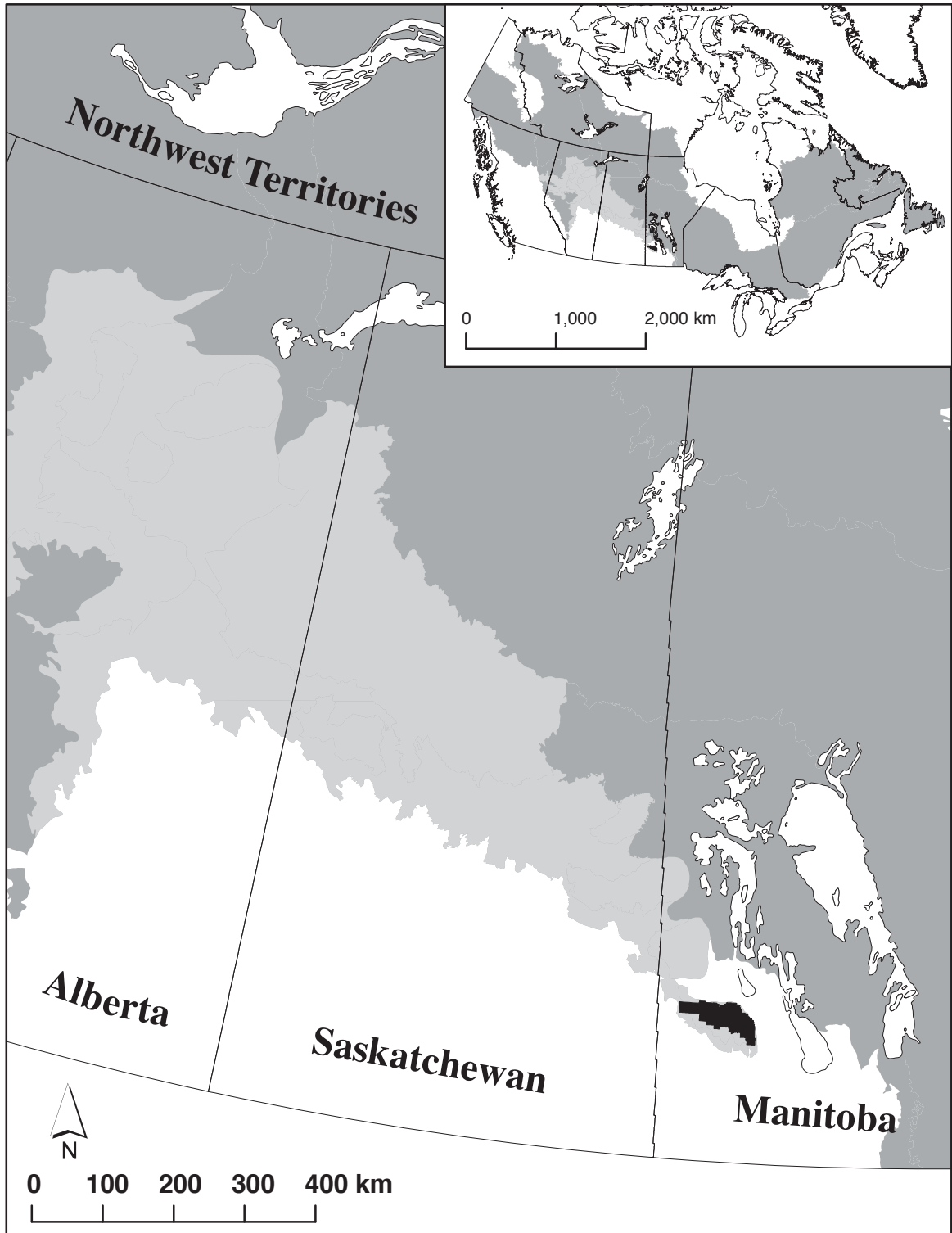
Figure 2.2: A map showing the extents of the boreal forest (dark grey) and the western boreal mixedwood forest (light grey). The study area, Riding Mountain National Park is highlighted in black.

CHAPTER 3
STUDY AREA AND OBJECTIVES

3.1 RIDING MOUNTAIN FOREST EXPERIMENTAL AREA (RMFEA)

In 1918, the Dominion Forestry Branch established sixteen permanent sample plots (PSPs) at the Petawawa Forest Experiment Station (Campbell 1920). This served as a precedent for setting aside small areas of land for long-term forestry research in Canada (Campbell 1921). By 1938, permanent sample plot studies had been initiated in New Brunswick, Quebec, Ontario, Manitoba and Alberta (Cameron 1938). This Canada-wide research project focused on developing silvicultural practices for increasing merchantable timber volume (Campbell 1922). A series of permanent sample plots were initiated in the Riding and Duck Mountain Forest Reserves in the early 1920s, and research continued on these plots until 1939 when all research projects were transferred to a small set of new plots established at Riding Mountain (Campbell 1922; Fyk 1986).

Soon after World War II (1946 – 1948), 1480 permanent sample plots were established and enumerated in the Riding Mountain Forest Experimental Area (Pratt 1967). This large project, known as MS – 69, was intended as an inventory and growth-yield survey of the Riding Mountain region, with an emphasis on ameliorating problems associated with white spruce reproduction (Phelps 1948; Rowe 1955). The study was also intended to provide information on long-term stand development (Jarvis *et al*. 1966). A number of additional forest research projects were undertaken within the boundaries of the Riding Mountain Forest Experimental Area, including white spruce harvesting, site preparation (scalping, disking) for the planting and seeding of white spruce, thinning of white spruce stands, removal of the aspen overstory (manually, mechanically and herbicides),

and removal of competing tall shrubs (mainly beaked hazelnut) using herbicides (Johnson and Waldron 1992).

3.1.1 Site Description and Characterization

The 1480 MS-69 plots covered a rectangular area approximately 11.5 km (south to north) by 6.5 km (east to west) immediately north of the northeast shoreline of Clear Lake (50°42' N, 100°0' W). The topography is moderately to strongly rolling, with gently undulating to level ground occurring near Clear Lake. Elevation ranges from 615 m (Clear Lake) to about 700 m. The underlying bedrock is dark grey Cretaceous shale. Most of the study area is overlain with glacial till surficial deposits, although lacustrine deposits occur in channels and along lakeshores. Two major soil parent material or "site" types occur in upland forest stands within the study area (Jameson 1963). The most common is the "Fresh Waitville" type, which is characteristic of strongly to moderately rolling topography. The soils are clay-loam textured orthic grey-wooded luvisols, derived from yellow-brown stony calcareous glacial till. Sites are fresh to moderately moist (Jarvis *et al*. 1966), with an understory dominated by beaked hazelnut (*Corylus cornuta* Marsh.), wild sarsaparilla (*Aralia nudicaulis* L.), lungwort (*Mertensia paniculata* (Ait.) G. Don) and bunchberry (*Cornus canadensis* L.). The less common "Moist Granville" type is characteristic of level to gently undulating topography. The soils are clay-loam to clay-textured dark-grey-wooded luvisols, derived from dark grey-brown shaly, slightly calcareous tills. Sites are moderately to very moist (Jarvis *et al*. 1966), with an understory dominated by marsh reed-grass (*Calamagrostis canadensis* (Michx.) Beauv.), flat-topped white aster (*Doellingeria umbellata* (Miller) Nees var. pubens), and goldenrod (*Solidago* spp.).

Soil profiles from the "Fresh Wainville" and "Moist Granville" types are very similar (Jameson 1963):

Horizon	Depth (cm)	pH	Texture
O	5	-	duff mull
A	10	5.5-6.1	sandy loam to clay loam
AB	10-15	5.6-6.3	silty loam to clay loam
B	15-20	6.5-6.7	clay loam to clay

The C-horizon, which begins at about 40-50 cm depth, consists of basic (pH =7.3 or higher) clay loam containing some gravel and stones.

The dominant tree species of the Riding Mountain Forest Experimental Area are trembling aspen and white spruce on fresh to moist sites, with lesser amounts of white birch and balsam poplar. Jack pine and balsam fir occur rarely within the region. Poorly drained peat lands and wet depressions are dominated by black spruce and tamarack (Jameson 1963; Bella and Gál 1995).

The dominant tall shrub of fresh to moderately moist upland sites is beaked hazelnut (Jarvis *et al.* 1966), a characteristic species of older mixed-wood boreal stands in Manitoba and Saskatchewan (Waldron 1959). The light filtering through mature, open forest canopies promotes rapid clonal development of the species, resulting in extensive areas of a dense, luxuriant hazelnut growth (Hsiung 1951; Kurmis and Sucoff 1989). Beaked hazelnut averages 1.5 – 2.0 m in height and forms a dense understory canopy. In a typical upland site about 88% of the shrub stems are hazelnut, with a density of about 90,000 stems/ha and a leaf area index (LAI) of seven (Waldron 1959). In older stands, competition from beaked hazelnut is a major factor limiting the recruitment and growth of white spruce saplings and trembling aspen root suckers (Bella and Gál 1995). In an

experiment using planted white spruce seedlings, survival (57 versus 29%) and height growth after four years (42 versus 28 cm) were much greater in areas that were sprayed with herbicide to remove competing hazelnut shrubs (Waldron 1959).

When the MS-69 permanent sample plots were established in 1946-1948, the stands were described as "overmature", with "decadent" trembling aspen trees 100-120 years old and an all-aged, "thrifty" white spruce component (Jarvis *et al*. 1966). Sample cores taken during the establishment of MS-69 found at least one tree > 100 years in age (at breast height) in each plot. In 1955, a detailed analysis of the age structure of these stands obtained ages > 120 years in 5% of trembling aspen, and 2% of white spruce (age at breast height; Jameson 1963). Assuming conservatively that trees in the > 120 year age class are 125 years old, and noting that it takes about 5 years for white spruce and trembling aspen saplings to reach breast height (Jameson 1963), it is apparent that these stands established following a catastrophic fire in the early to mid 1820s. This estimate is in keeping with historical and fire scar evidence indicating that catastrophic fires occurred in the 1820s (as well as the 1850s and 1889-1891) in the Riding Mountain area (Gill 1930; Harrison 1934; Rowe 1955; Sentar 1992; Tardif 2004).

Following a stand-destroying fire, a dense stand of clonal trembling aspen as suckers from the surviving root system, and a few white spruce often establish contemporaneously. When these early established white spruce reach seed-bearing age (after about 60 years), delayed recruitment of spruce begins in earnest (Rowe 1955) and this initiates the conversion of young aspen-dominated stands to the mixed-wood condition (i.e. trembling aspen – white spruce co-dominance).

Rowe (1955) speculated that:

"*The mixedwoods which eventually develop from hardwood stands do not appear to represent a stable type ... Many of them clearly show evidence of succession toward a softwood type. In fact it may be stated that old stands are coniferous stands*".

Rowe (1955) went on to predict successional change in the MS-69 plots, based on observations of forest stand composition and structure made during the initial survey (1946-1948):

"*The overmature aspen is dying at present without replacement, while the spruce continues to increase. Thus an uneven-aged softwood type is in the making ... The invasion of poplar by spruce, either rapidly or over a long period, and the subsequent dying of the poplar represents the typical development of coniferous stands on medium moist soils.*"

Numerous other researchers with the Riding Mountain Forest Experimental Area project made similar inferences regarding the long-term successional trajectory of these stands (e.g. Jameson 1963; Jarvis *et al*. 1966).

3.1.2 Permanent Sample Plots

The MS-69 permanent sample plots are arranged in a regular grid (excluding roads, grasslands, wetlands and lakes) at an interval of 10 chains (220 yards or 201.2 m). Each plot is square and 1 x 1 chains (0.1 acre) in size (i.e. 20.12^2 m, or approximately 0.04 ha). Each plot was marked with aluminum corner posts and a numbered plaque to facilitate relocation and re-measurement.

All 1480 of the MS-69 permanent sample plots were measured in 1946-1948 to obtain the following information:

1. Stem Data: Diameter at breast height (DBH) and species identification of all stems greater than 2 m in height (DBH measured to the nearest inch). In each plot, subsets of representative trees of each species were measured for height (nearest foot), and others were cored (at DBH level) for age determination.

2. Disturbance: The type of disturbance (wind-throw, fungi, logging and fire), and disturbance severity (light, moderate, heavy or severe) were noted in each plot, including the species and the number of trees affected.

3. Site Characteristics: Plot slope and aspect were measured, and drainage and topography classes noted. A general measure of soil texture (presence-absence of sand, silt and clay) was also made.

Most (1356 of the 1480) plots were re-measured (stem DBH only) at ten-year intervals, in 1956-1958 (Johnson and Waldron 1992) and again in 1966-1968 (Pratt 1967-1969).

A large permanent headquarters was established within the Riding Mountain Forest Experimental Area, and numerous manipulative experiments and field trials were undertaken on or near many of the permanent sample plots (summarized in Waldron 1991; Johnson and Waldron 1992). Fortunately, excellent records of these projects, and of timber harvesting in the region, were maintained so that it can readily determined which plots were affected by human impacts (Pratt 1964-1969; Johnson and Waldron 1992).

The Riding Mountain Forest Experimental Area was decommissioned in 1970, following a change in the mandate of Parks Canada dictating that no human interventions or impacts should occur within natural areas of National Parks. All experiments were abandoned, headquarters buildings were removed, and access roads and trails were no longer maintained. The marker posts and plaques associated with the MS-69 permanent sample plots remained in place, but most of the plots were not re-measured between 1967 and 2000 (Johnson and Waldron 1992).

In 2000 – 2001 forestry crews from Louisiana-Pacific Canada, in cooperation with Parks Canada, relocated a number of the original permanent sample plots. The purpose was to obtain information on long-term changes in mixed-wood forest stand composition and structure in the absence of fire and human disturbance. For this reason, no attempt was made to relocate plots in areas that were subjected to manipulative experiments or timber harvesting. Of the relocated plots, 266 were re-enumerated in 2001-2002 by Louisiana-Pacific Canada crews. The following criteria were used to select plots for re-enumeration:

1. Stand Composition: Only boreal mixed-wood stands dominated by trembling aspen and/or white spruce, with lesser amounts of paper birch and balsam poplar, were considered. Stands dominated by paper birch, balsam poplar, other species (e.g. black spruce) were not included.

2. Site Characteristics: Only fresh to mesic upland sites on mineral soil were considered. Sites with organic substrates, and those disturbed by beaver activity (flooding or tree felling), were not included.

3. Human Disturbance: Sites on or near a former Forest Experimental Area manipulation, and those having undergone timber harvesting in the past (determined from historical records, and the presence of stumps in the plot) were not included.

4. Stand Age: Only stands undisturbed by fire since the 1820s were considered. Plots in the southeast corner of the study area, which were burned in the 1880s (Sentar 1992), were not included.

5. Historic Data: In a few of the permanent plots, data from the earlier surveys were missing or contained major errors. These plots were not re-enumerated.

Unfortunately, the Louisiana-Pacific re-enumeration failed to tally stems < 9 cm DBH, making comparisons with earlier survey results impossible (all stems > 1.3 m in height were enumerated in earlier surveys). The same plots (and a few additional ones) were therefore independently re-enumerated in 2002-2004 in order to tally all stems > 1.3 m in height. The results of this independent re-enumeration (undertaken by Peter Sinkins and Matthew Lazowski of the Quantitative Plant Ecology Laboratory, University of Manitoba) were then compared to the Louisiana-Pacific survey results, to check for and ensure data consistency and accuracy.

3.2 OBJECTIVES

The overall objective of this thesis is to develop a synoptic model of long-term boreal mixed-wood forest stand dynamics for the Riding Mountain region of Manitoba, based on long-term (55 years) permanent sample plot data spanning stand ages 120 – 175 years. Specific objectives are:

- To determine whether standard models of boreal forest succession (replacement of trembling aspen by white spruce) in fact occurs in old-growth (>100 years) mixed-wood stands in Manitoba.

- To determine the recruitment dynamics of trembling aspen and white spruce in old-growth stands, and the factors affecting recruitment dynamics, using permanent sample plot data.

- To develop a model of boreal mixed-wood stand dynamics (0 – 175 years), based on data from the permanent sample plots.

CHAPTER 4

A LONG-TERM STUDY OF BOREAL MIXED-WOOD OLD-GROWTH STAND DYNAMICS: RESULTS FROM 266 PERMANENT SAMPLE PLOTS OVER 55 YEARS

4.1 INTRODUCTION

The boreal mixed-wood forests of western Canada are dominated by two tree species, trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) (Rowe 1972). Historical succession models have hypothesized that canopy break-up of the initial aspen cohort, which begins at about 60 – 80 years, allows white spruce to establish, grow, and inevitably replace trembling aspen as the dominant canopy species (Rowe 1956, 1961). More recent stand dynamic models have continued to hypothesize replacement of trembling aspen by white spruce, although some authors acknowledge that trembling aspen can occasionally persist in older stands (Bergeron *et al.* 1999; Bergeron 2000; Chen and Popadiouk 2002; Purdy *et al.* 2002). Even so, boreal succession models continue to subscribe to the notion of a predominant and characteristic late-succession community dominated by coniferous species (Kneeshaw and Bergeron 1998; Bergeron 2000; Taylor and Chen 2011). While this deterministic view of forest succession has been questioned and criticized (Kenkel *et al.* 1997; Pickett *et al.* 2009), boreal succession models continue to emphasize notions of species turnover and canopy replacement that were first inferred through casual observations of the composition and canopy structure of "mature" (typically 100-120 year old) stands (e.g. Rowe 1956, 1961).

Boreal succession studies concluding that conifers dominate during the late stages of succession may reflect a sampling bias resulting from the lack of long-term permanent sample plot data, which are essential to the study of forest

dynamics in real time. As Johnson (1979) notes, "the time required for succession to 'occur' is long enough that it preclude[s] direct observation of it". In the absence of reliable long-term data on boreal forest dynamics, the chronosequence approach (also known as "space for time substitution" (Pickett 1989 or "time-space conversion" (Johnson 1979)) is widely used to infer temporal changes in forest composition, structure and productivity (e.g. Frelich and Reich 1995; Paré and Bergeron 1995; Bergeron 2000; Taylor and Chen 2011). In this approach, forest stands at various post-disturbance ages are sampled, and succession changes inferred by summarizing changes in forest composition and structure over the temporal sequence. The chronosequence approach can be criticized on a number of fronts. It implicitly assumes that all sampled stands are environmentally similar (e.g. edaphics, mesoclimate), have the same disturbance history (e.g. herbivores, pests and pathogens, wind-throw), and have the same potential floristics (e.g. seed and clonal propagation sources). Furthermore, it is difficult to collect such data in a completely neutral and theory-free manner (Johnson 1979), with the result that researchers may simply find what they are looking for (Jones 1959). The direct interpretation of chronosequence data almost invariably leads to a deterministic summary of forest changes over time (Bergeron 2000; Krebs 2009).

In this study, forest composition and structure data collected over a 55-year period from 266 permanent sample plots located in boreal mixed-wood stands at Riding Mountain National Park, Manitoba are analyzed and summarized. The permanent sample plots were established and initially surveyed in 1947, when the stands were approximately 120 years old. The plots were re-sampled in 1957, 1967 and 2002, thus providing long-term direct observations of forest stand change between 120 and 175 years post-disturbance. Observations on these forest stands during the initial survey led Rowe (1955) to conclude that:

"*The overmature aspen is dying at present without replacement, while the spruce continues to increase. Thus an uneven-aged softwood type is in the making ... The invasion of poplar by spruce, either rapidly or over a long period, and the subsequent dying of the poplar represents the typical development of coniferous stands on medium moist soils.*"

The objective of this study is to provide unequivocal evidence using long-term direct observational data to validate or refute the succession hypothesis espoused by Rowe (1955) and others, i.e. replacement of trembling aspen by white spruce as the dominant canopy species in older boreal mixed-wood forest stands.

4.2 METHODS AND MATERIALS

4.2.1 Study Area

This study was conducted in Riding Mountain National Park (RMNP), Manitoba (50° 30' - 51° 01' N, 99° 33' - 101°06'W). RMNP is located on undulating hummocky terrain of the Manitoba Escarpment. The area is at the eastern limit of the western boreal mixed-wood forest that extends from west-central Manitoba to central Alberta (Rowe 1972; details in Chapter 2). The upland forest stands of RMNP consist of a mixture of deciduous trees (trembling aspen, balsam poplar, white birch) and coniferous evergreen trees (white spruce, black spruce, jack pine and balsam fir) occurring on well drained, mesic, moderately rich, slightly acidic to basic soils. The climate is continental, with a mean annual temperature of 0.1°C (ranging from –19.6°C in January to 16.5°C in July). The mean annual precipitation is 52 cm, about two-thirds of which falls as rain during the summer months (Environment Canada 2009).

In 1946, a forest experimental area (FEA) was designed within RMNP to promote research into the silvics and sustainable harvesting of white spruce and trembling aspen. To achieve this objective, an 11.5 km by 6.5 km study area was established north of Clear Lake, and a series of 1480 permanent sample plots were located approximately 200 m apart in a regular square grid pattern. All plots were square and approximately 20 x 20m in size. These forests were approximately 120 years of age (termed "old growth" (Kneeshaw and Gauthier 2003) or "decadent" (Jarvis *et al*. 1966) stands) at the time of plot establishment, and were of fire origin (see Chapter 3 for details). All stands were initially enumerated in 1946 – 1948 (stand age =120 years), 1956 – 1958 (stand age = 130 years), and again in 1966 – 1968 (stand age =140 years; Pratt 1969). Following closure of the FEA facility in the 1970s, the permanent sample plots were abandoned. However, in 2002 (stand age = 175 years) crews from Louisiana-Pacific Canada and the University of Manitoba were able to relocate and re-sample a large number of the original permanent sample plots. Of these re-sampled plots, a total of $n = 266$ were deemed suitable for the analysis of long-term trends in stand dynamics of old-growth boreal mixed-wood forest over the 55 year sampling period (stand ages 120 – 175 years). Additional details on the permanent sample plots, and the criteria used to select the plots analyzed here, are presented in Chapter 3.

4.2.2 Classification of Stands

For analytical purposes, three size-classes of trees are recognized: saplings (DBH ≤ 7.6 cm), sub-canopy trees (DBH = 10.2 – 20.3 cm), and canopy trees (DBH ≥ 22.9 cm). Careful examination and preliminary analysis of the 1947 data (stand age 120 years, $n = 266$) indicated that the stands could be conveniently classed into one of two groups based on the size distribution of the dominant hardwood tree species (trembling aspen and balsam poplar) in the plots:

1. Mature Stands ($n = 161$): In these plots, most hardwood trees were in the canopy class (i.e. trees with DBH ≥ 22.9 cm); there were few sub-canopy trees, or no saplings as defined above.

2. Regenerating Stands ($n = 105$): In these plots, there were one or more canopy hardwood trees (DBH ≥ 22.9 cm) and a larger number of sub-canopy trees present (DBH = 10.2 – 20.3 cm). These sub-canopy trees represent a secondary hardwood cohort established beneath the initial post-fire canopy cohort.

Examination of the size-class distributions of softwoods (i.e. white spruce) in the 1947 plots indicated two patterns of softwood recruitment: delayed recruitment (only hardwoods in the canopy, softwoods present in the sub-canopy and sapling classes only), and contemporaneous recruitment (both hardwood and softwood canopy trees present). This dichotomy is consistent with recruitment patterns of white spruce recruitment observed in Alberta mixed-wood forests (Peters *et al.* 2006):

1. Delayed Recruitment ($n = 78$): In these plots there were no softwood trees in the canopy class (DBH ≥ 22.9 cm), but there were one or more individuals in the sapling (DBH ≤ 7.6 cm) and/or sub-canopy (10.2 – 20.3 cm DBH) classes. Softwood trees with DBH ≤ 22.9 cm were < 60 years old, indicating that softwood recruitment was delayed by at least 60 years (since these stands were about 120 years old in 1947; *cf.* Peters *et al.* 2006).

2. Contemporaneous Recruitment ($n = 188$): In these plots, there was at least one white spruce in the canopy class (DBH ≥ 22.9cm); in most cases there was more than one canopy white spruce, and many trees were much greater than 23 cm DBH. This indicates that in these stands white spruce recruited

contemporaneously, i.e. within the first 10 years post-fire (the recruitment "window of opportunity", Peters *et al.* (2006)).

A cross-classification (contingency table) was then produced, using these two classification dichotomies (i.e. mature vs. regenerating hardwoods, and delayed vs. contemporary white spruce recruitment) to obtain four physiognomic groups for the 266 plots (**Figure 4.1**):

GROUP A (*n* = 43)

These stands are defined as having a mature hardwood canopy, little or no hardwood regeneration (second cohort), and delayed white spruce recruitment. The hardwood trees in these plots mostly occur in the canopy class (DBH ≥ 22.9 cm), and all white spruce trees are in the sapling and/or sub-canopy classes (DBH < 22.9 cm).

GROUP B (*n* = 35)

These stands are defined as having both a mature hardwood canopy and hardwood regeneration (second cohort present), and delayed white spruce recruitment. In most cases these plots had only a few canopy hardwood trees, but numerous sub-canopy trees (DBH = 10.2 – 20.3 cm). All white spruce trees are in the sapling and/or sub-canopy classes (DBH < 22.9 cm).

GROUP C (*n* = 118)

These stands are defined as having a mature hardwood canopy, little or no hardwood regeneration (second cohort), and contemporaneous white

spruce recruitment. Most of the hardwood trees in these plots occur in the canopy class (DBH ≥ 22.9 cm). In these plots, there is at least one white spruce tree in the canopy class (DBH ≥ 22.9 cm) and usually a number of white spruce trees in the sub-canopy and sapling classes.

GROUP D ($n = 70$)

These stands have both a mature hardwood canopy and hardwood regeneration (second cohort present), and contemporaneous white spruce recruitment. Typically, these plots have only a few canopy hardwood trees but numerous sub-canopy trees (DBH = 10.2 – 20.3 cm), and at least one white spruce tree in the canopy class (DBH ≥ 22.9 cm). In most cases, these plots had a number of white spruce trees in the sub-canopy and sapling classes.

The four groups are summarized by species in **Table 4.1**. These structural-physiognomic groups were used in all subsequent analyses to summarize and characterize changes in species composition and stand structure (density and basal area) for the permanent sample plots over a 55-year period (1947 – 2002), which corresponds to stand ages 120 to 175 years. In the following, results are presented for the years 1947 (stand age 120), 1967 (stand age 140) and 2002 (stand age 175). The results from the 1957 plot enumerations were used mainly to error-check the data.

