MODELLING LANDSCAPE LEVEL VEGETATION DYNAMICS IN THE BOREAL FORESTS OF NORTHWESTERN ONTARIO

BY

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A Thesis
Submitted to the Faculty of Graduates Studies
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. . . As is he who dreaming sees, and after the dreams the passion remains imprinted, and the rest returns not to the mind, such am I;

for my vision almost wholly fails, while the sweetness that was born of it yet distils within my heart.

Thus the snow is by the sun unsealed; thus on the wind, in the light leaves, was lost the saying of the Sibyl.

FROM Dante: The Divine Comedy: Paradise, ca 1318 AD

Translated by Charles Eliot Norton

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ABSTRACT

Studies of succession in the boreal forest have improved our understanding of the role of disturbance in vegetation dynamics. However, the influence of edaphic variables on landscape-level succession has received less attention. Successional trends in the boreal forest have been inferred using two approaches: (i) analysis of size and/or age class distributions of trees, and species vital attributes; (ii) enumeration of stands at different ages. The first approach assumes that mortality, natality and growth rates, and life-history strategies, are similar between species. The second approach is restricted to self-regenerating, monodominant forests and assumes that the reconstructed successional trends are not confounded by intersite environmental variation. The objective of this study was to develop a succession (vegetation dynamics) model for the boreal forests of northwest Ontario using these two approaches.

The data used in this study were collected between 1983 and 1988 as part of the North Western Ontario Forest Ecosystem Classification (FEC) project. A total of 1389 plots enumerated within the ca. 184,000 km^2 study area were retained for further analysis. Percent cover estimates were obtained for all vascular plants and terricolous cryptogams species within 10x10 m plots. Tree and shrub cover were separately enumerated in four height-based vegetation strata. In addition, extensive edaphic data were collected within each plot. An analysis was undertaken to ascertain vegetation-environment relationships and soil variable redundancy. In addition, a synoptic stand dynamic model for the boreal forests of northwestern Ontario was developed. The analysis proceeded in four steps: (i) stands ≤ 85 years old were classified into one of twelve discrete vegetation 'stand-types' using cluster analysis; (ii) stands ≥ 85 yr. were assigned to one of the twelve stand-types using a discriminant function classifier, based on vegetation and soil variables; (iii) successional trajectories, including moisture status and surficial-topographic variants, were summarized for each of the twelve stand-types; (iv) successional trajectories for the twelve

stand-types were synthesized to create a synoptic forest succession model.

The synoptic model recognizes two self-perpetuating forest canopy types. The black spruce type occurs primarily in nutrient-deficient sites, while the mixed-wood (fir-spruce-birch) type occurs in areas where nutrients are less limiting. Within the black spruce type, a hygric-xeric gradient is recognized, from peat moss to feathermoss to reindeer lichen in the understory. Ericaceous shrubs are also abundant in the understory. Within the mixed-wood type, canopy sub-types are differentiated along a moisture-nutrient gradient. Succession toward eastern white cedar occurs under hygric, nutrient-rich conditions, whereas balsam fir and white spruce dominate when mesic, somewhat nutrient-limited conditions occur. Birch dominates in areas where nutrients and moisture are most limited. Transition between the two major types, and within the subtypes, may also occur with changing edaphic conditions and/or disturbance regimes. This synoptic model explicitly incorporates edaphic, topographic and landform variables into boreal forest successional processes at the landscape level.

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CHAPTER 1
STRUCTURE AND DYNAMICS OF BOREAL FOREST ECOSYSTEMS

1.1 INTRODUCTION

In this chapter, I summarize the available literature on the structure, composition, temporal dynamics, and vegetation-environmental relationships of boreal forest ecosystems in central North America. Important factors determining recurrent patterns and processes in boreal forest ecosystems such as disturbance, climate, edaphic factors, geology, and glacial history are discussed. I also outline various forest succession models and theories, and discuss their application to boreal forest ecosystems.

1.2 THE BOREAL FOREST

The boreal forest is one of the largest biomes in the world, covering an area of 12 x 10^6 km^2 or approximately 8% of the world's continental land mass (Whittaker 1975). This biome is restricted to the northern hemisphere continents of North America and Eurasia. Over 80% of Canada's forests occur within the boreal ecoregion, which extends longitudinally from Labrador to the Yukon (Larsen 1980). Canada's boreal forests are economically important to the timber, mining, and recreational sectors (Pye 1991).

1.2.1 Climate

The influence of climate on the boreal forest is all-pervasive (Larsen 1980). The boreal forest is characterized by a continental climate of short, cool to moderately warm summers and long, cold to severe winters. Annual precipitation is ≥ 90 cm in the eastern and far western portions of the Canadian boreal forest, but is generally < 75 cm in the more continental regions of north-western Ontario and the prairie provinces (Hare and Thomas 1979). Although precipitation occurs throughout the year, well over half is deposited as rain during the relatively short growing season. Forest fire frequency and intensity are largely determined by climatic factors (temperature, precipitation), with drier and warmer regions experiencing shorter fire cycles than moist, cool ones (Rowe and Scotter 1973; Viereck 1983).

Floristic composition and vegetation dynamics of the boreal forest are affected by climate both directly (e.g. physiological adaptation of species) and indirectly (e.g. soil development, fire frequency). The southern border of the boreal forest corresponds roughly to the mean January position of the Arctic Front, which separates the dry, cold Arctic air from the comparatively warm, moist Pacific air masses (Bryson 1966). In northern Ontario, the boundary between the Boreal and Great Lakes-St. Lawrence forests corresponds roughly to the 2°C mean annual isotherm (Oechel and Lawrence 1985; Liu 1990). The dominance distribution of several boreal tree species can be accurately predicted using a combination of five climatic parameters related to air temperature and moisture (Lenihan 1993). Climatic variables such as precipitation and temperature also influence soil thermal regime and moisture content, which in turn determine nutrient cycling rates. In general, nutrient turnover and decomposition rates in the boreal forest are low (Prescott et al. 1989).

1.2.2 Quaternary Ecology

Most of northern Ontario was glaciated at ca. 11,000 BP, although recently deglaciated areas in the extreme north-west were flooded by glacial Lake Agassiz at this time. The early postglacial (10,000 BP) forest that colonized the Canadian Shield of northern Ontario was dominated by white spruce, although oak, elm and poplar were also present. The base-rich, unleached soils of these newly deglaciated surfaces favored white spruce over black spruce (Liu 1990). Continued climate warming after 9000 BP resulted in the replacement of white spruce by jack pine, and the invasion of shade-intolerant shrubs and herbs. The much warmer and drier climate of the Hypsithermal (beginning 7400 BP) favored the northward expansion of Great Lakes-St. Lawrence species such as white pine, eastern hemlock, beech and eastern white cedar (Delcourt and Delcourt 1987; Holloway and Bryant 1985). This northward expansion continued from 7000 to 3000 BP, moving the boreal ecotone to approximately 140 km north of its present position (Ritchie and Yarranton 1978; Liu 1990). By 3000 BP, neoglacial cooling resulted in much wetter, cooler conditions. This sudden change in climate decimated northern populations of white pine and eastern white cedar, while favoring spruce, jack pine and balsam fir. As a result, the boreal ecotone retreated dramatically between 3000-2500 BP, and continued to do so until it reached its present position about 1000 BP (Liu 1990).

1.2.3 Surficial Geology

The boreal forest of northwestern Ontario occurs mainly on shallow sandy till over early-Precambrian granitic bedrock ('Canadian Shield') that was formed about 3 billion years ago (Zoltai 1961, 1965, 1967). Late-Precambrian Proterozoic rocks are found in the Lake Nipigon area, and along the north-west shore of Lake Superior. Localized greenstone belts are found throughout the area (Thurston et al. 1991). The granitic parent material results in soils that are typically acidic and nutrient-deficient.

Exposed Canadian Shield bedrock is encountered throughout the region, but it is particularly common around Lake of the Woods and Rainy Lake, and along the shore of Lake Superior. Lacustrine clay deposits occur mainly in areas flooded by glacial Lake Agassiz (a belt that includes Lake of the Woods, Lac Seul and Lake Nipigon). A large area dominated by coarse glacial outwash (material deposited by meltwaters along an ice front) is found west of Lake Nipigon. Subsequent modification of the landscape has occurred through the actions of erosion, alluvial deposition, soil profile development, formation of bogs and dunes, frost action, and the damming of watercourses by beaver.

1.2.4 Landscape and Landform

Landform, which incorporates parent material and surficial topography, determines local patterns of insolation and drainage. These in turn affect soil development, nutrient and moisture status, community composition, and the prevailing disturbance regime (Ritchie 1956; Viereck 1983; Oechel and Lawrence 1985; Host et al. 1987; Leduc et al. 1992).

These factors are thought to become increasingly important at higher latitudes (Viereck et al. 1993). Landform is an important determinant of the distribution, abundance and regeneration dynamics of boreal tree species (Heinselman 1973, 1981; Bergeron and Brisson 1990; Frelich and Reich 1995a,b). Greater landform variability results in more ecologically patchy landscapes, which may promote forest habitat diversity and complexity (Foster and King 1986).

1.2.5 Edaphic Factors

Edaphic factors play a central role in determining the distribution and regeneration dynamics of boreal forest species. Important factors include:

Soil Drainage and Soil Texture

Various species of pine (jack pine in the east, lodgepole pine in the west, and red and white pine in the south-east), and black spruce, are most abundant on well to excessively drained sandy soils. On finer-textured silt and clay soils, species such as paper birch, trembling aspen, white spruce and balsam fir are generally favoured.

Soil Nutrient Status and Nutrient Availability

Well-drained sandy soils supporting pine or black spruce stands are generally nutrient-poor, while trembling aspen, balsam fir and white spruce occur on more mesotrophic silt-clay substrates. Deep organic soils of low nutrient status (oligotrophic bogs) are dominated by black spruce, while eastern larch is found on more minerotrophic organic soils (at least in early successional stages). Alluvial soils enriched by organic matter may support stands of eastern cedar, black ash or balsam poplar. High soil acidity reduces the availability of many essential mineral nutrients (Fitzpatrick 1974; Barber 1995). As a result, the large areas of the boreal forest occurring on the acidic, granitic Canadian Shield are dominated by species that tolerate nutrient-deficient conditions, such as the pines, black spruce, ericaceous shrubs and the feathermosses.

Organic Matter Accumulation

Large areas of the boreal forest consist of poorly-drained bogs with considerable accumulations of poorly-decomposed organic peat (primarily the *Sphagnum* mosses). Peat accumulation greatly impedes drainage and ties up essential plant nutrients. Oligotrophic to ombrotrophic bogs are dominated by stands of black spruce, ericaceous shrubs, and peat mosses. Peat accumulation may eventually 'drown' forest stands in northern areas, a process known as paludification (Heilman 1966).

Permafrost

The presence of permafrost likely determines the northern range limits of deep-rooted species such as the pines, white birch and trembling aspen (Viereck 1983). Species characteristic of the tree line (white and black spruce, and balsam poplar) have shallow root systems that are better adapted to the presence of permafrost.

1.2.6 Vegetation Studies

The floristic composition and structure of the boreal forest has sometimes been described as a being relatively "simple" (e.g. Ritchie 1956; Larsen 1980; Oechel and Lawrence 1985). Despite this, some boreal vegetation associations have been described as "surprising" (e.g. Ritchie 1956), while others are sufficiently rare, ecologically or geographically, to be placed into a catch-all "other" category (e.g. La Roi 1992). Early phytosociological studies in the boreal forest were largely descriptive, though many workers speculated as to the dynamic nature of these stands (e.g. Ritchie 1956; La Roi 1967; Rowe 1961,1983). These early studies laid the groundwork for more quantitative investigations undertaken to examine vegetation-environmental relationships (e.g. Carleton and Maycock 1978; Kenkel 1986, 1987), and successional trends (e.g. Dix and Swan 1971; Cogbill 1985; Bergeron and Dubuc 1989; Zoladeski and Maycock 1990). While the plant species composition of the boreal forest community varies across North America, recurrent vegetation-environmental relationships and floristic associations characterize much of the biome (La Roi 1967).

1.3 The Role Of Disturbance

1.3.1 Fire

Comprehensive reviews of the role of fire in the boreal forest include Rowe and Scotter (1973), Heinselman (1973, 1981), Wein and MacLean (1983) and Johnson (1992). At the landscape level, fire is undoubtedly the most important disturbance feature in the boreal forest (Ritchie 1956; Dix and Swan 1971; Heinselman 1973; Carleton and Maycock 1978; Wein and MacLean 1983; Payette 1992; Bonan 1992). Larsen (1980) emphasized that fire, climate and soils form a multifactorial complex defining the boreal ecosystem. In the absence of human intervention, fire cycles in North American upland boreal forests range from < 50 years in southern and central areas of the prairie provinces, to 250 years or more in the mesic boreal forests of eastern Canada. Such fire frequencies are well within the longevity range of most boreal tree species. Poorly-drained bogs, swamps, marshes, and forests at the boreal-tundra transition zone burn much less frequently. However, fire plays an important role in the stand and landscape dynamics of these areas as well (Payette 1992).

While forest fires occur throughout the boreal forest, some areas are burned more frequently and intensely than others (Heinselman 1973). At the landscape level, this results in a patchwork mosaic of forest stands at various ages having different disturbance histories. The long-term cumulative fire history of a site is thought to play an important role in determining present-day vegetation (Heinselman 1973; Cogbill 1985; Bergeron and Dubuc 1989; Zasada et. al. 1992).

The frequency and intensity of boreal forest fire affect both the floristic composition (LaRoi 1967; Dix and Swan 1971; Rowe 1983; Diotte and Bergeron 1989) and vegetation dynamics (Ritchie 1956; Dix and Swan 1971; Wright and Heinselman 1973; Carleton and Maycock 1978; Bergeron and Dansereau 1993; DeGrandpré et. al. 1993; Shafi and Yarranton 1973a,b) of these ecosystems. This result in boreal forest landscapes that are a mosaic of communities adapted to fire cycles of varying duration. Under short fire cycles, 'pioneer' species that endure or evade fires come to dominate, while 'seed-banking' fire-intolerant species are favored in areas where fires are less frequent and/or severe (Rowe 1983; Zasada et al. 1992). Payette (1992) describes the boreal flora as consisting of robust 'generalist' species capable of withstanding recurrent environmental change. One adaptation to recurrent fire (seen in jack, lodgepole and red pines, and black spruce) is the production of fully to semi-serotinous cones. White birch, balsam poplar, trembling aspen, and the majority of boreal shrub and forb species, reproduce both vegetatively and by seed (Rowe 1983; Zasada et. al. 1992). Trembling aspen suckers after a fire (or after logging), and the species continues to reproduce vegetatively until stands are overmature (Peterson and Peterson 1992). Particularly severe fires may kill underground plant parts and deplete the soil seed bank (Rowe and Scotter 1973).

Fire is critical to the regeneration dynamics of most boreal forest species. All boreal tree species have optimal seed germination and seedling survival (establishment) on exposed mineral substrates (Van Wagner 1983). A major result of fire is the removal of accumulated litter, thus exposing mineral soil for seed germination and seedling establishment (Johnson 1992). Successful germination and establishment rates (as well as layering) on organic substrates are more prevalent in hydric species such as larch (Johnston 1990a), black spruce (Viereck and Johnston 1990), and white cedar (Johnston 1990b). Mesic species such as balsam fir (Furyaev 1983) and white spruce (Peterson and Peterson 1992) may also germinate and establish on organic substrates, but generally at lower rates than the more hydric species.

Increased post-fire soil temperature is the result of loss of vegetation cover, which increases insolation. Furthermore, the burning (blackening) of the substrate increases soil albedo (Viereck 1983). Fire also results in an overall nutrient 'pulse'. Despite a significant loss of nitrogen due to volatilization, this nutrient pulse (together with increased decomposition, nitrogen fixation, and soil temperatures) favors rapid re-establishment of vegetation (Johnson 1992). An increase in soil pH following a fire (MacLean et. al. 1983) also increases nutrient uptake and mineralization. Ground-to-air thermal exchange is also affected by the loss of vegetation cover. As trees no longer provide a windbreak, fluctuations in soil temperatures increase on a daily, seasonal, and annual basis (Viereck 1983; Bonan 1992). Fire is also believed to reverse the trend towards paludification in poorly-drained sites in the far north (Viereck 1983).

Rowe (1983) believes that the general "successional path" of boreal forest stands is dependent on fire cycle duration, with frequent fires favoring resprouting, shade-intolerant species and seed-banking ephemerals. Bergeron and Dubuc (1989) and DeGrandpré et. al. (1993) assert that convergent succession can only occur on sites where a seed bank of shade-tolerant tree species is present; such a seed bank may not exist in areas where forest fires are frequent. It is often assumed that shade-tolerant tree species such as balsam fir and/or eastern white cedar, which are frequently encountered in the subcanopy of established boreal forest stands, will eventually form a "climax" community in the absence of fire (Ritchie 1956; LaRoi 1967; Dix and Swan 1971; Carleton and Maycock 1978; Cogbill 1985; Archambault and Bergeron 1992). This rarely occurs, however, since fire almost invariably interrupts the successional process (Archambault and Bergeron 1992). Furthermore, spruce budworm infestations often interrupt the invasion of balsam fir (Zoladeski and Maycock 1990; Archambault and Bergeron 1992). Both understory floristic composition (Carleton and Maycock 1978; Bergeron and Dubuc 1989; DeGrandpré et. al. 1993, Taylor et al 1987) and species richness and diversity (Shafi and Yarranton 1973a) have been shown to vary with time-since-fire, particularly during the first few years of vegetation re-establishment.

1.3.2 Herbivory

Herbivores may play a much greater role in boreal forest vegetation dynamics than has been previously acknowledged by plant ecologists. Ungulate herbivores, for example, can be quite selective in their choice of browse. Differential browsing of tree saplings may dramatically alter successional trajectories. For example, balsam fir saplings are actively sought out by many ungulate herbivores (e.g. white-tailed deer), thereby suppressing balsam fir regeneration. Infestations of spruce budworm may reverse the course of succession by selecting against balsam fir and white spruce (Archambault and Bergeron 1992). Similarly, an infestation of larch sawfly in the mid-1930's decimated stands of eastern larch over large areas of the North American boreal forest (Johnson et al. 1995). A host of insect larvae feed on both coniferous and deciduous boreal tree species, and can cause massive defoliation and stand mortality in trembling aspen and other species (Burns and Honkala 1990). The harvesting of boreal conifer and deciduous tree seeds by mammalian granivores may also be important.

Beaver activity is important to boreal forest dynamics at more local spatial scales. Beaver damming often result in the flooding of low-lying forests, killing the trees. Beaver ponds are important temporary catchment basins that accumulate organic matter and nutrients (Naiman 1988). The damming of streams may have adverse effects on downstream hydrology. Beaver activity also results in the removal of deciduous species such as trembling aspen and willows from the catchment area, resulting in competitive release of sub-canopy conifers (Peterson and Peterson 1992).

1.3.3 Human Activity

Clear-cutting and selective cutting are both practiced in the boreal forest. Selective cutting of white and red pine in central Ontario in the late 1800's dramatically reduced the abundance of these species. Clear-cutting with reseeding/replanting is the standard silvicultural practice in much of the boreal forest. The long-term effects of clear-cutting on forest stand dynamics remains largely unknown. However, a recent study in eastern Manitoba suggests that logging does not drastically affect species composition, but does alter relative abundances (Ehnes and Shay 1995).

Fire suppression may have long-term effects on boreal forest composition, structure, and dynamics. In particular, forest stands adapted to recurrent fires (usually within the lifespan of the first generation of trees) may undergo unpredictable and largely unknown changes in response to the suppression of this natural disturbance. Fire suppression may also favor late-successional species such as balsam fir and white spruce, which in turn increases the frequency and severity of spruce budworm outbreaks (Blais 1983). Other potential effects of human activity include changes in the distribution and abundance of ungulate herbivores, and climate change.

1.3.4 Gap Dynamics

Windthrows are relatively common in the boreal forest, and are particularly common in shallow-rooting species such as white spruce and white pine (Foster 1988), as well as trees growing on rock outcrops. On deep mineral soils, deep-rooting species such as jack pine are generally not susceptible to windthrow (Burns and Honkala 1990). The exposure of mineral soil that results from a windthrow may be important in boreal forest regeneration dynamics (Jonsson and Dynesius 1993). While a number of studies have examined gap dynamics in the eastern deciduous forest, comparable studies have yet to be undertaken in the boreal forest (but see Frelich and Reich 1995a,b).

1.3.5 Pathogens

A large number of fungal pathogens have been recorded on boreal forest tree species (Burns and Honkala 1990; Peterson and Peterson 1992). Like windthrow, pathogens may open up gaps in the forest canopy, by killing individual trees and/or by disturbance caused by the treefall. Parasitic dwarf mistletoes may attack boreal tree species (particularly jack pine and white spruce) in western regions of the boreal forest.

1.4 Boreal Forest Succession and Vegetation Dynamics

1.4.1 Introduction

Johnson (1979) notes that the history of succession theory can be broken down into four time periods. The underpinnings of succession theory were developed prior to 1900, based on empirical field investigations such as Cowles' (1899) classic study of forest dynamics along the south shore of Lake Michigan. Further development and elaboration of succession theory concepts occurred between 1900-1930, a period very much dominated by the works of Clements (1916, 1936). The Clementsian, 'community-unit' (Collins et al. 1993) or 'holistic' (Finegan 1984) model of succession viewed the community as a natural 'organism', in which individual species are held together by the 'social bonds' of the dominants. Plant species were thought to modify their environment, paving the way for later-successional species while rendering the habitat unsuitable for themselves. A self-replacing climax community develops once the full 'potential' of a particular environment (defined mainly by climate) is realized. Johnson (1979) notes that "contemporary ecologists cannot read Clements and hope to understand him. He is a product of another age, he speaks a different language and expresses a different cognitive commitment, appropriate for a different world view". An alternative view of vegetation dynamics was offered by Gleason (1926), a contemporary of Clements. His is a 'reductionist' (Finegan 1984) or 'individualistic-based' model, in which a plant community is viewed as nothing more than a fortuitous assemblage of species populations. Under such a model, species replacements occur on a plant-by-plant basis (driven by differences in life-history traits), and stochastic processes predominate. The third period (the "scholastic interval" from 1930-1947, Johnson 1979) was notable as a period in which the views of Clements were largely rejected in favor of the reductionist approach advocated by Gleason.

1.4.2 Contemporary Views of Succession

The fourth (post-1947) period in the development of forest succession models was characterized by a loss of faith in the major ideas of classical Clementsian succession; a view that persists today (Cook 1996). This alternative view of succession recognizes that disturbance is an integral component of vegetation dynamics. Disturbance was "the nemesis of classical succession because it ... introduced heterogeneity and lack of compositional stability" (Johnson 1979). In ecosystems where disturbances are relatively frequent, the classic notion of a 'climax' community characterized by a self-replacing species assemblage is meaningless (Horn 1976).

Watt (1947) is generally acknowledged as the first researcher to explicitly incorporate disturbance into a model of vegetation dynamics. In his model, the community is viewed as a mosaic of patches, each of which undergoes cyclical, rather than seral, changes in composition and structure. Watt also recognized the stochastic nature of community structure and dynamics, and the role that plant life-histories and biotic interactions play in directing vegetation trajectories.

Finegan (1984) has characterized Egler's (1954) 'initial floristic composition' model as the "cornerstone of a new succession theory". In this model, succession is viewed as proceeding from (and indeed constrained by) the propagules available at a site following disturbance. Propagule availability is largely determined by site history and stochastic factors (see also McCune and Allen 1985a,b). Wilson et al. (1992) suggest that two versions of Egler's model should be distinguished. The 'complete' initial floristic model states that all species involved in succession are present at the beginning; thus, succession represents the 'unfolding' of this initial flora, as determined by differences in species life-history attributes. Conversely, the 'preemptive' initial floristics model recognizes that dominant species, which initially preempt a site, have a long-term influence on the site. Succession is therefore somewhat unpredictable, since vegetation development depends on 'who gets there first'.

More recent developments in vegetation succession theory have involved the integration, refinement, and elaboration of the ideas advocated by Watt, Egler and their contemporaries. Connell and Slatyer (1977) note that proposed mechanisms of succession are based largely on plant-plant interactions, and that other factors such as herbivory have been largely ignored. They proposed a series of theoretical succession models. The neo-Clementsian 'facilitation' hypothesis holds that succession is controlled by the vegetation itself, with one group of species making the environment more suitable for the next group (in effect, facilitating change). The 'tolerance' model holds that succession results in a species assemblage that is most efficient at exploiting limiting resources. The tolerance model anticipated Tilman's (1985) 'resource-ratio' model, which states that succession is driven by changes in resource ratios (e.g. light, nutrients) over time. Finally, the neo-Eglerian 'inhibition' model proposes that the species present at a site inhibit the establishment of potential competitors.

A number of authors have focused on differences in species life-histories as the driving force of succession. Pickett (1976) viewed the landscape as consisting of patches of different successional environments. These patches are continually changing in relative size and position in response to the prevailing disturbance regime. A climax community is defined when the level of adaptation of the species present equals or exceeds that of potential competitors. In addition, since a given species is best adapted to a particular set of conditions, different species are favored at different successional stages. Grime (1977) expanded on these ideas, noting that some species ('ruderals') are best adapted to a disturbance environment, others ('stress tolerators') to extreme environments, and still others ('competitors') to relatively undisturbed and productive habitats. The incorporation of life-history attributes into a Gleasonian model led to the concept of 'vital attributes' (Cattelino et al. 1979, Noble and Slatyer 1980). A species' vital attributes are determined by the method of arrival or persistence at the site during and following disturbance, the ability to establish and grow to maturity in the developing community, and the time taken to reach critical life-history stages such as reproduction. Depending on disturbance frequency, different vital attributes will be favored. Attributes that are favoured when disturbances are rare will prove maladaptive in environments where disturbances are comparatively frequent. The 'life history' model (Huston and Smith 1987) incorporates many of the ideas discussed above into a comprehensive model of vegetation dynamics that explicitly incorporates the role of disturbance. The model is based on three premises: (a) that competition for limiting resources occurs between all individuals in the community, though the specific resource(s) and the intensity of competitive interactions may change through time and between plant communities; (b) that plants alter their environment such that the relative availability of resources changes though time, which in turn affects competitive ability; (c) that physiological and energetic constraints preclude any one species being a superior competitor under all circumstances. Their model indicates that although a competitive equilibrium is rarely achieved, a steady-state dynamic equilibrium reflecting a balance between the prevailing disturbance regime and local successional dynamics can occur.

A number of other investigators have contributed to contemporary forest succession theory, as summarized in the review papers of Finegan (1984), McCook (1994) and Cook (1996). Finegan (1984) is of the opinion that tolerance and life-history traits cannot by themselves provide a complete description of vegetation dynamics. He cites a number of empirical investigations demonstrating the importance of facilitation, and suggests that the concept should not be abandoned solely because of its Clementsian connotations. He is also somewhat critical of reductionist approaches, stating that stochasticism is "a disorganizing power as elusive as the emergent properties of the holists". Despite such criticisms, an overall common consensus is emerging:

1. Disturbance is frequent and ubiquitous enough that it must be incorporated into any model of vegetation dynamics. Disturbances are recognized as operating at various spatial and temporal scales.
2. The classic Clementsian 'climax community' is rarely if ever reached. Multiple successional pathways are possible, retrogression may occur, and succession may be arrested.
3. Stochastic factors may play a significant role in vegetation dynamics. Such factors operate at many spatial and temporal scales, and cumulative effects are expected.
4. Species life-histories and vital attributes, and their evolution, are important and must be considered.

5. The mechanisms driving succession vary in both space and time. In addition, more than one mechanism may be at work simultaneously. A pluralistic approach to the study of vegetation dynamics is therefore required.

1.4.3 Boreal Forest Succession

The historical development of forest succession models was largely based on empirical investigations in temperate deciduous forest ecosystems. Such ecosystems are characterized by a relatively high diversity of tree species having different life-history characteristics. Furthermore, these forests are infrequently subjected to catastrophic natural disturbances. By contrast, the boreal forest is species-poor, and the majority of species show life-history adaptations to frequent, catastrophic fires.

Early boreal studies were frequently surveys of specific regions (e.g. Ritchie 1956) or broad-scale studies (LaRoi 1967). In these early studies, community dynamics were inferred by comparing the vertical stratification and composition of younger vs. older stands. Rowe (1961) was the first to critically apply concepts of succession theory to the boreal forest, which he characterized as a disturbance-driven ecosystem. He notes that while fire is a 'catastrophe' at the stand level, fire promotes vegetation heterogeneity at the landscape level and is critical to maintaining ecosystem health and vigor. Fire is such a frequent occurrence in the boreal forest that Clementsian successional concepts are not applicable (see also Engelmark et al. 1993). Rowe recognized that stochasticism, site history, edaphic conditions, and species life-history characteristics are important determinants of the composition, structure and dynamics of the boreal forest. Multi-directional successional trajectories are possible due to edaphic variation and differences in propagule availability. Rowe also suggested that no western Canadian boreal tree possesses all the vital attributes required of a self-perpetuating Clementsian climax species.

Dix and Swan (1971) developed successional trajectories for boreal central Saskatchewan by sampling the canopy strata in 89 stands. They suggested that recurrent forest fires (well within the lifespan of the dominant tree species) 'stabilize' species composition at a given site, in the sense that the post-fire vegetation is floristically similar to that existing before the fire. Community composition and succession were explained in terms of vital attributes and life-history characteristics of the major trees species. Most boreal forest trees are 'pioneers', in the sense that they do not regenerate beneath themselves. Such species include trembling aspen, jack pine, birch, and balsam poplar. Black and white spruce were also deemed to be 'chiefly pioneer', since their presence in the sub-canopy of many stands is probably the result of suppression by canopy dominants rather than continuous long-term establishment. The authors also suggest, based on life-history characteristics, that balsam fir is the only late-successional species in boreal Saskatchewan, although this species never dominated the upper canopy and was rarely abundant in the sub-canopy.

Carleton and Maycock (1978) used canopy information obtained from 152 stands in north-eastern Ontario to obtain successional vectors (trajectories) in ordination space. They found that stand trajectories were generally short, circular and somewhat divergent. Most upland sites were dominated by young monocultures of pioneer species adapted to recurrent fires. Stand degeneration was noted in older jack pine stands, and there was little regeneration by black spruce or balsam fir. In deciduous forests (mostly trembling aspen), a shift to conifer dominance (balsam fir and/or black spruce) may occur in the absence of fire. Their main findings were that a self-regenerating vegetation complex is absent in boreal forests, that fire is an integral part of the system, and that boreal forest composition and dynamics reflects species adaptations to recurrent and unpredictable fire events.

Similar results were obtained from a study of 212 stands in north-western Ontario (Zoladeski and Maycock 1990). Balsam fir showed continuous recruitment into most stands, but was only dominant in sites protected from fire. Balsam fir communities may self-perpetuate, but are subject to periodic outbreaks of spruce budworm. Trembling aspen and jack pine stands both develop toward a mixed black spruce-balsam fir forest, but fire will normally halt such a trend. The canopy of black spruce bogs tends to become more open over time, and the species successfully regenerates though layering. Upland black spruce stands also become more open with time, but appear to undergo little compositional change.

Taylor et al. (1987) suggest that understory vegetation changes in upland black spruce stands are related to increased soil moisture as a stand ages. Terricolous macrolichens (*Cladina*, *Cladonia*) were only found in the youngest stands. Cover of *Pleurozium schreberi* increased up to age 60, while other feathermosses (particularly *Ptilidium crista-castrensis* and *Hylocomium splendens*) and some herbaceous species increased in abundance in the oldest stands. Shafi and Yarranton (1973b) found that many of the understory species present after a fire were the result of vegetative regeneration. Invader species (e.g. *Epilobium angustifolium*) were present for the first few years, but were competitively excluded within a few years.

Cogbill (1985) aged a total of 1785 trees from eleven boreal forest stand-types in central Québec to establish patterns of stand development. On average, 71% of tree recruitment occurred within the first 30 years (range: about 60% in black spruce and balsam fir stands, and 85% in jack pine, trembling aspen and white birch stands). These results indicate that "apparent succession is simply an expression of differential longevity and conspicuousness of species" (c.f. the Eglerian 'complete initial floristics' model of Wilson et al. 1992). Black spruce regenerated well in bogs, but larch abundance declined over time. Upland black spruce stands showed a small increase in balsam fir and white birch, but tended to degenerate over time. Balsam fir stands showed good regeneration, but were subject to spruce budworm attacks. Stands dominated by 'pioneer' tree species (jack pine, trembling aspen, and white birch) were thought to represent, in theory, transitional stages toward a forest dominated by balsam fir and/or black spruce. In practice, however, older upland stands invariably become decadent, displaying "rapid deterioration and degeneration" and little regeneration. Cogbill hypothesized that the moss-humus layer slows vegetation change by retarding seedling establishment. Dense ericaceous and alder shrub thickets may have similar effects.

Yves Bergeron and colleagues have undertaken a series of investigations on boreal forest dynamics on the morainal-lacustrine clay deposits at Lake Duparquet, west-central Québec. Bergeron and Bouchard (1984) summarize the forest stands present in the region. Bergeron and Dubuc (1989) used size-class ordination analysis to examine successional trends on exposed bedrock, morainal, and clayey surface deposits in the region. With size-class analysis, "points (on the ordination diagram) representing diameter classes of the same stand were linked in decreasing order of diameter classes". There are two major criticisms of this approach: (a) mortality of the younger age classes may differ between species; (b) differential growth rates of species can mask successional changes. Jack pine or red pine dominated the overstory on exposed bedrock sites. Stands of trembling aspen and white spruce were present on morainal deposits, while mixed-canopy stands (trembling aspen, white spruce, black spruce, white birch, and balsam fir) occurred on clay and some morainal sites. In all cases, the lower canopies (smaller size classes) were dominated by balsam fir and eastern white cedar, suggesting that these two species have 'later successional' status. The authors cite this as evidence of successional convergence, although they question the concept of self-replacement (climax) as applied to the boreal forest. All tree species were present within the first 50 years following fire, and the current forest composition was similar to the pre-burnt one. These results are consistent with the initial floristic composition (Egler 1954) and tolerance (Connell and Slatyer 1977) models. Species life-history attributes were also thought to be important. Some species resprout following fire (e.g. white birch, trembling aspen), while others store seed in serotinous (jack pine, red pine) or semi-serotinous (black spruce) cones. Only balsam fir and white cedar appear to have the vital attributes (longevity, shade tolerance) characteristic of later-successional species. Furthermore, the seeds of these two species are able to germinate on organic substrates. In the absence of fire, the authors hypothesize that mesic and hygric sites will be dominated by balsam fir and eastern white cedar, while eastern white cedar and black spruce will predominate on xeric sites. However, patch dynamics (windthrow, spruce budworm outbreaks) may alter these 'ideal' successional pathways. Bergeron and Dansereau (1993) reached a similar conclusion based on their model of boreal forest composition and structure under different fire cycles. If fires are infrequent, deciduous stands become increasingly dominated by coniferous species, although this trend is periodically interrupted by outbreaks of spruce budworm. The result is a patchwork mosaic of mixed coniferous-deciduous forest. Spruce budworm outbreaks also have an important influence on understory dynamics, as canopy openings favor ruderal, pioneer species (DeGrandpré et al. 1993).

Heinselman (1973, 1981) emphasized the importance of fire and other disturbances in determining succession trajectories of 'near-boreal' forests in northern Minnesota. He noted considerable variation in stand dynamics. Whereas some red and jack pine stands showed evidence of early invasion by balsam fir and eastern white cedar, other stands showed no such invasion after 350 years. Potential factors contributing to these differences include seed rain, rooting space, soil physical structure and nutrient status, herbivory, light availability, and surface organic accumulation (including litter and bryophyte cover). Frelich and Reich (1995a,b) incorporated spatial scale into a study of successional processes in the Boundary Waters area of Minnesota. Their analysis of two upland stands (both on sandy substrates over granitic rock) suggested a successional sequence from uniform, even-aged stands of jack pine (occasionally red pine) or trembling aspen to old-growth, multi-aged mixed stands of balsam fir, black spruce, paper birch and/or eastern white cedar (see also Buell and Niering 1957). In the absence of fire, they hypothesized that fine-scale (10-30 m) canopy openings caused by wind, insect and disease drive this successional process. Canopy openings are colonized by one of the later-successional species (c.f. founder-controlled patch dynamics), so that uniform, even-aged pine or trembling aspen canopies are gradually "chipped away" over time. As a result, stands deemed to be 'pure' at a fine scale are part of a more complex mosaic at coarser scales. The authors also hypothesized that fire suppression may result in the local extirpation of jack pine, resulting in trembling aspen becoming the dominant post-fire species.

1.4.4 Edaphic Factors and Boreal Forest Succession

Organic decomposition rates in the boreal forest are generally low (Prescott et al. 1989). This has generally been attributed to a combination of the short growing season and suboptimal edaphic conditions. Large amounts of highly flammable detritus accumulate in dry upland conifer sites, decreasing the availability of limiting nutrients (e.g. nitrogen, phosphorus) over time (Paré et al. 1993). In addition, a dense carpet of feathermosses (mainly *Pleurozium schreberi*) often develops, tying up nutrients and creating a substrate less suited for seed germination. Deciduous litter appears to limit the development of a continuous moss layer (Paré et al. 1993).

Poorly-decomposed peats (*Sphagnum* spp.) often accumulate in wet, poorly drained environments, leading to increased substrate moisture content and decreased availability of nitrogen, phosphorus and potassium (Heilman 1966; Heinselman 1981). In Alaska, peat moss accumulations of 25-50 cm per century are not uncommon (Heilman 1968).

1.4.5 Determining Successional Trends in the Boreal Forest

Permanent Plots

The establishment and regular enumeration of permanent plots offers the most powerful approach to studying boreal forest dynamics (Carleton 1982a,b). Unfortunately, the time required for succession to occur is normally so long as to preclude its direct observation (Finegan 1984). Indirect approaches to studying succession thus require a theoretical framework to provide guidelines for data collection and interpretation (Johnson 1979).

Chronosequencing

In chronosequencing, successional trends are inferred by enumerating stands of different ages (e.g. Crocker and Major 1955). This approach assumes that stand histories and environments are similar, i.e. the reconstructed successional trends are not confounded by site-to-site variation. Given the acknowledged importance of initial floristic composition to boreal forest dynamics, this assumption must be questioned. Another problem with this approach is that older stands are often poorly represented, particularly in fire-prone areas (Heinselman 1973). Adequate stand replication, and the enumeration of a large number of plots in each age class, will greatly increase the reliability and accuracy of reconstructed chronosequences. Chronosequencing studies in the boreal forest have been used to examine understory dynamics (e.g. Taylor et al. 1987; De Grandpré et al. 1993), while an approach combining chronosequencing and canopy-subcanopy relationships (see below) has generally been used to infer succession trends in the tree canopy.

Canopy-Subcanopy Relationships

This approach utilizes the size and/or age class distributions of tree species to infer successional trends (Horn 1976). For example, a stand dominated by species *A* in the canopy and by species *B* in the subcanopy and/or sapling layer indicates a possible successional trend towards dominance by species *B*. This approach implicitly assumes that mortality, natality and growth rates, and life-history strategies, are similar between species. These assumptions are probably unrealistic when applied to boreal tree species. For example, the relative contribution of balsam fir and trembling aspen saplings in later successional stages may be overestimated, since these species are preferentially browsed by ungulates and other herbivores. Similarly, the slow growth rate of black spruce (particularly when it is shaded) may result in an underestimation of its relative contribution (Cogbill 1985). Despite these limitations, canopy-subcanopy relationships (usually done in conjunction with chronosequencing) have been widely used to infer probable successional sequences in the absence of fire and other natural disturbances (e.g. Dix and Swan 1971; Cogbill 1985; Zoladeski and Maycock 1990). A similar approach, involving size-class ordination, has also been used to infer canopy succession trajectories (Carleton and Maycock 1978, 1980; Bergeron and Dubuc 1989).

CHAPTER 2
BACKGROUND AND OBJECTIVES

2.1 INTRODUCTION

In the previous chapter, I presented an overview of boreal forest composition, structure and dynamics. This chapter outlines the objectives of my research and presents information specific to the study area. In addition, I give important background information on the data utilized and the statistical analyses undertaken.

2.2 OBJECTIVES

This study had two primary objectives: (1) to reconstruct and summarize boreal forest successional trends, and (2) to develop a stand dynamic model for the boreal forests of north-western Ontario. Since succession proceeds from the post-disturbance environment, it was also necessary to quantify the strength of vegetation-environment relationships within the study area (see Chapter 3). All results are based on data collected by the Ontario Ministry of Natural Resources (OMNR) in northwest Ontario.

2.3 STUDY AREA

2.3.1 Location

The study area is ca. 184,000 km^2 in size and includes the Ontario Ministry of Natural Resources North-Central (NCR) and North-Western (NWR) administrative regions (Baldwin and Sims 1989; Racey et. al. 1989). The western and southern limits of the study area are the Manitoba-Ontario and Ontario-Minnesota borders respectively. The easternmost limit occurs near the town of Marathon. The northern border is close to the limit of commercial forestry in the province, which corresponds roughly to the southern border of the Hudson Bay lowland physiographic region (**Fig 2.1**). The study area includes a small portion of Great Lakes-St. Lawrence Forest Region (Quetico, Rainy River), but most of the region falls within the Boreal Forest Region (Rowe 1972; Baldwin and Sims 1989).

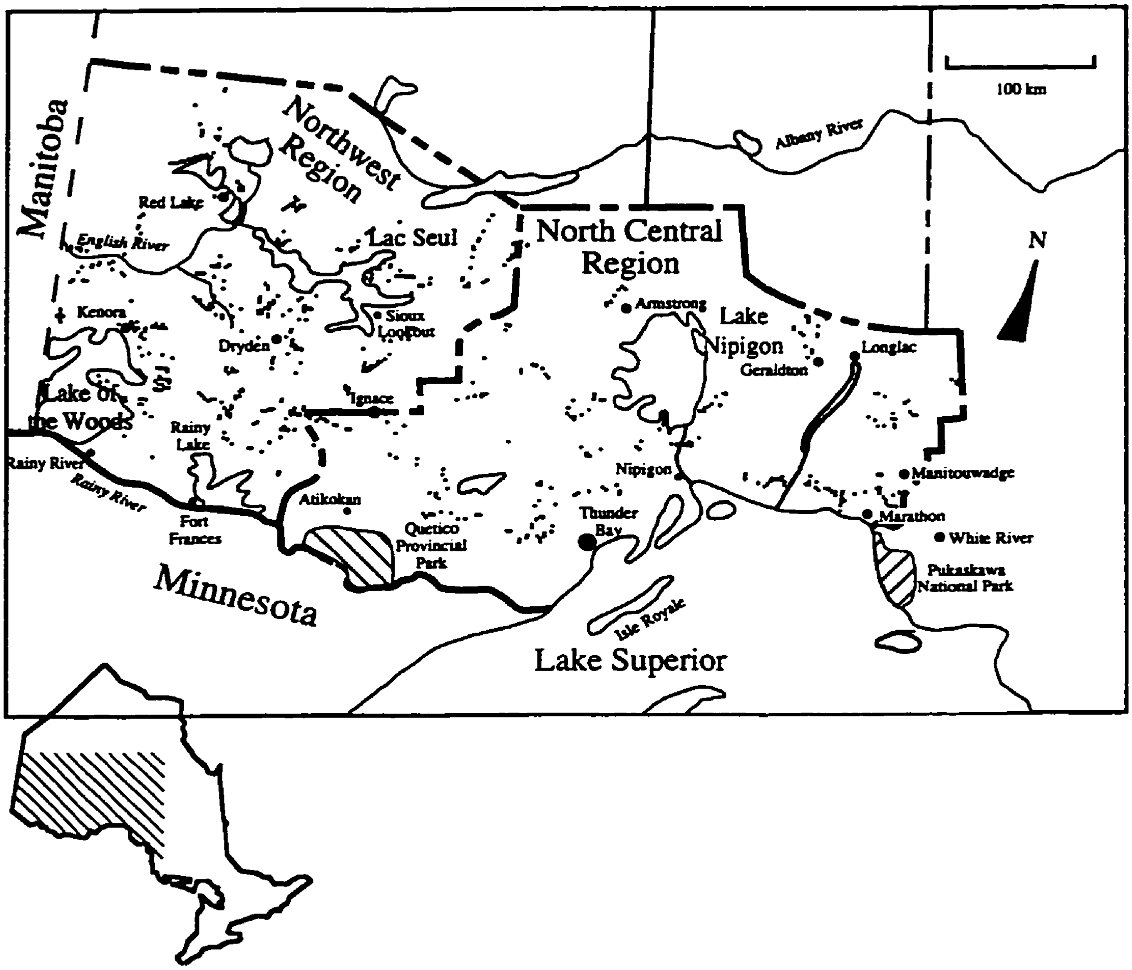


Fig. 2.1 Map of the study area in northwestern Ontario, showing administrative regions, plot locations (small dots), and key geographic characteristics. (Modified from Racey et. al. 1989).

2.3.2 Climate

The study area lies within Köppen's Dfb (continental cool summer) climatic region (Eichenlaub 1979). It is characterized by a continental climate of short, cool to moderately-warm summers and long, cold-severe winters. The mean January temperature varies from south to north, from ca. -14°C along the coast of Lake Superior to ca. -20°C to the north of Lac Seul and Lake Nipigon. Variation in mean July temperature occurs mainly from east to west, ranging from ca. 15°C along the shore of Lake Superior to ca. 19°C in the Lake of the Woods region. The mean annual frost-free period ranges from 70-80 days in the central portion of the study area (a band extending from Quetico Provincial Park to Lake Nipigon) to 100-120 days near Lake Superior and the Lake of the Woods region. Mean annual precipitation ranges from ca. 60 cm (16 cm as snow) near the Manitoba border to ca. 75 cm (25 cm as snow) at Marathon. Annual water deficits of 2.5 to 5.0 cm are experienced in the westernmost portion of the study area. Winds are predominantly from the north-west in winter, and from the south-west during the summer. Mean annual bright sunshine hours ranges from ca. 1800 in the east to >2000 in the west (data from Hare and Thomas 1979).

2.3.3 Regional History

The study area is sparsely populated, with most of the settlements occurring along the Trans-Canada highway and around Lake of the Woods. Extensive logging at the turn of the century involved mainly the selective harvesting of mature red and white pine stands in the Quetico and Rainy River regions. Logging and tourism, and associated secondary and tertiary industries, drive the economy of the region.

Recurrent forest fires are characteristic of the study area. Fire frequency is dependent upon topography and site-climatic conditions. Fires occur every 50-100 years in dry jack pine uplands, but 300 years or more may pass between fire events in mesic-hygric habitats where white spruce, black ash and eastern white cedar predominate (Heinselman 1981). Forest fire frequencies vary as a function of the synergistic influences of climate and fuel accumulations. Fires were particularly frequent during the warm, dry 15th and 16th centuries, but fire frequency declined after 1600 AD (Clark 1988). Within the study area, forest fires are more prevalent in drier regions near the Manitoba border.

2.3.4 Geology

The Canadian Shield, a colloquial term for early-Precambrian granitic bedrock, is characteristic of the study area (Baldwin and Sims 1989; Pye 1991). Late-Precambrian Proterozoic rocks are found in the Lake Nipigon area and along the north-west shore of Lake Superior, and localized greenstone belts are found throughout the region (Thurston et al. 1991).

2.3.5 Surficial Geology and Glacial History

The Wisconsin ice sheet retreated from the study area between 12,000 and 10,000 years BP. Glacial Lake Agassiz formed from water dammed behind the ice sheet, flooding much of the study area from Lake of the Woods to the Lac Seul - Lake Nipigon region. Sedimentation resulted in the localized deposition of lacustrine clays. Canadian Shield bedrock outcrops are encountered throughout the study area, but are particularly common around Lake of the Woods, Rainy Lake, and along the shoreline of Lake Superior (Zoltai 1961, 1965, 1967). A large area dominated by coarse glacial outwash (materials deposited by meltwaters along an icefront) occurs west of Lake Nipigon, and end moraines occur sporadically throughout the area. The landscape has been subsequently modified by processes such as erosion, alluvial deposition, soil profile development, bog and dune formation, frost action and the damming of watercourses by beaver. Poorly-decomposed organic peats are commonly encountered in low-lying areas, but expansive poorly-drained wetlands such as those found in the clay belt regions of Ontario and Manitoba are not common in the study area (Baldwin and Sims 1989).

2.3.6 Edaphic Factors

The study area is dominated by coarse-textured, poorly-developed humo-ferric podzolic soils over a hilly, rolling terrain. Numerous phases of gray-wooded luvisols, fibrisols and mesisols also occur (Soils of Canada 1977). Common surficial deposits include shallow drift, undulating ablation and basal tills, and morainal and drumlin features (Baldwin and Sims 1989). The granitic parent material produces soils that are acidic and often nutrient-deficient. A gradient of increasing precipitation from west to east results in an overall trend of higher soil moisture, increased soil development, and greater accumulations of organic matter as one moves eastward (Minning et. al. 1994; Fullerton 1994; Soils of Canada 1977). Colder temperatures in the north result in colder soil thermal regimes, lower rates of decomposition and nutrient cycling, and increased soil moisture (Viereck 1983).

2.3.7 Vegetation

Even-aged stands of jack pine and/or black spruce are characteristic of moderately to excessively drained, nutrient-deficient sandy soils and granitic rock outcrops throughout the region. More mesic stands (e.g. fine sandy and loamy soils) often support pure or mixed stands of trembling aspen, white birch, balsam fir and black and white spruce. Black spruce is abundant in poorly-drained, nutrient-deficient peaty lowlands (Zoladeski and Maycock 1990). Wet, nutrient-rich habitats (e.g. riverine areas, rich fens) support species such as black ash, cedar, eastern larch, and balsam poplar. In the Quetico and Rainy River regions, suitable habitats are often dominated by red and white pine.

Zoladeski and Maycock (1990) undertook an extensive survey of the boreal forests of north-western Ontario. Stand age-class distributions indicated that tree recruitment occurs mainly during the first few years of stand regeneration, leading the authors to conclude that succession is largely determined by initial floristic composition. Black spruce lowlands and uplands were found to be stable and self-regenerating, although the canopy of upland stands tended to become more open over time. Jack pine and trembling aspen stands, in the absence of fire, appeared to be slowly succeeding toward a mixture of black spruce and balsam fir. Balsam fir showed continuous recruitment, but balsam fir stands were only common in areas protected from fire. Similar forest dynamic trends have been found in adjacent regions of northern Minnesota (Heinselman 1981; Frelich and Reich 1995b).

2.4 Data Collection

The data used in this study were collected as part of the northwest Ontario Forest Ecosystem Classification (FEC) project. Vegetation sampling in the North Central Region (NCR) took place between 1983 and 1987, and soil samples were analyzed at the Great Lakes Forestry Centre (Canadian Forest Service). Sampling in the North West Region (NWR) took place between 1983 and 1988, and soil samples were analyzed by the Ontario Ministry of Natural Resources (Ontario Forest Research Institute) and by the Ontario Institute of Pedology (Agricultural Centre, University of Guelph).

2.4.1 Sampling Criteria

Sampling areas were located using a nested stratification method, incorporating: (a) the forest region classification of Rowe (1972); (b) broad surficial characteristics, based on the Ontario Land Inventory and Northern Ontario Engineering and Geological Terrain classification (1:250,000 maps); (c) overstory composition, based on 1:15,480 Forest Resources Inventory (FRI) maps; and (d) stand productivity based on FRI site classes.

To ensure that plots were representative, transects were randomly located within the areas sampled and the centers of 10 x 10 m study plots were subjectively located based on prevailing stand conditions. Only stands meeting the following conditions were enumerated: (a) mature, fully-stocked, and of harvestable age and condition; (b) accessible by road or water; (c) not previously logged, or showing evidence of human disturbance; (d) representative of a wide variety of vegetation and site conditions; and (e) located on surficial materials common within the sampling area.

2.4.2 Vegetation

A complete inventory of vascular plant and terricolous cryptogam species was undertaken in each plot. Because epiphytic cryptogams were not consistently collected, I did not include them in this study. In each 10 x 10 m plot, cover-abundance estimates were obtained for all species. Cover estimates for trees and shrubs were assessed separately in each of four vegetation strata: (1) canopy; (2) subcanopy; (3) lower subcanopy, 2-10 m in height; (4) saplings, less than 2 m in height. Shrub species rarely occurred in the first two strata.

Mensurative data were collected for trees >10 cm diameter at breast height (DBH), although methods differed between NCR and NWR inventories. In the NCR, three individuals of each of the most abundant tree species were selected as being "representative" of conditions within the plot. Height, age, and DBH measurements were made on these trees. In the NWR, all trees of DBH ≥ 10 cm were enumerated. DBH measures were made on all trees within the plot, heights were estimated for most (> 75%) trees, and approximately half were aged. In addition, the basal area (BA) and number of stems per ha (SPH) were estimated for the most "abundant" trees within the plot.

2.4.3 Environment

Detailed soil and site description data were collected from many of the study plots. There were some differences in the information collected in the NCR and NWR inventories, and environmental information was more consistently collected in the NWR study; many of the NCR plots had only vegetation information. Variation in edaphic conditions resulted in inconsistent data collection: for example, sites over bedrock or on organic substrates did not always have information on soil particle size (percentage sand, silt and clay). The following soil and site description variables (common to the NCR and NWR inventories) were available for use in this study:

(1) Soil Information

- Canadian System of Soil Classification (CSSC 1978) soil description.
- Mineral and organic horizon pH.
- Humus form.
- Soil horizon descriptions (organic and mineral horizons).
- Soil texture (sand, silt, clay).
- Nutrient information, including
  - Total nitrogen (mineral and/or organic horizon).

- Cation exchange capacity.
- Total exchangeable bases.
- Total base saturation.
- Percent organic matter (mineral and/or organic horizons).

(2) Site Description Data

- Time since last disturbance (stand age).
- Location (latitude, longitude).
- Genetic material.
- Moisture regime (MR).
- Drainage regime (DR).
- Seepage (Se).
- Depth to bedrock (DBR).
- Depth to water table (DWT).
- Depth to gleying (DGl).
- Depth to distinct mottling (DDM).
- Aspect (0° = 360° = North).
- Slope (%).
- Plot topography (e.g. concave, convex, straight).
- Plot position on slope.

2.5 DATA COLLATION

The entire northwest Ontario FEC data set (NWR and NCR inventories), consisting of 2183 plots, was available for use in this study. However, a number of plots were missing information that was considered essential in developing a model of boreal forest dynamics. Therefore, only those plots having all of the following data were retained:

1. Complete vegetation cover data.
2. Stand age.

3. Tree mensurative data (height, DBH).

4. Soil profile information (named horizons and depths).

5. Site description data (e.g. location, moisture and drainage regime, aspect).

Using these criteria, 1483 plots were retained for further consideration. The majority of the excluded plots lacked information on stand age. Following careful individual inspection of the data for these 1483 plots, a further 94 plots were excluded since they lacked critical information and/or contained data that were clearly in error. A total of 1389 stands were used in this study, with 588 occurring in the NCR and 801 in the NWR.

2.5.1 Vegetation Data

The species list was exhaustively checked for errors and 'outliers' (species outside their expected range, and rare species). Some rare and difficult taxonomic groups were combined into broader generic categories. Species nomenclature follows Scoggan (1978) for vascular plants, Anderson et al. (1990) for mosses, Schuster (1966-1974) for hepatics, and Hale (1979) for lichens. Common and scientific names are given in Tables 5.1-5.24 (trees) and in Appendices I-XII (shrubs, herbs, and cryptogams). In some analyses, tree and shrub cover values for each strata were summed to obtain a single species cover value.

2.5.2 Stand Age

A stand age file was available for the NWR inventory. Values in this file were carefully checked against the mensuration data collected for each plot. For the NCR plots, stand age was determined from the oldest tree found in the plot, except in cases where the oldest tree was clearly a fire-remnant.

2.5.3 Soil Data

Differences between data collected in the NCR and NWR regions were too great to permit amalgamation of the soil data sets. These differences included:

1. Soil pit depth was 1 m for NCR vs. 2 m for NWR.

2. Soil horizons were ordered (top to bottom of profile) in NWR, but not in NCR.

3. Nutrient analyses were available for organic horizons in NWR, but not in NCR.

4. Soil texture, nutrient analyses, and so forth were determined for each mineral horizon in NWR, but only for "representative" horizon(s) in NCR.

Soil information was carefully checked for errors and internal-external inconsistencies. Cation exchange capacity (CEC), total exchangeable bases (TEB), and total base saturation (TBS) values proved to be inconsistent between the NCR and NWR data sets. After discussions with personnel at OMNR, it was eventually determined that the NCR values were in error. Therefore, only the nutrient data collected from the NWR sites were used. For each plot, mean values of nutrient (TEB, TBS, CEC, percent nitrogen) and particle-size (percent sand, silt, clay) variables, and mineral horizon pH and organic content, were calculated.

In both the NWR and NCR inventories, depths to bedrock, water table, carbonates, and distinct mottling were recorded in the first 2 m of the soil profile (if the variable did not occur, it was recorded as 2 m). In this study, these variables have been expressed as proportions (e.g. "bedrock occurred within the first 2m in 52% of plots belonging to vegetation class I"). Other soil variables used in this study include genetic material, CSSC soil type, humus form, depth of organic horizon, depths of A and B horizons, moisture regime (0-9, dry-wet), drainage regime (0-7, very rapid-very poor), percent slope, organic layer pH and percent nitrogen, and stoniness (0-5, non-stony-excessively stony, NWR only).

2.6. Data Analysis: A Methodological Overview

2.6.1 Cluster Analysis

Cluster analysis refers to a set of numerical classification procedures for placing n individuals into k non-overlapping categories (where $k < n$). Most clustering methods operate from a matrix of dissimilarities between individuals. Groups are formed by successively fusing individuals or groups that are 'nearest' to each other, based on the computed dissimilarity values.

The clustering algorithm used in this study was Ward's method, a hierarchical agglomerative method based on minimizing the increase in the error sum of squares at each fusion (Orlóci 1978). The resemblance measure used was chord distance (Orlóci 1978), which represents individuals as unit-length vectors based on their species composition. This vector transformation alleviates discrepancies in cover estimates obtained by different field workers and over different years. Percent cover values were square-root transformed to 'down-weight' the importance of ubiquitous species of high cover. The analysis was performed in SPSS (Norusis 1994). In this study, I used cluster analysis to classify sites ≤ 85 years in age (based on their vegetation composition) into 12 boreal forest stand-types (see Chapter 4).

2.6.2 Ordination Methods

Ordination methods are numerical strategies used to represent data structures in a lower dimensional space, while maximally preserving the trended variation present in the data. The data are mapped from the original n-dimensional space into an optimized space of fewer dimensions (Pielou 1984). Ordination axis are extracted in order, with each axis summarizing the maximum amount of trended information not yet accounted for by previous axes. Thus, the first axis is always the "most important", followed by the second, the third, and so forth. Higher (smaller) axes are then discarded on the assumption that most of the intrinsic structure of the data is preserved in first few axes (Pielou 1984).

Principal Component Analysis (PCA)

Principal component analysis (PCA) is a linear ordination method that maps the original data into an optimized space through rigid axis rotation. This is accomplished by performing an eigenanalysis of a dispersion (correlation or covariance) matrix **S**:

$$|\mathbf{S} - \lambda \mathbf{I}| = 0,$$

where λ is a vector of p eigenvalues. PCA repartitions the variance into linearly uncorrelated components. If the data has an underlying linear structure, and if the original variables are highly correlated, the first few components will offer a good representation of the underlying data structure. In this study, I used PCA to quantify the degree redundancy of environmental variables measured in the study plots.

Correspondence Analysis (CA)

Correspondence analysis (CA) is an ordination method that is well-suited to the analysis of non-linear data structures (Hill 1973). The method partitions the total contingency chi-square (χ^2) of the data matrix **X** into a series of linearly additive components. This partitioning is achieved by eigenanalysis of the square symmetric matrix:

$$\mathbf{S} = \mathbf{U}\mathbf{U}'$$

where $U_{ij} = \{[X_{ij}/\sqrt{(X_{i.}X_{.j})}] - [\sqrt{(X_{i.}X_{.j})/X_{..}}]\}$, $X_{i.}$ and $X_{.j}$ are row and column totals respectively, and $X_{..}$ is the grand total. The eigenvalues ($\lambda_i = R^2$) range from 0 to 1, and are squared canonical correlations measuring the strength of the relationship (redundancy) between the rows (variables) and columns (individuals). In this study, I used CA to quantify and summarize vegetation trends.

Canonical Correspondence Analysis (CCA)

Canonical correspondence analysis (CCA) is an extension of CA that was developed to examine the redundancy between two sets of variables (e.g. vegetation and environment) measured on the same set of individuals. This method uses the environmental data to 'constrain' the vegetation ordination axes, using a multiple regression approach (ter Braak 1987). In this study, I used CCA to examine vegetation-environmental relationships in the study plots.

2.6.3 Classification by Discriminant Functions

Discriminant functions analysis is used to classify an individual into g pre-existing classes (Morrison 1990). The model uses a multiple-group classification rule based on minimization of the squared Mahalanobis distance:

$$D_i^2 = (\mathbf{x} - \bar{\mathbf{x}}_i)'\mathbf{S}^{-1}(\mathbf{x} - \bar{\mathbf{x}}_i)$$

Assignment of the 'unknown' individual X is made to the class with the smallest D_i^2. Under the assumption of multivariate normality, D_i^2 follows the χ^2 distribution (Klecka

1980). Following assignment of the 'unknown' individual to class m, the Bayesian misclassification probability (the *a posteriori* probability that X does not belong to class m) is given by:

$$1 - p(H_m \mid X) = \frac{p(X \mid H_m)}{\sum_{i=1}^{g} p(X \mid H_i)}$$

where $p(X \mid H_i)$ is the *a priori* probability of belonging to class i. In this study, I use discriminant functions classification to individually assign older stands (> 85 years in age) to vegetation types or groups (see Chapter 5).

CHAPTER 3
VEGETATION-ENVIRONMENT RELATIONSHIPS

3.1 INTRODUCTION

In boreal forest ecosystems, vegetation composition is thought to be determined primarily by environmental factors (e.g. Ritchie 1956; Maycock and Curtis 1960; Dix and Swan 1971; Frey 1973; Carleton and Maycock 1980; Leduc et al. 1992). However, few studies have examined boreal forest vegetation-environmental relationships at the landscape scale. Instead, boreal communities are described in terms of 'typical' species assemblages and/or 'average' environmental attributes. However, other factors such as fire (Heinselman 1973), herbivory (Blais 1983) and initial floristic composition (Egler 1954) may also affect floristic composition. It is important to examine and quantify the relative roles of these various factors in determining boreal forest stand composition.

Vegetation-environment relationships are scale-dependent. At the vegetation biome scale, macroclimate exerts a strong controlling influence (Bonan and Sirois 1992; Lenihan 1993). At the landscape level, soil moisture and nutrient status are considered to be important determinants of floristic composition (Dix and Swan 1971; Carleton and Maycock 1978, 1980; Kenkel 1986, 1987; Tonteri et al. 1990), although topographic variation may also exert a strong effect vegetation complexity (Frelich and Reich 1995b). At the stand level, clonal species may be less responsive to environmental variation than non-clonal species (Leduc et al. 1992). Finally, microclimatic factors strongly affect species composition and structure in the understory and cryptogam layers of boreal forest ecosystems (Carleton 1990; Økland and Eilertsen 1994).

At the landscape level, studies of vegetation-environment relationships in boreal forest ecosystems can be categorized according to spatial scale (large vs. small geographical area) and the number of environmental variables utilized in the analysis (**Table 3.1**). Unfortunately, most studies have used very few or no environmental variables. Økland and

TABLE 3.1. Examples of previous boreal forest studies based on area and environmental data collected.

	Extensive Geographic Area	Restricted Geographic Area
No Environmental Data	Ritchie 1956; La Roi 1967; Tonteri et al. 1990	Mueller-Dombois 1964
Minimal Environmental Data	Carleton & Maycock 1978, 1980; Zoladeski & Maycock 1990	Dix & Swan 1971; Kenkel 1986, 1987; La Roi 1992
Extensive Environmental Data		Økland & Eilertsen 1994

Eilertsen (1994) had 33 environmental variables at their disposal, but their study was over a very small region (eight transects, 80-450 m in length) in southern Norway and was primarily concerned with species composition in the understory. A comprehensive examination of vegetation-environmental relationships at a landscape scale is lacking for boreal forest ecosystems.

In this chapter, I undertake a detailed study of vegetation-environmental relationships in boreal forest vegetation, utilizing 29 environmental variables measured in 320 forest stands in northwest Ontario. The specific objectives are: (1) to examine the degree of redundancy amongst the 29 measured environmental variables; (2) to determine which environmental factors are most important in determining vegetation structure and composition; and (3) to quantify the strength of the relationship between the vegetation and environmental factors.

3.2 Materials and Methods

3.2.1 Data Description

A total of 320 stands containing 252 species were used in the analysis. Only stands from the NWR were considered, since the NCR soil data were incomplete. To minimize potential confounding of vegetation-environmental relationships and successional dynamics, only stands less than 100 years old were included. The analysis was also restricted to stands on mineral substrates that contained complete data for 29 soil variables. Twenty-one of these soil variables were measured on a ratio-scale: depth (cm) of the O, A and B horizons, and solum depth; pH of the O, A, B and C horizons; percent available nitrogen of the O, A and B horizons; percent organic matter of the O, A and B horizons; total exchangeable bases (TEB, meq/100g) and percent total base saturation (TBS) of the A and B horizons; and soil particle size (percentage of sand, silt and clay, as a weighted average over the mineral horizons to 2 m). All ratio-scale variables except pH were log-transformed in order to meet assumptions of multivariate normality. Three ordinal variables were also included: moisture regime (1=7, with 1 representing the driest stands); drainage regime (1-6, with 1 representing very poorly drained sites); and stoniness (1-6, with 1 representing no stones). Finally, presence-absence of the five variables in the first 2 m of the soil profile were included: carbonates, bedrock, water table, mottling, and seepage.

3.2.2 Data Analysis

Principal Component Analysis (PCA)

Principal component analysis, based on a correlation matrix, was used to quantify variable redundancy and summarize relationships between the 29 soil variables. This analysis was performed using the program SYNTAX-5 (Podani 1995).

Canonical Correspondence Analysis (CCA)

Canonical correspondence analysis (ter Braak 1986) was used to summarize and quantify vegetation-environmental relationship in the 320 stands. The vegetation data were square root transformed and rare species were 'down-weighted'. This analysis was performed using the CANOCO package (ter Braak 1987).

3.3 Results

3.3.1 Redundancy of Soil Variables

Intervariable redundancy among the twenty-nine soil variables is high. The first ordination axis alone accounts for ca. 25% of the total variance, and about half of the total (ca. 48%) is accounted for by the first three axes. The eigenvalue scree plot (**Fig. 3.1**) suggests that the first three PCA axes offer a parsimonious representation of the data structure.

Biplot scores of the 29 variables on the first two PCA ordination axes are displayed in **Fig. 3.2**. The first axis is broadly interpretable as a soil nutrient gradient, from acidic and nutrient-deficient sands to pH-neutral to basic, nutrient-rich clays. Clay soils have higher pH, TBS, and TEB values, and a well-developed A-horizon. Carbonates are often present in the first 2 m of the soil profile. By contrast, the larger particle size of sandy soils results in fewer bonding sites for cations (reduced surface area per unit volume), resulting in lower cation exchange capacity and higher acidity (Fitzpatrick 1974). The second axis is interpreted as a soil moisture gradient from well-drained, thick solum soils to moist soils with a prominent organic layer. Since particle size affects soil structure and porosity (Barber 1995), clay soils tend to be moister and less well-drained than sandy soils. The third axis (not shown) separates the shallow and/or stony soils from the moist, organic substrates.

3.3.2 Vegetation-Environment Relationships

Approximately 14.8% of the total contingency chi-squared was accounted for by the first two CCA ordination axes, compared to ca. 20% from the correspondence analysis (CA) of the vegetation data alone (CA results not shown). This suggests that the major trends in the vegetation data are strongly correlated with environmental variation. The first two canonical eigenvalues account for 41.6% and 13.0% respectively of the canonical or 'constrained' eigenstructure (or 54.6% on the first two CCA axes). Redundancy between the vegetation and environmental data (the ratio of totals of the constrained and unconstrained eigenvalues) is 0.821/3.142 = 26.13%. A bootstrap Monte Carlo test with 99 permutations (ter Braak 1987) confirmed a statistically significant relationship ($p < 0.001$) between the vegetation and environment data sets.