When necessary, correlations between saplings in 1967 and established trees in 2002 were used to analyze successful establishment of the recruiting aspen cohort (Zar 1999). A logistic regression was used to model the successful recruitment of the aspen cohort of group C. The successful establishment of aspen in 2002 was the y response variable (1= successful recruiment, 0 =

unsuccessful recruitment) and the stand basal area (m^2/ha) of 1967, the independent x-variable (Gotelli and Ellison 2004). The general logistic equation is:

$$\pi(X) = \exp(\beta_0 + \beta_1 x_1)/1 - \exp(\beta_0 + \beta_1 x_1)$$

where $\pi(X)$ is the probability of an aspen second cohort establishment. β_1 represents the rate of change in $\pi(X)$ as a function of x. Figures were created using Mircosoft Excel and analyses were run using Data Desk 6.2.1 (Data Description Inc. Ithaca NY).

4.3 RESULTS

As described above, each of the $n = 266$ plots were classified into one of four physiognomic-structural groups: group A ($n = 43$), canopy hardwoods and delayed white spruce recruitment; group B ($n = 35$), canopy and regenerating hardwoods and delayed white spruce recruitment; group C ($n = 118$), canopy hardwoods and contemporaneous white spruce recruitment; group D ($n = 70$), canopy and regenerating hardwoods and contemporaneous white spruce recruitment. Stand dynamics trends for each of the four physiognomic groups over the 55-year period are summarized below.

4.3.1 Group A: Canopy Hardwoods, Delayed White Spruce Recruitment ($n = 43$)

Trembling Aspen

In 1947 (stand age of 120 years), these stands had large trembling aspen trees in the canopy but very limited or no aspen regeneration (i.e. limited second cohort). Most of the trees were mature, with a mean DBH = 28.6 cm. Almost 85% of trembling aspen are canopy trees (DBH ≥ 22.9 cm; **Figure 4.2a**); there are few

sub-canopy trees (14.3% of the total), and very few saplings (DBH < 10.2 cm). The majority of the trembling aspen trees in these stands (73%, or nearly three-quarters) are between 22.9 and 35.6 cm DBH, and very few are > 36 cm DBH. This range in DBH values indicates a mean canopy height of 21 – 22 m, and trees that are 110 – 120 years old (Jameson 1963).

Considerable changes occurred in stand demographics of trembling aspen by 1967 (stand ages = 140 years; **Figure 4.2a**). Overall densities of both canopy and sub-canopy aspen declined over the twenty-year period (1947 and 1967), from 126.2 to 86.8 trees/ha for the canopy trees, and from 21.5 to only 1.2 trees/ha for the sub-canopy trees. The remaining trees are large, with a mean DBH = 34.3 cm. This indicates some sub-canopy trees have grown into canopy trees, while others have probably died. In addition, many of the large canopy trees present in 1947 have died. Other mature canopy trees present in 1947 have grown even larger: DBH classes > 40 cm makes up 27% of all canopy trees in 1967, compared to only 7.5% in 1947 (a total of 40 trees in 1967, versus only 16 trees in 1947). This indicates that by a stand age of 140 years, the post-disturbance canopy is "breaking up"; in 1967 the number (and basal area) of canopy aspen is low, and there are very few sub-canopy trees. The stands at this stage have a very open, "broken" canopy with many large gaps. This canopy break-up is expected at this stage of stand development, since the maximum longevity of trembling aspen is 140 years or so (Jones and Schier 1985). Corresponding to senescence (canopy break-up) of the initial post-fire cohort is the substantial recruitment of a second cohort of aspen root suckers (present in the sapling class, particularly the 2.54 and 5.08 cm DBH classes; **Figure 4.2a**). This "flush" of root sucker or ramets (secondary recruitment) is a direct result of senescence of the initial post-fire canopy. Canopy tree mortality results in both the loss of apical dominance and increased light to the forest floor, promoting root suckering. At this stage of stand development, over 90% of all aspen stems

belong to the sapling class, and < 10% to the sub-canopy and canopy classes. This second cohort of aspen was present in most, but not all, of the 43 plots. There were on average 31 saplings per plot (773 saplings/ha). Only four plots showed no sapling recruitment at this stage of stand development, and nearly half of the plots (20/43 = 46.5%) contained over 30 saplings (large root suckers) in 1967 (i.e. > 750 saplings/ha). Most of these saplings are in the 2.54 cm DBH class, and would therefore be 2 – 5 m in height and 5 – 10 years old (Bella 1975).

   Some of the trees from this second recruitment flush had reached the canopy class by 2002 (particularly the 22.9 – 30.5 cm DBH classes, and possibly larger as well), as indicated by the Gaussian-like distribution of size classes centered on the 17.8 and 20.3 cm diameter classes (**Figure 4.2a**). For the 43 plots, the number of root suckers in 1967 was a good predictor of the number of sub-canopy aspen present in 2002 (R^2 = 57.9%, P < 0.001), confirming successful recruitment of the second cohort. Most of the largest trees in 2002 (i.e. DBH > 32 cm) are likely very old trees that were also present in the canopy in 1967; some of these very large trees, which represent about 4.5% of all trees present in 2002, would be about 175 years old. Most of the trees in the sub-canopy class (10 – 23 cm diameter classes) are typically 12 – 18 m in height and 25 – 50 years old (Jameson 1963). It is also notable that very few saplings (< 3% of all aspen stems) were encountered in the 2002 survey, indicating that root suckering is episodic (i.e. discontinuous recruitment) and occurs mainly during canopy senescence (e.g. in 1967), when canopy break-up results in a loss of apical dominance and increased light reaching the forest floor.

Balsam Poplar

   The overall temporal trends for balsam poplar are remarkably similar to those
of trembling aspen (**Figure 4.2b**). This suggests that these two species have
similar life history characteristics, and are distinguished mainly by differences in
habitat preferences: balsam poplar prefers more mesic sites (Halliday and Brown
1943).

   In 1947 (stand age of 120 years), about two-thirds of balsam poplars were
canopy trees. Most of the remaining trees occur in the sub-canopy, and there are
very few saplings (**Figure 4.2b**). Most of the trees were mature, with a mean
DBH = 25.8 cm. The total density of canopy and sub-canopy trees is 72.1
trees/ha. Two-thirds of the trees are between 20.3 and 35.6 cm DBH, and there
are very few large trees (only 5% of trees have a DBH > 35.6 cm). Only one of
the 43 plots contained balsam poplar saplings (root suckers), indicating that the
closed canopy is inhibiting root suckering at this stage of stand development.

As with trembling aspen, there were considerable changes in balsam poplar
stand structure and physiognomy by 1967, just 20 years later (stand age of 140
years). Canopy and sub-canopy tree density has declined to 61.0 trees/ha, but
tree size has increased to a mean DBH = 30.7 cm. Very large trees (DBH > 35.6
cm) make up about 17% of the canopy trees at this stage of stand development.
There are very few sub-canopy trees (DBH = 10.2 – 20.3 cm) at this stage of
stand development, 6.4 trees/ha compared to 22.7 trees/ha just 20 years earlier.
Corresponding to this decline in canopy and sub-canopy balsam poplar is a
"flush" of root suckers (sapling class). At this stage of stand development, over
80% of the balsam poplar trees occur in the sapling class (**Figure 4.2b**). Nearly
two-thirds (62.8%, or 27 of 43) of the stands contained recruited saplings,
averaging 72 saplings/ha.

The 2002 survey results (stand age = 175 years) clearly indicate that the balsam poplar saplings, recruited by 1967 following senescence of the initial cohort of trees, have established successfully. Over half of balsam poplar trees at this stage of stand development occur in the sub-canopy class, originating from the second cohort of root suckers from 1967. For the 43 plots, the number of saplings present in a given plot in 1967 is a significant predictor (R^2 = 58.5%, P < 0.001) of the abundance of sub-canopy and canopy balsam poplar trees in 2002.

By 2002 the density of sub-canopy and canopy balsam poplar trees has more than doubled, from 61.0 trees/ha in 1967 to 133.7 trees/ha in 2002. As with trembling aspen, some of the trees from the second recruitment flush have reached the canopy class by 2002 (particularly the 22.9 – 30.5 cm DBH classes, and possibly larger as well), as indicated by the Gaussian-like distribution of size classes centered on the 20.3 cm diameter class (**Figure 4.2b**). Some of the largest individuals in 2002 (i.e. DBH > 32 cm) are likely relict trees from the initial post-fire canopy cohort, and are therefore about 175 years old. As with trembling aspen, very few balsam poplar saplings (root suckers) were encountered in the 2002 survey.

<u>White Spruce</u>

In 1947, the majority of white spruce trees were in the sapling class (79%), and a few had reached the lower end of the sub-canopy class, but none had reached the canopy class. Most of the trees are small (mean DBH = 6.2 cm). This size class distribution, and the lack of white spruce in the canopy of these stands, indicates that white spruce recruitment was greatly delayed in these stands. The white spruce trees present are < 21 cm DBH, which corresponds to about 40 – 50 years of age and younger (Jameson 1963). However, some of these saplings

may actually be somewhat older (60 or 70 years, perhaps), since white spruce found beneath a dense aspen canopy are often suppressed and grow very slowly (Gutsell and Johnson 2002). Nonetheless, it is apparent that white spruce recruitment was delayed by 40 – 60 years (or more) in these stands. These suppressed white spruce trees are likely to undergo a "release" following break-up of the hardwood canopy, as greater amounts of light reach the forest floor.

There is strong evidence of competitive release of established white spruce saplings by 1967 (stage age 140 years). Break-up of the hardwood canopy has clearly promoted both the establishment and growth of white spruce (**Figure 4.2c**). Many of the saplings present in 1947 have reached the sub-canopy (42% of trees), and few have even reached the lower end of the canopy class (6% of trees). These trees have grown considerably, mean DBH increasing from 6.2 cm in 1947 to 10.2 cm in 1967. Canopy break-up has also promoted overall white spruce recruitment, with density nearly doubling in only twenty years from 146 trees/ha in 1947 to 279 trees/ha by 1967. The shape of the size-distribution curve at this stage of stand development indicated continuous recruitment of white spruce over the past 30 – 50 years (**Figure 4.2c**), which is attributable to increased light levels to forest floor resulting from break-up of the hardwood canopy. Hardwood canopy senescence offers a "window of opportunity" (lasting 20 years or more, Lieffers *et al.* 1996) for the recruitment of white spruce seedlings, as well as the rapid growth ("release") of established (but formerly suppressed) white spruce saplings.

By 2002 (stand age of 175 years), many of the sub-canopy white spruce present in 1967 have reached the canopy, and some of these trees are quite large: 31 trees have a DBH > 40 cm (about 6% of all trees in these stands). At this stage of stand development, nearly half (48.5%) of the white spruce trees have reached the canopy class (DBH > 22.9 cm). Most of the trees are quite

large: mean DBH = 21.8 cm. Recruitment into the sapling class continues, but at a much lower rate compared to earlier stages of stand development: 45.9 saplings/ha in 2002, versus 87.8/ha in 1947 and 143.6/ha in 1967. In 2002, less than two-thirds (61%) of plots contained white spruce saplings, versus 86% of the plots in both 1947 and 1967. In addition, there were relatively few white spruce trees in the sub-canopy class in 2002 (particularly at the lower end of the range, DBH = 10 – 15 cm), suggesting that the "window of opportunity" for white spruce recruitment (between stand ages 120 - 150 years) has closed. A dense canopy and sub-canopy of white spruce has developed by this stage of stand development, considerably reducing the amount of light reaching the forest floor. Reduced light levels are detrimental to white spruce recruitment, and inhibit root suckering in trembling aspen and balsam poplar.

4.3.2 Group B: Canopy and Regenerating Hardwoods, Delayed White Spruce Recruitment (*n* = 35)

Trembling Aspen

   In 1947 (stand age of 120 years), these stands contained relatively few canopy trembling aspen but had considerable amounts of secondary aspen regeneration, as indicated by the large number of individuals in the sub-canopy and sapling classes (**Figure 4.3a**). About 88% of the trembling aspen in these plots occurred in sub-canopy or sapling classes; mean DBH = 11.7 cm. The few trembling aspen in the canopy are remnant trees from the initial post-fire cohort, and are about 120 years old (Jameson 1963). The majority of individuals of the second cohort (i.e. sub-canopy trees) have DBH = 7.6 – 10.2 cm, making them about 30 – 40 years old and 10 – 14 m in height (Bella and DeFranceschi 1980). These results indicate that canopy break-up in these stands occurred about 30 – 40 years earlier, i.e. at stand age 80 – 90 years, or 30 – 40 years earlier than in the

group A stands. In the stands of group B, initial cohort tree mortality (canopy break-up) occurred between the years 1925 and 1935. This resulted in loss of apical dominance and increased light to the forest floor, promoting aspen root suckering and establishment of the second cohort (i.e. sub-canopy trees) seen in 1947.

By 1967 (stand age of 140 years), individual trees of the second cohort have grown in size (**Figure 4.3a**); mean tree DBH = 18.0 cm (excluding saplings at DBH = 2.54). The majority of the sub-canopy trees occur in the 10 – 20 cm diameter classes, corresponding to 50 – 70 years of age and 12 – 18 m in height (Jameson 1963). The number and size distribution of large canopy trees in 1967 is similar to that seen in 1947, reflecting the combined effects of loss due to density-independent mortality and gain through the growth of sub-canopy trees into the canopy. Interestingly, a tertiary cohort of aspen suckers (sapling class, DBH = 2.54 cm) is also apparent in the 1967 data, although the density of the sapling cohort (160 saplings/ha) is considerably lower than the second cohort "flush" of aspen suckering seen in group A plots in 1967 (773 saplings/ha). This aspen suckering occurred in about half (17 of 35) of the plots. It is notable that the size-class distribution of sub-canopy and canopy trembling aspen in 1967 is remarkably similar to that of group A in 2002 (compare **Figure 4.2a** in 2002 with **Figure 4.3a** in 1967). This indicates that the principal difference between group A and B plots is the timing of hardwood canopy break-up and recruitment of the second cohort. This occurred at a stand age of 110 years for group A plots, versus about 80 years of age for group B plots. It is apparent that dynamic changes in stand structure in groups A and B plots are remarkably similar; they are simply shifted in time by about 30 years.

A number of trees from the second recruitment flush have reached the canopy class by 2002 (**Figure 4.3a**). This is confirmed by noting that, over the 35 plots,

the number of sub-canopy trees in 1947 is a significant predictor of the number of canopy trees in 2002 (R^2 = 47.5%, $P <$ 0.001). Most of the trees at this stage of stand development are large: mean DBH = 26.1 cm (excluding saplings of DBH = 2.54 cm). It is possible that a few of the largest canopy trees present (DBH > 40 cm) may be relict individuals from the initial cohort, which would make them about 175 years old. The presence of individuals in the sub-canopy class suggests that some of the saplings from the root sucker "flush" of 1967 were able to successfully establish and grow. Interestingly, a cohort of aspen suckers (sapling class, DBH = 2.54 cm) is also present in 2002, in about half (17 of 35) of the plots. This contrasts with the lack of saplings in the group A plots in 2002.

Balsam Poplar

   The size-class distribution of balsam poplar in 1947 is very similar to that of trembling aspen (**Figures 4.3 a,b**). The stands contain mostly sub-canopy trees (about 70% of trees), with relatively few balsam poplar trees present in the canopy. Most of the trees are small (mean DBH = 14.3 cm). The few canopy balsam poplar trees present (about 13% of trees) are remnant individuals from the initial post-fire cohort. Most individuals of the second cohort (i.e. subcanopy trees) have DBH = 7 – 15 cm, making them about 25 – 55 years old and 10 – 18m in height (Bella and DeFranceschi 1980; Jameson 1963). These results suggest that canopy break-up occurred about 30 – 40 years earlier, confirming the same finding based on the size-class distribution data for trembling aspen (summarized above).

   By 1967 (stand age of 140 years), second cohort balsam poplar trees have grown in size (Figure 4.4b): mean DBH has increased from 14.3 to 20.3 cm (excluding saplings of DBH = 2.54 cm). Most of the sub-canopy trees occur in the 12 – 23 cm diameter classes, and a few trees have entered the lower end of the

canopy class (25 – 30 cm DBH). About one-quarter (23.5%) of the balsam poplars occur in the canopy class, versus only 12.6% in 1947. As with trembling aspen, a tertiary cohort of balsam poplar suckers (sapling class, DBH = 2.54 cm) is apparent in the 1967 data, although regeneration density is well below that seen in the group A at this date (56.4 saplings/ha, versus 276.2 saplings/ha for group A plots).

Most of the balsam poplar trees recruited in the second cohort flush have reached the canopy class by 2002 (**Figure 4.3b**), and the trees are much larger: mean DBH = 26.3 cm. Nearly three-quarters of the trees are in the canopy class, indicating successful recruitment of second cohort trees into the canopy. A few of the very large balsam poplar trees (DBH > 40 cm) may be relict individuals from the initial post-fire cohort, making them about 175 years old. As with trembling aspen, the presence of a few individuals in the sub-canopy class in 2002 indicates that some of the saplings (DBH = 2.54 cm) recruited in 1967 were able to successfully establish and have grown into sub-canopy trees.

White Spruce

Overall, temporal trends in white spruce recruitment for group B are very similar to those seen for group A (compare **Figure 4.2c** and **Figure 4.3c**). However, white spruce sapling recruitment in 1947 is somewhat lower in these plots: 68.6 saplings/ha, versus 87.8 saplings/ha in group A plots. About three-quarters of the white spruce trees occur in the sapling class (DBH < 7.6 cm). There are no individuals in the canopy class, indicating that white spruce recruitment was greatly delayed in these stands. The white spruce present at this stage of stand development are small: mean DBH = 6.9 cm. As in group A, the white spruce trees present are all < 20.9 cm DBH, which corresponds to maximum age of 40 –

50 years (Jameson 1963). This indicates that white spruce recruitment has been delayed by about 40 – 60 years in these stands.

There is evidence for the growth of established white spruce in the sapling and sub-canopy classes by 1967 (stand age of 140 years): the mean DBH has increased from 6.9 cm in 1947 to 12.6 cm. However, white spruce establishment and growth into the sub-canopy and canopy classes is somewhat lower than in group A plots: 107 trees/ha, versus 136 trees/ha in group A plots. The size-distribution curves for groups A and B also differ somewhat. For group A, the size-class distribution is a continuous declining series (**Figure 4.2c**, 1967), whereas that of group B is somewhat truncated (or flattened) at DBH classes 7 – 17 cm (**Figure 4.3c**, 1967). This indicates that development of the second cohort hardwoods during this period has inhibited somewhat the establishment and growth of white spruce saplings. Most of the sub-canopy white spruce trees are 7 – 15 cm DBH in size, or 25 – 40 years old and 6 – 12 m in height (Jameson 1963). At this stage of stand development, only about 7% of the white spruce trees in these stands (16.4 trees/ha) have reached canopy size (DBH $\geq$ 22.9 cm).

By 2002 (stand age of 175 years), a number of the sub-canopy white spruce trees present in 1967 had reached canopy size (101.4 trees/ha, versus only 16.4 trees/ha in 1967), and some trees are very large (**Figure 4.3c**): the mean DBH = 20.3 cm. The 2002 size-class distributions for white spruce in group A and B plots are very similar, although canopy density is about one-third higher in group A (141.9 canopy trees/ha) than group B (101.4 canopy trees/ha). Sub-canopy densities for the two groups are very similar: 80.7 trees/ha for group B plots, and 91.9 trees/ha for group A plots. Conversely, sapling recruitment for group B is over twice that for group A (119.3 saplings/ha, versus just 45.9 saplings/ha for group A). Survivorship of these recruited saplings is low, however, as evidenced by the low number of trees in size classes 7.6 – 12.7 cm DBH in both groups A

and B (**Figures 4.2c** and **4.3c**). The higher sapling recruitment of group B may reflect the lower density (basal area) of white spruce: 9.2 m^2/ha for group B, versus 13.4 m^2/ha for group A.

4.3.3 Group C: Canopy Hardwoods, Contemporaneous White Spruce Recruitment (*n* = 118)

Trembling Aspen

In 1947 (stand age of 120 years), these stands were structurally similar to those of group A (compare **Figures 4.4a** and **4.2a**). Large trembling aspen trees were present in the canopy, and there is little aspen regeneration. About 80% of the trees occur in the canopy class, and most of the others are larger sub-canopy trees (20.3 – 22.9 cm DBH). The size distribution is approximately Gaussian, with a mean DBH = 26.6 cm. The majority of the aspen trees are between 20.3 and 30.5 cm DBH, and there are very few trees > 36 cm DBH. These DBH ranges indicate a mean canopy height of 21 – 22 m, and trees that are 110 – 120 years old (Jameson 1963).

The demography of trembling aspen has been considerably altered by 1967, just twenty years later (**Figure 4.4a**). The canopy trees have increased in size (mean DBH = 30.7 cm, excluding saplings of 2.54 cm DBH), but stand density (excluding saplings) has declined substantially, from 160.8 trees/ha in 1947 to 103.6 trees/ha by 1967. This decline in density is particularly notable in the sub-canopy classes: from 32.4 trees/ha in 1947 to 4.9 trees/ha just twenty years later. This result indicates that while some of the 1947 sub-canopy trees have entered the canopy size, others have died. It is clear that the initial post-fire aspen canopy is "breaking up" at this stage of stand development, resulting in numerous canopy gap openings. As a consequence, there is a substantial recruitment

"flush" of a second cohort of aspen suckers (trees in the sapling class, particularly DBH = 2.54 cm; **Figure 4.4a**), similar to that also seen in the group A plots in 1967. However, the density of this second cohort is considerably lower: 273.5 saplings/ha, versus 773.3 sapling/ha in group A plots. The higher basal area of white spruce trees of group C plots (11.0 m^2/ha, versus 3.2 m^2/ha in group A) likely accounts for the reduced amount of root sucker recruitment in these stands. Almost all the 1967 saplings fall into the 2.54 cm DBH class, and would therefore be 2 – 5 m in height and 5 – 10 years old (Bella 1975).

By 2002, it is clear that some of the secondary recruitment saplings from 1967 have grown into the sub-canopy and the lower canopy class (DBH = 22 – 26 cm) (**Figure 4.4a**). However, trembling aspen canopy/sub-canopy density is just 97.7 trees/ha, versus 272.1 trees/ha in the group A plots. The higher basal area of canopy white spruce (9.1 m^2/ha in 1967, versus 1.0 m^2/ha in group A) during the period of aspen secondary recruitment has clearly had an inhibitory effect on trembling aspen recruitment, growth and survivorship. Many of the largest trees present in 2002 (i.e. DBH > 35 cm) are likely very old relict trees present in the 1967 canopy and therefore members of the initial post-fire cohort; these trees would be about 175 years old. There is a very wide range of tree sizes at this stage of stand development: mean DBH = 23.5 cm (**Figure 4.4a**), and a minor tertiary sapling cohort (56.8 saplings/ha) is also present in some plots.

Further examination of the group C data revealed that about half (57 of 118) of the plots showed successful secondary recruitment of trembling aspen. To examine this, the data for group C were divided into two sub-groups: plots showing successful secondary recruitment of aspen (*n* = 57 plots; **Figure 4.5a**), and those showing no secondary recruitment in 2002 (*n* =61 plots; **Figure 4.6a**). In the 57 group C plots with successful secondary recruitment (**Figure 4.5a**), trends in trembling aspen stand demographics are very similar to those seen in

group A (**Figure 4.2a**). In 1947 (stand age of 120 years), most trees occur in the canopy (mean DBH = 26.1 cm) and the stand is moderately dense (146.3 trees/ha). Twenty years later (1967), canopy trees are somewhat larger (mean DBH = 31.6 cm), but stand density (excluding saplings) has declined by 43%, from 146.3 trees/ha in 1947 to 84.0 trees/ha by 1967. This break-up of the initial post-fire aspen canopy has promoted considerable root suckering (435.7 saplings/ha) in all 57 plots. Many of these saplings have successfully recruited into the sub-canopy and lower canopy to form a second aspen cohort by 2002 (**Figure 4.5a**). As a consequence, trembling aspen density (excluding saplings) by 2002 increased to 154.5 trees/ha (about the same as in 1947), with a mean DBH = 20.5 cm (excluding sapling of 2.54 cm DBH). In about half the plots (26 of 57), tertiary aspen recruitment (71.7 saplings/ha) is evident in 2002.

In 1947, the stand structures of the two sub-groups are quite similar (compare **Figures 4.5a** and **4.6a**). Trembling aspen trees are almost identical in size (mean DBH = 27.1 and 26.1 cm respectively), but stand density is somewhat higher for the 61 plots without successful secondary recruitment (176.3 trees/ha, versus 146.3 trees/ha). Stand structures are also similar in 1967: mean DBH of canopy trees are 31.7 and 31.6 cm respectively. As in 1947, canopy stand density is higher (by about one-third) in the 61 plots (no second cohort) subgroup: 126.6 trees/ha, versus 84.0 trees/ha. This indicates that aspen canopy break-up is not as pronounced in these plots, resulting in fewer canopy gaps and less light reaching the forest floor. As a result, sapling density in 1967 is substantially lower: 100 saplings/ha versus 435.7 saplings/ha in the 57 plots showing successful establishment of a second aspen cohort, and almost half the plots (30 of 61 plots, contained no aspen saplings at all. By 2002, none of these plots contained sub-canopy trees indicating that a second aspen cohort failed to establish. At this stage of stand development, the aspen canopy is completely dominated by a few very large remnant trees from the initial post-fire cohort

(mean DBH = 37.0 cm, and a stand density of only 36.8 trees/ha: **Figure 4.6a**). These results indicate that comparatively rapid and pronounced canopy break-up is a necessary prerequisite to successful establishment of a second cohort in trembling aspen. Extensive and rapid canopy break-up encourages both prolific root suckering (due to loss of apical dominance) and the successful establishment of saplings (due to high light levels in canopy gaps). A slower, less pronounced break-up of an aspen canopy results in limited root suckering, and high mortality of saplings due to insufficient light reaching the forest floor. For the 118 group C plots, there is a statistically significant negative relationship between canopy tree basal area (m^2/ha) in 1967 and the successful establishment of a second aspen cohort by 2002 (β_1= -0.0936; χ_1^2 = 12.02; P = 0.0005; **Figure 4.7**).

Balsam Poplar

The demographic trends for balsam poplar are similar to those of trembling aspen (**Figure 4.4b**). In 1947 (stand age of 120 years), the size distribution of balsam poplar is approximately Gaussian, with a mean DBH = 23.9 cm and a stand density of 30.7 trees/ha. About two-third of the trees occur in the canopy class.

By 1967 (stand age of 140 years), the canopy trees are larger (mean DBH = 27.6 cm (excluding sapling), but stand density (excluding saplings) has declined by about one-quarter, from 30.7 to 23.7 trees/ha (**Figure 4.4b**) indicating mortality of some canopy trees. As a result, there is a flush of root sucker recruitment (sapling density 75.2 trees/ha). These saplings would be approximately 8 – 12 years old (Bella and DeFranceschi 1980). Sapling density in these stands is considerably less than was seen in the group A plots in 1967 (273.5 saplings/ha). This lower recruitment is likely attributable to the presence of

white spruce in the canopy, which limits the root suckering through light attenuation.

Results from the 2002 survey (stand age of 175 years) indicate that some of the balsam poplar saplings recruited in 1967 (following break-up of the initial hardwood canopy cohort) have established successfully (**Figure 4.4b**). Trees in DBH range 10.2 – 25.4 cm (i.e. sub-canopy and lower canopy classes) show an approximate Gaussian distribution. Trees in this size range are approximately 40 – 50 years old (Jameson 1963), and are most certainly derived from the root suckers recruited in 1967. The largest trees in the stand (DBH > 35.6 cm and larger) are relict individuals from the initial post-fire canopy cohort, and are therefore about 175 years old.

As in trembling aspen, a second cohort of balsam poplar had established in 2002 in some group C plots, but not in others. This was examined using the same two subgroups of the group C plots described above (**Figures 4.5b** and **4.6b**). In 1947 (stand age of 120 years), balsam poplar trees were large in both sub-groups: DBH = 24.3 cm in the 61 plots with no second cohort, and 22.7 cm in the 57 plots with a second cohort in 2002. Balsam poplar density was much higher in the former group, however: 46.9 trees/ha, versus 15.6 trees/ha. By 1967, the canopy trees grew larger but density declined in both groups: DBH = 28.9 cm and 34.6 trees/ha for the 61 plots with no second cohort, and DBH = 24.5 cm and 13.5 trees/ha for the 57 plots with a second cohort in 2002. The break-up of the hardwood canopy by 1967 promoted balsam poplar root suckering, particularly in the 57 second cohort plots: 105 suckers/plot, versus only 41 suckers/plot in the other subgroup. This likely reflects differences in the density of the hardwood canopy at this stage of stand development: 97.5 trees/ha (basal area = 8.12 m^2/ha) in the 57 second-cohort plots, versus 159.2 trees/ha (basal area = 12.88 m^2/ha) in the 61 plots with no second cohort. This difference

strongly affected recruitment of a second cohort of balsam poplar. By 2002, the 57 plot sub-group contained 63.8 trees/ha in both the sub-canopy and canopy classes (mean DBH = 20.0 cm), indicating successful recruitment of a second cohort (**Figure 4.5b**). By contrast, in 2002 the 61 plot sub-group contained only 27.2 trees/ha, and most of these were very large relict trees in the canopy (mean DBH = 31.1 cm). These 61 plots contained few sub-canopy trees, indicating limited second cohort recruitment (**Figure 4.6b**).

White Spruce

   In 1947 (stand age of 120 years), the size-class distribution of white spruce is continuous with a monotonic decline in abundance with increasing DBH (**Figure 4.4c**). Such a distribution is "stable", i.e. continuous recruitment and cumulative mortality with increasing size (Hett and Loucks 1976). The mean DBH = 17.1 cm is quite low, reflecting relatively high densities of sapling (98.7 trees/ha) and sub-canopy (68.4 trees/ha) trees. About one-third of the trees occur in the canopy class (82.6 trees/ha), and many of the plots contained at least one very large (DBH > 35 cm) tree, corresponding to 24 – 28 m in height and 90 – 110 years in age (Jameson 1963). The presence of these large trees indicates contemporaneous recruitment, i.e. germination and establishment within the first 10 – 30 years post-fire. Density is highest in the sapling class indicating that white spruce recruitment is continuing but that sapling mortality is high.

   Twenty years later (1967, stand age of 140 years), stand density of the sub-canopy white spruce class increased from 68.4 to 97.9 trees/ha while canopy tree density remained stable (82.6 trees/ha in 1947, versus 81.8 trees/ha in 1967 (**Figure 4.4c**). The increase in sub-canopy white spruce density is a result of substantial recruitment from the sapling class, likely driven by increased light levels following break-up of the hardwood canopy. Sapling recruitment has also

increased, from 99 saplings/ha in 1947 to 161 saplings/ha in 1967. Again, this is likely attributable to break-up of the hardwood canopy. The distribution of size-class indicates high white spruce survivorship in the smaller size classes (DBH < 20.3 cm) at this stage of stand development compared to 1947. As a result of increased recruitment in the smaller size classes, mean DBH declined to 14.9 cm in 1967.

By 2002 (stand age of 175 years), the size-class distribution of white spruce closely resembles that seen in 1947 (**Figure 4.4c**). Tree density in the canopy class has increased somewhat, from 81.8 trees/ha in 1967 to 106.8 trees/ha. Most of this increase has occurred in the smaller size classes of the canopy (i.e. DBH range 22.9 – 35.6 cm); the number of trees in this size range increased by more than half, from 49.2 trees/ha to 76.3 trees/ha. This increase is a direct result of release of the sub-canopy trees during break-up of the hardwood canopy in 1967. Saplings continue to recruit into these stands (130.3 trees/ha), but the sapling survivorship is lower as evidenced by the low number of trees of DBH 5.1 – 10.2 cm range. Nonetheless, survivorship is sufficient to ensure continued recruitment into the sub-canopy class: the density of sub-canopy trees in 2002 (88.3 trees/ha) nearly matches that in 1967 (97.9 trees/ha), indicating long-term perpetuation of white spruce in these stands (**Figure 4.4c**).

The two sub-groups of group C described above (successful hardwood second cohort, $n = 57$; no hardwood second cohort in 2002, $n = 61$) were examined for differences in white spruce recruitment and density. The two sub-groups had very similar white spruce population structures in 1947 and 1967 (**Figures 4.5c** and **4.6c**). In 1947, stand densities were 154 and 147 trees/ha (basal area = 9.04 and 10.4 m^2/ha) respectively. In 1967, stand densities were 172 and 188 trees/ha (basal area = 11.7 and 10.4 m^2/ha) respectively. For the 118 plots, the relationship between white spruce basal area in 1967 and the successful

establishment of a second trembling aspen cohort by 2002 was not significant ($\chi_1^2 = 0.41$, $P = 0.52$). This indicates that successful hardwood secondary recruitment is unaffected by white spruce abundance, being driven instead by the degree of hardwood canopy break-up. Interestingly, successful recruitment of a second hardwood cohort (trembling aspen and balsam poplar) by 2002 has adversely affected white spruce abundance. In plots without a second hardwood cohort ($n = 61$), white spruce density in 2002 was 217 trees/ha (basal area = 15.3 m^2/ha), considerably greater than in the 57 plots with a second hardwood cohort (175 trees/ha, basal area = 10.2 m^2/ha). As a result, white spruce contributes over two-thirds of total basal area in the 61 plots without a hardwood second cohort, versus only about half in the 57 plots with a second hardwood cohort in 2002 (**Table 4.2**).

4.3.4 Group D: Canopy and Regenerating Aspen, Contemporaneous White Spruce Recruitment ($n = 70$)

Trembling Aspen

In 1947 (stand age of 120 years), the trembling aspen in these stands are quite variable in size (**Figure 4.8a**), with mean DBH = 16.7 cm and a stand density of 369 trees/ha. The size distribution is bimodal (peaks at 7.6 and 20.3cm DBH), indicating distinct recruitment events. The peak at 7.6 cm DBH corresponds to trees 10 – 18 m in height and 20 – 40 years old (Bella and DeFranceschi 1980). As in group C, the presence of these trees indicates break-up of the initial post-fire canopy at about 80 – 100 years of age. Approximately three-quarters of the trees in these stands occur in the sapling and sub-canopy classes, and represent a second cohort. The canopy trees (28% of the total) include very large remnant individuals (DBH > 35 cm) from the original post-fire cohort, and are about 100 – 120 years old (Jameson 1963).

By 1967 (stand age of 140 years), the second cohort aspen have grown in size (DBH = 22.7 cm, excluding saplings at DBH = 2.54 cm), and density has declined slightly to 327 trees/ha (excluding saplings). The size-class distribution is approximately Gaussian, with about 70% of the trees occurring in the canopy class. Some of the plots (27 of 70) contained aspen saplings (from root suckers) at this stage of stand development (density of 84.3 saplings/ha), representing a third cohort.

In 2002 (stand age of 175 years), tree density of the sub-canopy and canopy classes has declined by over half, to 140 trees/ha, but these trees are somewhat larger (DBH = 27.6 cm). Only 14% of the trees occur in the sub-canopy class, indicating limited recruitment of root suckers into the sub-canopy at this stage of stand development. Aspen saplings (151.1 saplings/ha, or nearly half the trees in these stands) occurred in about two-thirds of the plots, and the presence of trees in the 5.1 and 7.6 cm size classes suggests that some of these may grow into the sub-canopy in later years.

Balsam Poplar

In 1947 (stand age of 120 years), balsam poplar trees in these plots are mostly medium-sized (mean DBH = 17.3 cm). Balsam poplar is uncommon in these plots (it occurs in only 19 of the 70 plots); as a result, density is low (29.3 trees/ha). Over half of the trees occur in the sub-canopy class, and there are few trees in the sapling class at this stage of stand development (**Figure 4.8b**).

By 1967 (stand age of 140 years), the trees have grown in size (mean DBH = 20.5 cm) but density has not changed, indicating little mortality. Saplings (from root suckering) are present at this stage of stand development in 8 of the 19 plots containing balsam poplar.

By 2002 (stand age of 175 years), balsam poplar density (excluding saplings at DBH = 2.54 cm) has declined to 20.3 trees/ha. Over half of the trees now occur in the canopy class, increasing the average tree diameter to 24.8 cm (**Figure 4.8b**). There are relatively few trees in the sub-canopy, indicating limited recruitment from saplings (root suckers). Some stands continue to produce a few root suckers at this stage of stand development (1 – 6 per plot), although prolific root suckering (46 saplings) was observed in one plot.

White Spruce

In 1947 (stand age of 120 years), the size-class distribution of white spruce in these plots is similar to that seen for group C. The size-class distribution is continuous, with abundance declining monotonically with increasing DBH (**Figure 4.8c**). Such a distribution is "stable" in that it indicates continuous recruitment and cumulative mortality with increasing tree size (Hett and Loucks 1976). The mean DBH = 12.8 cm is quite low, reflecting the high densities of saplings (248.6 trees/ha) and sub-canopy trees (160.4 trees/ha). About one-fifth of the trees occur in the canopy class (95.4 trees/ha), and many plots contained at least one large (DBH > 35 cm) tree, corresponding to 24 – 28 m in height and 90 – 110 years in age (Jameson 1963). The presence of these large trees confirm that white spruce recruitment was contemporaneous, i.e. seed germination and sapling establishment within the first 10 – 30 years post-fire. White spruce density in these plots is much higher than for group C plots, particularly for saplings (248.6 saplings/ha, versus 98.7 saplings/ha in group C) and sub-canopy trees (160.4 trees/ha, versus 68.4 trees/ha). This indicates very high recruitment in these stands compared to the other three groups.

In 1967 (stand age of 140 years), the size-class distribution of white spruce is virtually identical to that in 1947 (**Figure 4.8c**). Tree size and density have

increased marginally (mean DBH = 13.2 cm, density = 538.2 trees/ha), and abundances in the sapling, sub-canopy and canopy classes are very similar. Total basal area has increased from 11.62 to 13.32 m^2/ha between 1947 and 1967.

By 2002 (stand age of 175 years), the size-class distribution of white spruce has changed somewhat, due to reduced sapling recruitment and fewer trees in the sub-canopy (**Figure 4.8c**). The abundance of saplings has declined by 40% to 160.7 trees/ha, while the abundance of sub-canopy trees has declined by about one-third, to 108.2 trees/ha. About one-third of the white spruce occur in the canopy at this stage of stand development (128 trees/ha), and their presence and abundance in the canopy is inhibiting the recruitment, growth and survivorship of saplings and sub-canopy individuals. As a result, mean tree size has increased to 16.4 cm DBH, but white spruce density has declined by over one-quarter to 396.8 trees/ha. Increased abundance of large canopy trees has increased the basal area of white spruce to 14.22 m^2/ha at this stage of stand development (56% of total stand basal area).

4.3.5 All Plots (*n* = 266)

Temporal trends in size-class distribution, stand density and basal area were examined for each of the three tree species (trembling aspen, balsam poplar and white spruce) to obtain a "landscape-level" synopsis of forest stand dynamics over the 55-year sampling period (stand ages 120, 140 and 175 years).

Trembling Aspen

In 1947 (stand age of 120 years), stand density was 276 trees/ha with a basal area of 9.89 m^2/ha (**Tables 4.3 and 4.4**). The size-class distribution is clearly bi-

modal, reflecting the presence of a second cohort (peaking at 7.6 and 10.2 cm DBH) recruited at stand ages 80 – 100 years (mainly groups C and D). There are very few young saplings (root suckers of DBH = 2.5 cm) at this stage of stand development (**Figure 4.9a**).

By 1967 (stand age of 140 years), the second cohort has grown into the upper sub-canopy, resulting in a relatively even distribution of trees over the 12.7 – 33.0 cm DBH classes (**Figure 4.9a**). There are very few trees in the large sapling and lower sub-canopy classes (5.1 – 10.2 cm BH) at this stage of stand development. However, there is considerable recruitment of young root suckers (saplings of DBH = 2.5 cm) attributable to the break-up of the hardwood canopy (particularly in groups A and B). Stand density has declined slightly to 190 trees/ha (excluding the smallest sapling class), but basal area has increased to 10.16 m^2/ha (**Tables 4.3 and 4.4**).

In 2002 (stand age of 175 years), trembling aspen density had declined slightly to 182 trees/ha (excluding the smallest sapling class), and basal area has also declined to 8.93 m^2/ha (**Tables 4.3 and 4.4**). The size-class distribution indicates a relatively equitable distribution of trees in the 5.1 – 40.6 cm DBH size classes; higher densities in the 15.2 – 22.9 cm DBH range reflect the growth of second cohort individuals recruited in 1967 and earlier. Root suckers (saplings at 2.5 cm DBH) are present in many stands at this stage of stand development.

Balsam Poplar

In 1947 (stand age of 120 years), balsam poplar stand density was 56.3 trees/ha with a basal area of 1.99 m^2/ha (**Tables 4.3 and 4.4**). The size-class distribution is slightly bi-modal, reflecting a second cohort (peaking at 10.2 cm DBH) recruited at stand ages 80 – 100 years (mainly groups C and D). As with

trembling aspen, there are very few young balsam poplar saplings (root suckers of DBH = 2.5 cm) at this stage of stand development (**Figure 4.9b**).

By 1967 (stand age of 140 years), the second cohort has grown into the upper sub-canopy and lower canopy, resulting in a relatively even distribution of trees over the 15.2 – 35.6 cm DBH range (**Figure 4.9b**). There are very few trees in the large sapling and lower sub-canopy classes (7.6 and 10.2 cm BH) at this stage of stand development. However, there is considerable recruitment of young root suckers (saplings of 2.5 and 5.1 cm DBH) attributable to the break-up of the hardwood canopy (particularly in groups A and B). Stand density has declined to 41.4 trees/ha (excluding the two smallest sapling classes), but basal area has increased to 2.38 m^2/ha (**Tables 4.3 and 4.4**).

In 2002 (stand age of 175 years), balsam poplar density has increased to 60.5 trees/ha (excluding the smallest sapling class), and basal area has also increased to 3.33 m^2/ha (**Tables 4.3 and 4.4**). The size-class distribution is approximately Gaussian (though skewed to the right), peaking at DBH = 17.8 and 20.3 cm. There are many more large trees (> 40 cm DBH) in 2002 compared to the other years. Root suckers (saplings at 2.5 cm DBH) are present in some stands.

White Spruce:

In 1947 (stand age of 120 years), the size-class distribution is continuous, with abundance declining monotonically with increasing tree size (**Figure 4.9c**). Such a distribution indicates an equilibrium state of continuous recruitment and cumulative mortality with increasing tree size (Hett and Loucks 1976). Stand density is 274 trees/ha, with 132.4 trees/ha in the sapling class. White spruce

basal area is 7.52 m^2/ha at this stage of stand development (**Tables 4.3 and 4.4**).

The size-class distribution has an almost identical shape in 1967, but density has increased to 369 trees/ha, with 183 trees/ha in the sapling class. White spruce basal area has increased by nearly 25% over twenty years, to 9.24 m^2/ha (**Tables 4.3 and 4.4**).

By 2002, the shape of the size-class distribution curve has changed (**Figure 4.9c**). The number of trees in each of the size classes 7.6 – 27.9 is similar, indicating lower survival rates of sub-canopy trees (DBH = 5.1 – 20.3 cm). Sapling recruitment (DBH = 2.5 cm) continues to be high, but comparatively fewer of these young saplings are surviving or growing into sub-canopy. Tree density remains high at 334 trees/ha, but the number of trees in the sapling class has declined to 123 trees/ha (**Table 4.3**). White spruce basal area has increased by over one-third from 1967, to 12.74 m2/ha. This is mainly attributable to the increased abundance of large trees (DBH > 30 cm), which constitute 30.6% of the white spruce population (versus and 26.9 and 22.3% in 1947 and 1967 respectively).

4.3.6 Forest Stand Dynamics

Changes in the total basal area of hardwoods (trembling aspen, balsam poplar) and softwoods (white spruce) over the 55-year period (1947-2002, stand ages 120 – 175 years) for each of the four groups A – D and for all plots (n = 266), are summarized in **Figure 4.10**.

As expected, the basal area of softwoods in groups A and B increased considerably over the 55-year period, reflecting the growth of delayed recruitment white spruce. For group A, total stand basal area increased from 14.53 m^2/ha in 1947 (> 95% of which is hardwood) to 29.78 m^2/ha in 2002 (53% hardwood). Softwood basal area increased greatly in these stands, while hardwood basal area increased only modestly. Within the hardwood class, trembling aspen declined over time, from 9.97 m^2/ha in 1947 to 9.07 m^2/ha in 2002, whereas the basal area of balsam poplar increased from 4.04 to 7.32 m^2/ha over the same period. For group B, total stand basal area increased from 14.19 m^2/ha in 1947 (> 95% of which is hardwood) to 30.76 m^2/ha in 2002 (70% hardwood). White spruce recruitment and growth in these stands appears to be limited by the earlier development of a second hardwood cohort (80 – 90 years, versus 110 – 120 years in the group A plots). Both hardwood and softwood basal area increased in these stands. Within the hardwood class, basal area increased for both trembling aspen (10.17 to 16.11 m^2/ha) and balsam poplar (3.47 to 5.46 m^2/ha).

Changes in hardwood and softwood basal area over the 55-year study period were more modest for group C and D plots, which is expected given the contemporaneous establishment of white spruce in these stands. For group C, total stand basal area increased slightly from 20.82 to 21.35 m^2/ha. Hardwood basal area declined by 22% (from 11.10 to 8.68 m^2/ha): basal area of trembling aspen declined (9.58 to 6.13 m^2/ha), while that of balsam poplar increased (1.52 to 2.55 m^2/ha). Over the same period, the basal area of white spruce increased by about one-third, from 9.72 to 12.67 m^2/ha. The trajectory for group C suggests a temporal trend of increasing softwood and declining hardwood basal area. For group D, total basal area showed a modest increase from 22.63 m^2/ha in 1947 to 25.35 m^2/ha in 2002. Harwood basal area increased slightly, from 11.01 to 11.13 m^2/ha, reflecting a small decline in trembling aspen basal area (10.22 to 9.98

m^2/ha) and a modest increase in the basal area of balsam poplar (0.79 to 1.15 m^2/ha). Over the same period, white spruce basal area increased by about one-quarter, from 11.62 to 14.22 m^2/ha.

The trajectory for all 266 plots is indicative of the overall "direction" of succession change on the landscape. Over all 266 plots, total basal area increased by about 30%, from 19.40 m^2/ha in 1947 to 25.00 m^2/ha in 2002. Almost all of this increase was attributable to white spruce, which increased by about 70% from 7.52 to 12.74 m^2/ha. Much of this increase occurred in the group A and B plots, reflecting the delayed recruitment of white spruce into these stands. Hardwood basal area also increased, but only by a modest 3%: from 11.88 to 12.26 m^2/ha. The basal area of trembling aspen declined (from 9.89 to 8.93 m^2/ha), while that of balsam poplar increased (from 1.99 to 3.33 m^2/ha). Over the 55-year period, the proportion of hardwood basal area attributable to balsam poplar increased considerably, from 17.5% in 1947 to 27.2% in 2002.

4.4 DISCUSSION

Long-term studies on the succession dynamics of mixed-wood forests have invariably used space-for-time substitution to infer changes in forest tree composition, structure and productivity (Frelich and Reich 1995; Bergeron 2000; Taylor and Chen 2011). Such an approach is necessitated by the lack of long-term permanent sample plot (i.e. direct observational) data for these ecosystems. However, space-for-time substitution has an inherent bias, resulting from the prior selection of stands that are thought to converge deterministically over time (Johnson and Miyanishi 2008). The Riding Mountain permanent sample plots, enumerated for 55 years since the late 1940s, provide a rare opportunity to confirm or refute, using unequivocal long-term direct observations, projections of

forest succession change that have been inferred using the indirect space-for-time substitution approach.

The mixed-wood boreal forest has been described as a deterministic system, in which the initial post-disturbance colonizers (i.e. shade intolerant species, trembling aspen) are upon their senescence replaced by shade species such as white spruce (Rowe 1955, 1961; Bergeron 2000). Such deterministic models are widely used to describe boreal mixed-wood forest dynamics (Bergeron 2000; Chen and Popadiouk 2002), despite increasing evidence that questions this deterministic paradigm (e.g. Cumming *et al.* 2000; Gutsell and Johnson 2002). It is now well established that recruitment of white spruce following a catastrophic disturbance event may either be contemporaneous or delayed (Peters *et al.* 2006), and that trembling aspen has the capacity for long-term persistence through the development of a second cohort from vegetative root suckers (Cumming *et al.* 2000). These findings suggest the need to objectively re-examine the simple, deterministic views of boreal mixed-wood forest succession that prevail to this day.

The dichotomy in white spruce recruitment (i.e. contemporaneous versus delayed) arises from differences in post-disturbance hardwood densities (Peters *et al.* 2005), and the presence or absence of a white spruce seed source (Greene 2000). My results clearly demonstrate that white spruce shows both delayed and contemporaneous recruitment (stand groups A and C, versus B and D). Contemporaneous white spruce recruitment occurs when a seed source occurs within 200 m of the area during stand initiation (Greene and Johnson 1995), although much greater seed dispersal distances have also be recorded (Stewart *et al.* 1998). At 80 – 120 years, the hardwood canopy begins to break apart and white spruce recruits and grows into the canopy (Dix and Swan 1971; Kneeshaw and Bergeron 1998; Bergeron 2000). My results confirm that white spruce

density does indeed increase following break-up of the initial hardwood canopy. However, my results also show that a flush of second cohort hardwood recruitment occurs following canopy break-up. As a result, older stands (175 years in age) contain a mixture of both hardwoods and softwoods. This coincides with field and modelled observations of hardwood persistence (Bella 1975; Crawford *et al*. 1998; Cumming *et al*. 2000; Kurzel *et al*. 2007).

Long-term persistence of trembling aspen and balsam poplar is also characteristic of boreal mixed-wood stands with delayed white spruce recruitment. In these stands, white spruce recruitment did not begin until after the density dependent mortality stage of hardwood stand development (i.e. aspen canopy break-up, 60 – 100 years; Pothier *et al*. 2004). The delayed recruitment white spruce saplings and small sub-canopy trees present at stand age 120 years recruited into these stands at about age 60 – 80 years post-disturbance. During the break-up of the initial hardwood canopy, increased light levels resulted in a flush of new white spruce recruitment and release of the suppressed white spruce sapling already present (Lieffers *et al*. 1996). As the initial hardwood canopy breaks apart, the stand becomes more susceptible to smaller scale disturbances that create more canopy gaps (Gardiner *et al*. 1997; Senecal *et al*. 2004). The rapid release of suppressed saplings, combined with a flush of new recruitment, fills the canopy gaps and creates an uneven-aged stand (Kneeshaw and Bergeron 1998). Importantly, my results also indicate that the breaking up of the hardwood canopy results in root sucker initiation by both trembling aspen and balsam poplar, reflecting a combination of apical dominance release and increased light to the forest floor. As a result, by a stand age of 175 years these stands consist of a mixture of both hardwoods and softwoods.

My results demonstrate that both trembling aspen and balsam poplar exhibit not only a stand initiation recruitment flush of root suckers following a stand-

replacing disturbance (typically fire), but also a later recruitment (second cohort) flush following break-up of the initial canopy. Hardwood canopy break-up may occur as early as 60 years, or as late as 100+ years (Peterson and Peterson 1992). Rapid canopy tree mortality during the break-up phase results in a loss of apical dominance, which if combined with an adequate supply of carbohydrates in the lateral roots (Schier 1973; Landhäusser and Lieffers 1997) stimulates prolific root suckering. My results show that the successful establishment of recruited root suckers is negatively correlated with hardwood canopy density. Rapid canopy break-up greatly increases light penetration to the forest floor, raising soil temperatures to levels required to initiate root suckering (Landhäusser and Lieffers 1998). These higher light levels also promote rapid growth of trembling aspen and balsam poplar root suckers. Competition for canopy space ensues, as both hardwoods and softwoods enter a "race" to obtain canopy dominance. However, if canopy break-up is limited, less light reaches the forest floor and hardwood root suckering is less prolific. Furthermore, the lower light levels result in greatly reduced survivorship of recruited root suckers. As a result, smaller canopy gaps tend to be ceded to the more shade-tolerant white spruce saplings.