Soil Variables

The first CCA ordination axis is interpretable as a gradient of increased soil nutrient availability, from right to left (**Fig. 3.3**). Sites with clay soils of high cation exchange capacity (CEC), total exchangeable bases (TEB), pH and nitrogen availability in the O and A soil horizons occur at the left, while sandy, nutrient-deficient soils are found at the right. The second axis represents a gradient of decreasing soil moisture. Stands on well-drained substrates (sandy and/or stony soils, bedrock sites) occur at the bottom of the ordination, while poorly-drained, moist stands with high organic matter accumulation, a mottled soil profile occur toward the top of the scatterplot. The third axis (not shown) separates acidic from basic substrates.

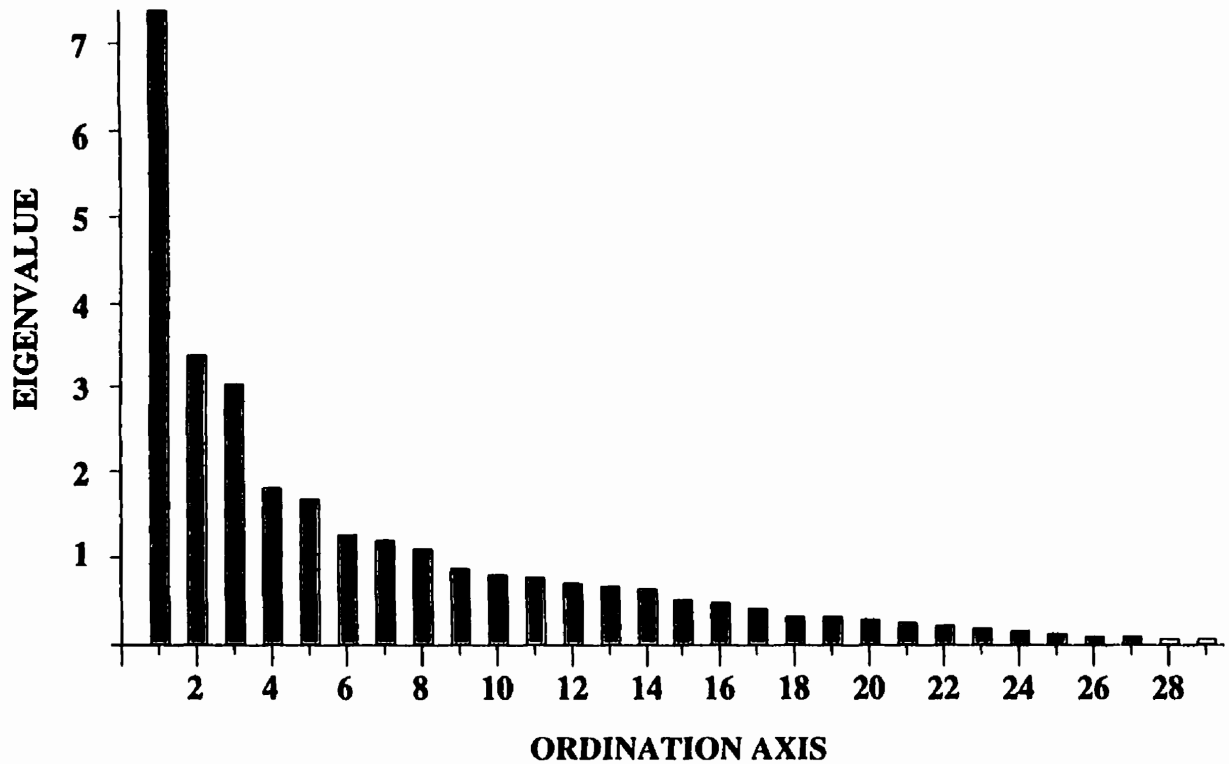


Figure 3.1. Eigenvalue scree plot (ordination axis vs. eigenvalue) for the principal component analysis of the 29 environmental variables measured on 320 plots, based on a correlation matrix.

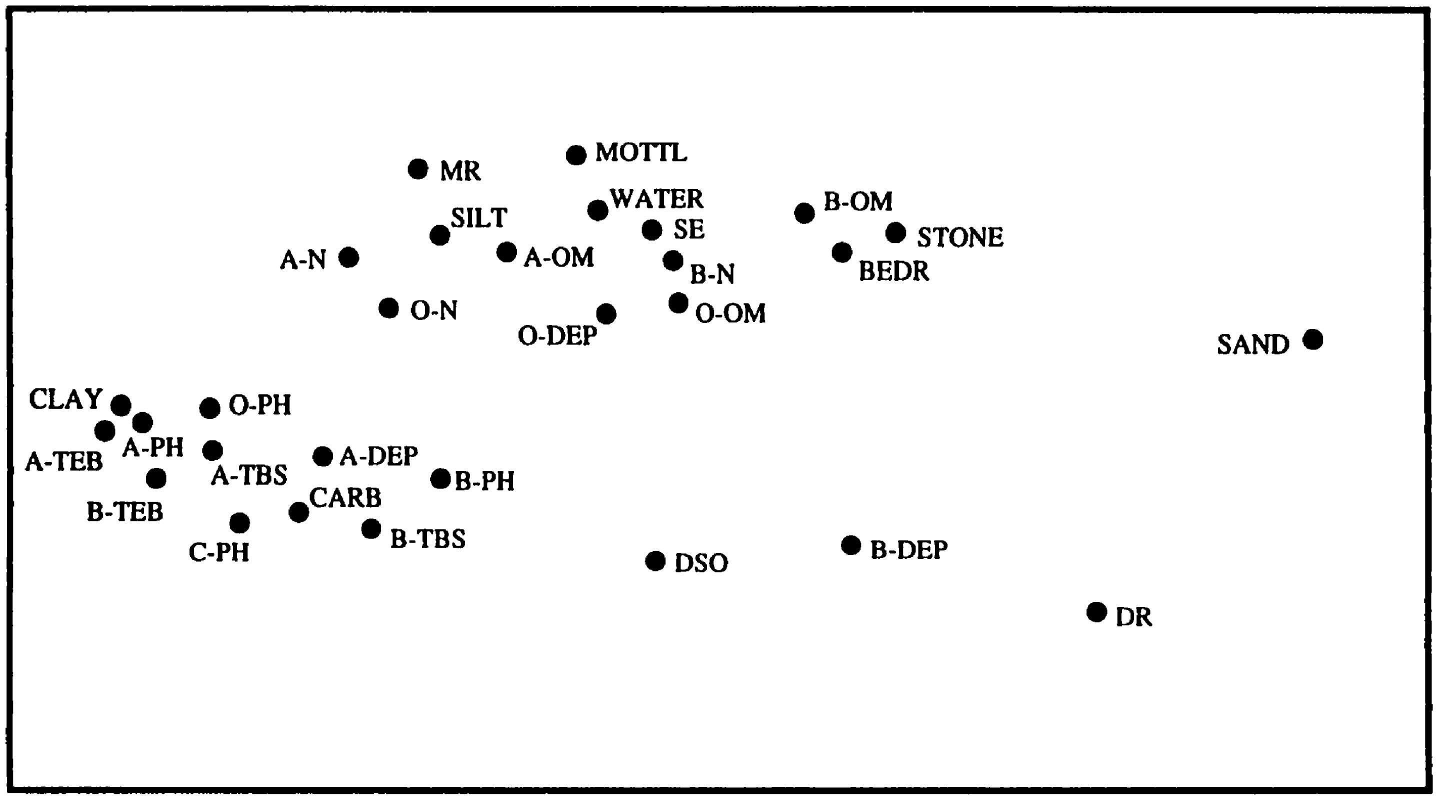


Figure 3.2. Principal component analysis (axis 1 vs. axis 2), showing the biplot positions of the 29 environmental variables: Codes: O = O-horizon, A = A-horizon, B = B-horizon, C = C-horizon, DR = drainage regime, MR = moisture regime, TEB = total exchangeable bases, TBS = total base saturation, OM = organic matter, DSO = depth of solum, N = nitrogen, CARB = presence of carbonates, MOTTL = presence of prominent mottling, BEDR = presence of bedrock, SEEP = presence of seepage, STONE = stoniness (refer to text for details).

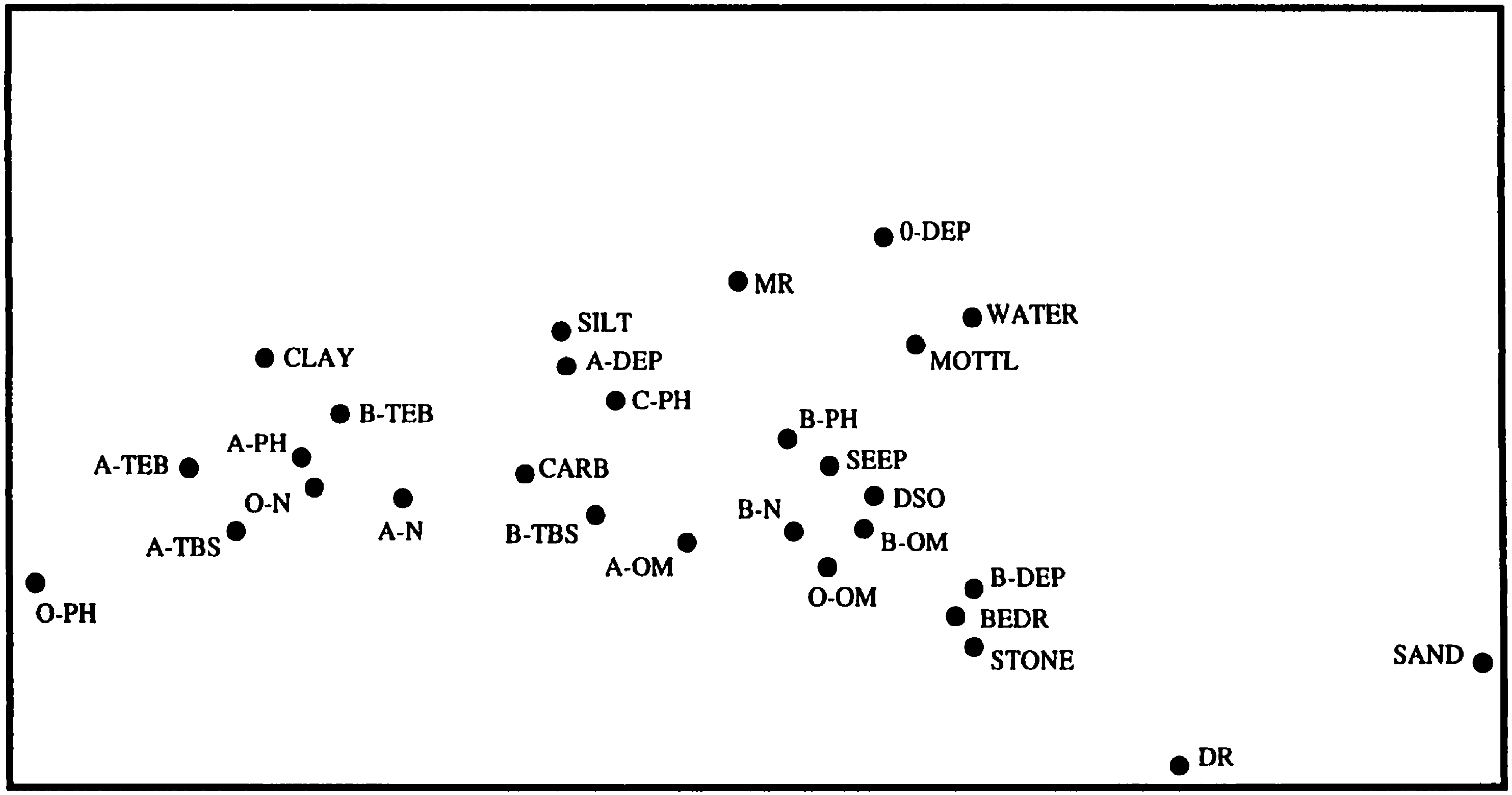


Figure 3.3. Canonical correspondence analysis (axis 1 vs. axis 2), showing positions of the 29 soil variables. Symbols code: O = O-horizon, A = A-horizon, B = B-horizon, C = C-horizon, DR = drainage regime, MR = moisture regime, TEB = total exchangeable bases, TBS = total base saturation, OM = organic matter, DSO = depth of solum, N = nitrogen, CARB = presence of carbonates, MOTTL = presence of prominent mottling, BEDR = presence of bedrock, SEEP = presence of seepage, STONE = stoniness (refer to text for details).

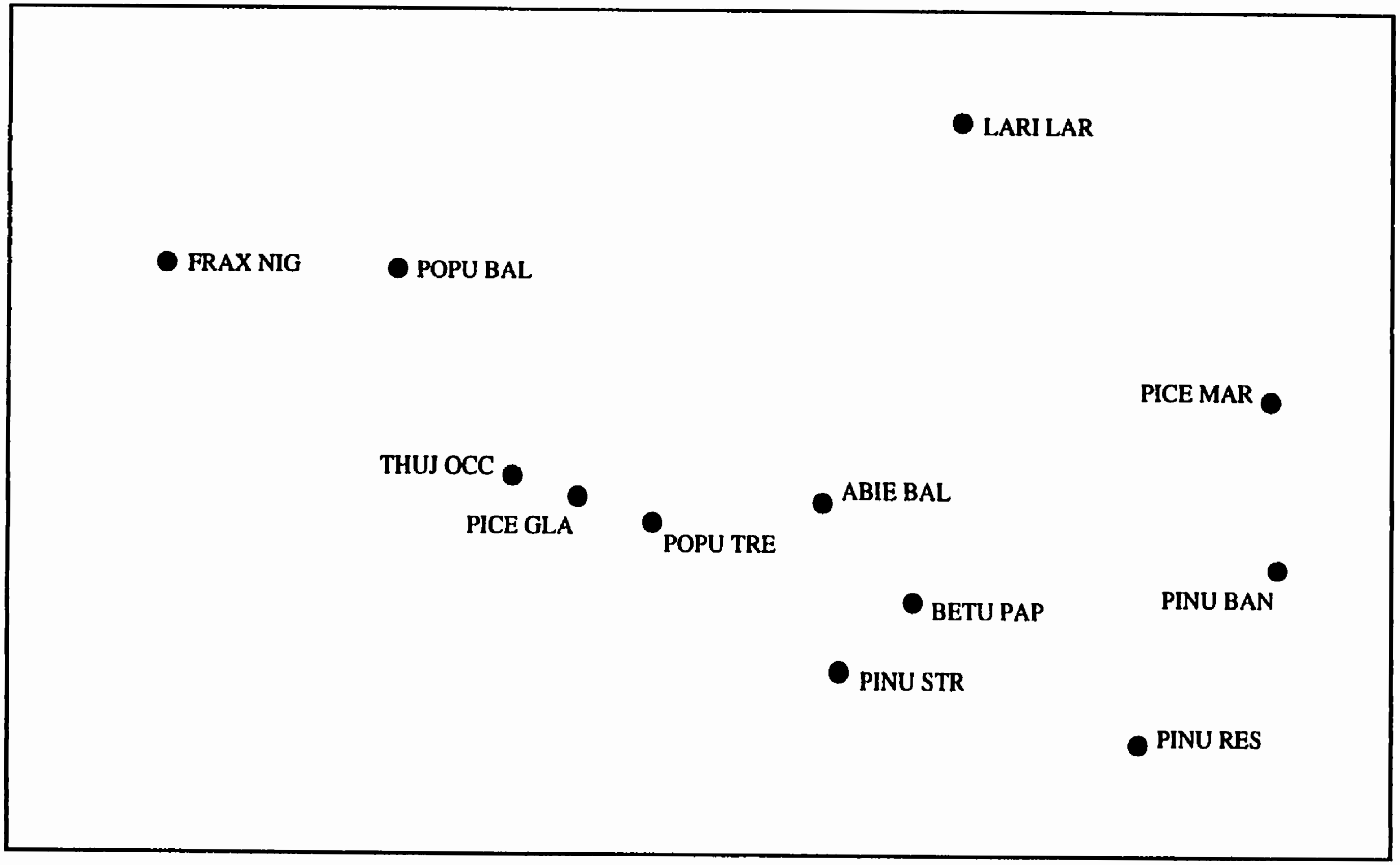


Figure 3.4. Canonical correspondence analysis (axis 1 vs. axis 2), showing positions of 12 of the most abundant tree species. Codes: ABIE BAL = *Abies balsamea* (balsam fir); BETU PAP = *Betula papyrifera* (paper birch); FRAX NIG = *Fraxinus nigra* (black ash); LARI LAR = *Larix laricina* (eastern larch); PICE GLA = *Picea glauca* (white spruce); PICE MAR = *Picea mariana* (black spruce); PINU BAN = *Pinus banksiana* (jack pine); PINU RES = *Pinus resinosa* (red pine); PINU STR = *Pinus strobus* (white spruce); POPU BAL = *Populus balsamifera* (balsam poplar); POPU TRE = *Populus tremuloides* (trembling aspen); THUJ OCC = *Thuja occidentalis* (eastern white cedar).

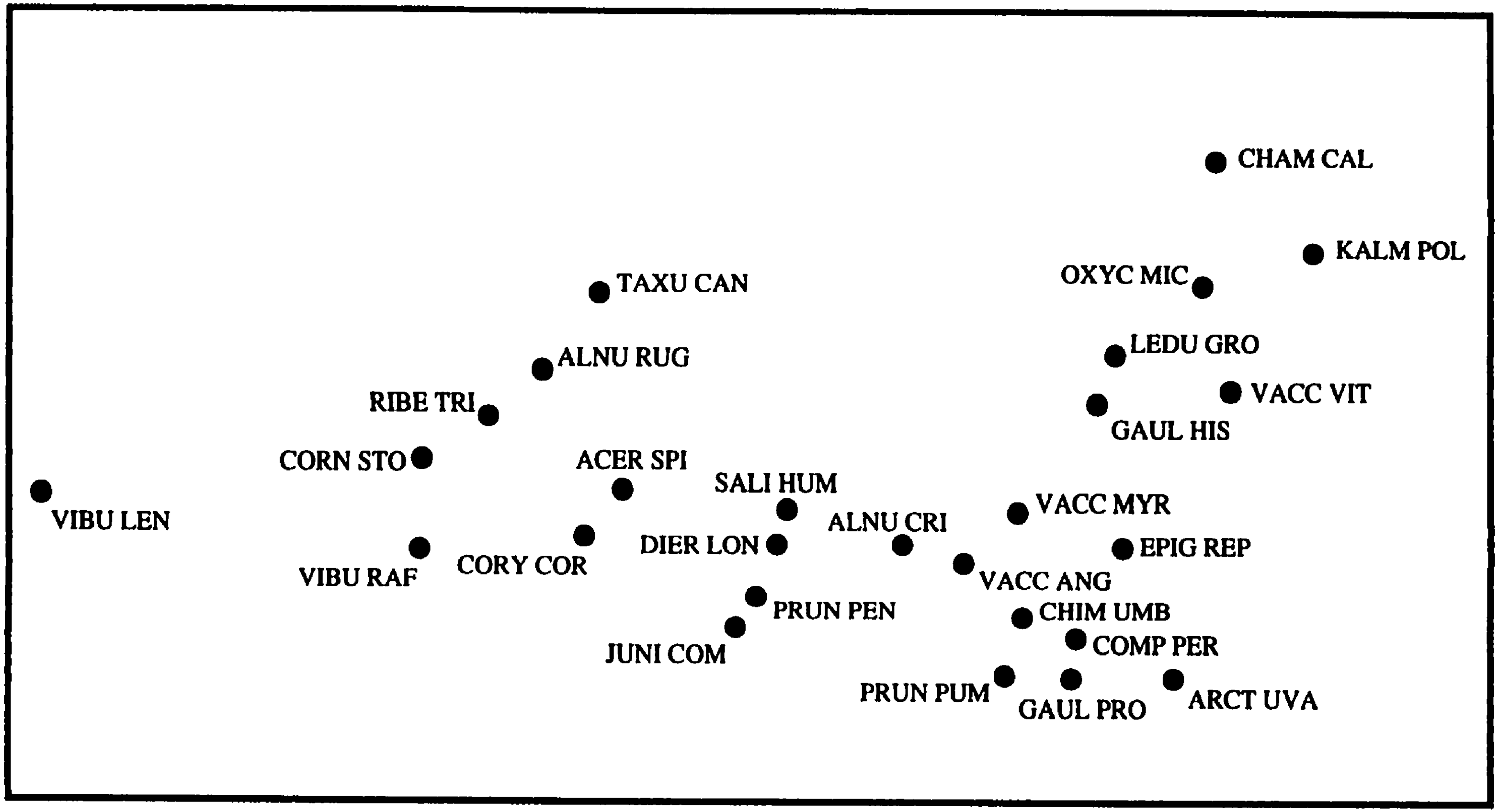


Figure 3.5. Canonical correspondence analysis (axis 1 vs. axis 2), showing positions of 27 representative shrub species. Codes: ACER SPI = *Acer spicatum* (mountain maple); ALNU CRI = *Alnus crispa* (green alder); ALNU RUG = *Alnus rugosa* (speckled alder); ARCT UVA = *Arctostaphylos uva-ursi* (bearberry); CHAM CAL = *Chamaedaphne calyculata* (leatherleaf); CHIM UMB = *Chimaphila umbellata* (prince's pine); COMP PER = *Comptonia peregrina* (sweet fern); CORN STO = *Cornus stolonifera* (red-osier dogwood); CORY COR = *Corylus cornuta* (beaked hazel); DIER LON = *Diervilla lonicera* (bush honeysuckle); EPIG REP = *Epigaea repens* (wintergreen); GAUL HIS = *Gaultheria hispidula* (creeping snowberry); GAUL PRO = *Gaultheria procumbens* (wintergreen); JUNI COM = *Juniperus communis* (common juniper); KALM POL = *Kalmia polyfolia* (bog laurel); LEDU GRO = *Ledum groenlandicum* (labrador tea); OXYC MIC = *Oxycoccus microcarpon* (bog cranberry); ; PRUN PUM = *Prunus pumila* (sand cherry); PRUN PEN = *Prunus pensylvanica* (pin cherry); RIBE TRI = *Ribes trieste* (gooseberry); SAL HUM = *Salix humilis* (upland willow); TAXU CAN = *Taxus canadensis* (Canada yew); VACC ANG = *Vaccinium angustifolium* (blueberry); VACC MYR = *V. myrtylloides* (blueberry); VACC VIT = V. *vitis-idaea* (cranberry); VIBU RAF = *Viburnum rafinesquianum* (downy arrowwood); VIBU LEN = *V. lentago* (nannyberry).

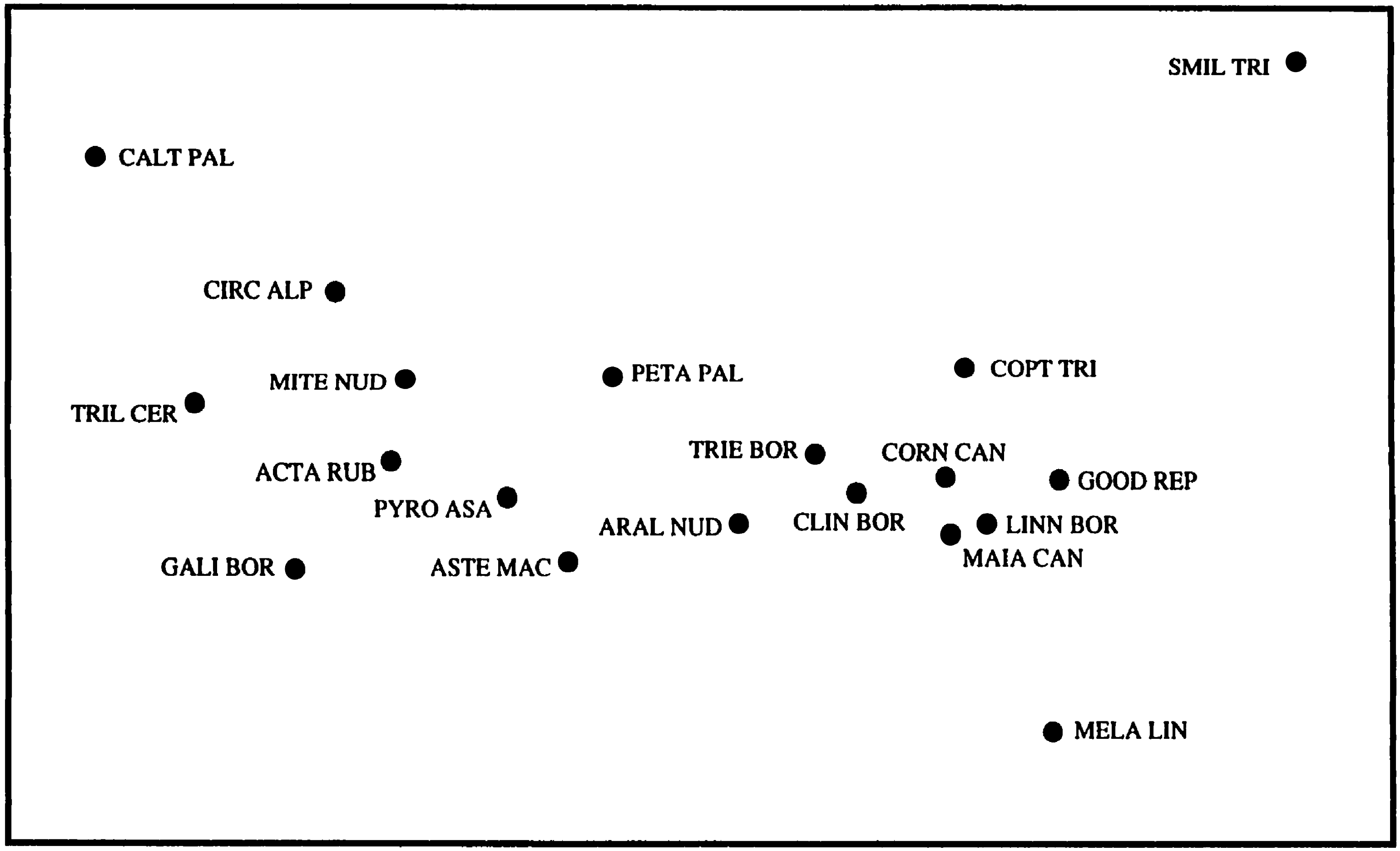


Figure 3.6. Canonical correspondence analysis (axis 1 vs. axis 2), showing positions of 19 representative herbaceous species. Codes: ACTA RUB = *Actaea rubra*; ARAL NUD = *Aralia nudicaulis*; ASTE MAC = *Aster macrophyllus*; CALT PAL = *Caltha palustris*; CIRC ALP = *Circaea alpina*; CLIN BOR = *Clintonia borealis*; COPT TRI = *Coptis trifoliata*; CORN CAN = *Cornus canadensis*; GALI BOR = *Galium boreale*; GOOD REP = *Goodyera repens*; LINN BOR = *Linnaea borealis*; MAIA CAN = *Maianthemum canadense*; MITE NUD = *Mitella nuda*; PETA PAL = *Petasites palmatus*; PYRO ASA = *Pyrola asarifolia*; SMIL TRI = *Smilacina trifoliata*; TRIE BOR = *Trientalis boralis*; TRIL CER = *Trillium cernuum*.

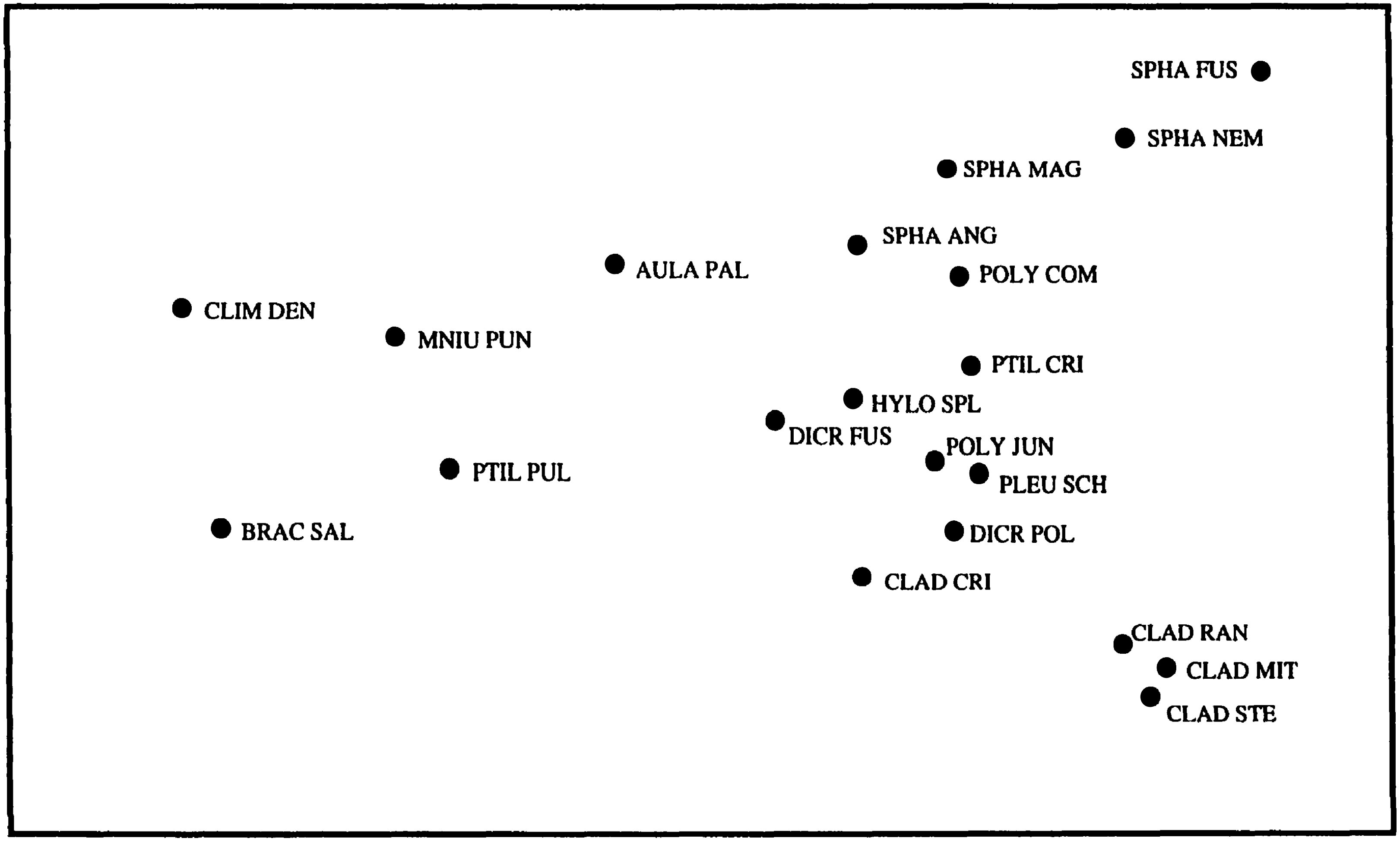


Figure 3.7. Canonical correspondence analysis (axis 1 vs axis 2), showing the positions of 20 representative cryptogam species. Codes: AULA PAL = *Aulacomium palustre*; BRAC SAL = *Bracythecium salebrosum*; CLAD MIT = *Cladina mitis*; CLAD RAN = *Cladina rangiferina*; CLAD STE = *Cladina stellaris*; CLAD CRI = *Cladonia cristatella*; CLIM DEN = *Climacium dendroides*; DICR FUS = *Dicranum fusescens*; DICR POL = *Dicranum polysetum*; HYLO SPL = *Hylocomium splendens*; MNIU PUN = *Mnium punctatum*; PLEU SCH = *Pleurozium schreberi*; POLY COM = *Polytrichum commune*; POLY JUN = *Polytrichum juniperinum*; PTIL CRI = *Ptilium crista-castrensis*; PTIL PUL = *Ptilidium pulcherrum*; SPHA ANG = *Sphagnum angustifolium*; SPHA FUS = *Sphagnum fuscum*; SPHA MAG = *Sphagnum magellanicum*; SPHA NEM = *Sphagnum nemoreum.*

Vegetation

The tree species most prevalent on nutrient-deficient substrates are jack pine, red pine and black spruce (**Fig. 3.4**). Black spruce also shows a preference for moister sites. At intermediate nutrient levels, eastern larch is most prevalent in hygric environments, white pine and white birch in more xeric sites, and balsam fir, trembling aspen and white spruce in mesic sites. Black ash, balsam poplar, and eastern white cedar are most prevalent in moist, nutrient-rich sites. Similar trends are seen in the shrub species (**Fig. 3.5**). Moist, nutrient-deficient stands are dominated by ericaceous shrubs such as leatherleaf, labrador tea, bog cranberry and northern bog-laurel. Dry, nutrient-deficient stands are typified by bearberry, blueberry species, prince's-pine, juniper, green alder, bush honeysuckle, sweet fern and upland willow. Moister, more nutrient-rich stands contain speckled alder, Canada yew, mountain maple and pussy willow, while drier areas are dominated by beaked hazelnut and chokecherry. High-nutrient sites are characterized by species such as red-osier dogwood, downy arrowwood and nannyberry. These same environmental trends are repeated in the herb and cryptogam layers (**Figs. 3.6-3.7**). Species characteristic of moist, nutrient-limited habitats include the herb *Smilacina trifoliata* and the *Sphagnum* mosses. Drier sites are dominated by herbs *Melampyrum lineare*, *Linnaea borealis*, *Geocaulon lividum* and *Goodyera repens*, reindeer lichens (*Cladina* spp.), and the mosses *Pleurozium schreberi* and *Polytrichum* spp. Nutrient-rich stands are characterized by species such as *Osmunda claytoniana*, *Trillium cernuum*, *Actaea rubra*, *Circaea alpina* and *Mitella nuda*, and by the mosses *Climacium dendroides*, *Mnium punctatum*, and *Brachythecium* spp. A number of species occur at intermediate nutrient levels, including *Aster macrophyllus*, *Trientalis borealis*, *Aralia nudicaulis*, and *Viola* spp. Overall, mosses dominate the nutrient-deficient stands, while herbs are more abundant where nutrient levels are higher.

3.4 DISCUSSION

The results reveal that the 29 environmental variables are highly redundant. This suggests that it may be sufficient to obtain data on a few carefully selected variables when examining landscape-level vegetation-environmental relationships in the boreal forest. The results reveal two main environmental gradients related to soil nutrient and moisture availability, suggesting that the collection of variables relating to nutrient status (e.g. soil texture, total exchangeable bases), moisture availability (e.g. moisture and drainage regime), and potential rooting depth (e.g. depth to bedrock) may be sufficient to characterize the environmental conditions of a stand.

A strong relationship has been demonstrated between boreal forest stand composition and environmental (mainly soil) variables, suggesting that environmental variation plays a critical role in determining boreal forest vegetation composition. Previous studies have suggested that soil moisture and nutrient status are important factors, but did not define this relationship in a rigourous way (e.g. Ritchie 1956; Dix and Swan 1971; Carleton and Maycock 1978, 1980; Kenkel 1986, 1987; Tonteri et al. 1990). The constrained CCA ordination is broadly triangular in shape, with the three vertices defining wet-rich, wet-poor, and dry-poor soil moisture-nutrient combinations. The combination dry-rich is rare, possibly because nutrient cycling and decomposition in boreal ecosystems is moisture-limited. The strong vegetation-environmental relationship elucidated in this study suggests that environmental information can be used to broadly classify vegetation, or conversely that floristic composition is a strong indicator of the environmental conditions that prevail at a site (Kenkel 1987). Nonetheless, an appreciable proportion of variation in the data structure remains unexplained by vegetation-environmental redundancy. Some of this remaining variation is undoubtedly attributable to random effects or 'noise' (Gauch 1982). Other potential factors include variation in initial floristic composition (Egler 1954), herbivory (Blais 1983), disturbance history and regimes (Wein and MacLean 1983; Johnson 1992), and landscape structure and complexity (Frelich and Reich 1995a,b).

CHAPTER 4

STAND-TYPES: CLASSIFICATION, DESCRIPTION AND RELATIONSHIPS

4.1 INTRODUCTION

Using a combined classification (TWINSPAN) and ordination (correspondence analysis) approach, the forest ecosystem classification (FEC) for north-western Ontario recognized 38 vegetation-types and 11 treatment units (Sims et al. 1989). These vegetation types provided a diagnostic summary of variation in boreal forest composition and community structure in the ecoregion. Since the data used to produce the FEC included stands of various ages, vegetation-environment relationships and stand dynamics (succession) are undoubtedly confounded. Thus some of the vegetation types described may represent different successional stages of the same forest-stand type. An approach that recognizes the dynamic aspect of forest stand structure and composition would be useful in relating vegetation-types to their relative successional status. In this chapter, I describe and summarize twelve stand-types obtained by classifying 721 young (≤ 85 years old) stands. The successional trajectories for these twelve stand-types are summarized in Chapter 5.

4.2 MATERIALS AND METHODS

4.2.1 Data Structure

I used the following approach to develop forest stand successional trajectories:

1. Develop a classification based on vegetation composition using only younger (≤ 85 years) stands. Limiting the classification to younger stands minimizes potential confounding between vegetation-environment relationships and temporal stand dynamics. I used the relationships developed in Chapter 3 to determine the environmental factors having the greatest influence on stand floristic composition.

2. Assign each of the older stands (> 85 years) to one of the vegetation classes defined in the above step. Assignments are based on: (a) environmental variables, particularly those that are invariant over time, e.g. soil particle size; (b) vegetation composition, e.g. an older stand with high cover of black ash should be assigned to a class having high cover of this species.
3. Develop successional (stand dynamic) trajectories for each vegetation class, based on comparisons of the structure-composition of younger (≤ 85 years) and older (> 85 years) stands. Compare the successional trajectories of the different vegetation classes to determine degrees of convergence or divergence.

Of the 1389 stands used in this study, 721 (304 from NCR, 417 from NWR) were ≤ 85 years in age, and the remaining 668 (284 from NCR, 384 from NWR) were >85 years old. While a division at stand age 85 is necessarily somewhat arbitrary, it can be justified:

1. In boreal forest stands, initially-establishing trees (following a fire, for example) are still present in the upper canopy by age 85, while later successional trees only occur in the lower canopy layers (Heinselman 1973; Cogbill 1985; Frelich and Reich 1995a,b).
2. The data are conveniently divided approximately in half. Thus, the initial classification is based on a large sample size (721 stands), as is the development of successional trajectories (688 stands).

4.2.2 Classification and Description of Stand-Types

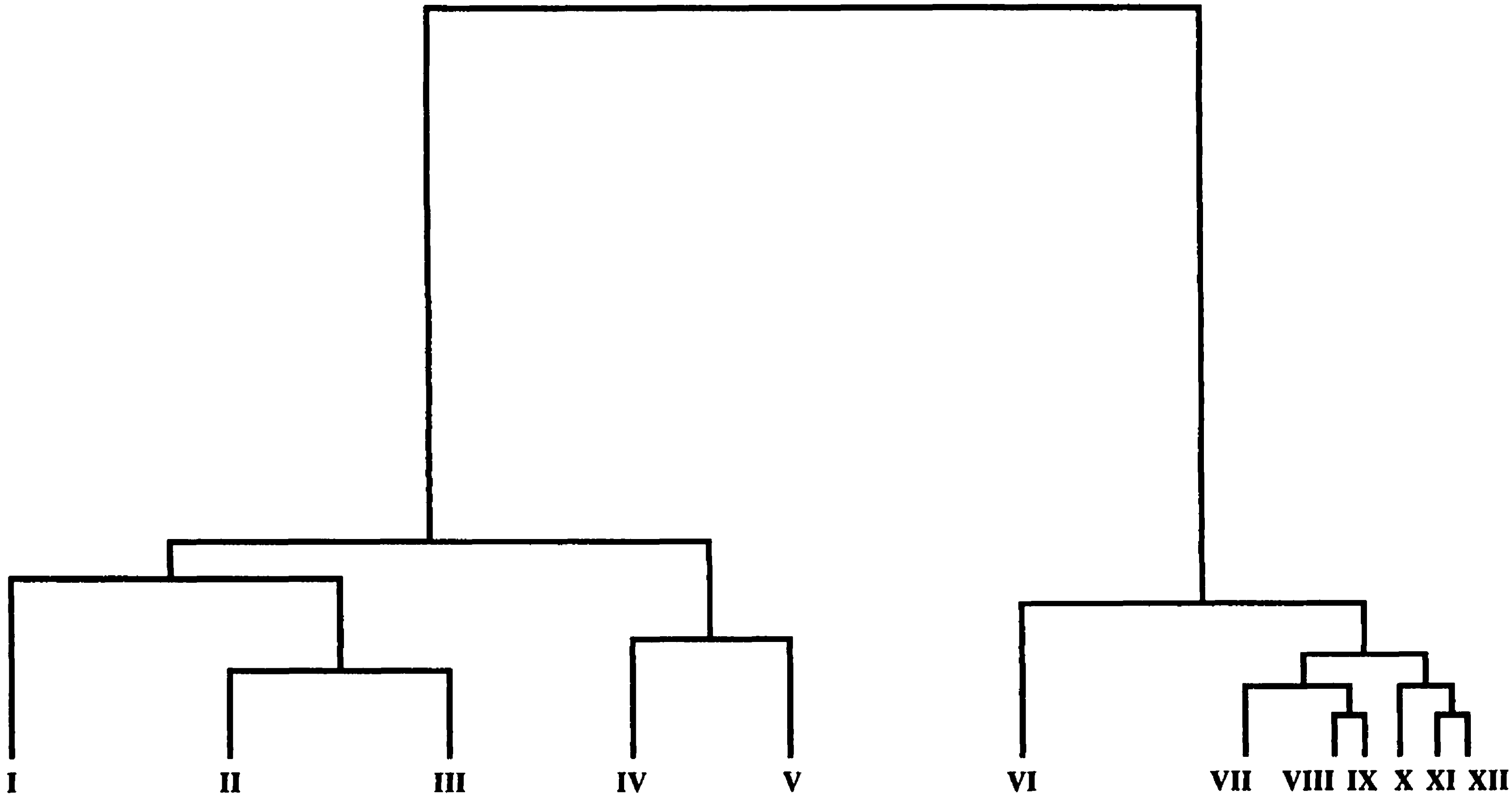
A stand classification was obtained using cluster analysis (Ward's method), based on a chord distance dissimilarity matrix between stands. The cluster analysis was performed using the SPSS statistical package (Norusis 1994). Chord distance standardizes stands to unit vector length, thus alleviating discrepancies in cover estimates by different field workers and over different years. Percent cover values were square-root transformed to down-weight the importance of ubiquitous species of high cover. An initial analysis based on separate tree cover estimates in the four canopy layers ('pseudo-species') proved uninterpretable. Species cover values were therefore summed across all canopy layers to obtain a single cover value for each tree species. Correspondence analysis (CA), performed in CANOCO (ter Braak 1987), was used to produce a two-dimensional summarization of the relationship between the twelve stand-types delineated by cluster analysis. In CA, percent cover values were square-root transformed and rare species were downweighted to reduce the importance of ubiquitous species of high cover.

For each of the twelve stand-types delineated in the cluster analysis, summary tables (mean, standard deviation, sample size) were produced for the following: (a) species richness, diversity and evenness; (b) soil particle size, texture and nutrient status; (c) soil order class; (d) genetic material class; (e) presence of bedrock, carbonates, distinct mottling and water in the soil profile; (f) soil humus-form type. Summary tables were based on data from both younger (≤ 85 years old) and older (> 85 years old) stands assigned to the twelve stand-types (see Chapter 5). Principal component analysis (PCA), based on mean values, was also used to summarize environmental relationship among the twelve stand-types. Two data sets were analyzed in PCA: (a) 'soil-landscape' variables (percent sand, silt and clay, depth of organic matter, A-, and B-horizons, pH, moisture regime); (b) 'nutrient' variables (percent nitrogen and organic matter in mineral soil, TBS and TEB). For these two data sets, means were computed based on log-transformed data to meet the assumption of multivariate normality. These analyses were performed using the SYNTAX-V package (Podani 1994).

4.3 Results and Discussion

4.3.1 Cluster Analysis

The cluster analysis result for the 721 younger stands (≤ 85 years in age) is presented in dendrogram form in **Fig. 4.1**. Twelve stand-types (labelled I-XII) were recognized, and successional trajectories were developed for each (see Chapter 5). The number of stands in each stand-type (721 younger stands classified in cluster analysis, and the 668 assigned older stands, see Chapter 5) are presented in **Table 4.1**. The initial dichotomy in the



I. Jack Pine - Feathermoss, *n = 103*
II. Jack Pine - Black Spruce - Feathermoss, *n = 92*
III. Black Spruce - Feathermoss, *n = 111*
IV. Black Spruce - Sphagnum, *n = 58*
V. White Spruce - Balsam Fir Mixed Wood, *n = 78*
VI. Trembling Aspen, *n = 130*
VII. Birch - Trembling Aspen Mixed Wood, *n = 65*
VIII. Red Pine, *n = 18*
IX. White Pine, *n = 14*
X. Birch - Tall Shrub Mixed Wood, *n = 26*
XI. Balsam Poplar, *n = 17*
XII. Black Ash, *n = 9*

Figure 4.1. Cluster analysis dendrogram of 721 stands less than 85 years old. Ward's clustering method, based on a chord distance matrix.

TABLE 4.1. Number of stands by stand-type, stand age (≤ 85 vs. > 85 years), and location (NCR vs. NWR).

						Stand-Type							
	all	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**	**XII**
≤ 85 years													
NCR	**304**	36	22	45	31	45	63	21	1	8	18	9	5
NWR	**417**	67	70	66	27	33	67	44	17	6	8	8	4
Total	**721**	103	92	111	58	78	130	65	18	14	26	17	9
> 85 years													
NCR	**284**	19	18	67	54	22	45	11	8	7	15	13	5
NWR	**384**	59	36	75	78	17	21	20	36	23	2	7	10
Total	**668**	78	54	142	132	39	66	31	44	30	17	20	15
Grand Total	**1389**	**181**	**146**	**253**	**190**	**117**	**196**	**96**	**62**	**44**	**43**	**37**	**24**

dendrogram separated the feathermoss-dominated 'true' boreal coniferous stands (jack pine, black spruce, balsam fir, white spruce) from a group consisting of herb-rich deciduous stands (trembling aspen, white birch, balsam poplar and black ash) and near-boreal conifer stands (red and white pine). On the left branch, a second dichotomy separated upland jack pine-black spruce stands from a group containing black spruce bogs and mixed balsam fir-white spruce stands. On the right branch, the second dichotomy separated out closed trembling aspen stands from the remaining stands.

4.3.2 Stand-Type Descriptions

The following overview of the 12 stand-types emphasizes both the floristic composition of younger (≤ 85 years old) stands and vegetation-environment relationships. Summative information is presented in **Tables 4.2 - 4.9.**

I. Jack Pine - Feathermoss

The canopy is dominated by jack pine, with black spruce, trembling aspen and white birch as occasional codominants. Black spruce generally dominates the sub-canopy and sapling layers, although regeneration of jack pine is occasionally seen. Feathermosses (mostly *Pleurozium schreberi*), reindeer lichens (*Cladina* spp.) and low ericaceous shrubs dominate the understory. Species diversity and richness are comparatively low. Soils are acidic, coarse-textured sands (glaciofluvial brunisols) of low nutrient status. Many stands occur over bedrock, and substrates are often stony.

II. Jack Pine - Black Spruce - Feathermoss

The canopy typically consists of a codominant mixture of jack pine and black spruce. Black spruce is abundant in the subcanopy and sapling layers. The understory is dominated by feathermosses, low ericaceous shrubs, *Cornus canadensis*, and *Maianthemum canadense*. Species richness and diversity are low, as is evenness (lowest of all the stand-types). Soils are similar to those of stand-type I, but are somewhat finer-textured, less acidic, and of higher nutrient status. Distinct mottling occurs in about one-third of the soil profiles.

III. Black Spruce - Feathermoss

The canopy is dominated by black spruce, with jack pine and trembling aspen as occasional codominants. Black spruce also dominates the subcanopy, while both balsam fir and black spruce occur as saplings. The understory is dominated by feathermosses. Shrub and herb cover are low, with ericaceous shrubs and *Cornus canadensis* predominating. As with stand-types I and II, species richness, diversity and evenness are low. These stands occur on more finely-textured soils than stand-types I and II. Soil moisture is also greater: over half of the stands show distinct mottling in the soil profile, and depth to water table is < 2 m in over 25% of the stands.

IV. Black Spruce - Sphagnum

Most of these stands have black spruce as the canopy dominant, although eastern larch, eastern white cedar, jack pine and balsam fir are occasional codominants. Black spruce and balsam fir are common in the subcanopy and sapling layers. Dominant understory species include *Alnus rugosa*, *Ledum groenlandicum*, *Carex* spp., peat-mosses (*Sphagnum* spp.), and feathermosses (mostly *Pleurozium schreberi*). These stands are mainly closed-canopy bogs and fens with a thick, poorly-decomposed peaty organic layer. Species richness and diversity are somewhat higher than in stand-types I-III, attributable mainly to a higher number of cryptogam species (mainly from the genus *Sphagnum*). Soil moisture is higher and drainage is generally poor. The soil profile shows distinct mottling in most stands, and depth to the water table is generally < 2 m.

V. White Spruce - Balsam Fir Mixed Wood

These mixed-wood stands are generally dominated by a mixture of mostly coniferous species (white spruce, black spruce, balsam fir, jack pine) in the canopy, although deciduous species (mainly trembling aspen and white birch) are occasional codominants. The subcanopy and sapling layers are dominated by balsam fir, although both black and white spruce are also relatively common. Tall shrubs (e.g. *Acer spicatum*, *Corylus cornuta*, *Sorbus* spp.) are frequent (though generally of low cover) as is the low shrub *Diervilla* *lonicera*. The rich herb layer is dominated by *Cornus canadensis*, *Clintonia borealis*, *Maianthemum canadense*, *Aralia nudicaulis*, and *Lycopodium* spp. The most common cryptogams are *Pleurozium schreberi* and *Bracythecium* spp. Species richness and diversity are relatively high, in large part attributable to the large number of herbaceous species. Soils are much more fine-textured and of higher nutrient status than those of stand-types I-III. Many of these stands occur on slopes, and almost half are of lacustrine origin. Over 25% of the stands have luvisolic soils. Carbonates occur in the soil profile of about one-third of the stands, and distinct mottling in the soil profile is common (> 40% of stands).

VI. Trembling Aspen

The canopy is dominated by trembling aspen, with balsam fir, white spruce and white birch occasionally occurring as codominants. The subcanopy and saplings layers are dominated by balsam fir, although trembling aspen, white birch and white spruce are also found in the sapling layer of some stands. Tall shrubs often occur at high cover, particularly *Corylus cornuta* and *Acer spicatum*. The low shrub *Diervilla lonicera* is also common. The rich herb layer is dominated by *Aster macrophyllus*, *Aralia nudicaulis*, *Maianthemum canadense*, *Rubus pubescens*, *Cornus canadensis* and *Clintonia borealis*. Cryptogam cover is low. Species richness and diversity are high. Edaphic conditions are similar to those of stand-type V.

VII. Birch - Trembling Aspen Mixed Wood

These mixed wood stands are variable in their canopy cover. Although deciduous species (trembling aspen, white birch and large-toothed aspen) dominate most stands, jack pine and black spruce are also occasionally important. The subcanopy and sapling layers are dominated by balsam fir, white spruce, white birch and black spruce. The tall shrubs *Alnus crispa* and *Corylus cornuta* are common, as are the low shrubs *Diervilla lonicera* and *Vaccinium* spp. The herb layer is relatively rich and dominated by the same species that occur in the understory of stand-type VI. *Pleurozium schreberi* occurs in most stands, though at low cover. Species richness and diversity are comparatively high. Soils texture is intermediate between stand-types I-III and V-VI, and are less nutrient-rich than those of stand-type VI. Depth to bedrock is < 2 m in about one-third of the stands, and the substrate is often stony.

VIII. Red Pine

These stands are dominated by red pine in the canopy layer, although jack pine, trembling aspen, white pine and large-toothed aspen are occasional codominants (particularly in stands over bedrock). The subcanopy is dominated by balsam fir and white birch, although regeneration by red and white pine also occurs in some stands. The most frequently encountered shrubs are *Diervilla lonicera*, *Chimaphila umbellata*, and *Vaccinium* spp, but their cover is generally low. Herb cover is also low; frequent species include *Maianthemum canadense*, *Aralia nudicaulis*, *Lycopodium* spp., *Cornus canadensis*, and *Aster macrophyllus*. Cryptogams are common, particularly *Pleurozium schreberi*, *Dicranum polysetum*, and *Cladina* spp. Species richness and diversity are comparatively low (similar to values for stand-types I-III). Soil texture and edaphic conditions are similar to those of stand-type I. Over 25% of these stands occur over bedrock, and many are on slopes. Red pine, a 'near-boreal' Great Lakes-St. Lawrence species, is most commonly found in the Quetico - Rainy River - Dryden area.

IX. White Pine

These stands are dominated by white pine, sometimes forming pure stands but more often found in mixture with red pine, white birch, trembling aspen and/or balsam fir. Red maple is occasional. Total canopy cover is high. The tall shrubs *Corylus cornuta* and *Acer spicatum* are frequent, and usually occur at moderate cover. *Diervilla lonicera* and *Rubus strigosus* are common low shrubs. The rich herb layer is dominated by *Aster macrophyllus* and *Aralia nudicaulis*. Cryptogams are a minor component of most stands. These stands generally occur on sandy loam or coarser substrates. Sites are less xeric and nutrient-deficient than those dominated by red pine (stand-type VIII). Over 40% of these stands occur on bedrock, and the substrate is often stony. Many of these stands occur on slopes.

Stands of this Great Lakes-St. Lawrence species are most frequently encountered in the Quetico - Rainy River area.

X. Birch - Tall Shrub Mixed Wood

These stands are characterized by high tree and tall shrub cover. White birch is the dominant canopy species in most stands, although trembling aspen, jack pine and/or balsam fir usually occur as codominants. *Acer spicatum*, the dominant tall shrub in these stands, occurs at moderate to high cover. *Diervilla lonicera* is frequent but usually occurs at low cover. The herb layer is relatively species-rich. The most frequently encountered species are *Clintonia borealis*, *Cornus canadensis*, *Maianthemum canadense*, *Streptopus roseus*, *Aralia nudicaulis*, *Lycopodium* spp. and *Trientalis borealis*. Total cryptogam cover is low, although *Pleurozium schreberi* and *Dicranum* spp. occur in most stands. Lichens are infrequent. Sites are nutrient-deficient, moderately acidic and well-drained. Soils are generally coarse-textured brunisols derived from morainal, glaciofluvial or lacustrine parent materials. Depth to bedrock is < 2m in 25% of sites, and about 40% of stands show distinct mottling in the soil profile. Terrain varies from gentle to steep slopes.

XI. Balsam Poplar

Balsam poplar dominates the canopy of these stands. Balsam fir, white spruce and black spruce are the most common species in the upper subcanopy, while balsam poplar, balsam fir, white spruce, white birch and eastern white cedar are frequently encountered in the subcanopy and sapling layers. Tall shrub cover is usually moderate (occasionally high). *Cornus stolonifera* is the most frequent and abundant species. *Alnus rugosa* and *Acer spicatum* may also occur at moderate cover, but are only present in about half the stands. Herb diversity and cover are high. Species occurring at high frequency and cover include *Rubus pubescens*, *Mitella nuda*, *Aralia nudicaulis*, *Aster macrophyllus*, and *Carex* spp. Cryptogams form a minor component of the vegetation. *Pleurozium schreberi* is frequently encountered but occurs at low cover. Lichens are infrequent. These stands occur on moist-wet, nutrient-rich, weakly acidic substrates. Soils are fine-textured, often gleyed, and usually derived from lacustrine deposits. Organic matter accumulation is relatively high, and mor-humus predominates.

XII. Black Ash

Black ash dominates the canopy, often forming pure stands. White birch and balsam poplar are occasional codominants. The subcanopy and sapling layers are dominated by black ash, although balsam fir and white spruce also occur. The tall shrubs *Acer spicatum*, *Alnus rugosa* and *Corylus cornuta* are frequent, and usually occur at moderate cover. *Ribes* spp. are ubiquitous but typically occur at low cover. Ericaceous species are absent. The herb layer is very species-rich, and total herb cover is moderate to high. *Rubus pubescens*, and species of the genera *Carex*, *Galium* and *Viola*, are ubiquitous and often occur at moderate cover. Total cryptogam cover is low, but species richness is high. *Climacium dendroides* and *Plagiomnium* spp. are the most frequently encountered species. Lichens are infrequent and occur at low cover. These sites are moist-wet, very nutrient-rich, and characterized by fine-textured, mildly acidic, organic-rich soils. Depth to the water table is usually < 2 m.

4.3.3 Stand-Type Relationships

Vegetation

The twelve 'stand-types' (721 stands) are plotted in two-dimensional CA ordination space in **Fig. 4.2**. A strong correspondence between the ordination and cluster analysis results is apparent. The first ordination axis is interpretable as a gradient of decreasing nutrient status from left to right. The second axis corresponds to a gradient of increasing moisture status from bottom to top. These overall trends in soil moisture and nutrient status are confirmed by the corresponding species ordination (**Fig. 4.3**). These results are similar to those obtained in Chapter 3.

Mean per-stand species richness, and Shannon-Weaver diversity and evenness, are summarized for each of the twelve stand-types in **Table 4.2**. Highest per-stand species diversity (H > 2.5) were found in stand-types V-VII, XI and XII. Intermediate diversity

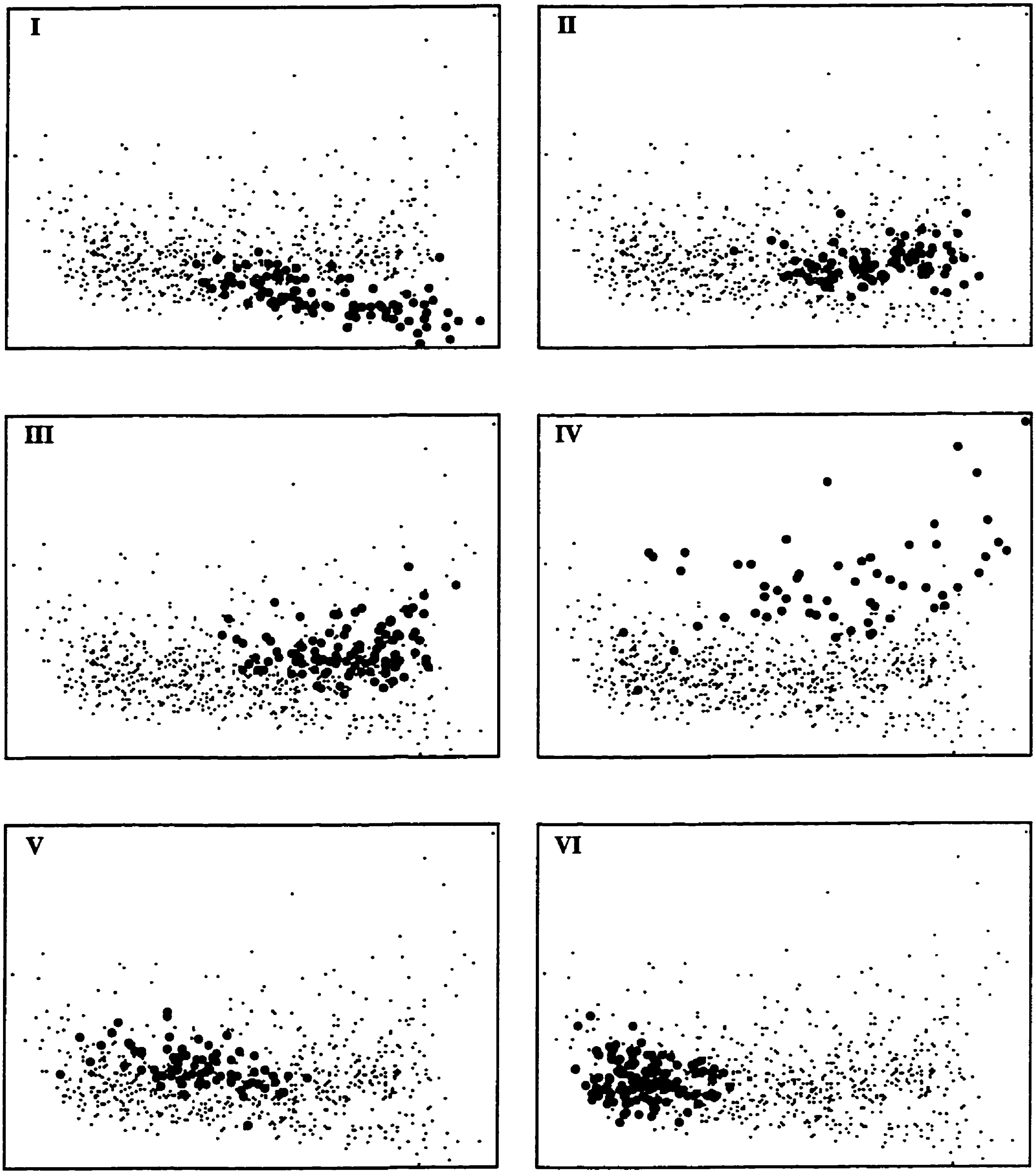


Figure 4.2a. Correspondence analysis ordination biplot of 721 stands ≤ 85 years old (axes I and II). Positions of stands in stand-types I-VI are shown.

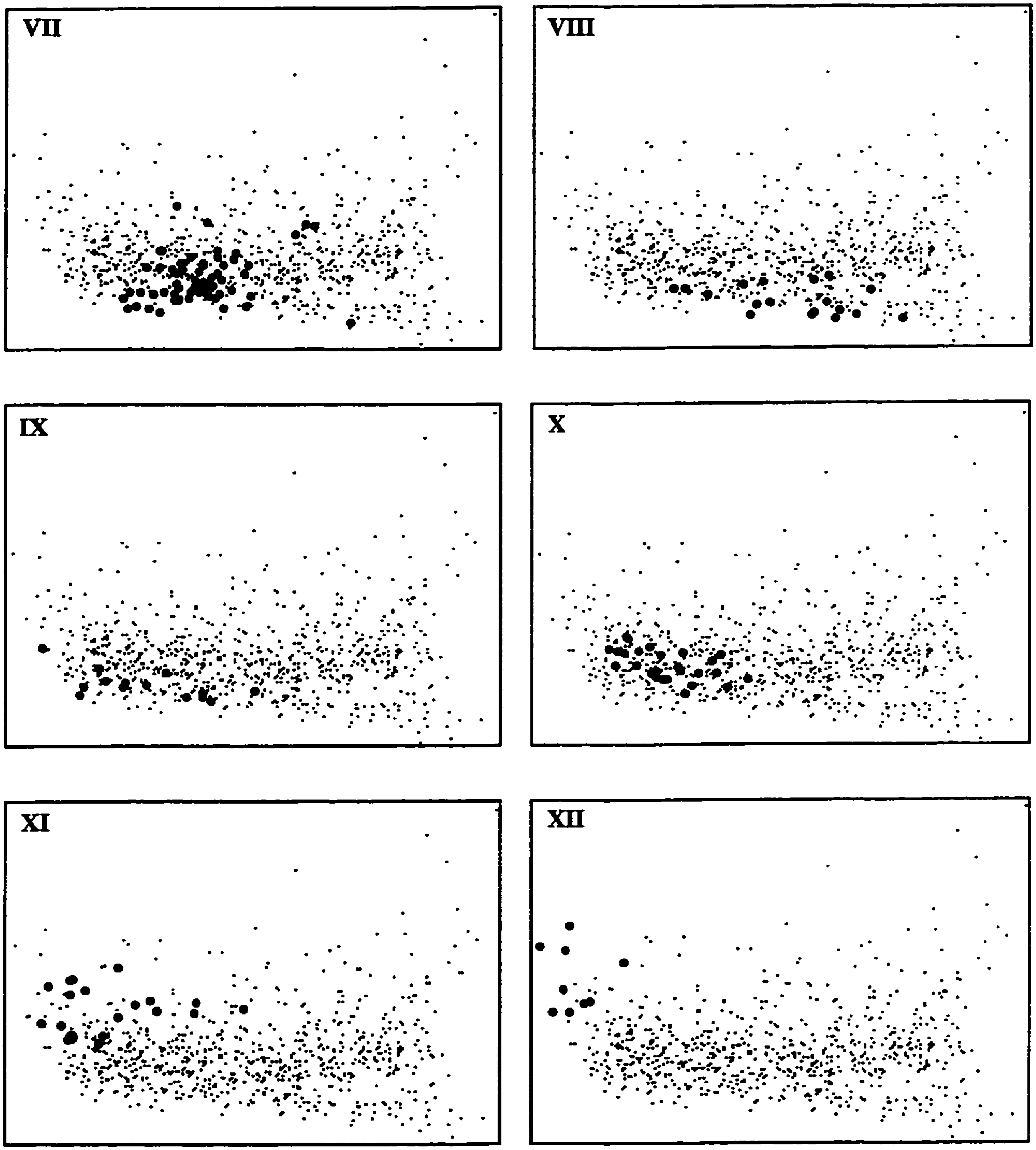


Figure 4.2b. Correspondence analysis ordination biplots of 721 stands ≤ 85 years old (axes I and II). Positions of stands in stand-types VII-XII are shown.

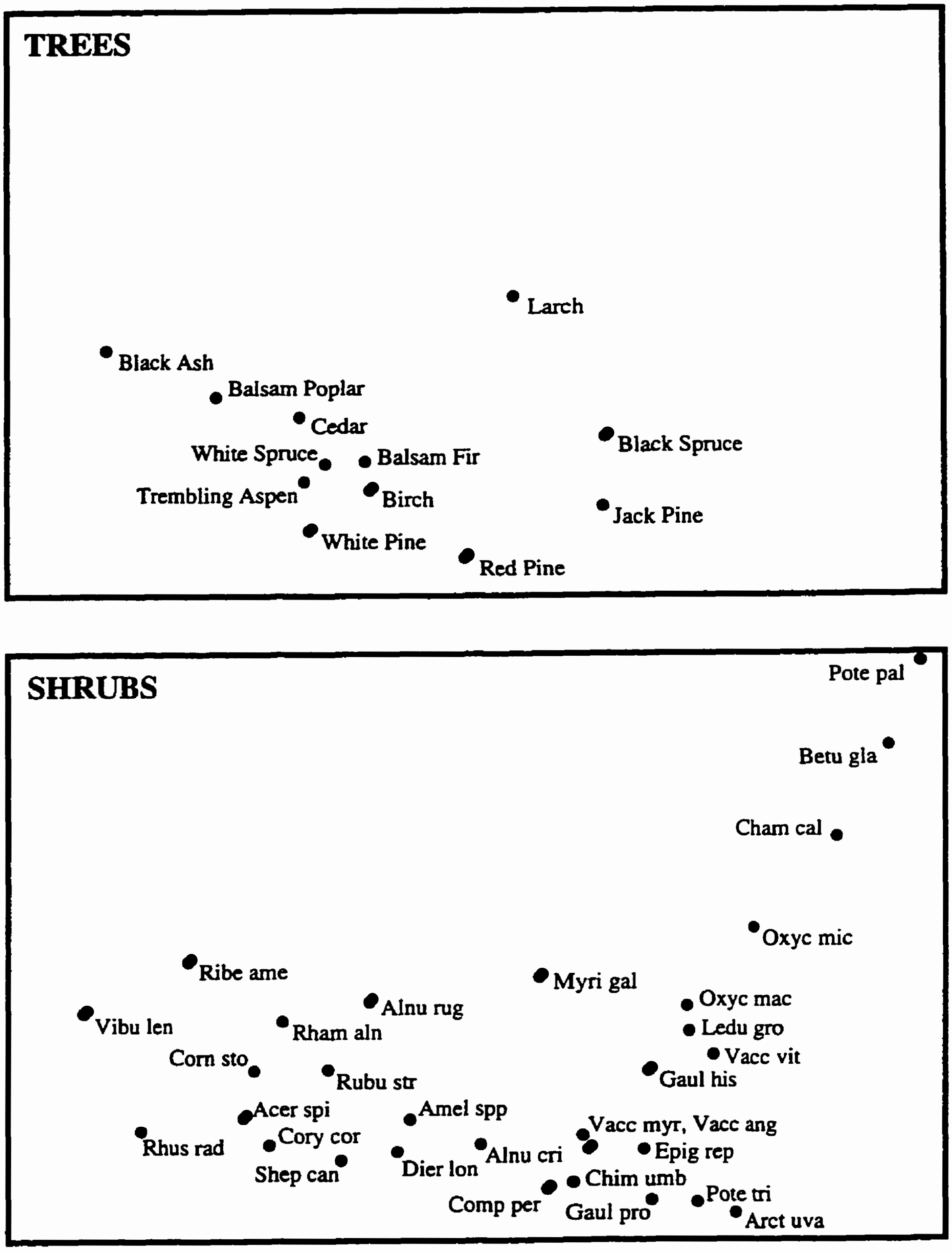


Figure 4.3a. Correspondence analysis ordination biplots of stands ≤ 85 years old (axes I and II). Selected tree and shrub species are shown. Species codes as in Chapter 3.