The flush of hardwood recruitment (root suckering) leading to successful establishment of a second tree cohort confirms that vegetative (asexual) reproduction is a critically important life history trait during later stages of stand development (Cumming *et al.* 2000; Baret and DesRochers 2011). My results indicate the need for a paradigm shift in our understanding of stand dynamics in the boreal mixed-wood forests of western Canada. I have shown that hardwoods (i.e. trembling aspen and balsam poplar) have the ability to successfully recruit from root suckers during later stages of stand development (i.e. following break-up of the initial canopy cohort). Succession in the boreal mixed-wood forest is not a simple, predefined deterministic pathway from deciduous to coniferous tree

dominance. Instead, this study has demonstrated that long-term coexistence of a mixture of hardwood and softwood species is characteristic of this ecosystem. The boreal mixed-wood forest is not a "transitional" phase, but rather a stable and self-sustaining ecosystem that persists as a dynamic equilibrium in both space and time.

My results demonstrate that balsam poplar, unlike trembling aspen, shows an appreciable increase in both density and basal area at later stages of stand development. Although trembling aspen and balsam poplar are often considered to be ecologically similar based on their common phylogeny (e.g. Peterson and Peterson 1992), the life history characteristics of these two species are in fact quite distinct (Landhäusser *et al*. 2003). Interestingly, an earlier study of mixed-wood boreal forest dynamics in central Alberta also found that balsam poplar increases in abundance in older stands (Plochmann 1956), but this finding was dismissed by Rowe (1961).

My results also indicate that white spruce, once established, maintains itself through continuous recruitment and growth. A closed canopy (hardwood and/or softwood) limits the amount of light reaching the forest floor, resulting in white spruce sapling suppression and reduced survivorship (Lieffers *et al*. 1996; Gutsell and Johnson 2002). Canopy openings or gaps result in increased light to the forest floor, increasing the recruitment (seed germination and establishment) of white spruce and releasing formerly suppressed saplings and sub-canopy trees. My results show a gradual increase in white spruce density and basal area over time, suggesting the possibility of higher softwood dominance at later years of stand development. However, the continued presence and successful recruitment of hardwood species through root suckering will likely preclude the development of a softwood-dominated system for many years to come.

The classification of boreal tree species based on their relative shade tolerance (as a proxy to their long-term persistence) has long dominated succession studies (e.g. Dix and Swan 1971; Cogbill 1985; Huston and Smith 1987; Dansereau and Bergeron 1993; Bergeron 2000; Chen and Popadiouk 2002; Taylor and Chen 2011). In a simplistic comparison of a shade intolerant species (e.g. trembling aspen) and a shade tolerant one (e.g. white spruce), the "logical" climax community is necessarily one dominated by the shade tolerant species (Rowe 1961; Huston and Smith 1987; Bergeron 2000). My results are clearly at odds with this simple "tolerance" view of boreal forest stand dynamics. Break-up of the initial post-disturbance canopy at 60 – 100 years is beneficial not only to white spruce, but to the clonal hardwood species (trembling aspen and balsam poplar) as well. Despite differences in shade tolerance among tree species, the canopy gaps formed during stand break-up are often sufficiently large to promote the regeneration of both hardwoods (through root sucker development and growth) and softwoods (through seedlings recruitment and establishment, and the growth of suppressed trees).

It is clear from my results that shade tolerance is not, on its own, a particularly useful life history trait for modelling long-term boreal forest stand dynamics. The canopy gaps created during stand break-up are generally sufficiently large and frequent enough to promote the regeneration of both sexually reproducing, shade tolerant tree species (e.g. white spruce) and asexually reproducing, shade intolerant ones (e.g. trembling aspen and balsam poplar).

There is considerable variation among species in the relative importance of those life history traits that ensure long-term persistence. Emphasis of a single trait (e.g. shade tolerance), and/or ignoring potentially important traits (e.g. rapid clonal growth), may result in misleading or wholly erroneous models of long-term

stand dynamics. The need to parameterize a given species' niche is essential to determining the environmental conditions under which it can exist (niche model: Clark *et al.* 2004). Equally important, however, is the inherent ability of species to persist on the landscape where environmental and biotic conditions vary continuously, and in which stochastic mortality and reproduction helps ensure long-term persistence at all spatial and temporal scales (neutral model: Hubbell 2001). This raises the fundamental question of the relative importance of niche versus neutral theory in explaining the long-term persistence and coexistence of species. I propose that the long-term persistence of tree species in boreal mixed-wood stands is attributable to both niche and neutral processes, which together produce a dynamic equilibrium of high tree diversity in these ecosystems.
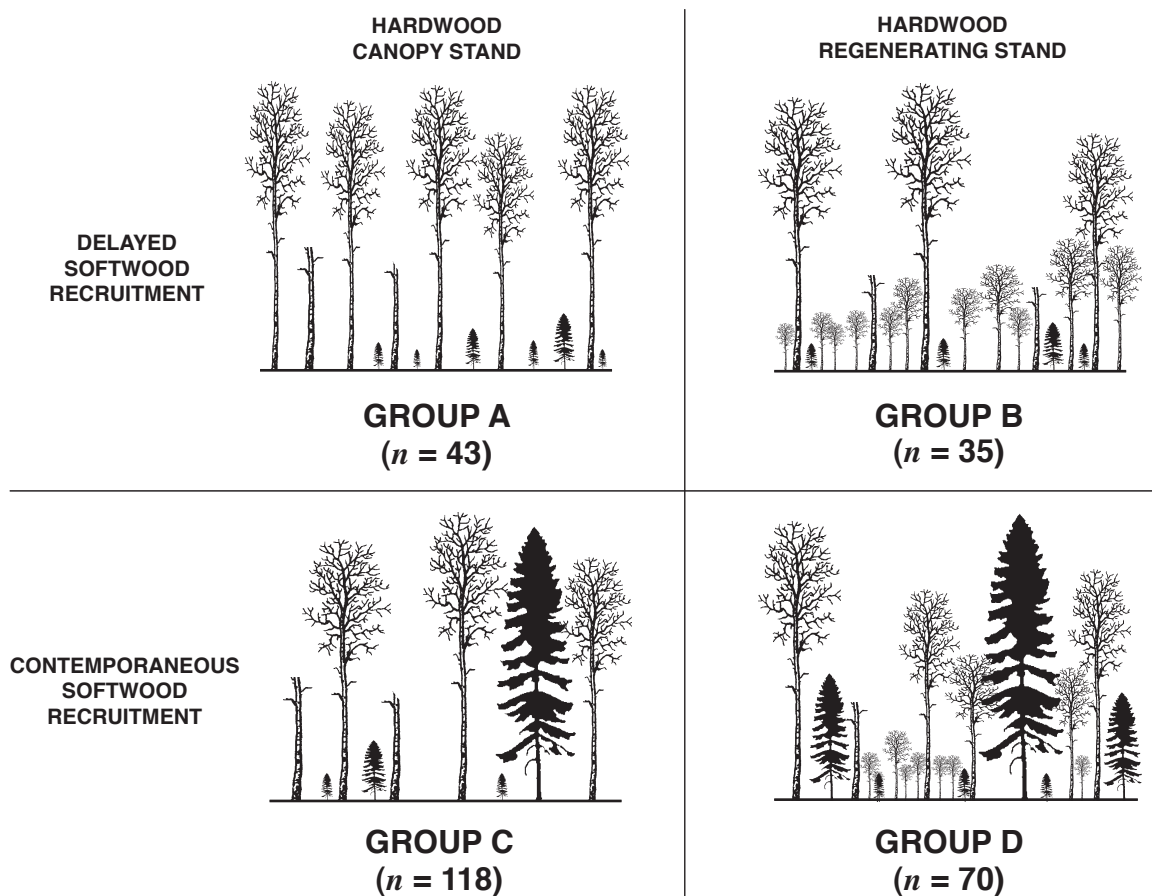
Figure 4.1: A 2 x 2 cross classifcation of 1947 (stand age = 120 years) softwood recruitment (delayed vs. contemporaneous) and hardwood stand types (canopy vs. regenerating).

TABLE 4.1: Summary of the four groups by (a) densities (trees/ha), and (b) basal area (m²/ha). The data used to populate the table to was collected in 1947 and separated into 3 classes: saplings (I; DBH <7.6cm), subcanopy (II; DBH = 7.6 – 20.3cm), and canopy (III; DBH >22.9cm). NOTE: Total columns represent the total value of subcanopy and canopy trees together.

(a)

GROUP	n	TREMBLING ASPEN				BALSAM POPLAR				WHITE SPRUCE			
		I	II	III	II+III	I	II	III	II+III	I	II	III	II+III
A	43	2.3	21.5	126.2	147.7	0.6	22.7	49.4	72.1	87.8	23.8	0.0	23.8
B	35	302.9	271.4	80.0	351.4	30.0	122.1	22.1	144.3	68.6	26.4	0.0	26.4
C	118	0.8	32.4	128.4	160.8	0.6	10.0	20.8	30.7	98.7	68.4	82.6	151.1
D	70	89.3	175.4	104.3	279.6	4.3	16.8	8.2	25.0	248.6	160.4	95.4	255.7

(b)

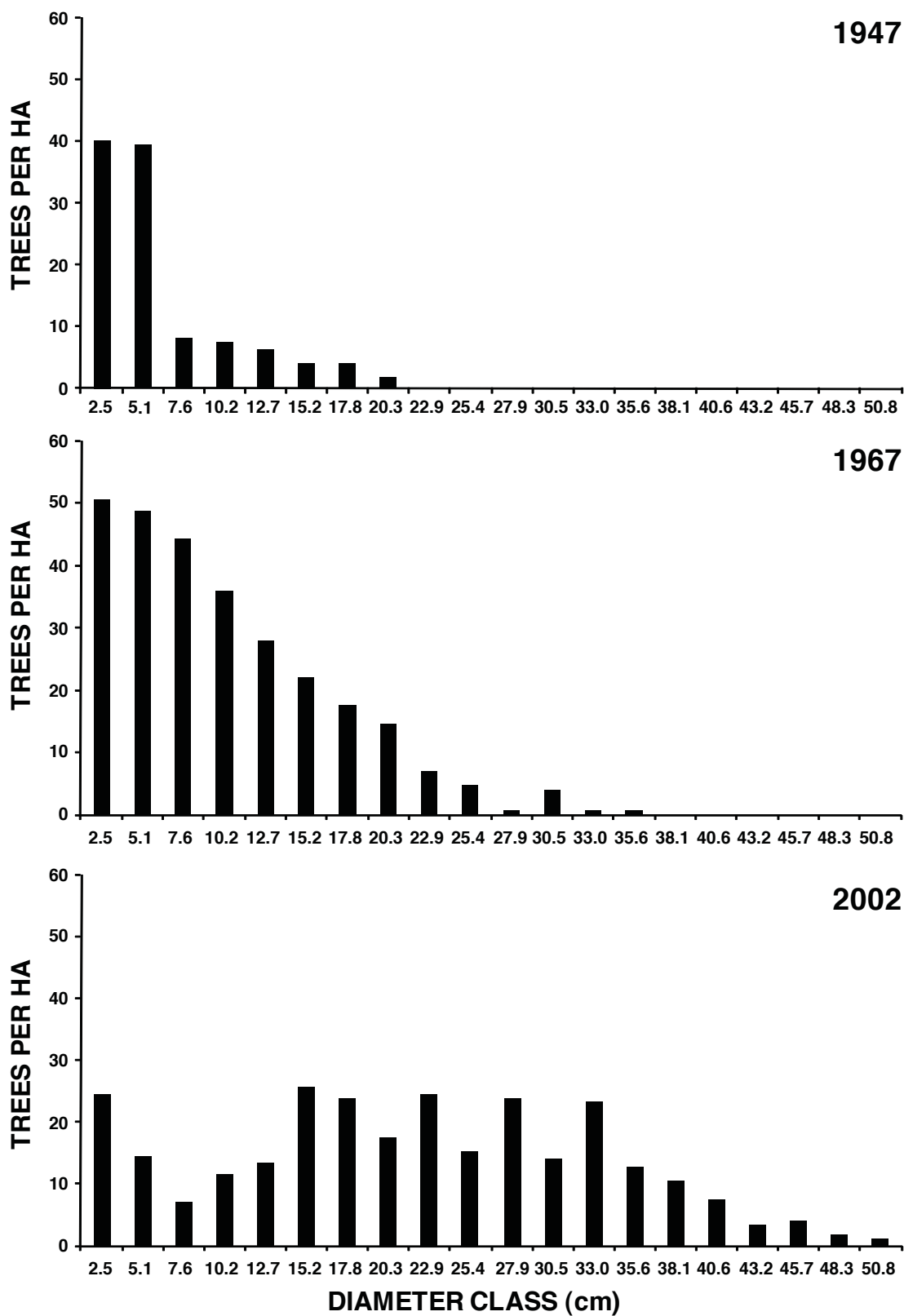| GROUP	n	TREMBLING ASPEN				BALSAM POPLAR				WHITE SPRUCE			
		I	II	III	II+III	I	II	III	II+III	I	II	III	II+III
A	43	0.01	0.56	9.40	9.97	0.00	0.56	3.48	4.04	0.14	0.38	0	0.52
B	35	1.06	3.35	5.76	10.17	0.12	1.79	1.56	3.47	0.11	0.43	0	0.54
C	118	0.00	0.86	8.72	9.58	0.00	0.22	1.29	1.51	0.18	1.21	8.33	9.72
D	70	0.32	3.29	6.62	10.22	0.01	0.32	0.45	0.78	0.47	2.59	8.56	11.62
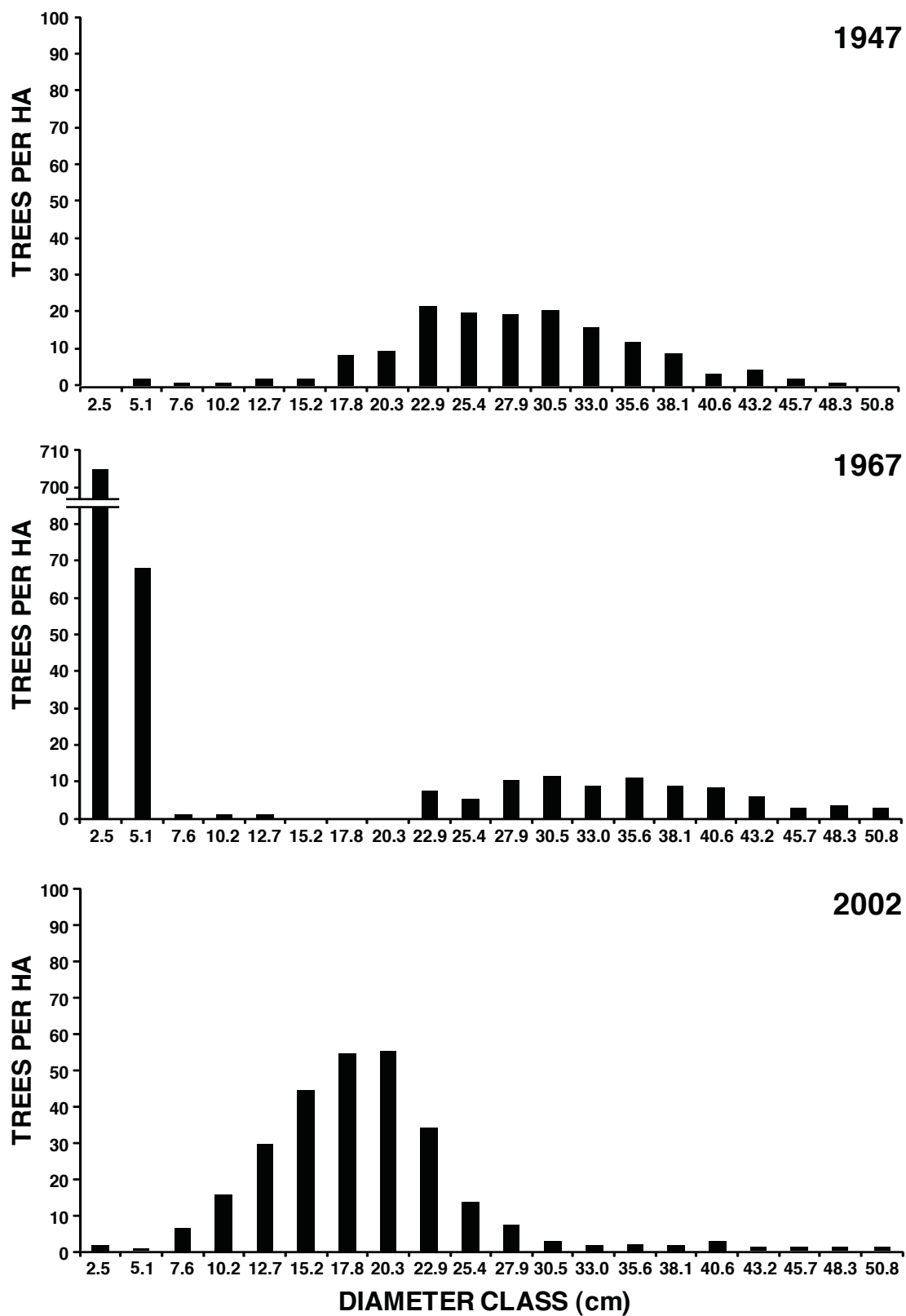
Figure 4.2 (a): Trembling aspen diameter class distributions in 1947, 1967, and 2002 of group A (n = 43 stands).
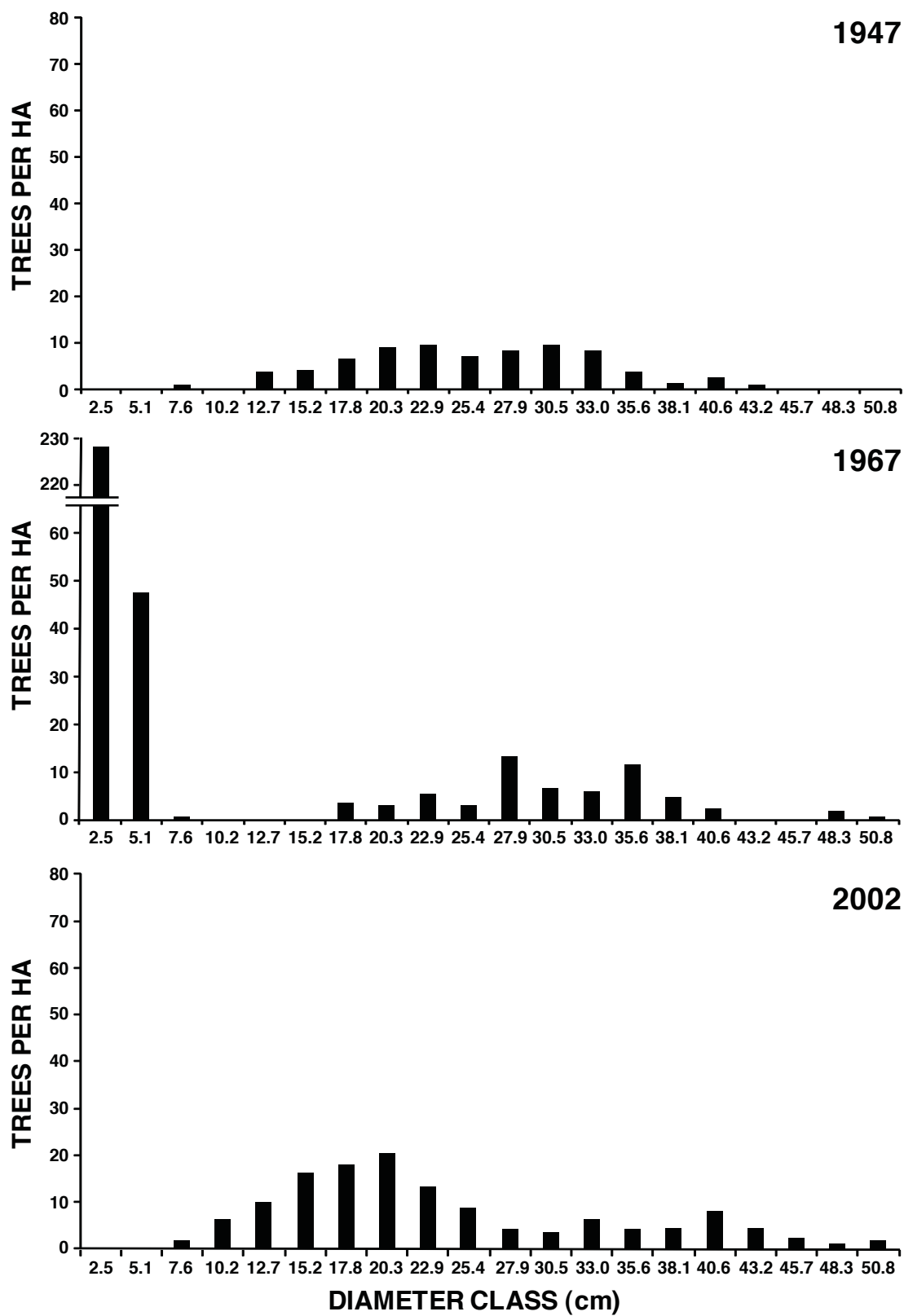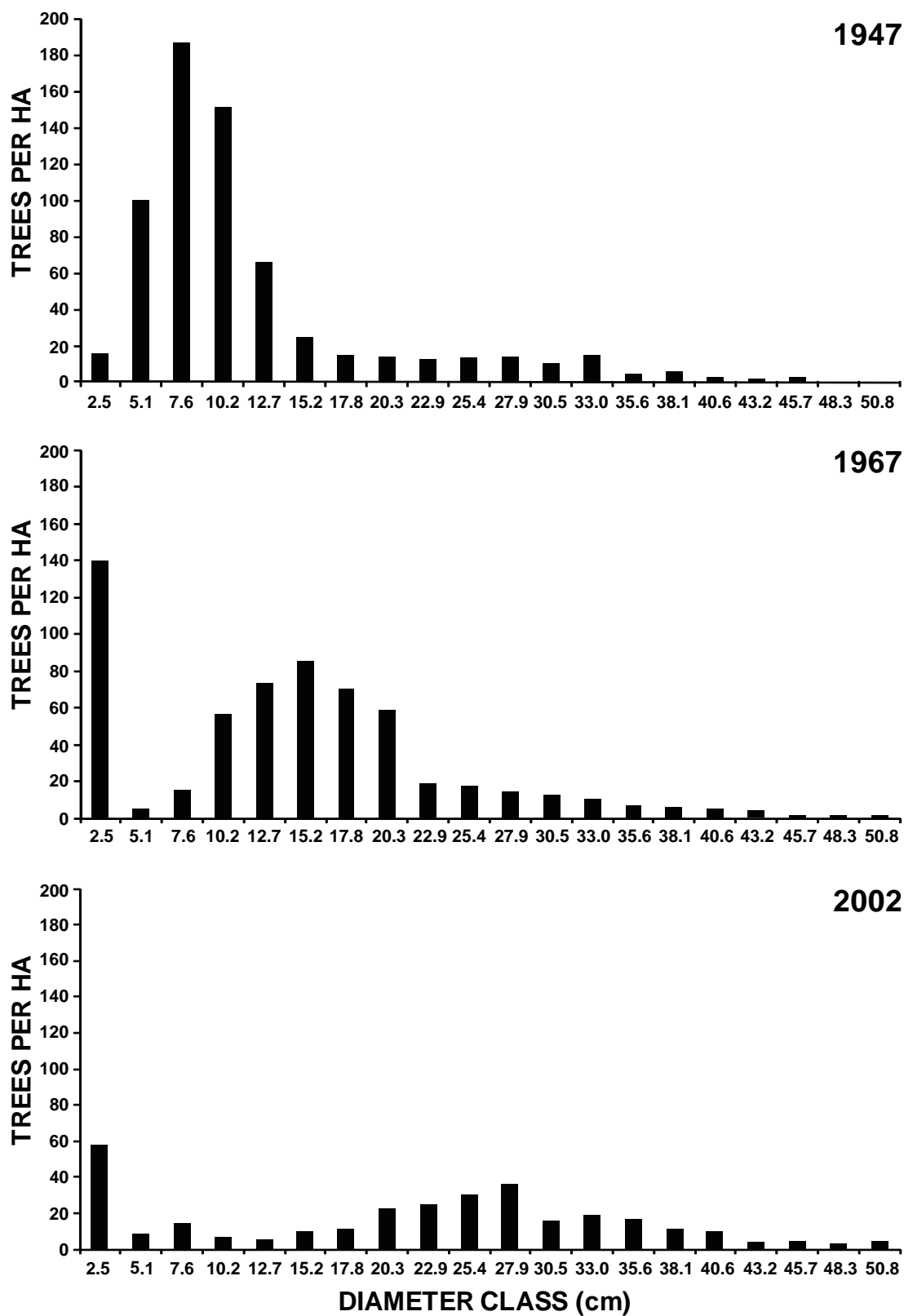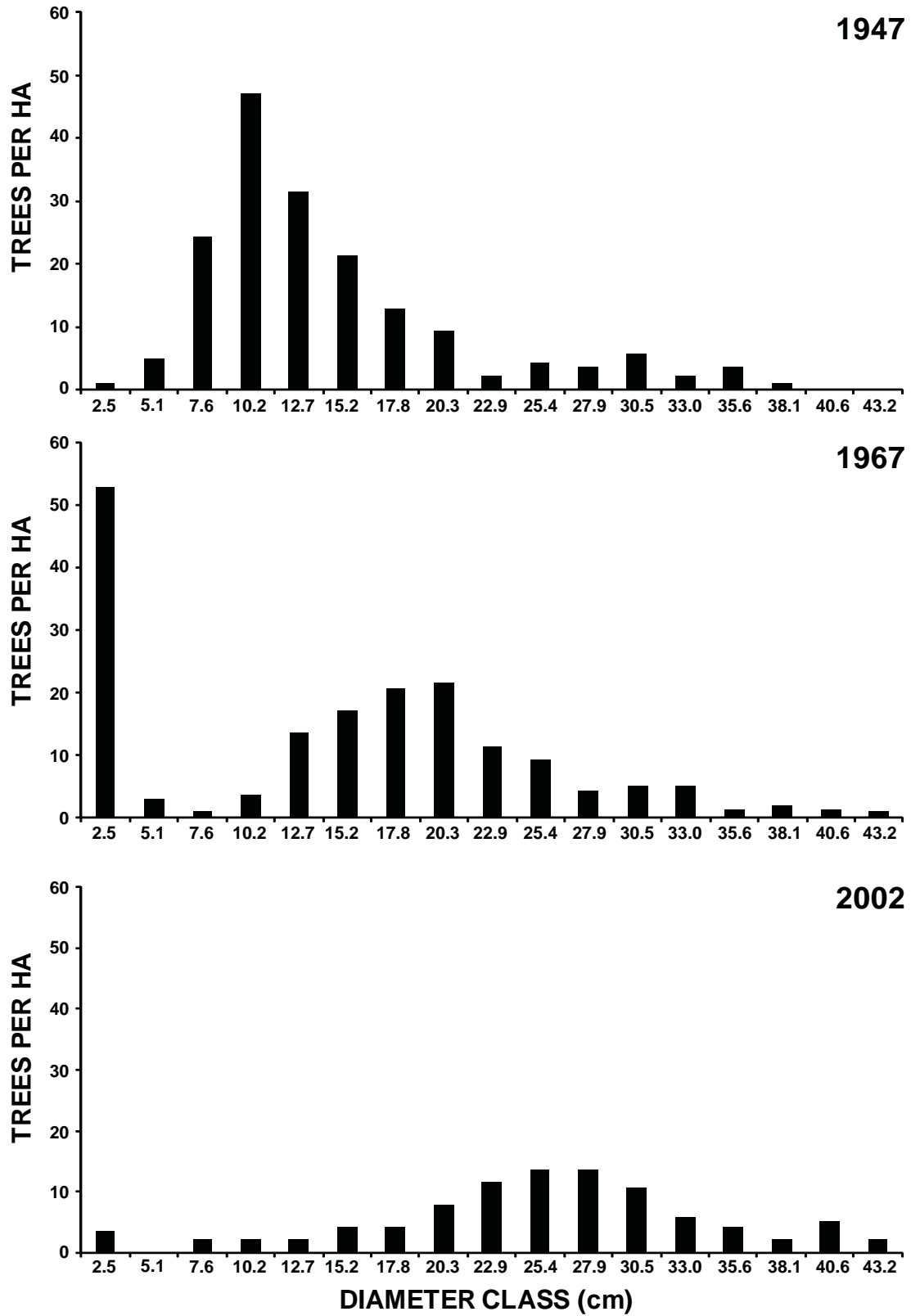
Figure 4.2 (b): Balsam poplar diameter class distributions in 1947, 1967, and 2002 of group A (n = 43 stands).
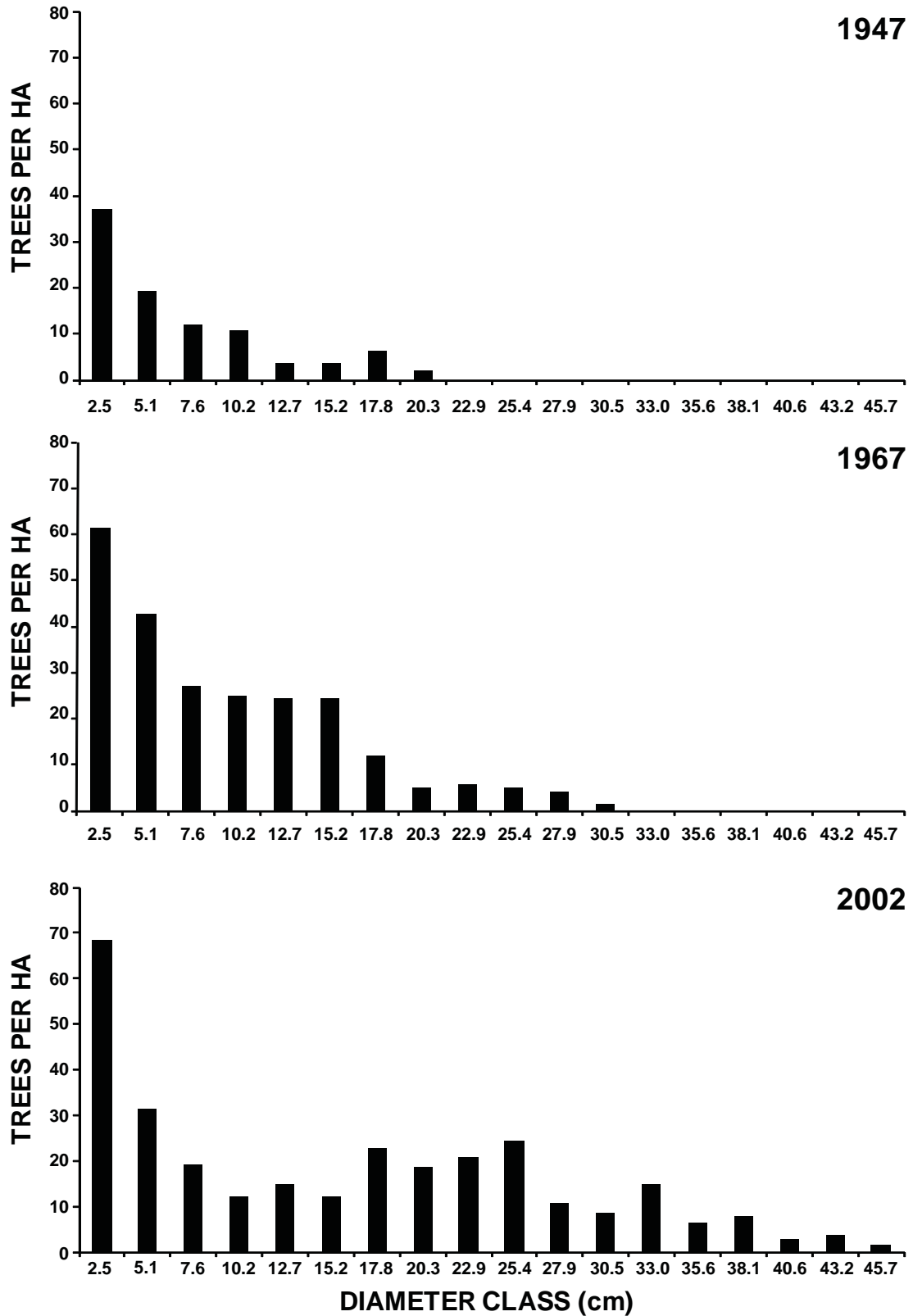
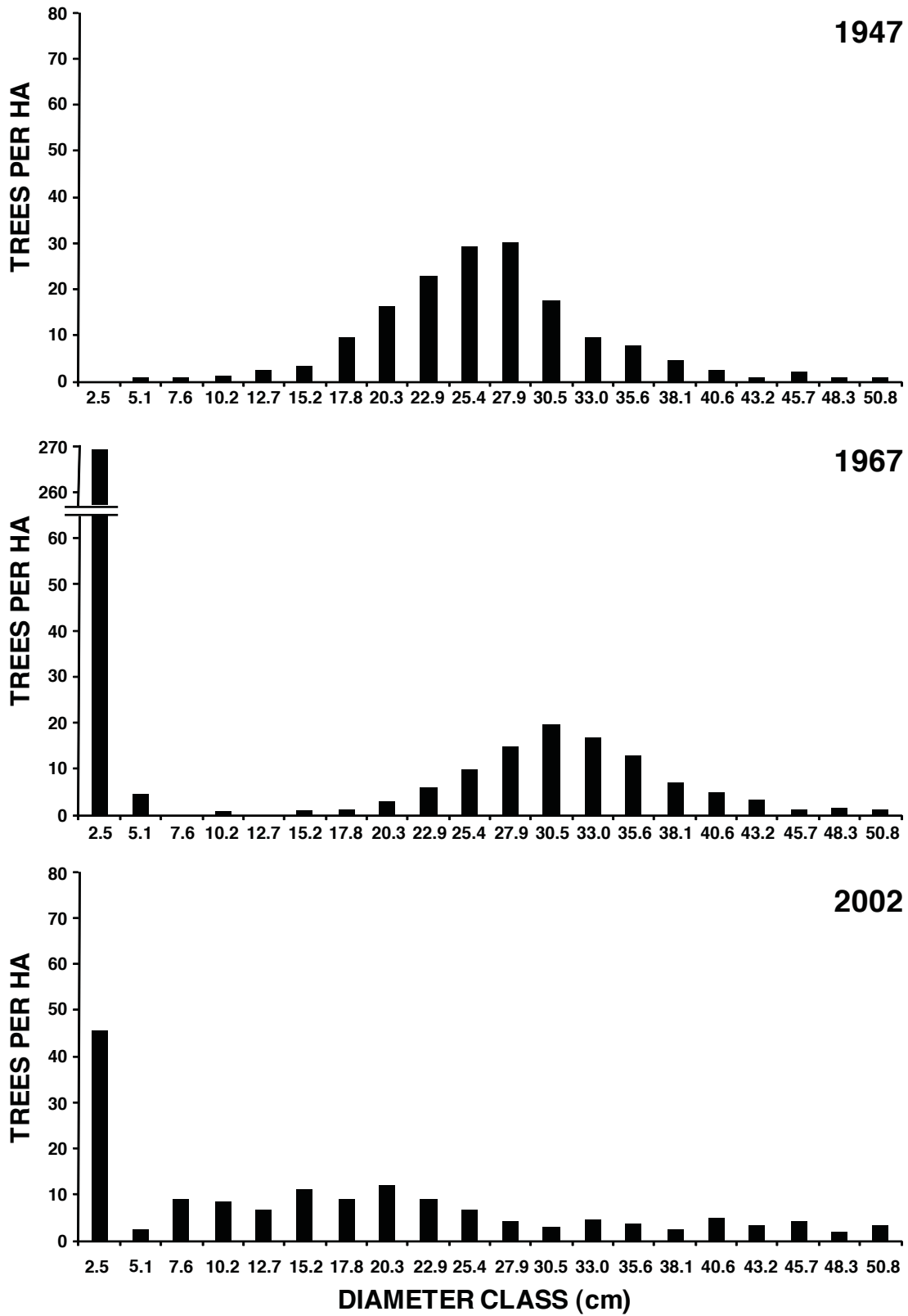**Figure 4.2 (c):** White spruce diameter class distributions in 1947, 1967, and 2002 of group A (n = 43 stands).

Figure 4.3 (a): Trembling aspen diameter class distributions in 1947, 1967, and 2002 of group B (*n* = 35 stands).
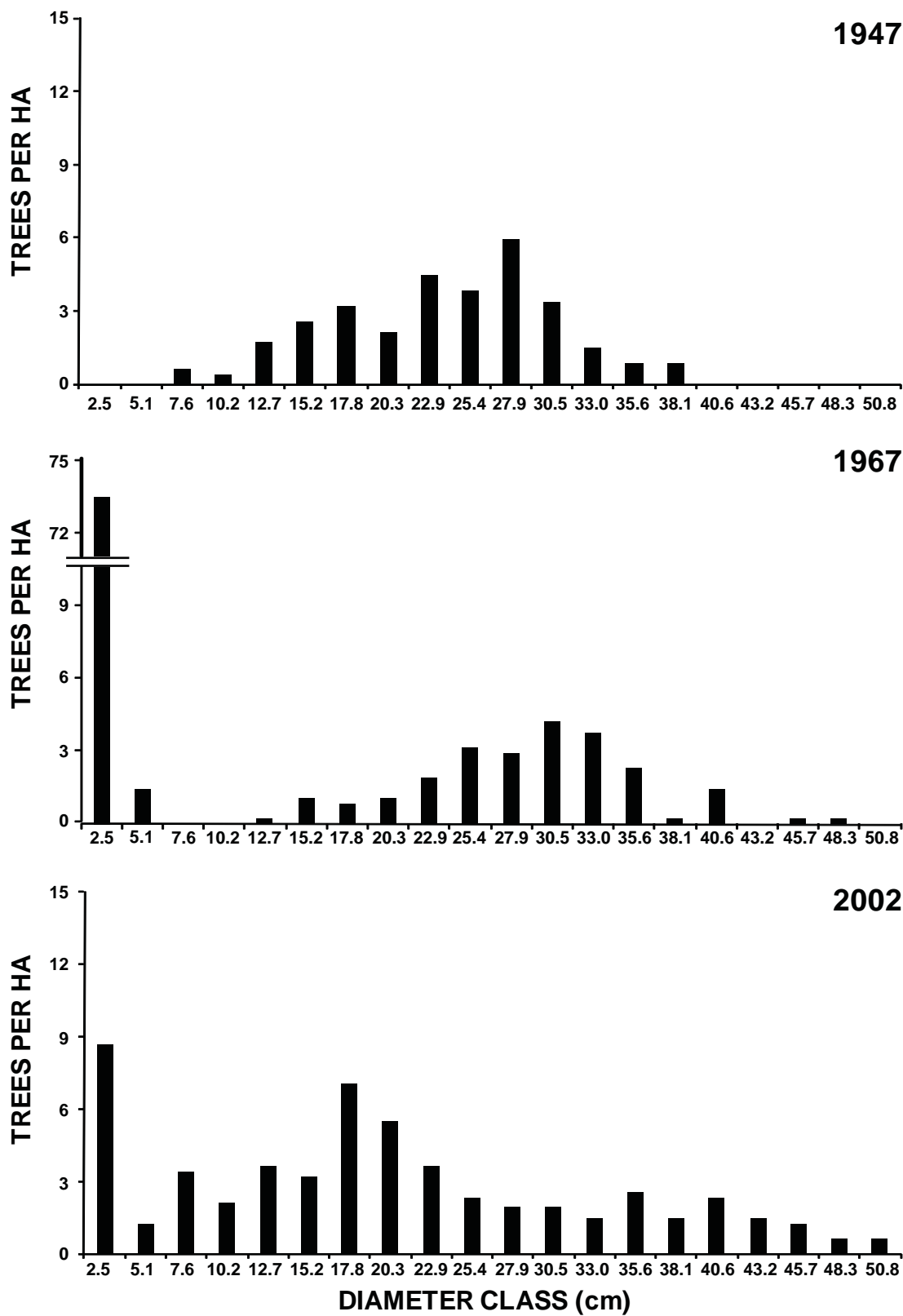
Figure 4.3 (b): Balsam poplar diameter class distributions in 1947, 1967, and 2002 of group B (*n* = 35 stands).
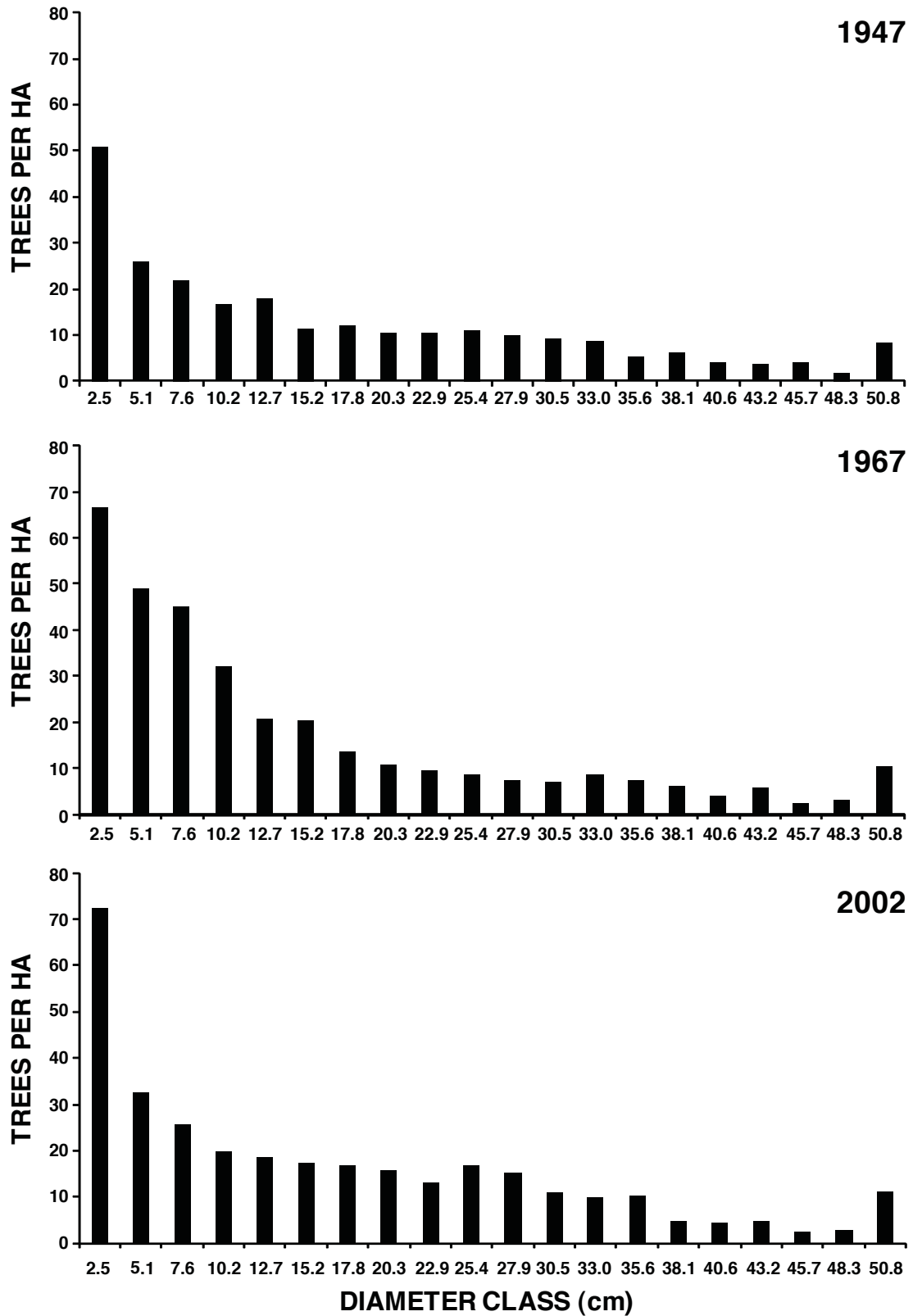
Figure 4.3 (c): White spruce diameter class distributions in 1947, 1967, and 2002 of group B (*n* = 35 stands).

Figure 4.4(a): Trembling aspen diameter class distributions in 1947, 1967, and 2002 of group C (n = 118 stands).
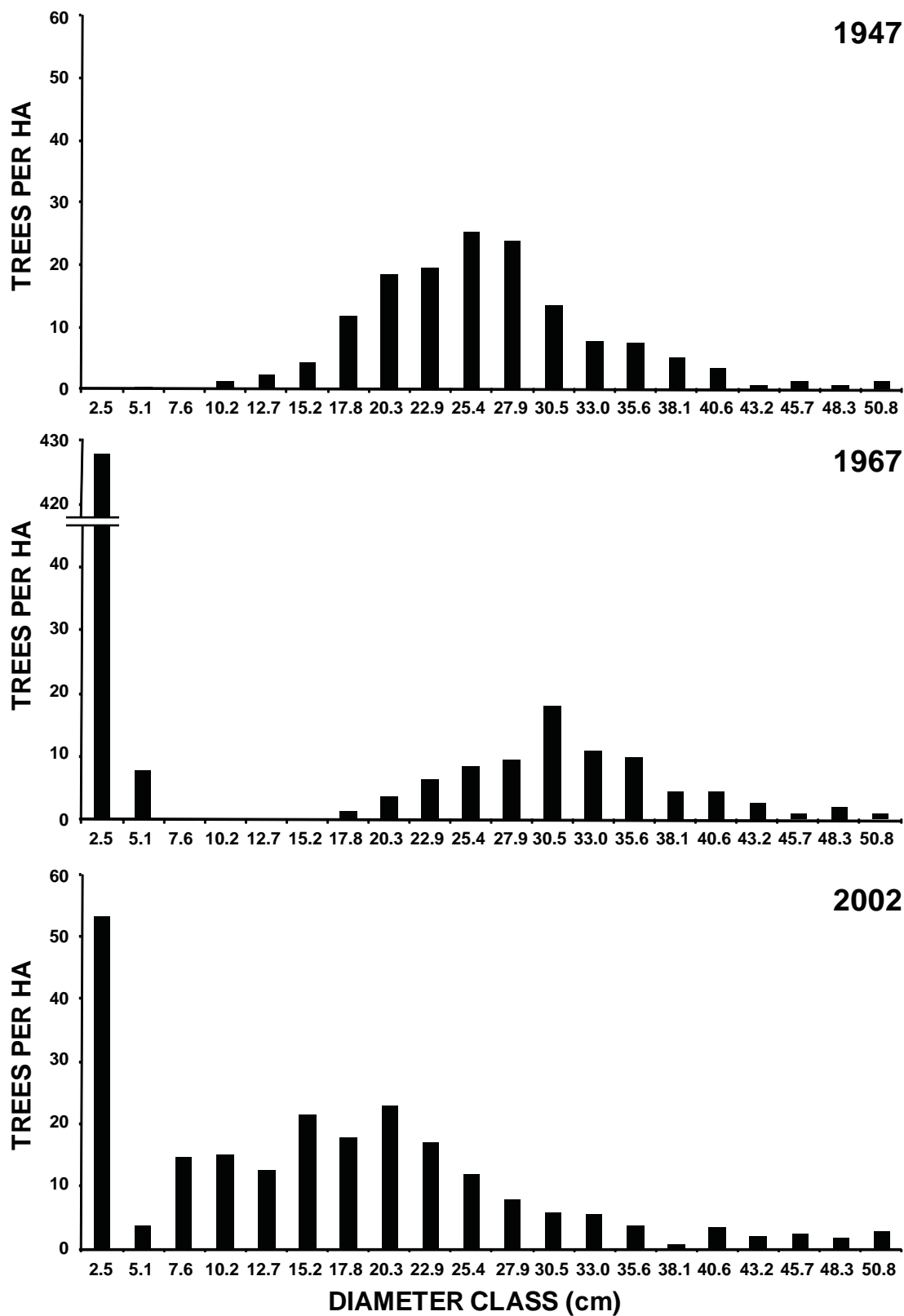
Figure 4.4 (b): Balsam poplar diameter class distributions in 1947, 1967, and 2002 of group C (*n* = 118 stands).

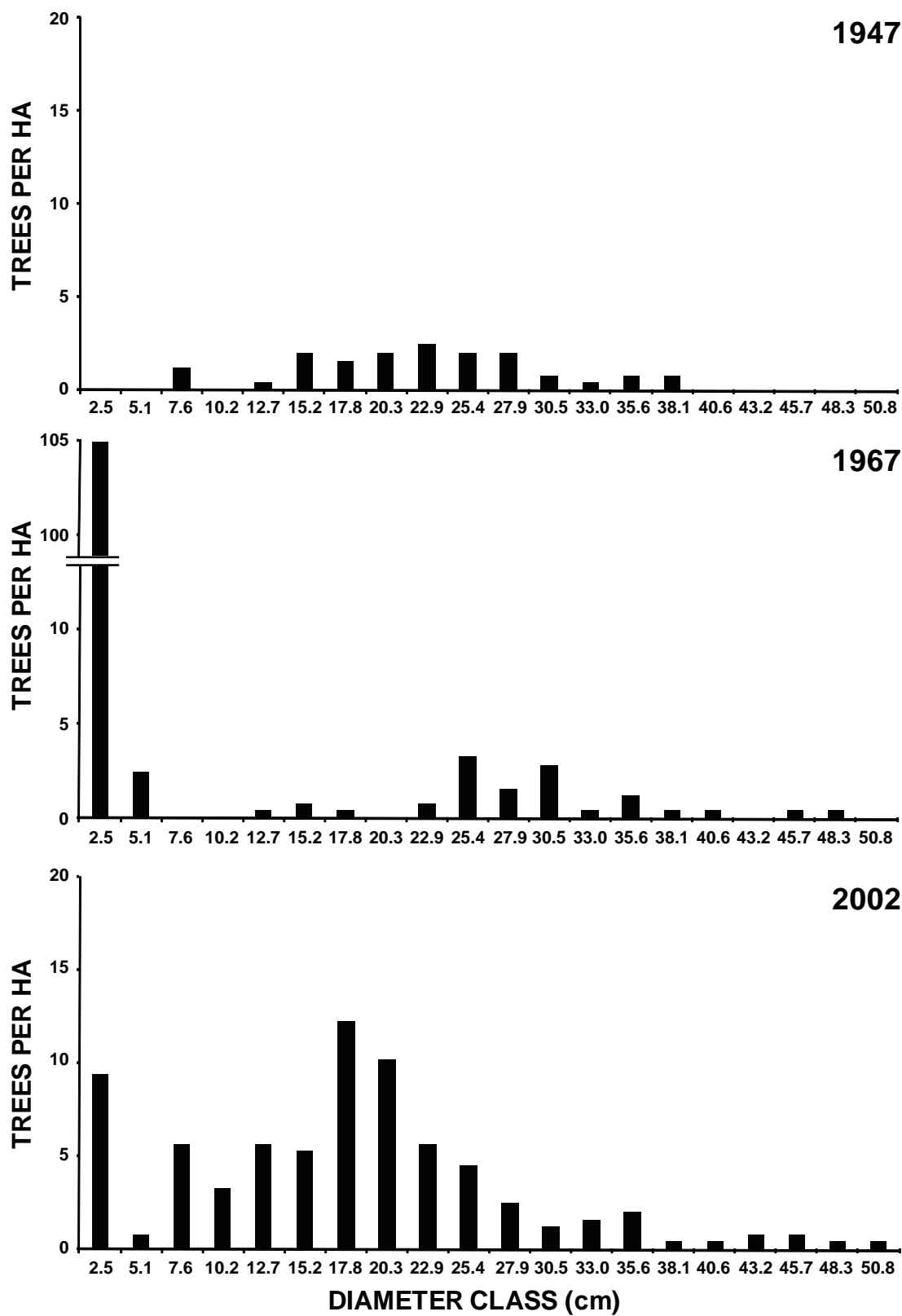**Figure 4.4(c):** White spruce diameter class distributions in 1947, 1967, and 2002 of group C (n = 118 stands).