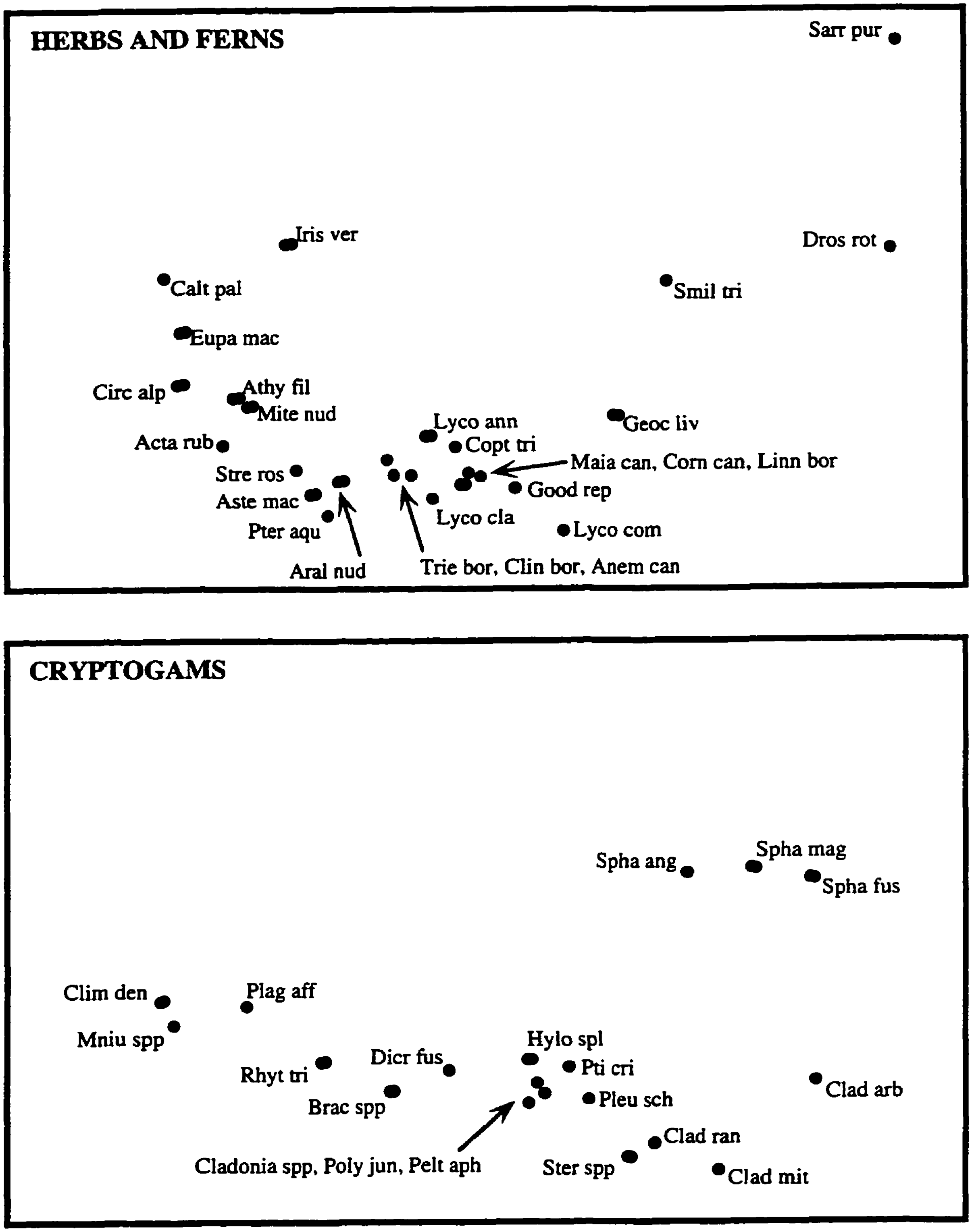


Figure 4.3b. Correspondence analysis ordination biplots of 721 stands ≤ 85 years old (axes I and II). Selected herb and cryptogam species are shown. Species codes as in Chapter 3.

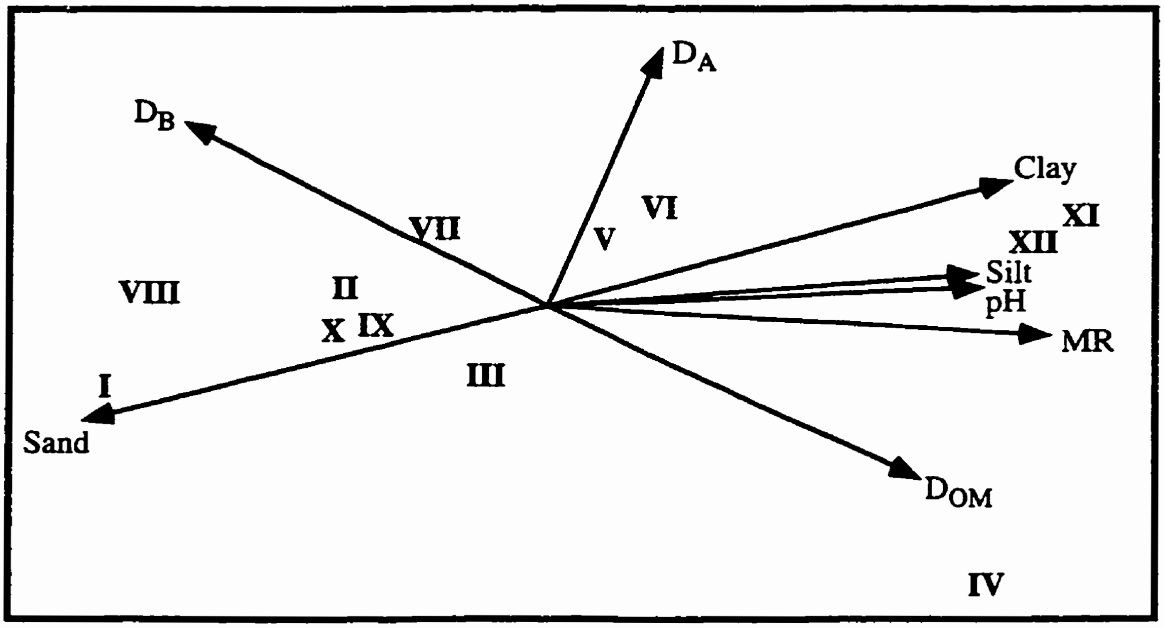


Figure 4.4. Principal component analysis ordination biplot (axes I and II, correlation) of stand-types (I-XII) and soil variables. Codes: Sand = percent sand; Silt = percent silt; Clay = percent clay; MR = moisture regime; pH = mineral horizon pH; D_{OM} = depth of organic layer; D_A = depth of A-horizon; D_B = depth of B-horizon.

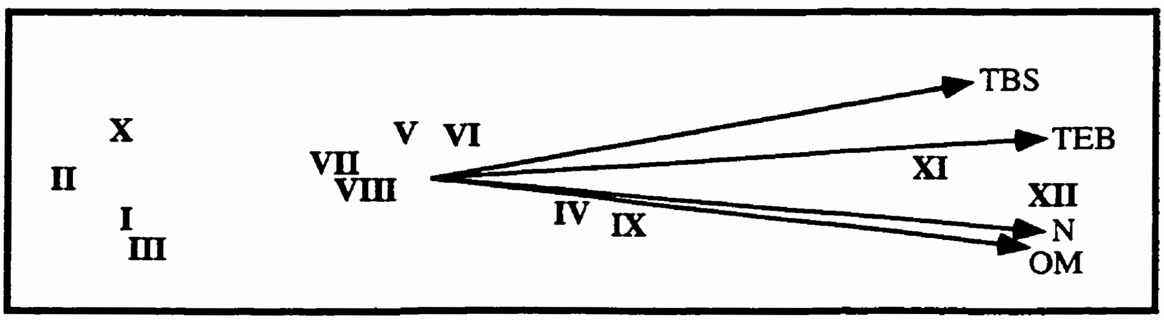


Figure 4.5. Principal component analysis ordination biplot (axes I and II, correlation) of stand-types (I-XII) and soil nutrient variables. Codes: TEB = total exchangable bases; TBS = total base saturation; N = percent nitrogen in mineral horizon; OM = percent organic matter in the mineral horizon.

TABLE 4.2. Species richness, diversity and evenness by stand-type.

	Stand-Type											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
	181	*146*	*253*	*190*	*117*	*196*	*96*	*62*	*44*	*43*	*37*	*24*
Species Richness												
All Species	26.56	25.82	25.64	32.96	40.66	39.80	34.92	27.79	29.45	35.70	46.54	41.42
Trees	3.47	3.45	3.11	2.51	3.82	3.96	4.48	5.05	4.70	3.65	4.38	4.29
Shrubs	6.83	6.23	5.55	7.93	7.87	9.01	8.95	7.73	7.23	6.51	9.19	7.29
Herbs	9.64	10.37	8.22	11.87	18.47	19.35	15.28	9.69	11.98	15.47	22.51	23.96
Cryptogams	6.63	5.77	8.77	10.65	10.49	7.48	6.21	5.32	5.55	10.07	10.46	5.88
Diversity	2.175	1.995	2.001	2.426	2.538	2.554	2.602	2.349	2.354	2.267	2.717	2.576
Evenness	0.671	0.620	0.628	0.708	0.691	0.698	0.738	0.711	0.701	0.640	0.711	0.699

TABLE 4.3. Means (bold), standard deviations, and sample sizes (italics) of soil variables by stand-type.

Stand-Type	Organic Matter Depth (cm)	A-horizon Depth (cm)	B-horizon Depth (cm)	Sand (%)	Silt (%)	Clay (%)	Moisture Regime	Drainage Regime	Slope (degrees)	Stoniness
I	**6.54**	**6.04**	**40.42**	**71.34**	**22.24**	**6.42**	**0.94**	**2.22**	**5.31**	**2.83**
	4.01	6.32	29.65	20.02	15.77	6.16	1.25	1.18	6.60	2.01
	181	*181*	*181*	*139*	*139*	*139*	*181*	*181*	*181*	*126*
II	**7.84**	**9.45**	**49.89**	**60.73**	**24.85**	**14.41**	**1.88**	**3.14**	**3.46**	**1.65**
	3.19	9.03	33.83	29.87	17.56	20.91	1.64	1.32	3.72	1.99
	146	*146*	*146*	*124*	*124*	*124*	*146*	*146*	*146*	*106*
III	**14.17**	**8.26**	**40.53**	**59.44**	**27.88**	**12.68**	**2.82**	**3.60**	**4.17**	**2.16**
	17.89	8.42	31.38	23.65	15.18	17.09	2.17	1.71	5.04	2.15
	253	*253*	*253*	*193*	*193*	*193*	*253*	*253*	*253*	*141*
IV	**88.08**	**5.81**	**12.61**	**51.41**	**31.60**	**16.99**	**6.19**	**6.14**	**0.47**	**0.55**
	70.22	13.60	24.13	28.09	18.63	19.04	1.75	1.21	1.43	1.34
	190	*190*	*190*	*74*	*74*	*74*	*190*	*190*	*190*	*105*
V	**9.32**	**9.76**	**46.76**	**45.67**	**31.22**	**23.11**	**2.50**	**3.54**	**5.78**	**1.44**
	5.88	8.50	22.60	28.67	17.55	24.22	1.71	1.34	6.26	2.00
	117	*117*	*117*	*83*	*83*	*83*	*117*	*117*	*117*	*50*
VI	**8.47**	**11.85**	**47.46**	**41.83**	**29.38**	**29.34**	**2.83**	**3.77**	**4.42**	**1.38**
	4.97	10.11	26.89	27.28	16.44	27.94	1.72	1.31	4.58	1.93
	196	*196*	*196*	*128*	*129*	*128*	*196*	*196*	*196*	*88*
VII	**7.47**	**10.48**	**50.34**	**53.31**	**28.71**	**17.98**	**1.80**	**3.00**	**4.37**	**2.59**
	4.33	8.98	33.60	26.28	15.21	21.88	1.57	1.23	4.05	2.12
	96	*96*	*96*	*82*	*82*	*82*	*96*	*96*	*96*	*64*
VIII	**6.52**	**7.65**	**68.21**	**69.24**	**23.40**	**7.36**	**0.98**	**2.31**	**6.85**	**2.89**
	2.85	6.34	50.49	20.14	16.96	6.25	1.08	1.11	5.84	2.21
	62	*62*	*62*	*55*	*55*	*55*	*62*	*62*	*62*	*53*
IX	**7.75**	**7.68**	**46.75**	**55.69**	**33.47**	**10.85**	**1.32**	**2.50**	**8.07**	**3.45**
	4.14	12.11	34.35	20.30	15.38	12.26	1.41	1.23	9.08	1.82
	44	*44*	*44*	*32*	*32*	*32*	*44*	*44*	*44*	*29*
X	**9.74**	**9.30**	**52.00**	**62.42**	**25.52**	**12.06**	**2.35**	**2.91**	**7.77**	**1.90**
	6.39	6.77	35.54	22.01	13.25	16.87	1.91	1.52	7.08	2.33
	43	*43*	*43*	*26*	*26*	*26*	*43*	*43*	*43*	*10*
XI	**17.70**	**12.57**	**33.73**	**32.58**	**37.19**	**30.23**	**4.35**	**4.54**	**3.34**	**0.40**
	17.12	11.07	28.00	22.36	18.76	22.42	1.75	1.26	7.68	0.83
	37	*37*	*37*	*28*	*28*	*28*	*37*	*37*	*37*	*15*
XII	**41.88**	**11.63**	**33.17**	**30.98**	**31.02**	**38.00**	**5.71**	**5.75**	**0.53**	**0.71**
	56.59	12.96	43.73	20.67	14.25	21.37	1.68	1.07	0.79	1.33
	24	*24*	*24*	*17*	*17*	*17*	*24*	*24*	*24*	*14*

TABLE 4.4. Means (bold), standard deviations, and sample sizes (italics) of soil nutrient variables by stand-type.

Stand-Type	Organic Horizon pH	Mineral Horizon pH	Organic Horizon Organic Matter (%)	Mineral Horizon Organic Matter (%)	Organic Horizon Nitrogen (%)	Mineral Horizon Nitrogen (%)	Cation Exchange Capacity (meq/100g)	Total Exchangable Bases (meq/100g)	Total Base Saturation (%)
I	**4.27**	**5.27**	**57.11**	**2.25**	**1.01**	**0.07**	**1.52**	**0.92**	**63.82**
	0.46	0.58	15.40	3.17	0.31	0.11	1.01	0.84	24.23
	124	*141*	*124*	*117*	*121*	*115*	*115*	*115*	*115*
II	**4.19**	**5.36**	**56.82**	**1.15**	**1.06**	**0.05**	**1.74**	**1.31**	**66.89**
	0.51	0.49	13.26	0.94	0.38	0.08	1.33	1.41	24.74
	105	*124*	*105*	*106*	*105*	*105*	*106*	*106*	*106*
III	**4.03**	**5.24**	**57.12**	**2.60**	**1.06**	**0.07**	**2.18**	**1.52**	**56.54**
	0.64	0.81	11.78	7.03	0.30	0.07	2.13	2.22	27.89
	140	*192*	*140*	*137*	*133*	*137*	*130*	*130*	*130*
IV	**4.91**	**6.03**	**62.78**	**3.27**	**1.27**	**0.10**	**2.74**	**2.42**	**80.39**
	0.89	0.93	17.21	4.43	0.46	0.13	1.96	2.09	25.78
	100	*67*	*100*	*36*	*97*	*35*	*34*	*34*	*34*
V	**4.91**	**5.44**	**61.37**	**1.68**	**1.33**	**0.05**	**3.11**	**2.84**	**81.95**
	0.66	0.76	11.92	1.92	0.26	0.04	2.78	2.88	18.32
	50	*83*	*50*	*50*	*49*	*50*	*48*	*48*	*48*
VI	**5.57**	**5.65**	**55.38**	**2.40**	**1.45**	**0.07**	**3.26**	**2.96**	**83.51**
	0.66	0.80	10.54	5.21	0.32	0.07	2.34	2.45	19.59
	87	*127*	*86*	*87*	*86*	*87*	*86*	*86*	*86*
VII	**5.05**	**5.22**	**59.77**	**2.01**	**1.31**	**0.07**	**2.49**	**2.12**	**76.51**
	0.63	0.59	13.89	2.44	0.32	0.06	2.44	2.51	19.02
	64	*82*	*64*	*63*	*60*	*61*	*61*	*61*	*61*
VIII	**4.65**	**5.41**	**60.72**	**2.13**	**0.99**	**0.06**	**1.61**	**1.25**	**77.41**
	0.51	0.49	10.15	3.02	0.25	0.04	0.86	0.82	17.00
	53	*55*	*53*	*52*	*53*	*52*	*52*	*52*	*52*
IX	**4.98**	**5.35**	**58.76**	**2.93**	**1.16**	**0.09**	**2.40**	**1.93**	**79.28**
	0.54	0.51	11.15	2.88	0.26	0.08	1.04	1.08	22.18
	28	*31*	*28*	*25*	*28*	*25*	*25*	*25*	*25*
X	**5.14**	**5.21**	**59.35**	**1.19**	**1.33**	**0.05**	**1.47**	**1.19**	**78.46**
	0.73	0.77	6.85	0.53	0.37	0.02	0.87	0.97	21.74
	10	*26*	*10*	*9*	*9*	*9*	*9*	*9*	*9*
XI	**6.13**	**6.96**	**54.24**	**3.57**	**1.17**	**0.13**	**3.73**	**3.67**	**98.69**
	0.58	0.75	12.50	4.09	0.51	0.09	0.89	0.86	1.47
	14	*27*	*14*	*15*	*13*	*15*	*15*	*15*	*15*
XII	**6.13**	**6.04**	**60.47**	**7.07**	**1.91**	**0.39**	**5.22**	**5.12**	**93.01**
	0.40	0.60	10.01	12.02	0.54	0.42	4.41	4.47	10.18
	10	*17*	*10*	*11*	*10*	*11*	*10*	*10*	*10*

TABLE 4.5. Frequency distributions of soil texture classes by stand-type. Values in italics are sample sizes. Values > 20% are bolded.

Soil Texture Class	Stand-Type												
	all	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**	**XII**
	981	*139*	*124*	*193*	*74*	*83*	*128*	*82*	*55*	*32*	*26*	*28*	*17*
Clay	0.153		0.145	0.104	0.149	**0.217**	**0.360**	0.172	0.018	0.031	0.115	**0.250**	**0.470**
Silt	0.115	0.072	0.121	0.093	0.176	**0.205**	0.063	0.085	0.109	0.156	0.038	**0.285**	0.059
Loam	**0.464**	**0.468**	**0.330**	**0.534**	**0.420**	**0.397**	**0.454**	**0.500**	**0.418**	**0.594**	**0.577**	**0.429**	**0.471**
Sand	**0.268**	**0.460**	**0.403**	**0.269**	**0.257**	0.180	0.126	**0.244**	**0.455**	**0.219**	**0.269**	0.036	

Clay = heavy clay, silt clay, clay and sandy clay.
Silt = silty clay loam, silty loam and silt.
Loam = clay loam, sandy clay loam, loam, and sandy loam.
Sand = loamy sand and sand.

TABLE 4.6. Frequency distributions of soil order classes by stand-type. Values in italics are sample sizes. Values > 20% are bolded.

Soil Order	Stand-Type												
	all	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
	1389	*181*	*146*	*253*	*190*	*117*	*196*	*96*	*62*	*44*	*43*	*37*	*24*
Non-Soil	0.014	0.077	0.007							0.091			
Regosol	0.018	0.017	0.007	0.036	0.026	0.009	0.010	0.010			0.023	0.054	
Brunisol	**0.482**	**0.724**	**0.582**	**0.478**	0.063	**0.436**	**0.454**	**0.604**	**0.887**	**0.659**	**0.535**	**0.324**	0.167
Luvisol	0.117	0.011	0.171	0.083	0.037	**0.248**	**0.250**	0.156	0.016	0.091	0.093	0.108	0.083
Gleysol	0.122	0.022	0.089	0.170	**0.211**	0.120	0.128	0.052		0.023	0.070	**0.297**	**0.458**
Podzol	0.135	0.105	0.144	0.186	0.037	0.171	0.153	0.167	0.081	0.114	**0.279**	0.162	
Organic	0.111	0.044		0.048	**0.626**	0.018	0.005	0.010	0.016	0.023		0.054	**0.292**

TABLE 4.7. Frequency distributions of genetic material classes by stand-type. Values in italics are sample sizes. Values > 20% are bolded.

Genetic Material	Stand- Type												
	all	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**	**XII**
	1389	*181*	*146*	*253*	*190*	*117*	*196*	*96*	*62*	*44*	*43*	*37*	*24*
Morainal	**0.296**	**0.370**	0.192	**0.375**	0.042	**0.256**	**0.296**	**0.427**	**0.468**	**0.705**	**0.419**	0.135	0.042
Glaciofluvial	**0.281**	**0.448**	**0.514**	**0.312**	0.116	**0.214**	0.163	**0.219**	**0.484**	0.159	**0.279**	0.135	0.083
Lacustrine	**0.274**	0.088	**0.274**	**0.257**	0.174	**0.470**	**0.474**	**0.333**	0.016	0.114	**0.279**	**0.514**	**0.375**
Organic	0.108	0.017		0.047	**0.642**		0.005					0.081	**0.333**
Fluvial	0.029	0.017	0.021	0.008	0.026	0.060	0.051		0.016		0.023	0.108	0.167
Bedrock	0.009	0.055							0.016	0.023			
Colluvial	0.002						0.005	0.010				0.027	
Eolian	0.001	0.006					0.005						

TABLE 4.8. Proportion of stands in which bedrock, carbonates, distinct mottling and water table are present within the first 2 m of the soil profile, by stand-type. Values in italics are sample sizes. Values > 20% are bolded.

Variable	Stand- Type												
	all	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**	**XII**
	1389	*181*	*146*	*253*	*190*	*117*	*196*	*96*	*62*	*44*	*43*	*37*	*24*
Bedrock	**0.257**	**0.448**	**0.233**	**0.387**	0.095	0.179	0.112	**0.323**	**0.242**	**0.386**	**0.279**	0.135	0.125
Carbonates	0.166	0.033	0.110	0.142	0.168	**0.333**	**0.296**	0.167	0.016		0.116	**0.514**	0.083
Distinct Mottling	**0.458**	0.133	**0.329**	**0.534**	**0.937**	**0.436**	**0.485**	0.198	0.161	0.114	**0.419**	**0.811**	**0.958**
Water Table	**0.258**	0.022	0.130	**0.281**	**0.837**	0.179	0.199	0.073			0.186	**0.378**	**0.708**

TABLE 4.9. Frequency distributions of humus-form by stand-type. Values in italics are sample sizes. Values > 20% are bolded.

Humus Form	Stand- Type												
	all	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**	**XII**
	1389	*181*	*146*	*253*	*190*	*117*	*196*	*96*	*62*	*44*	*43*	*37*	*24*
Mull	0.047	0.017	0.007	0.020	0.026	0.043	0.143	0.042	0.032	0.045	0.047	0.054	**0.250**
Moder	**0.206**	0.061	0.137	0.198	0.053	**0.333**	**0.388**	**0.260**	0.097	**0.273**	**0.512**	**0.297**	0.167
Fibrimor	**0.567**	**0.884**	**0.842**	**0.660**	0.116	**0.521**	**0.398**	**0.656**	**0.871**	**0.682**	**0.302**	**0.378**	0.083
Humimor	0.043	0.028	0.007	0.055	0.011	0.094	0.056	0.031			0.116	0.189	0.042
Peatymor	0.138	0.011	0.007	0.067	**0.795**	0.009	0.015	0.010			0.023	0.081	**0.458**

(2.2 < H < 2.5) occurred in stand-types IV and VIII-X, and the lowest diversity (H < 2.2) in stand-types I-III. In general, the higher diversity values were attributable to greater species richness in the herb layer. Evenness values were generally similar across stand-types, although evenness was somewhat lower in stand-types II and III.

Soil - Environment

Measured soil and environmental variables are summarized (mean, standard deviation, sample size) by stand-type in **Tables 4.3** and **4.4**. Note that some soil variables were only measured for mineral soils, so that values for stand-types in which organic soils dominate (particularly stand-type IV) are somewhat biased. Site-types I, II and IX have the most coarse-textured soils (sand and sandy loam), stand-types III, IV, VII, VIII and X have intermediate-textured soils (loams and loamy sands), and stand-types V, VI, XI and XII have finer-textured clays and loams (**Table 4.5**). About half of the stands occur on soils of the brunisol order, and these are particularly predominant in stand-types I and VIII (**Table 4.6**). Organic or gleysol soil orders dominate stand-types IV, XI and XII, while luvisolic soils are most commonly encountered in stand-types V and VI (about 25% of stands). Soil genetic material is mostly morainal in stand-type X, although morainal materials are also common in stand-types I, III, and V-VII (**Table 4.7**). Glaciofluvial material is most common in stand-types I, II, VIII, and is relatively common in stand-types III and X. Lacustrine material is found predominantly in stand-types V, VI, XI and XII, with lesser amounts in stand-types II, III and VII. Organics predominate in stand-types IV and XII.

Table 4.8 summarizes, for each stand-type, the proportion of stands in which bedrock, carbonates, distinct mottling, and water table are encountered within the first 2 m of the soil profile. Bedrock was most commonly encountered in stand-type I (almost half the stands), but was also common (>25% of stands) in stand-types II, VII, IX and X. Carbonates were most commonly encountered in stand-type XI, but were also common in stand-types V and VI. Distinct mottling predominated in the wet, organic-rich sites (stand-types IV, XI and XII), although it was also comparatively common (>40% frequency) in stand-types III, V, VI and X. Humus forms are predominately fibrimoric (**Table 4.9**), particularly in conifer stands on mineral soil (stand-types I-III, V and VII-IX). Moder and fibrimor humus forms were most commonly encountered in stand-types VI, X and XI, while peatymors were found mainly in stand-types IV and XII. Mulls were rarely encountered except in stand-type XII (25% frequency).

A two-dimensional ordination of the 12 stand-types and 8 edaphic variables is presented in **Fig. 4.4**. The two axes account for 87.7% of the variance, indicating considerable intervariable correlation. The first axis separates the dry, acidic, coarse textured soils (stand types I and VIII, and to a lesser extent II, III, VII, IX and X) from moist, pH-neutral, fine textured soils (stand-types XI and XII). Site-type IV is an outlier strongly associated with deep organic soils. Site-types V and VI occur at the top-center of the ordination, indicating fresh conditions and a well-developed A-horizon.

Fig 4.5 presents a two-dimensional nutrient status ordination of the 12 stand-types and 4 'soil-nutrient' variables. Variable redundancy is high, with the first axis alone accounting for 79.5% of the variance. This axis reflects a gradient in overall nutrient status from left to right. Site-types I-III and X have the lowest nutrient status, stand-types IV-IX have intermediate values, and stands XI and XII have the highest values. Note that the position of stand-type IV is probably biased, since values were available only for stands on mineral soil (which probably have higher nutrient status than the peaty organic soils that dominate stand-type IV).

CHAPTER 5
SUCCESSIONAL TRAJECTORIES

5.1 INTRODUCTION

Few studies have attempted to delineate the diverse range of community types, and their successional trends, across large areas of the boreal forest. Instead, a few community types over a limited region are generally the focus of a given study. One of the primary reasons for this approach lies in the difficulty of obtaining sufficient data (replicate plots). Furthermore, successional trends have generally been inferred from relative abundance of tree species present in the lower strata, instead of more directly determining successional trends by comparing younger and older stands. Finally, the successional dynamics of the shrub, herb and cryptogam layers have often been ignored.

In Chapter 4, I provided a synoptic description of twelve stand-types delineated using data from younger (≤ 85 years) stands. In this chapter, I develop and summarize successional trajectories for each of these twelve stand-types. Descriptions of successional dynamics by stand-type include trends in the tree, shrub, herb and cryptogam layers.

5.2 MATERIALS AND METHODS

5.2.1 Development of Successional Trajectories

Assignment of Older (>85 Years) Stands

Each of the 668 older stands (> 85 years old) was assigned to one of twelve stand-types delineated in the classification of 721 younger (≤ 85 years old) stands described in Chapter 4. In some cases, assignments were relatively straightforward. For example, a 100-year-old pure stand of red pine clearly belongs to stand-type VIII (Red Pine). In other cases, a given stand could only reasonably 'belong' to a subset of the 12 stand-types. For example, a 120-year-old stand with jack pine in the canopy and high cover of feathermoss could only belong to one of the three jack pine stand-types. In such cases, the stand was assigned to one of these 'subset' stand-types using a multivariate discriminant function classifier (Morrison 1990: 269). This assignment method uses a multiple-group classification rule, based on the Mahalanobis distance, to compute likelihood and Bayesian misclassification probabilities for each potential stand-type. To avoid circularity of argument, vegetation composition was not used in making the assignments. Instead, temporally-invariant soil variables such as particle size were used. Consider again a 120-year-old jack pine stand: this stand must be assigned to one of three stand-types (I, II or III). Each of these three stand-types is described by a set of soil variables (e.g. percent sand, silt and clay). The assignment is made by first comparing the soil variables of the 120-year-old 'unassigned' stand to those of the three stand-types. Assignment is then made to the most similar stand-type.

The strategy used to assign each of the 668 older stands to one of the 12 stand-types can be summarized as follows (beginning with the complete data set):

1. Separate out stands on organic substrates: these were defined as stands with an organic matter depth >50 cm. These were then classified into one of three stand-types (III. Black Spruce-Sphagnum; XI. Balsam Poplar; XII. Black Ash) based on floristic composition and environmental information (e.g. humus form; nutrient status).
2. Separate out stands with red or white pine in the canopy: the literature indicates that these two pine species are very long-lived (Heinselman 1973). Stands dominated by red pine were assigned to the stand-type VIII (Red pine), and those dominated by white pine to stand-type IX (White Pine). Environmental information and floristic composition were carefully checked to ensure that these assignments were reasonable.
3. Separate out stands with jack pine in the canopy: jack pine is a pioneer species that rarely regenerates under its own canopy (Zoladeski and Maycock 1990). Its presence in the canopy of older stands (> 85 years) indicates that it was present at stand initiation following fire. Such stands were assigned to one of four stand-types (I. Jack Pine-Feathermoss; II. Jack Pine-Black Spruce-Feathermoss; III. Black Spruce-Feathermoss;

VII. Birch-Trembling Aspen Mixed Wood). Stands with moderate to high cover of feathermoss (primarily *Pleurozium schreberi*) were assigned to one of classes I-III using the multiple discriminant classifier. Stands with low feathermoss cover and white birch and/or trembling aspen present in the canopy were assigned to site type VII.

4. Separate out stands with black spruce in the canopy: black spruce regenerates well in many stands, but is comparatively slow-growing (Cogbill 1985). Older stands dominated by black spruce in the canopy, and high feathermoss cover in the understory, were therefore classified into one of three stand-types (I. Jack Pine-Feathermoss; II. Jack Pine-Black Spruce-Feathermoss; III. Black Spruce-Feathermoss) using the multiple discriminant classifier. Mixed-wood stands on richer sites with black spruce in the canopy were assigned to stand-type V (White Spruce-Balsam Fir Mixed Wood).
5. Assign the remaining stands: the remaining stands were usually dominated by white spruce, balsam fir, trembling aspen and/or white birch in the canopy. These stands were assigned to one of four stand-types (V. White Spruce-Balsam Fir Mixed Wood; VI. Trembling Aspen; VII. Birch-Trembling Aspen Mixed Wood; X. Birch-Tall Shrub Mixed Wood) using the multiple discriminant classifier.
6. Refine the initial assignments: following the initial assignments, the data from each stand were manually examined for consistency in vegetation cover (particularly the shrub, herb and cryptogam layers) and environmental factors (e.g. soil particle size, substrate type). Particular attention was paid to the oldest stands (>150 years), those containing 'late-successional' species such as balsam fir in the canopy, and stands having high misclassification probabilities in the initial discriminant classifications. Based on this manual examination, fifty-six of the stands (8.4%) were reassigned. In all cases, a reassignment was made only if both vegetation cover and soil factors clearly indicated that the initial assignment was 'suboptimal'. In the majority of cases, these reassignments were relatively minor, e.g. from stand-type I (Jack Pine-Feathermoss) to II (Jack Pine-Black Spruce-Feathermoss).

5.2.2 Description of Successional Trajectories

Age Class Distributions and Summary Tables

Stand age class frequency histograms were produced for each of the twelve stand-types. As well, summary tables were produced to compare vegetation and environmental variables between younger (≤ 85 years) and older (> 85 years) stands. The following variables were summarized: (a) frequency and mean cover of trees species by canopy class; (b) frequency and mean cover of the most common shrubs, herbs and cryptogams; (c) mean and standard deviation of species richness and diversity for all species, and individually for trees, shrubs, herbs, and cryptogams layers; (d) mean and standard deviation of selected soil variables.

Succession Profiles

Site-type successional trajectories were fully described, and pictorial physiognomic-successional profiles for each stand-type were produced using standard illustrative symbols (**Fig. 5.1**). Three successional stages were illustrated: young stands (≤ 85 years), intermediate stands (85-120 years), and old stands (> 120 years). These pictorial profiles were based on mean cover values of tree and tall shrub species in each successional period. Variations in landform and edaphic factors within each stand-type were also considered.

Temporal Trajectories

For each stand-type, the following variables were plotted as a function of stand age: (a) total percent cover of trees, shrubs, herbs and cryptogams; (b) total percent cover of trees in each of four vertical strata (canopy, subcanopy, lower subcanopy, and sapling); (c) total percent cover of tall, low and ericaceous shrubs. The scatterplots were smoothed using robust locally weighted regression analysis (Cleveland 1979) to summarize temporal trends in each variable. These analyses were performed using Data Desk (Velleman 1992).

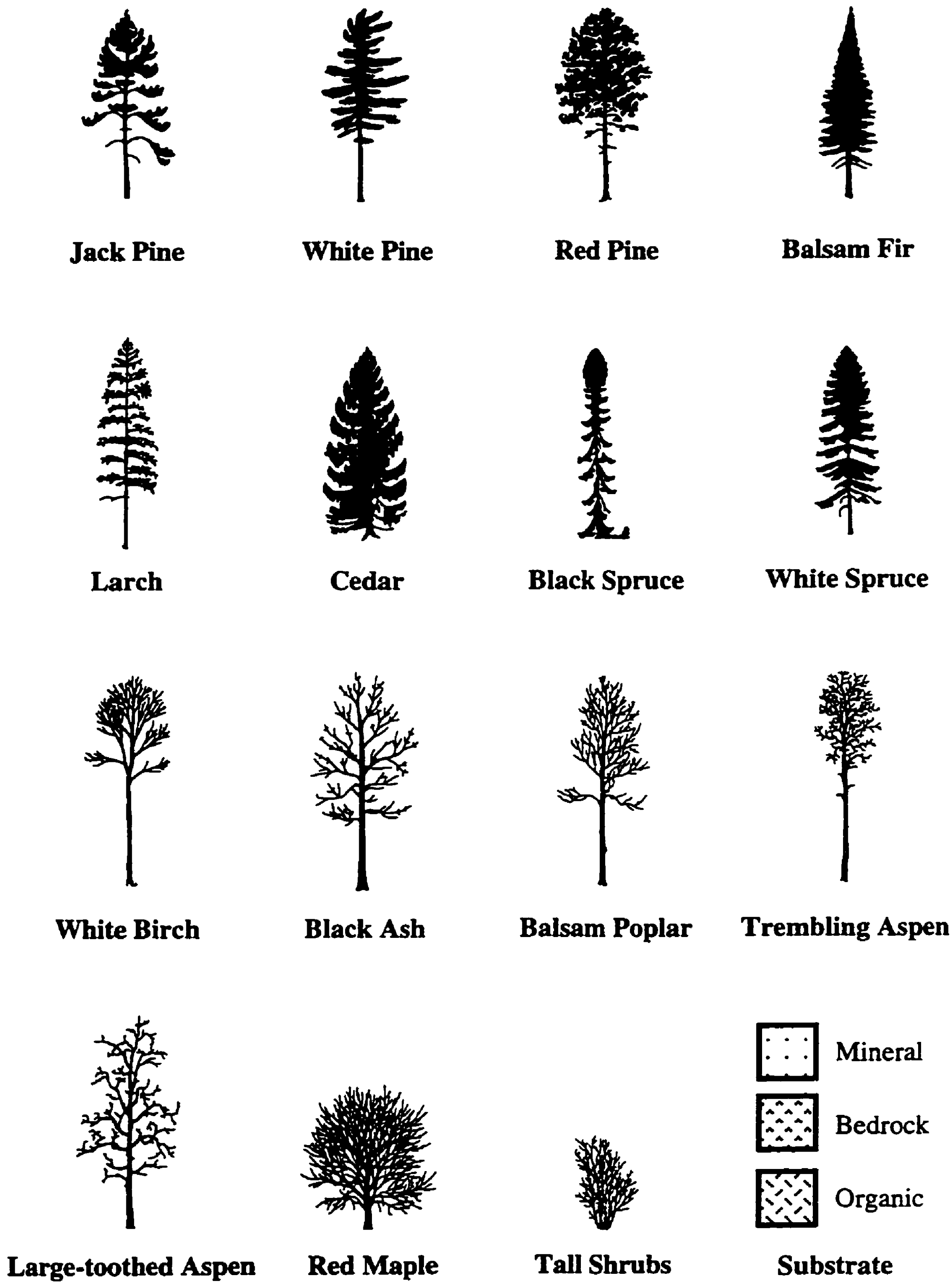


Fig. 5.1. Symbols used in the description of successional trajectories.

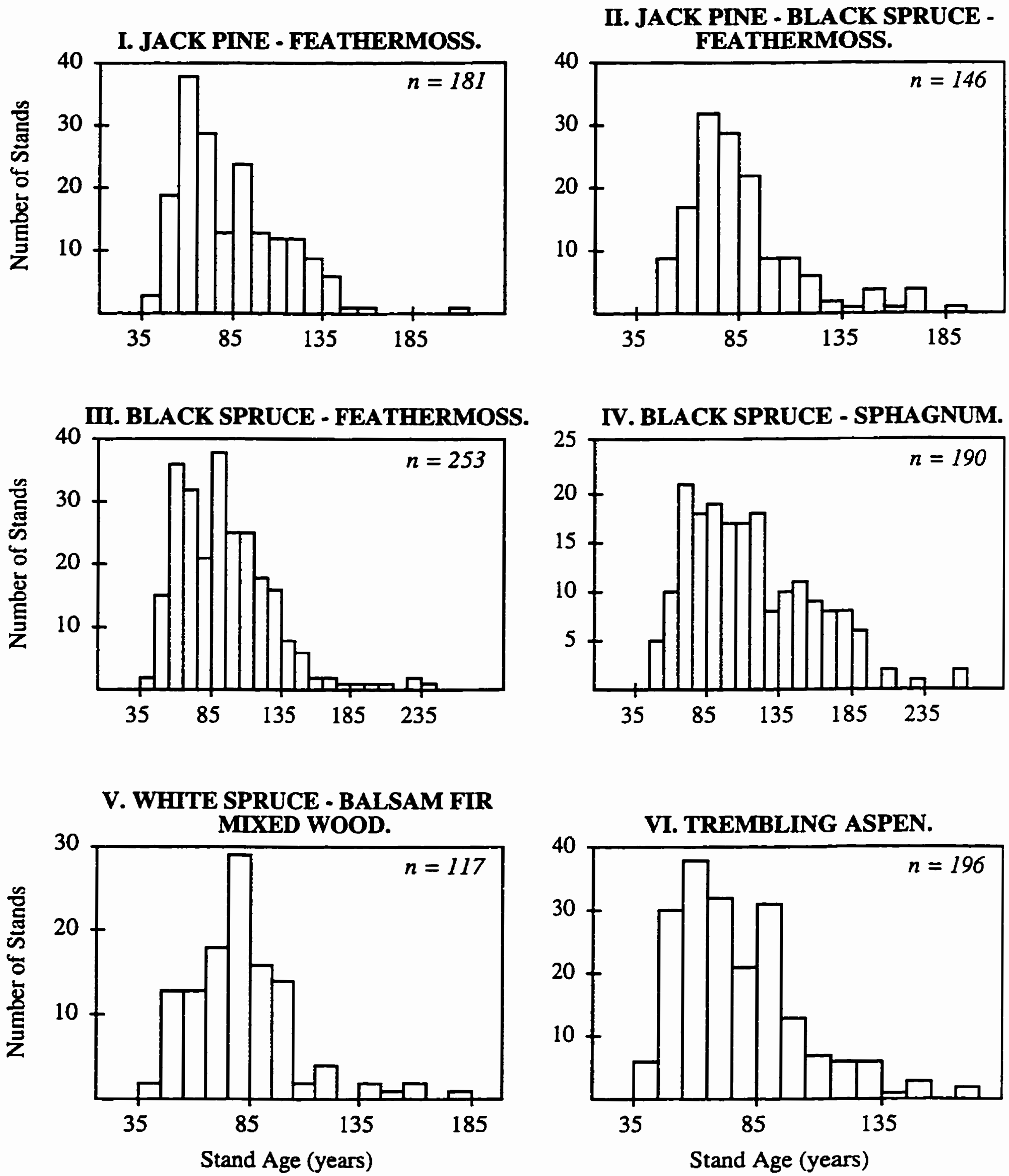


Figure 5.2a. Age-class histograms for stand-types I-VI.

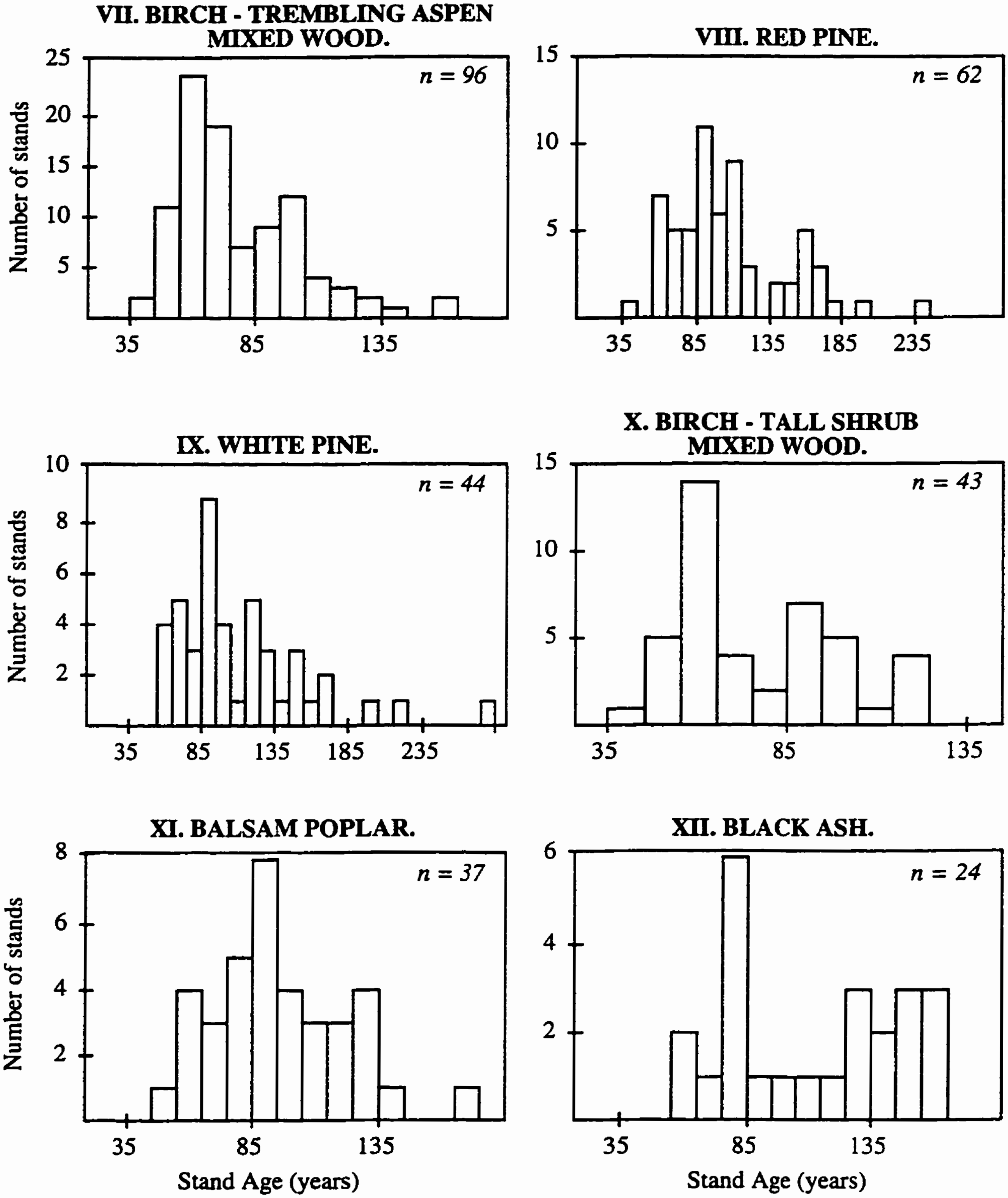


Figure 5.2b. Age-class histograms for stand-types VII-XII.

5.3 Results and Discussion

Age-class frequency histograms for each stand-type are presented in **Fig. 5.2**. Note that stands >150 years in age are infrequent in most stand-types, with the exception of white pine, red pine, and black spruce stands. Successional trajectories for each of the twelve stand-types are summarized below.

5.3.1 Stand-Type I: Jack pine - Feathermoss

Stand-Type Description

Soil-Environment

Most sites are classified as 'excessively drained', indicating very xeric conditions. Depth to the water table is > 2m in virtually all sites, and distinct mottling of the soil profile is rare. Most stands are on level to gently sloping terrain, although a few have slopes >10°. Glaciofluvial and morainal genetic materials predominate. Bedrock occurs within 2 m in about one-third of the stands. Soils are primarily coarse-textured (sand to sandy loam) eluviated Dystric Brunisols. Nutrient availability is very limited (mean TEB = 0.97, the lowest of any of the stand-types). Organic horizon depth is < 10 cm in most stands (mean depth = 6.5 cm), and fibrimor humus forms predominate.

Vegetation

Jack pine is ubiquitous and often occurs as pure stands, although black spruce, white birch and/or trembling aspen may also occur in the canopy-subcanopy layers. Subcanopy regeneration is usually sparse and dominated by black spruce. Balsam fir and black spruce saplings are relatively common. Saplings of 'pioneer' tree species (trembling aspen, white birch, and jack pine) are surprisingly common, occurring in over half the stands. This is the only stand-type where regeneration of jack pine was common: over 25% of stands ≤ 85 years in age contained jack pine saplings. Total shrub cover is generally moderate to high. Low ericaceous shrubs predominate, and blueberry species (*Vaccinium angustifolium and V. myrtilloides*) are ubiquitous. *Arctostaphylos uva-ursi* is less common, but often occurs at high cover when present. The low shrub *Diervilla lonicera* is both common and abundant. *Chimaphila umbellata*, *Rosa acicularis*, and *Lonicera*. spp. are also frequently encountered. Tall shrubs are a minor component of most stands. *Amelanchier* spp. occur in about half the stands, though at low cover. *Salix humilis*, *Sorbus* spp., *Alnus crispa*, and *Corylus cornuta* are occasionally encountered.

Common herbaceous species in these stands are *Maianthemum canadense*, *Linnaea borealis* and *Aralia nudicaulis*, but they usually occur at low cover. *Cornus canadensis* is less frequent but may have moderate cover. Other commonly encountered species include *Melampyrum lineare*, *Lycopodium* spp., and *Clintonia borealis*. *Aster macrophyllus*, although not frequent, may occur at moderate to high cover when present. The feathermoss *Pleurozium schreberi* is ubiquitous and generally occurs at high cover. *Dicranum polysetum* is frequently encountered at low to moderate cover. Lichens may occur at low to high cover; reindeer lichens (*Cladina* spp.) are frequent, and often abundant, in plots of low canopy cover. Club lichens (*Cladonia* spp.) are less frequent and occur at low cover.

Stand Dynamics

<u>Summary</u>

These stands are succeeding toward very open-canopy, mixed black spruce and jack pine forests (**Fig. 5.3**) in which feathermosses form a continuous understory. A steady decrease in total tree cover over time is largely attributable to declining canopy cover (**Figs. 5.4, 5.5**). Regeneration is primarily to black spruce, although jack pine saplings are also encountered in some stands. The overall frequency, cover and diversity of shrubs declines over time, since non-ericaceous species are largely eliminated from older stands (**Fig. 5.5**). Herbs similarly decline over time (**Fig. 5.4**), but cryptogam cover increases as succession proceeds (**Fig. 5.4**). Trend toward increased organic accumulation, decreased pH, and lower nutrient availability are apparent (see **Appendix I**). Increased organic matter accumulation further ties up already limiting nutrients, while higher substrate acidity reduces microbial activity and slows nutrient cycling.

I. Jack Pine - Feathermoss

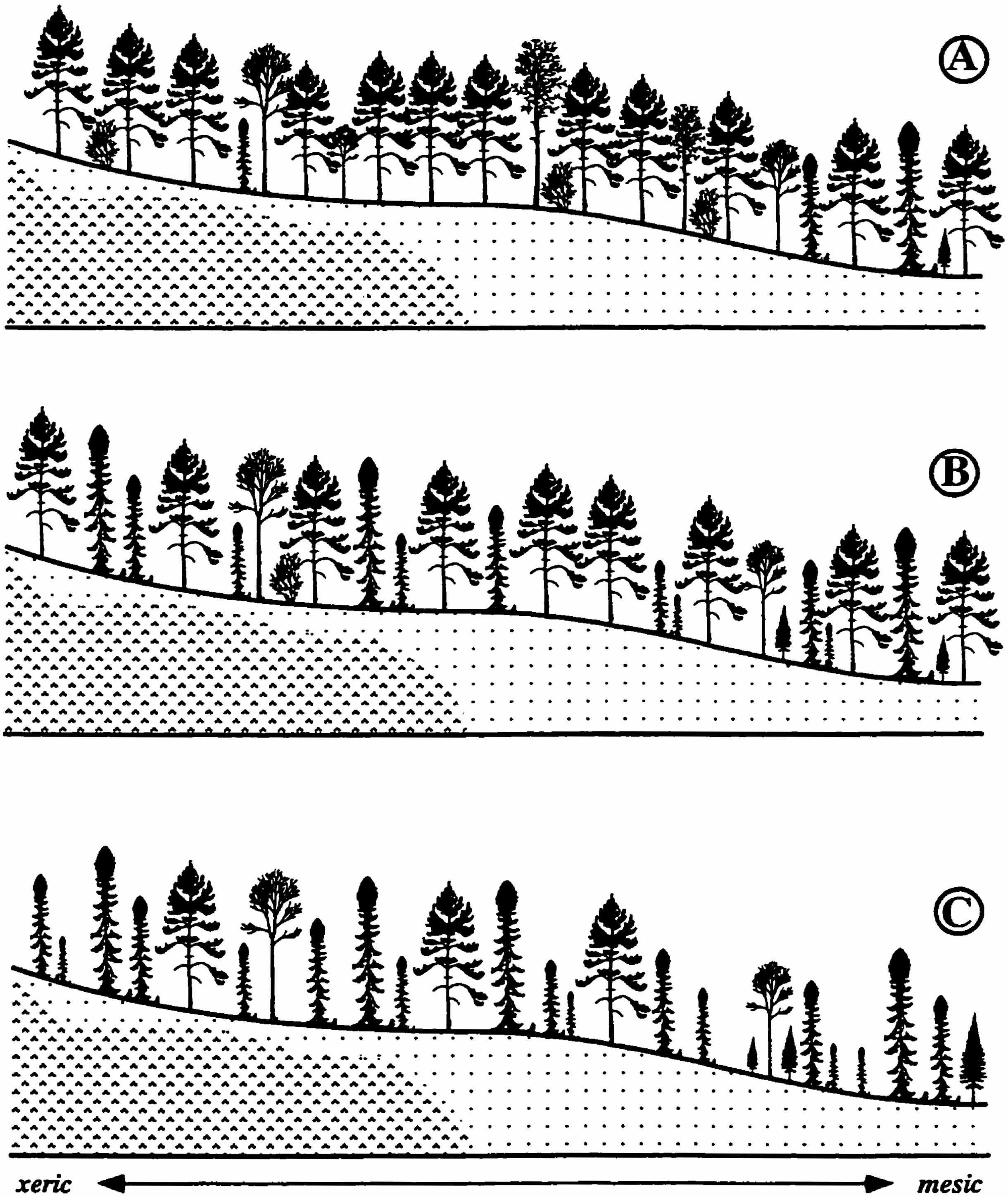


Figure 5.3. Successional trajectory based on mean tree canopy cover.
A = ≤ 85 years; B = 86-120 years; C = > 120 years.

I. Jack Pine - Feathermoss

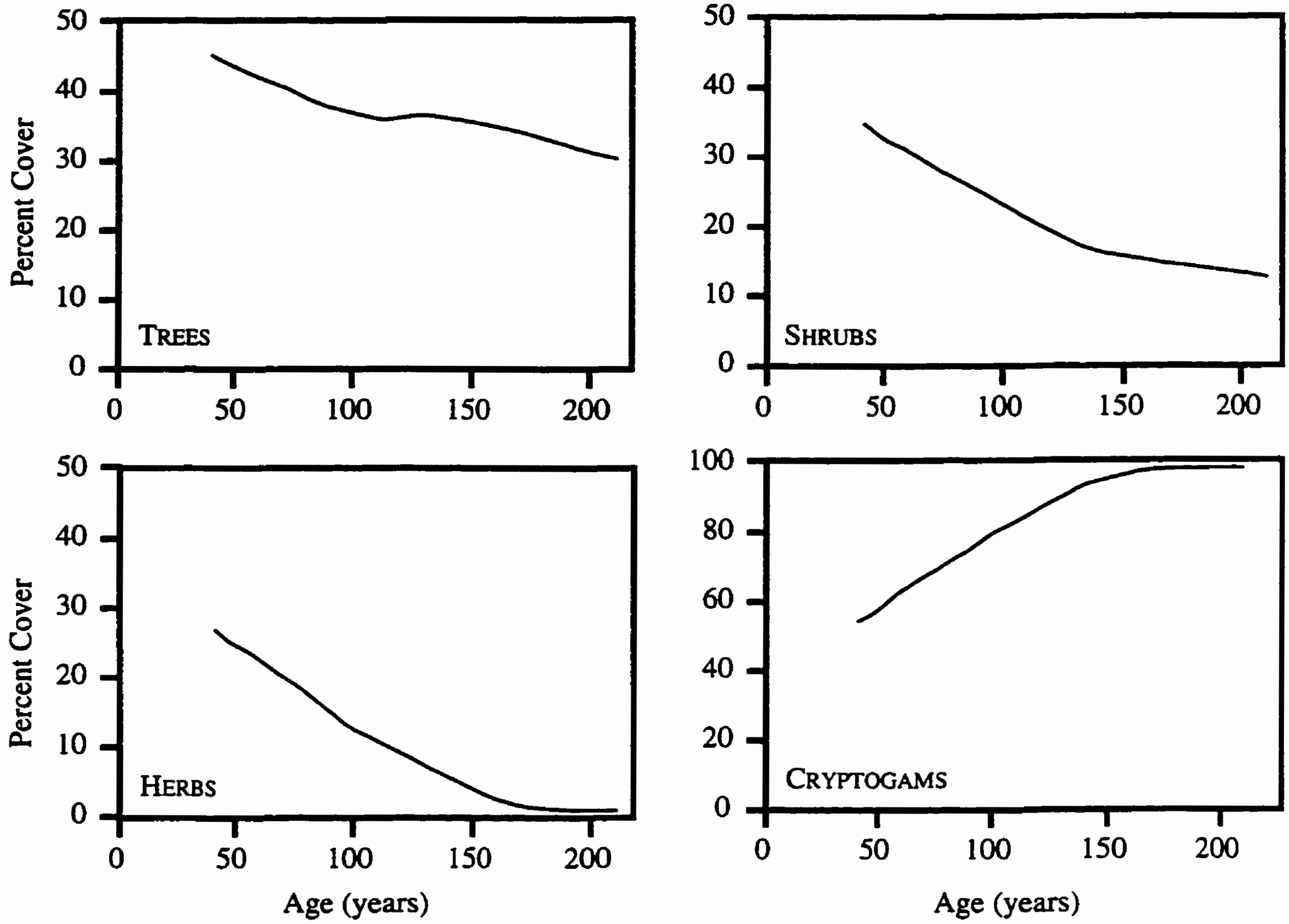


Figure 5.4. Changes in total tree, shrub, herb and cryptogam cover over time. Lines fitted using locally weighted regression analysis.

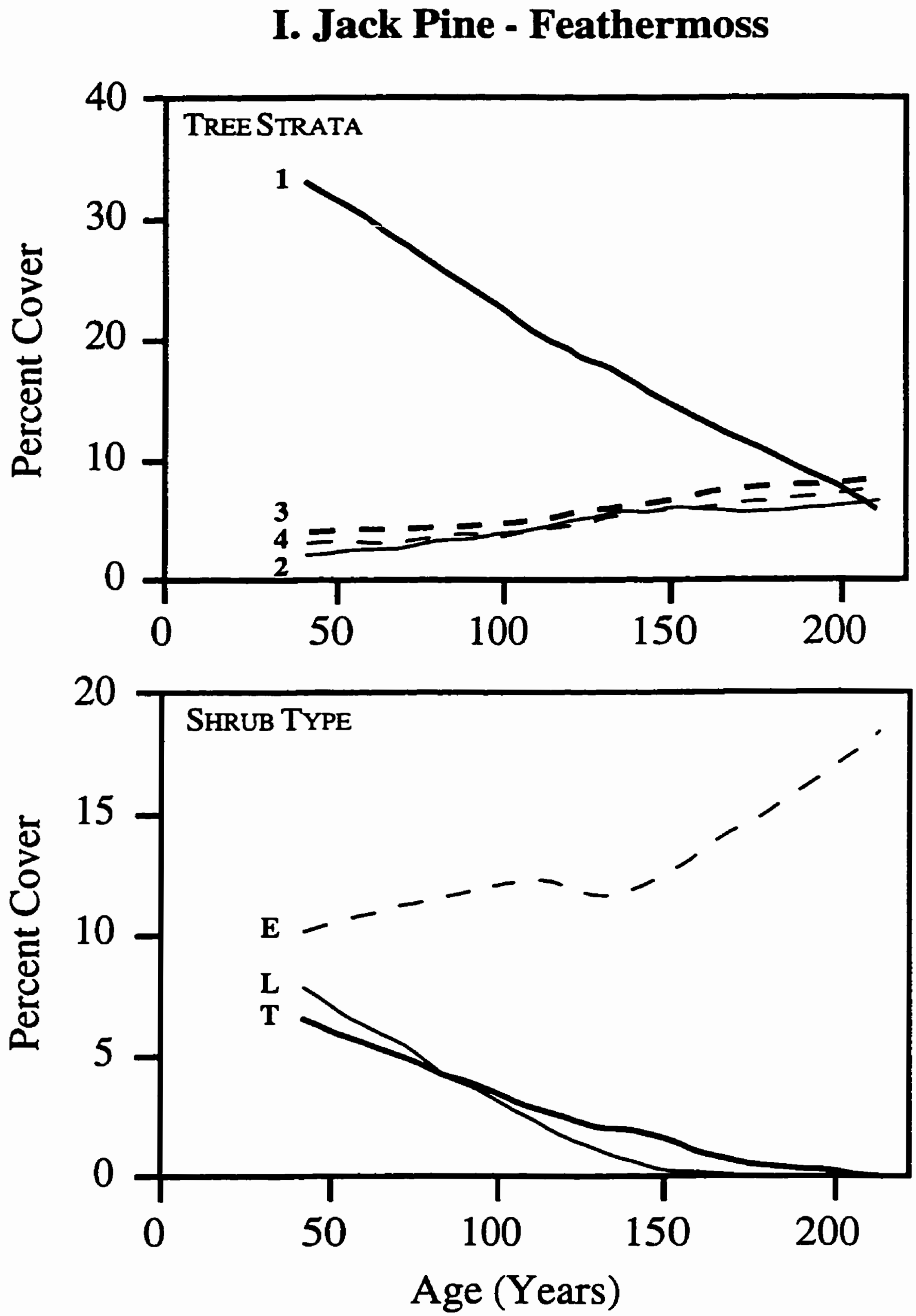


Figure 5.5. Changes in total tree cover by strata (codes: 1 = canopy; 2= upper subcanopy; 3 = lower subcanopy; 4 = sapling layer) and shrub cover by shrub-type (codes: T = tall shrubs; L = low shrubs; E = ericaceous shrubs). Lines fitted using locally weighted regression analysis.

TABLE 5.1. Mean cover of tree species in stand-type I by canopy strata (1-4), in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	Stands ≤ 85 years *n = 103*					Stands > 85 years *n = 78*				
		Total	1	2	3	4	Total	1	2	3	4
Pinus banksiana	Jack Pine	25.67	25.20	0.17	0.11	0.19	16.62	16.18	0.09	0.15	0.19
Picea mariana	Black Spruce	6.10	1.09	2.32	1.74	0.95	14.60	5.32	4.09	2.72	2.47
Betula papyrifera	White Birch	5.68	0.99	1.65	2.38	0.66	2.58	0.37	0.92	0.76	0.53
Populus tremuloides	Trembling Aspen	4.04	2.86	0.19	0.55	0.43	1.01	0.63		0.14	0.24
Abies balsamea	Balsam Fir	2.45	0.03	0.46	0.86	1.10	3.19	0.09	0.89	1.39	0.83
Picea glauca	White Spruce	0.87	0.29	0.04	0.17	0.38	0.60	0.22	0.09	0.18	0.12
Acer rubrum	Red Maple	0.12			0.06	0.06	0.01		0.01		
Populus balsamifera	Balsam Poplar	0.08		0.05	0.01	0.02					
Thuja occidentalis	White Cedar	0.04				0.04	0.21			0.10	0.10
Fraxinus nigra	Black Ash	0.03				0.03					
Pinus strobus	White Pine	0.02			0.01	0.01	0.10		0.06		0.04
Populus grandidentata	Large-toothed Aspen	0.01				0.01					
Quercus rubra	Red Oak						0.03			0.03	
Populus deltoides	Cottonwood						0.01			0.01	

TABLE 5.2. Frequency of tree species in stand-type I by canopy strata 1-4, younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 103*					> 85 years *n = 78*				
		Total	1	2	3	4	Total	1	2	3	4
Pinus banksiana	Jack Pine	0.97	0.96	0.07	0.08	0.18	0.86	0.86	0.03	0.05	0.19
Picea mariana	Black Spruce	0.72	0.14	0.25	0.48	0.47	0.85	0.45	0.44	0.56	0.71
Betula papyrifera	White Birch	0.57	0.06	0.17	0.30	0.45	0.50	0.06	0.18	0.24	0.41
Populus tremuloides	Trembling Aspen	0.49	0.23	0.07	0.18	0.40	0.22	0.08		0.09	0.15
Abies balsamea	Balsam Fir	0.54	0.01	0.08	0.21	0.52	0.50	0.03	0.13	0.28	0.45
Picea glauca	White Spruce	0.23	0.03	0.02	0.07	0.19	0.14	0.03	0.03	0.05	0.08
Acer rubrum	Red Maple	0.08			0.04	0.06	0.01		0.01		
Populus balsamifera	Balsam Poplar	0.03		0.01	0.01	0.02					
Thuja occidentalis	White Cedar	0.02				0.02	0.03			0.03	0.03
Fraxinus nigra	Black Ash	0.02				0.02					
Pinus strobus	White Pine	0.01			0.01	0.01	0.05		0.01		0.04
Populus grandidentata	Largetooth Aspen	0.01				0.01					
Quercus rubra	Red Oak						0.01			0.01	
Populus deltoides	Cottonwood						0.01			0.01	

Successional Trajectory

In the vast majority of stands, the jack pine-dominated canopy is slowly being replaced by black spruce. Canopy cover of white birch and trembling aspen also decline over time. Tree cover in the subcanopy and sapling layers increases slightly over time but remains low (**Tables 5.1, 5.2**). Regeneration in most stands is poor, and in some cases virtually nonexistent. These latter stands will probably degenerate into decadent, open-canopy jack pine barrens, although they may be slowly invaded by black spruce if there is a nearby seed source. Stands having more vigorous regeneration will develop into uneven-aged stands of black spruce, with some relict jack pine trees remaining for at least 200 years. Balsam fir, white birch and trembling aspen may form a very minor component in some stands. The presence of young jack pine in some highly xeric stands suggests its continued persistence.

Low ericaceous species become increasingly dominant over time (**Fig. 5.5**). Blueberries (*Vaccinium angustifolium, V. myrtylloides*) remain an important component of older stands. *Gaultheria hispidula* and *Ledum groenlandicum* are more frequent and abundant in older stands, while *Arctostaphylos uva-ursi* and *Gaultheria procumbens* are less frequent. The overall decline in herb cover is reflected in reduced frequency and cover of individual species as succession proceeds. With the exception of *Polytrichum* spp., the more common cryptogram species increase in frequency and cover as succession proceeds. *Pleurozium schreberi*, already abundant in younger stands, forms an almost continuous carpet in most older stands. The feathermosses *Ptilium crista-castrensis* and *Hylocomium splendens* increase in both frequency and cover. The cover of *Cladina* spp. increases slightly over time, and *Peltigera* spp. are more frequently encountered (see **Appendix I**).

Successional Variants

1. BEDROCK SITES (DEPTH TO BEDROCK < 2 M)

Younger stands over bedrock have lower tree cover than the stand-type as a whole. Regeneration is primarily black spruce in the subcanopy, while white birch and balsam fir are frequent in the sapling layer. Jack pine regeneration also occurs, though at low frequency. Shrub composition is similar to the stand-type, but overall cover is lower and *Arctostaphylos uva-ursi* is less frequently encountered. Tall shrubs cover is low. The herb layer is similar to the stand-type. Total cryptogam cover is somewhat higher, in large part attributable to higher cover and frequency of *Cladina* spp.

A successional trend toward black spruce dominance is indicated on bedrock sites. However, remnant jack pine and the occasional white birch or trembling aspen may be found in older stands. Overall, shrub and herb trajectories are similar to those of the stand-type. A notable exception is *Ledum groenlandicum*, which increases in frequency and cover in older stands. *Gaultheria procumbens* and *G. hispidula* are also more frequently encountered. *Cladina* spp. increase in cover as succession proceeds. The feathermosses *Pleurozium schreberi*, *Ptilium crista-castrensis* and *Hylocomium splendens* increase in frequency and cover, as does *Dicranum polysetum*.

2. Xeric Sites (Moisture Regime < 3)

Total tree cover in these stands is initially higher than in the stand-type as a whole. These are generally pure jack pine stands, although black spruce and trembling aspen may be encountered in the canopy. In general, black spruce is less frequent here (in all canopy layers) compared to the other variants. The subcanopy and sapling layers are predominantly black spruce, although white birch and balsam fir also occur. Jack pine saplings occur in about one-third of the stands. *Diervilla lonicera* and *Arctostaphylos uva-ursi* are initially common, and herb and cryptogam species composition are similar to the stand-type.