Figure 4.5 (a): Trembling aspen diameter class distributions in 1947, 1967, and 2002 of group C with an established second cohort in 2002 (*n* = 57 stands).

Figure 4.5 (b): Balsam poplar diameter class distributions in 1947, 1967, and 2002 of group C with an established aspen second cohort in 2002 (*n* = 57 stands).

Figure 4.5 (c): White spruce diameter class distributions in 1947, 1967, and 2002 of group C with an established aspen second cohort in 2002 (*n* = 57 stands).
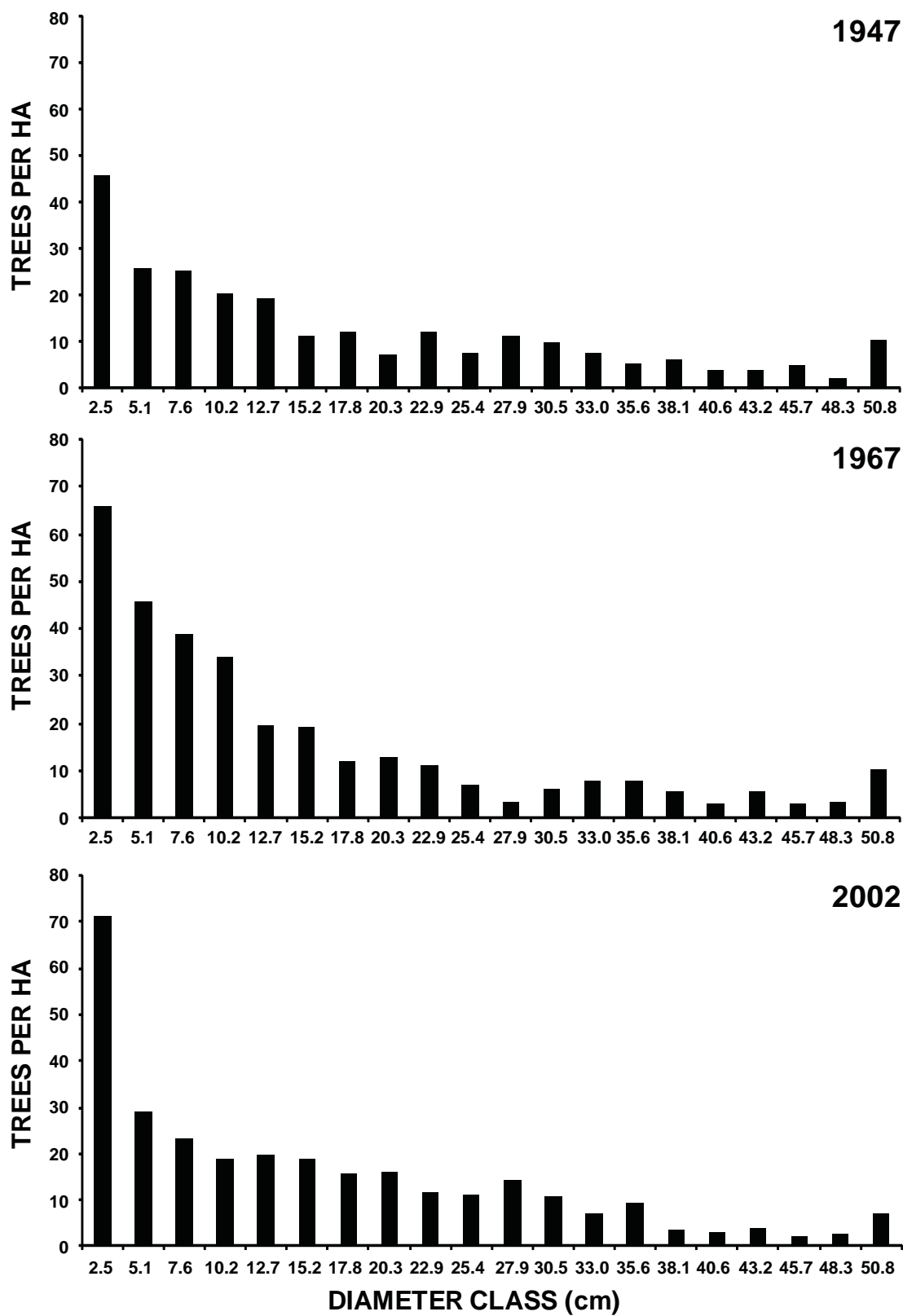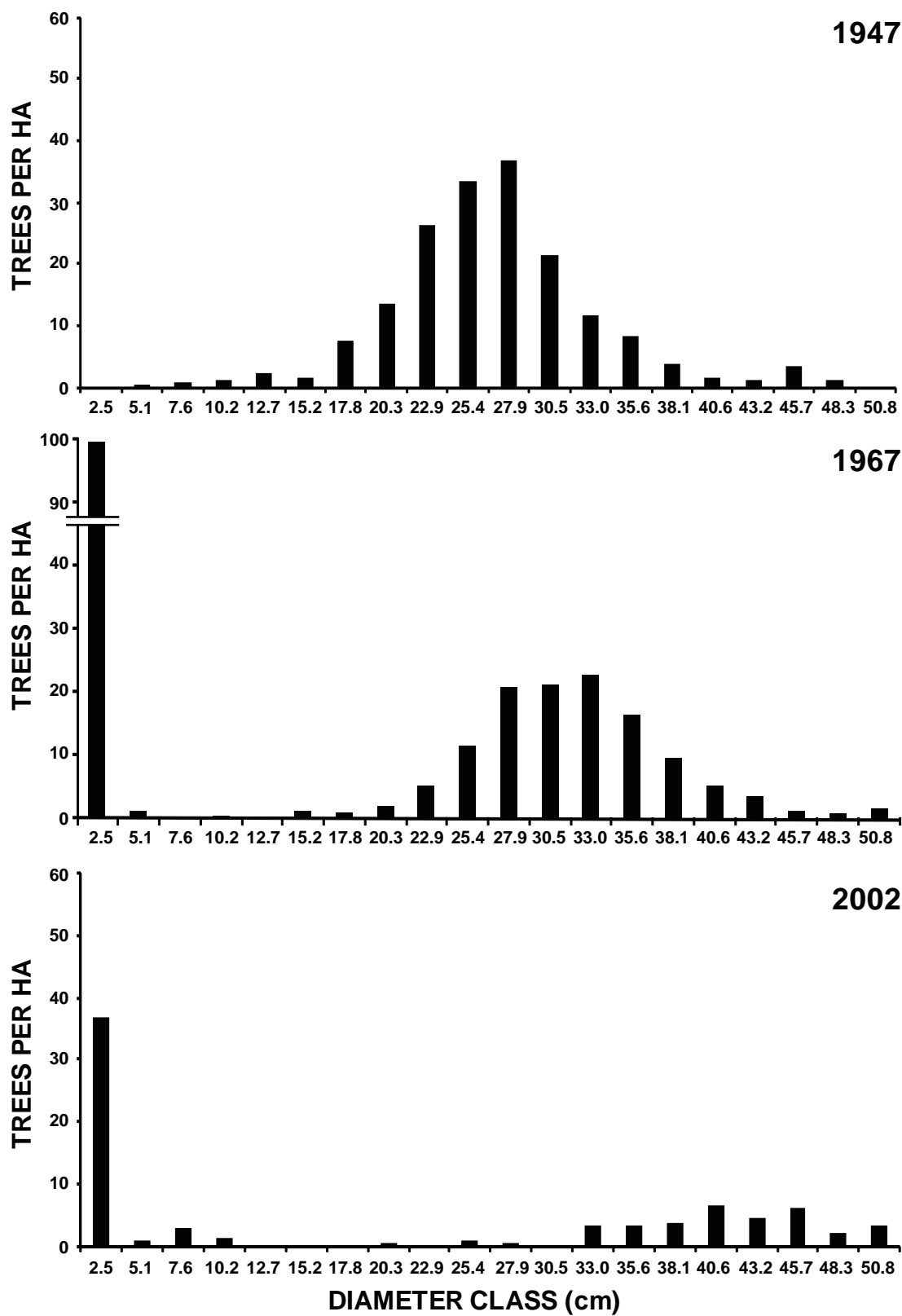
Figure 4.6 (a): Trembling aspen diameter class distributions in 1947, 1967, and 2002 of group C with no established second cohort in 2002 (*n* = 61 stands).
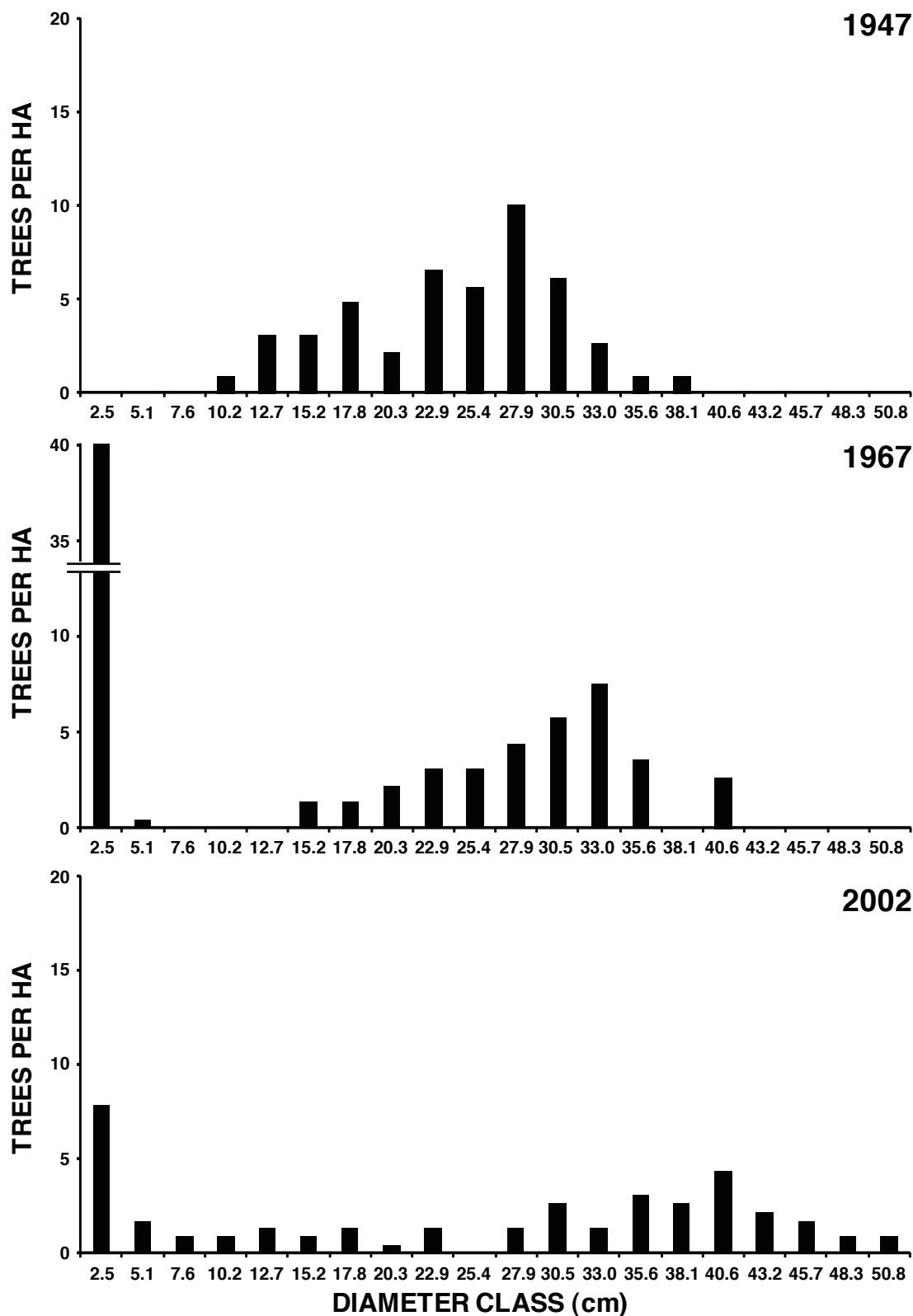
Figure 4.6 (b): Balsam poplar diameter class distributions in 1947, 1967, and 2002 of group C with no established aspen second cohort in 2002 ($n = 61$ stands).
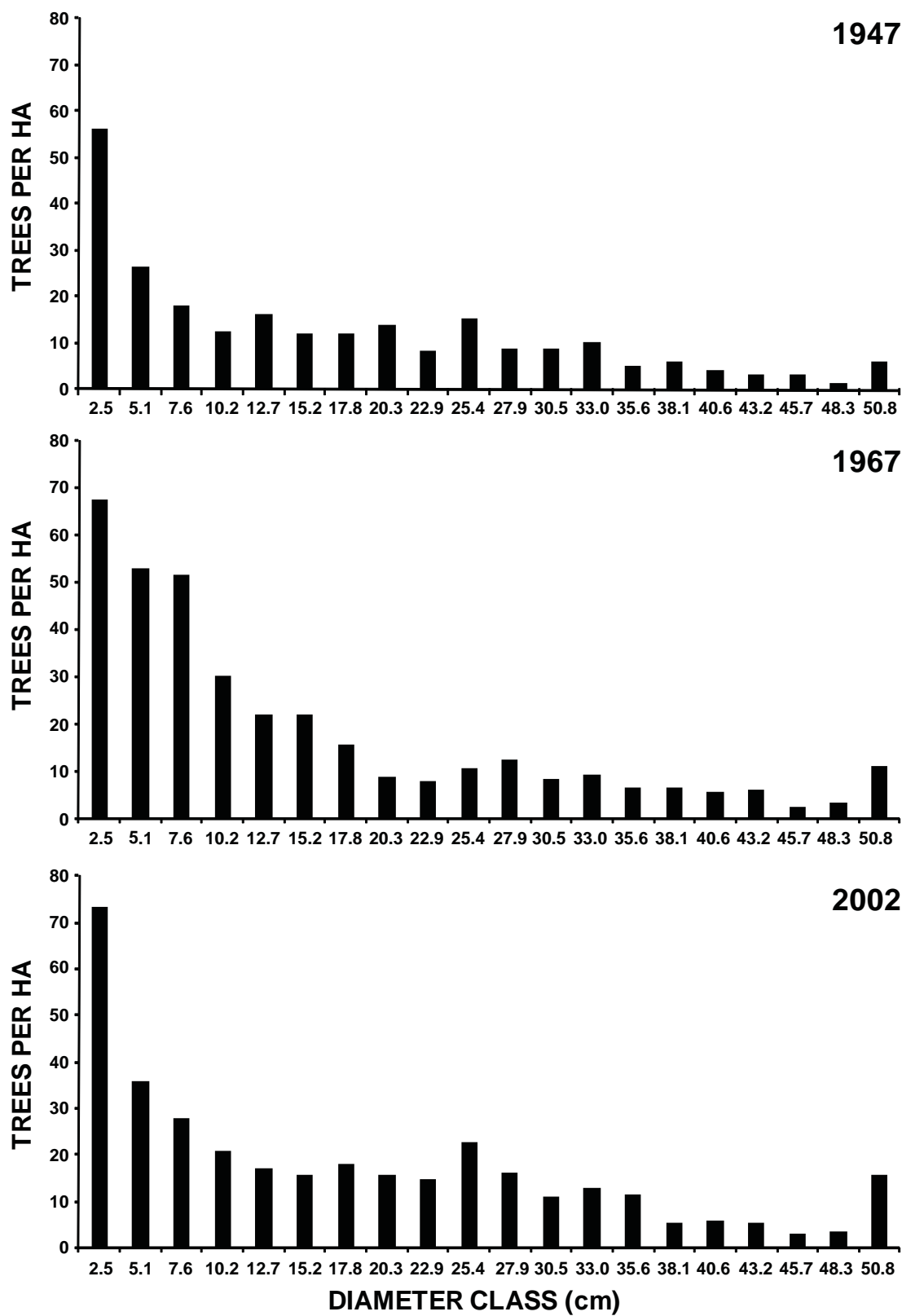
Figure 4.6 (c): White spruce diameter class distributions in 1947, 1967, and 2002 of group C with no established aspen second cohort in 2002 (*n* = 61 stands).

$$\pi(X) = \frac{e^{1.025-0.094\,X}}{1+e^{1.025-0.094\,X}}$$
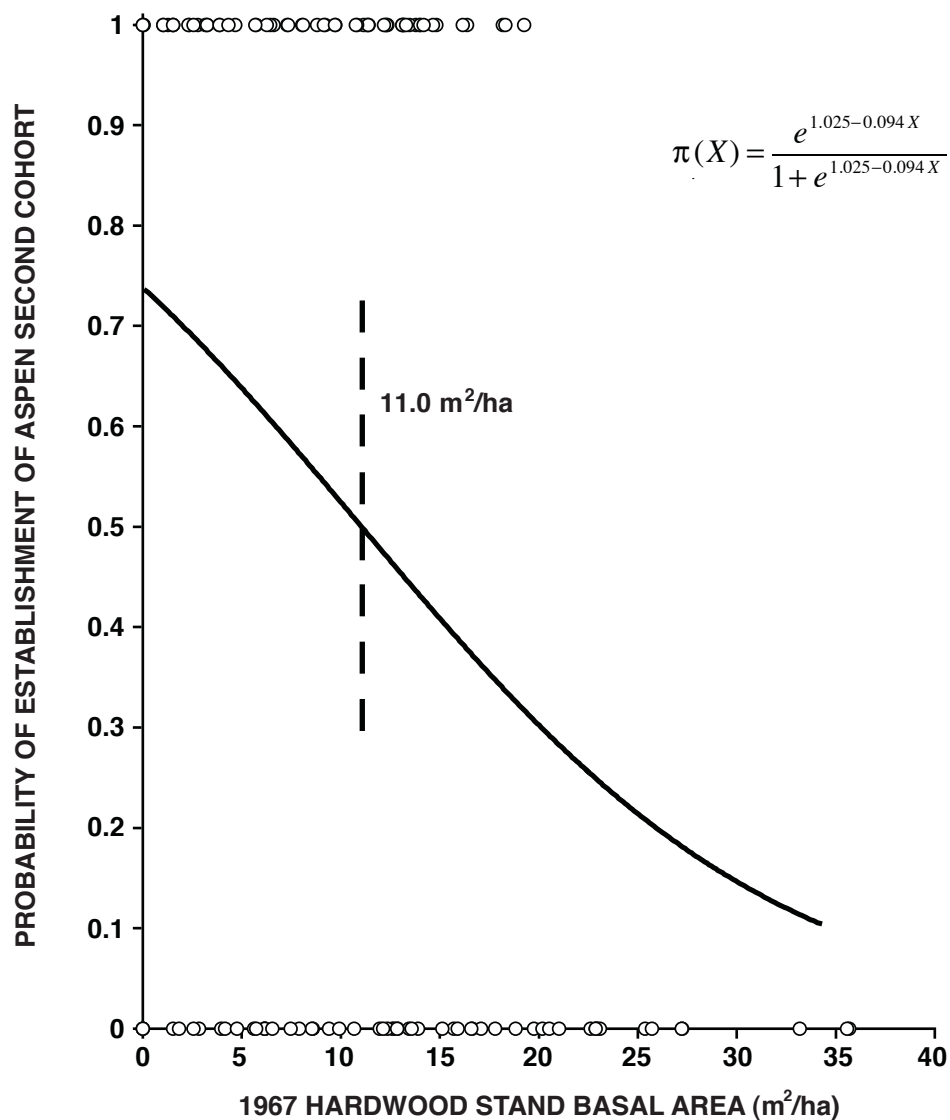
FIGURE 4.7: Logistic regression of the probability that a second trembling aspen cohort successfully establishes in 2002, as a function of hardwood basal area of group C plots in 1967 (Wald statistic (χ^2) = 12.02, $P < 0.001$). The probability of successful establishment declines with increasing stand basal area in 1967, and is less than 0.5 at stand basal area greater than 11.0 m^2/ha.

Table 4.2: Density and basal areas of C subgroups.

	SECOND HARDWOOD COHORT IN 2002							
	PRESENT (n = 57)				ABSENT (n = 61)			
	WS	TA	BP	HW	WS	TA	BP	HW
DENSITY (trees/ha)								
1947	154.5	146.3	15.6	161.9	147.4	176.3	46.9	223.2
1967	172.1	84.0	13.5	97.5	188.2	124.6	34.6	159.2
2002	175.0	154.5	57.8	212.3	216.7	36.8	27.2	64.0
BASAL AREA (m^2/ha)								
1947	10.35	8.42	0.76	9.18	9.04	10.83	2.33	13.16
1967	10.38	7.12	1.00	8.12	11.68	10.40	2.44	12.84
2002	10.19	7.22	2.44	9.66	15.33	4.96	2.67	7.63
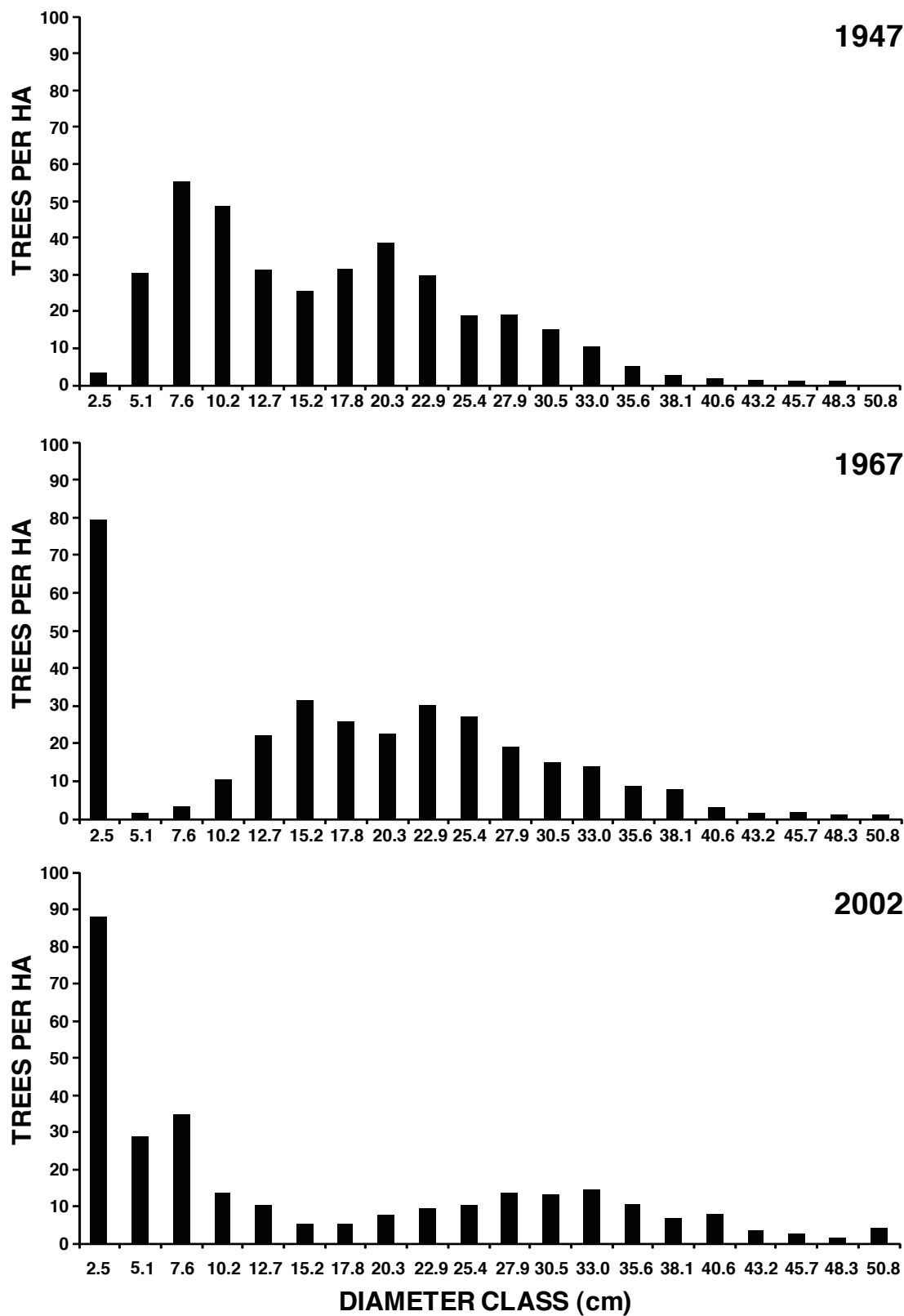
Figure 4.8(a): Trembling aspen diameter class distributions in 1947, 1967, and 2002 for group D (n = 70 stands).
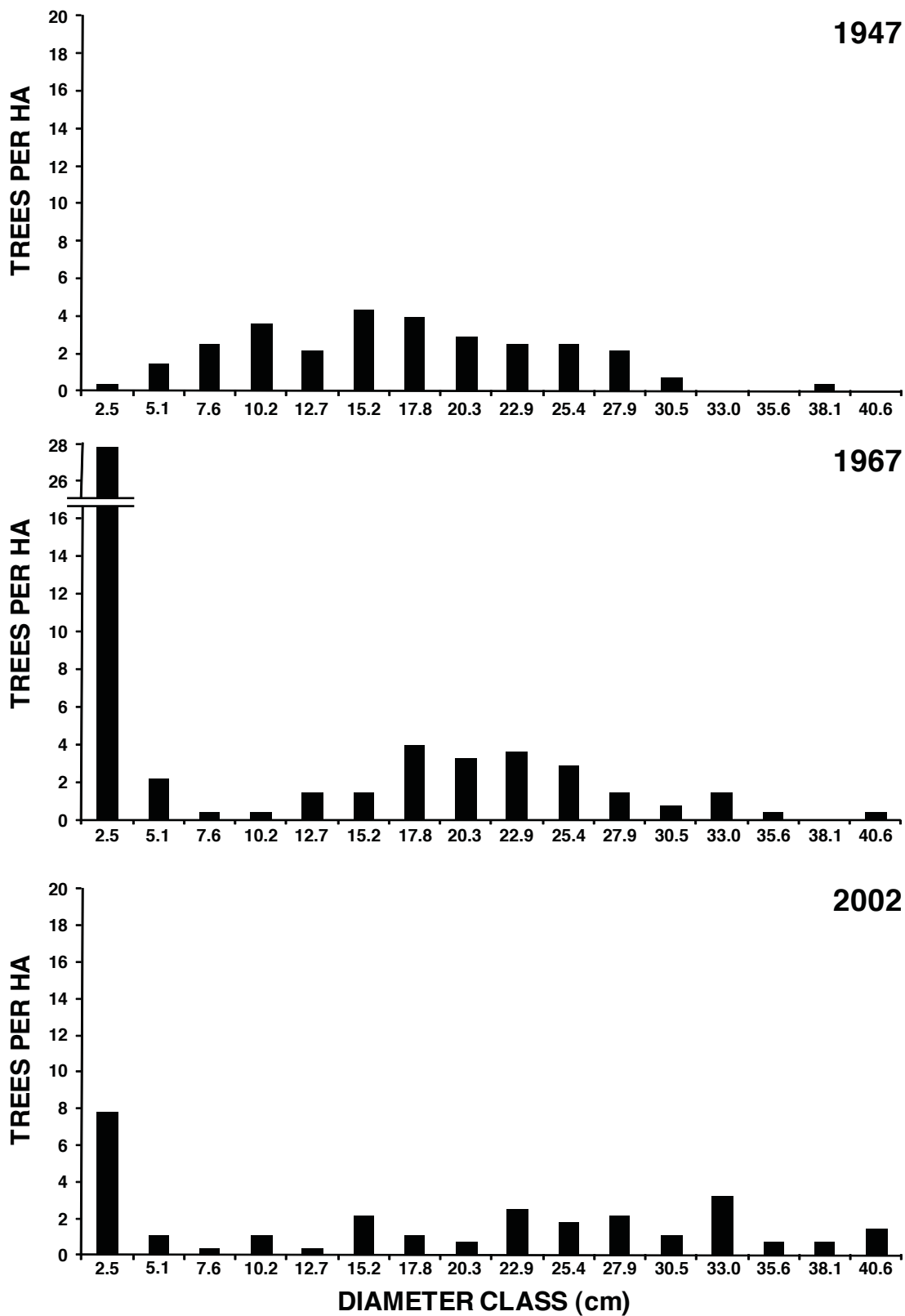
Figure 4.8 (b): Balsam poplar diameter class distributions in 1947, 1967, and 2002 of group D (n = 70 stands).