Compared to the other two successional variants, jack pine persists well in these stands. Black spruce is invading the canopy, but slowly and sporadically. Although balsam fir is common in the sapling layer, it rarely occurs in the canopy or subcanopy of even the oldest stands. Vaccinium *myrtilloides* and *V. vitis-idaea* increase in cover and/or frequency, while *Diervilla lonicera* and *Arctostaphylos uva-ursi* decline in importance. Successional trends in the herb and cryptogam layers are similar to the overall stand-type trajectory.

3. MESIC SITES (MOISTURE REGIME ≥ 3)

Younger stands on more mesic sites are dominated by jack pine, but black spruce cover is higher (in all canopy layers) than in the stand-type as a whole. White birch, balsam fir, and trembling aspen are less frequent in the canopy, but more common in the subcanopy and sapling layers. The subcanopy is dominated by black spruce, while black spruce, balsam fir and white birch are found in the lower subcanopy and sapling layers. *Diervilla lonicera* is infrequent and occurs at low cover when present. *Vaccinium angustifolium* is very abundant. Total herb cover is slightly lower than the stand-type as a whole. Total cryptogam cover is similar, though *Cladina* spp. are more frequent.

Succession in these stands is similar to the overall stand-type trajectory, although canopy replacement occurs more quickly and total canopy cover remains higher. These stands develop into an uneven-aged, mixed canopy of relict jack pine and regenerating black spruce, with some white birch and balsam fir. Overall shrub cover declines over time, particularly shade-intolerant species such as *V. angustifolium* and *Arctostaphylos uva-ursi*. Herbaceous cover also declines, although *Cornus canadensis* increases in both frequency and cover in older stands. *Pleurozium schreberi* slowly decreases in cover, while *Ptilium crista-castrensis* cover increases. *Cladina* spp. is uncommon from older stands.

Discussion

The overall successional trajectory for this stand-type is clear. Jack pine is being succeeded by black spruce, although the rate of succession varies considerably depending on environmental conditions. In the majority of stands, the canopy becomes more open with time. Some species in the sapling layer rarely if ever reach the canopy, particularly balsam fir, white birch and trembling aspen. The cover of non-ericaceous shrubs and herbs declines over time, whereas cryptogams (mainly feathermosses, reindeer lichens) and ericaceous shrubs increase. Organic matter accumulation further reduces nutrient availability and results in an unsuitable tree seedbed (Carleton 1982a; Burns and Honkala 1990).

Jack pine saplings were observed in many open-canopy xeric stands, suggesting that long-term regeneration is possible. This was also noted in xeric habitats in western Québec (Gauthier et al. 1993). Although jack pine cones are often assumed to be serotinous (e.g. Dix and Swan 1971; Carleton and Maycock 1978), the loss of serotiny may be favoured in environments where non-lethal fires are common (e.g. islands, Gauthier et al. 1996; Rudolph and Laidly 1990). In the absence of strong regeneration, jack pine stands in xeric habitats become more open and savanna-like (Carleton and Maycock 1978).

Carleton (1982a,b) concluded that black spruce regenerates well under jack pine canopies in north-eastern Ontario, but that regeneration patterns vary widely. Some stands showed contemporaneous establishment of jack pine and black spruce, whereas others showed gradual or episodic black spruce recruitment. Episodic recruitment generally occurred following a low-intensity surface fire. In eastern Québec, by contrast, the majority of recruitment in jack pine stands occurs within 30 years (Cogbill 1985). In older stands, fallen timber (tip-up mounds) may assist seedling establishment by exposing mineral soil. Carleton (1982a) speculated that granivore foraging may limit regeneration in mature stands, and that black spruce recruitment is highly dependent on seed source proximity.

Jack pine is a short-lived, shade-intolerant species that forms a monodominant pyric climax in fire-prone, dry-sandy habitats (Cayford and MacRae 1983). Jack pine may become locally extinct if fire cycles exceed 200 years (Heinselman 1973; Cogbill 1985; Bergeron and Dubuc 1989). In the absence of fire, closed stands are gradually replaced by black spruce (Carleton and Maycock 1978; Kenkel 1986) and/or balsam fir. However, my results indicate that balsam fir rarely if ever succeeds jack pine, even though balsam fir often occurs in the sapling layer. Ungulate herbivory and/or spruce budworm attack may prevent balsam fir dominance (Zoladeski and Maycock 1990). Environmental conditions are undoubtedly important in the regeneration dynamics of these stands. Xeric, nutrient-deficient and acidic conditions may explain why many sapling rarely enter the canopy layer, even in the oldest stands. Decreased nutrient availability over time favours species that are tolerant of nutrient deficiencies, particularly ericaceous shrubs and some cryptogams.

5.3.2 Stand-Type II: Jack pine - Black spruce - Feathermoss

Stand-Type Description

Soil-Environment

Most sites in this stand-type are classified as xeric-mesic, although in general they are not as moisture-deficient as those of stand-type I. Depth to water table is < 2 m in only 14% of stands, and the soil profile of about one-third of show distinct mottling. Few stands (about 18%) occur over bedrock, and the majority are on flats or very gentle slopes. Substrates are primarily sands and sandy loams, but loams and clays also occur. Brunisolic soils predominate, but Podzols and Luvisols are also relatively common. Parent materials are primarily glaciofluvial, but lacustrine and morainal are also seen. Stands are relatively nutrient-poor (mean TEB = 1.28), but nutrient-deficiency is not as strongly pronounced as in stand-type I. Depth of organic horizons are slightly greater than stand-type I (mean DOM= 7.84 cm), and most stands have a poorly-developed fibrimoric humus form.

Vegetation

These stands are characterized by a mixture of jack pine and black spruce. Jack pine is found almost exclusively in the canopy, whereas black spruce is distributed throughout the canopy, subcanopy and sapling layers. White birch, balsam fir, trembling aspen and/or white spruce may also occasionally be present in the upper two canopies, but they are uncommon. Regeneration in the lower subcanopy and saplings layers is predominately to black spruce. Balsam fir, white birch and trembling aspen are occasionally encountered in the sapling layer. Total cover of shrubs is low, and ericaceous species predominate. Blueberries (particularly *Vaccinium myrtilloides*) are found in virtually all stands. *Gaultheria hispidula* is frequently encountered at low cover, while *Ledum groenlandicum* occurs at moderate to high cover when present. Tall shrubs are of minor importance.

Amelanchier spp. are most frequently encountered (40% of stands) but occur at low cover. *Alnus crispa* is less frequent, but may occur at moderate cover when present. *Diervilla lonicera* is the most frequent and abundant low shrub, occurring in about half the stands.

Maianthemum canadense, *Cornus canadensis*, and *Linnaea borealis* are ubiquitous, but generally occur at low cover. However, the cover of *C. canadensis* may be high in some stands. *Clintonia borealis*, *Aralia nudicaulis* and *Lycopodium* spp. are also relatively frequent. Minimum cryptogam cover in these stands is 30%, and over two-thirds of the stands have >80% cryptogam cover. With few exceptions, the feathermoss, *Pleurozium schreberi*, dominates the understory of these stands (mean cover >80%). *Dicranum polysetum* and *Ptilium crista-castrensis* are also frequent but far less abundant. *Hylocomium splendens* and *Cladina* spp. occur in about half the stands at low cover.

Stand Dynamics

<u>Summary</u>

These stands are succeeding towards a more open, uneven-aged monodominant canopy of black spruce (**Fig. 5.6**). Regeneration of black spruce is strong in all stands. Balsam fir sometimes regenerates well in moist sites, but in most stands regeneration by other tree species is poor. Total shrub cover declines after 100 years (**Fig. 5.7**), as does the cover of most tall, low and ericaceous shrubs (**Fig. 5.8**). Herb cover declines steadily as succession proceeds (**Fig. 5.8**). Cryptogam cover declines until 100 years (**Fig. 5.8**), largely due to a decline in *Pleurozium schreberi* cover, then stabilizes. No clear changes in soil variables are apparent: soil pH and nutrient status are largely invariant, and organic matter accumulation is minimal (see **Appendix II**).

<u>Successional Trajectory</u>

Canopy closure is not complete after 85 years, and virtually all stands are following a successional trend from even-aged, mixed jack pine-black spruce stands toward more closed-canopy, uneven-aged stands dominated by black spruce (**Fig. 5.6**). Total tree cover increases over time (**Fig. 5.7**), attributable primarily to the higher frequency and

II. Jack Pine - Black Spruce - Feathermoss

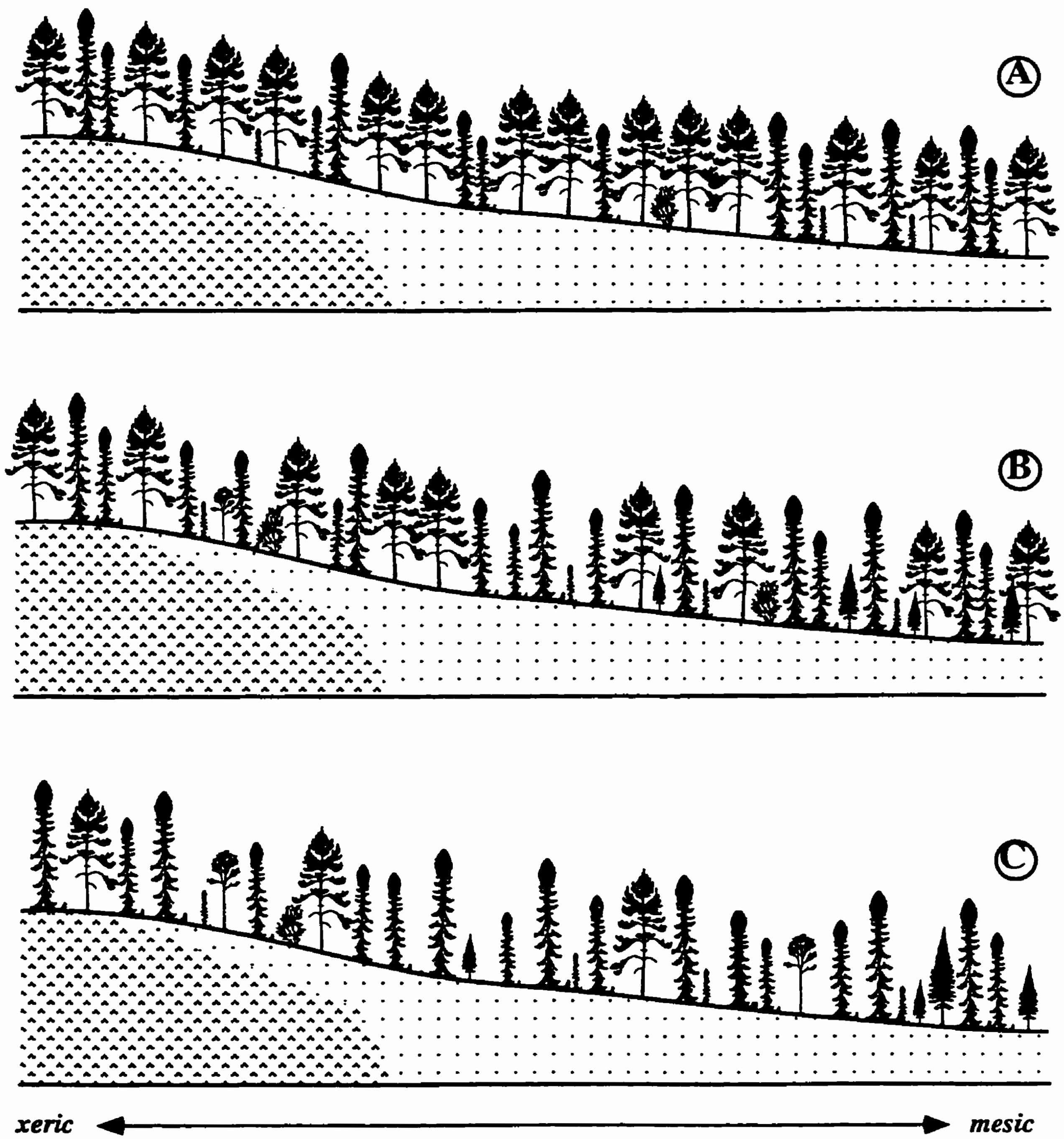


Figure 5.6. Successional trajectory based on mean tree canopy cover.
A = ≤ 85 years; B = 86-120 years; C = > 120 years.

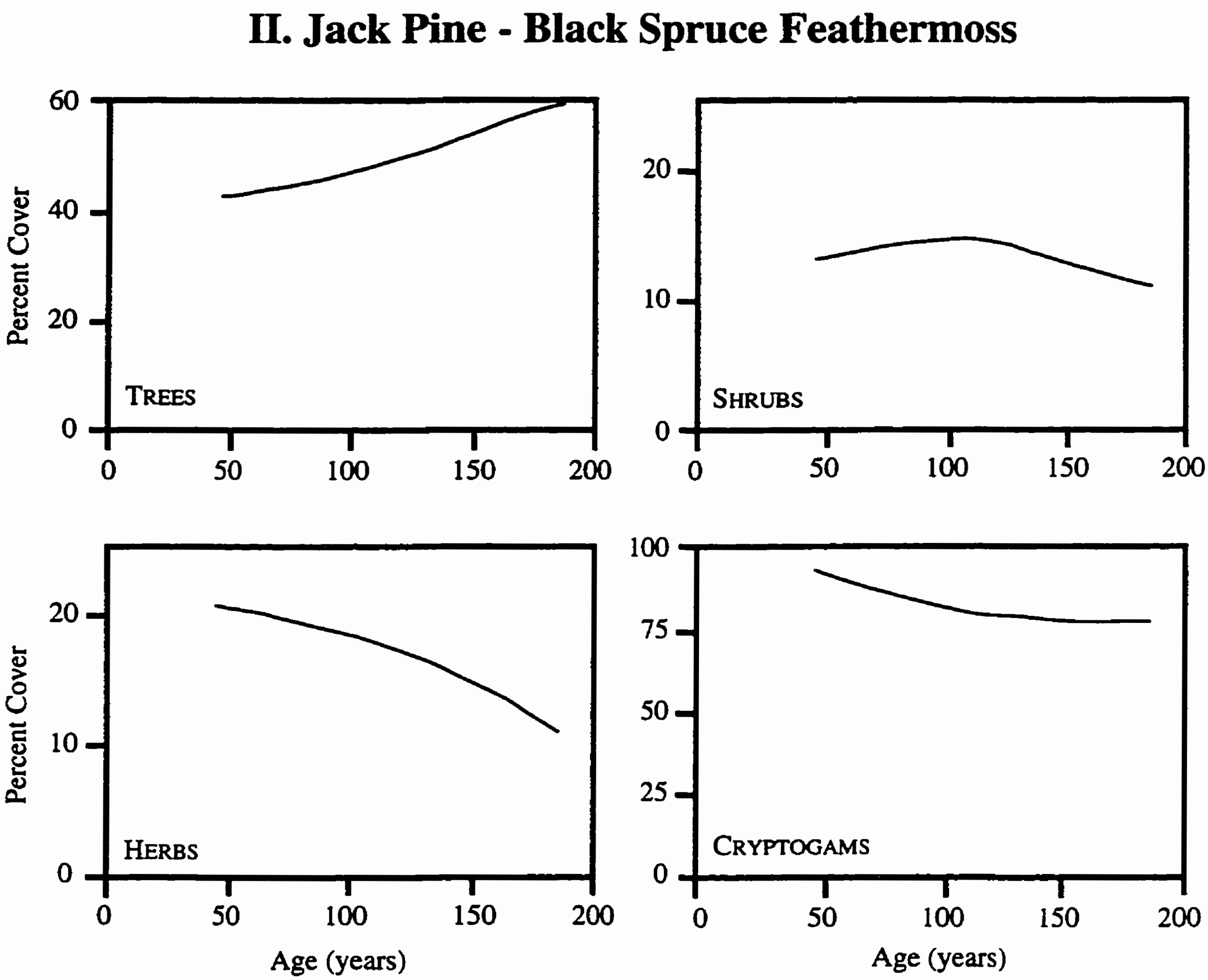


Figure 5.7. Changes in total tree, shrub, herb and cryptogam cover over time. Lines fitted using locally weighted regression analysis.

II. Jack Pine - Black Spruce Feathermoss

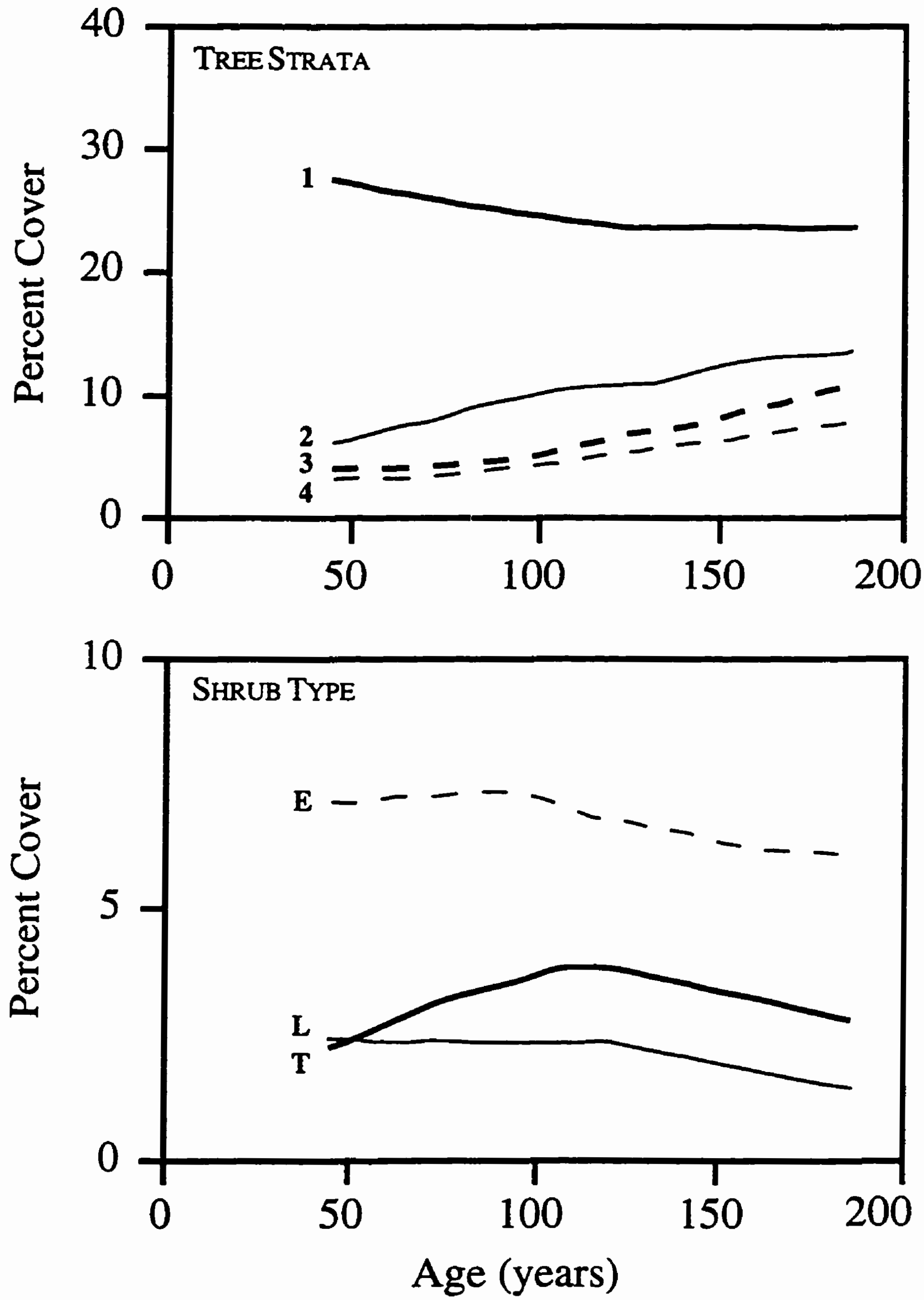


Figure 5.8. Changes in total tree cover by strata (codes: 1 = canopy; 2 = upper subcanopy; 3 = lower subcanopy; 4 = sapling layer) and shrub cover by shrub-type (codes: T = tall shrubs; L = low shrubs; E = ericaceous shrubs). Lines fitted using locally weighted regression analysis.

TABLE 5.3. Mean cover of tree species in stand-type II by canopy strata (1-4), in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years					> 85 years				
		n = 92					n = 54				
		All	1	2	3	4	All	1	2	3	4
Pinus banksiana	Jack Pine	20.49	20.16	0.27	0.01	0.04	14.61	14.54	0.02	0.02	0.04
Picea mariana	Black Spruce	20.12	5.30	8.35	4.11	2.36	20.72	8.02	7.43	2.43	2.85
Abies balsamea	Balsam Fir	1.77	0.11	0.29	0.51	0.86	8.76		2.98	3.85	1.93
Betula papyrifera	White Birch	1.49	0.21	0.36	0.64	0.28	2.91	0.39	1.52	0.48	0.52
Populus tremuloides	Trembling Aspen	0.78	0.41	0.05	0.14	0.17	2.13	1.65	0.07	0.09	0.31
Picea glauca	White Spruce	0.47	0.20	0.09	0.13	0.05	1.46	0.74	0.50	0.11	0.11
Pinus strobus	White Pine	0.08	0.05			0.02	0.22	0.15			0.07
Acer rubrum	Red Maple	0.07				0.07	0.11				0.11
Pinus resinosa	Red Pine	0.07	0.02		0.03	0.01	0.17	0.17			
Populus balsamifera	Balsam Poplar	0.03			0.02	0.01					
Populus deltoides	Cottonwood						0.22		0.06	0.02	0.02
Thuja occidentalis	White Cedar						0.07		0.04		0.04
Larix laricina	Eastern Larch						0.02				0.02
Quercus marcocarpa	Bur Oak						0.02				0.02

TABLE 5.4. Frequency of tree species in stand-type II by canopy strata, younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years					> 85 years				
		n = 92					n = 54				
		All	1	2	3	4	All	1	2	3	4
Pinus banksiana	Jack Pine	0.99	0.99	0.04	0.01	0.04	0.96	0.96	0.02	0.02	0.04
Picea mariana	Black Spruce	0.98	0.46	0.73	0.72	0.82	0.91	0.59	0.67	0.56	0.74
Abies balsamea	Balsam Fir	0.49	0.01	0.05	0.19	0.41	0.61		0.22	0.44	0.52
Betula papyrifera	White Birch	0.36	0.03	0.10	0.19	0.26	0.43	0.07	0.22	0.11	0.35
Populus tremuloides	Trembling Aspen	0.20	0.08	0.03	0.07	0.16	0.39	0.24	0.04	0.07	0.30
Picea glauca	White Spruce	0.11	0.03	0.02	0.05	0.05	0.22	0.11	0.07	0.06	0.07
Pinus strobus	White Pine	0.02	0.01			0.02	0.09	0.02			0.07
Acer rubrum	Red Maple	0.04				0.04	0.11				0.11
Pinus resinosa	Red Pine	0.01	0.01		0.01	0.01	0.04	0.04			
Populus balsamifera	Balsam Poplar	0.02			0.01	0.01					
Populus deltoides	Cottonwood						0.02	0.02	0.02	0.02	0.02
Thuja occidentalis	White Cedar						0.04		0.02		0.04
Larix laricina	Eastern Larch						0.02				0.02
Quercus marcocarpa	Bur Oak						0.02				0.02

cover of black spruce in all four canopy layers (**Tables 5.3, 5.4**). A slight increase in tree diversity reflects the higher frequency of balsam fir, white birch, trembling aspen and white spruce in older stands. While regeneration by black spruce predominates, balsam fir is occasionally abundant in the subcanopy of older stands and may occasionally reach the canopy. White birch shows moderate to strong regeneration where the canopy is more open and may persist in older stands. Relict jack pine trees may persist for 200 years or more, but most older stands are dominated by black spruce.

Shrubs are rarely an important component of these stands. The decline in total shrub cover after 100 years (**Fig. 5.7**) is largely attributable to decreased frequency and cover of tall shrubs (e.g. *Alnus crispa*, *Acer spicatum*, *Sorbus* spp.). Shrub cover declines as tree cover increases. Shade-intolerant ericaceous shrubs such as *Vaccinium myrtylloides* and *Arctostaphylos uva-ursi* are much less frequent in older stands, suggesting a shading effect. The herb layer is rarely important in these stands (**Fig. 5.7**). *Cornus canadensis* is the most abundant herb species in both younger and older stands. The understory is dominated by feathermosses, particularly *Pleurozium schreberi*. Cryptogams remain abundant but cover decreases over time (**Fig. 5.7**). *P. schreberi* cover decreases in older stands, but this is offset somewhat by increased cover and frequency of other species, particularly *Dicranum polysetum*, *Ptilium crista-castrensis* and *Hylocomium splendens*. Lichens are a very minor component of both young and old stands (see **Appendix II**).

<u>Successional Variants</u>

1. BEDROCK SITES (DEPTH TO BEDROCK < 2 M)

Black spruce cover is somewhat higher in these stands, and total tree cover is slightly lower. Black spruce regeneration is similar to the stand-type as a whole, and balsam fir and white birch are more commonly encountered in the lower subcanopy. Shrub species composition is similar, but total shrub cover is lower (attributable to low cover of *Ledum groenlandicum* and the absence of *Arctostaphylos uva-ursi*.). Species composition and cover of the herb layer is typical of the stand-type. The cryptogam layer is also similar in composition, although lichens are slightly more frequent (although cover remains low).

The successional trajectory for these stands is typical of the stand-type, although canopy replacement by black spruce occurs more quickly. White birch persists in the subcanopy of some stands, and tall shrubs (particularly *Alnus crispa*) and *Ledum groenlandicum* are more frequently encountered. Cover of *Aster macrophyllus* increases over time, although it remains low. The shrub and herb layers both remain relatively unimportant. The cover of *Pleurozium schreberi* declines to < 50% in older stands, but this is offset somewhat by increases in the cover of *Ptilium crista-castrensis* and *Dicranum polysetum*.

2. MESIC SITES (MOISTURE REGIME ≥ 3)

These stands are characterized by higher cover of black spruce, and lower cover of jack pine. Regeneration is primarily to black spruce, but balsam fir and trembling aspen are more frequently encountered than in the stand-type as a whole. Total shrub cover is initially higher, attributable to the higher frequency and cover of *Ledum groenlandicum* (which accounts over half the total shrub cover). Cover of *Cornus canadensis* is also higher. Cryptogam species composition and cover are similar to the stand-type as a whole.

Balsam fir regeneration is an important component of many of these stands, and some stands develop a mixed balsam fir-black spruce canopy. Relict jack pine may persist, but not as commonly as in the drier variants. Total canopy cover is high, resulting in a deeply shaded understory. As a result, total shrub and herb cover decline. *Ledum groenlandicum* shows a particularly large decline in cover. *Maianthemum canadense*, *Linnaea borealis*, *Clintonia borealis* and *Trientalis borealis* increase in frequency, but their cover remains low. *Pleurozium schreberi* cover declines to <40% in older stands, as does the cover of *Dicranum polysetum*. *Ptilium crista-castrensis*, *Hylocomium splendens and Brachythecium* spp. all increase in frequency and cover over time.

3. Dry Sites (Moisture Regime < 3)

Compared to the stand-type average, jack pine and white birch cover are higher while black spruce and balsam fir are lower. Regeneration is primarily to black spruce, although balsam fir may also occur in the lower subcanopy and sapling layers. Shrub, herb and cryptogam species composition and cover are similar to the stand-type as a whole.

The successional trajectory is similar to that of stand-type I. Black spruce succeeds jack pine, but succession occurs more slowly. Relict jack pine trees may persist for 200 years or more, and balsam fir very rarely enters the canopy. Total tree canopy cover is lower than that of the stand-type as a whole. Successional trends in the shrub and herbs largely parallel those of the stand-type. *Ledum groenlandicum*, *Lycopodium annotinum*, *Fragaria virginiana* and *Streptopus roseus* show slight increases in cover over time, but total cover remains low. *Pleurozium schreberi* persists in older stands (mean cover of 65%).

Discussion

The successional trajectory is similar to that of stand-type I, but the transition toward black spruce dominance occurs more quickly. Jack pine recruitment is restricted to the first few years after fire (Dix and Swan 1971; Zoladeski and Maycock 1990; St-Pierre et al. 1992), while black spruce recruitment continues for at least 60 years (Dix and Swan 1971; Foster and King 1986; Zoladeski and Maycock 1990). Although relict jack pine may persist for 200 years or more (Cayford and MacRae 1983), it has been suggested that jack pine will be extirpated should fire cycles exceed 200 years (Heinselman 1973; Bergeron and Dubuc 1989). Older stands of this stand-type have a more closed canopy than those of stand-type I , and jack pine regeneration is rare. The cover of non-ericaceous shrubs and herbs decline over time, though not as dramatically as in stand-type I. Older, uneven-aged stands are dominated by black spruce, ericaceous shrubs and feathermosses.

It has been speculated that mixed jack pine-black spruce stands represent a successional stage toward fir-spruce dominance (e.g. Ritchie 1956; Dix and Swan 1971; Carleton and Maycock 1978, 1980; Cayford and MacRae 1983; Cogbill 1985; Bergeron and Dubuc

1989; Zoladeski and Maycock 1990). Balsam fir recruitment often does not occur until at least 30 years after stand initiation (Foster and King 1986; Frelich and Reich 1995b). Zoladeski and Maycock (1990) note that balsam fir recruitment into mixed jack pine-black spruce stands increases over time. However, the results presented here demonstrate that although balsam fir is often present in the sapling layer, it rarely enters the canopy of older stands. Differential mortality of balsam fir saplings may be attributable to the combined effects of low nutrient availability, ungulate herbivory, and spruce budworm infestation (Blais 1983; Bergeron and Dubuc 1989; Bergeron and Dansereau 1993). Balsam fir seedlings are also sensitive to drought and frost (Frank 1990), which could account for the scarcity of balsam fir in the more xeric variants of this stand-type.

5.3.3 STAND-TYPE III: BLACK SPRUCE - FEATHERMOSS

Stand-Type Description

Soil-Environment

Compared to stand-types I and II, these sites are relatively mesic (mean moisture regime = 3). Depth to water table is < 2 m in about one-third of the sites, and distinct mottling of the soil profile occurs in ca. 25% of sites. Most stands occur on sandy or loamy soils, although clay soils are occasional. Brunisols predominate, but Podzols are relatively common in the NCR region. Organic soils and Gleysols may also occur. Most stands are on level to gently sloping ground. Bedrock is found in the first 2 m in ca. 30% of stands. Morainal, glaciofluvial and lacustrine parent materials are all common. Organic matter depth is twice that of stand-types I and II (mean DOM = 14.17 cm), and raw moders and fibrimors predominate. Nutrient status is marginally higher than in stand-type II.

Vegetation

This stand-type is dominated by dense, monodominant stands of black spruce. Jack pine, and more occasionally white birch, trembling aspen and/or white spruce, may occur as canopy codominants. Regeneration in the subcanopy layers is overwhelmingly to black spruce; balsam fir, white birch, and trembling aspen are occasional. Black spruce and balsam fir are equally frequent in the sapling layer. Ericaceous shrubs are ubiquitous, and occur at low to moderate cover. *Ledum groenlandicum*, *Vaccinium angustifolium* and *V. myrtilloides* are the most common species. *Gaultheria hispidula* is also frequent but generally occurs at low cover. Tall and low shrubs are relatively uncommon, and generally have low cover when present.

Total herb cover is low in most stands. *Cornus canadensis* is the most frequent species, and may occur at moderate cover. Other common herbs include *Maianthemum canadense*, *Linnaea borealis*, and *Lycopodium* spp. Stands are characterized by high cover of *Pleurozium schreberi*. *Ptilium crista-castrensis* and *Dicranum polysetum* are also common, generally occur at lower cover. *Hylocomium splendens* and *Polytrichum* spp. are also found in many stands. Peat mosses (*Sphagnum* spp.) may be abundant when present.

Stand Dynamics

Summary

Succession in this stand-type is straightforward: strong black spruce regeneration results in a more open, uneven-aged black spruce forest (**Fig. 5.9**). *Ledum groenlandicum* dominates the shrub layer of older stands, and *Pleurozium schreberi* persists at high cover on the forest floor. Total shrub cover increases over time (**Fig. 5.10**), attributable to an increase in the frequency and cover of ericaceous shrubs (**Fig. 5.11**). Tall and low shrubs show little change in composition and cover. Species composition in the herb and cryptogam layers shows little change, and cover declines slightly over time (**Fig. 5.10**). Most soil variables show little change over time. Total base saturation (TBS) declines over time, but total exchangeable bases (TEB) does not. The rate of organic matter accumulation is low. Soil pH declines in both the mineral and organic horizons. Older stands are characterized by a highly acidic (pH < 4) litter (see **Appendix III**).

III. Black Spruce - Feathermoss

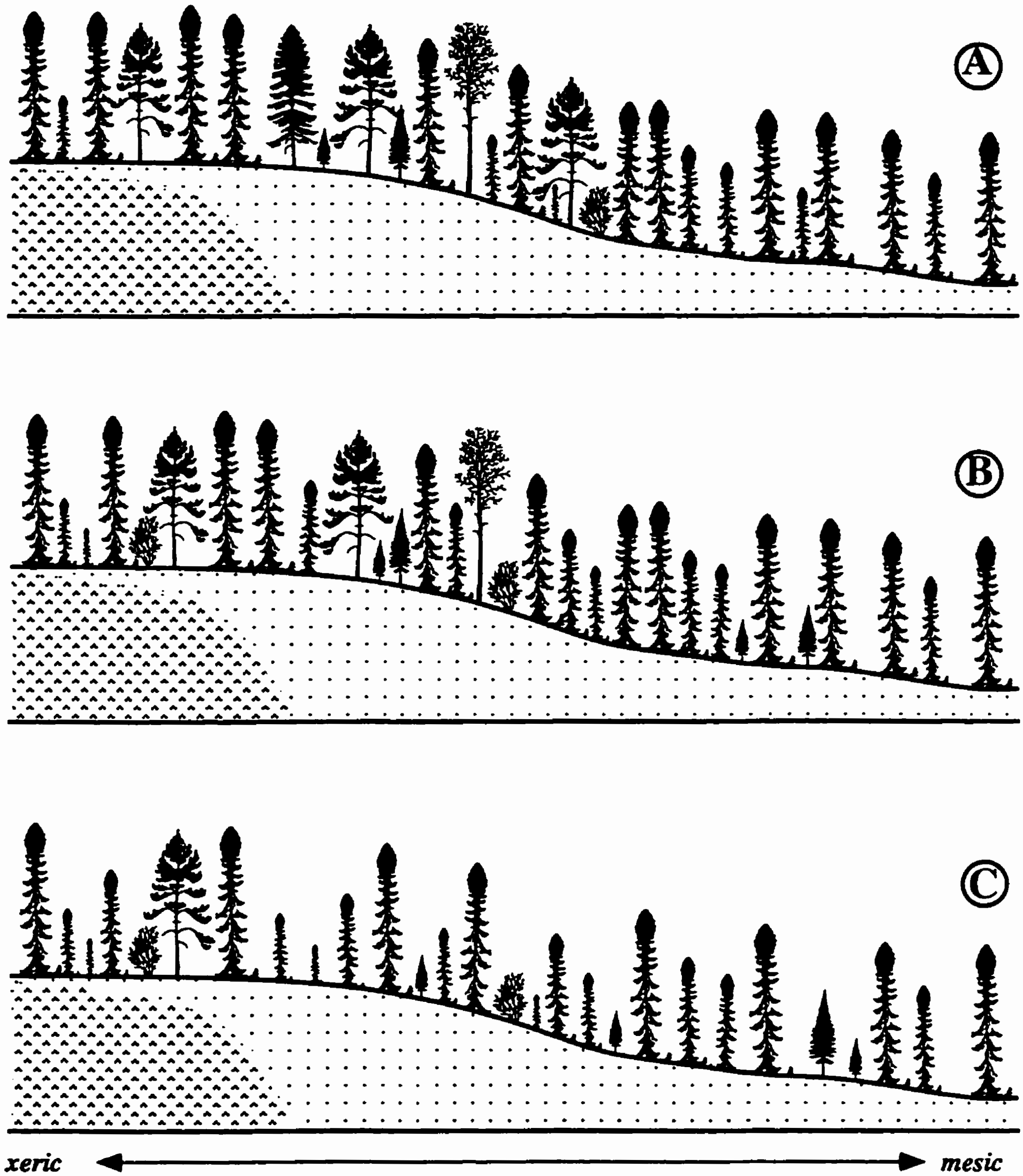


Figure 5.9. Successional trajectory based on mean tree canopy cover.
A = ≤ 85 years; B = 86-120 years; C = > 120 years.

III. Black Spruce - Feathermoss

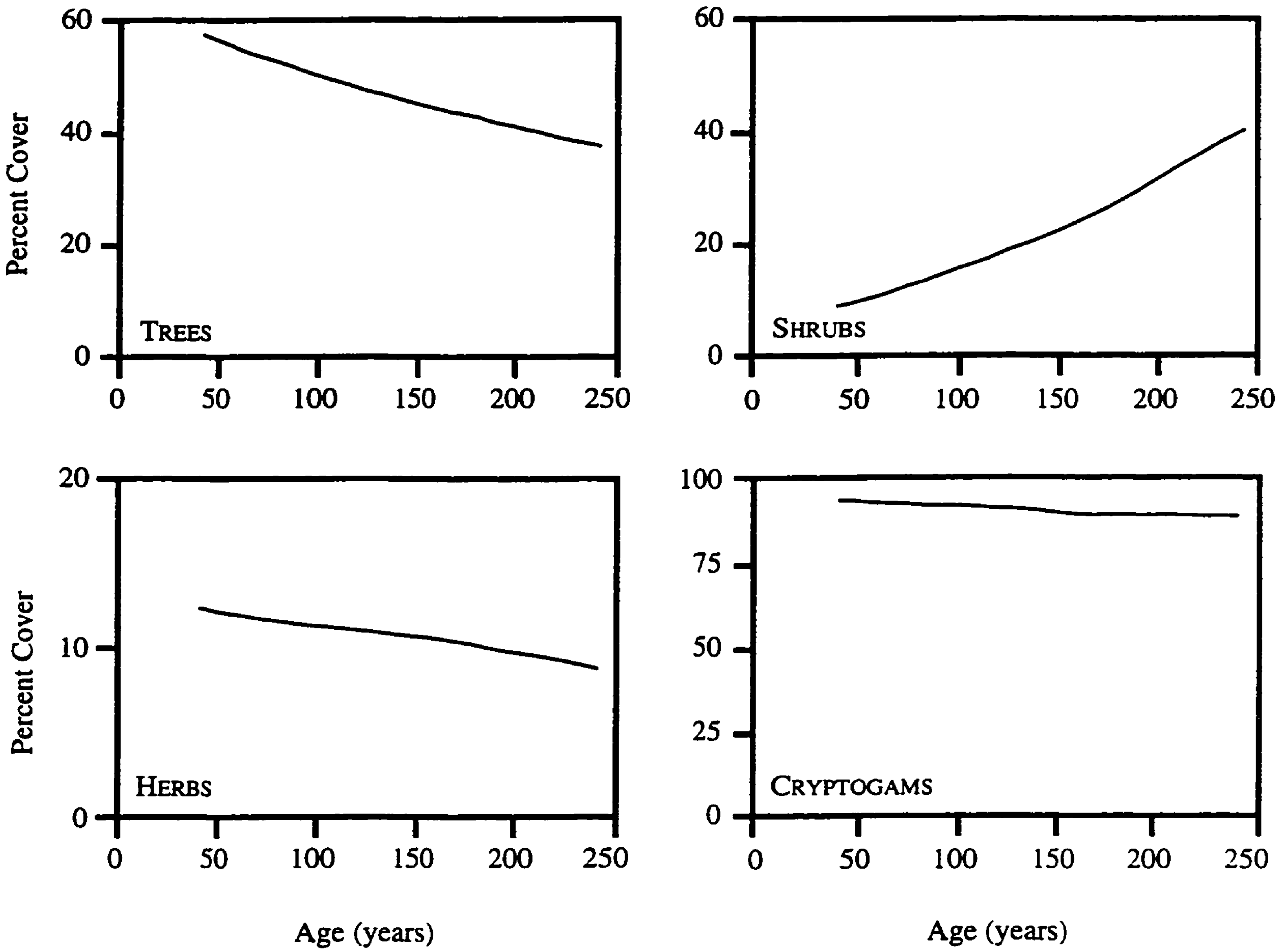


Figure 5.10. Changes in total tree, shrub, herb and cryptogam cover over time. Lines fitted using locally weighted regression analysis.

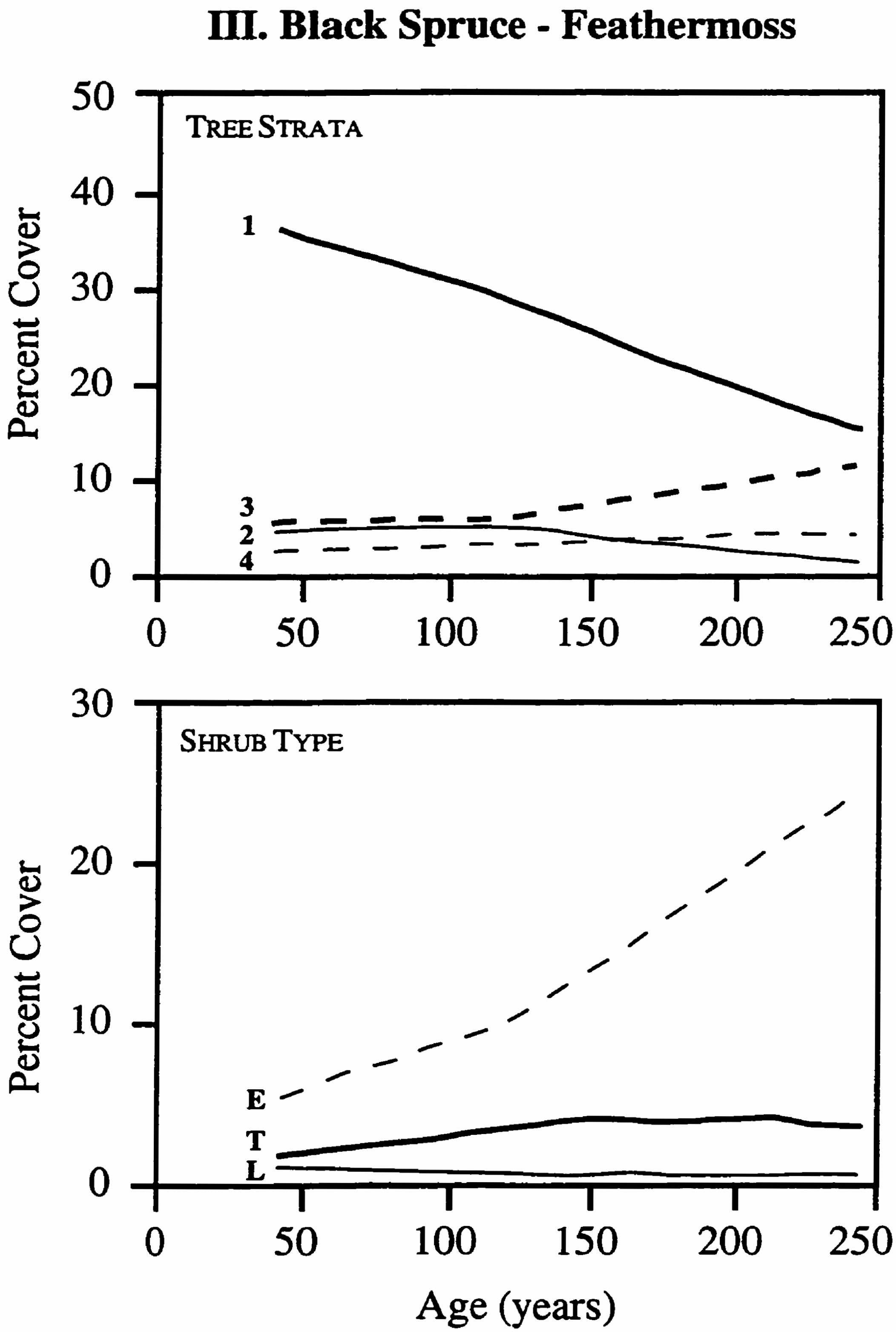


Figure 5.11. Changes in total tree cover by strata (codes: 1 = canopy; 2 = upper subcanopy; 3 = lower subcanopy; 4 = sapling layer) and shrub cover by shrub-type (codes: T = tall shrubs; L = low shrubs; E = ericaceous shrubs). Lines fitted using locally weighted regression analysis.

TABLE 5.5. Mean cover of tree species in stand-type III by canopy strata (1-4), in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 111*					> 85 years *n = 142*				
		Total	1	2	3	4	Total	1	2	3	4
Picea mariana	Black Spruce	37.77	23.65	6.20	6.15	1.77	31.65	20.79	4.56	3.79	2.51
Pinus banksiana	Jack Pine	5.95	5.93	0.01	0.02		6.55	6.44	0.08	0.01	0.02
Abies balsamea	Balsam Fir	3.29	0.55	0.30	1.23	1.21	6.25	0.78	1.73	2.49	1.25
Populus tremuloides	Trembling Aspen	2.31	1.67	0.30	0.13	0.22	2.61	2.28	0.01	0.09	0.22
Betula papyrifera	White Birch	2.21	0.61	0.50	0.83	0.26	3.67	1.61	0.83	0.82	0.41
Picea glauca	White Spruce	1.99	1.62	0.13	0.19	0.05	0.41	0.27	0.09	0.02	0.02
Larix laricina	Eastern Larch	0.92	0.84	0.05	0.04						
Thuja occidentalis	White Cedar	0.32	0.05	0.05	0.11	0.11	0.04			0.02	0.02
Populus balsamifera	Balsam Poplar	0.12	0.09		0.01	0.02	0.32	0.26			0.06
Acer rubrum	Red Maple	0.04				0.04	0.06			0.04	0.02
Fraxinus nigra	Black Ash	0.04		0.04							
Pinus strobus	White Pine	0.02				0.02	0.13	0.11			0.01
Pinus resinosa	Red Pine						0.06	0.06			
Populus deltoides	Eastern Cottonwood						0.01	0.01			0.01

TABLE 5.6. Frequency of tree species in stand-type III by canopy strata, younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 111*					> 85 years *n = 142*				
		Total	1	2	3	4	Total	1	2	3	4
Picea mariana	Black Spruce	0.98	0.83	0.56	0.69	0.68	0.99	0.91	0.51	0.62	0.72
Pinus banksiana	Jack Pine	0.48	0.46	0.01	0.02		0.60	0.57	0.04	0.01	0.01
Abies balsamea	Balsam Fir	0.55	0.10	0.11	0.28	0.48	0.51	0.13	0.16	0.30	0.45
Populus tremuloides	Trembling Aspen	0.32	0.20	0.05	0.08	0.20	0.30	0.17	0.01	0.06	0.20
Betula papyrifera	White Birch	0.40	0.09	0.14	0.16	0.24	0.48	0.15	0.14	0.20	0.35
Picea glauca	White Spruce	0.17	0.14	0.03	0.05	0.04	0.10	0.06	0.02	0.01	0.02
Larix laricina	Eastern Larch	0.08	0.08	0.03	0.01						
Thuja occidentalis	White Cedar	0.03	0.01	0.01	0.02	0.03	0.01			0.01	0.01
Populus balsamifera	Balsam Poplar	0.02	0.01		0.01	0.02	0.06	0.02			0.06
Acer rubrum	Red Maple	0.04				0.04	0.04			0.01	0.02
Fraxinus nigra	Black Ash	0.01		0.01							
Pinus strobus	White Pine	0.02				0.02	0.02	0.01			0.01
Pinus resinosa	Red Pine						0.01	0.01			
Populus deltoides	Eastern Cottonwood						0.01	0.01			0.01

<u>Successional Trajectory</u>

Total tree cover declines over time, which is primarily attributable to a decrease in black spruce cover in the canopy (**Tables 5.5, 5.6**) . Regeneration is primarily to black spruce, which often forms a multi-layered canopy in older stands. Balsam fir cover increases in moist, older stands, but rarely reaches the canopy. Relict jack pine trees may be present in older stands, particularly on drier sites. White birch, trembling aspen and white spruce are only occasionally encountered, and become less common in older stands. The overall trend is toward more open, uneven-aged stands of black spruce.

Total shrub cover increases, due in large part to increased abundance of *Ledum groenlandicum* (mean cover >9% in older stands). Other shrub species are uncommon, and species composition and cover are remarkably stable over time. Total herb cover is low and tends to decline slightly over time. Species composition is similar in young and older stands. *Cornus canadensis* and *Maianthemum canadense* show the largest declines in cover over time. Cryptogams dominate the understory of these stands and species composition, frequency and cover are stable over time. *Pleurozium schreberi* is ubiquitous at all successional stages, and is abundant (> 50% cover) in most older stands. *Ptilium crista-castrensis*, *Hylocomium splendens*, and *Dicranum* spp. are also frequent, but they generally occur at lower cover. Lichens are infrequent, and have low cover at all successional stages (see **Appendix III**).

<u>Successional Variants</u>

1. BEDROCK SITES (DEPTH TO BEDROCK < 2 M)

Tree species composition is similar to the stand-type as a whole, but black spruce cover is slightly higher in the subcanopy and sapling layers. The subcanopy is almost entirely dominated by black spruce. Black spruce is also found in the lower subcanopy and sapling layers, but balsam fir and white birch may also occur. Shrub and herb species composition and cover are typical of the stand-type, although *Vaccinium* spp. are more common and herb cover is slightly lower. Compared to the stand-type as a whole, *Pleurozium schreberi* and *Dicranum polysetum* cover are higher, while *Hylocomium splendens* and *Ptilium crista-castrensis* cover is lower.

The successional trajectory for these stands is typical of the stand-type. Black spruce cover declines over time as the canopy opens and becomes increasingly multi-tiered. Relict jack pine trees persist on these sites. Balsam fir occurs in the subcanopy and sapling layers but very rarely reaches the canopy. Shrub cover (*Ledum groenlandicum* and *Vaccinium* spp.) in older stands is higher than in the stand-type as a whole. Herb cover remains low. The understory is dominated by *Pleurozium schreberi* at all successional stages.

2. MESIC SITES (MOISTURE REGIME ≥ 3)

These stands are characterized by high canopy cover of black spruce. Larch may be present in some stands. Jack pine, trembling aspen and white birch are less common in this variant. Black spruce shows strong regeneration, but balsam fir is also commonly encountered in the lower subcanopy layers. *Ledum groenlandicum* cover is higher, and *Vaccinium* spp. lower, than in the stand-type as a whole. Species composition and cover in the herb layer are typical of the stand-type. Cryptogam cover is high: *Sphagnum* spp. and *Ptilium crista-castrensis* have higher cover, while cover of *Pleurozium schreberi*, *Dicranum polysetum* and *Hylocomium splendens* are lower. Lichens are infrequent.

Succession in this variant is similar to the stand-type as a whole, but canopy cover is higher and balsam fir occurs at higher cover. Balsam fir regeneration is common in some stands, and it may occasionally reach the canopy-subcanopy. White birch may be present in a few stands, but is never abundant. Eastern larch and jack pine are rarely present in older stands. *Ledum groenlandicum* is by far the most dominant shrub species in older stands. Overall herb cover declines over time. Cryptogams dominate the understory in these stands, but relative abundance changes over time. *Pleurozium schreberi* and *Ptilium crista-castrensis* decline slightly in cover, while *Hylocomium splendens* cover increases considerably (mean = 1.8%, to 9.4% in older stands). Cover of *Sphagnum* spp. also increases, although they are never abundant. *Rhytidiadelphus triquestrus*, which is absent in younger stands, is present in about one-fifth of the older stands.

3. DRY SITES (MOISTURE REGIME < 3)

Total tree cover is slightly lower than the stand-type mean. Black spruce canopy cover is somewhat lower, and jack pine is more commonly encountered. White spruce and balsam fir are more common in the lower canopy and sapling layers in these sites, but black spruce is also common. Total ericaceous shrub cover is lower due the lower frequency of *Ledum groenlandicum*. However, cover of *Vaccinium angustifolium* and *Gaultheria hispidula* are higher than the stand-type average. Tall shrubs are also somewhat more frequent in this variant. Herb species composition and cover are similar to the stand-type as a whole. Bryophytes dominate the understory, although cover of all species is lower than the stand-type mean. Lichens are more common but generally occur at low cover.

The successional trajectory for these stands is similar to that of the stand-type as a whole. A multi-tiered, uneven-aged black spruce canopy develops, but relict jack pine trees may also be present. Balsam fir, white birch and trembling aspen may occur in the subcanopy, but rarely reach the canopy. Cover of *Ledum groenlandicum* increases substantially over time, but *V. angustifolium* declines. Herb layer composition change is minimal, but cover declines. *Pleurozium schreberi* and *Ptilium crista-castrensis* decrease slightly in cover, while *Hylocomium splendens* increases. Lichen cover declines.

Discussion

The overall successional trajectory for this stand-type is clear. These are self-regenerating black spruce stands with feathermosses and ericaceous shrubs (mainly *Ledum groenlandicum*) in the understory. *Pleurozium schreberi* continues to dominate, but *Hylocomium splendens* and *Ptilium crista-castrensis* increase in abundance over time (Viereck 1983). Soil moisture is higher than stand-types I and II, but nutrients remain limiting as evidenced by feathermoss and ericaceous shrub dominance. *Hylocomium splendens* is thought to be an indicator of nitrogen deficiency (Klinka et al. 1990).

Black spruce is highly shade-tolerant; only balsam fir and eastern white cedar are more shade-tolerant (Burns and Honkala 1990). Reproduction may occur from seed or by vegetative layering (Stanek 1961; Viereck and Johnston 1990), although the former is more important in upland stands. Feathermosses may provide a suitable seedbed during wet years (Frelich and Reich 1995b), but may dry out before root penetration to the mineral soil occurs. Fires that completely remove the surface organic layer usually provide the best seedbed for black spruce (Viereck and Johnston 1990).

Self-regenerating closed black spruce stands have been reported from northwestern Ontario (Zoladeski and Maycock 1990), northern Alberta (Rowe 1961) and northern Manitoba (Ritchie 1956). Balsam fir recruitment may occur in older stands, but is limited by crown closure (Rowe 1961). Ritchie (1956) asserts that closed, upland black spruce stands are the climax type in northern Manitoba. Early post-fire stands are generally even-aged (Viereck and Johnston 1991), but older stands are more 'decadent' and multi-aged (Cogbill 1985). In northern regions, stand paludification may occur in older stands after feathermosses form a continuous mat (Taylor et al. 1987; Heilman 1966,1968).

5.3.4 STAND-TYPE IV: BLACK SPRUCE - SPHAGNUM

Stand-Type Description

Soil-Environment

These sites are characterized by a thick, peaty organic layer (mostly > 30 cm in depth, and often > 1 m deep) and high soil moisture content. Fibrimor humus forms predominate. Most stands occur on level ground, and are generally poorly drained, relatively nutrient-poor, and somewhat acidic. Depth to the water table is < 2 m in most stands, and bedrock is rarely encountered in the first 2 m. Most stands with mineral horizons show distinct mottling in the soil profile and have a soil texture that is generally finer than in stand-types I-III. Genetic material is mainly organic, but lacustrine or (rarely) glaciofluvial material may also occur. Soil classification for most sites is Organic or Gleysol.

Vegetation

Black spruce dominates most stands. It is most frequently monodominant in the canopy-subcanopy, but may be codominant with eastern larch or (very occasionally) jack pine. Regeneration is primarily black spruce, but balsam fir and white birch are also present in the lower subcanopy and sapling layers. Trembling aspen and eastern larch are occasional in the sapling layer. Black spruce is uncommon in mesotrophic-eutrophic sites, where eastern white cedar, eastern larch or a mixture of the two is found. These nutrient-rich stands are regenerating to eastern white cedar. Ericaceous and tall shrubs are relatively common in most stands. *Ledum groenlandicum* is frequent and often occurs at moderate cover. *Gaultheria hispidula* and *Vaccinium* spp. are also common, but typically occur at low cover. *Chamaedaphne calyculata* is uncommon but may occur at moderate cover when present. *Alnus rugosa* is found in over half the stands, usually at moderate cover. Low shrubs are neither particularly common nor abundant.

The herb layer is usually fairly diverse, with one or more species often occurring at moderate cover. *Cornus canadensis* and *Carex* spp. are the most frequently encountered species; *Equisetum* spp. and *Lycopodium* spp. are also relatively common. Cryptogam cover is high in most stands. *Sphagnum* spp. are present in most stands and occur at high cover. *Pleurozium schreberi* is found in most stands, but generally occurs at much lower cover than in stand-types I-III. *Dicranum polysetum* and *Ptilium crista-castrensis* are also frequent, but typically occur at low cover. *Hylocomium splendens* is present in about half the stands, generally at low cover. Lichens are infrequent and of low cover when present.

Stand Dynamics

Summary

Most of these stands are succeeding toward uneven-aged, relatively open-canopy black spruce stands (**Fig. 5.12**). Tree regeneration in often poor, although black spruce may layer in some stands. Eastern white cedar usually dominates mesotrophic-eutrophic sites, and larch is rarely encountered in older stands. Total shrub cover increases (**Fig. 5.13**)

IV. Black Spruce - Sphagnum

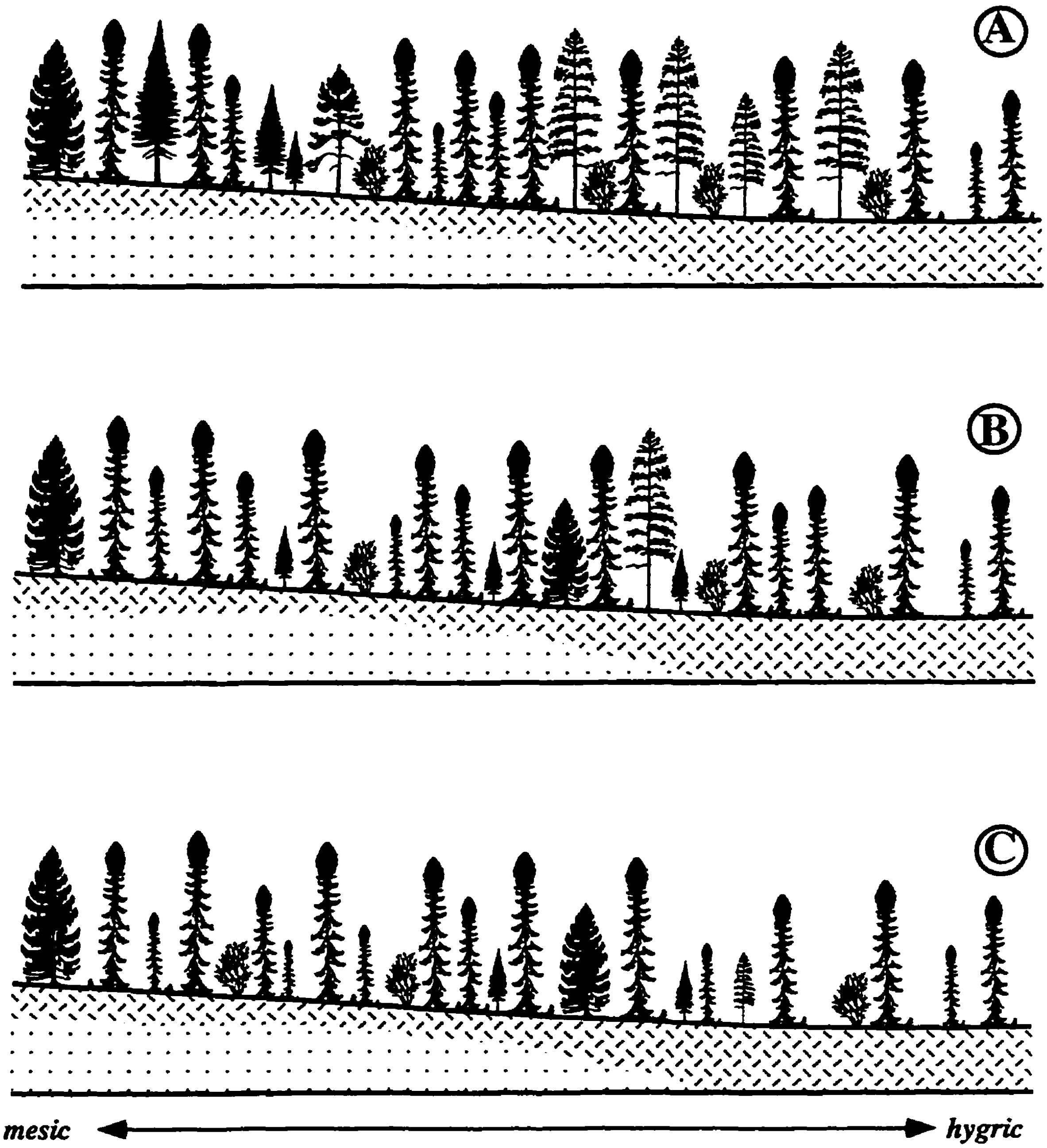


Figure 5.12. Successional trajectory based on mean tree canopy cover. A = ≤ 85 years; B = 86-120 years; C = > 120 years.

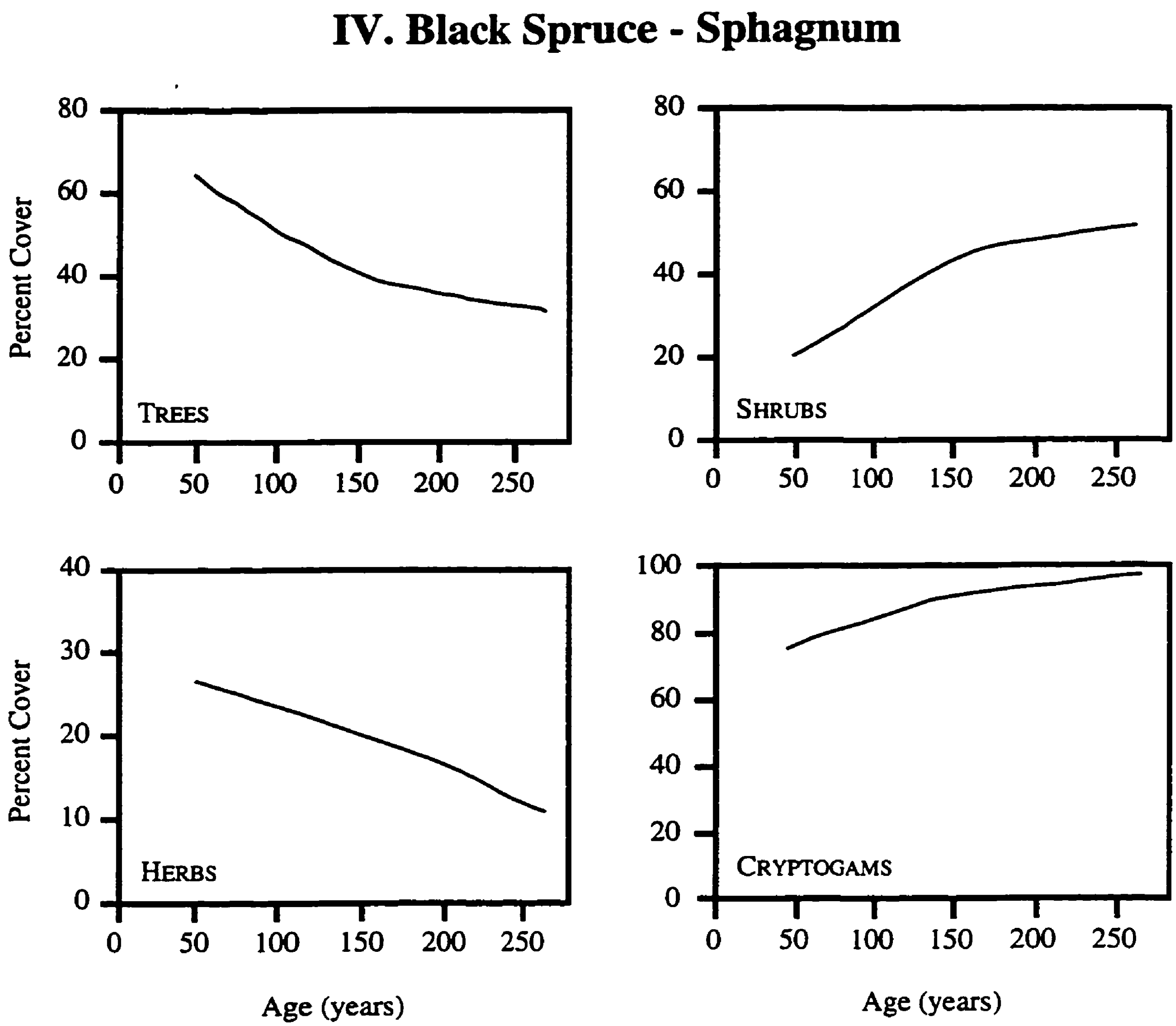


Figure 5.13. Changes in total tree, shrub, herb and cryptogam cover over time. Lines fitted using locally weighted regression analysis.

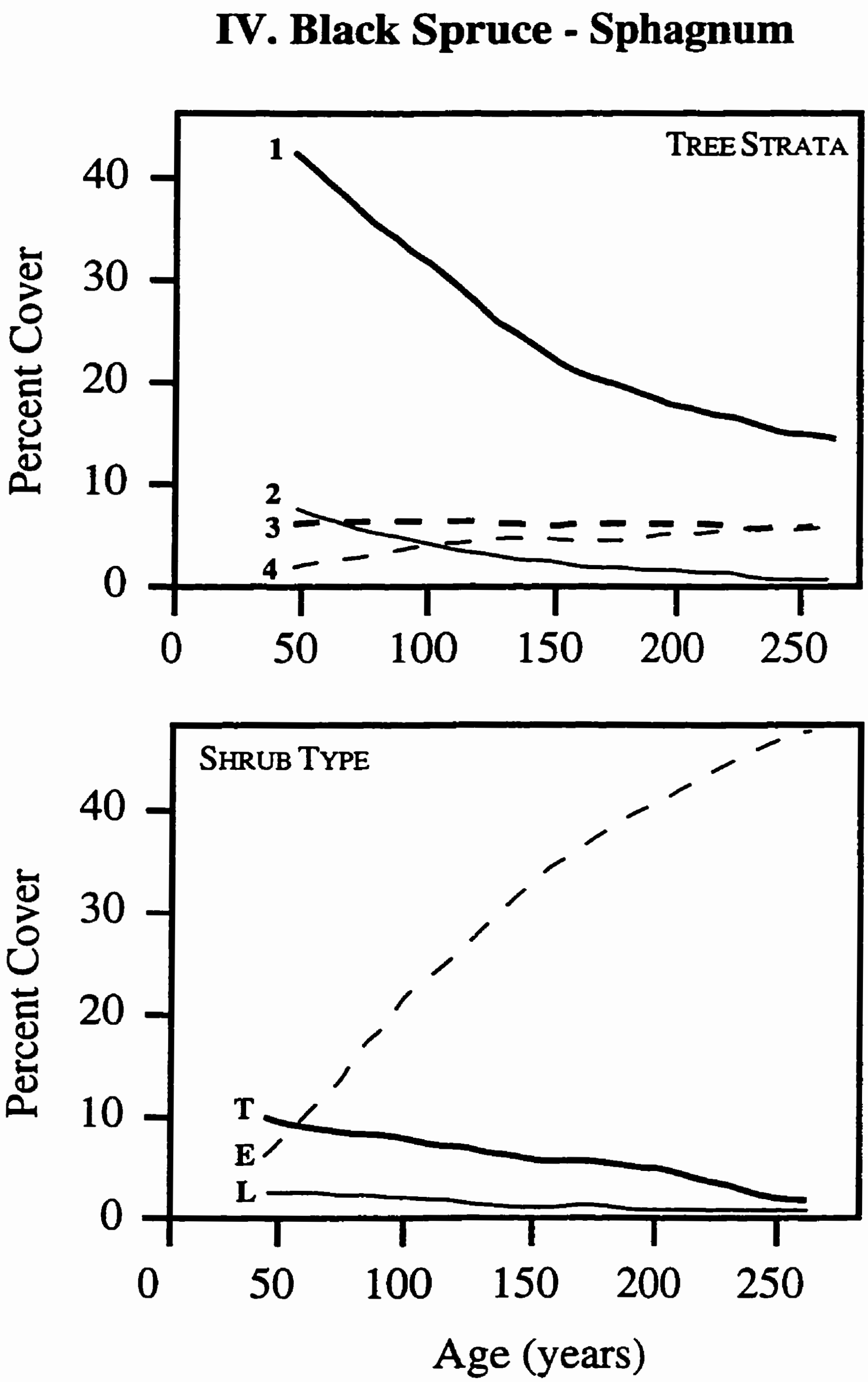


Figure 5.14. Changes in total tree cover by strata (codes: 1 = canopy; 2 = upper subcanopy; 3 = lower subcanopy; 4 = sapling layer) and shrub cover by shrub-type (codes: T = tall shrubs; L = low shrubs; E = ericaceous shrubs). Lines fitted using locally weighted regression analysis.