Figure 4.8 (c): White spruce diameter class distributions in 1947, 1967, and 2002 of group D (n = 70 stands).

Table 4.3: Change of density (trees/ha) over time of trembling aspen, balsam poplar and white spruce in all 266 plots and within the four groups. I = saplings, II = subcanopy, III = canopy, ALL = II + III.

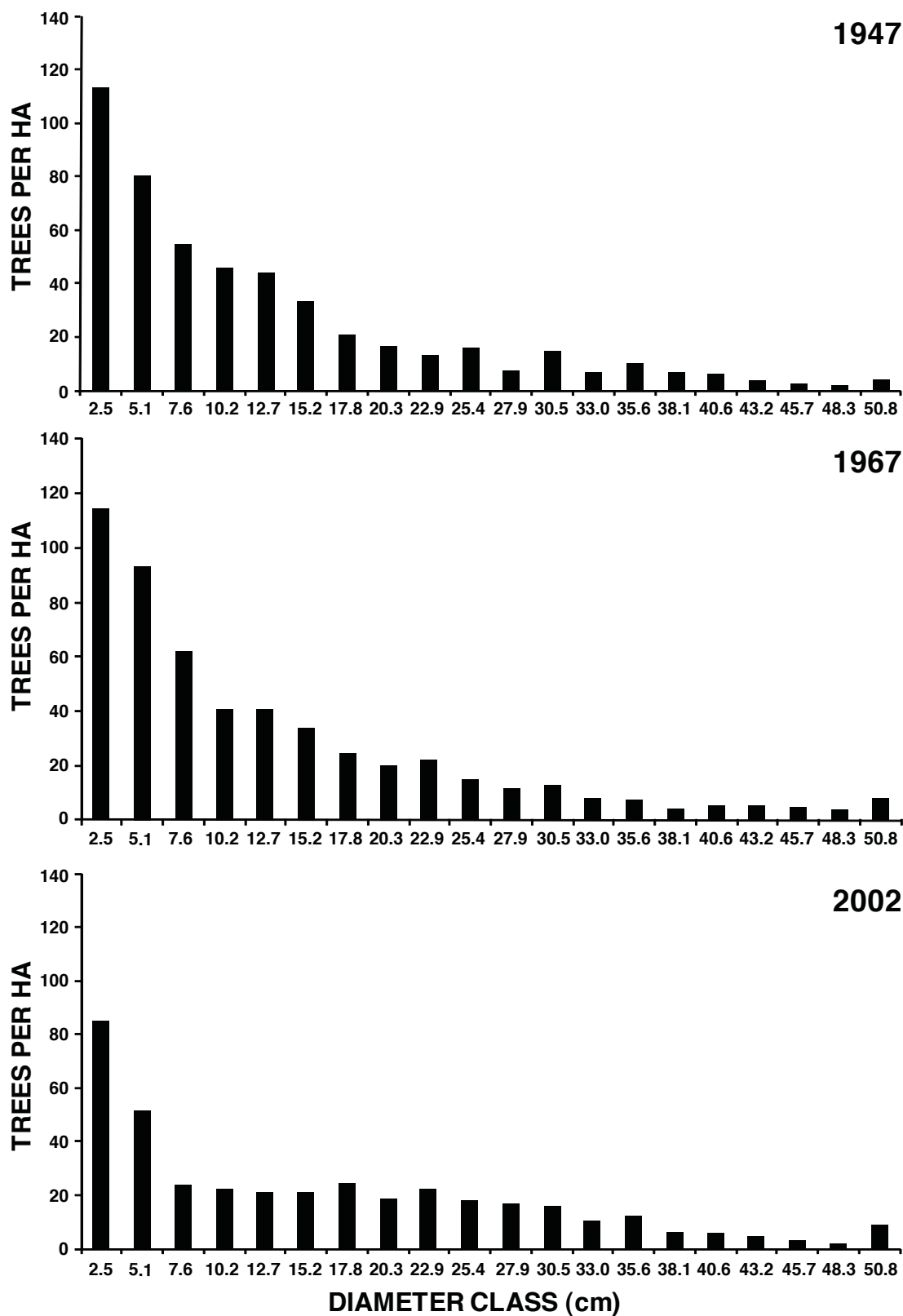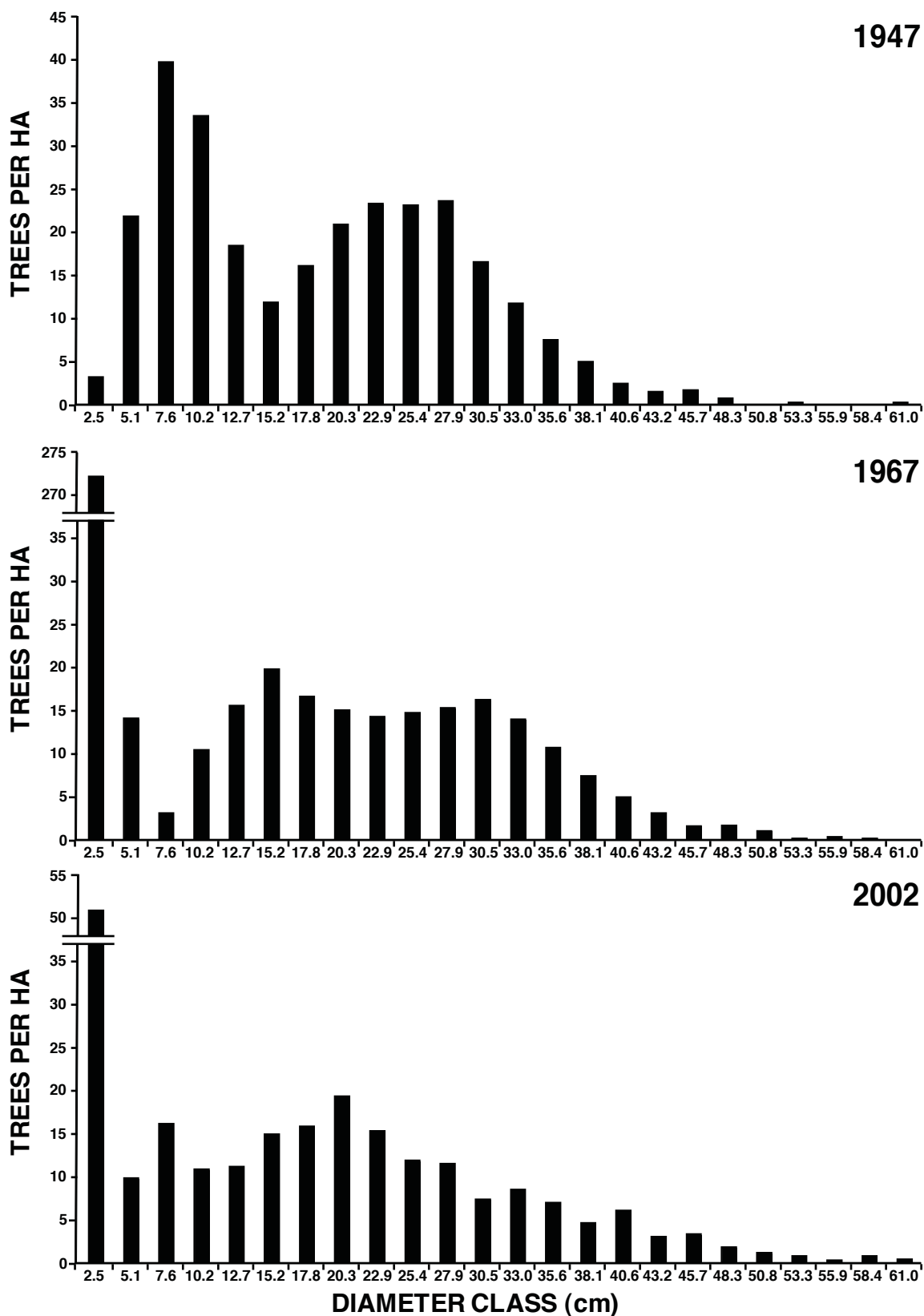|	TREMBLING ASPEN				BALSAM POPLAR				WHITE SPRUCE			
	I	II	III	ALL	I	II	III	ALL	I	II	III	ALL
GROUP A (*n*=43)												
1947	2.3	21.5	126.2	147.7	0.6	22.7	49.4	72.1	87.8	23.8	0.0	23.8
1967	773.3	1.2	86.6	87.8	276.2	6.4	54.7	61.0	143.6	118.0	17.4	135.5
2002	8.7	200.0	72.1	272.1	1.7	70.9	62.8	133.7	45.9	91.9	141.9	233.7
GROUP B (*n*=35)												
1947	302.9	271.4	80.0	351.4	30.0	122.1	22.1	144.3	68.6	26.4	0.0	26.4
1967	160.0	342.9	95.0	437.9	56.4	76.4	40.7	117.1	131.4	90.7	16.4	107.1
2002	80.7	56.4	178.6	235.0	5.7	20.7	68.6	89.3	119.3	80.7	101.4	182.1
GROUP C (*n*=118)												
1947	0.8	32.4	128.4	160.8	0.6	10.0	20.8	30.7	98.7	68.4	82.6	151.1
1967	273.5	4.9	98.7	103.6	75.2	3.2	20.6	23.7	161.0	97.9	81.8	179.7
2002	56.8	47.2	50.4	97.7	13.3	21.4	21.6	43.0	130.3	88.3	106.8	195.1
GROUP D (*n*=70)												
1947	89.3	175.4	104.3	279.6	4.3	16.8	8.2	25.0	248.6	160.4	95.4	255.7
1967	84.3	112.5	130.0	242.5	30.4	10.4	10.7	21.1	270.0	160.0	108.2	268.2
2002	151.1	42.1	97.9	140.0	9.3	5.4	13.6	18.9	160.7	108.2	127.9	236.1
ALL (*n*=266)												
1947	64.1	99.7	115.3	215.0	5.5	28.6	22.3	50.8	132.4	79.9	61.7	141.6
1967	289.6	77.1	104.5	181.6	93.4	15.2	26.1	41.4	183.0	116.5	69.7	186.3
2002	77.0	71.8	83.3	155.1	9.4	25.1	32.3	57.4	123.2	93.1	117.3	210.4

Table 4.4: Change of basal area (m²/ha) over time of trembling aspen, balsam poplar and white spruce in all 266 plots and within the four groups. I = saplings, II = subcanopy, III = canopy.

	TREMBLING ASPEN				BALSAM POPLAR				WHITE SPRUCE			
	I	II	III	ALL	I	II	III	ALL	I	II	III	ALL
GROUP A (*n* = 43)												
1947	0.01	0.56	9.40	9.97	0.00	0.56	3.48	4.04	0.14	0.38	0.00	0.52
1967	0.50	0.01	8.55	9.06	0.21	0.18	4.57	4.97	0.33	1.95	0.96	3.24
2002	0.03	4.47	4.57	9.07	0.01	1.58	5.73	7.32	0.07	1.89	11.43	13.39
GROUP B (*n* = 35)												
1947	1.06	3.35	5.76	10.17	0.12	1.79	1.56	3.47	0.11	0.43	0.00	0.55
1967	0.15	6.57	7.02	13.74	0.04	1.72	2.67	4.43	0.24	1.42	0.85	2.51
2002	0.11	1.33	14.67	16.11	0.01	0.48	4.96	5.46	0.19	1.68	7.32	9.19
GROUP C (*n* =118)												
1947	0.00	0.86	8.72	9.58	0.00	0.22	1.29	1.52	0.18	1.21	8.33	9.72
1967	0.15	0.14	8.42	8.70	0.04	0.08	1.58	1.70	0.34	1.59	9.09	11.01
2002	0.07	0.97	5.09	6.13	0.02	0.47	2.05	2.55	0.22	1.64	10.81	12.67
GROUP D (*n* = 70)												
1947	0.32	3.29	6.62	10.22	0.01	0.32	0.45	0.79	0.47	2.59	8.56	11.62
1967	0.06	2.31	9.11	11.48	0.02	0.25	0.64	0.90	0.53	2.73	10.06	13.32
2002	0.26	0.72	9.00	9.98	0.01	0.10	1.04	1.15	0.26	2.05	11.91	14.22
ALL (*n* = 266)												
1947	0.23	1.78	7.89	9.89	0.02	0.51	1.46	1.99	0.24	1.33	5.96	7.52
1967	0.18	1.54	8.44	10.16	0.06	0.36	1.96	2.38	0.37	1.92	6.95	9.24
2002	0.12	1.52	7.29	8.93	0.01	0.56	2.76	3.33	0.20	1.80	10.74	12.74

Figure 4.9(a): Trembling aspen diameter class distributions in 1947, 1967, and 2002 of all groups (*n* = 266 stands).
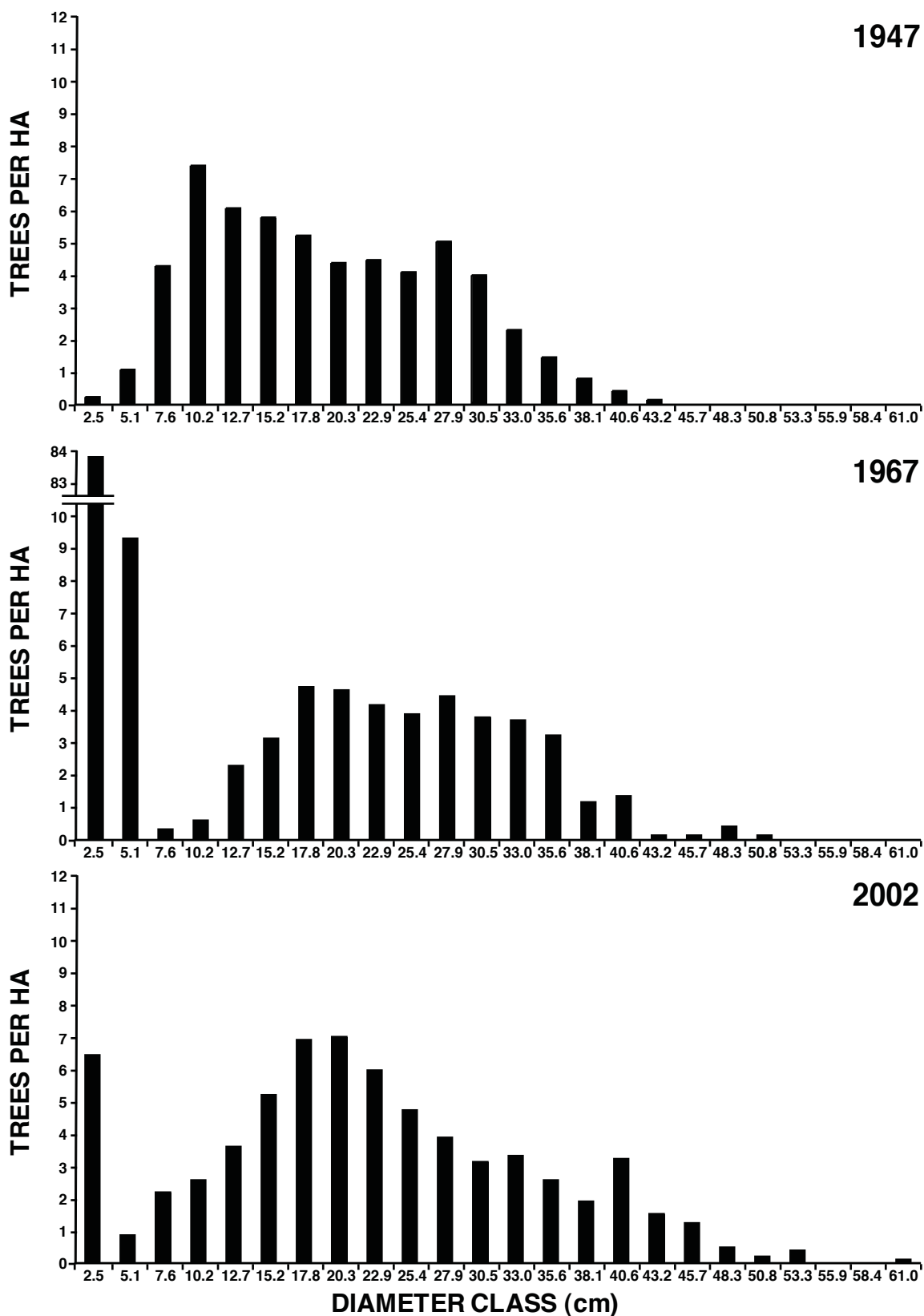
Figure 4.9(b): Balsam poplar diameter class distributions in 1947, 1967, and 2002 of all groups (n = 266 stands).

1947

1967

2002
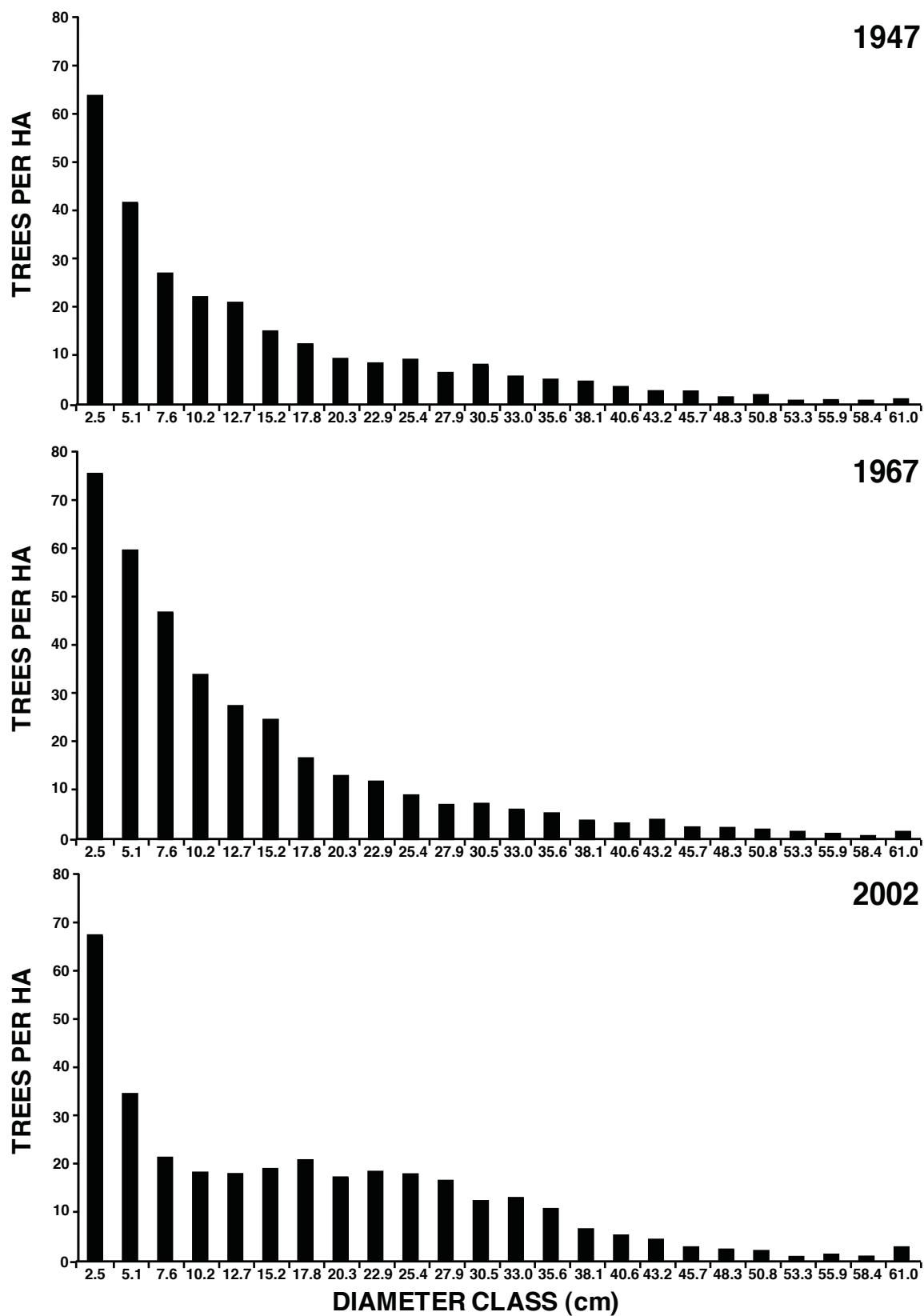
DIAMETER CLASS (cm)

Figure 4.9(c): White spruce diameter class distributions in 1947, 1967, and 2002 of all groups (n = 266 stands).
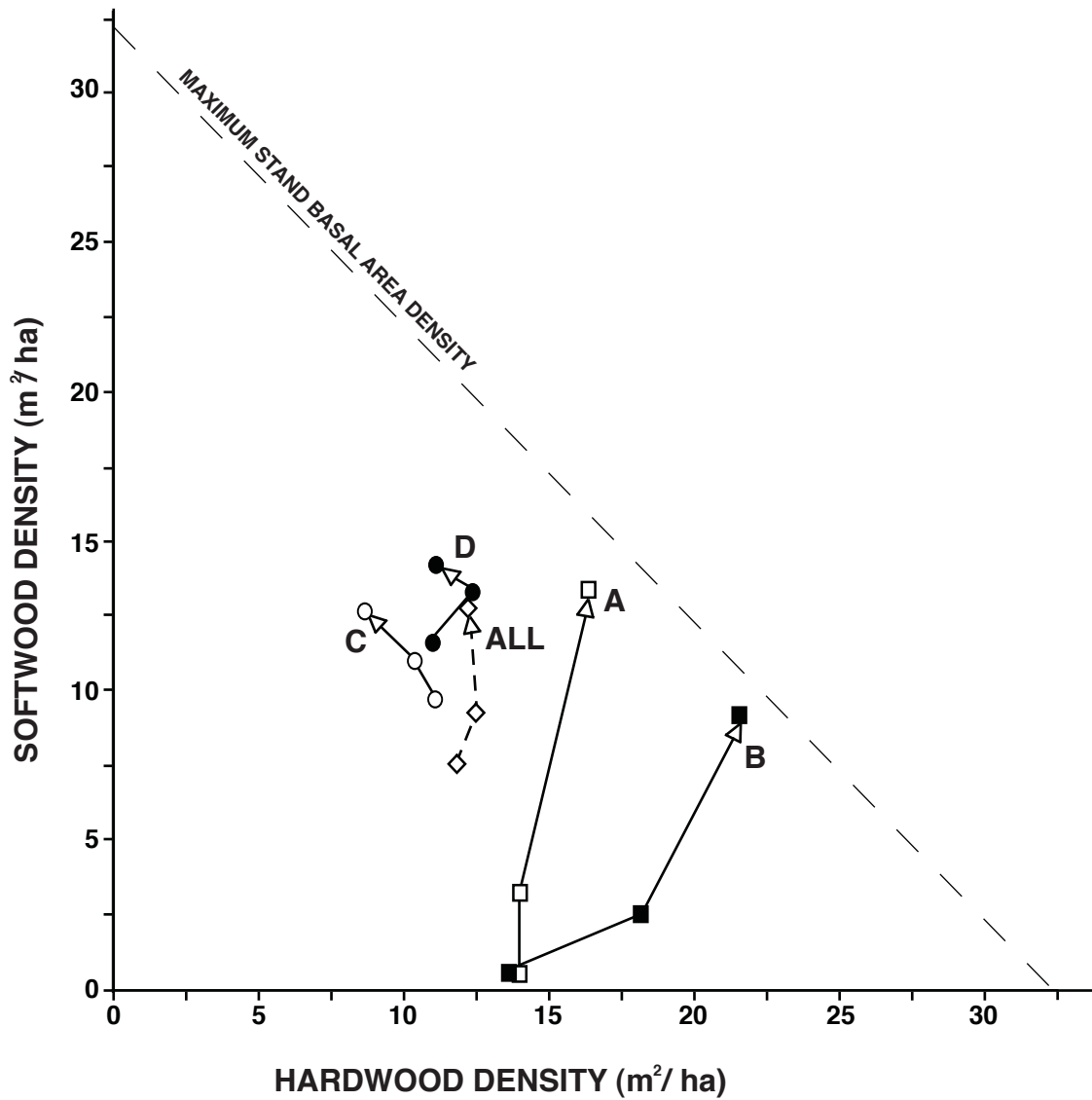
FIGURE 4.10: Basal area trajectories of hardwood and softwood species over time at a localized scale (A, B, C, D) and a landscape scale (ALL). Dotted line reperesents maximum stand basal area density of 34.6 m^2/ha (Comeau 2002).

CHAPTER 5

SUMMARY AND CONCLUSIONS

Life history characteristics are critical to our understanding of the long-term species persistence and coexistence (Bond and Midgley 2001). An understanding of the long-term persistence of species allows us to forecast how communities will change through time (Huston and Smith 1987; Grime 2002), which in turn allows us to predict the development of a community (Keddy 1992; Lavorel and Garnier 2002). Succession theory, which is historically rooted in a deterministic view wherein communities develop toward a specific endpoint or "climax" (Johnson 1979), is unable to incorporate the many exceptions and anomalies that inevitably arise in empirical studies of long-term forest dynamics (e.g. Bergeron 2000). In this thesis, I have used long-term direct observational data to demonstrate unequivocally that the long-term dynamics of the boreal mixed-wood stands in western Canada do not follow the long-assumed trajectory from hardwood to softwood dominance (**Figure 1.1a**). Instead, my results clearly demonstrate that hardwoods (trembling aspen and balsam poplar) and softwoods (white spruce) co-exist and persist on the landscape for at least 175 years, and probably much longer (**Figure 1.1b**).

Post-disturbance mixed-wood forest stands show either contemporaneous (within 5 – 10 years) or delayed (for 50 – 80 years) white spruce recruitment (Peters *et al.* 2005). As the initial cohort grows and stands develop (stand ages < 120 years), a dichotomy in forest composition and structure develops. Stands with delayed white spruce recruitment have a canopy dominated by hardwoods, with small and suppressed white spruce in the sub-canopy and sapling layers recruited at about 50 to 80 years post-disturbance (Groups A & B in this study).

Conversely, contemporaneous white spruce recruitment results in a forest canopy containing both hardwoods and softwoods, often with softwoods in the sub-canopy and sapling layers that have recruited over an extended period (Groups C & D in this study).

Mixed-wood forest stand development and structure is also affected by fire severity, which strongly affects the initial tree densities of post-fire communities (Johnstone *et al*. 2010). Initial post-fire tree growth and stand development (stand ages < 120 years) creates a second structural dichotomy. Dense hardwood stands at initiation undergo an extended period of self-thinning during which only the largest individuals survive, which by 80 – 100 years results in homogeneous stands of large, similar-sized canopy trees (Groups A & C in this study). Conversely, less dense hardwood stands at initiation develop a more heterogeneous canopy (often with early secondary recruitment) consisting of variable-sized canopy and sub-canopy trees (Groups B & D in this study).

These two dichotomies result in the recognition of four distinct physiognomic (compositional-structural) groups in the 120 year old boreal mixed-wood stands examined in this study. Following the development of each of these four stand groups in "real time", from 120 to 175 years in age, revealed that hypothesized temporal trajectories of shifting dominance from hardwoods to softwoods are not confirmed. The overall stand development for each of the four physiognomic groups is summarized below.

5.1 GROUP A

Immediately following catastrophic fire disturbance, the hardwoods in these stands regenerate at very high densities from root suckers, excluding all other tree species (**Figure 5.1**). As these stands age, the fastest-growing individuals

inhibit the growth of neighbouring ramets. Strong density-dependent mortality (self-thinning) ensues, in which only the largest individuals survive. As these stands mature, tree growth slows and there is an eventual shift from density dependent to density independent mortality. At this stage the canopy begins to break apart. As individual canopy trees die, canopy gaps are created and light begins to reach the forest floor. The suppressed sub-canopy and sapling white spruce benefit from this increased light, and begin to grow rapidly as they are undergoing a competitive "release" and soon reach the canopy.

  Continued die-off of the hardwood canopy results in the loss of apical dominance, which together with increased light levels promotes the prolific production of vegetative root suckers by about 130 – 140 years stand age. These root suckers grow rapidly to form a second hardwood cohort that by 175 years stand age has successfully recruited into the upper sub-canopy and canopy layers. As a result, by stand age 175 years these stands consist of a near-even mixture of hardwoods and softwoods in both the canopy and sub-canopy layers.

5.2 GROUP B

Immediately following catastrophic fire disturbance, the hardwoods in these stands regenerate at relatively low densities from root suckers (**Figure 5.2**). Lower root sucker density may be the result of very intense fires (Johnstone *et al.* 2010), or may simply reflect natural genetic variation in genets or other biotic factors (Stevens 1998, Hazell *et al.* 1998). Density-dependent mortality (self-thinning) is less intense in these stands, resulting in a heterogeneous canopy of large and smaller individuals. Lower stand density also results in the development of an earlier second hardwood cohort in these stands. This cohort is recruited at about 80 – 100 years post-fire, so that at age 120 years these stands are structurally heterogeneous: they contain a mixture of initial cohort hardwoods

(120 years of age) and much smaller second cohort individuals (20 – 40 years of age).

White spruce recruitment into these stands is delayed by 60 – 100 years; this most likely reflects the lack of a proximate seed source (Greene and Johnson 2000). These trees remain suppressed for an extended period, due to the relatively high hardwood canopy density throughout stand development. As a result, by stand age 175 years these stands remain dominated by hardwoods, although some white spruce have reached the canopy and continuous white spruce recruitment is occurring.

5.3 GROUP C

A proximate white spruce was present in these stands, resulting in contemporaneous softwood recruitment (i.e. within the first 5 – 10 years of stand initiation). As in group A, the hardwoods in these stands regenerate at very high densities from root suckers immediately following catastrophic fire disturbance (**Figure 5.3**). Within a few years the fast-growing hardwoods (established from root suckers, not seeds) overtop the established white spruce saplings, suppressing their growth for many years (Peters *et al.* 2002). As these stands age, the hardwoods undergo strong density-dependent mortality (self-thinning), and only the largest individuals survive. As the hardwood canopy trees mature, their growth slows and density independent canopy mortality ensues. At this stage the canopy begins to "break apart" as individual canopy trees die. Canopy gaps are thus created, increasing the amount of light reaching the forest floor. The suppressed sub-canopy and sapling white spruce benefit from this increased light, and begin to grow rapidly as they undergo a competitive "release" (Gutsell and Johnson 2002). As a result, by 120 years of age the canopy of these stands consists of both hardwoods and softwoods.

In these stands, successful development of a second hardwood cohort is dependent on the extent and rapidity of break-up of the initial hardwood canopy cohort (i.e. canopy hardwood basal area). If hardwood canopy break-up is rapid, loss of apical dominance combined with increased light levels ensures the successful recruitment of a second hardwood cohort through root suckering. Under this scenario, hardwood persistence is ensured and by age 175 years these stands contain both hardwoods and softwoods in the canopy and sub-canopy layers. Conversely, a more benign break-up of the hardwood canopy results in lower root sucker production, and a low-light environment that greatly reduces root sucker survivorship. Under this scenario, hardwoods fail to produce a second cohort, and by age 175 years these stands contain softwoods in the canopy and sub-canopy, and a few old, initial cohort hardwoods in the upper canopy. Balsam poplar may successfully regenerate to a limited extent in these stands, but light levels are generally insufficient to ensure the perpetuation of trembling aspen.

5.4 GROUP D

Immediately following catastrophic fire disturbance, the hardwoods in these stands regenerated at relatively low densities from root suckers (**Figure 5.4**). In addition, a proximate white spruce was present in these stands, resulting in contemporaneous softwood recruitment (i.e. within the first 5 – 10 years of stand initiation). Less intense density-dependent mortality (self-thinning) of hardwoods results in a heterogeneous canopy containing large and smaller individuals. Lower hardwood stand density also results in the development of an earlier second hardwood cohort. This cohort is recruited at about 80 – 100 years post-fire, so that by age 120 years these stands are structurally heterogeneous: they contain a mixture of initial cohort hardwoods (120 years of age) and much smaller second cohort individuals (20 – 40 years of age). Contemporaneous white spruce recruitment results in the co-occurrence of hardwoods and

softwoods in the canopy by a stand age of 120 years. The composition and structure of these stands remained remarkably similar over time, with relatively few changes in the abundance and basal area of trembling aspen, balsam poplar and white spruce over the 55-year study period. Canopy gaps are created through senescence of both hardwoods and softwoods, but there is little evidence for the competitive replacement of hardwoods by softwoods in these stands.

5.5 CLOSING THOUGHTS

The results of this study clearly indicate that the boreal mixed-wood forest succession trends of softwood dominance proposed for Québec by Bergeron (2000) are not tenable in western Canada. This most likely reflects differences in environmental conditions, the frequency and types of natural disturbances, and floristic variation (e.g. the dominance of balsam fir in eastern Canada, versus its relative rarity in western Canada).

Both the direct regeneration and intermediate disturbance hypotheses acknowledge the importance of disturbance in modeling forest stand dynamics. Together these hypotheses predict the occurrence of multiple succession pathways that almost invariably converge on a forest dominated by shade-tolerant conifers (Taylor and Chen 2011). My results demonstrate that a deterministic succession trajectory of this type does not occur in western Canada. Multiple pathways may occur, but they do not converge on a single endpoint or "climax". Instead, the western boreal mixed-wood forest can be viewed as a continuum in species composition wherein small-scale disturbances create canopy gaps (vacant spaces) that may be filled by either hardwoods or softwoods. Gap recruitment is stochastic, and softwood and hardwood species will fill occurring gaps using fundamentally different recruitment strategies. White spruce recruitment employs a "sit and wait" strategy (i.e. saplings tolerant of low

light conditions), whereas hardwoods are "opportunistic", recruiting from vegetative root suckers that are initiated in response to increased light levels. When this life history trait of hardwoods is acknowledged as an important adaptation promoting long-term persistence, our understanding of long-term boreal stand dynamics is greatly increased (Baret and DesRochers 2011).

My results offer support for the recognition of species life history traits, particularly vegetative reproduction in hardwoods (trembling aspen and balsam poplar) as being of great importance to our understanding of the long-term dynamics of boreal mixed-wood forests. Others have speculated that hardwoods might conceivably persist in boreal stands for much longer than previously thought (Cumming *et al.* 2000), this study provides the first unequivocal evidence in support of the long-term persistence of boreal hardwoods through the successful recruitment of a second cohort of root suckers. These findings represent a paradigm shift in our understanding of the ecology and management of boreal mixed-wood forests in western Canada.
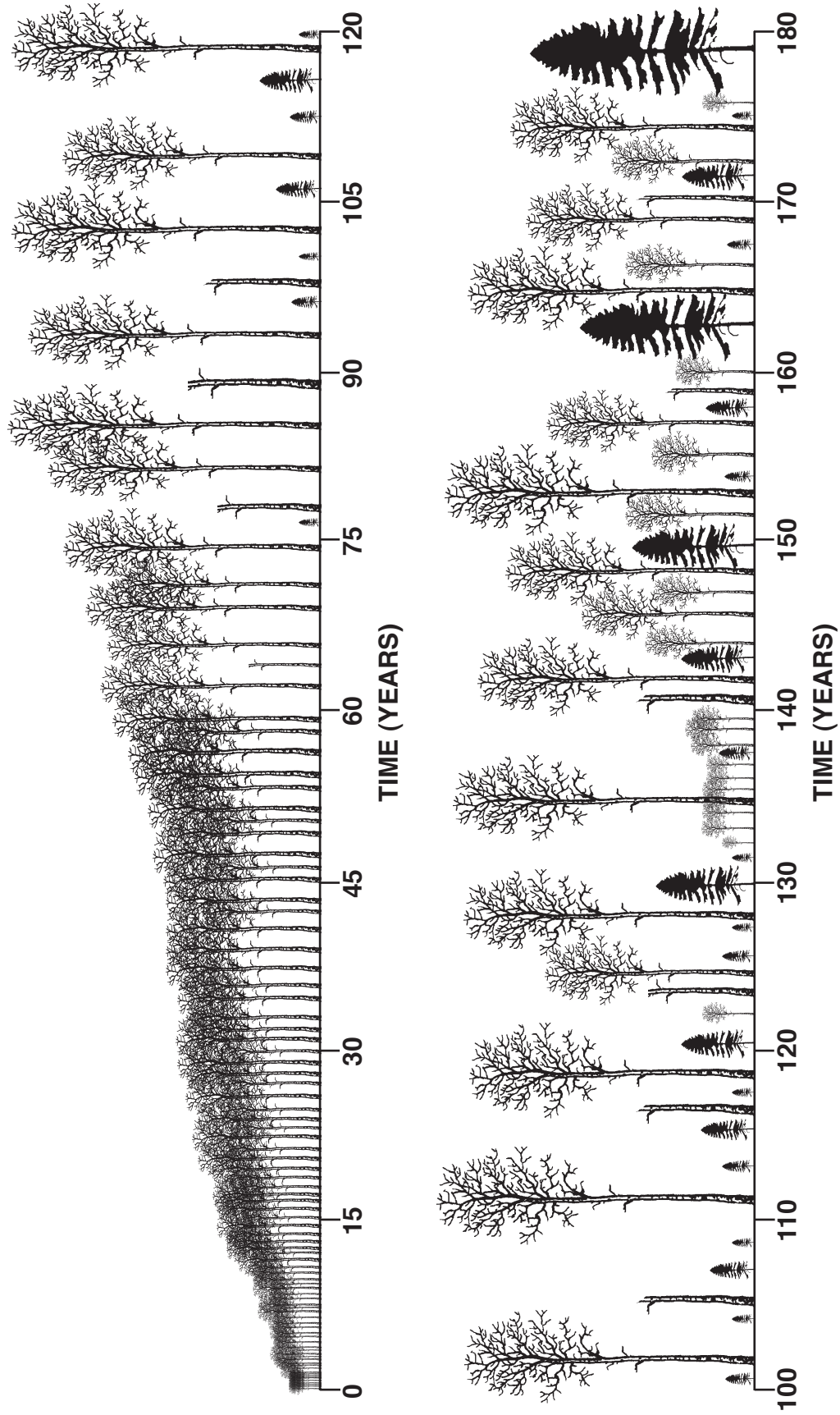
Figure 5.1: The typical stand dynamics of group A from 0 - 120 years (top) and 100 - 180 years (bottom). The bottom diagram is proportional to the average stand density and basal area of group A. Note tree heights are scaled to 1cm:6m
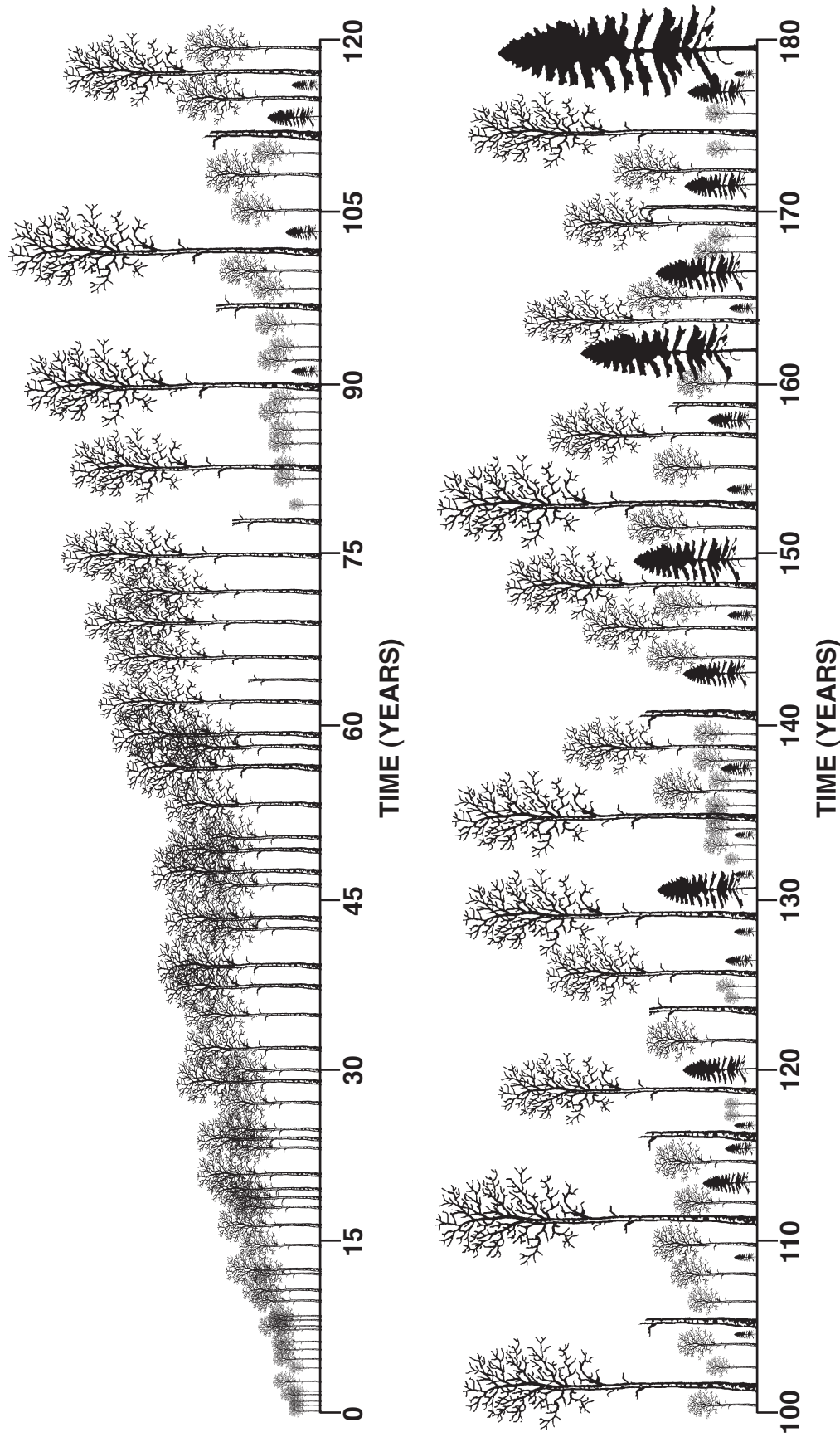
Figure 5.2: The typical stand dynamics of group B from 0 - 120 years (top) and 100 - 180 years (bottom). The bottom diagram is proportional to the average stand density and basal area of group B. Note tree heights are scaled to 1cm:6m

Figure 5.3: The typical stand dynamics of group C from 0 - 120 years (top) and 100 - 180 years (bottom). The bottom diagram is proportional to the average stand density and basal area of group C. Note tree heights are scaled to 1cm:6m
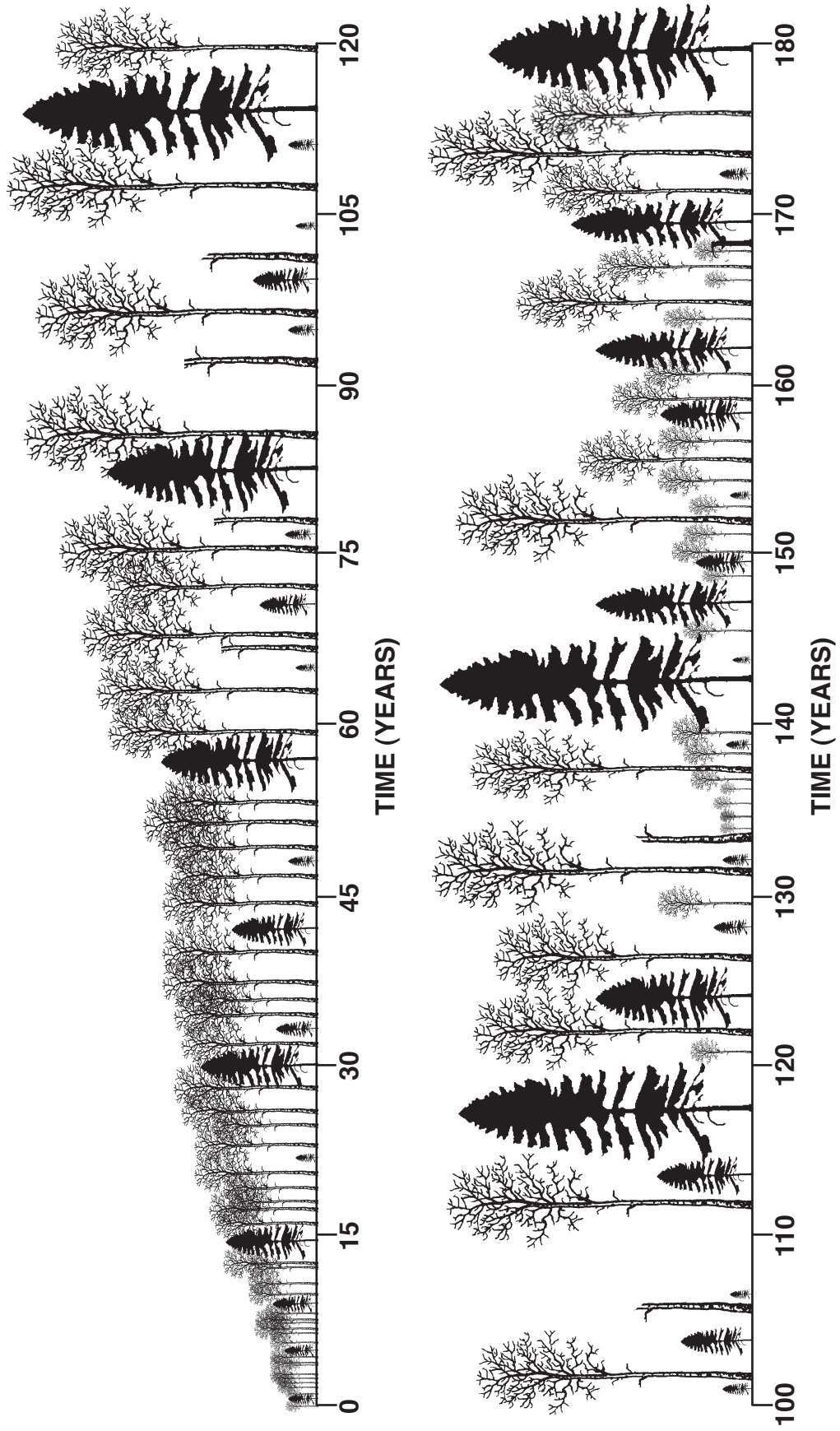
Figure 5.4: The typical stand dynamics of group D from 0 - 120 years (top) and 100 - 180 years (bottom). The bottom diagram is proportional to the average stand density and basal area of group D. Note tree heights are scaled to 1cm:6m
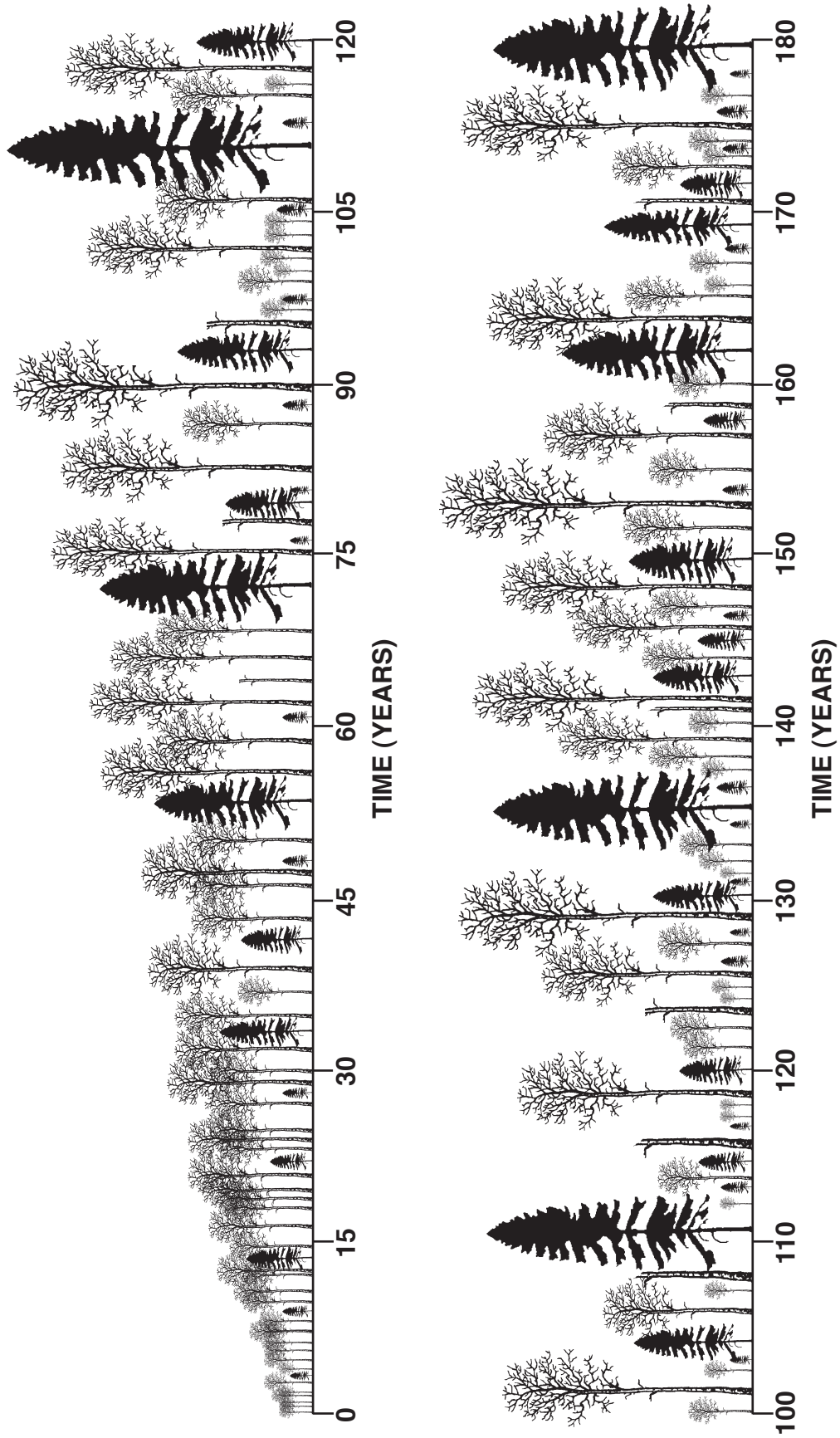
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