TABLE 5.7. Mean cover of tree species in stand-type IV by canopy strata (1-4), in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n* = 58					> 85 years *n* = 132				
		Total	1	2	3	4	Total	1	2	3	4
Picea mariana	Black Spruce	34.41	22.16	5.83	5.28	1.16	28.82	19.22	3.49	3.78	2.33
Larix laricina	Eastern Larch	13.36	11.02	1.52	0.66	0.17	1.71	1.47	0.03	0.06	0.15
Thuja occidentalis	White Cedar	5.36	2.17	2.24	0.41	0.53	8.44	5.01	1.30	0.92	1.21
Abies balsamea	Balsam Fir	5.16	1.26	1.10	1.71	1.09	5.31	0.64	0.79	2.33	1.56
Pinus banksiana	Jack Pine	2.55	2.55				0.06	0.06			
Populus tremuloides	Trembling Aspen	0.98	0.74	0.12		0.12	0.12	0.11			0.01
Picea glauca	White Spruce	0.76	0.64	0.10	0.02		0.19	0.06	0.08	0.02	0.02
Betula papyrifera	White Birch	0.66	0.31		0.16	0.19	1.59	0.89	0.17	0.38	0.16
Acer rubrum	Red Maple	0.28	0.14	0.07	0.03	0.03	0.16			0.07	0.09
Fraxinus nigra	Black Ash	0.28		0.07	0.16	0.05	0.11	0.05	0.05		0.02
Populus balsamifera	Balsam Poplar	0.05				0.05	0.08		0.04	0.02	0.03
Ulmus americana	White Elm	0.05			0.02	0.03					
Pinus resinosa	Red Pine	0.02	0.02								
Pinus strobus	White Pine	0.02				0.02	0.05				0.05
Populus grandidentata	Large-toothed Aspen	0.02				0.02					

TABLE 5.8. Frequency of tree species in stand-type IV by canopy strata, younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n* = 58					> 85 years *n* = 132				
		Total	1	2	3	4	Total	1	2	3	4
Picea mariana	Black Spruce	0.88	0.74	0.45	0.59	0.55	0.96	0.84	0.39	0.67	0.73
Larix laricina	Eastern Larch	0.50	0.47	0.14	0.17	0.10	0.21	0.11	0.02	0.04	0.11
Thuja occidentalis	White Cedar	0.16	0.07	0.09	0.07	0.12	0.19	0.13	0.06	0.09	0.17
Abies balsamea	Balsam Fir	0.66	0.12	0.14	0.40	0.60	0.51	0.08	0.08	0.29	0.49
Pinus banksiana	Jack Pine	0.14	0.14				0.02	0.02			
Populus tremuloides	Trembling Aspen	0.14	0.07	0.03		0.12	0.02	0.01			0.01
Picea glauca	White Spruce	0.09	0.05	0.03	0.02		0.04	0.02	0.02	0.01	0.01
Betula papyrifera	White Birch	0.22	0.09		0.07	0.14	0.23	0.07	0.03	0.11	0.15
Acer rubrum	Red Maple	0.03	0.02	0.02	0.02	0.03	0.06			0.03	0.05
Fraxinus nigra	Black Ash	0.03		0.02	0.02	0.03	0.02	0.02	0.01		0.02
Populus balsamifera	Balsam Poplar	0.05				0.05	0.03		0.01	0.02	0.02
Ulmus americana	White Elm	0.03			0.02	0.03					
Pinus resinosa	Red Pine	0.02	0.02								
Pinus strobus	White Pine	0.02				0.02	0.03				0.03
Populus grandidentata	Large-toothed Aspen	0.02				0.02					

due to increasing cover of ericaceous shrubs (especially Ledum *groenlandicum*). Tall shrub cover declines and low shrubs remain a minor component (**Fig. 5.14**). Total herb cover declines over time (**Fig. 5.14**). Increased cryptogam cover (**Fig. 5.14**) is attributable to increased accumulation of *Sphagnum* spp. In these stands, organic matter depth and acidity increase over time as *Sphagnum* peat accumulates. Other soil variables show no clear trends (see **Appendix IV**).

Successional Trajectory

Total tree cover declines over time, although the rate of decline decreases after age 150 (**Fig. 5.13**). Black spruce becomes proportionately more dominant over time. Eastern larch is very uncommon in older stands, and jack pine is entirely absent (**Tables 5.7, 5.8**). Eastern white cedar increases over time but remains infrequent, being largely restricted to more mesotrophic-eutrophic sites. Balsam fir occurs occasionally in the subcanopy and sapling layers, but very rarely reaches the canopy.

The increase in shrub cover over time is largely attributable to increased abundance of *Ledum groenlandicum*. Other ericaceous species such as *Gaultheria hispidula*, *Vaccinium angustifolium*, *Chamaedaphne calyculata.*, *Kalmia polifolia* and *Oxycoccus* spp. show more modest increases in cover. Tall shrub cover declines slightly over time (**Fig. 5.14**), although *Alnus rugosa* (the most common and abundant tall shrub) is relatively common in both young and old stands, occurring at moderate cover. Herb cover declines somewhat over time, although overall species composition, frequency and cover are similar in younger and older stands. *Cornus canadensis* and *Lycopodium* spp. (mainly *L. annotinum*) show the largest decreases in cover. *Smilacina trifolia* is the only common species that increases in both frequency and cover over time. Cryptogam cover is high in both younger and older stands, and *Sphagnum* spp. increase in both frequency and cover over time. *Pleurozium schreberi* remains ubiquitous, but cover increases only slightly. *Aulocomnium palustre* and *Hylocomium splendens* are less frequently encountered. Lichens remain a minor component of older stands. Interestingly, *Peltigera* spp. are absent in younger stands but occur in about one-quarter of the older stands (see **Appendix IV**).

Successional Variants

1. SITES WITH DEPTH TO WATER TABLE > 2 M

These stands are somewhat similar to the wettest stands of stand-type III. Younger stands of this variant often have some "upland" floristic affinities. Eastern white cedar, balsam fir and jack pine are more frequent and abundant relative to the stand-type as a whole. Subcanopy regeneration is primarily to black spruce, although balsam fir, eastern larch and eastern white cedar also occur. The sapling layer is predominantly balsam fir; while black spruce and eastern white cedar are of secondary importance. Shrub composition and cover differ somewhat from the stand-type as a whole. Ericaceous shrubs, particularly *Ledum groenlandicum* and *Gaultheria hispidula*, are much less abundant, whereas *Alnus rugosa* is more common. Herb species composition and cover differ somewhat from the stand-type average as well. *Equisetum* spp. and *Lycopodium* spp. are more frequent, whereas *Carex* spp. are less frequently encountered. The cover of all common cryptogam species is lower.

The successional trajectory for these stands is toward a more open, uneven-aged canopy dominated by black spruce. Larch and jack pine are absent from older stands, and balsam fir regeneration declines. Black spruce cover declines, in large part due to its virtual absence in the subcanopy of older stands. Regeneration in the lower subcanopy and sapling layers is primarily to black spruce. White birch and balsam fir are also present in the lower canopies of older stands, but they rarely reach the canopy. Ericaceous shrubs increase in cover over time, particularly *Ledum groenlandicum*. *Gaultheria hispidula* also increases in abundance, although its cover remains comparatively low. *Alnus rugosa* decreases in both frequency and cover. Herb cover declines during succession, being particularly pronounced in *Cornus canadensis*, *Lycopodium* spp. and *Equisetum* spp. Cryptogam cover increases as succession proceeds. *Pleurozium schreberi* becomes much more abundant. *Sphagnum* spp. also increase in cover, although species composition changes somewhat: *S. girgensohnii*, *S. angustifolium*, *S. magellanicum*, and *S. nemoreum*. increase in cover, whereas *S. warnstorfii* , *S. russowii* and *S. wulfianum* are much less frequent in older stands. *Ptilium crista-castrensis* and *Hylocomium splendens* increase in abundance, although they remain a relatively minor understory component in older stands.

2. SITES WITH DEPTH TO WATER TABLE < 2 M

Most stands are dominated by black spruce and/or eastern larch, while balsam fir and jack pine are less frequent relative to the stand-type as a whole (eastern white cedar, while infrequent, is characteristic of mesotrophic-eutrophic sites). Regeneration is predominantly to black spruce, although balsam fir and eastern larch are sometimes found in the sapling layer. The shrub layer is predominantly ericaceous: *Ledum groenlandicum* cover is slightly higher than the stand-type average. *Alnus rugosa* is somewhat less abundant here than in the stand-type as a whole, while *Carex* spp., *Equisetum* spp. and *Lycopodium* spp. are more abundant. Cryptogams are abundant: cover values for *Pleurozium schreberi*, *Sphagnum* spp. and *Hylocomium splendens* are all higher than the stand-type average.

Like the previous variant, the successional trajectory here is toward open, uneven-aged stands dominated by black spruce (except for less acidic, mesotrophic-eutrophic sites, which continue to be dominated by eastern white cedar). Larch is rarely present in older stands. Regeneration of black spruce (by seedling establishment and/or layering) is common. Balsam fir is sometimes encountered in the sapling and subcanopy layers, but it rarely reaches the canopy. Ericaceous species (mainly *Ledum groenlandicum*, but also *Gaultheria hispidula* and *Vaccinium myrtilloides*) dominate the shrub layer, although their cover is somewhat lower than the other variant. The cover of most herbaceous species declines over time, and herbs are a minor component of older stands. *Pleurozium schreberi* and *Ptilium crista-castrensis* cover decline as *Sphagnum* spp. abundance increases. *S. angustifolium* is less common in older stands, but the cover of *S. girgensohnii* and *S.*

magellanicum increases over time. Other species of *Sphagnum* (e.g. *S. fuscum*, *S. nemoreum* and *S. russowii*) show more modest increases in cover over time.

Discussion

These stands are remarkably stable over time (see also Carleton and Maycock 1980; Zoladeski and Maycock 1990). Oligotrophic, acidic, poorly-drained conditions prevail in most stands, leading to increased dominance of black spruce and hydrophytic ericaceous shrubs, and continued accumulation of poorly-decomposed *Sphagnum* peat. *Alnus rugosa* may be abundant in some older stands. Black spruce can regenerate from seed or by vegetative layering into the moist peat (Zoladeski and Maycock 1990). Larch, a highly shade-intolerant pioneer species (Beeftink 1951, Johnston 1990), is rarely present in the canopy of older stands although saplings are occasionally encountered when sufficient light is available (Johnston 1990). Eastern larch is also susceptible to larch sawfly infestations (Johnson et al. 1995). Eastern white cedar (together with sedges and/or *Sphagnum*) may be abundant in less acidic, mesotrophic-eutrophic sites that are subject to water-level fluctuations (Jeglum 1974; Kenkel 1987). Balsam fir may also seed into the organic substrate (Frank 1990), but rarely persists due to the acidic, low nutrient conditions prevailing in most stands.

Over time, nutrients are increasingly tied up in the poorly-decomposed organic peats of acidic bogs (Viereck and Johnston 1990). *Sphagnum* accumulation also leads to paludification, which favours hydrophytic species. Viereck (1983) concluded that fire reverses the trend toward paludification in black spruce-*Sphagnum* bogs by recycling nutrients and increasing substrate temperature, which favours microbial activity.

5.3.5 Stand-Type V: White Spruce - Balsam Fir Mixed Wood

Stand-Type Description

Soil-Environment

These stands are found on sandy loam or more finely-textured substrates. They occur over a wide range of soil orders, although Brunisols, Podzols, Luvisols and Gleysols predominate. Approximately half the stands occur on lacustrine parent material, while the remaining occur on morainal (primarily NCR stands) and glaciofluvial (primarily NWR stands) material. Nutrient availability is higher than in stand-types I - IV. Depth to bedrock is < 2m in ca. 20% of the sites. Approximately half the stands are found on gently sloping ground, but a few occur on steep slopes. In most sites the depth to water table is > 2m, and distinct mottling in the soil profile is uncommon. Most sites are moderately-well to well drained. Stands are much less acidic than stand-types I-III (mean mineral soil pH = 5.4) and organic horizons are somewhat deeper. Humus forms are raw moders or fibrimors.

Vegetation

Coniferous tree species dominate most stands, but a strong deciduous component (white birch, trembling aspen) characterizes some stands. Balsam fir is the most frequent and abundant species, and may occasionally occur as pure stands. However, in most stands balsam fir occurs with white or black spruce, or less commonly with white birch, jack pine and/or trembling aspen, to form a mixed canopy. Balsam fir shows strong regeneration in all canopy layers. Black and white spruce are also common in the lower subcanopy and sapling layers, although white spruce occurs less frequently. White birch and trembling aspen may occur in the sapling layer of more open stands. Total shrub cover is generally low to moderate. Most of the species present are relatively common but generally occur at low cover. *Sorbus* spp. and *Amelanchier* spp. are frequent but never abundant. *Acer spicatum* and *Corylus cornuta* are less frequent, but may occur at moderate cover when present. The low shrub *Diervilla lonicera* is frequently encountered and occurs at moderate cover in some stands. *Rosa acicularis* and *Ribes* spp. are relatively frequent but have low cover. Ericaceous shrubs are uncommon, except *Vaccinium* spp. which occur in about two-thirds of the stands, at low cover.

Most stands are quite herb-rich, and total herb cover can be quite high (often > 30%). *Cornus canadensis*, *Aralia nudicaulis*, and *Rubus pubescens* are frequently encountered and often occur at moderate cover. *Maianthemum canadense*, *Linnaea borealis* and *Trientalis borealis* are usually also present, but at low cover. Less frequent species that may occur at moderate cover when present include *Lycopodium* spp., *Aster macrophyllus*, *Dryopteris* spp. and *Mitella nuda*.. Total cryptogam cover is comparable to stand-types I-IV, but the cryptogam flora is more diverse. *Pleurozium schreberi* is found in most stands at moderate cover (mean cover = 30%). Other frequently encountered species include *Dicranum polysetum*, *Ptilium crista-castrensis*, *Rhytidiadelphus triquestrus*, *Brachythecium* spp., *Drepanocladus uncinatus*, and *Hylocomium splendens*. These species occur at low to moderate cover when present. Lichens are infrequently found and occur at low cover.

Stand Dynamics

<u>Summary</u>

These stands succeed toward more open-canopy, mixed-wood stands. Coniferous species (balsam fir, white spruce and black spruce) dominate older stands, but white birch may be common in well-drained sites. The presence of balsam fir, white spruce, black spruce and/or white birch in the lower subcanopy and sapling layers suggests that these mixed wood stands are self-regenerating (**Fig. 5.15**). An increase in total shrub (**Fig. 5.16**) cover is attributable to an increase in tall shrubs, particularly *Acer spicatum*. Overall herb cover declines (**Fig. 5.17**). Total cryptogam cover changes little over time, but cryptogams become more diverse as a decline in cover of *Pleurozium schreberi* is offset by increases in other species. Organic matter depth increases over time, and a slight increase in soil pH is indicated. Total exchangeable bases (TEB) decline, but remains higher than in stand-types I-IV (see **Appendix V**).

Vegetation

Although total tree cover does not change over time, canopy cover decreases as subcanopy cover increases (**Fig. 5.17**), indicating that an uneven-aged, multi-tiered canopy develops over time. Shade-intolerant species (particularly jack pine and trembling aspen) decrease over time, and are rarely present in older stands. Balsam fir and white spruce are the most abundant canopy species in older stands (**Tables 5.9**, **5.10**), but black spruce and white birch are often present as well. Black spruce regeneration declines over time, suggesting that it may eventually disappear from many of these stands. The lower subcanopy and sapling layers are usually dominated by balsam fir, although white spruce and white birch are also common in many stands. On steep slopes, eastern white cedar may be present in older stands.

Total shrub cover increases over time (**Fig. 5.17**). Much of this increase is attributable to increased frequency and abundance of tall shrubs, particularly *Acer spicatum* and to a lesser extent *Alnus rugosa*. Such species may be favoured as the canopy becomes increasingly open and multi-tiered. *Diervilla lonicera* frequency and cover decline over time. Ericaceous species remain unimportant in older stands. Total herb species cover declines over time, but most stands retain a floristically diverse herb layer. Species showing the largest declines in mean cover include *Aralia nudicaulis*, *Clintonia borealis*, and *Lycopodium* spp. A few species such as *Mitella nuda*, *Mertensia paniculata*, and *Gymnocarpium dryopteris* show modest increases in frequency and/or cover, although they remain a minor component of the flora. The cover of *Pleurozium schreberi* declines over time, but this is offset by increases in the frequency and/or cover of *Ptilium crista-castrensis*, *Hylocomium splendens* and *Rhytidiadelphus triquestris*. Although lichens remain an unimportant component of the flora of older stands, *Peltigera* spp. increase in frequency and occur in about half of the older stands (see **Appendix V**).

V. White Spruce - Balsam Fir Mixed Wood

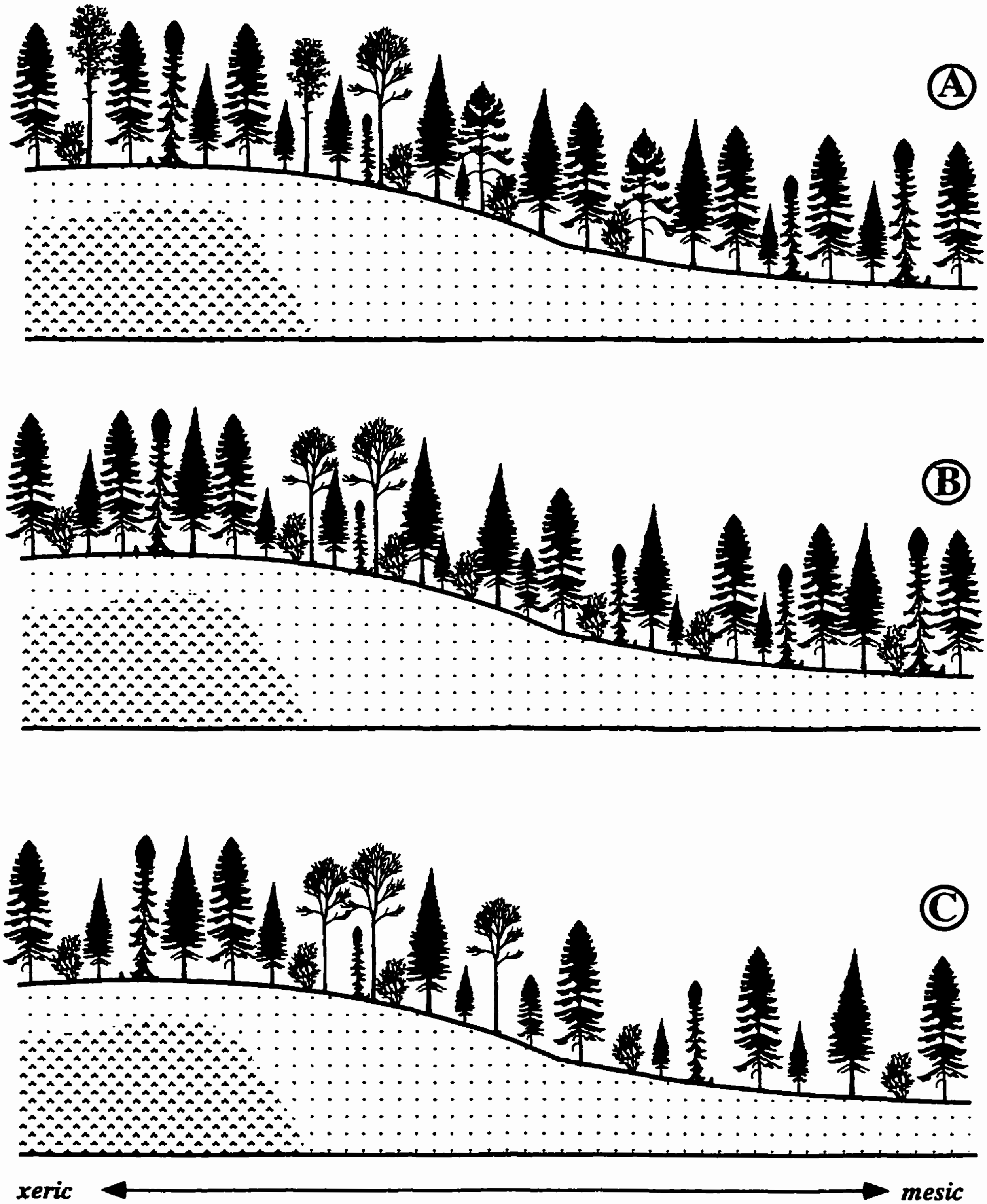


Figure 5.15. Successional trajectory based on mean tree canopy cover.
A = ≤ 85 years; B = 86-120 years; C = > 120 years.

V. White Spruce - Balsam Fir Mixed Wood

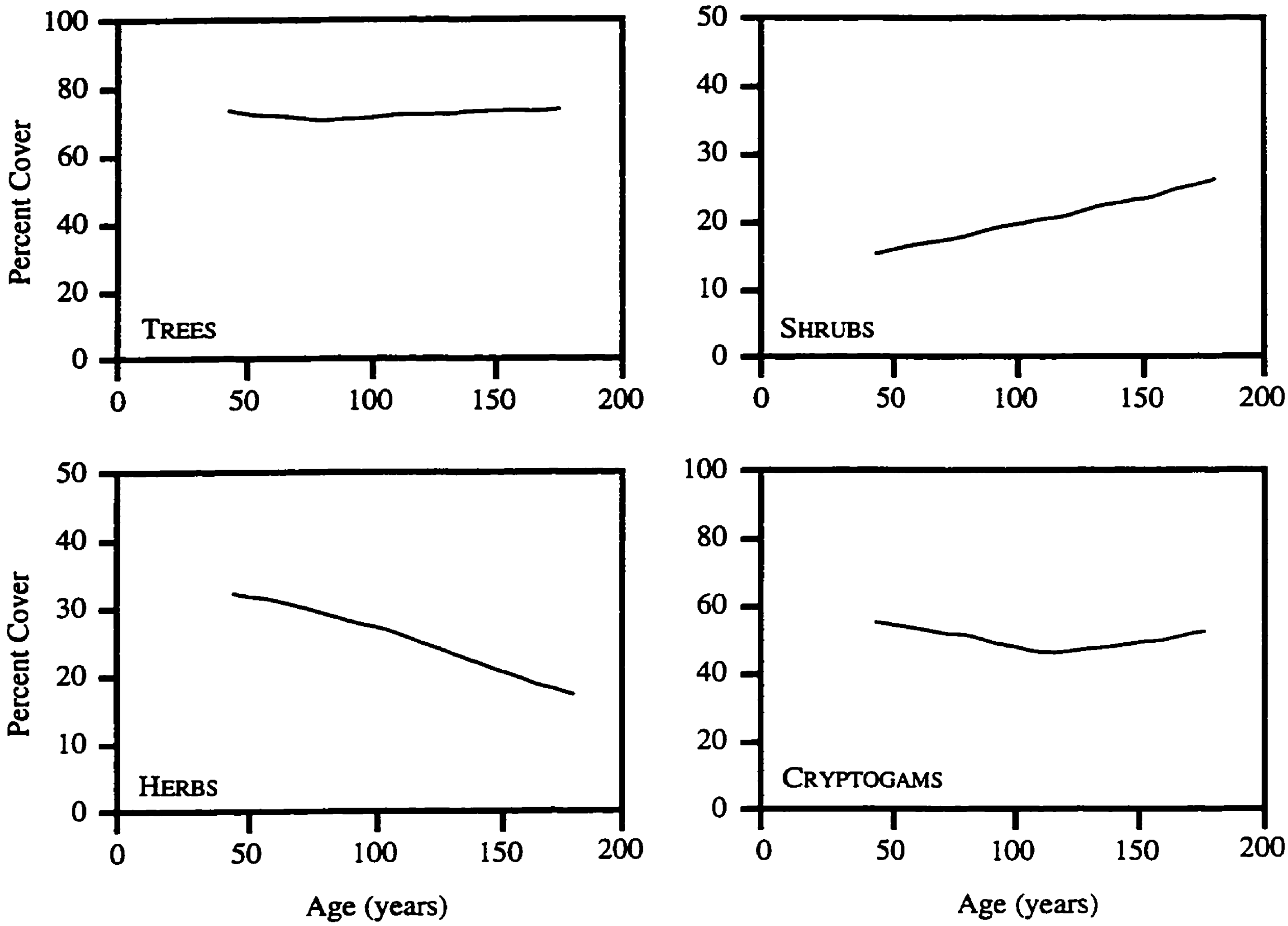


Figure 5.16. Changes in total tree, shrub, herb and cryptogam cover over time. Lines fitted using locally weighted regression analysis.

V. White Spruce - Balsam Fir Mixed Wood

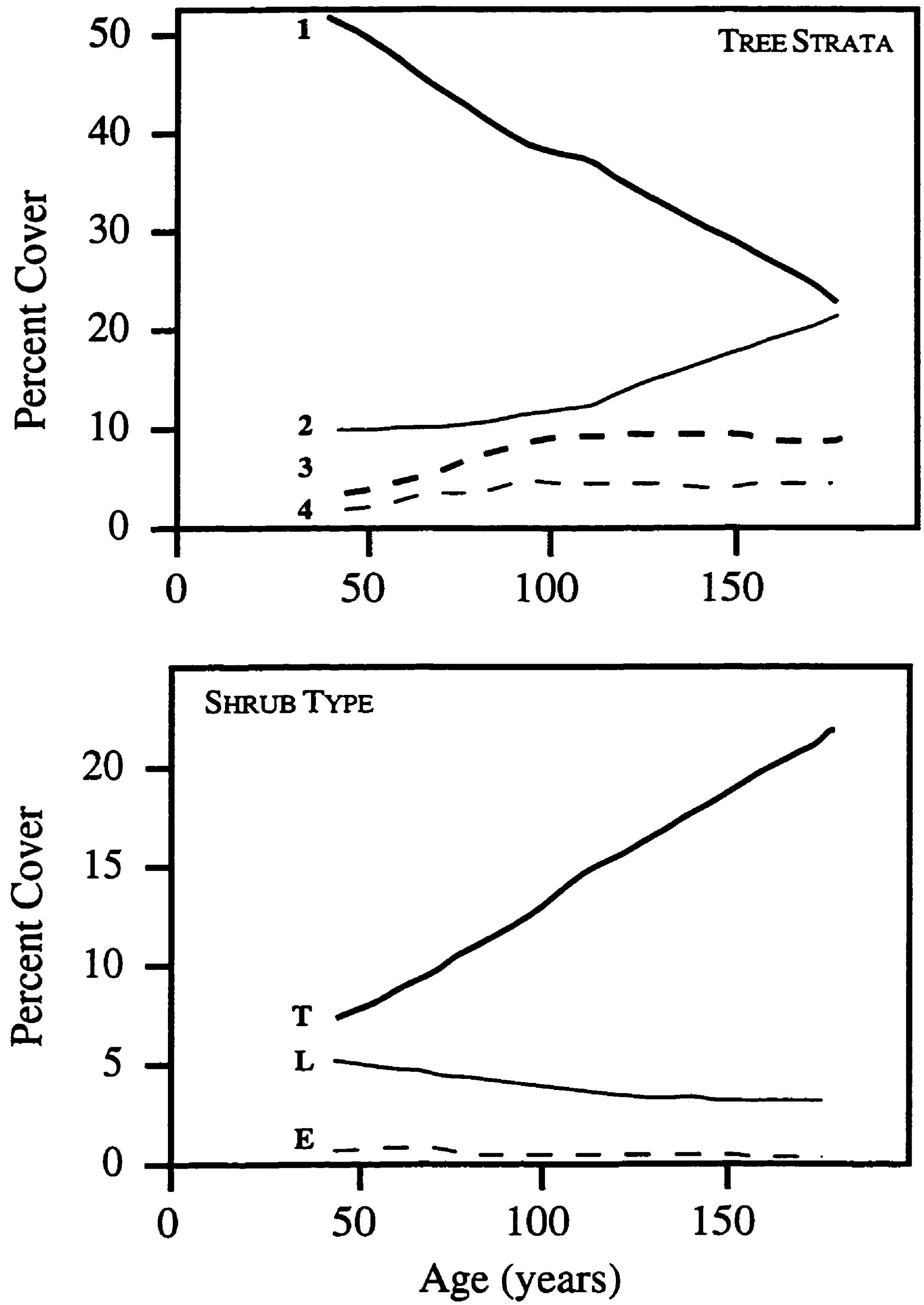


Figure 5.17. Changes in total tree cover by strata (codes: 1 = canopy; 2 = upper subcanopy; 3 = lower subcanopy; 4 = sapling layer) and shrub cover by shrub-type (codes: T = tall shrubs; L = low shrubs; E = ericaceous shrubs). Lines fitted using locally weighted regression analysis.

TABLE 5.9. Mean cover of tree species in stand-type V by canopy strata (1-4), in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n* = 78					> 85 years *n* = 39				
		Total	**1**	**2**	**3**	**4**	**Total**	**1**	**2**	**3**	**4**
Abies balsamea	Balsam Fir	25.31	8.96	8.31	5.40	2.64	30.49	9.49	6.72	9.31	4.97
Picea glauca	White Spruce	18.96	16.96	1.28	0.49	0.23	18.10	16.26	1.05	0.51	0.28
Picea mariana	Black Spruce	10.72	5.09	3.82	1.28	0.53	5.77	4.31	0.82	0.31	0.33
Populus tremuloides	Trembling Aspen	5.96	5.21	0.23	0.18	0.35	3.08	2.51	0.23	0.03	0.31
Pinus banksiana	Jack Pine	5.21	4.67	0.54			0.31	0.31			
Betula papyrifera	White Birch	3.22	1.95	0.58	0.39	0.31	9.10	6.69	0.97	1.05	0.39
Larix laricina	Eastern Larch	0.76	0.76								
Thuja occidentalis	White Cedar	0.73	0.24	0.19	0.08	0.22	5.41	0.72	4.13	0.36	0.21
Populus balsamifera	Balsam Poplar	0.21	0.08		0.01	0.12	0.82	0.72			0.10
Populus deltoides	Eastern Cottonwood	0.04	0.01			0.03					
Fraxinus nigra	Black Ash	0.01				0.01					
Pinus strobus	White Pine						0.36	0.33	0.03		
Acer rubrum	Red Maple						0.03				0.03

TABLE 5.10 Frequency of tree species in stand-type V by canopy strata, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n* = 78					> 85 years *n* = 39				
		Total	**1**	**2**	**3**	**4**	**Total**	**1**	**2**	**3**	**4**
Abies balsamea	Balsam Fir	0.97	0.44	0.50	0.72	0.90	1.00	0.39	0.51	0.77	0.95
Picea glauca	White Spruce	0.62	0.56	0.26	0.19	0.23	0.80	0.77	0.21	0.26	0.21
Picea mariana	Black Spruce	0.68	0.39	0.37	0.31	0.39	0.56	0.41	0.15	0.10	0.13
Populus tremuloides	Trembling Aspen	0.51	0.33	0.08	0.10	0.33	0.44	0.28	0.03	0.03	0.31
Pinus banksiana	Jack Pine	0.35	0.33	0.04			0.03	0.03	0.00		
Betula papyrifera	White Birch	0.46	0.15	0.14	0.15	0.31	0.67	0.41	0.18	0.31	0.39
Larix laricina	Eastern Larch	0.06	0.06								
Thuja occidentalis	White Cedar	0.03	0.03	0.01	0.03	0.01	0.18	0.05	0.08	0.13	0.10
Populus balsamifera	Balsam Poplar	0.12	0.01		0.01	0.12	0.10	0.05		0.00	0.10
Populus deltoides	Eastern Cottonwood	0.03	0.01			0.03					
Fraxinus nigra	Black Ash	0.01				0.01					
Pinus strobus	White Pine						0.03	0.03	0.03		
Acer rubrum	Red Maple						0.03				0.03

Successional Variants

1. Bedrock Sites (Depth to Bedrock < 2 m)

Black spruce, white spruce and trembling aspen occur at higher cover compared to their overall stand-type means, whereas cover of balsam fir and jack pine are lower. White spruce is the canopy dominant in many stands. The lower subcanopy and sapling layers are dominated by balsam fir and black spruce, although white spruce and white birch are commonly encountered as well. Tall shrub cover is lower than the stand-type average, whereas the low shrub *Diervilla lonicera* is more prevalent. Ericaceous shrubs occur at low cover. The herb layer is rich, but cover of *Rubus pubescens* is much lower than its stand-type mean. *Pleurozium schreberi* cover is comparatively high (averaging 50%), while other species (e.g. *Ptilium crista-castrensis*, *Hylocomium splendens*, *Rhytidiadelphus triquestrus*, and *Brachythecium* spp.) have considerably lower cover than their stand-type means.

These stands are succeeding toward an uneven-aged mixed canopy of balsam fir, white spruce, black spruce and/or white birch. Balsam fir and white birch increase in frequency and cover over time. Balsam fir is more commonly found in the canopy of older stands, while white birch occurs primarily in the subcanopy. The regenerating layers of older stands are dominated by balsam fir and white birch, but white and black spruce also occur (though less frequently than in younger stands). Tall shrubs (particularly *Acer spicatum*, but also *Sorbus* spp. and *Alnus crispa*) increase in frequency and/or cover over time, whereas *Diervilla lonicera* declines in cover. Ericaceous shrubs (particularly *Vaccinium myrtilloides* and *Ledum groenlandicum*) increase in cover, but remain a minor component of the understory. *Pleurozium schreberi* cover increases, and it remains the dominant species in older stands. Unlike the other variants, the remaining cryptogam species do not increase in cover over time.

2. Mesic Sites (Moisture Regime ≥ 3)

These stands are primarily coniferous: white and black spruce, and balsam fir are more frequent and abundant here compared to their stand-type means. White and black spruce form a dense canopy, while balsam fir is most common in the subcanopy and sapling layers. Jack pine and trembling aspen are generally absent, and white birch is infrequent except in the sapling layer. Regeneration is predominantly to balsam fir, although white spruce, black spruce and white birch are also found in the lower subcanopy and sapling layers. The tall shrub *Alnus rugosa* is frequent and may occur at moderate cover when present. *Diervilla lonicera* is uncommon, but *Rubus strigosus* is a common low shrub. Herb species composition and cover are similar to the stand-type as a whole, but *Cornus canadensis* and *Aralia nudicaulis* are less common while *Rubus pubescens* is much more common. The cover of *Pleurozium schreberi* is lower than the stand-type average, while *Brachythecium curtum*, *Hylocomium splendens* and *Plagiomnium* spp. occur with higher frequency and cover.

As succession proceeds, black spruce becomes a less important component of the canopy. The subcanopy of older stands is almost completely dominated by balsam fir. Regeneration is mainly to balsam fir, although white birch and white spruce often occur in the lower subcanopy and sapling layers of older stands. The tall shrubs *Alnus rugosa*, *Corylus cornuta* and *Acer spicatum* all increase in frequency and/or cover over time. *Rubus strigosus* cover decreases over time. The herb layer of older stands are similar in species composition to the younger stands. *Rubus pubescens*, *Equisetum* spp, *Circaea alpina*, and *Clintonia borealis* decrease in cover, while *Aster macrophyllus*, *Maianthemum canadense*, *Linnaea borealis*, *Dryopteris* spp, and *Coptis trifolia* increase. *Brachythecium curtum* and *Plagiomnium* spp. decline in cover over time, while *Rhytidiadelphus triquetrus*, *Hylocomium splendens* and *Ptilium crista-castrensis* increase.

3. DRY SITES (MOISTURE REGIME < 3)

White spruce is comparatively infrequent in these stands, while jack pine and trembling aspen are more commonly encountered. Balsam fir is common in the canopy, usually in mixture with jack pine, trembling aspen, black spruce and/or white spruce. Balsam fir and black spruce are the most commonly encountered species in the lower subcanopy and sapling layers. The tall shrubs *Acer spicatum* and *Corylus cornuta* are common, but *Alnus rugosa* is rarely present. The cover and species composition of low shrubs and ericaceous shrubs are similar to the stand-type as a whole. Herb composition and cover are also similar, although *Rubus pubescens* is lower in frequency and cover than the stand-type mean. Cryptogam species composition and cover are also similar to the stand-type.

Balsam fir, white spruce, and white birch increase in frequency and cover over time, while the cover of black spruce declines. Trembling aspen and jack pine are not present in older stands. Balsam fir dominates the subcanopy, although white spruce, white birch and black spruce may also be present. The lower subcanopy and sapling layers are dominated by balsam fir. Eastern white cedar may be present on slopes. *Acer spicatum* shows large increases in frequency and cover over time, while *Corylus cornuta* declines in cover but not frequency. The herb layer remains floristically diverse, and individual species cover values do not change appreciably over time. The bryophytes *Brachythecium curtum* and *Rhytidiadelphus triquestris* increase in cover over time.

Discussion

The overall successional trajectory for this stand-type indicates continued persistence of a mixed-wood forest dominated by balsam fir, white spruce, and white birch in the canopy and regenerating layers. Black spruce may also occur, particularly in nutrient-limited sites. Balsam fir and white spruce regenerate from seed, while white birch regenerates both from seed and by resprouting. Pioneer tree species such as trembling aspen and jack pine are not found in older stands. Tall shrubs (particularly *Acer spicatum*) increase in cover, while herb cover declines. Higher soil nutrients favours herbs over cryptogams in the understory.

Mixed wood (fir-spruce-birch) stands in northwestern Ontario are characterized by continuous high recruitment of balsam fir, and low to moderate recruitment of white and black spruce; white birch recruitment occurs only in the first 60 years (Zoladeski and Maycock 1990). It has been hypothesized that white birch stands represent an early successional variant of this stand-type (Carleton and Maycock 1980), since recruitment of balsam fir into white birch stands is usually high (Frelich and Reich 1995b). In the boreal forests of Saskatchewan, balsam fir rarely enters the canopy although it is frequently abundant in the sapling layer (Dix and Swan 1971). White spruce is larger than most of its common associates, and its longevity is surpassed only by eastern white cedar, red pine and white pine (Burns and Honkala 1990). Dix and Swan (1971) concluded that white spruce is both an initial colonizer and a 'climax' species. However, white spruce rarely forms pure stands throughout most of its range (Blais 1983; Grigal and Ohmann 1975). Lieffers et. al. (1996) found that later white spruce establishment is greatest on rotten logs.

Given that balsam fir is the most shade-tolerant boreal tree species (Burns and Honkala 1990), a number of workers have concluded that, in the absence of disturbance, it is a late-successional or 'climax' species (e.g. Carleton and Maycock 1978, 1980; Grigal and Ohmann 1975). Although balsam fir dominates the regenerating layer of many boreal stands, the species is comparatively less abundant in the canopy layer. This is due at least in part to windthrow (Sprugel 1976) and/or recurrent outbreaks of spruce budworm (Cogbill 1985). Spruce budworm, which favours balsam fir but will also attack white spruce, is critical to understanding the dynamics of these mixed wood stands (Blais 1983). Periodic infestations of spruce budworm kill mature stands of balsam fir, releasing balsam fir seedlings (Ostaff and MacLean 1995) and favouring the regeneration of less shade-tolerant species such as white birch, black spruce and white spruce (Holling 1973; Bergeron and Dubuc 1989; Bergeron and Dansereau 1993; Frelich and Reich 1995b). Holling (1992) notes that spruce budworm outbreaks tend to be self-propagating once initiated, and that outbreak severity is positively correlated with the proportion of balsam fir in the canopy. Outbreaks are the result of a complex of factors related to climatic conditions and forest stand age, composition and structure. Spruce budworm and balsam fir form an interdependent, self-regulating system in which cyclical budworm outbreaks confer long-term ecological stability (Morin 1994). In general, mixed forests (at both the stand and landscape levels) contribute to decreased budworm outbreak frequency and intensity (Bergeron et al. 1995). A recent study in New Brunswick found that defoliation of balsam fir decreases as the proportion of hardwoods (mainly white birch) increases (Su et al. 1996). It was hypothesized that the presence of hardwoods increases habitat diversity, which in turn supports larger populations of budworm predators and pathogens.

5.3.6 Stand-Type VI: Trembling Aspen

Soil-Environment

Humus forms are predominantly fibrimors (mainly NWR sites) and raw moders (mainly NCR sites). Organic matter depth is slightly greater than in the upland conifer-dominated stands (stand-types I-III, V). The organic and mineral layers are less acidic and nutrient status is higher than the upland conifer stands. Most stands occur on sandy loams or more fine-textured soils, and are moderately drained. Most stands occur on lacustrine or morainal (occasionally glaciofluvial) deposits. Soils are generally Brunisols or Luvisols; Podzols and Gleysols are occasional. Depth to bedrock is < 2 m in ca. 10% of the stands, and many occur on gentle slopes. Depth to water table is > 2 m in most stands, but almost half the stands show distinct mottling in the soil profile.

Vegetation

Total tree cover is high. The canopy of younger stands is often pure trembling aspen, or less frequently a mixture of trembling aspen with balsam fir, white spruce and/or white birch. Balsam fir, white spruce, black spruce and/or white birch may be present in the subcanopy. Balsam fir is common in the regenerating layers, although white birch and black spruce may also occur. Trembling aspen regeneration (probably suckering) is common in many stands. Red maple is occasionally encountered in stands located in the south-west portion of the study area. Total shrub cover is high, and is dominated by the tall shrubs *Corylus cornuta* and *Acer spicatum*. These two species are frequent, and generally occur at moderate or occasionally high cover. *Amelanchier spp. and Cornus stolonifera* are also frequent, but occur at much lower cover. *Alnus rugosa* and *A. crispa* are infrequent but may be moderately abundant where found. *Diervilla lonicera* is the only low shrub that is both frequent and abundant. *Rosa acicularis*, *Rubus strigosus*, *Ribes* spp. and *Lonicera* spp. are occasional. Ericaceous shrubs are uncommon.

The herb layer is very diverse, and total cover is moderate to high. *Aralia nudicaulis* and *Aster macrophyllus* are found in most stands at moderate cover. Other frequently encountered species include *Maianthemum canadense*, *Streptopus roseus*, *Rubus pubescens*, *Cornus canadensis*, *Clintonia borealis*, *Trientalis borealis*, *Viola* spp. and *Galium* spp. These latter species generally occur at low cover. Total cryptogam cover is low. *Pleurozium schreberi* is the most commonly encountered species, but is far less abundant (mean cover < 2%) than in the upland conifer stand-types. *Peltigera* spp. occur in about one-third of the stands, again at low cover.

Stand Dynamics

Summary

As succession proceeds, trembling aspen is being replaced by conifers, resulting in mixed, uneven-aged stands dominated by a mixture of balsam fir, white spruce and occasionally black spruce (**Fig. 5.18**). The oldest stands have a more open canopy and show strong conifer regeneration in the subcanopy and sapling layers. Regeneration is almost entirely coniferous, with balsam fir predominating. Shrub cover is stable over time (**Fig. 5.19, 5.20**), although changes in individual species cover do occur. Total herb cover declines after age 100 years (**Fig. 5.19**) and many species decline in cover or frequency. A steady increase in cryptogam cover (**Fig. 5.19**) reflects increased conifer domination. Few changes in soil factors are apparent. Depth of the organic layer increases slightly, while total exchangeable bases (TEB) decreases. The organic horizon becomes slightly more acidic over time (see **Appendix VI**).

Vegetation

Canopy cover increases up to age 100 (**Fig. 5.18**) and then begins to decline as trembling aspen is replaced by coniferous species, particularly balsam fir but also white spruce and/or black spruce (on more acidic substrates). Balsam fir predominates in the oldest stand canopies, but white and black spruce are also more frequent and relict trembling aspen trees may persist for 200 years or more. Eastern white cedar and white birch may occur on well-drained slopes. Subcanopy cover increases as canopy cover declines (after age 100), indicating that stands are becoming more multi-tiered and uneven-aged. The lower subcanopy and sapling layers are dominated by coniferous species (**Tables 5.11, 5.12**), particularly balsam fir but also white and black spruce. Trembling aspen is often present in the sapling layer of older stands, but rarely enters the subcanopy.

Tall shrubs dominate the shrub layer in both young and older stands. *Acer spicatum* is the most frequent and abundant species in older stands. *Corylus cornuta* decreases in frequency and cover, but *Alnus rugosa* increases. Cover of the low shrub *Diervilla lonicera* declines over time. Ericaceous shrubs remain an inconspicuous component of older stands (**Fig. 5.20**). Herb cover begins to decline after age 100 (**Fig. 5.19**) as the canopy becomes more conifer-dominated; species richness remains high, however. Declines in cover are greatest in *Aralia nudicaulis* and *Aster macrophyllus*. *Cornus canadensis*, *Rubus pubescens*, *Mitella nuda*, and *Clintonia borealis* show modest declines in mean cover over time. Cryptogam cover increases during succession, but they remain a minor component of the understory. Modest increases in the frequency and/or cover occur in *Pleurozium schreberi*, *Dicranum polysetum*, *Ptilium crista-castrensis*, *Rhytidiadelphus triquetrus*, and *Hylocomium splendens* (see **Appendix VI**).

VI. Trembling Aspen

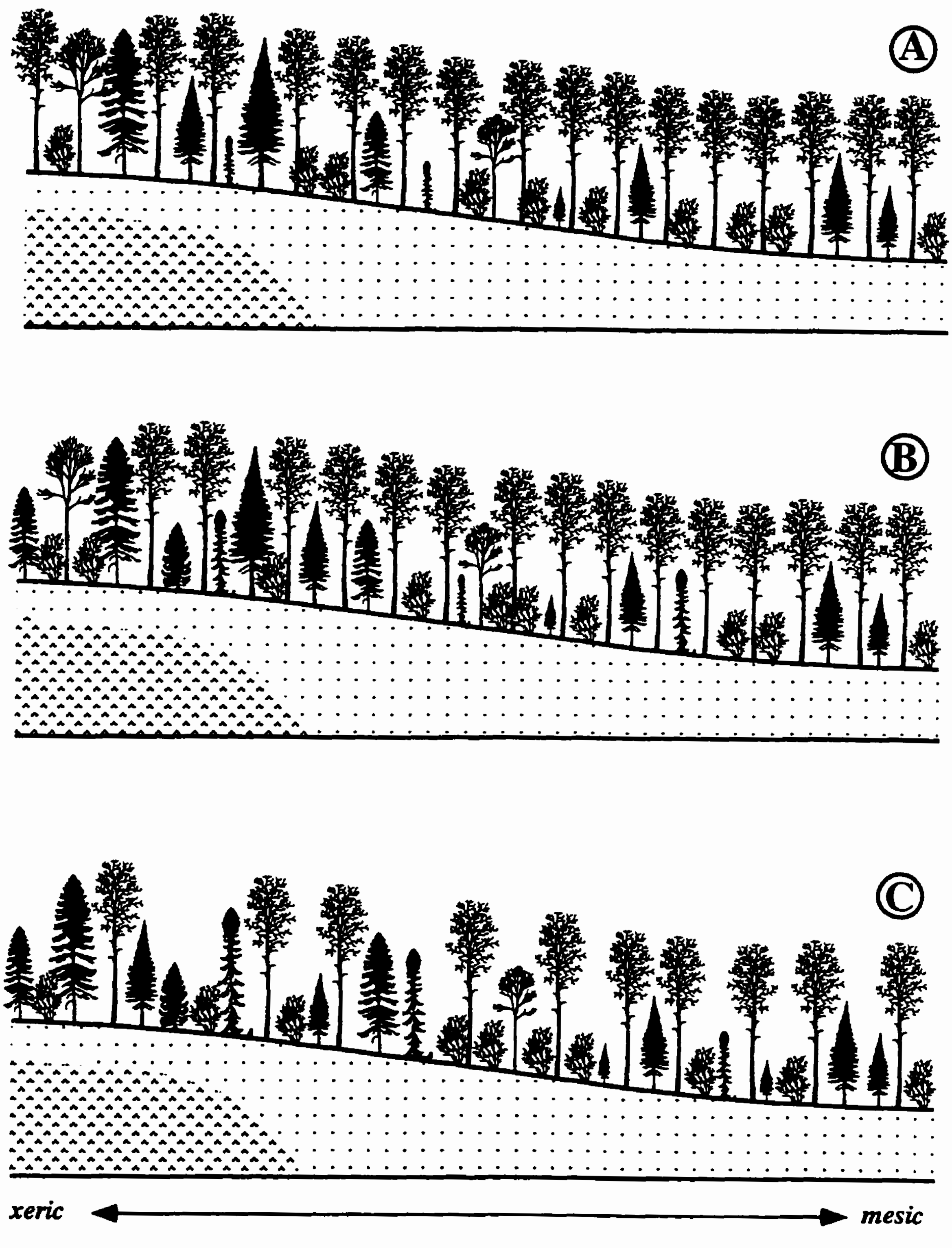


Figure 5.18. Successional trajectory based on mean tree canopy cover.
A = ≤ 85 years; B = 86-120 years; C = > 120 years.

VI. Trembling Aspen

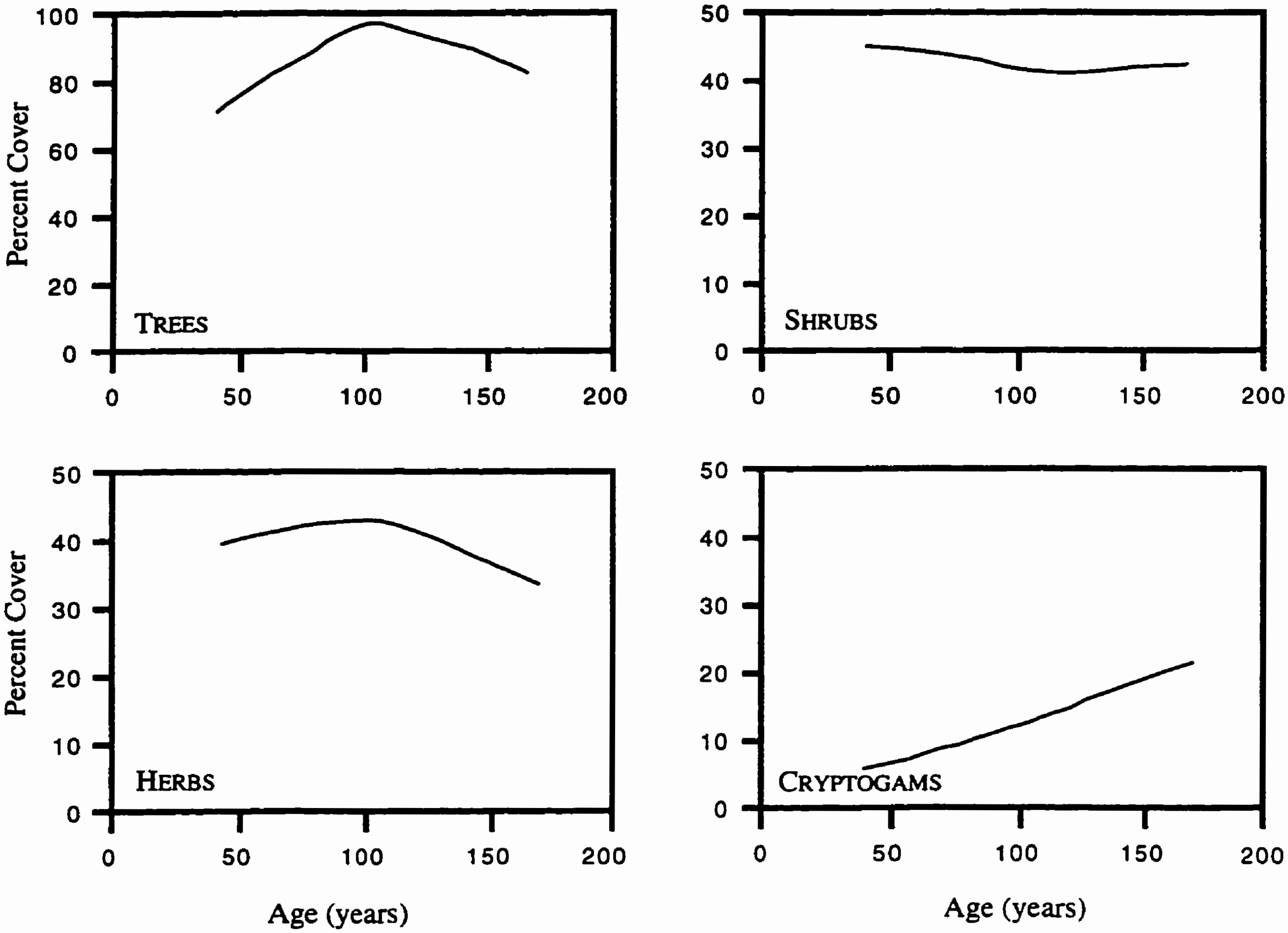


Figure 5.19. Changes in total tree, shrub, herb and cryptogam cover over time. Lines fitted using locally weighted regression analysis.

VI. Trembling Aspen

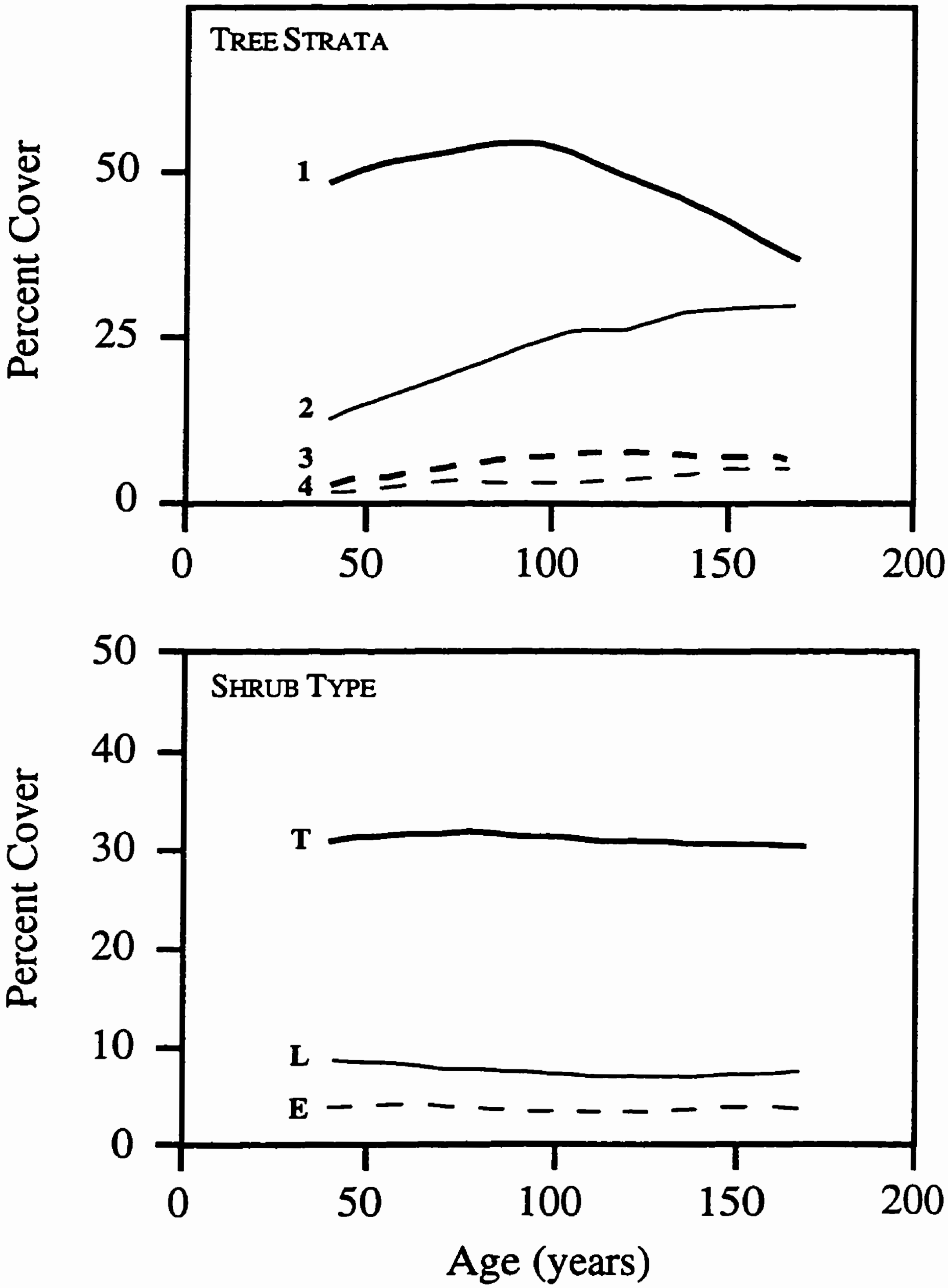


Figure 5.20. Changes in total tree cover by strata (codes: 1 = canopy; 2 = upper subcanopy; 3 = lower subcanopy; 4 = sapling layer) and shrub cover by shrub-type (codes: T = tall shrubs; L = low shrubs; E = ericaceous shrubs). Lines fitted using locally weighted regression analysis.

TABLE 5.11. Mean cover of tree species in stand-type VI by canopy strata (1-4), in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 130*					> 85 years *n = 66*				
		Total	1	2	3	4	Total	1	2	3	4
Populus tremuloides	Trembling Aspen	46.25	44.30	0.80	0.51	0.64	47.50	45.29	0.99	0.35	0.88
Abies balsamea	Balsam Fir	18.32	2.86	10.16	3.01	2.29	23.18	1.50	12.36	6.47	2.85
Betula papyrifera	White Birch	7.32	1.97	3.79	1.14	0.42	6.08	1.74	3.30	0.77	0.26
Picea glauca	White Spruce	6.08	3.06	2.42	0.36	0.24	6.74	2.00	3.77	0.68	0.29
Picea mariana	Black Spruce	2.09	0.31	1.36	0.28	0.15	8.64	1.24	6.46	0.39	0.55
Acer rubrum	Red Maple	1.42	0.20	0.28	0.75	0.19	2.03		0.53	1.06	0.44
Fraxinus nigra	Black Ash	0.75		0.19	0.34	0.22	1.83	0.15	1.29	0.15	0.24
Populus balsamifera	Balsam Poplar	0.71	0.49	0.11	0.02	0.09	1.08	0.89	0.06	0.03	0.09
Thuja occidentalis	Eastern Cedar	0.31		0.20	0.02	0.09	1.24		1.05	0.05	0.15
Pinus banksiana	Jack Pine	0.29	0.23	0.05			0.39	0.27	0.11	0.02	
Pinus strobus	White Pine	0.15	0.13			0.02	1.02	0.49	0.53		
Tilia americana	Basswood	0.08	0.06		0.01	0.01					
Quercus macrocarpa	Bur Oak	0.03			0.01	0.02					
Ulmus americana	White Elm	0.03			0.02	0.02					
Fraxinus pennsylvanica	Green Ash	0.02			0.01	0.02					
Betula alleghenienisis	Yellow Birch	0.02			0.02						
Populus grandidentata	Large-toothed Aspen	0.01				0.01	0.02				0.02
Populus deltoides	Eastern Cottonwood						0.02			0.02	

TABLE 5.12. Frequency of tree species in stand-type VI by canopy strata, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 130*					> 85 years *n = 66*				
		Total	1	2	3	4	Total	1	2	3	4
Populus tremuloides	Trembling Aspen	1.00	1.00	0.16	0.17	0.60	0.99	0.97	0.08	0.11	0.76
Abies balsamea	Balsam Fir	0.90	0.19	0.56	0.53	0.88	0.89	0.08	0.65	0.71	0.88
Betula papyrifera	White Birch	0.62	0.13	0.36	0.32	0.29	0.64	0.12	0.39	0.20	0.23
Picea glauca	White Spruce	0.49	0.21	0.22	0.14	0.21	0.55	0.17	0.35	0.24	0.26
Picea mariana	Black Spruce	0.29	0.04	0.14	0.06	0.14	0.58	0.12	0.42	0.15	0.21
Acer rubrum	Red Maple	0.14	0.02	0.02	0.09	0.12	0.05		0.02	0.03	0.05
Fraxinus nigra	Black Ash	0.07		0.03	0.07	0.06	0.08	0.02	0.03	0.03	0.08
Populus balsamifera	Balsam Poplar	0.12	0.04	0.02	0.02	0.09	0.11	0.05	0.02	0.03	0.09
Thuja occidentalis	Eastern Cedar	0.07		0.03	0.02	0.05	0.09		0.05	0.03	0.06
Pinus banksiana	Jack Pine	0.07	0.05	0.02			0.11	0.08	0.05	0.02	
Pinus strobus	White Pine	0.02	0.01			0.02	0.05	0.03	0.02		
Tilia americana	Basswood	0.01	0.01		0.01	0.01					
Quercus macrocarpa	Bur Oak	0.02			0.01	0.02					
Ulmus americana	White Elm	0.02			0.02	0.02					
Fraxinus pennsylvanica	Green Ash	0.01			0.01	0.01					
Betula alleghenienisis	Yellow Birch	0.01			0.01						
Populus grandidentata	Large-toothed Aspen	0.01				0.01	0.02				0.02
Populus deltoides	Eastern Cottonwood						0.02			0.02	

Successional Variants

1. BEDROCK SITES (DEPTH TO BEDROCK < 2 M)

Pure stands of trembling aspen over bedrock are uncommon; most stands are a mixture of trembling aspen, balsam fir and/or white spruce. Black spruce and red maple are also occasionally encountered. The lower subcanopy and sapling layers are dominated by balsam fir and white birch, although white and black spruce may also occur. The shrub layer is dominated by *Corylus cornuta* and *Diervilla lonicera*, which are more common here than in other variants. *Acer spicatum* is less common. Herb species composition and cover are similar to the stand-type mean, but *Aster macrophyllus* cover is higher. Cryptogam cover is low, but *Pleurozium schreberi* has higher cover here than the stand-type mean.

These stands succeed toward a mixture of balsam fir, white spruce, trembling aspen and white birch. Eastern white cedar may be present in the subcanopy of some stands. White birch and balsam fir are common in the lower subcanopy and sapling layers of older stands. The cover of *Corylus cornuta* and *Diervilla lonicera* decline over time. *Aster macrophyllus* cover also declines, but remains higher than the stand-type mean. *Maianthemum canadense*, *Cornus canadensis* and *Lycopodium obscurum* also decline in cover. Cryptogam cover increases in these stands. The successional trajectory indicates convergence toward stand-type V stands over bedrock .

2. MESIC SITES (MOISTURE REGIME ≥ 3)

Monodominant stands of trembling aspen are common, although balsam fir is often present in the subcanopy. White spruce is less frequent here than in the stand-type as a whole. Balsam fir is common in the lower subcanopy and sapling layers, although white birch, black spruce and trembling aspen suckers are often present as well. *Corylus cornuta* is less frequent and abundant than the stand-type mean, while *Alnus rugosa* is more frequent and often occurs at higher cover. The herb layer is species-rich. *Aster macrophyllus* cover is lower, while *Rubus pubescens* occurs at higher cover. Other hydrophytic species such as *Mitella nuda* and *Athyrium filix-femina* also have higher cover than the stand-type average. Cryptogam cover is low.

These sites show succession toward mixed, uneven-aged stands. Older stands consist of a mixture of over-mature trembling aspen with balsam fir and/or black spruce in the canopy-subcanopy. Regeneration is strongly to balsam fir. Overall tree cover declines somewhat as the canopy opens. White spruce and white birch are infrequent in older stands. *Diervilla lonicera* and *Corylus cornuta* decline in cover over time. The herb layer of older stands remains diverse. *Aster macrophyllus* and *Actaea rubra* decline somewhat in cover, while *Coptis trifoliata* and *Cornus canadensis* increase. Cryptogams remain a minor component of the understory, though *Ptilium crista-castrensis* increases over time.

3. DRY SITES (MOISTURE REGIME < 3)

Tree composition and cover are similar to the stand-type as a whole. Trembling aspen dominates the canopy, forming pure or mixed stands. Codominants in the canopy are balsam fir and white spruce, although black spruce and white birch may also occur. Balsam fir predominates in the lower subcanopy and sapling layers, although white birch, white spruce, black spruce and trembling aspen are also found. Shrub composition and cover are similar to the stand-type mean, although *Corylus cornuta* cover is lower and *Acer spicatum* higher. Herb composition and cover are also similar. Cryptogams occur at low cover.

Trembling aspen persists well in older stands, although cover declines. Balsam fir, white spruce, and black spruce becomes increasingly abundant in the canopy-subcanopy. White birch is found in the subcanopy of some stands. Balsam fir is common in the lower subcanopy and sapling layers, although white birch, black spruce and white spruce also occur. *Corylus cornuta* increases in cover over time, whereas *Acer spicatum* decreases. Changes in the herb and cryptogam layers are very similar to the stand-type as a whole.

Discussion

The successional trajectory for these stands indicates a progression from almost pure, even-aged trembling aspen stands to mixed, uneven-aged stands dominated by balsam fir, white and black spruce, and white birch (c.f. stand-type V). Herb and shrub cover decline once the shade-tolerant coniferous trees reach the canopy, but diversity remains high. Feathermoss cover increases, approaching cover values for stand-type V, but remains low relative to stand-types I-IV. The regeneration dynamics of older stands are similar to stand-type V.

Trembling aspen remains the canopy dominant for at least 100 years (Heinselman 1973; Cogbill 1985). However, trembling aspen is highly shade-intolerant and regeneration beneath a closed canopy is low (Dix and Swan 1971; Perala 1990; Peterson and Peterson 1992). Propagation is mainly vegetative (root suckering), with 'sapling' suckers being produced for at least 250 years (Kneeshaw and Bergeron 1996). Disturbances such as fire and logging promote suckering. Trembling aspen suckers are a favoured summer browse of ungulates (Peterson and Peterson 1992), which may limit successful regeneration of the species. Trembling aspen in also favoured by beaver, which use the species for construction material and food (Novakowski 1987). The loss of mature stands of aspen along watercourses speeds up the succession toward conifer dominance.

Pure stands of trembling aspen gradually deteriorate and may become decadent, showing sparse regeneration and increased domination by shrubs (Zoladeski and Maycock 1990). However, in most stands the invasion of shade-tolerant conifers (balsam fir and white spruce) results in a gradual replacement of trembling aspen (Carleton and Maycock 1978; Perala 1990; Alban et al. 1991; Cogbill 1985). Recruitment of white spruce may occur immediately if there is a ready seed source and seedbed conditions are optimal, i.e. exposed mineral soil. Otherwise, white spruce recruitment is delayed and is much more sporadic (Lieffers et al. 1996). Similarly, balsam fir recruitment is often delayed due to the lack of a ready seed source (Frelich and Reich 1995b).

Succession in these stands may be driven in part by changes in nutrient dynamics and availability. Compared to conifer needles, deciduous litter decays relatively quickly and is recycled more rapidly (Peterson and Peterson 1992). Once conifers invade a stand, nutrient cycling is slowed and trembling aspen (a relatively nutrient-demanding species) is less favoured. In addition, Strong and LaRoi (1983) suggest that the comparatively shallow root system of white spruce effectively intercepts water and nutrients before they can reach the deeper trembling aspen roots.

5.3.7 STAND-TYPE VII: BIRCH- TREMBLING ASPEN MIXED WOOD

Stand-Type Description

Soil-Environment

Soils are generally coarse-textured, with sandy loams and sands predominating. Many sites are quite stony, and in about one-third the depth to bedrock is < 2 m. Brunisol soils predominate, although Luvisols and Podzols are occasional. Parent materials are most commonly morainal, but lacustrine and glaciofluvial parent materials also occur. Sites vary from level to moderately sloping. Most stands are moderately to excessively-drained, and depth to water table is > 2 m in almost all stands. However, distinct mottling is found in approximately 20% of stands. The organic layer is thin, and fibrimors predominate. Sites are less acidic than in the upland coniferous stand-types (I-III, V). Nutrient status is comparable to the upland conifer stand-types, but is lower than Stand-Type V.

Vegetation

A mixed-canopy of white birch, trembling aspen, and/or jack pine is characteristic of most stands. In some stands, black spruce and large-toothed aspen are also present, and red maple and red pine occur in a few stands. Black spruce is frequently found in the subcanopy beneath trembling aspen and jack pine, while most white birch dominated stands also have white birch in the subcanopy. The lower subcanopy and sapling layers are dominated by white birch, black spruce and/or balsam fir. Suckering by trembling aspen is also common. Total shrub cover is moderate to high in most stands. Tall and low shrubs are the most prevalent, but ericaceous shrubs may occur at moderate cover in some stands. The most abundant tall shrubs are *Alnus crispa* and *Corylus cornuta*. *Amelanchier* spp. are also frequent, but generally occur at much lower cover. The low shrub *Diervilla lonicera* is ubiquitous and usually occurs at moderate cover. Ericaceous shrubs are a minor component in most stands, although *Vaccinium* spp. often present at low cover.

Total herb cover is generally moderate to high. The most frequent and abundant species are *Cornus canadensis*, *Aralia nudicaulis* and *Aster macrophyllus*. *Maianthemum canadense*, *Clintonia borealis*, and *Lycopodium* spp. are also frequent, but typically occur at low cover. Total cryptogam cover is low. *Pleurozium schreberi* is ubiquitous, but usually occurs at low cover (mean cover < 5%). *Dicranum polysetum* is often present as well. Lichens are uncommon and occur at low cover when present.

Stand Dynamics

Summary

Stand succession is towards more open, multi-tiered and uneven-aged stands containing a mixture of black spruce and white birch (**Fig. 5.21**). Regeneration is diverse: paper birch, black spruce, balsam fir and trembling aspen are all common in one or both of the lower subcanopy or sapling layers. Total shrub cover declines over time (**Fig. 5.22**). This is attributable to cover declines in tall and low shrubs, whereas ericaceous shrub cover increases somewhat (**Fig. 5.23**). Total herb cover declines, although species composition is similar. Overall cryptogam cover increases (**Fig. 5.22**) and most species increase in cover and/or frequency. The depth of the organic layer increases marginally over time, while soil pH increases slightly. Nutrient status (TEB) declines slightly, but this decrease in not as pronounced as in the upland, conifer-dominated stands. Incorporation of organic material into the mineral horizon increases over time (see **Appendix VII**).

Vegetation

Black spruce is becoming increasingly dominant over time, although white birch regenerates well in many stands and often remains dominant in the canopy-subcanopy (**Fig. 5.21**). The canopy of most older stands contain a mixture of black spruce and white birch, although white spruce may also be present. Relict jack pine may persist (occasionally

VII. Birch - Trembling Aspen Mixed Wood

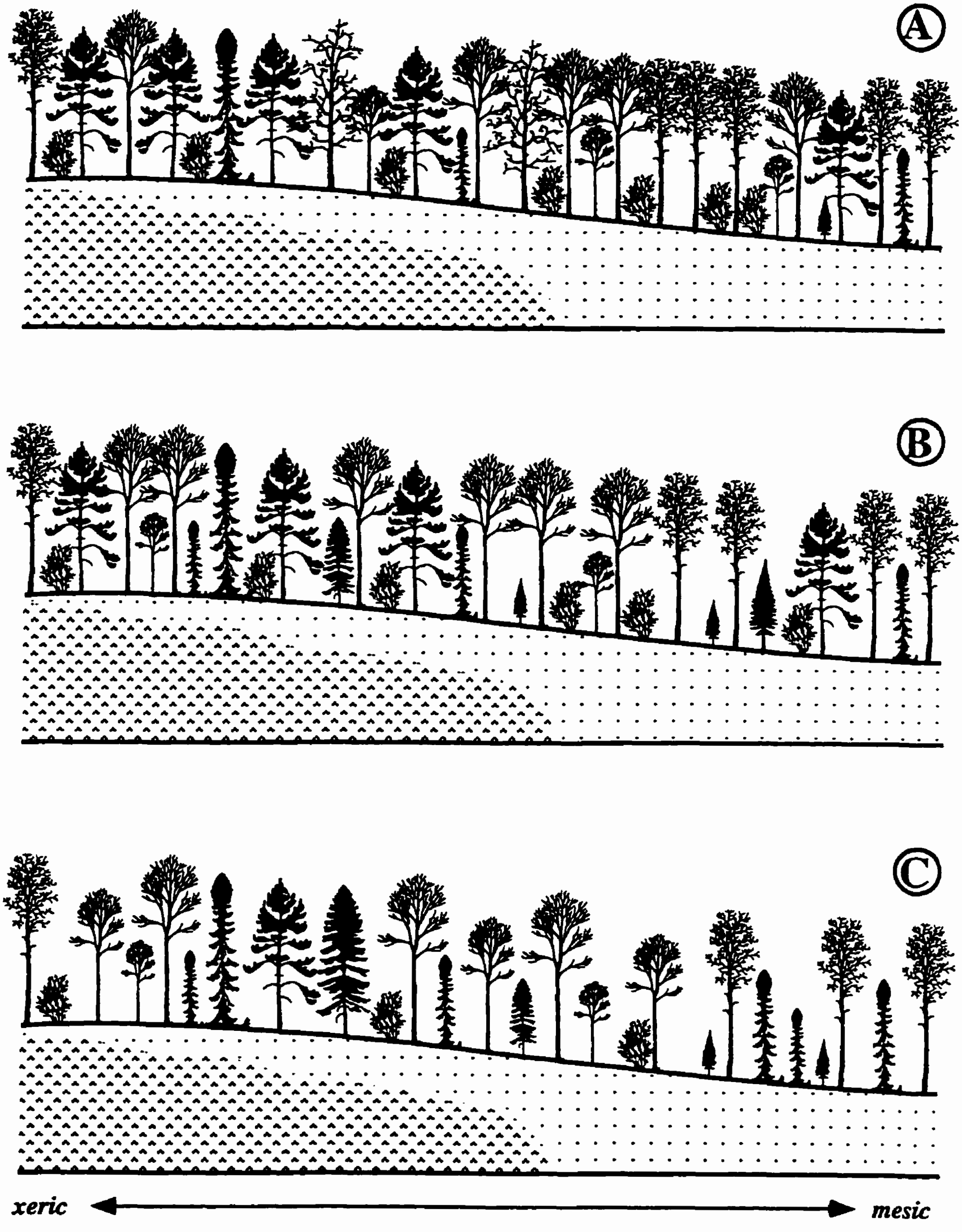


Figure 5.21. Successional trajectory based on mean tree canopy cover. A = ≤ 85 years; B = 86-120 years; C = > 120 years.

VII. Birch - Trembling Aspen Mixed Wood

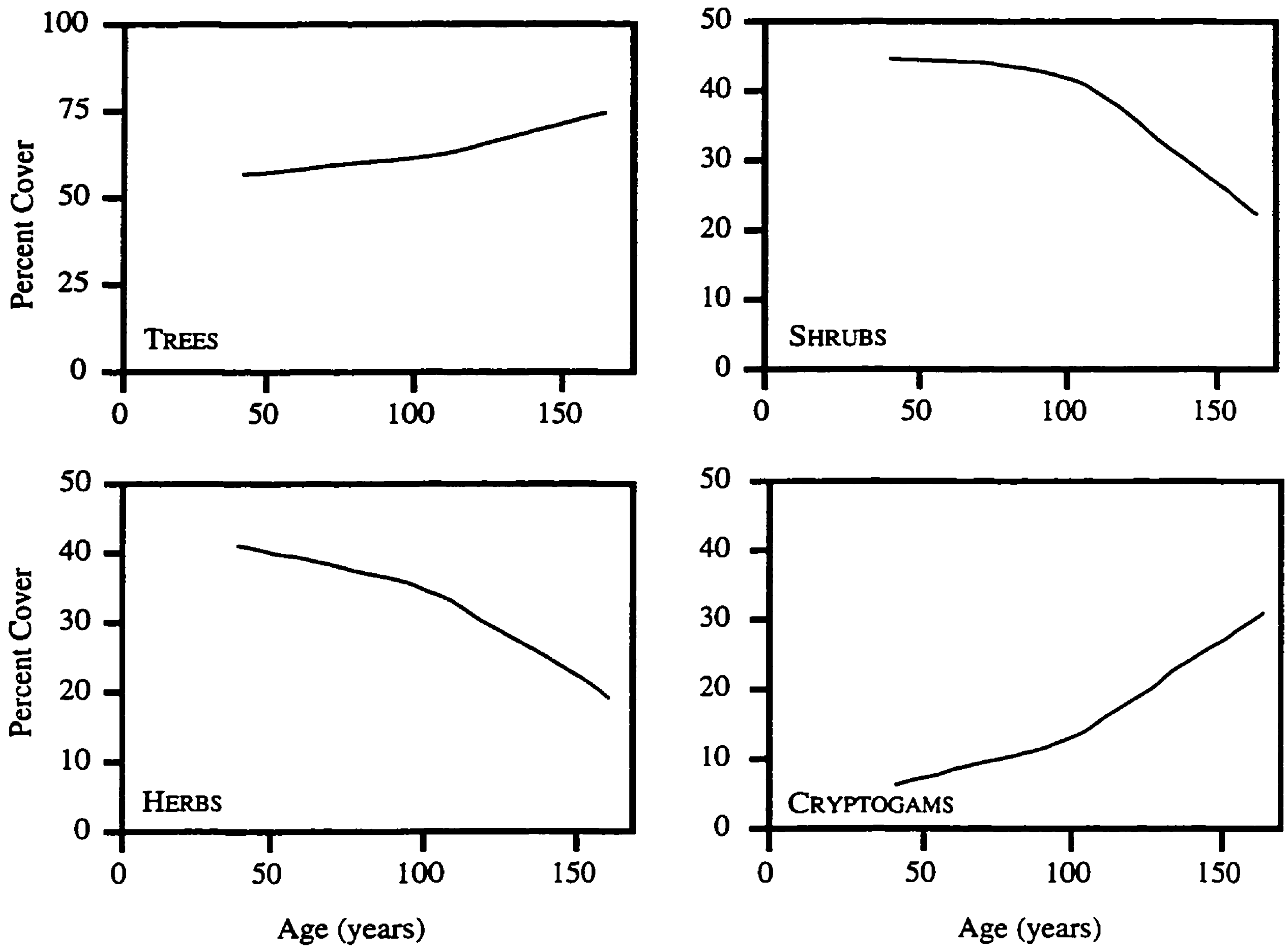


Figure 5.22. Changes in total tree, shrub, herb and cryptogam cover over time. Lines fitted using locally weighted regression analysis.

VII. Birch - Trembling Aspen Mixed Wood

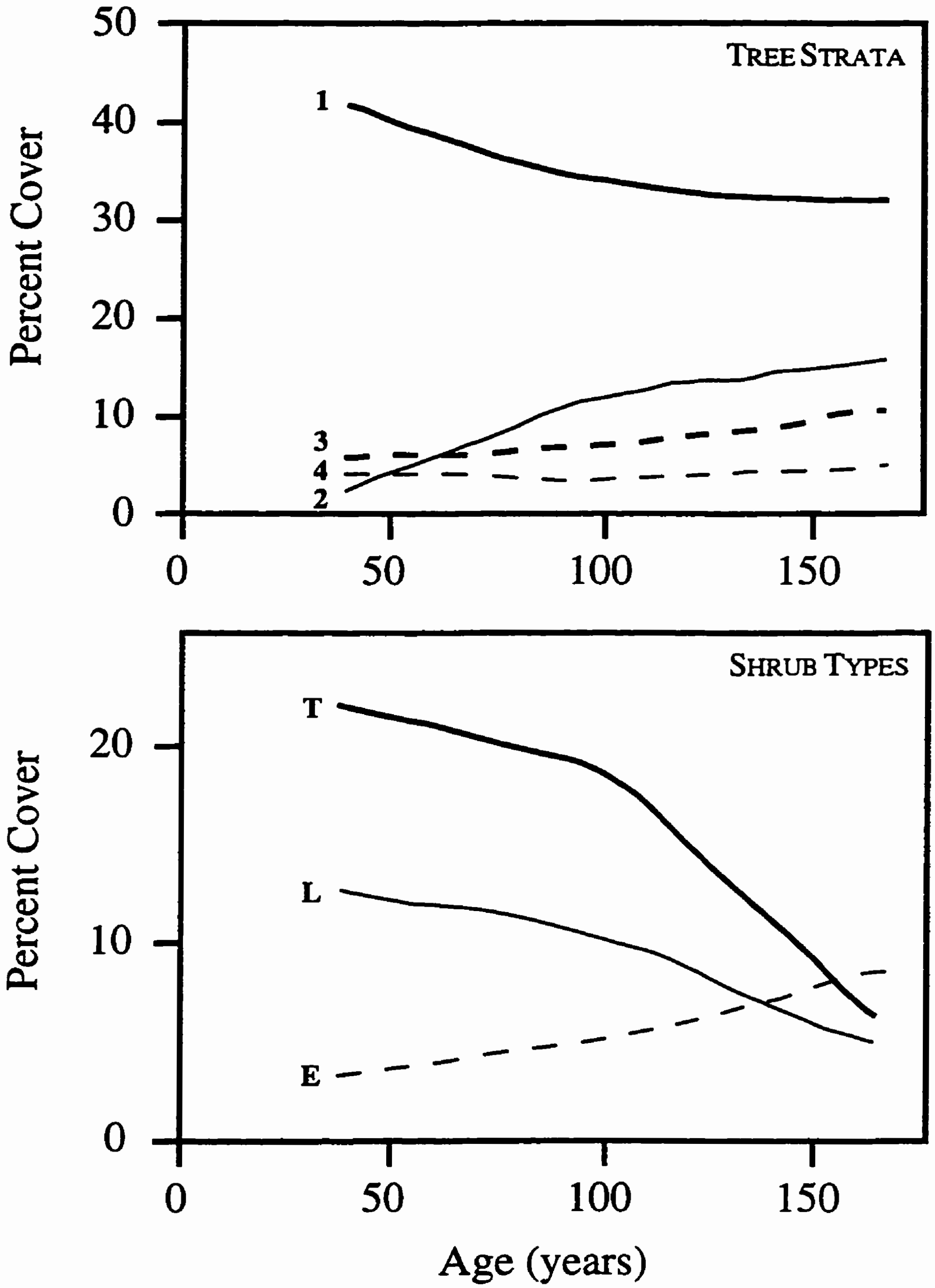


Figure 5.23. Changes in total tree cover by strata (codes: 1 = canopy; 2 = upper subcanopy; 3 = lower subcanopy; 4 = sapling layer) and shrub cover by shrub-type (codes: T = tall shrubs; L = low shrubs; E = ericaceous shrubs). Lines fitted using locally weighted regression analysis.

TABLE 5.13. Mean cover of tree species in stand-type VII by canopy strata (1-4), in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n* = 65					> 85 years *n* = 31				
		Total	1	2	3	4	Total	1	2	3	4
Betula papyrifera	White Birch	17.48	10.48	2.66	3.66	0.68	13.97	7.84	3.16	2.48	0.48
Populus tremuloides	Trembling Aspen	14.55	12.63	0.52	0.72	0.68	18.32	14.90	1.94	0.84	0.65
Pinus banksiana	Jack Pine	9.79	9.46	0.17	0.14	0.02	9.13	9.10			0.03
Picea mariana	Black Spruce	6.29	1.39	3.22	1.05	0.65	11.42	1.61	6.29	2.39	1.13
Abies balsamea	Balsam Fir	3.57	0.06	0.65	1.23	1.63	8.07	0.29	3.52	1.71	2.55
Populus grandidentata	Large-toothed Aspen	3.26	3.12		0.09	0.05					
Picea glauca	White Spruce	2.12	1.15	0.37	0.31	0.29	3.03	0.52	1.19	0.77	0.55
Acer rubrum	Red Maple	1.60	0.15	0.60	0.42	0.43	1.03		0.23	0.52	0.29
Pinus resinosa	Red Pine	1.31	1.25		0.06		0.19	0.19			
Thuja occidentalis	Eastern Cedar	0.66		0.62	0.02	0.03	0.19				0.19
Populus balsamifera	Balsam Poplar	0.35	0.31		0.02	0.03	0.07		0.07		
Pinus strobus	White Pine	0.20	0.03	0.09	0.03	0.05	0.03				0.03
Quercus rubra	Red Oak	0.03			0.02	0.02					
Fraxinus nigra	Black Ash						0.10				0.10

TABLE 5.14. Frequency of tree species in stand-type VII by canopy strata, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n* = 65					> 85 years *n* = 31				
		Total	1	2	3	4	Total	1	2	3	4
Betula papyrifera	White Birch	0.77	0.32	0.34	0.35	0.45	0.87	0.32	0.39	0.52	0.45
Populus tremuloides	Trembling Aspen	0.71	0.46	0.11	0.26	0.55	0.84	0.65	0.23	0.32	0.61
Pinus banksiana	Jack Pine	0.63	0.59	0.08	0.03	0.02	0.71	0.68			0.03
Picea mariana	Black Spruce	0.57	0.12	0.29	0.29	0.35	0.65	0.19	0.42	0.45	0.45
Abies balsamea	Balsam Fir	0.72	0.02	0.09	0.31	0.68	0.58	0.03	0.19	0.36	0.55
Populus grandidentata	Large-toothed Aspen	0.12	0.11		0.02	0.05					
Picea glauca	White Spruce	0.35	0.06	0.08	0.09	0.17	0.52	0.10	0.16	0.26	0.26
Acer rubrum	Red Maple	0.34	0.03	0.05	0.12	0.31	0.13		0.07	0.07	0.13
Pinus resinosa	Red Pine	0.08	0.08		0.02		0.07	0.07			
Thuja occidentalis	Eastern Cedar	0.03		0.02	0.02	0.03	0.03				0.03
Populus balsamifera	Balsam Poplar	0.05	0.03		0.02	0.03	0.03		0.03		
Pinus strobus	White Pine	0.06	0.02	0.02	0.02	0.05	0.03				0.03
Quercus rubra	Red Oak	0.03			0.02	0.02					
Fraxinus nigra	Black Ash						0.07				0.07

at moderate cover) on bedrock sites. Large-toothed aspen are rarely present in older stands. Trembling aspen persist mainly in moister sites, and suckers from these trees can be found in the subcanopy in about one-quarter of stands. White birch, balsam fir (which rarely reaches the canopy) and black spruce regenerate well in most stands, while white spruce is occasional (**Tables 5.13, 5.14**).

Total shrub cover begins to decline after age 100. Tall shrub cover declines, most notably in *Corylus cornuta* and *Alnus crispa*. The low shrub *Diervilla lonicera* is also less abundant in older stands. Ericaceous shrubs increase in cover over time, particularly *Vaccinium* spp. *Ledum groenlandicum* and *Gaultheria hispidula* also increase in frequency and cover, but remain minor components of the forest understory. As with the shrubs, total herb cover declines after age 100 (**Fig. 5.23**). *Aster macrophyllus* shows the greatest decline, but other species show modest declines in frequency and/or cover as well. Overall herb species richness and diversity do not change appreciably over time. Total cryptogam cover increases over time, although cryptogams remain a relatively minor component of the vegetation. *Pleurozium schreberi* remains the most frequent and abundant species in older stands. *Dicranum polysetum*, *Ptilium crista-castrensis*, *Hylocomium splendens* and *Rhytidiadelphus triquestris* also increase slightly in cover. Lichens also increase in frequency and cover, but remain a minor component (see **Appendix VII**).

Successional Variants

1. BEDROCK SITES (DEPTH TO BEDROCK < 2 M)

Total tree cover is low in these stands compared to the stand-type as a whole. Jack pine is more frequent and abundant, whereas trembling aspen and balsam fir are uncommon. Large-toothed aspen is not present in these stands. Tall and low shrub cover is somewhat lower, whereas ericaceous shrubs (particularly *Vaccinium* spp.) are more abundant. The species composition and cover of the herb layer are similar to the stand-type means, although *Aster macrophyllus* is more frequent and abundant.

Succession is toward an open, uneven-aged canopy dominated by white birch and black spruce. Jack pine and trembling aspen are infrequently present in older stands, although cover may be high when present. White spruce is present in a few stands. The lower subcanopy and sapling layers of older stands are dominated by black spruce and white birch. Balsam fir is also present in the sapling layer, but rarely occurs in the canopy of older stands. The tall shrubs (particularly *Corylus cornuta* and *Alnus crispa*) decline in cover over time, as do the low shrubs *Diervilla lonicera* and *Rosa acicularis*. Overall herb cover declines over time, but stands remain herb-rich. *Aster macrophyllus* cover declines considerably, but most other species show more modest declines. *Pleurozium schreberi* cover increases considerably to >16% in older stands.

2. SITES WITH DEPTH TO BEDROCK > 2 M

These stands have higher cover of white birch and trembling aspen than the bedrock variant, while jack pine is less common. In the south-west portion of the study area, large-toothed aspen may occur on well-drained sites. Black spruce and white birch are the most frequently encountered subcanopy species, while balsam fir is common in the sapling layer. Shrub composition and cover are similar to the stand-type as a whole. Herb species composition and cover are also similar, except that *Aster macrophyllus* is less common and abundant in this variant. Cryptogam species composition and cover are also similar.

Like the bedrock variant, older stands are characterized by open, uneven-aged canopies dominated by white birch and black spruce. Jack pine and large-toothed aspen are absent from older stands. Trembling aspen persist in more mesic sites. White birch regeneration is not as strong as in the bedrock sites. Balsam fir, black spruce and white spruce are frequently encountered in the lower subcanopy and sapling layers of older stands. Balsam fir may enter the subcanopy but rarely reaches the canopy. Shrub cover declines over time but remains higher than the stand-type average. Ericaceous shrub cover is low. Herb cover also declines, but stands remain relatively species-rich. *Ptilium crista-castrensis* and

Pleurozium schreberi increase slightly in cover over time. *Rhytidiadelphus triquestris*, which is infrequent in younger stands, occurs at low cover in over half of the older stands.

Discussion

These stands represent a dry, nutrient-deficient variant of stand-type VI. The overall successional trajectory indicates convergence toward fairly open-canopied, uneven-aged mixed-wood stands. However, prevailing soil moisture and nutrient conditions are more favourable to white birch and black spruce, and less favourable to white spruce and balsam fir (c.f. stand-types V and VI). Trembling aspen regeneration may also occur. Herbs and low shrubs (particularly *Diervilla lonicera*) continue to dominate the understory, although feathermosses become more abundant as stands age.

Although white birch is considered to be highly shade-intolerant, a number of studies have indicated that the species regenerates well in older stands (Ohmann and Grigal 1975; Kneeshaw and Bergeron 1996; Frelich and Reich 1995b). Much of this regeneration is probably due to the resprouting ability of the species (Safford et al. 1990). Germination and establishment may also occur in large forest gaps created by intermediary disturbances (Frelich and Reich 1995b). Black spruce regeneration may be favoured in forest gaps. In addition, low nutrient status is favourable to black spruce since potential competitors (particularly balsam fir and white spruce) are comparatively nutrient-demanding.

5.3.8 Stand-Type VIII: Red Pine

Stand-Type Description

<u>Soil-Environment</u>

Sites dominated by red pine are typically xeric and excessively drained. The water table is > 2 m from the surface in all stand, and distinct mottling of the soil profile is uncommon. Depth to bedrock is < 2 m in about one-quarter of the sites, and many are stony. Stands occur on coarse-textured substrates (sandy to sandy loam) derived from glaciofluvial or morainal parent materials. Soils of the Brunisolic order predominate. Organic accumulation is low (mean organic layer depth = 5.8 cm, the lowest of any stand-type), and humus form is predominately fibrimoric. The mineral and organic soil layers are relatively acidic, and nutrient status is low (though higher than stand-types I-III). Most sites are level, but some stands occur on gentle, or occasionally steep, slopes.

Vegetation

The canopy is dominated by red pine, which often forms monodominant stands. Jack pine, trembling aspen and large-toothed aspen are occasional canopy codominants. Canopy cover is relatively high in most stands, but subcanopy cover is usually low. Balsam fir, white birch, black spruce and white pine may occur in the lower subcanopy. Red pine is regenerating in some but not all stands. The sapling layer is dominated by balsam fir and white birch, although trembling aspen, white pine, black spruce, large-toothed aspen and jack pine saplings may also be present. Total shrub cover is usually low to moderate. Tall shrubs are infrequent and no one species predominates. *Amelanchier* spp. are found in about two-thirds of the stands, but occur at low cover. *Alnus crispa*, *Corylus cornuta* and *Acer spicatum* are less frequent but can occur at moderate or (rarely) high cover when present. *Diervilla lonicera* is ubiquitous and occurs at low to moderate cover, while *Chimaphila umbellata* occurs in most stands at low cover. *Vaccinium* spp. are ubiquitous, but generally occur at low cover. *Arctostaphylos uva-ursi* is infrequent but may occur at moderate cover when present.

Total herb cover is usually low to moderate. *Maianthemum canadense* and *Aralia nudicaulis* are ubiquitous and occur at low, or occasionally moderate, cover. *Lycopodium* spp., *Cornus canadensis* and *Aster macrophyllus* occur in over half the stands, again at low cover. Other species are infrequent and inconspicuous in most stands. *Dicranum polysetum* and *Pleurozium schreberi* are ubiquitous, and usually occur at low to moderate cover. *Cladina* spp. are also commonly encountered at low cover.

Stand Dynamics

Summary

Succession in this stand-type indicates continued dominance of red pine in the canopy (**Fig. 5.24**). Regeneration in both the subcanopy and sapling layers is primarily coniferous (predominantly balsam fir). Replacement by balsam fir, white spruce or white pine may occur, but is unlikely in the more xeric, nutrient-poor sites. Given the size and longevity of red pine, canopy replacement by these available species (excluding perhaps white pine) is improbable. The decrease in total shrub cover (**Fig. 5.25**) over time is attributable to decreases in tall and low shrub cover. Ericaceous shrubs cover increases marginally as stands age (**Fig. 5.26**). Total herb cover also declines, particularly in older stands (**Fig. 5.25**). Cryptogam cover increases over time (**Fig. 5.25**), attributable mainly to increased abundance of *Pleurozium schreberii*. Changes in soil variables over time are minor. Organic matter depth increases slightly, but other variables show no clear trends (see **Appendix VIII**).

Vegetation

Canopy cover declines over time, particularly after age 100 (**Fig. 5.25**). Red pine dominates the canopy of older stands, usually forming pure stands but occasionally occurring with white pine. Trembling aspen, jack pine and large-toothed aspen decline in frequency and cover over time (**Tables 5.15, 5.16**). The lower canopies are increasingly dominated by balsam fir and black spruce, and many older stands have a distinctive two-tiered profile (red pine in the canopy, balsam fir/black spruce in the lower subcanopy). However, balsam fir and black spruce rarely enter the canopy or subcanopy. The sapling layer of older stands is dominated by balsam fir and black spruce. Red pine, white pine and white birch saplings are found in about one-third of the stands.

The cover of most tall and low shrubs decline over time. Species composition remains similar, however, and individual changes in frequency and cover are minor. Ericaceous

VIII. Red Pine

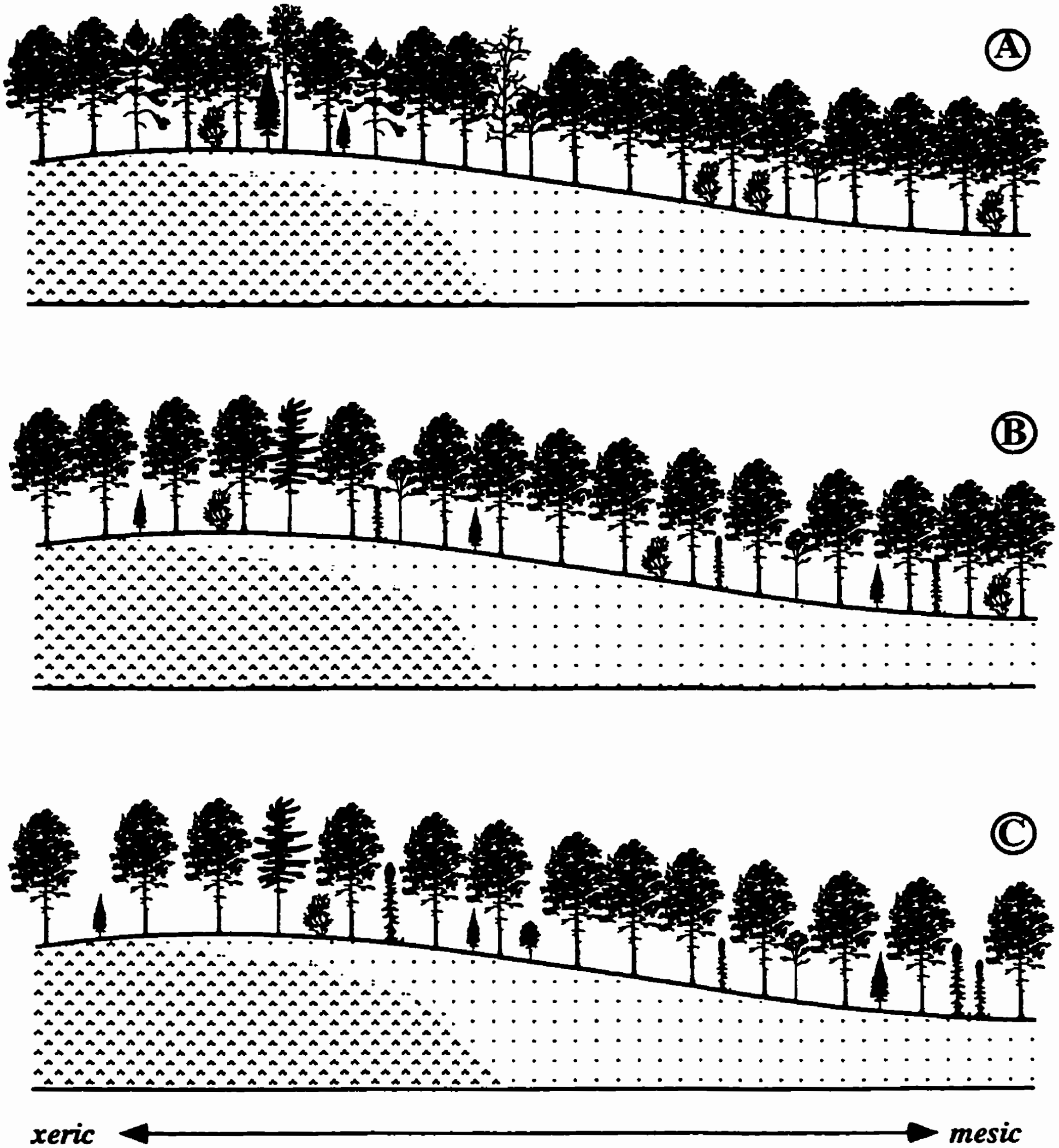


Figure 5.24. Successional trajectory based on mean tree canopy cover.
A = ≤ 85 years; B = 86-120 years; C = > 120 years.

VIII. Red Pine

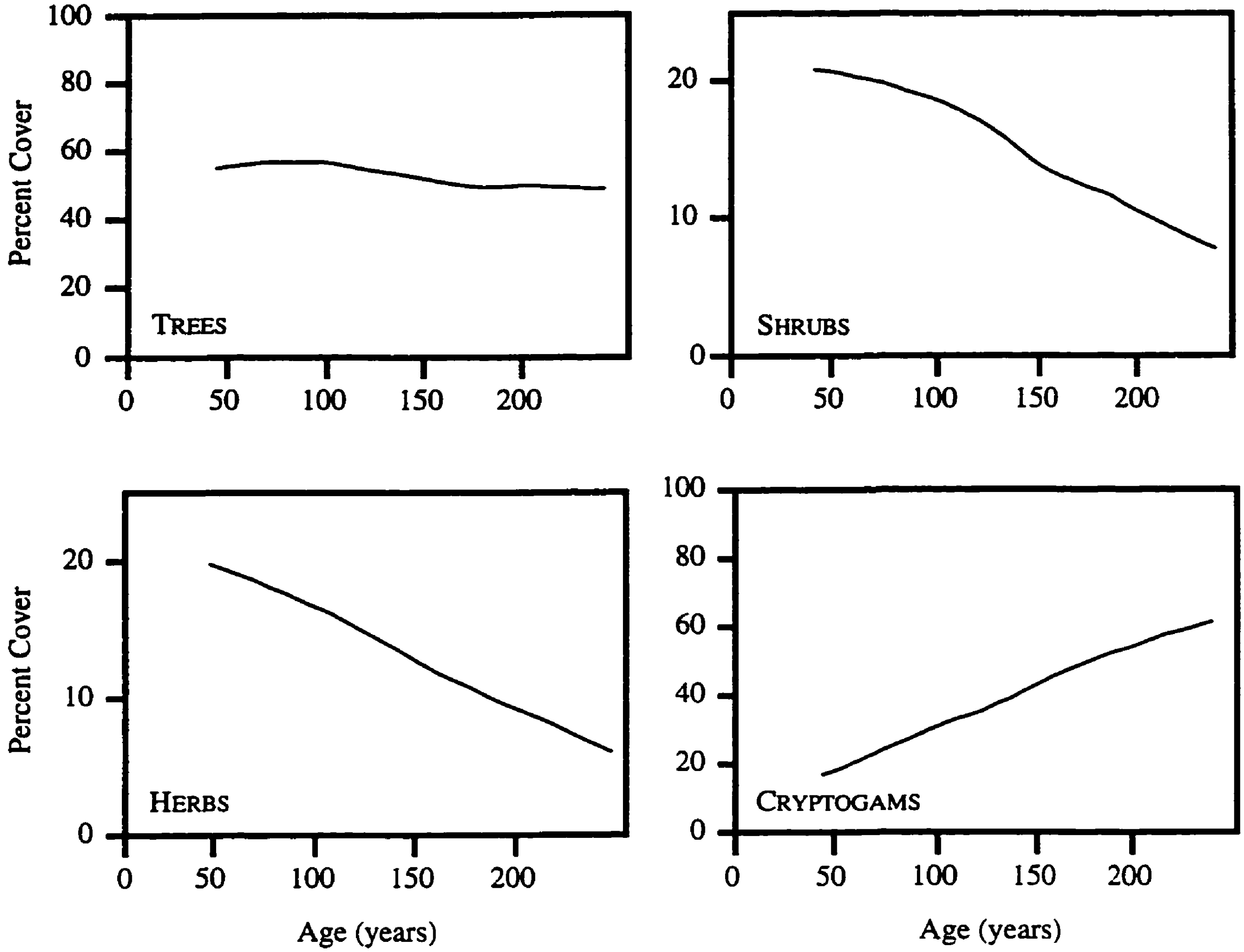


Figure 5.25. Changes in total tree, shrub, herb and cryptogam cover over time. Lines fitted using locally weighted regression analysis.

VIII. Red Pine

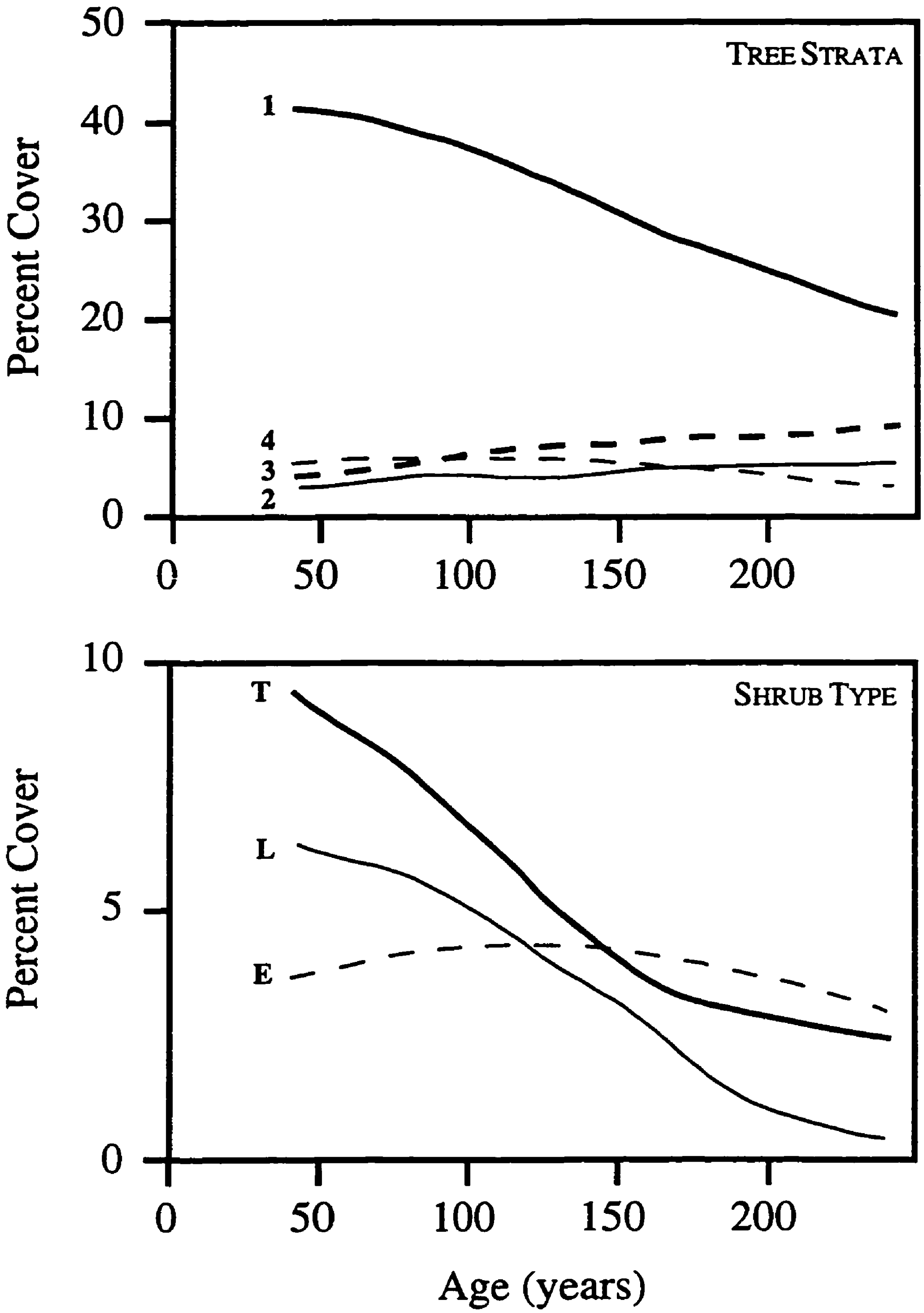


Figure 5.26. Changes in total tree cover by strata (codes: 1 = canopy; 2 = upper subcanopy; 3 = lower subcanopy; 4 = sapling layer) and shrub cover by shrub-type (codes: T = tall shrubs; L = low shrubs; E = ericaceous shrubs). Lines fitted using locally weighted regression analysis.

TABLE 5.15. Mean cover of tree species by in stand-type VIII canopy strata (1-4), in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 18* Total	1	2	3	4	> 85 years *n = 44* Total	1	2	3	4
Pinus resinosa	Red Pine	29.78	27.94	0.44	0.89	0.50	35.14	34.07	0.41	0.21	0.46
Abies balsamea	Balsam Fir	4.39		2.00	0.94	1.44	9.09	0.11	1.71	4.82	2.46
Betula papyrifera	White Birch	3.61	0.28	1.33	1.33	0.67	3.84	0.30	1.09	2.02	0.43
Pinus banksiana	Jack Pine	3.22	2.89	0.22		0.11	1.32	1.27		0.05	
Populus tremuloides	Trembling Aspen	2.44	1.56		0.11	0.78	1.50	0.48	0.07	0.59	0.36
Pinus strobus	White Pine	1.78	0.89	0.33	0.33	0.22	3.66	1.89	0.98	0.34	0.46
Populus grandidentata	Large-toothed Aspen	1.78	1.28	0.17	0.17	0.17	0.71	0.59		0.02	0.09
Picea mariana	Black Spruce	0.83	0.17	0.06	0.39	0.22	4.05	0.23	1.14	1.32	1.36
Thuja occidentalis	Eastern Cedar	0.56			0.22	0.33	1.64		0.57	0.39	0.68
Picea glauca	White Spruce	0.39	0.22		0.06	0.11	0.89	0.25	0.09	0.32	0.23
Acer rubrum	Red Maple	0.22			0.11	0.11	0.25			0.07	0.18
Populus balsamifera	Balsam Poplar						0.02				0.02

TABLE 5.16. Frequency of trees in stand-type VIII by canopy strata, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 18* Total	1	2	3	4	> 85 years *n = 44* Total	1	2	3	4
Pinus resinosa	Red Pine	1.00	1.00	0.11	0.39	0.17	1.00	1.00	0.16	0.11	0.30
Abies balsamea	Balsam Fir	0.78		0.28	0.28	0.78	0.89	0.02	0.25	0.64	0.82
Betula papyrifera	White Birch	0.72	0.11	0.22	0.33	0.56	0.75	0.07	0.25	0.48	0.36
Pinus banksiana	Jack Pine	0.39	0.33	0.06		0.11	0.32	0.27		0.05	
Populus tremuloides	Trembling Aspen	0.44	0.28		0.11	0.28	0.34	0.09	0.02	0.11	0.23
Pinus strobus	White Pine	0.39	0.11	0.11	0.11	0.22	0.41	0.21	0.11	0.14	0.36
Populus grandidentata	Large-toothed Aspen	0.28	0.28	0.06	0.11	0.17	0.09	0.05		0.02	0.09
Picea mariana	Black Spruce	0.33	0.06	0.06	0.22	0.17	0.66	0.07	0.23	0.39	0.55
Thuja occidentalis	Eastern Cedar	0.06			0.06	0.06	0.27		0.05	0.18	0.23
Picea glauca	White Spruce	0.22	0.06		0.06	0.11	0.25	0.07	0.05	0.16	0.14
Acer rubrum	Red Maple	0.11			0.06	0.06	0.18			0.05	0.16
Populus balsamifera	Balsam Poplar						0.02				0.02

shrubs are equally abundant in young and older stands. *Vaccinium* spp. and *Arctostaphylos uva-ursi* increase over time, but other ericaceous species decline.

Total herb cover declines over time. *Maianthemum canadense*, *Lycopodium* spp., *Aster macrophyllus* and *Melampyum lineare* all decline in frequency and/or cover, while *Cornus canadensis* and *Linnaea borealis* show modest increases. Total cryptogam cover increases over time, attributable mainly to increasing abundance of *Pleurozium schreberi*. *Cladina* spp. decline in cover and frequency over time (see **Appendix VIII**).

Successional Variants

1. BEDROCK SITES (DEPTH TO BEDROCK < 2 M)

Stands over bedrock are more likely to have a mixed canopy. Jack pine, trembling aspen and white pine are more frequent and abundant compared to the stand-type as a whole. The lower subcanopy is dominated by balsam fir and red pine. The sapling layer is dominated by balsam fir, although white birch, white pine and trembling aspen may also occur. Red pine saplings are present in about one-third of the stands. Tall shrubs such as *Corylus cornuta* and *Acer spicatum* are less frequent, and their cover is lower. *Diervilla lonicera* and *Rosa acicularis* are more frequent than the stand-type mean. *Aster macrophyllus* occurs with much higher cover on these sites, but otherwise herb composition and cover are similar. Cover of *Pleurozium schreberi* and *Dicranum polysetum* are lower than the stand-type means, but *Cladina* spp. are more common.

Mean tree cover declines over time in these stands, and older stand are often quite open. Black spruce, white spruce and white pine increase in frequency and cover, but only white pine reaches the canopy. Jack pine and trembling aspen decrease in frequency and cover over time. The subcanopy of older stands may contain white birch, balsam fir and/or black spruce, but cover values are generally low. The sapling layer has trembling aspen, white pine, and white birch, but more frequently red pine and black spruce. Temporal changes in shrub cover are similar to the stand-type mean. Tall shrub cover declines, and *Diervilla lonicera* decreases in both frequency and cover. Ericaceous shrubs also decline in cover and frequency, except for *Vaccinium angustifolium* which becomes almost ubiquitous in older stands. *Aster macrophyllus* decreases in both frequency and cover, while *Linnaea borealis* is more frequently encountered in older stands. *Pleurozium schreberi* increases over time, while frequency and cover of *Cladina* spp. decline.

2. Sites With Depth to Bedrock > 2m

Jack pine and white pine are less frequently encountered in these stands, while white birch and black spruce are more common. Large-toothed aspen is occasional. The lower subcanopy and sapling layers are dominated by balsam fir, white birch and black spruce. Tall shrubs (particularly *Corylus cornuta* and *Acer spicatum*) are more abundant, though they remain a relatively minor component of most stands. *Diervilla lonicera* and *Aster macrophyllus* are less frequent and abundant compared to the stand-type average, whereas *Pleurozium schreberi* and *Dicranum polysetum* are more abundant. *Cladina* spp. are infrequent in these stands.

Changes in canopy composition are very similar to the stand-type as a whole. Jack pine, trembling aspen and large-toothed aspen decline over time and are absent from the oldest stands. The canopy is generally pure red pine, while black spruce, white birch, and occasionally balsam fir, are found in the subcanopy. The sapling layer of older stands is dominated by balsam fir, black spruce and white birch. Red pine and white pine saplings may also be present in some stands. Cover of *Vaccinium* spp. and *Arctostaphylos uva-ursi* increase over time, but otherwise temporal trends in the shrub, herb and cryptogam layers are similar to the stand-type as a whole.

Discussion

In northwestern Ontario, red pine usually occurs in pure stands on xeric, oligotrophic substrates (coarse sand or bedrock). The successional trajectory indicates that canopies become more open over time, and that ericaceous shrub and feathermoss dominate the understory of older stands. Black spruce and balsam fir are common in the subcanopy and sapling layers, but are rarely abundant. Red pine regeneration occurs in about half of the older stands. Three possible successional trends are suggested: (a) red pine self-regeneration; (b) long-term succession toward open-canopy black spruce-ericaceous shrub-feathermoss stands; (c) long-term succession toward open-canopy white pine-feathermoss stands. Because red pine is a comparatively long-lived species, these proposed successional trajectories are somewhat tentative.

In Ontario, red pine generally occurs in pure (or almost pure) stands (Carleton et al. 1996). It is a relatively shade-intolerant species (Rudolf 1990; Puettman and Wright 1995). Although red pine cones are not serotinous, fire is critical to its regeneration. Specifically, periodic low-intensity surface fires are required to reduce shrub competition and expose a mineral soil seedbed. Because red pine bark is fire-resistant, few of the mature trees are killed by these light fires. Regeneration of red pine is greatest in stands where light surface fires occur every 20-40 years, and where the interval between catastrophic crown fires is >100 years (Heinselman 1973, 1981). Such conditions generally occur in specific physiographic settings, such as exposed ridges (Engstrom and Mann 1991) and islands in large lakes (Bergeron and Brisson 1990). Such sites are insulated from the larger, more intense fires characteristic of 'mainland' areas.

Red pine regeneration is highly variable: sapling are common in some stands, while in others none are encountered (Rudolf 1990; Carleton and Arnup 1993; Carleton et al. 1996). In northern Québec, occasional low-intensity fires promote red pine regeneration (Bergeron and Brisson 1990). The more intense surface fires of xeric sites kill a proportion of mature trees, which opens the canopy and promotes regeneration. By contrast, saplings are shaded out in more mesic sites where surface fires are less intense (Bergeron and Gagnon 1987). Red pine requires approximately 35 years to develop bark thick enough to withstand low-intensity fires (Bergeron and Brisson 1990).

The successional dynamics of red pine stands is dependent on substrate conditions, fire frequency and intensity, and physiography. Mesic red pine stands are often replaced by a spruce-fir mix, whereas red pine forms a self-perpetuating 'subclimax' in more xeric habitats (Rudolf 1990). Horton and Bedell (1960) suggested that red pine may be succeeded by shade-tolerant hardwoods or softwoods, or by white pine.

5.3.9 STAND-TYPE IX: WHITE PINE

Stand-Type Description

Soil-Environment

Organic matter accumulation is <10 cm in all stands, and raw moder and fibrimor humus forms predominate. Most stands occur on Brunisolic or Luvisolic loamy soils derived from lacustrine or morainal parent material. Depth to bedrock is < 2 m in over one-third of stands, and sites are often stony. Sites are well-drained, but are usually not as dry as those of stand-type VIII. The water table is not found in the first 2 m of any of the stands, and distinct mottling of the soil profile is uncommon. Soils are relatively acidic, though less so than stand-types I-III. Nutrients are limited, but stands have higher nutrient status than stand-types I-III and VIII. Most stands occur on level to gently sloping ground.

Vegetation

Total canopy cover is high, and white pine dominates the canopy of all stands. White pine may occur as pure stands, but is more often found in mixture with red pine, white birch, trembling aspen and/or balsam fir. Red maple and eastern white cedar are occasional. Balsam fir, white birch and white pine are the most frequently encountered species in the subcanopy. The lower subcanopy and sapling layers are dominated by balsam fir, although trembling aspen, white birch, red maple, white spruce and eastern white cedar may also be encountered. The shrub layer is dominated by *Corylus cornuta* and *Acer spicatum*, which occur at high frequency and moderate cover. *Amelanchier* species are also frequent but usually occur at low cover. *Alnus crispa*, *Cornus stolonifera* and *C. rugosa* are occasionally encountered, occurring at low cover when present. The low shrubs *Diervilla lonicera* and *Rubus strigosus* are frequent and usually occur at moderate cover. Ericaceous shrubs are infrequent and occur at low cover. *Vaccinium* spp. occur in half the stands.

The herb layer is relatively rich. *Aster macrophyllus* and *Aralia nudicaulis* are frequent, and usually occur at moderate cover. *Maianthemum canadense*, *Oryzopsis* spp., *Cornus canadensis*, *Lycopodium* spp. and *Clintonia borealis* are also frequently encountered, but generally occur at low cover. The fern *Pteridium aquilinum* occurs in about one-third of the stands. Total cryptogam cover is low. The most frequent species are *Pleurozium schreberi* and *Dicranum polysetum*, but they occur at low cover. Lichens are infrequent.

Stand Dynamics

Summary

As succession proceeds, older stands are typically characterized by a semi-closed canopy of white pine, with a mixed subcanopy of balsam fir, white spruce, white birch and/or eastern white cedar (**Fig. 5.27**). Regeneration in the lower subcanopy and sapling layer is predominantly balsam fir, and to a lesser extent white pine. Total shrub cover shows little change in each of the tall, low and ericaceous strata (**Fig. 5.28**, **5.29**). Total herb cover declines over time (**Fig. 5.28**), primarily due to lower cover of *Aster macrophyllus* and *Aralia nudicaulis*. Cryptogam cover (primarily *Pleurozium schreberi*) increases over time (**Fig. 5.28**). Depth of the organic layer increases over time, and both the mineral and organic layers become less acidic. Total exchangeable bases decrease as stands age, but other soil variables show no clear trends (see **Appendix IX**).

Vegetation

The canopy becomes somewhat more open over time, but canopy cover remains comparatively high. Older stands are characterized by a semi-closed canopy of white pine, although red pine may occur as a minor canopy codominant on bedrock sites. Trembling aspen cover declines steadily over time and is absent from the oldest stands. A subcanopy consisting of a mixture of balsam fir, white spruce, white birch and/or eastern white cedar develops in most older stands. Red maple may occur as a minor component of the subcanopy. Balsam fir dominates the sapling layer of older stands, but rarely reaches the

IX. White Pine

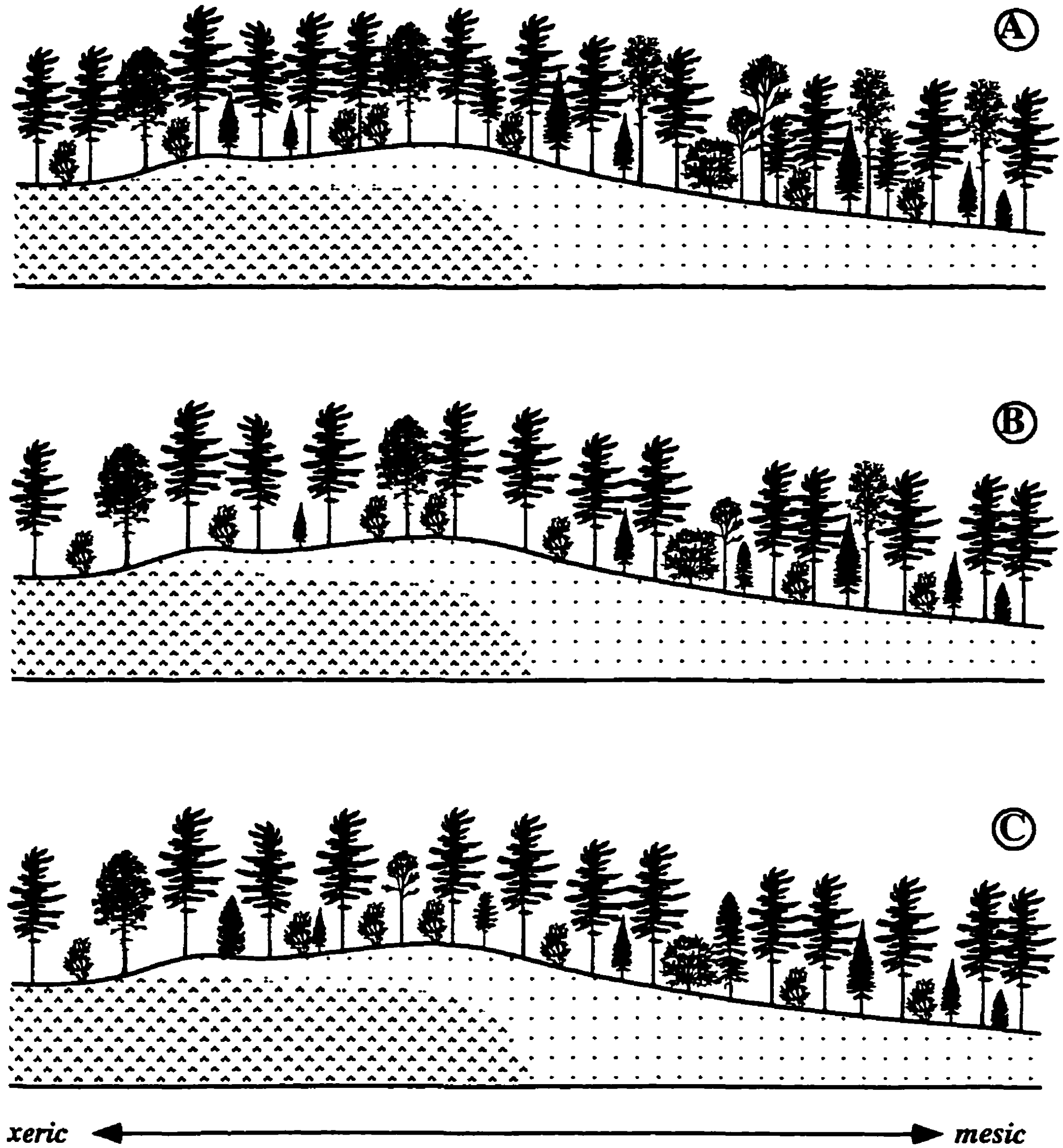


Figure 5.27. Successional trajectory based on mean tree canopy cover. A = ≤ 85 years; B = 86-120 years; C = > 120 years.

IX. White Pine

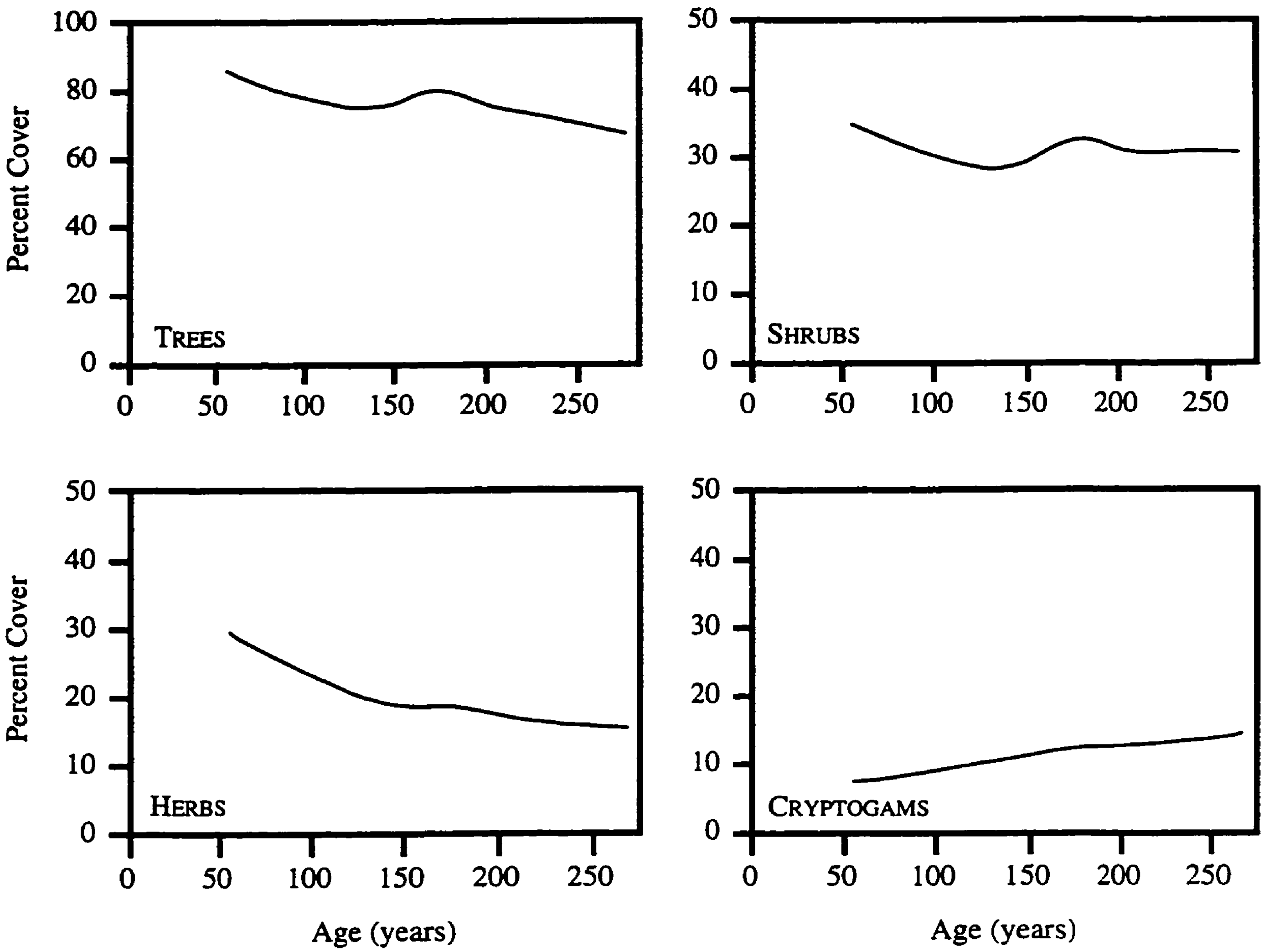


Figure 5.28. Changes in total tree, shrub, herb and cryptogam cover over time. Lines fitted using locally weighted regression analysis.

IX. White Pine

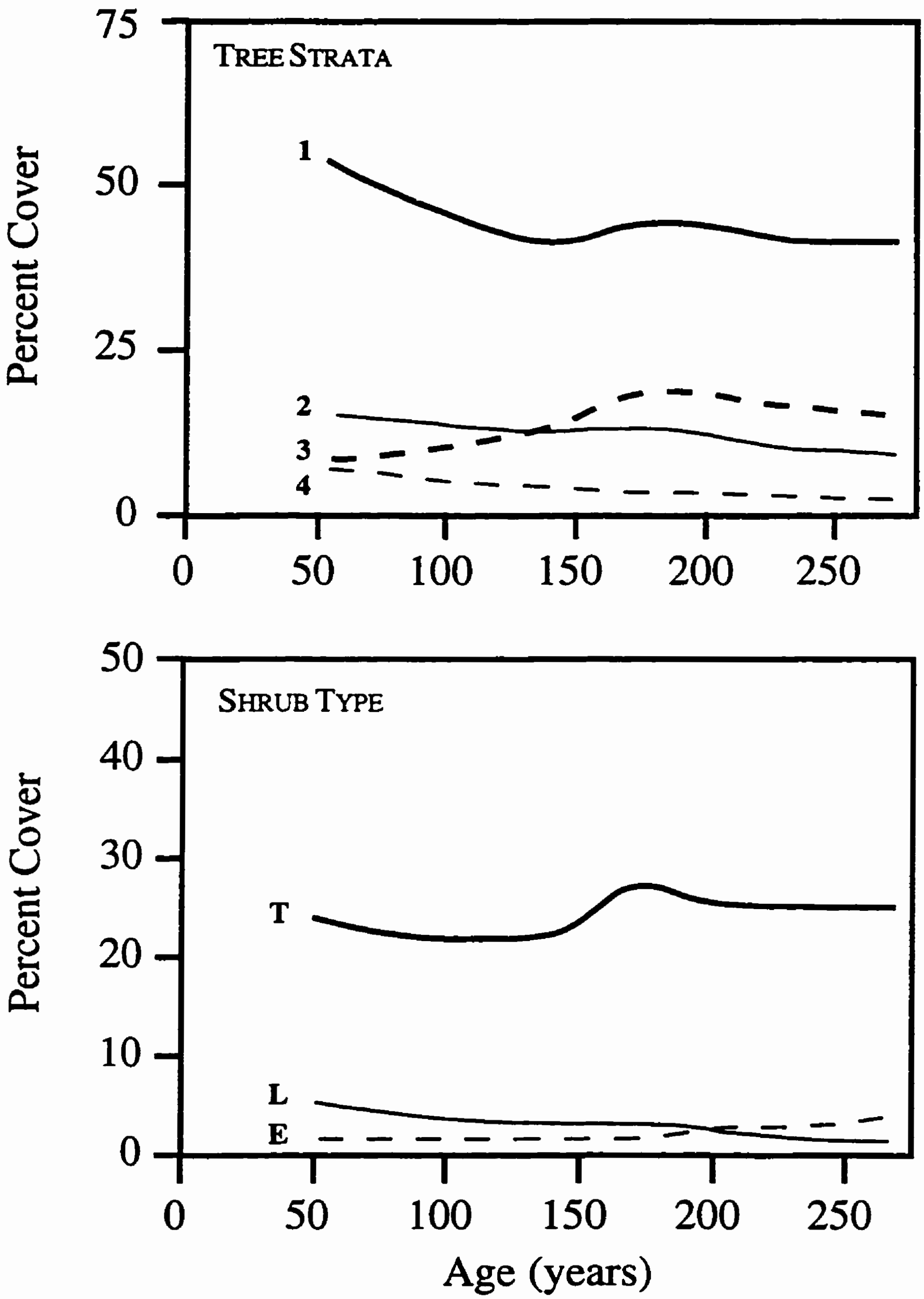


Figure 5.29. Changes in total tree cover by strata (codes: 1 = canopy; 2 = upper subcanopy; 3 = lower subcanopy; 4 = sapling layer) and shrub cover by shrub-type (codes: T = tall shrubs; L = low shrubs; E = ericaceous shrubs). Lines fitted using locally weighted regression analysis.

TABLE 5.17. Mean cover of tree species in stand-type IX by canopy strata (1-4), in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n* = 14					> 85 years *n* = 30				
		Total	1	2	3	4	Total	1	2	3	4
Pinus strobus	White Pine	48.64	39.14	9.14	0.21	0.14	33.67	31.80	0.60	0.70	0.57
Abies balsamea	Balsam Fir	20.07	0.29	7.07	9.29	3.43	13.10		4.10	6.80	2.20
Populus tremuloides	Trembling Aspen	11.07	8.86	1.43	0.14	0.64	2.57	1.93	0.07	0.23	0.33
Betula papyrifera	White Birch	8.00	3.14	3.07	1.50	0.29	4.63	1.53	2.23	0.63	0.23
Pinus resinosa	Red Pine	6.43	6.29		0.14		3.97	3.30	0.47	0.17	0.03
Thuja occidentalis	Eastern Cedar	5.64		0.43	2.57	2.64	4.03		2.90	0.87	0.27
Acer rubrum	Red Maple	5.29		0.36	3.43	1.50	5.20		0.67	3.83	0.70
Picea glauca	White Spruce	1.14		0.93		0.21	1.93	0.50	0.97	0.30	0.17
Picea mariana	Black Spruce	1.07		0.79		0.29	0.87	0.03	0.23	0.37	0.23
Populus grandidentata	Large-toothed Aspen	0.93	0.50	0.21	0.21						
Pinus banksiana	Jack Pine						0.10	0.07			0.03
Quercus macrocarpa	Bur Oak						0.07				0.07
Fraxinus pensylvanica	Green Ash						0.03			0.03	

TABLE 5.18. Frequency of tree species in stand-type IX by canopy strata, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n* = 14					> 85 years *n* = 30				
		Total	1	2	3	4	Total	1	2	3	4
Pinus strobus	White Pine	1.00	0.79	0.50	0.07	0.14	1.00	1.00	0.23	0.23	0.47
Abies balsamea	Balsam Fir	0.86	0.07	0.29	0.86	0.79	0.93		0.43	0.63	0.83
Populus tremuloides	Trembling Aspen	0.71	0.36	0.21	0.07	0.57	0.33	0.13	0.07	0.07	0.27
Betula papyrifera	White Birch	0.64	0.14	0.29	0.14	0.29	0.53	0.17	0.27	0.20	0.20
Pinus resinosa	Red Pine	0.36	0.36		0.07		0.47	0.40	0.10	0.10	0.03
Thuja occidentalis	Eastern Cedar	0.36		0.14	0.14	0.29	0.23		0.13	0.17	0.20
Acer rubrum	Red Maple	0.43		0.07	0.21	0.36	0.30		0.03	0.17	0.27
Picea glauca	White Spruce	0.29	0.00	0.14	0.00	0.21	0.37	0.13	0.13	0.13	0.13
Picea mariana	Black Spruce	0.14		0.07		0.14	0.27	0.03	0.07	0.13	0.17
Populus grandidentata	Large-toothed Aspen	0.21	0.07	0.14	0.07						
Pinus banksiana	Jack Pine						0.07	0.03			0.03
Quercus macrocarpa	Bur Oak						0.03				0.03
Fraxinus pensylvanica	Green Ash						0.03			0.03	

canopy. White pine regeneration increases as stands age, particularly over bedrock, where saplings occur in half the stands (**Tables 5.17, 5.18**).

Shrubs remain an important component of older stands. The tall shrub *Corylus cornuta* declines in cover. *Acer spicatum* cover increases, but this is largely attributable to high cover values in a few older stands. Most other tall shrub species also decline in cover. The low shrubs *Diervilla lonicera* and *Rubus strigosus* are much less frequent and abundant in older stands. Ericaceous shrubs remain a minor component of older stands and the most frequent and abundant (*Vaccinium* spp.) decline in cover. Total herb cover also declines over time. *Aster macrophyllus* and *Aralia nudicaulis* decrease in cover. Temporal changes in most other herb species are relatively minor. *Linnaea borealis* has the largest increase in both frequency and cover over time, but remains a relatively minor component. Cryptogams increase over time, but they remain a minor component. Both *Pleurozium schreberi* and *Dicranum polysetum* increase in frequency and cover. Other bryophyte species are uncommon at all ages. *Cladina* spp. increase in both frequency and cover over time, but lichens remain a minor component of the cryptogam layer (see **Appendix IX**).

Successional Variants

1. BEDROCK SITES (DEPTH TO BEDROCK < 2 M)

Total canopy cover is lower than the stand-type average, and balsam fir, white birch and trembling aspen are less frequent and abundant. Red pine cover is higher. Most stands have a pure white pine canopy, or a mixed canopy of white and red pine. Regeneration in the lower subcanopy and sapling layers is somewhat lower than the stand-type average. Balsam fir is occasionally encountered in the lower subcanopy. Balsam fir, trembling aspen, red maple, white birch, and eastern white cedar are found in the sapling layer in ca. 20% of younger stands. Shrub cover is similar to the stand-type as a whole, although *Diervilla lonicera* cover is higher. *Aster macrophyllus* and *Aralia nudicaulis* cover are lower than the stand-type mean, but *Maianthemum canadense* is more abundant. *Pleurozium schreberi* and *Dicranum polysetum* cover are slightly higher than the stand-type average.

These stands are characterized by a large decline in canopy cover over time. Older stands are characterized by an open canopy of white pine, with red pine as an occasional codominant. Black spruce and eastern white cedar are the most frequently encountered species in the subcanopy, but cover is low. Trembling aspen, white birch and red maple are less frequent in the sapling layer. Balsam fir is found less frequently in the sapling layer, and it rarely enters the subcanopy. White pine regeneration increases considerably over time: only 20% of younger stands contain white pine saplings, compared to >90% of the older stands. *Corylus cornuta* and *Acer spicatum* are often absent from older stands, or occur at low cover. *Diervilla lonicera* declines in both frequency and cover over time, while *Chimaphila umbellata* increases. *Juniperus communis* is more frequent and abundant in older stands. Herb cover declines over time, with the largest decreases occurring in *Maianthemum canadense*, *Cornus canadensis* and *Aster macrophyllus*. *Oryzopsis asperifolia* and *Polypodium vulgare* increase in frequency and cover over time. *Pleurozium schreberi* and *Dicranum polysetum* increase in frequency and cover, as do *Cladina* spp. The overall cryptogam abundance of older stands is much higher than the stand-type mean.

2. SITES WITH DEPTH TO BEDROCK > 2 M

Tree cover is somewhat higher than the stand-type mean, particularly in more mesic locations. Pure stands of white pine may be encountered, but more often the canopy is mixed. Trembling aspen, white birch, and/or balsam fir are common codominants on mesic sites, while red pine is more frequent in drier areas. White pine, balsam fir, and to a lesser extent white birch and red maple may be found in the subcanopy, sometimes at high cover. The lower subcanopy and sapling layers are dominated by balsam fir; other species are infrequent. Shrub composition and cover values are similar to the stand-type as a whole, although *Corylus cornuta* and *Diervilla lonicera* have lower cover. Herb composition is also similar, but *Aster macrophyllus* and *Aralia nudicaulis* have higher cover. Cryptogam cover is much lower than in the bedrock variant.

Succession in these stands is toward a canopy increasingly dominated by white pine, although most stands retain a somewhat mixed canopy. Red pine, trembling aspen and white birch decline in canopy cover as stands age. Balsam fir, white spruce, red maple, white birch and/or red pine occur in the subcanopy. The lower subcanopy and sapling layers are dominated by balsam fir, although eastern white cedar, white spruce, white birch and white pine are also encountered. Total tree cover remains high in older stands, but white pine cover increases at the expense of other species. *Acer spicatum* has a much higher cover in older stands, while *Corylus cornuta* shows a more modest increase. Other tall shrubs (e.g. *Amelanchier* spp., *Alnus crispa*) decline in cover over time. The low shrubs *Diervilla lonicera* and *Rubus parviflorus* are infrequent in older stands. Ericaceous shrubs also decline in cover, particularly *Vaccinium angustifolium*. Herb species cover also decreases over time, particularly *Aster macrophyllus*, *Aralia nudicaulis* and *Pteridium aquilinum*. Cryptogam cover increases over time but remains below the stand-type mean.

Discussion

The successional trajectory for this stand-type indicates that shade-intolerant species such as trembling aspen do not persist, while recruitment of balsam fir, white birch, white spruce and eastern white cedar increases as stands age. White pine regeneration is seen in most older stands, particularly on bedrock substrates. Because white pine is a large and very long-lived species (>500 years), it will remain an important canopy component over the long term. Open-canopy white pine stands on rapidly-drained substrates are probably self-regenerating, whereas more mesic, closed-canopy stands are increasingly dominated by a fir-spruce-birch mix. The understory of older stands is dominated by shrubs. Herb cover declines over time, but remains higher than cryptogam cover.

White pine is moderately shade-tolerant (more so than red pine, Wendel and Smith 1990), but does not regenerate well in closed-canopy stands (Carleton and Arnup 1993; Lowe 1994; Elliot and Vose 1995; Carleton et al. 1996). White pine saplings are adversely affected by competition from understory vegetation (Wendel and Smith 1990), but respond well to release in the first 30 years (Wendel and Smith 1990; Stiell et al. 1994). As with red pine, periodic light surface fires promote white pine regeneration (Heinselman 1973).

Seven hundred-year-old white pine stands near Temagami, Ontario are uneven-aged, indicating continuous recruitment (Quinby 1991). Stand recruitment is thought to be facilitated by local disturbances such as surface fires, windthrow, and mortality of mature individuals, casting doubt on the notion that a catastrophic fire is required to regenerate white pine stands (Quinby 1991). Similar results were obtained for white pine stands in northwestern Ontario (Holla and Knowles 1988). In northern Minnesota, older white pine stands in mesic habitats are characterized by a 'supercanopy' of relict white pine above a mixed fir-spruce-birch canopy (Heinselman 1973). Peterson and Squiers (1995) suggest that regional physiography and landform features are important factors determining succession trajectories in old-growth white pine forests (see also Horton and Bedell 1960). Stands on rapidly-drained sites succeed to a white pine-eastern hemlock mix, while more mesic sites are eventually dominated by balsam fir and eastern white cedar. In eastern North America, regenerating white pine stands are encountered on bedrock ridges and other habitats where occasional, light surface fires are favoured (Leak 1987). These observations suggest that white pine stands show landform-mediated differences in their successional pathways (c.f. Host et al. 1987).

5.3.10 Stand-Type X: Birch - Tall Shrub Mixed Wood

Stand-Type Description

Soil-Environment

These sites are typically dry and well-drained. The water table rarely occurs in the first 2 m of the soil profile, but distinct mottling occurs in over 40% of stands. Soils are generally coarse-textured, eluviated dystric Brunisols derived from morainal, glaciofluvial or lacustrine parent materials. Raw moder and fibrimor humus forms predominate, and organic matter depth averages 7.3 cm. Depth to bedrock is < 2m in about one-quarter of the sites, and terrain varies from gentle to steep slopes. Soils are moderately acidic and nutrient-deficient (TEB = 1.19, second lowest of all stand-types).

Vegetation

White birch is the canopy dominant in most stands, often in mixture with jack pine, trembling aspen and/or balsam fir (and more rarely, white and black spruce). White birch and balsam fir show strong regeneration in the subcanopy and sapling layers. Black spruce, white spruce and trembling aspen may also occur in the sapling layer, usually at low cover. *Acer spicatum* is ubiquitous and abundant in younger stands, averaging over 50% cover. *Corylus cornuta*, *Sorbus* spp., and *Amelanchier* spp. are also frequent but usually occur at low or occasionally moderate cover. The low shrub *Diervilla lonicera* is found in most stands at low to moderate cover. *Vaccinium* spp. occur in about half the stands at low cover.

The herb layer is quite species-rich. The most frequent and abundant species are *Clintonia borealis*, *Aralia nudicaulis*, *Lycopodium* spp. and *Aster macrophyllus*. *Cornus canadensis*, *Maianthemum canadense*, *Streptopus roseus* and *Trientalis borealis* are also frequent but occur at lower cover. Total cryptogam cover is low in most stands. The most frequent species are *Pleurozium schreberi* and *Dicranum polysetum*, which occur at low to moderate cover. Other species are much less frequent and abundant. Lichens are infrequent and occur at low cover when present.

Stand Dynamics

Summary

The oldest stand in this stand-type was 121 years and most were ≤ 85 years old. Since the age range for this stand-type is small, inferred successional trajectories are necessarily tentative. Stand succession is toward a more open, mixed canopy of white birch and balsam fir (**Fig. 5.30**). Balsam fir, and to a lesser extent white birch, regenerate well and are present in both the subcanopy and sapling layers of older stands. The decline in total shrubs cover (**Fig. 5.31, Fig. 5.32**) is mainly attributable to the decline in tall shrubs

Acer spicatum. Low and ericaceous shrubs remain a minor component of most stands. Total herb cover increases as shrub cover declines (**Fig. 5.31**), but composition changes little. The cover of most species increases, particularly members of the genus *Lycopodium*. Cryptogams remain a minor component of most stands (**Fig. 5.31**). Depth of the organic layer increases over time, and mineral soil pH declines. Trends for other variables are unclear due to a lack of replication in older stands (see **Appendix X**).

Vegetation

Total tree cover increases up to age 120, due primarily to increasing subcanopy cover (**Fig. 5.31**). Jack pine and trembling aspen decline in cover and are usually not present in older stands. Succession is toward an uneven-aged, mixed birch-balsam fir canopy, with white and black spruce forming a minor canopy-subcanopy component in some sites. White birch and balsam fir dominate the subcanopy and sapling layers of older stands. Older stands become more open over time, and resemble the dry, nutrient-poor variant of stand-type V.

The rapid decline of total shrub cover reflects increased canopy-subcanopy cover of balsam fir and other conifers (**Tables 5.19, 5.20**). This decline is largely attributable to decreased frequency and cover of the tall shrub *Acer spicatum*, and to a lesser extent *Corylus cornuta*. The low shrub *Diervilla lonicera* also declines in cover over time. Most other shrub species show no clear changes over time. Ericaceous shrubs remain a minor component of older stands. Total herb cover increases over time, particularly in the younger (≤ 85 years) stands. Large increases in cover are seen in *Lycopodium annotinum*, *Maianthemum canadense*, and *Cornus canadensis*. Overall species composition and diversity are invariant over time. Cryptogams remain a minor component of older stands. *Pleurozium schreberi* cover declines over time, but other bryophyte species show no clear trends. *Cladonia* spp. marginally increase in frequency and cover over time, but remain a minor component of the vegetation (see **Appendix X**).

X. Birch - Tall Shrub Mixed Wood

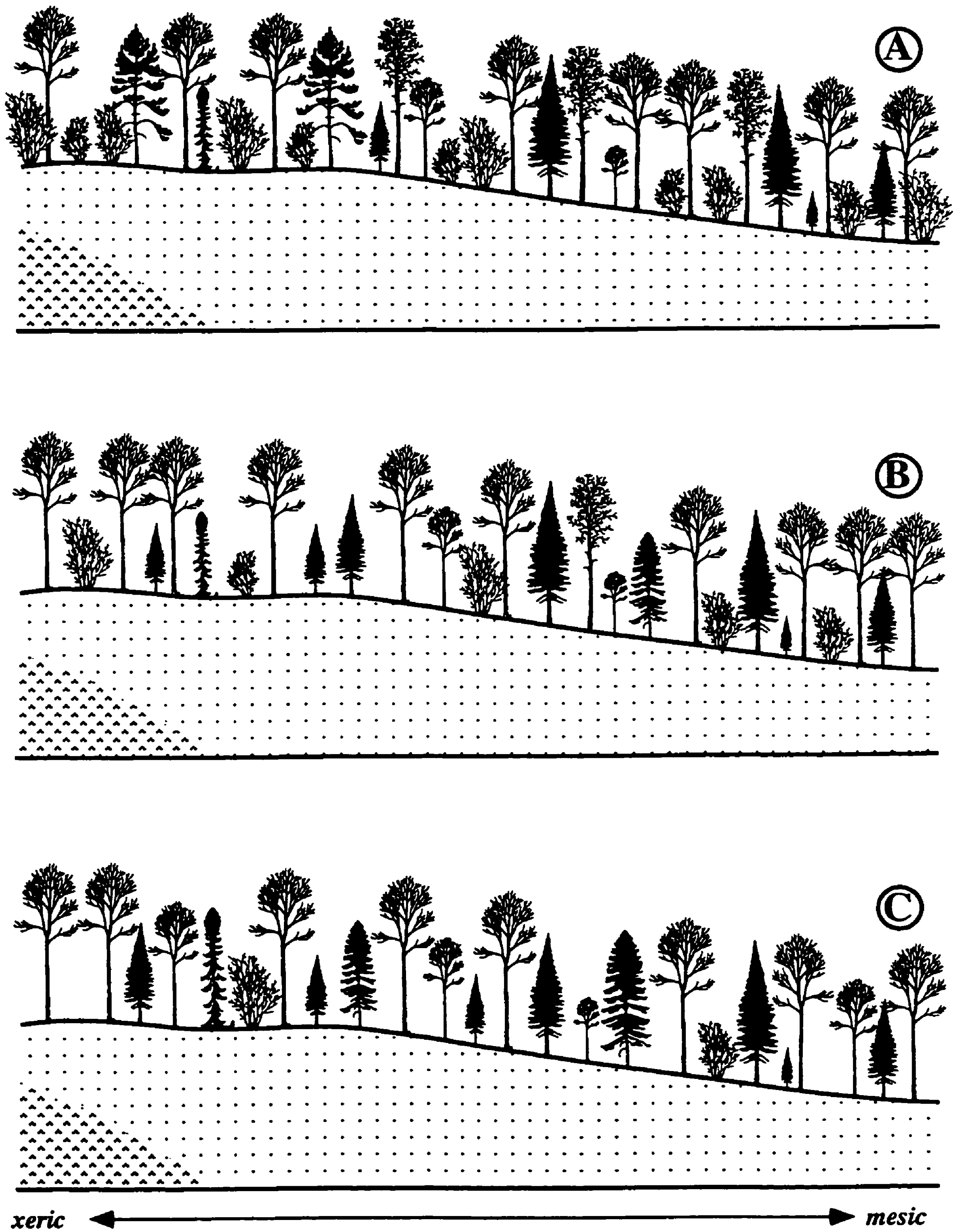


Figure 5.30. Successional trajectory based on mean tree canopy cover.
A = ≤ 85 years; B = 86-120 years; C = > 120 years.

X. Birch - Tall Shrub Mixed Wood

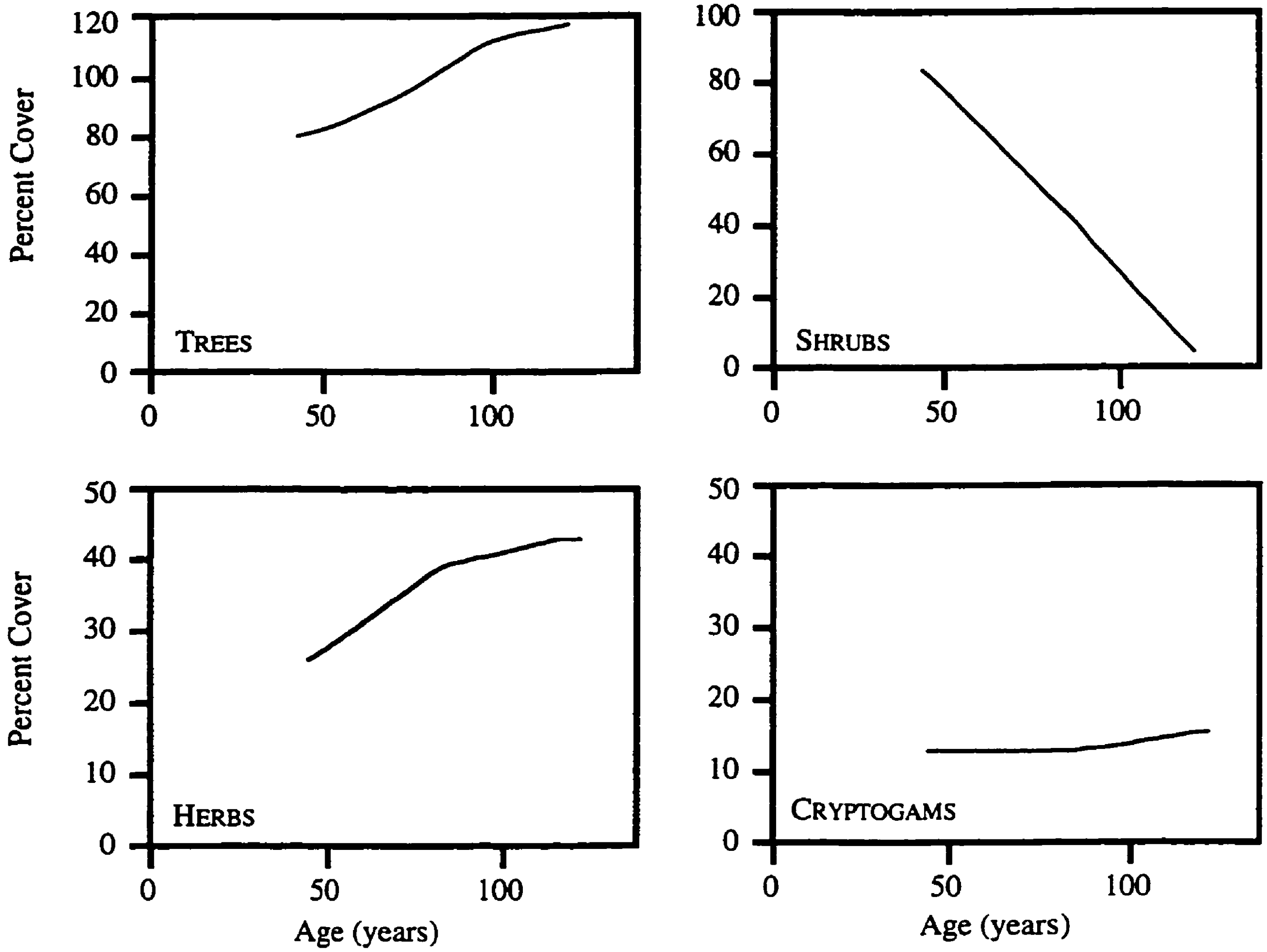


Figure 5.31. Changes in total tree, shrub, herb and cryptogam cover over time. Lines fitted using locally weighted regression analysis.

X. Birch - Tall Shrub Mixed Wood

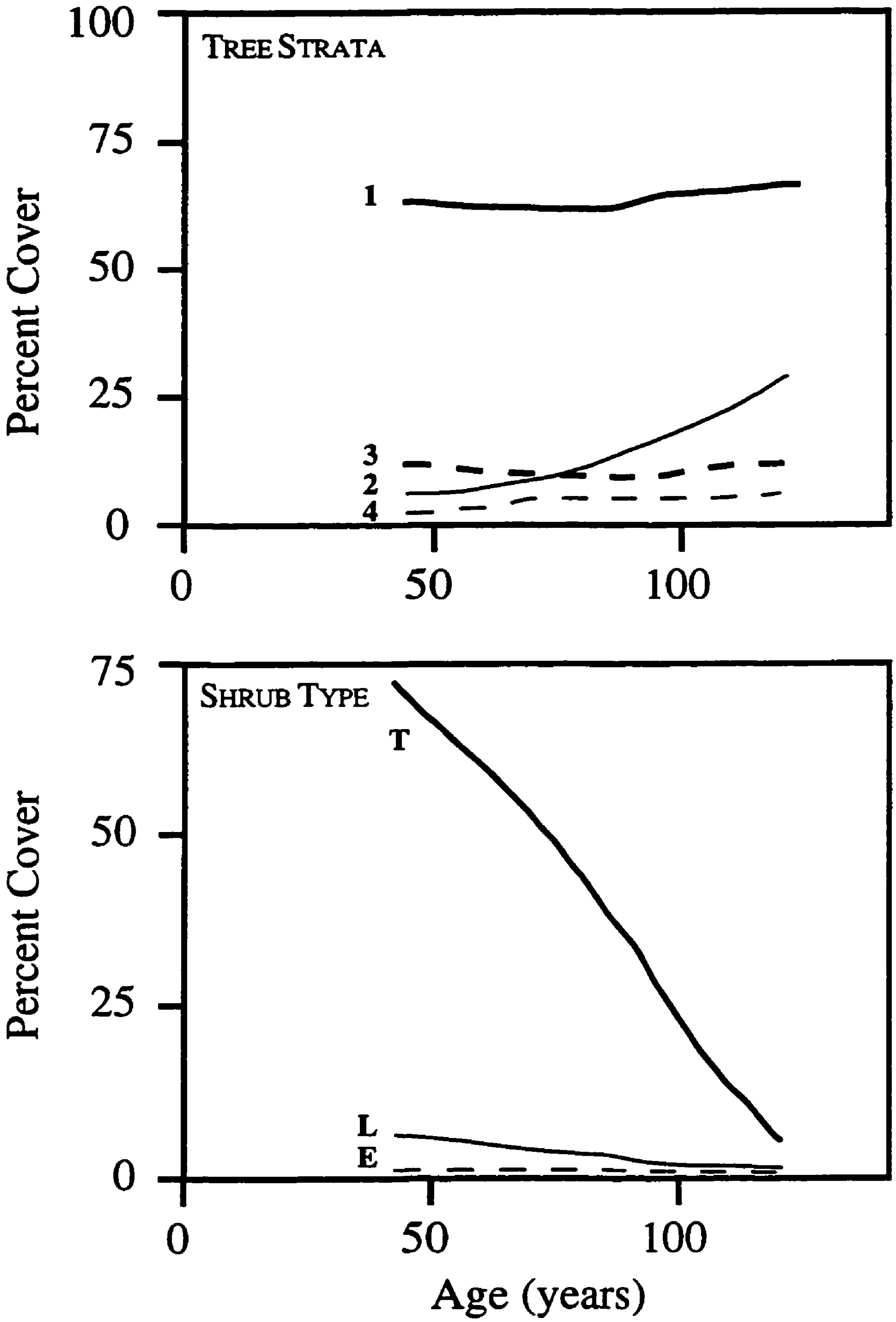


Figure 5.32. Changes in total tree cover by strata (codes: 1 = canopy; 2 = upper subcanopy; 3 = lower subcanopy; 4 = sapling layer) and shrub cover by shrub-type (codes: T = tall shrubs; L = low shrubs; E = ericaceous shrubs). Lines fitted using locally weighted regression analysis.

TABLE 5.19. Mean cover of tree species in stand-type X by canopy strata (1-4), in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n* = 26					> 85 years *n* = 17				
		Total	1	2	3	4	Total	1	2	3	4
Betula papyrifera	White Birch	41.39	31.81	3.77	5.00	0.81	63.24	55.77	6.65	0.35	0.47
Abies balsamea	Balsam Fir	17.46	8.08	4.31	3.65	1.42	42.59	4.53	16.94	15.06	6.06
Populus tremuloides	Trembling Aspen	12.92	12.27	0.08	0.12	0.46	3.47	0.29	2.94	0.12	0.12
Pinus banksiana	Jack Pine	6.73	6.58	0.15							
Picea mariana	Black Spruce	3.12	0.69	1.31	0.65	0.46	1.06	0.35	0.18		0.53
Picea glauca	White Spruce	1.73	0.62	0.23	0.77	0.12	3.71	2.12	1.29	0.18	0.12
Acer rubrum	Red Maple	0.19			0.19		0.35	0.29			0.06
Thuja occidentalis	Eastern Cedar	0.12				0.12	1.06	0.88			0.18
Fraxinus nigra	Black Ash	0.04				0.04					
Populus balsamifera	Balsam Poplar						0.18	0.18			
Pinus strobus	White Pine						0.06				0.06

TABLE 5.20. Frequency of tree species in stand-type X by canopy strata, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n* = 26					> 85 years *n* = 17				
		Total	1	2	3	4	Total	1	2	3	4
Betula papyrifera	White Birch	1.00	0.77	0.31	0.54	0.69	1.00	0.94	0.35	0.18	0.35
Abies balsamea	Balsam Fir	0.81	0.23	0.35	0.50	0.73	1.00	0.41	0.82	0.88	1.00
Populus tremuloides	Trembling Aspen	0.58	0.46	0.04	0.08	0.46	0.29	0.12	0.06	0.12	0.12
Pinus banksiana	Jack Pine	0.42	0.39	0.04							
Picea mariana	Black Spruce	0.46	0.15	0.19	0.19	0.31	0.41	0.06	0.06		0.35
Picea glauca	White Spruce	0.31	0.08	0.04	0.19	0.12	0.53	0.29	0.24	0.06	0.12
Acer rubrum	Red Maple	0.08			0.08		0.06	0.06			0.06
Thuja occidentalis	Eastern Cedar	0.08				0.08	0.06	0.06			0.06
Fraxinus nigra	Black Ash	0.04				0.04					
Populus balsamifera	Balsam Poplar						0.06	0.06			
Pinus strobus	White Pine						0.06				0.06

Successional Variants

1. Dry Sites (Moisture Regime < 3)

These stands are dominated by white birch, but jack pine and trembling aspen are also frequently encountered. Black spruce cover is higher than the stand-type mean, while balsam fir cover is lower. Shrub composition and cover are similar to the stand-type means. This is also true of the herb layer, although *Aralia nudicaulis* has higher cover while *Lycopodium* spp. is lower. *Pleurozium schreberi* cover is higher than the stand-type mean.

The successional trajectory for this variant is similar to the stand-type as a whole. Jack pine and trembling aspen decline in cover over time, while balsam fir, black spruce and white spruce become more abundant. Older stands are dominated by white birch in the canopy, and by a mixture of white birch, balsam fir, and black and white spruce in the subcanopy. The latter two species may enter the canopy of the oldest stands. The sapling layer is dominated by balsam fir, black spruce and white birch. Temporal changes in the shrub, herb and cryptogam layers are very similar to the stand-type.

2. Mesic Sites (Moisture Regime ≥ 3)

This variant is characterized by higher cover of balsam fir and trembling aspen, and lower cover of jack pine, black spruce and white spruce. Balsam fir and white birch dominate the lower subcanopy and sapling layers. Shrub species composition and cover are typical of the stand-type. Herb composition and cover are also similar, although *Aralia nudicaulis* cover is lower, and *Lycopodium* spp. cover higher, than the stand-type means. Cryptogram cover is low, due primarily to low cover of *Pleurozium schreberi*. *Callicladium haldanium* is present in most stands, but occurs at low cover.

Trembling aspen cover declines over time. Older stands have a mixed canopy of white birch and balsam fir, and occasionally white spruce. White birch and balsam fir are commonly encountered in the subcanopy and sapling layers, indicating strong regeneration. Canopy cover is higher than the stand-type average. Changes in the shrub and herb layers are similar to the stand-type as a whole. Cryptogam cover remains low in older stands.

Discussion

The successional trajectory for this stand-type indicates a decline in shade-intolerant species (jack pine, trembling aspen), and a corresponding increase in balsam fir and white spruce. Tall shrub cover (particularly *Acer spicatum*) declines as the more shade-tolerant conifers invade. The understory is dominated by herbaceous species, while cryptogams are a minor component. Succession toward a herb-rich, mixed forest of white birch, balsam fir and white spruce is indicated. White birch will likely persist in these stands, due to its ability to resprout and seed into canopy gaps. The high cover of *Acer spicatum* in young stands may be indicative of past human disturbance (Farrar 1995).

White birch is a fast-growing, shade-intolerant pioneer species (Dix and Swan 1971). Seeds are wind-dispersed and readily germinate on both organic and mineral substrates. White birch is easily killed by fire, but resprouts from root collars provided that the fire is not too intense (Safford et al. 1990). Pure stands are most commonly encountered on stony, well-drained, moist sites. White birch litter decomposes quickly relative to conifer needles (Foster and King 1986).

Succession in white birch stands is toward a mixed forest of balsam fir and/or white spruce (Carleton and Maycock 1980; Pastor and Mlandenoff 1992; Foster and King 1986), although white birch often persists in older stands (Cogbill 1985). This persistence is explained in part by the resprouting ability of white birch (Buell and Neiring 1957; Heinselman 1973). In addition, the species readily seeds into canopy gaps created by intermediary disturbances (Frelich and Reich 1995a,b; Kneeshaw and Bergeron 1996). In Labrador, white birch is most frequently encountered on slopes and valleys where fire frequency and intensity are comparatively low (Foster and King 1986). These fire-protected stands serve as an important seed source for adjacent post-fire stands.

5.3.11 Stand-Type XI: Balsam Poplar

Stand-Type Description

Soil-Environment

These stands are generally nutrient rich, pH-neutral (mean pH = 6.9) and moist-wet. Depth to water table is < 2 m in many sites, and most soil profiles show distinct mottling. Organic matter accumulation is high (mean = 18 cm). Humus forms are predominantly fibrimors and moders, but humimors also occur. Fine-textured Brunisolic or Gleysolic soils predominate, but Luvisols and Podzols may also be encountered. Most stands occur on lacustrine deposits, but morainal, glaciofluvial and fluvial parent materials also occur. Depth to bedrock is generally > 2 m, and most stands occur on flats or gentle slopes.

Vegetation

Balsam poplar is the dominant canopy species in most sites. It may form pure stands, but usually occurs in mixture with balsam fir, trembling aspen, black spruce, white spruce, white birch and/or eastern white cedar. Balsam fir, white spruce and black spruce are generally restricted to the subcanopy. The most frequently encountered species in the lower subcanopy and sapling layers are balsam poplar, balsam fir, white spruce, white birch and eastern white cedar. Black ash and black spruce occur occasionally. Tall shrubs are frequently encountered and are moderately abundant. *Cornus stolonifera* has the highest frequency and cover. *Alnus rugosa* and *Acer spicatum* are present in about half the stands at moderate to high cover. *Ribes* spp. are ubiquitous but usually occur at low cover. The low shrubs *Rosa acicularis*, *Rubus strigosus* and *Lonicera* spp. occur in over half the stands. Ericaceous shrubs are infrequent and occur at very low cover in these stands.

The herb layer is very diverse and total cover is moderately high. *Rubus pubescens*, *Mitella nuda*, *Aralia nudicaulis*, *Aster macrophyllus*, and *Carex* spp. are frequent and occur at moderate cover. Other frequently encountered species include *Actaea rubra*, as well as members of the genera *Galium*, *Viola*, *Petasites*, *Fragaria* and *Equisetum*. *Calamagrostis canadensis* and *Streptopus roseus* are somewhat less frequently encountered, but often occur at moderate cover when present. Ferns and fern-allies are common compared to other stand-types. Cryptogams are a minor component of these stands, although species richness is quite high. *Pleurozium schreberi* is the most frequently encountered species, but cover is low. Lichens are infrequent and occur at low cover when present.

Stand Dynamics

Summary

As succession proceeds, balsam poplar is increasingly replaced by coniferous species in the canopy and subcanopy. Stands are become increasingly open, multi-tiered and uneven-aged (**Fig. 5.33**). Regeneration is primarily balsam fir, balsam poplar and/or white birch. Total shrub cover declines over time (**Fig. 5.34**), in large part attributable to declines in frequency and cover of tall shrubs (primarily Cornus *stolonifera*) and low shrubs (**Fig. 5.35**). The herb layer remains floristically diverse, although cover of most species declines over time. Frequency and cover of most cryptogam species increase as stands age, but overall cover remains low to moderate. Few clear changes in soil-environmental variables are apparent. Mineral soil pH increases slightly, while organic pH declines. Nutrient status remains comparatively high (see **Appendix XI**).

Vegetation

Total tree cover increases to age 100 and then begins to decline (**Fig. 5.34**). Canopy diversity increases as stands age. Canopy cover declines slightly over time, but is largely matched by increasing subcanopy cover (**Fig. 5.35**). A multi-tiered, uneven-aged forest canopy increasingly dominated by white spruce, eastern white cedar, balsam fir and black spruce develops over time. Balsam poplar frequency and cover decline over time (**Tables 5.21, 5.22**). Although balsam poplar saplings are frequently encountered in older stands, they seldom enter the canopy-subcanopy. Balsam fir is usually restricted to the subcanopy of older stands, whereas white spruce, black spruce and eastern white cedar occur in the canopy. Balsam fir, balsam poplar, white birch and white spruce are frequently

XI. Balsam Poplar

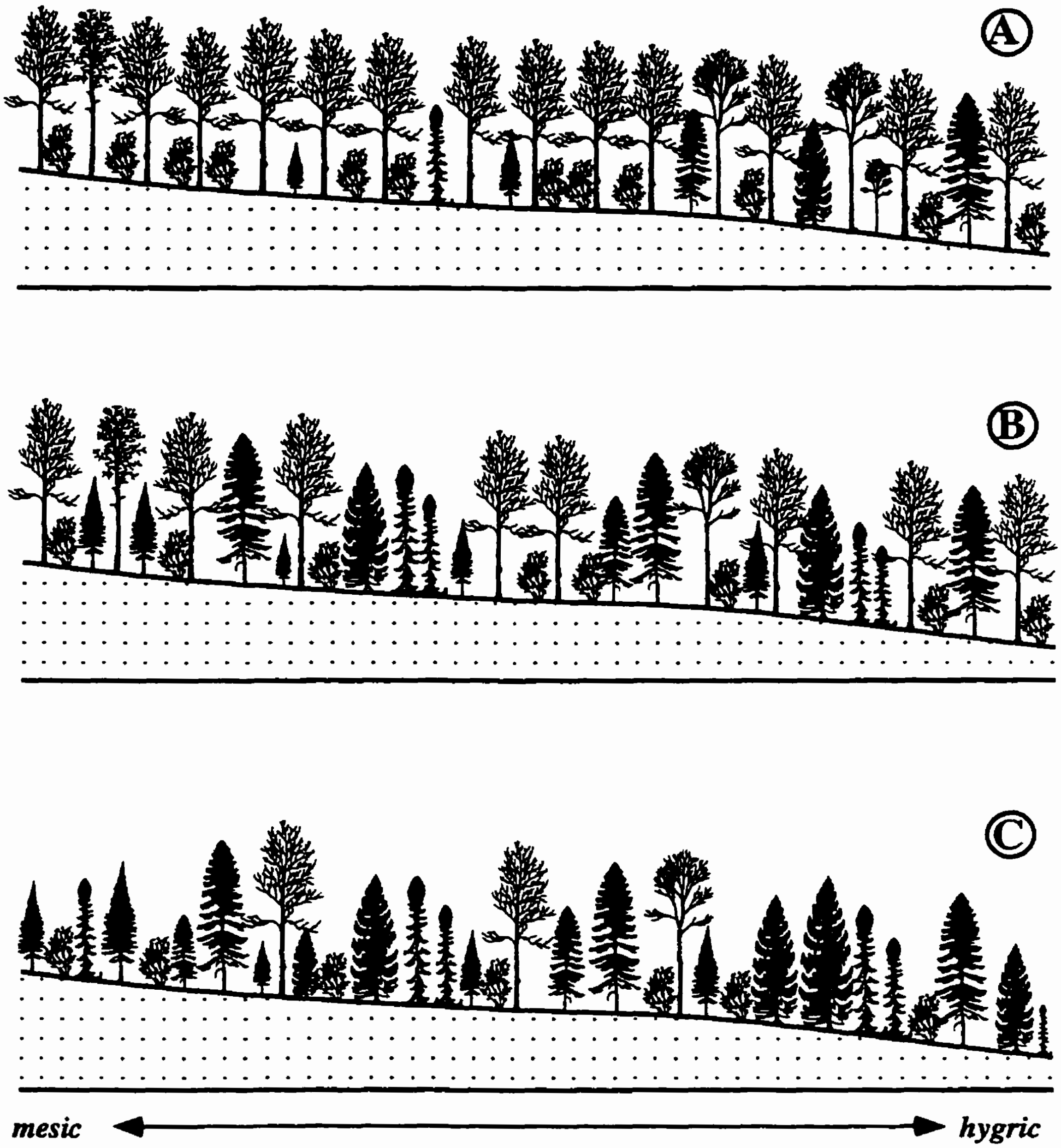


Figure 5.33. Successional trajectory based on mean tree canopy cover.
A = ≤ 85 years; B = 86-120 years; C = > 120 years.

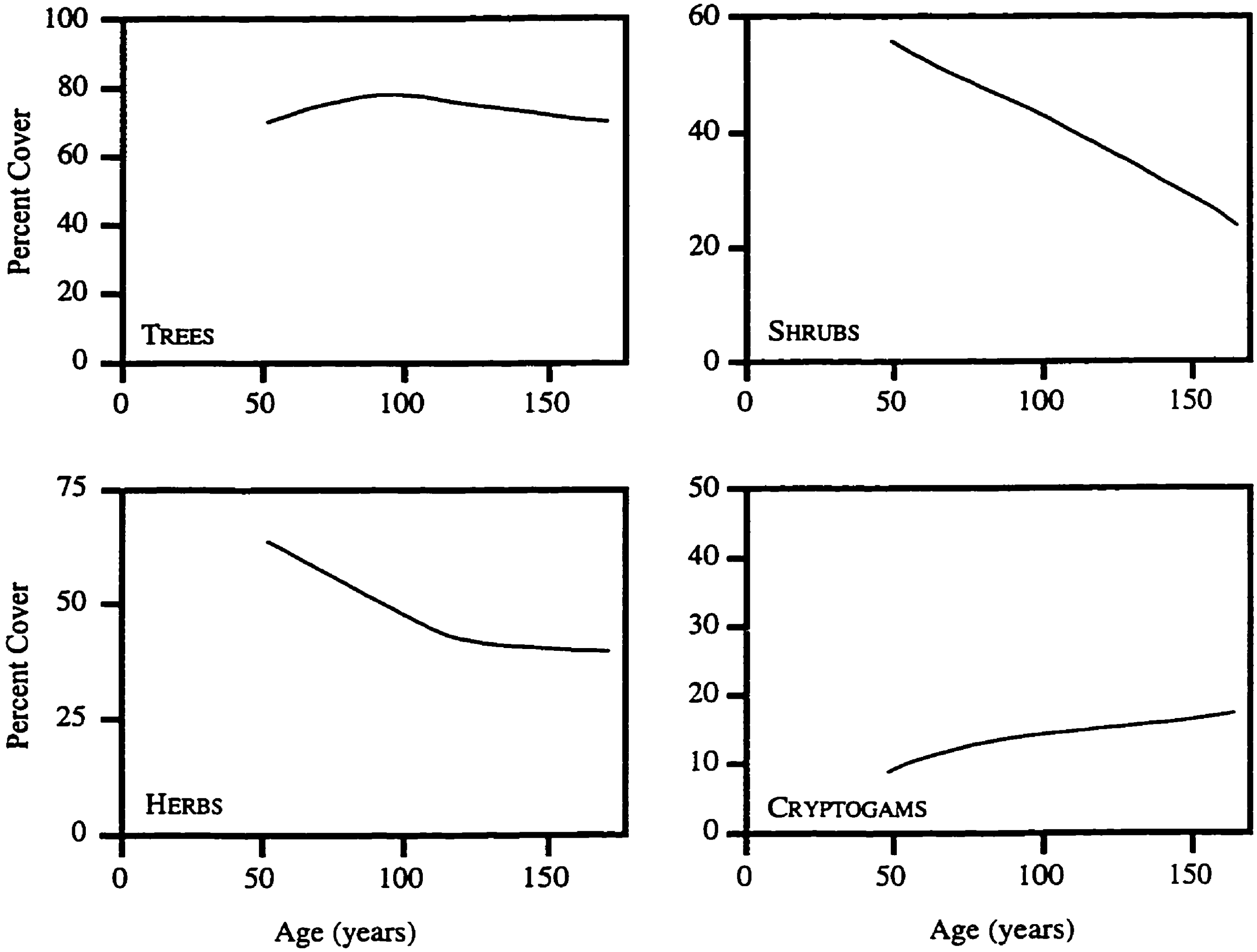


Figure 5.34. Changes in total tree, shrub, herb and cryptogam cover over time. Lines fitted using locally weighted regression analysis.

XI. Balsam Poplar

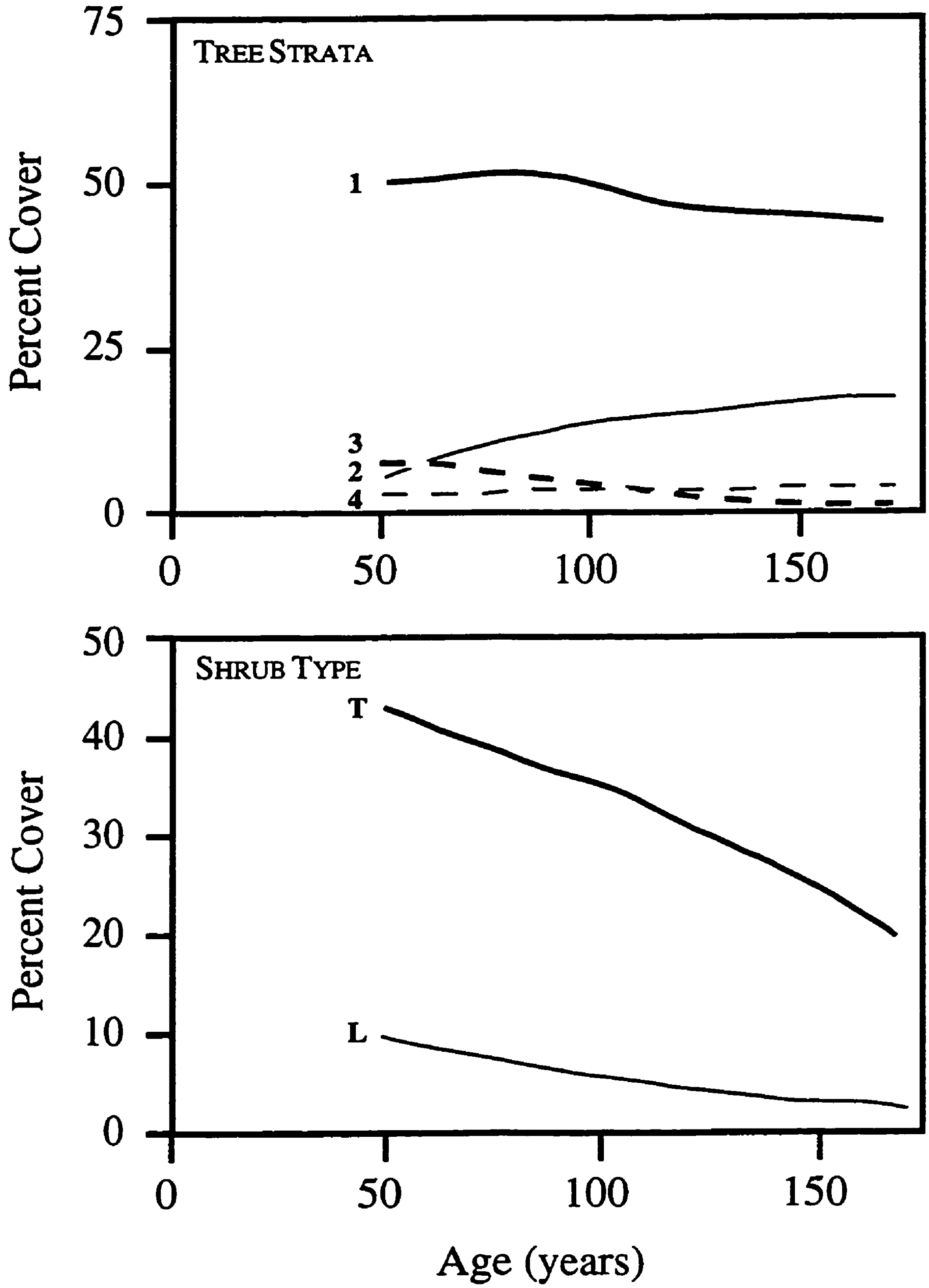


Figure 5.35. Changes in total tree cover by strata (codes: 1 = canopy; 2 = upper subcanopy; 3 = lower subcanopy; 4 = sapling layer) and shrub cover by shrub-type (codes: T = tall shrubs; L = low shrubs; E = ericaceous shrubs). Lines fitted using locally weighted regression analysis.

TABLE 5.21. Mean cover of tree species in stand-type XI by canopy strata (1-4), in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	> 85 years					> 85 years				
		n = 17					*n = 20*				
		Total	**1**	**2**	**3**	**4**	**Total**	**1**	**2**	**3**	**4**
Populus balsamifera	Balsam Poplar	40.53	39.00	0.47	0.24	0.82	29.10	27.30	0.65	0.45	0.70
Abies balsamea	Balsam Fir	6.77		1.53	2.88	2.35	15.90	2.45	9.60	2.55	1.30
Betula papyrifera	White Birch	6.53	4.77		1.29	0.47	4.55	1.45	2.60	0.15	0.35
Picea glauca	White Spruce	6.29	2.59	2.59	0.71	0.41	9.25	7.90	1.00	0.05	0.30
Picea mariana	Black Spruce	5.59	1.59	2.59	1.24	0.18	5.60	4.15	1.30		0.15
Populus tremuloides	Trembling Aspen	4.41	2.71	0.71	0.65	0.35	4.75	3.35	0.95	0.25	0.20
Thuja occidentalis	Eastern Cedar	3.00	1.18	0.71	0.24	0.88	10.25	4.35	5.35	0.35	0.20
Fraxinus nigra	Black Ash	1.65			0.65	1.00	0.90		0.60	0.20	0.10
Pinus banksiana	Jack Pine	0.59	0.06	0.53			0.45	0.35	0.10		
Larix laricina	Eastern Larch	0.24	0.24								
Fraxinus pensylvanica	Green Ash						0.05				0.05
Pinus strobus	White Pine						0.05				0.05
Quercus macrocarpa	Bur Oak						0.05				0.05

TABLE 5.22. Frequency of tree species in stand-type XI by canopy strata, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	> 85 years					> 85 years				
		n = 17					*n = 20*				
		Total	**1**	**2**	**3**	**4**	**Total**	**1**	**2**	**3**	**4**
Populus balsamifera	Balsam Poplar	1.00	0.94	0.18	0.12	0.71	1.00	1.00	0.20	0.20	0.70
Abies balsamea	Balsam Fir	0.77		0.29	0.53	0.65	0.80	0.20	0.45	0.55	0.75
Betula papyrifera	White Birch	0.41	0.18		0.12	0.35	0.55	0.10	0.40	0.05	0.35
Picea glauca	White Spruce	0.59	0.12	0.35	0.29	0.35	0.55	0.50	0.15	0.05	0.30
Picea mariana	Black Spruce	0.41	0.12	0.35	0.18	0.18	0.35	0.30	0.15		0.15
Populus tremuloides	Trembling Aspen	0.65	0.35	0.06	0.24	0.29	0.45	0.25	0.15	0.15	0.20
Thuja occidentalis	Eastern Cedar	0.29	0.06	0.06	0.12	0.29	0.25	0.10	0.20	0.10	0.10
Fraxinus nigra	Black Ash	0.12			0.06	0.12	0.10		0.10	0.10	0.10
Pinus banksiana	Jack Pine	0.12	0.06	0.06			0.15	0.10	0.05		
Larix laricina	Eastern Larch	0.06	0.06								
Fraxinus pensylvanica	Green Ash						0.05				0.05
Pinus strobus	White Pine						0.05				0.05
Quercus macrocarpa	Bur Oak						0.05				0.05

encountered in the subcanopy and sapling layers of older stands. The oldest stands usually have a mixed-conifer canopy with white birch and the occasional relict balsam poplar.

Total shrub cover declines over time. This decrease is largely attributable to lower frequency and cover of *Cornus stolonifera* and *Salix* spp. Other common tall shrub species (e.g. *Alnus rugosa*, *Acer spicatum*) are equally frequent and abundant in younger and older stands. Most common low shrub species (e.g. *Ribes* spp., *Rosa acicularis*, *Rubus strigosus* and *Lonicera* spp.) decrease in frequency and cover over time. Ericaceous shrubs remain a very minor component of the vegetation. Total herb cover declines over time. Most species decrease slightly in cover, but overall richness of the herb layer remains high. *Calamagrostis canadensis*, a common species in some young stands, is rare in older stands. *Equisetum* spp. have much higher mean cover in older stands. Total cover of bryophytes increases over time, but they remain a relatively minor component of the vegetation. *Pleurozium schreberi* shows the largest increase in cover. Lichens remain infrequent and occur at very low cover in older stands.

Successional Variants

1. SITES WITH DEPTH TO WATER TABLE > 2 M

Tree cover is similar to the stand-type mean. Balsam fir and trembling aspen are somewhat more abundant, while white birch and eastern white cedar are less abundant. Balsam fir is also more common in the lower subcanopy and sapling layers. *Acer spicatum* is more frequent and abundant, but otherwise shrub cover is similar to the stand-type mean. Species composition and cover in the herb and cryptogam layers are also similar.

The successional trajectory for this variant is very similar to that of the stand-type. Balsam fir is somewhat more common in the canopy, subcanopy and sapling layers. *Acer spicatum* and *Alnus rugosa* decrease in frequency and cover. Temporal trends in the herb and cryptogam layers are similar to the stand-type.

2. SITES WITH DEPTH TO WATER TABLE < 2 M

Trembling aspen, white birch and eastern white cedar are more abundant in this variant, while trembling aspen and balsam fir are less common. The subcanopy and sapling layers are dominated by balsam fir, black spruce and white spruce. Species composition and cover in the shrub, herb and cryptogam layers are similar to the stand-type as a whole.

Eastern white cedar, black spruce and white spruce dominate the canopy of older stands, although white birch and balsam fir may also be present. Relict balsam poplar trees may also be present. Temporal trends in the shrub, herb and cryptogam layers are similar to the stand-type as a whole.

Discussion

The successional trajectory for this stand-type indicates increased dominance of coniferous tree species over time. Very moist sites are invaded by white spruce, black spruce and eastern white cedar, while balsam fir and white birch are also present in better-drained sites. Shrub and herb cover declines over time, but they remain the dominant understory species in older stands. Cryptogam cover increases as the conifers invade.

Balsam poplar is a short-lived, shade-intolerant pioneer species that prefers moist, nutrient-rich soils (Zasada and Phipps 1990). It may reproduce vegetatively from suckers, but these are often short-lived since they are highly shade-intolerant. Balsam poplar is normally a minor component of stands >100 years of age (Zasada and Phipps 1990). Post-fire regeneration is by suckering and seed germination. Balsam poplar is a preferred summer browse by ungulates, and is utilized by beaver.

In absence of disturbance, balsam poplar stands are succeeded by white and black spruce, and balsam fir (Dix and Swan 1971). In Ontario, older stands are invaded mainly by white spruce, although balsam fir may also be important in drier sites (Carleton and Maycock 1978). On Alaskan floodplains, balsam poplar is succeeded by white spruce (van Cleve et al. 1993).

5.3.12 STAND-TYPE XII: BLACK ASH

Stand-Type Description

Soil-Environment

These sites are wet-moist. Depth to water table is < 2 m in most stands, and soil profiles show distinct mottling. Organic matter accumulation is considerable (mean depth = 42 cm), but varies considerably between stands. Peatymor humus forms predominate, but mulls and moders also occur. Soils are either Gleysols (occasionally Brunisols) derived from lacustrine or fluvial materials, or Organics. Soil texture varies: about half the stands occur on hard clay, the other half on clay loam. Depth to bedrock is generally > 2 m, and the terrain is always flat. Nutrient status is very high relative to the other stand-types. Soils are slightly acidic (mean pH of mineral soil = 6.0).

Vegetation

Total tree cover in these stands is high. Black ash dominates the canopy, often occurring in pure stands. White birch and balsam poplar are occasional canopy codominants. Black ash shows strong regeneration in the subcanopy and sapling layers. Balsam fir and white spruce are also commonly encountered in the sapling layer, while balsam poplar, white birch, trembling aspen and eastern white cedar are occasional. Tall shrubs are frequent and relatively abundant in these stands. *Acer spicatum* and *Alnus rugosa* are common, generally at moderate (occasionally high) cover. *Corylus cornuta* is also frequent but occurs at lower cover. *Ribes* spp. are ubiquitous in these stands, but usually occur at low cover.

Herb species richness and total cover are high. *Carex* spp. (mainly *C. disperma* and *C. vaginata*) are ubiquitous and usually occur at moderate (occasionally high) cover. *Rubus pubescens*, *Galium triflorum* and *Viola* spp. are also ubiquitous, but are usually found at low cover. Other frequently encountered species include *Athyrium felix-femina*, *Equisetum* spp., *Aster macrophyllus*, *Mitella nuda*, *Circaea alpina*, *Streptopus roseus*, *Asarum canadense*, *Caltha palustris* and *Dryopteris* spp. Cryptogam cover is low to moderate. The most frequently encountered bryophytes are *Climacium dendroides* and *Plagiomnium* spp., both of which have low cover. The genera *Thuidium*, *Calliergon* and *Brachythecium* are less frequent but may occur at moderate cover when present. Lichens are infrequent and occur at low cover when present. *Peltigera* spp. occur in about one-quarter of the plots.

Stand Dynamics

Summary

Successional trajectories indicate continued dominance of black ash in the canopy-subcanopy. Over time these stands become more open, multi-tiered and uneven-aged (**Fig. 5.36**). Regeneration is predominantly black ash, although balsam fir and eastern white spruce also regenerate well. The decline in total shrub cover over time is largely attributable to lower cover of tall shrubs (**Figs. 5.37, 5.38**). The herb layer of older stands remains species-rich, but total herb cover declines (**Fig. 5.37**). Cryptogam cover increases to age 100 and then declines (**Fig. 5.37**). Organic matter depth increases over time, but varies considerably between stands. The mineral and organic layers become slightly more acidic as stands age. Nutrient availability (as measured by TEB) declines over time, but values are highly variable. Incorporation of organic matter into the mineral horizon also increases over time (see **Appendix XII**).

Vegetation

Total tree cover begins to decline after age 100 (**Fig. 5.37**). This is largely attributable to declining canopy cover, which is offset somewhat by increased subcanopy cover. This trend indicates that stands are becoming more open, multi-tiered and uneven-aged as succession proceeds. Black ash regenerates well, and continues to dominate the canopy-subcanopy of older stands (**Tables 5.23, 5.24**). Birch and trembling aspen, which occurs as occasional canopy codominant in younger stands, are replaced by eastern white cedar and white spruce in older stands. Balsam fir also increases in cover over time, but it is restricted to the subcanopy and sapling layers. The lower subcanopy and sapling layers of older stands are dominated by black ash, although balsam fir, white spruce, white elm and eastern white cedar are also frequently encountered.

XII. Black Ash

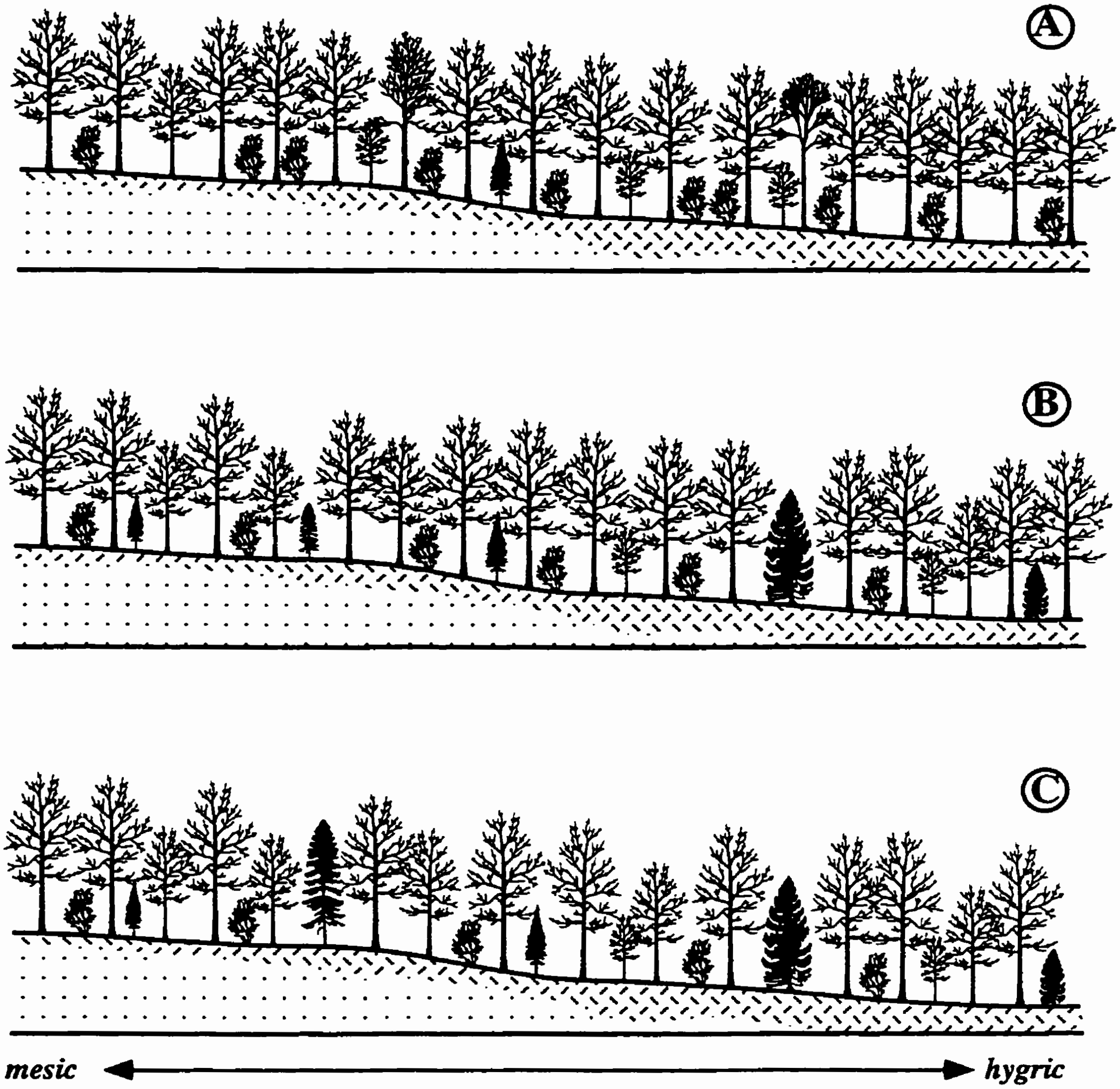


Figure 5.36. Successional trajectory based on mean tree canopy cover.
A = ≤ 85 years; B = 86-120 years; C = > 120 years.

XII. Black Ash

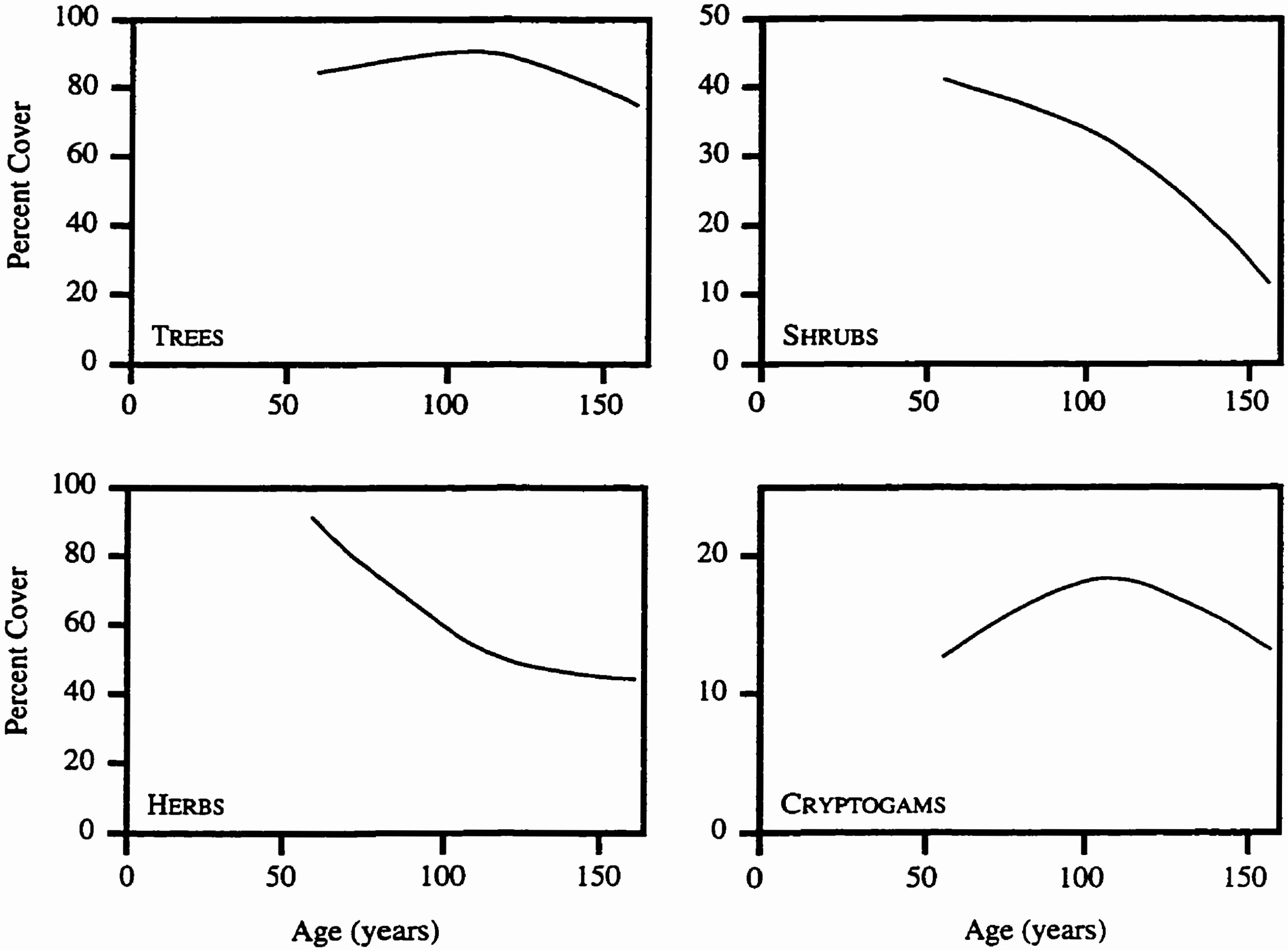


Figure 5.37. Changes in total tree, shrub, herb and cryptogam cover over time. Lines fitted using locally weighted regression analysis.

XII. Black Ash

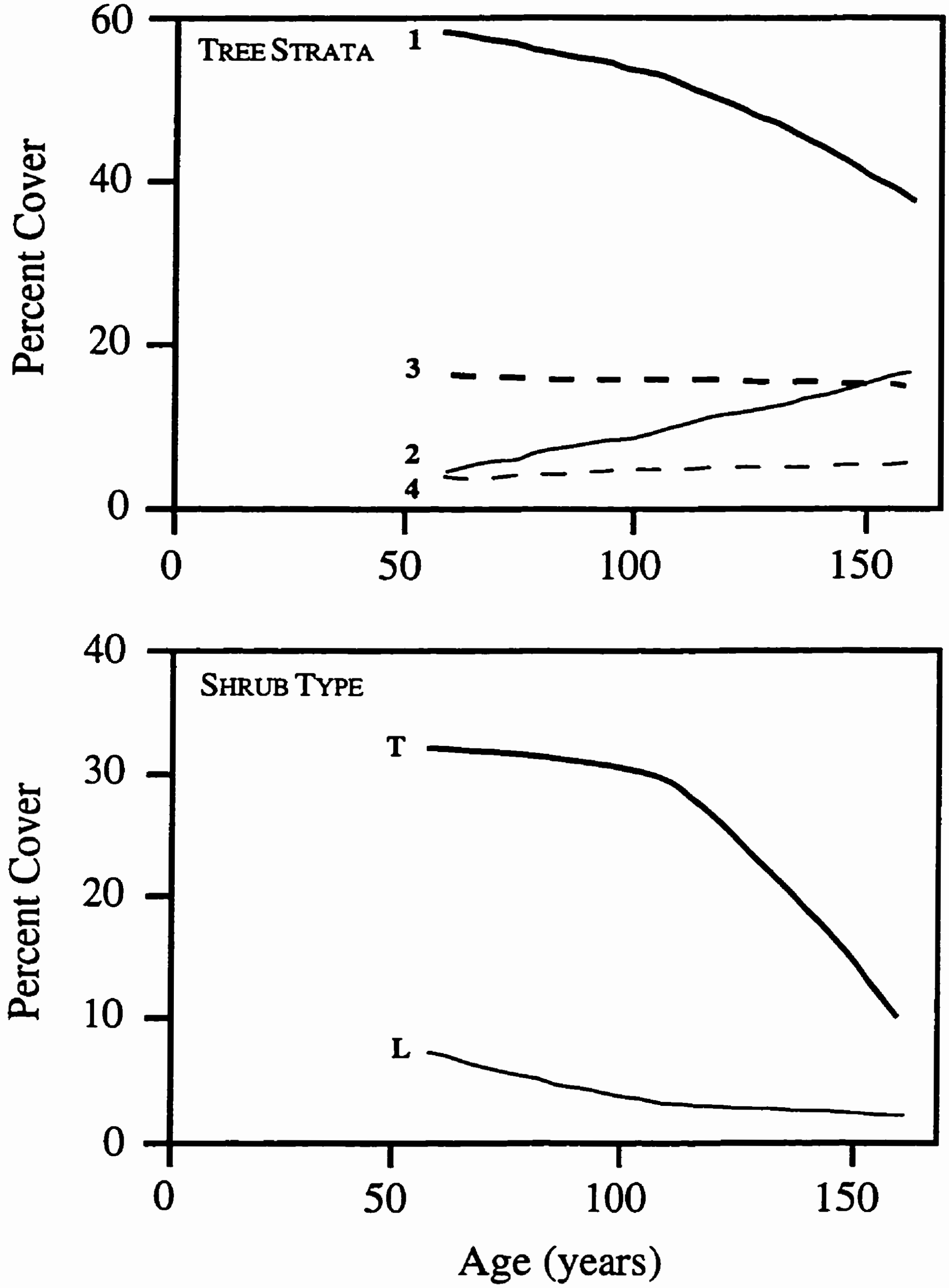


Figure 5.38. Changes in total tree cover by strata (codes: 1 = canopy; 2 = upper subcanopy; 3 = lower subcanopy; 4 = sapling layer) and shrub cover by shrub-type (codes: T = tall shrubs; L = low shrubs; E = ericaceous shrubs). Lines fitted using locally weighted regression analysis.

TABLE 5.23. Mean cover of tree species in stand-type XII by canopy strata (1-4), in younger (≤ 85 years) and older (> 85 years) stands.

Species	**Common Name**	**≤ 85 years** *n = 9*					**> 85 years** *n = 15*				
		Total	**1**	**2**	**3**	**4**	**Total**	**1**	**2**	**3**	**4**
Fraxinus nigra	Black Ash	64.67	49.33	4.00	10.22	1.11	56.40	41.20	7.40	6.67	1.13
Abies balsamea	Balsam Fir	7.00	0.11	1.78	4.00	1.11	4.47		1.20	1.93	1.33
Betula papyrifera	White Birch	3.89	3.56			0.33	0.87	0.47		0.20	0.20
Populus balsamifera	Balsam Poplar	3.22	2.33	0.11	0.33	0.44	0.87	0.73		0.07	0.07
Picea glauca	White Spruce	3.00	0.89		1.33	0.78	3.47		0.93	1.87	0.67
Ulmus americana	White Elm	1.44			1.33	0.11	7.60	1.40	1.60	4.00	0.60
Thuja occidentalis	Eastern Cedar	1.33		0.89	0.33	0.11	6.80		6.00	0.33	0.47
Populus deltoides	Eastern Cottonwood	0.89	0.89								
Populus tremuloides	Trembling Aspen	0.44	0.11		0.11	0.22	1.67	1.67			
Fraxinus pennsylvanica	Green Ash						2.40	1.87	0.27	0.20	0.07
Betula allaghaniensis	Yellow Birch						1.13		1.00	0.07	0.07
Picea mariana	Black Spruce						0.67	0.47		0.20	
Acer rubrum	Red Maple						0.47			0.07	0.40
Acer negundo	Manitoba Maple						0.33		0.27		0.07
Quercus macrocarpa	Bur Oak						0.13				0.13
Larix laricina	Eastern Larch						0.07			0.07	

TABLE 5.24. Frequency of tree species in stand-type XII by canopy strata, in younger (≤ 85 years) and older (> 85 years) stands.

Species	**Common Name**	**≤ 85 years** *n = 9*					**> 85 years** *n = 15*				
		Total	**1**	**2**	**3**	**4**	**Total**	**1**	**2**	**3**	**4**
Fraxinus nigra	Black Ash	1.00	1.00	0.56	0.89	0.89	1.00	1.00	0.53	0.93	0.80
Abies balsamea	Balsam Fir	0.78	0.11	0.22	0.33	0.67	0.87		0.27	0.60	0.67
Betula papyrifera	White Birch	0.44	0.22			0.33	0.20	0.07		0.07	0.20
Populus balsamifera	Balsam Poplar	0.56	0.22	0.11	0.33	0.44	0.07	0.07	0.00	0.07	0.07
Picea glauca	White Spruce	0.78	0.11	0.00	0.22	0.78	0.73	0.00	0.13	0.40	0.53
Ulmus americana	White Elm	0.11			0.11	0.11	0.27	0.13	0.07	0.27	0.27
Thuja occidentalis	Eastern Cedar	0.11		0.11	0.11	0.11	0.33		0.20	0.07	0.20
Populus deltoides	Eastern Cottonwood	0.11	0.11								
Populus tremuloides	Trembling Aspen	0.22	0.11		0.11	0.22	0.07	0.07			
Fraxinus pennsylvanica	Green Ash						0.13	0.13	0.07	0.07	0.07
Betula allaghaniensis	Yellow Birch						0.07		0.07	0.07	0.07
Picea mariana	Black Spruce						0.20	0.07		0.13	
Acer rubrum	Red Maple						0.20			0.07	0.20
Acer negundo	Manitoba Maple						0.07		0.07		0.07
Quercus macrocarpa	Bur Oak						0.13				0.13
Larix laricina	Eastern Larch						0.07			0.07	

Tall shrub cover decreases after age 120, attributable mainly to lower abundance of *Alnus rugosa*, *Corylus cornuta* and *Viburnum* spp. *Acer spicatum* remains frequent and abundant in older stands. The cover and frequency of low shrubs also declines, with the largest decrease occurring in *Rubus* spp. Ericaceous shrubs are absent from older stands. Total herb cover and diversity decline up to age 120 and then stabilize. Many of the frequent and abundant species in younger stands decline in cover, including *Carex disperma*, *C. vaginata*, *Galium triflorum*, *Rubus pubescens* and *Equisetum* spp. A few species are more abundant in older stands, most notably *Calamagrostis canadensis* and *Onoclea sensibilis*. Some species present in younger stands are absent in older ones, including *Cirsium arvense*, *Thalictrum* spp. and *Pyrola* spp. Cryptogam cover increases to age 100 and then begins to decline. *Climacium dendroides* and *Plagiomnium* spp. are more abundant in older stands; members of the genera *Calliergon* and *Brachythecium* decline in frequency and cover over time. Lichens remain an unimportant component of older stands, although *Peltigera* spp. increase in frequency (see **Appendix XII**).

Discussion

Most stands of this stand-type are self-regenerating. Older stands are uneven-aged, and black ash usually dominates the subcanopy and sapling layers. In sites less prone to flooding, eastern white cedar, white spruce and balsam fir may be present in older stands. White elm and green ash are also occasionally encountered. Shrub, herb and cryptogam cover decline over time. The understory of older stands is dominated by flood-tolerant, nutrient-loving herbaceous species. Ferns and graminoids are particularly common.

Black ash is generally found along rivers, streams, and other poorly-drained, seasonally flooded sites (Kenkel 1987; Walshe 1990). The species tolerates standing water for many weeks (Farrar 1995). It is most commonly encountered on peat and muck soils, although it may also be found on sandy tills underlain by clay (Wright and Rauscher 1990). Deer browse black ash saplings, and beaver will utilize the species if trembling aspen is scarce.

Spring and early summer flooding affect the dynamics of black ash stands. In Québec, regeneration declines as flooding frequency and duration increases (Tardif and Bergeron 1992, 1993). Black ash recruitment is continuous, however, indicating some degree of shade tolerance (Tardif et al. 1994). In less flood-prone sites, black ash stands may be succeeded by eastern white cedar (Wright and Rauscher 1990).

5.4 SUMMARIES

I. Jack Pine - Feathermoss

These stands are characteristically xeric, with a thin organic horizon, on sandy loam to sandy substrates, and frequently over bedrock. The stand-type is characterized by a forest canopy dominated by jack pine (often fairly open stands) and an understory of feathermoss (mainly *Pleurozium schreberi*), usually at high cover. Dry sites over bedrock often have a significant lichen component (mainly *Cladina* spp.). Total shrub cover is moderate, with ericaceous (*Vaccinium angustifolium*, *V. myrtylloides*) and low shrubs (*Diervilla lonicera*) predominating. Tall shrubs are occasionally encountered, but are rarely common or abundant. Total herb cover is low to moderate, and no single species predominates.

Total canopy tree cover is declining over time. In almost all plots black spruce is gradually replacing jack pine, although black spruce regeneration is sometimes limited. Some stands are becoming 'decadent' (minimal or no regeneration). This is the only stand-type with even moderate regeneration of jack pine. The overall successional trajectory indicates a trend to a more open canopy of aging jack pine trees and increased presence and cover of black spruce in the canopy-subcanopy layers. The understory becomes increasingly dominated by feathermoss (mainly *Pleurozium schreberi*) and ericaceous shrubs at the expense of shrubs and herbs.

II. Jack Pine - Black Spruce - Feathermoss

These sites are generally xeric-mesic, although typically not as dry as the previous stand-type. Soils are usually coarse-textured (sand to sandy loam) and nutrient-poor, but less so than those of the previous stand-type. These stands are characterized by a closed, mixed jack pine-black spruce canopy. They differ from those of the previous stand-type in having a much higher cover of black spruce in the canopy-subcanopy layers. Total shrub cover is low, and ericaceous shrubs predominate (mainly *Vaccinium* spp.). Non-ericaceous shrubs and herbs occur with low frequency and/or cover. Cryptogam cover is primarily *Pleurozium schreberi* (mean cover >80%). Species richness, diversity and evenness are low compared to other eleven stand-types.

The successional trajectory indicates increased dominance by black spruce, in both the canopy and subcanopy layers. Unlike the previous stand-type, black spruce regeneration is high and total canopy cover does not decline over time. Shrubs become less abundant in the older (>100 years) stands, and herb cover steadily declines. Cryptogams dominate the understory. *Pleurozium schreberi* remains the dominant cryptogam, although its cover declines substantially over time. Increases in other cryptogams (primarily *Dicranum polysetum*, *Ptilium crista-castrensis* and *Hylocomium splendens*) largely offset the decline in *Pleurozium schreberi.*

III. Black Spruce - Feathermoss

These stands occur on relatively coarse substrates, but are typically more mesic than those of the previous two stand-types. Depth to bedrock is < 2 m in one-third of the sites, and the water table occurs within 2 m in over one-third of the sites. Stands are characterized by a dense, monodominant canopy of black spruce with a nearly continuous carpet of cryptogams (mainly *Pleurozium schreberi*, but also *Ptilium crista-castrensis*) in the understory. Jack pine may occasionally occur as a canopy codominant. White birch, trembling aspen and/or white spruce are uncommon. Total tree and cryptogam cover are high, and shrub and herb cover low. As with the previous stand-type, species richness, diversity, and evenness are low.

The overall successional trajectory for this stand-type is straightforward: strong black spruce regeneration results in a more open, uneven-aged black spruce forest. Ericaceous shrubs increase in frequency and cover over time, while tall and low shrubs show little change in composition and cover. Species composition of the herb layer shows little change, but overall herb cover declines over time. Cryptogams composition and cover remains remarkably consistent.

IV. Black Spruce - Sphagnum

Stands of this stand-type generally occur on deep, moist peat-organic soils. Sites are poorly to moderately drained, and mottling occurs when mineral horizons are present. The canopy is typically dominated by black spruce, but eastern larch and/or eastern white cedar often dominate in mesotrophic-eutrophic sites. Most stands have high cover of *Sphagnum* species, but *Pleurozium schreberi* may also be abundant. Shrub and herb cover is often moderate to high. Species richness and diversity are higher than in the previous three stand-types. Regeneration is primarily to black spruce, but balsam fir may also be present in the lower subcanopy and sapling layers.

The overall successional trajectory for oligotrophic stands of this stand-type indicates increased dominance of black spruce. Older stands are uneven-aged, and typically have a relatively open canopy. Eastern white cedar dominates the canopy-subcanopy of moderately well-drained, mesotrophic-eutrophic sites. Larch, although relatively common in young stands, is rarely found in older (> 85 year) stands. Tree regeneration in most stands is low to moderate. Black spruce may layer in some stands. Ericaceous shrub cover (particularly *Ledum groenlandicum*) increases during succession, but total herb cover declines. *Sphagnum* spp. increase in frequency and cover over time.

V. White Spruce - Balsam Fir - Mixed Wood

These stands are characterized by relatively fine-textured, slightly acidic soils of moderate nutrient status. Most sites are mesic, have moderate drainage, and are of higher nutrient status than previous four stand-types. This stand-type is characterized by mixed-wood stands in which balsam fir and/or white spruce occur in the canopy. White birch, trembling aspen, black spruce and jack pine may also occur. Total shrub cover is moderate. Tall, low and ericaceous (primarily *Vaccinium* spp.) shrubs are often present, but their cover is generally low to moderate. The herb layer is species-rich, and individual species cover values are low to moderate. Cryptogam species richness is also high. *Pleurozium schreberi* is the most ubiquitous species, and generally occurs at moderate cover. *Brachythecium* spp. and *Rhytidiadelphus triquetrus*, which were rare or absent in the first three stand-types, occur in about half of the stands.

The overall successional trajectory for these stands indicates a trend toward more open-canopy, mixed-wood stands. Balsam fir, white spruce, white birch and black spruce regenerate well, but jack pine and trembling aspen are usually not present in older stands. Tall shrub cover increases over time (particularly *Acer spicatum*), while *Vaccinium* spp. decline in importance. Herb cover declines over time but species composition remains similar. Cryptogams continue to dominate the forest floor in older stands, but evenness increases: *Pleurozium schreberi* cover declines, whereas the cover of most other common species (e.g. *Hylocomium splendens*, *Rhytidiadelphus triquestris*) increases.

VI. Trembling Aspen

Edaphic-environmental characteristics are similar to those of the previous stand-type. Moderately-drained sandy loam or finer-textured soils predominate, and the majority of stands are found on lacustrine deposits. These stands are dominated by trembling aspen in the canopy. Pure canopies of trembling aspen are common, but white spruce, balsam fir, white birch and/or black spruce are occasional codominants. Balsam fir, white spruce and white birch are commonly encountered in the subcanopy. The regenerating layers are dominated by balsam fir. The tall shrubs *Corylus cornuta* and *Acer spicatum* are frequent, and often occur at moderate to high cover. *Diervilla lonicera* is also common. The herb layer is floristically rich, and cover is quite high. *Aster macrophyllus* and *Aralia nudicaulis* are the most abundant species. Cryptogams are frequently encountered, but almost always occur at low cover.

The overall successional trajectory for these stands is toward a more open, uneven-aged canopy of mixed species composition. Trembling aspen is slowly replaced by coniferous species, particularly white spruce and balsam fir but also black spruce (occasionally) and eastern white cedar (rarely). White birch persists in the subcanopy of some stands. Suckering may allow trembling aspen to persist in these stands, albeit at low cover. Tall shrubs are frequent, and occur at moderate cover in older stands. Total herb cover declines after age 110 (corresponding to increasing conifer cover), but the herb layer remains floristically diverse. Cryptogams increase in frequency and cover over time, but remain a relatively unimportant component of the vegetation in older stands.

VII. Birch - Trembling Aspen - Mixed Wood

These stands occur on dry, moderately to excessively-drained substrates, and often occur on slopes. Soils are generally coarse-textured and often stony. Soils are less acidic than in upland conifer-dominated stands. Stands typically have a mixed deciduous-coniferous canopy. The most frequently encountered canopy species are white birch, trembling aspen, and jack pine, but large-toothed aspen and black spruce may also be present. Balsam poplar and red maple are very occasionally encountered. Balsam fir and white spruce may be present in the subcanopy of younger stands. The tall shrubs *Corylus cornuta* and *Alnus crispa* are common and occur at moderate cover. The low shrub *Diervilla lonicera*, which is characteristic of these stands, usually occurs at moderate to high cover. The herb layer is species-rich and total herb cover is comparable to the previous stand-type. The most frequent and abundant species are *Aster macrophyllus*, *Cornus canadensis* and *Aralia nudicaulis*. Cryptogam cover is low, though *Pleurozium schreberi* is present in most stands at low cover.

The successional trajectory indicates a trend toward a more open, uneven-aged variant of stand-type V. White birch and trembling aspen are frequent in older stands, although their cover declines over time. White spruce may be present in the canopy-subcanopy of older stands. Black spruce cover increases, while jack pine and large-toothed aspen decline. Balsam fir, white birch and black spruce dominate the lower subcanopy and sapling layers, although white spruce may also occur. However, balsam fir and trembling aspen rarely reach the canopy of older stands. The cover of tall and low (*Diervilla lonicera*) shrubs decline over time, whereas ericaceous (*Vaccinium* spp.) shrubs increase in cover. Herb cover declines after age 100 as conifer cover increases. Cryptogam cover increases, with *Pleurozium schreberi* reaching a mean cover of 10% in older stands.

VIII. Red Pine

These stands are generally xeric (well to excessively-drained) and occur on coarse-textured, often stony substrates. Soil organic accumulation is low. Most stands are characterized by a pure canopy of red pine, although jack pine, trembling aspen, large-toothed aspen and white pine are occasional codominants. White birch is sometimes present in the subcanopy, but in most stands subcanopy cover is low. Balsam fir and white birch are the most frequent species in the sapling layer. Shrub and herb cover is low in most stands; few species are ubiquitous and none are abundant. Bryophytes (*Pleurozium schreberi*, *Dicranum* spp.) are ubiquitous and lichens (*Cladina* spp) are common, but they generally occur at low cover.

Succession in these stands is toward a more open canopy dominated primarily by red pine, with white pine as an occasional codominant. Black spruce frequency and cover increase over time, but it is generally restricted to the subcanopy of older stands. Tall and low shrub cover declines over time, while ericaceous shrub cover remains low. Bryophytes (mainly *Pleurozium schreberi*) cover increases over time, but lichens decrease in frequency and cover in older stands.

IX. White Pine

These stands generally occur on sandy loam or coarser substrates. Sites are generally less xeric and nutrient-deficient than those of the previous stand-type. The canopy is dominated by white pine, sometimes as pure stands but more often in mixture with red pine, white birch, trembling aspen and/or balsam fir. Red maple is occasional. Total canopy cover is high. The tall shrubs *Corylus cornuta* and *Acer spicatum* are frequent, and generally occur at moderate cover. *Diervilla lonicera* and *Rubus strigosus* are also common.

The herb layer is relatively rich, and is dominated by *Aster macrophyllus* and *Aralia nudicaulis*. Cryptogams are a minor component of most stands.

Older stands are typically characterized by a semi-closed canopy of white pine and a mixed subcanopy of balsam fir, white spruce, white birch and/or eastern white cedar. Total canopy cover declines slightly over time, but remains higher than most other stand-types. Red pine persists only on bedrock, and trembling aspen is absent from the oldest stands. White birch cover declines over time, and in older stands it is restricted to the subcanopy. The sapling layer of older stands is dominated by balsam fir, but this species rarely reaches the canopy-subcanopy. White pine saplings are found mainly on sites over bedrock. Shrub cover remains relatively consistent over time. Total herb cover declines over time, with the greatest decreases occurring in *Aster macrophyllus* and *Aralia nudicaulis*. Cryptogram cover increases, due mainly to increased abundance of *Pleurozium schreberi*.

X. Birch - Tall Shrub - Mixed Wood

These sites are xeric-mesic and well-drained. Depth to bedrock is < 2m in 25% of sites, and ca. 40% of stands show distinct mottling in the soil profile. Terrain varies from gentle to steep slopes. Soils are moderately acidic and quite nutrient-deficient. Young stands are characterized by high tree and tall shrub cover. White birch is the dominant canopy species in most stands, although trembling aspen, jack pine and/or balsam fir often occur as codominants. *Acer spicatum*, the dominant tall shrub in these stands, occurs at moderate to high cover. *Diervilla lonicera* is frequent but typically occurs at low cover. The herb layer is relatively rich and diverse. Total cryptogam cover is low, although *Pleurozium schreberi* and *Dicranum* spp. occur in most stands.

Succession in these stands is toward a more open, mixed conifer-deciduous canopy. Jack pine and trembling aspen decline in cover over time. White birch continues to dominate the canopy of most older stands, and regenerates well as evidenced by its presence in the subcanopy and sapling layers. Balsam fir is most commonly encountered as a canopy codominant, but white and/or black spruce may also occur. Balsam fir is abundant in the lower subcanopy and sapling layers. The decrease in total shrub cover is attributable to sharp declines in the abundance of *Acer spicatum* and *Corylus cornuta*. Herb cover increases to age 120, with the largest increases occurring in *Lycopodium* spp. Most bryophyte species show declines in frequency and cover over time. *Cladonia* spp. are more frequent in older stands, but remain a minor component.

XI. Balsam Poplar

These stands occur on moist-wet, nutrient-rich, weakly acidic substrates. Soils are fine-textured and often gleyed. Organic matter accumulation is relatively high, and mor-humus predominates. Balsam poplar dominates the canopy of younger stands, with white birch, white spruce, trembling aspen and black spruce as occasional codominants. Balsam fir, white spruce and black spruce are the most common species in the subcanopy, while balsam poplar, balsam fir, white spruce, white birch and eastern white cedar are frequently encountered in the lower subcanopy and sapling layers. Tall shrub cover is usually moderate and occasionally high. *Cornus stolonifera* is the most frequent and abundant species. Herb diversity and cover are high and ferns and fern-allies are relatively common in this stand-type. Cryptogams form a minor component of the vegetation.

Over time these stands become more open, multi-tiered and uneven-aged. Balsam poplar is largely replaced by coniferous species, particularly white spruce, eastern white cedar, balsam fir and/or black spruce. Balsam fir dominates the subcanopy of older stands. Balsam fir, balsam poplar, white spruce and white birch are the most frequently encountered species in the lower subcanopy and sapling layers. Shrub cover declines over time, mainly reflecting decreased abundance of *Cornus stolonifera*. The herb layer of older stands remains species-rich, although cover of most species declines. The frequency and cover of most cryptogam species increase over time, although cover remains low.

XII. Black Ash

These sites are moist-wet, very nutrient-rich, and characterized by fine-textured, mildly acidic, organic-rich soils. The water table is usually < 2 m from the surface. Stands are dominated by black ash in the canopy, usually as pure stands. Birch and balsam poplar are occasional canopy codominants. The lower subcanopy and sapling layers are dominated by black ash, although balsam fir and white spruce are also frequent. Tall and low shrubs are frequent and usually occur at moderate and low cover, respectively. Ericaceous species are absent. The herb layer is very species-rich, and total herb cover is moderate to high. Species of the genera *Carex* are ubiquitous and often occur at moderate to high cover. Total cryptogam cover is low, but species richness is high. *Climacium dendroides* and *Plagiomnium* spp. are the most frequently encountered species.

Black ash continues to predominate as stands age, but these forests become more open, multi-tiered and uneven-aged. White birch and balsam poplar decrease in cover over time. Eastern white cedar and white spruce increase in cover and may occur in the canopy of older stands. Balsam fir also increases in cover, but is generally restricted to the subcanopy layers. Tall shrubs remain frequent and abundant in older stands, while low shrub abundance declines. Herb cover also declines over time, but the herb layer remains species-rich. Species in the genera *Carex* decline in frequency and cover over time. Cryptogam cover increases to age 100, and then declines. *Climacium dendroides* and *Plagiomnium* spp. increase in cover over time.

CHAPTER 6
A SYNOPTIC MODEL OF BOREAL FOREST VEGETATION DYNAMICS

6.1 INTRODUCTION

In this chapter, I use the results summarized in Chapter 5 to develop a synoptic model (sensu Jeffers 1984) of boreal forest dynamics in northwest Ontario. I have also considered the following factors in developing the model:

Macroclimate

My study area incorporates both the extreme northwest portion of the Great Lakes-St. Lawrence (or 'near-boreal', Heinselman 1973) forest and the boreal forest ecoregion (Rowe 1972). Tree species that are largely or entirely restricted to 'near-boreal' forests include red and white pine, eastern white cedar, black ash, red maple and large-tooth aspen. Successional trajectories developed for 'near-boreal' forests of the United States (e.g. Ohmann and Grigal 1975; Frelich and Reich 1995a,b) are not directly applicable to northern boreal forests, which have a more extreme climate (colder and drier) and lower tree species richness.

Spatial Context

The model has been developed from a very large data set covering an extensive area of ca. 184,000 km^2 (Baldwin and Sims 1989). While some investigators have examined boreal forest succession at the broad spatial scale (e.g. Carleton and Maycock 1978; Cogbill 1985; Zoladeski and Maycock 1990), others have focussed on comparatively small regional landscapes (e.g. Dix and Swan 1971; Heinselman 1973, 1980; Bergeron and Dubuc 1989; Ohmann and Grigal 1975). Such 'local' models may not be robust when applied to other regions and/or over broader spatial scales. More general models such as the one developed in this Chapter lack some of the details of a more 'local' model, however.

Spatial Scale

Perceptions of successional dynamics are necessarily scale-dependent. A 'pure' stand at the scale of a research plot is part of a heterogeneous forest mosaic when viewed at coarser spatial scales (Frelich and Reich 1995a,b). A robust forest succession model should consider spatial scaling and changes in vegetation pattern at the landscape level.

Landform

Landform characteristics such as soil parent material and surficial topography determine insolation and drainage, and influence soil development, species composition, community structure, and disturbance regimes (Heinselman 1973; Foster and King 1986). Landform-mediated differences in successional pathways are therefore expected (Host et al. 1987).

Temporal Scale and Species Life-History Characteristics

Life-history characteristics of boreal and 'near-boreal' tree species vary considerably. Whereas some are relatively short-lived and highly shade-intolerant (e.g. jack pine, trembling aspen), other are relatively shade-tolerant (e.g. balsam fir, black spruce). Some 'near-boreal' species (e.g. red and white pine) are long-lived and grow to be much larger than most boreal tree species. Such life-history characteristics can render the development of successional trajectories difficult. For example, Heinselman (1973) describes a 450-year-old stand where white pine forms a 'supercanopy' above a temporally dynamic mixed stand of balsam fir, white birch and white spruce. Some authors speculate that changes in boreal canopy composition over time simply reflect the differential growth rates of individuals that established contemporaneously (e.g. Cogbill 1985; Zoladeski and Maycock 1990). However, some researchers have found that 'late-successional' species such as balsam fir can invade into older, established stands over time (Frelich and Reich 1995a,b).

Floristic Composition

Most boreal forest successional models have only considered changes in tree species composition. It is important to consider the temporal dynamics of the shrub, herb and cryptogam layers as well. Understory plants can reduce soil nutrient availability, and determine seedbed characteristics that are critical to forest stand regeneration. Interspecific competition from shrubs, herbs and cryptogams can substantially reduce tree recruitment in established stands.

Nutrient and Moisture Status

Few boreal forest succession models have incorporated edaphic variation, despite studies demonstrating the importance of nutrient and moisture gradients in determining forest stand composition and structure. Factors such as nutrient availability, rates of nutrient cycling, soil acidity and moisture status are undoubtedly critical in determining species composition and relative competitive ability. It has also been hypothesized that changes in nutrient availability over time might drive the dynamics of boreal mixed-wood stands (Pastor et al. 1987).

Differential Mortality of Seedlings and Saplings

A number of authors have used the presence and/or abundance of tree seedlings and sapling to infer boreal forest successional trajectories (e.g. Carleton and Maycock 1978; Bergeron and Dubuc 1989; Ohmann and Grigal 1975), or to determine species transitional probabilities (Frelich and Reich 1995a,b). Such investigations assume that the tree understory is indicative of future canopy composition. However, this important assumption has never been rigorously tested. My results suggest that this assumption may be untenable, particularly when applied to balsam fir, trembling aspen, balsam poplar and perhaps eastern white cedar. The most plausible explanation for this discrepancy is differential tree sapling mortality resulting from competition for limiting resources, or differential species selection by insect pests, fungal pathogens, and/or ungulate herbivores.

Seed Source

Boreal forest landscape pattern is determined by the combined effects of physiography and recurrent catastrophic fires. The cumulative effects of repeated forest fires have resulted in vast areas that are dominated by one or a few tree species. This is especially true in regions of low topographic relief and/or low surficial variability. As a result, fire-intolerant 'late-successional' species such as balsam fir, white spruce and eastern white cedar may be regionally rare or entirely absent. Absence of a seed source may severely limit successional trajectories (Heinselman 1973; Grigal and Ohmann 1975), allowing competitively subordinate species to occupy habitats from which they might otherwise be excluded.

Differential Stand Disturbance: Catastrophic Fire

Because long-term studies of boreal stand dynamics are unavailable, successional trajectories are inferred by comparing edaphically-similar stands at different ages. Such an approach implicitly assumes that the stands being compared have similar stand histories, initial floristic composition, environment, and habitat. Heinselman (1973) notes that the oldest forest stand in boreal ecosystems occur in habitats that are protected from fire, such as mesic microsites, lakeshores, islands and rock outcrops. These older stands are therefore not completely representative of the environmental conditions of more fire-prone areas. One must ask, for example: is it appropriate to compare an old stand of white pine adjacent to a lakeshore to a younger post-fire stand on a dry-sandy substrate?; are the successional trajectories for the two sites even related?

Differential Stand Disturbance: Pests, Pathogens, Herbivory and Weather

Frelich and Reich (1995a,b) note that boreal forest stand dynamics is dependent on the timing and frequency of small-scale disturbances that create canopy gaps allowing late-successional species to invade. Forest gaps may be created by windthrow, snow and winter storm damage, insect pests such as spruce budworm, fungal pathogens, dwarf mistletoe, and so forth. Ungulate browsing may also be important. Moose show a strong preference for balsam fir in winter (Belovsky 1981), whereas white-tailed deer prefer eastern white cedar (Grigal and Ohmann 1975). The cumulative effects of such localized disturbances may be critical in determining the direction and rate of successional change in boreal forest stands.

6.2 Materials and Methods

6.2.1 Vegetation Analysis

Mean cover values of all species were determined for younger (≤ 85 years) and older (> 85 years) stands, in each of the twelve stand-types. Correspondence analysis (CA) was then used to summarize relationships among the twelve stand-type successional trajectories.

6.2.2 Size-Class Analysis of Tree Species

Frequency of occurrence of each tree species over the four canopy stratal classes (canopy, upper sub-canopy, lower sub-canopy and sapling layers) were determined for each of the twelve stand-types (stands > 85 years in age only). Trends in this frequency table were then summarized using correspondence analysis (CA). Successional trajectories of tree species were inferred by connecting stratal classes for each stand-type, as in 'size-class' ordination analysis (Carleton and Maycock 1978; Bergeron and Dubuc 1989).

6.2.3 Synoptic Model of Boreal Forest Dynamics

The synoptic model summarized here incorporates the dynamic trends in the twelve site-types (see Chapter 5), as well as the results of the ordination analyses outlined above. The model was developed to serve as a framework for summarizing overall trends in boreal forest dynamics in northwest Ontario at the landscape level. As such, the model should be viewed as a conceptual structure for organizing and summarizing generalized trends in successional dynamics.

6.3 Results and Discussion

6.3.1 Vegetation Ordination Analysis

The initial CA ordination indicated that two of the twelve stand-types were strong outliers (**Fig. 6.1**). Stand-Type XII (Black Ash) is strongly separated along the first ordination axis, and the successional trajectory (arrow direction) indicates increasing floristic divergence over time. Stand-Type IV (Black Spruce-Sphagnum) is an outlier on the second ordination axis, and again increasing floristic divergence over time is indicated. The presence of these outliers resulted in successional trends for the remaining ten stand-types being somewhat obscured and/or relegated to higher ordination axes. To resolve their successional trajectories, a residual ordination was performed after removing the two outliers (**Fig. 6.2**). The results reveal that stand-types V (White Spruce-Balsam Fir Mixed Wood), VI (Trembling Aspen), X (Birch-Tall Shrub Mixed Wood) and XI (Balsam Poplar) are all converging toward mixed coniferous-deciduous stands dominated by balsam fir, white spruce, white birch and black spruce in the canopy, and a species-rich, herb-shrub understory. Stand-types II (Jack Pine-Black Spruce Feather-moss), III (Black Spruce-Feathermoss) and VII (Birch-Trembling Aspen Mixed Woods) are also converging, but toward stands dominated by black spruce in the canopy and a feathermoss-ericaceous shrub understory. The successional trajectory for stand-type I (Jack Pine-Feathermoss) indicates divergence from stand-types II and III toward very dry, open-canopy stands dominated by black spruce and remnant jack pine with a lichen-feathermoss understory. Stand-types VIII (Red Pine) and IX (White Pine) are slowly converging toward mixed coniferous-deciduous stands, but they remain floristically distinct.

6.3.2 Size-Class Ordination Analysis of Tree Species

The original CA ordination (based on all twelve stand-types) indicated that stand-types VIII (Red Pine), IX (White Pine) and XII (Black Ash) were strong outliers (**Fig. 6.3**). This result is not particularly surprising since red pine, white pine and black ash are 'near-boreal' (Great Lakes-St. Lawrence) species of restricted distribution within the study area. The size-class trajectories for these three stand-types indicate dominance by eastern white cedar, white spruce, balsam fir and/or white birch in their sapling-subcanopy layers. Because tree size-class trajectories for the nine remaining stand-types were obscured by the three 'near-boreal' outliers, a residual ordination was performed after removing them (**Fig. 6.4**). Two overall size-class trends are distinguished in the residual ordination. The first trend is toward increased dominance of black spruce in the sapling-subcanopy layers, as exemplified by stand-types I-IV. The remaining stand types (V-VII, X-XI) show a trend toward a more diverse sapling-subcanopy layer dominated by balsam fir, white birch,

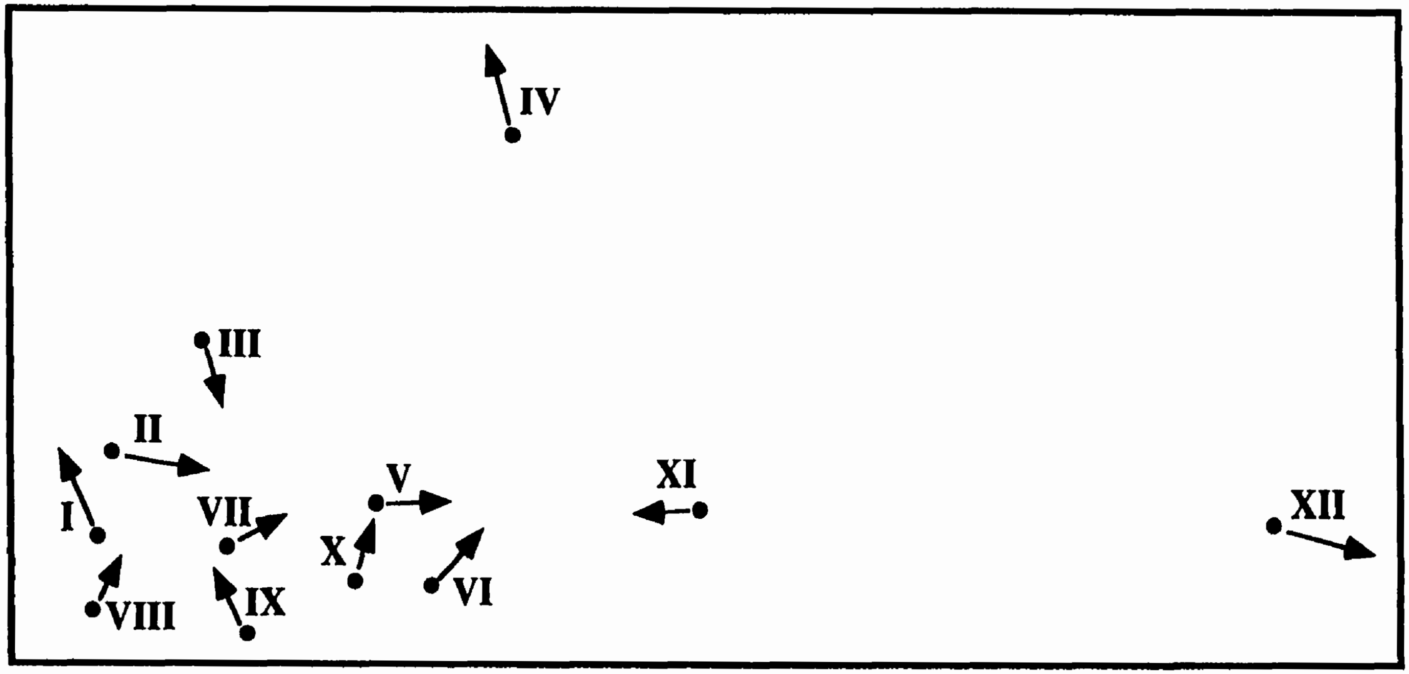


Figure 6.1. Correspondence analysis ordination (axes I and II) of the 12 stand-types, based on mean species cover in younger (≤ 85 years) and older (> 85 years) stands. The solid dots indicate the position of younger stands of each stand-type, and the end of the arrow the position of older stands. Note that stand-types IV and XII are outliers, and that they are 'moving away' from the other stand-types over time (as indicated by the direction of the arrows).

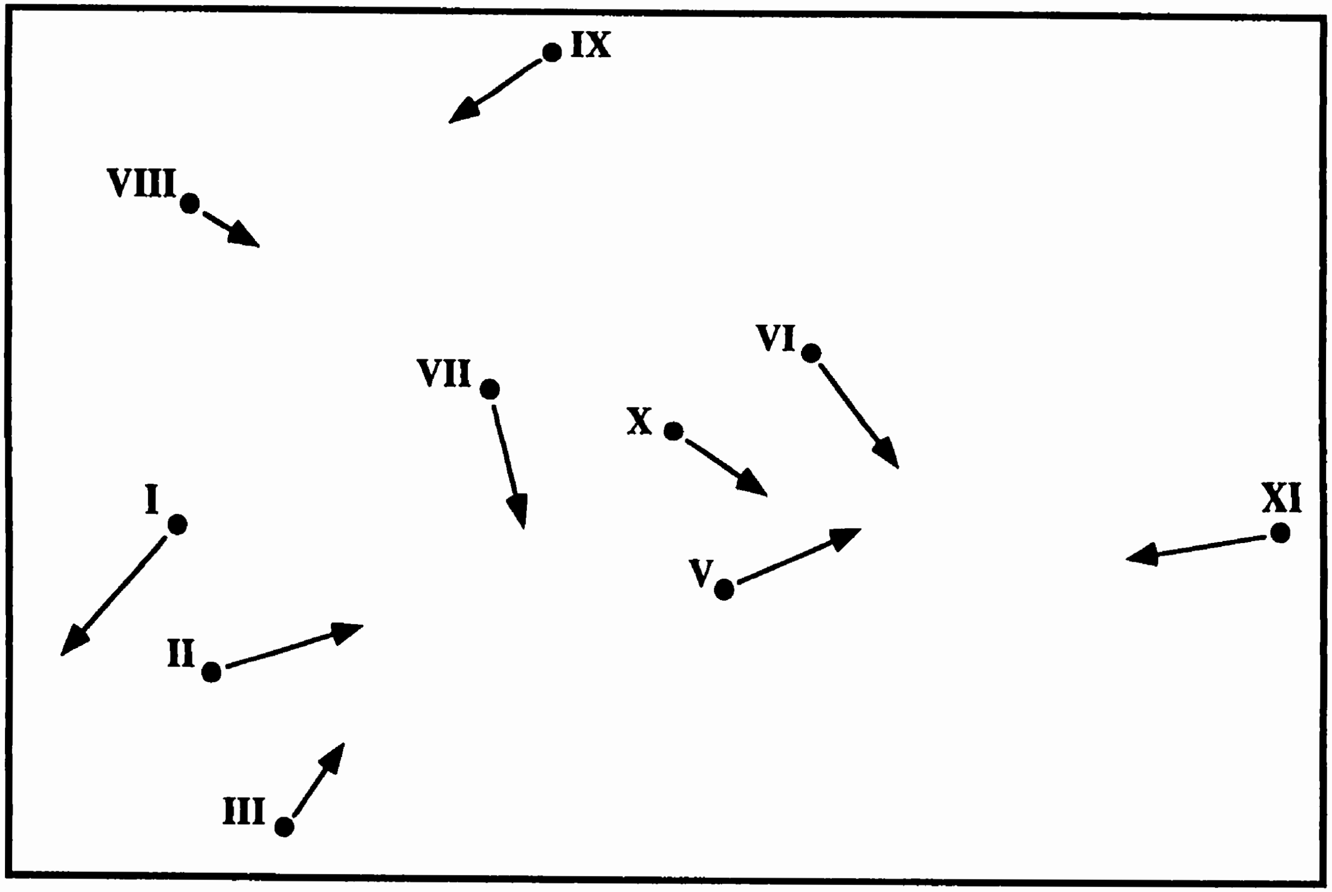


Figure 6.2. Correspondence analysis ordination (axes I and II) of 10 site-types, based on mean species cover in younger (≤ 85 years) and older (> 85 years) stands (outlier stand-types IV and XII removed, see **Fig. 6.1**). The solid dots indicate the position of younger stands of each stand-type, and the end of the arrow the position of older stands. Mean successional trends are indicated by the direction of the arrows.

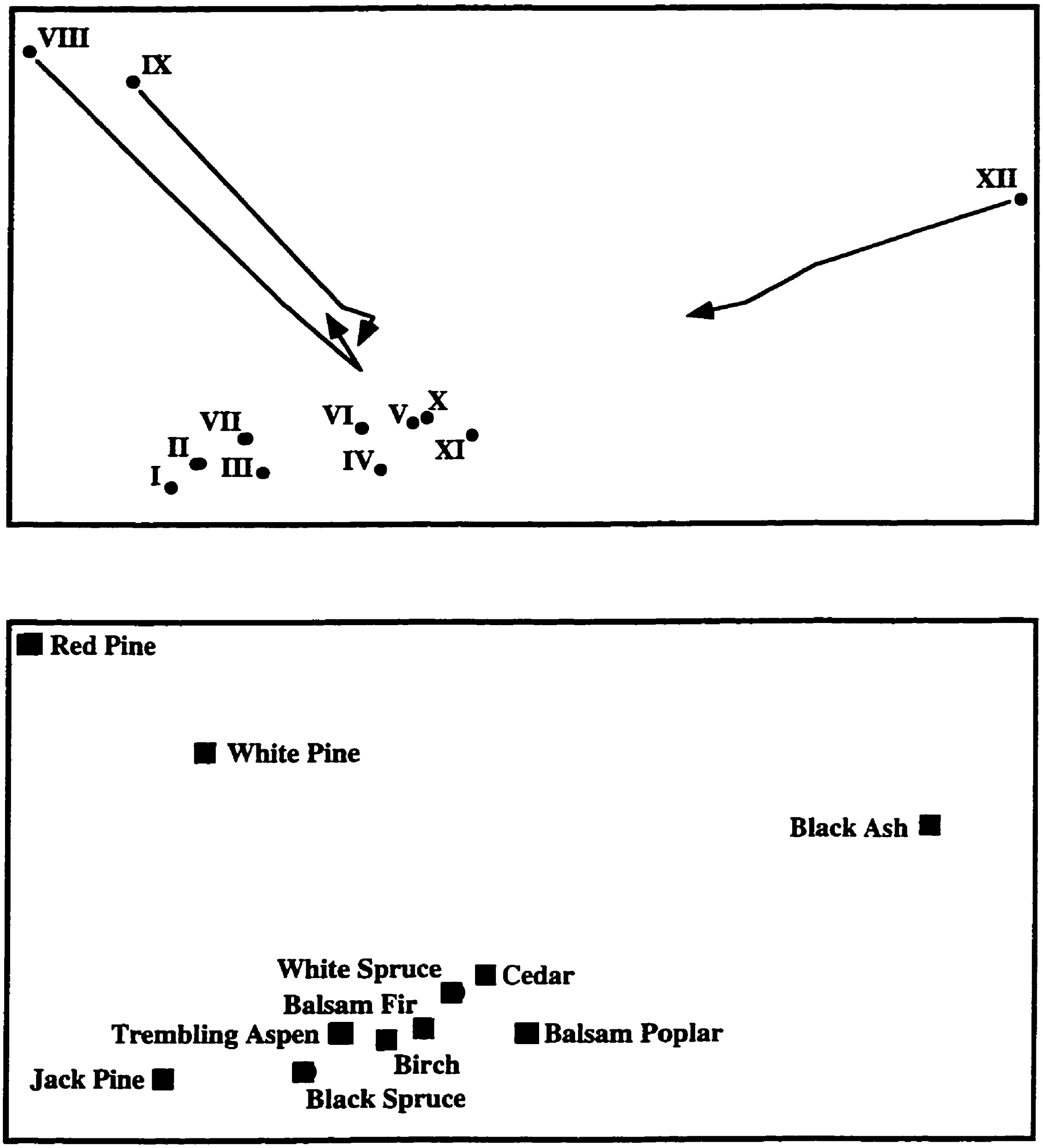


Figure 6.3. Correspondence analysis ordination (axes I and II) of stand-types by tree canopy strata, and the corresponding species ordination dual. The solid dots indicate the position of the canopy stratum of each stand-type. The arrows (drawn only for outlier stand-types VIII, IX, and XII) connect the canopy, upper subcanopy, lower subcanopy and sapling layers.

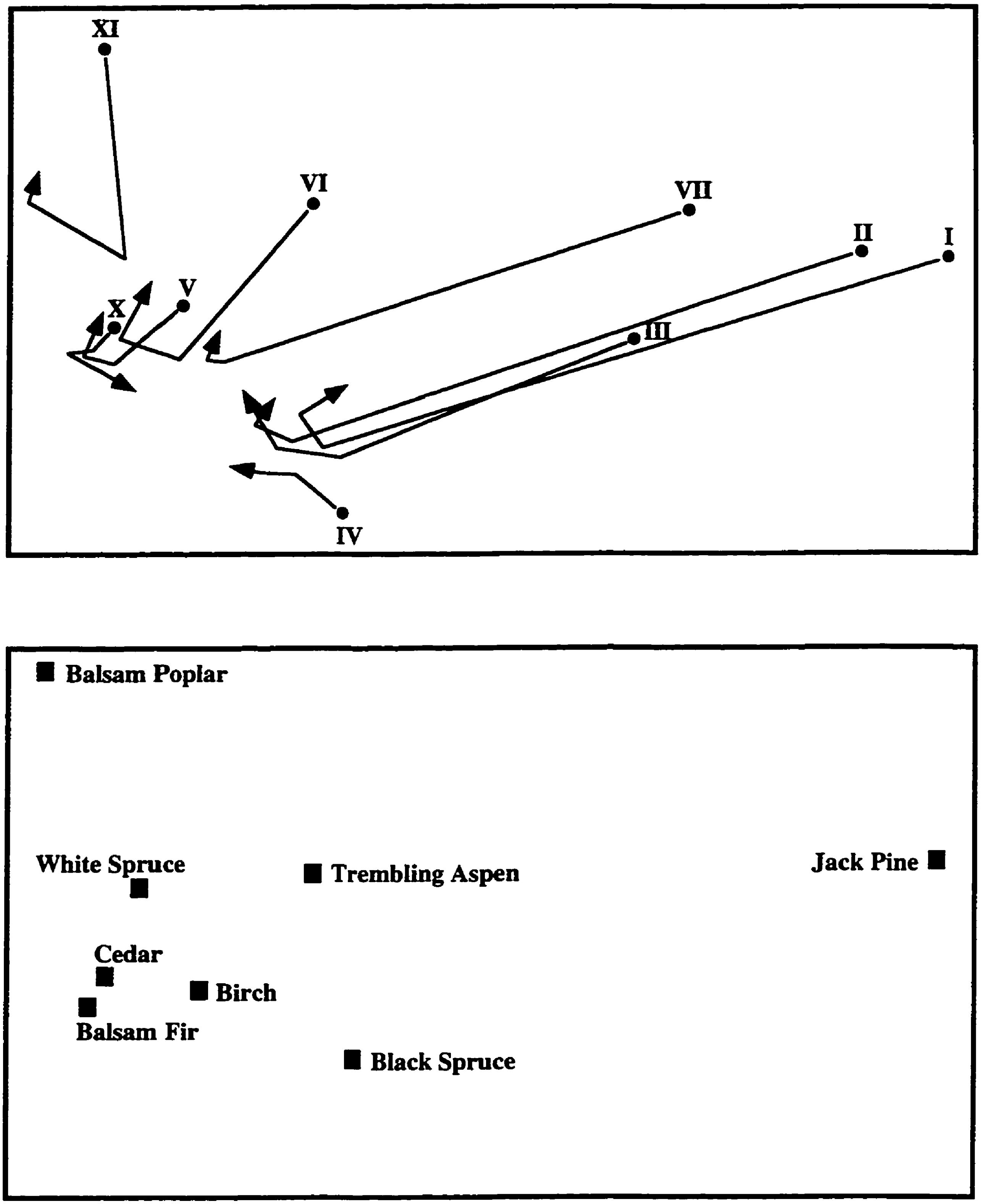


Figure 6.4. Correspondence analysis ordination (axes I and II) of site-types by tree canopy strata, and the corresponding species ordination dual. Outlier stand-types VIII, IX and XII are not included (see **Fig. 6.3**). The solid dots indicate the position of the canopy stratum of each stand-type. Arrows connect the canopy, upper subcanopy, lower subcanopy and sapling layers.

I. Jack Pine - Feathermoss
II. Jack Pine - Black Spruce - Feathermoss
III. Black Spruce - Feathermoss
IV. Black Spruce - Sphagnum
V. White Spruce - Balsam Fir Mixed Wood
VI. Trembling Aspen
VII. Birch - Trembling Aspen Mixed Wood
VIII. Red Pine
IX. White Pine
X. Birch - Tall Shrub Mixed Wood
XI. Balsam Poplar
XII. Black Ash

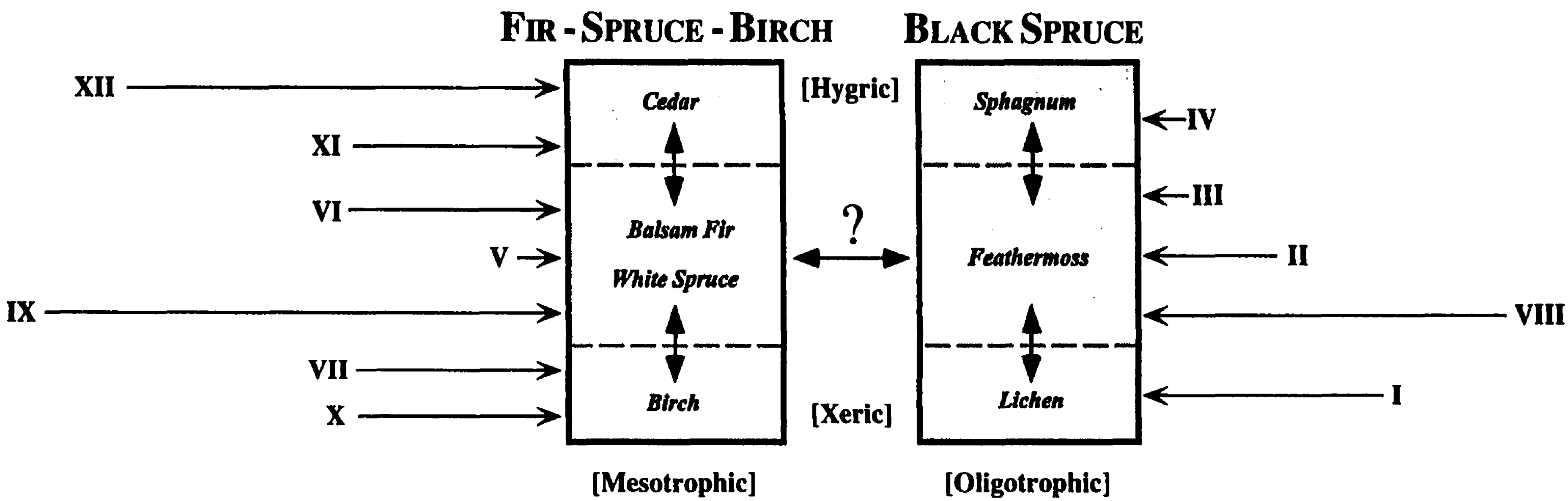


Fig. 6.5. Forest succession model for northwestern Ontario. Two self-perpetuating forest canopy types (shaded boxes) are hypothesized: black spruce in oligotrophic sites, and mixed fir-spruce-birch in mesotrophic sites. Within these two forest canopy types, moisture status (xeric-hygric gradient) determines specific floristic composition. Successional trajectories for the 12 stand-types are indicated by arrows, where arrow length is proportional to the convergence rate to the respective forest canopy type. Switching between forest canopy types (indicated by ?) may occur with changing nutrient status and/or dynamics. Double arrows within the shaded boxes indicate possible vegetation trajectories with changing moisture status.

white spruce and/or eastern white cedar. Note that stand-type XI is unique in having balsam poplar in the sapling-subcanopy layers.

6.3.3 Synoptic Boreal Forest Succession Model

The forest successional trajectories for each of the twelve stand-types (Chapter 5) reveal the following general trends:

(a) Physiognomic: young stands are even-aged and have a uniform closed canopy, whereas older stands are more open and have a multi-tiered, uneven-aged canopy.

(b) Canopy Tree Floristics: species richness, diversity and evenness of trees increase over time, although the extent of these increases vary by stand-type. This trend is attributable to the invasion and/or higher abundance of 'late-successional' species in older stands.

(c) Understory Floristics: diversity trends for shrub, herb and cryptogams are less clear, and vary considerably by stand-type. In most stand-types, herb and shrub diversity decline over time while cryptogam diversity increases.

(d) Environmental Factors: in both young and old stands, floristic composition and community structure are largely determined by moisture and nutrient status.

(e) Floristic Composition: most stand-types show evidence of floristic convergence over time (**Figs. 6.1, 6.2**). Stand-types IV (Black Spruce-Sphagnum) and XII (Black Ash) are the most floristically 'unique'. Over time, stands appear to converge toward one of two floristic types: (a) black spruce stands, with an ericaceous shrub-cryptogam understory; (b) mixed balsam fir, white spruce and white birch stands, with a tall shrub - herb understory. However, the rate of convergence is very slow for red and white pine stands (stand-types VIII and IX).

Based on these findings, a synoptic forest succession model was developed for northwest Ontario (**Fig. 6.5**). Two self-perpetuating forest canopy-understory types are recognized: (a) black spruce in oligotrophic sites; and (b) mixed fir-spruce-birch in more mesotrophic sites. Within these two self-perpetuating forest types, site moisture status (xeric to hygric gradient) determines the specific floristic compostion of a stand. Switching between these two self-perpetuating types may occur with changing nutrient status and/or stand dynamics. In this model, each of the twelve stand-types converges toward one of these two self-perpetuating types, albeit at different rates and to differing degrees as summarized below.

A. Black Spruce

These stands usually occur on acidic, nutrient-deficient substrates, ranging from excessively-drained coarse sands and rock outcrops to very poorly-drained undecomposed organic peats. In older stands, black spruce is the characteristic species of both the canopy and regenerating layers. The understory is dominated by ericaceous shrubs and cryptogams. Blueberries (*Vaccinium angustifolium*, *V. myrtilloides*) and reindeer lichens (*Cladina* spp.) are common in xeric sites, blueberries and feathermosses (*Pleurozium schreberi*, *Hylocomium splendens* and *Ptilium crista-castrensis*) in mesic sites, and labrador tea (*Ledum groenlandicum*) and peat mosses (*Sphagnum* spp.) in hygric sites.

Black spruce regenerates well in these sites. Although slow-growing, it is a long-lived species that tolerates nutrient-deficient, acidic conditions. It is also highly shade-tolerant, and is able to germinate and establish on living organic (usually moss) seedbeds. Vegetative propagation by layering may also occur in more open, mesic-hygric sites (Stanek 1961). Black spruce is also remarkably adaptable to changing soil moisture conditions: it occurs over the entire soil moisture gradient, particularly in northern areas.

The decomposition rate in these stands is often very low, due to the combination of a short growing season, high substrate acidity, and poor litter quality. In addition, xeric habitats are moisture-limited, while anaerobic conditions characterize hygric habitats. The result is high litter accumulation over time, further decreasing nutrient availability. Nutrient impoverishment over time may favour black spruce, since potential 'late-successional' invaders (e.g. balsam fir, white spruce, white birch, eastern white cedar) are intolerant of nutrient-deficient conditions.

Five of the twelve stand-types show convergence toward this canopy-understory type, as summarized below (refer also to **Fig. 6.5**).

I. Jack Pine-Feathermoss (xeric)

These stands occur on excessively drained coarse sands and rock outcrops. Succession is toward very open, unproductive black spruce-lichen-feathermoss stands. Jack pine may regenerate if semi-serotinous ecotypes are present. White birch may also be present in the canopy, particularly on rock outcrops. Reindeer lichens are favoured in older, open-canopy stands.

II. Jack Pine-Black Spruce Feathermoss (xeric-mesic)

Succession is toward increased dominance of black spruce in the canopy and regenerating layers, and declining jack pine abundance. Balsam fir and white birch may sometimes be present in the lower subcanopy at low abundance, but rarely enter the canopy. Feathermoss dominates the understory.

III. Black Spruce-Feathermoss (mesic)

These stand continue to be dominated by black spruce and feathermosses. The major changes are the development of a multi-tiered (self-regenerating) canopy, and declining abundance of other tree species. Balsam fir may be present in some older stands, but it rarely enters the canopy.

IV. Black Spruce-Sphagnum (hygric)

Most of these stands continue to be dominated by black spruce and *Sphagnum* mosses. Major changes include the development of a multi-tiered, self-regenerating canopy, and a considerable decline in larch (which is rarely present in older stands). Vegetative layering of black spruce may be important in these stands. Eastern white cedar may dominate mesotrophic-eutrophic habitats at the expense of black spruce.

VIII. Red Pine (xeric-mesic)

Because red pine is a comparatively long-lived species (>300 years), successional changes in these stands are expected to occur over an extended period (Heinselman 1973).

Older red pine stands in northern Minnesota are invaded mainly by white birch, eastern white cedar, balsam fir and black spruce, with very little red pine regeneration (Frelich and Reich 1995a,b). By contrast, the vast majority of stands in northwestern Ontario occur on excessively drained, nutrient-deficient substrates, which favour black spruce regeneration. Red pine may also be self-regenerating, especially in areas where occasional, low-intensity ground fires occur every 20–40 years (Heinselman 1973; Bergeron and Brisson 1990). Such a fire regime may also favour the invasion of white pine. Black spruce is expected to remain a relatively minor component of such self-regenerating stands.

B. Balsam Fir-White Spruce-White Birch Mixed Wood

These stands generally occur on substrates that are less acidic and nutrient-deficient than black spruce-dominated stands. Soils are usually medium to fine-textured, and well to moderately drained (some stands are seasonally flooded). Rates of organic decomposition and nutrient cycling are greater than in black spruce-dominated stands. Older stands are usually characterized by a self-regenerating mixture of balsam fir, white birch, white spruce and black spruce. Eastern white cedar may also be present, particularly in less acidic, mesic-hygric sites. Black spruce and white birch are somewhat more abundant in xeric sites. The understory is characterized by high herb diversity and cover. Tall and non-ericaceous low shrubs may also be abundant. Feathermosses are often present, but they rarely dominate the understory.

Regeneration dynamics in these mixed-wood stands is complex (Frelich and Reich 1995a,b; Kneeshaw and Bergeron 1996). The species involved are relatively to highly shade-tolerant, and quickly colonize patches created by small-scale intermediary disturbances (e.g. windthrow, pests and pathogens). Hardwood species may also persist through vegetative propagation (suckering in trembling aspen, resprouting in white birch). Possible factors controlling regeneration dynamics include patch size, nature and frequency of disturbance, competition from tall shrubs, ungulate herbivory, seed source proximity, stand age, soil moisture and nutrient status, and seedbed type. Recurrent spruce budworm infestations may favour balsam fir regeneration: by killing mature trees, suppressed saplings are released (Kneeshaw and Bergeron 1996).

Seven of the twelve stand-types show general convergence toward this canopy-understory type, though convergence rates differ considerably. Trends in each stand-type are summarized below (see also **Fig. 6.5**).

V. Balsam Fir - White Spruce Mixed Wood (mesic)

These are self-perpetuating stands that show little change in floristic composition and community structure over time. Early successional species such as jack pine and trembling aspen are absent from older stands, while the abundance of eastern white cedar increases. An uneven-aged, multi-tiered, mixed canopy of balsam fir, white spruce and white birch characterizes older stands.

VI. Trembling Aspen (mesic)

These stands are gradually invaded by balsam fir, white spruce and white birch, so that older stands are similar to those of stand-type V. The maximum longevity of trembling aspen is about 200 years (Heinselman 1973). Trembling aspen may persist, however, since it continues to produce sucker shoots for at least 250 years (see also Kneeshaw and Bergeron 1996). Whether these suckers persist is open to question, however, since they are highly shade-intolerant and are a preferred ungulate browse. In stands along watercourses, beaver activity may speed the succession from trembling aspen to conifer domination.

VII. Birch - Trembling Aspen Mixed Wood (xeric-mesic)

These stands are drier and more nutrient-deficient than those of stand-types V and VI. Succession is toward a balsam fir - white spruce - white birch mixed forest, but white birch is more prominent. Black spruce may also be an important species in some stands.

IX. White Pine (xeric-mesic)

Succession in these stands occurs slowly, since white pine is a large and very long-lived species (>500 years, Heinselman 1973). The subcanopy of most stands is gradually invaded by balsam fir, white spruce, eastern white cedar and white birch. These comparatively small trees eventually form an open canopy beneath a 'supercanopy' of mature white pine (Heinselman 1973). However, stands subject to occasional, low-intensity ground fires may show good regeneration of white pine and less invasion by other species. In northwest Ontario, white pine regeneration is most prevalent in bedrock sites.

X. Birch - Tall Shrub Mixed Wood (xeric-mesic)

Older stands of this type are similar to those of stand-type VII. Balsam fir invades these stands as tall shrub cover declines. Succession is toward a mixed canopy of balsam fir, white spruce and white birch.

XI. Balsam Poplar (mesic-hygric)

Balsam poplar is highly shade-intolerant and relatively short-lived. Hygric sites are invaded by white spruce, black spruce and eastern white cedar, while balsam fir and white birch are favoured in more mesic sites. The long-term successional trend in most stands indicates increased dominance of eastern white cedar.

XII. Black Ash (hygric)

Black ash stands in seasonally-flooded sites are self-regenerating. Eastern white cedar, white spruce and balsam fir may slowly invade stands that are less subject to flooding, or where the flooding regime is altered by humans.

6.4 Further Research

Underrepresented Stand-Types

Three of the deciduous stand-types were underrepresented (≤ 25 stands) in one or both of the younger (≤ 85 yr.) or older (> 85 yr.) age classes (**Table 4.1**). Both the Balsam Poplar (XI) and Black Ash (XII) stand-types were underrepresented in both the younger and older age classes, while the Birch - Tall Shrub Mixed Wood (X) had few stands ≥ 85 years old (and the oldest stand was 121 years old). The paucity of descriptive and successional studies focusing on these stand-types may be due to the relatively minor economic importance of white birch, balsam poplar and black ash. Succession in balsam poplar has been extensively studied in Alaska (e.g. Van Cleve et. al. 1993), but these studies may not be particularly relevant to more continental regions. More studies should be undertaken to describe the range of environmental conditions under which these communities occur and succession under these conditions.

The Red Pine (VIII) and White Pine (IX) stand-types were insufficiently replicated in younger stands. Both red and white pine are valuable economically and have been investigated in some detail (e.g. Carleton and Arnup 1993; Horton and Bedell 1960). Heinselman (1973) suggests that red and white pine regeneration is greatest in areas where low-intensity fires occur every 20-40 years. Thus, monodominant stands may be restricted to 'protected' sites, such as islands and rock outcrops. Further research should focus on edaphic and topographic factors influencing red and white pine abundance and succession.

Finally, eastern white cedar stands were not commonly encountered in this study. As a result, this species did not form a distinct stand-type. Additional sampling of eastern white cedar stands should be undertaken to characterize the environmental preferences and successional characteristics of this species.

Effects of Logging on Stand Dynamics

The differentiation between stand-types X and VII is primarily attributable to higher tall shrub abundance in stand-type X. In northwest Ontario, high tall shrub abundance may be an indicator of prior logging (Zoladeski and Maycock 1990). Few studies have compared the regeneration dynamics of naturally burned vs. logged stands. Ehnes and Shay (1995) found that the floristic composition of post-logging and post-fire stands is similar, but that species abundances are lower in post-logging stands.

Establishment Of Long-Term Permanent Plots

The establishment of long-term permanent plots, with sufficient replication of floristic, edaphic and topographic conditions, offers the best hope for understanding successional processes in the boreal forest. Field-scale experiments designed to assess the effects of logging and fire suppression on stand dynamics are also required. Since succession in forests dominated by black spruce and jack pine is relatively straightforward, greater emphasis should be placed on examining the dynamics of mixed-wood stands.

Concluding Remarks

Effective fire suppression is being practiced in most regions of boreal Canada, and formerly inaccessible regions are becoming more accessible as new roads are built. The successional trajectories developed in this study indicate that continued fire suppression will lead to an alteration in the driving forces controlling boreal forest vegetation dynamics (Frelich and Reich 1995a,b). Pioneer species such as jack pine and aspen may become locally extirpated (Hienselman 1973), and progressively slower rates of nutrient cycling may result in more open, 'park-like' stands (Carleton and Maycock 1978). Monodominant black spruce forests, and mixed-wood stands dominated by balsam fir, white spruce and/or white birch, will come to dominate the boreal ecosystem. This will result in declining habitat diversity at the landscape level, which will negatively impact the boreal flora and fauna.

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APPENDIX I

STAND-TYPE I : JACK PINE - FEATHERMOSS

STAND-TYPE L JACK PINE - FEATHERMOSS.

TABLE 1. Frequency and mean cover of common shrub taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years $n = 103$		> 85 years $n = 78$	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Tall Shrubs					
Amelanchier spp.	Serviceberries	0.49	1.28	0.35	0.53
Salix spp.	Willows	0.45	0.95	0.18	0.26
Sorbus spp.	Mountain Ashes	0.41	0.43	0.26	0.30
Alnus crispa	Green Alder	0.38	2.85	0.44	2.76
Corylus cornuta	Beaked Hazel	0.34	1.29	0.17	0.69
Acer spicatum	Mountain Maple	0.18	0.73	0.13	0.14
Prunus spp.	Cherries	0.17	0.27	0.06	0.06
Low Shrubs					
Diervilla lonicera	Low-Bush Honeysuckle	0.69	8.57	0.40	2.63
Chimaphila umbellata	Prince's Pine	0.41	0.52	0.24	0.32
Rosa acicularis	Wild Rose	0.31	0.41	0.30	0.31
Lonicera spp.	Honeysuckles	0.23	0.26	0.08	0.08
Rubus strigosus	Raspberry	0.18	0.24	0.09	0.09
Ribes spp.	Gooseberries	0.12	0.15	0.04	0.05
Ericaceous Shrubs					
Vaccinium spp.	Blueberries	0.99	10.71	0.97	9.41
Arctostaphylos uva-ursi	Bearberry	0.31	2.81	0.18	1.33
Gaultheria hispidula	Creeping Snowberry	0.27	0.41	0.49	0.89
Gaultheria procumbens	Wintergreen	0.24	0.78	0.13	0.64
Ledum groenlandicum	Labrador Tea	0.18	0.38	0.30	1.91
Epigaea repens	Trailing Arbutus	0.11	0.18	0.14	0.21

STAND-TYPE I. JACK PINE - FEATHERMOSS.

TABLE 2. Frequency and mean cover of common herb, fern and fern-ally taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n* = *103*		> 85 years *n* = *78*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Maianthemum canadense	Wild Lily-of-the-Valley	0.89	2.47	0.76	1.58
Linnaea borealis	Twinflower	0.80	1.79	0.58	0.99
Cornus canadensis	Bunchberry	0.73	6.79	0.64	2.51
Aralia nudicaulis	Wild Sarsaparilla	0.60	2.35	0.49	1.17
Melampyrum lineare	Cow-Wheat	0.59	0.71	0.27	0.27
Lycopodium spp.	Club Mosses	0.57	1.57	0.46	1.14
Clintonia borealis	Bluebead Lily	0.52	0.77	0.37	0.62
Aster macrophyllus	Large-leaved Aster	0.44	2.65	0.21	0.90
Epilobium angustifolium	Fireweed	0.40	0.41	0.10	0.10
Oryzopsis spp.	Rice Grasses	0.38	0.50	0.27	0.37
Goodyera repens	Rattlesnake Plantain	0.31	0.35	0.14	0.14
Trientalis borealis	Star Flower	0.30	0.30	0.28	0.30
Cypripedium acaule	Moccasin Flower	0.28	0.28	0.18	0.18
Fragaria spp.	Strawberries	0.26	0.35	0.10	0.10
Dryopteris spp.	Wood Ferns	0.25	0.27	0.04	0.04
Apocynum androsaemifolium	Dogbane	0.24	0.25	0.12	0.17
Rubus pubescens	Dewberry	0.24	0.28	0.14	0.15
Streptopus roseus	Twistedstalk	0.24	0.28	0.21	0.22
Pyrola spp.	Pyrolas	0.33	0.37	0.21	0.22

STAND-TYPE I. JACK PINE - FEATHERMOSS.

TABLE 3. Frequency and mean cover of common cryptogam taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 103*		> 85 years *n = 78*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Bryophytes					
Pleurozium schreberi	Schreber's Moss	0.99	47.05	0.97	55.99
Dicranum polysetum	Broom Moss	0.99	5.06	0.99	6.95
Polytrichum spp.	Hair-Cap Mosses	0.49	0.58	0.35	0.36
Ptilium crista-castrensis	Plume Moss	0.37	0.72	0.46	2.37
Hylocomium splendens	Stair-Step Moss	0.17	0.18	0.45	1.92
Lichens					
Cladina spp.	Reindeer Lichens	0.75	8.59	0.82	9.59
Cladonia spp.	Club Lichens	0.25	1.07	0.27	1.03
Peltigera spp.	Dog Lichens	0.07	0.08	0.21	0.40

STAND-TYPE I. JACK PINE - FEATHERMOSS.

TABLE 4. Species richness, diversity and evenness in younger (≤ 85 years) and older (> 85 years) stands.

	≤ 85 years *n = 103*		> 85 years *n = 78*	
	mean	s.d.	mean	s.d.
Species Richness				
All Species	29.29	8.75	22.96	7.85
Trees	3.69	1.51	3.18	1.27
Shrubs	7.66	2.83	5.73	2.82
Herbs	11.57	5.18	7.08	5.03
Cryptogams	6.37	3.38	6.97	3.06
Diversity (H)				
All Species	2.304	0.404	2.005	0.470
Trees	0.767	0.430	0.726	0.392
Shrubs	1.473	0.465	1.265	0.542
Herbs	1.954	0.642	1.546	0.808
Cryptogams	0.810	0.447	0.813	0.486
Evenness				
All Species	0.690	0.088	0.647	0.110
Trees	0.617	0.211	0.665	0.215
Shrubs	0.755	0.177	0.792	0.197
Herbs	0.862	0.143	0.936	0.077
Cryptogams	0.452	0.197	0.433	0.213

STAND-TYPE I. JACK PINE - FEATHERMOSS.

TABLE 5. Means and standard deviations of selected soil variables, in younger (≤ 85 years) and older (> 85 years) stands.

Variable	≤ 85 years			> 85 years		
	Mean	s.d.	*n*	Mean	s.d.	*n*
Organic Horizon Depth (cm)	**5.65**	2.79	*103*	**7.72**	4.99	*78*
Mineral Horizon Nitrogen (%)	**0.07**	0.10	*63*	**0.08**	0.12	*52*
Mineral Horizon Organic Matter (%)	**2.19**	3.70	*66*	**2.33**	2.39	*55*
Mineral Horizon pH	**5.40**	0.54	*65*	**5.09**	0.60	*52*
Organic Horizon Nitrogen (%)	**1.01**	0.32	*67*	**1.00**	0.29	*57*
Organic Horizon Organic Matter (%)	**57.97**	14.05	*82*	**56.09**	16.91	*59*
Organic Horizon pH	**4.42**	0.45	*67*	**4.09**	0.41	*57*
Total Base Saturation (%)	**70.29**	19.83	*65*	**55.41**	26.92	*50*
Total Exchangable Bases (meq/100g)	**0.97**	0.92	*65*	**0.86**	0.73	*50*

APPENDIX II

STAND-TYPE II: JACK PINE - BLACK SPRUCE - FEATHERMOSS

STAND-TYPE II. JACK PINE - BLACK SPRUCE - FEATHERMOSS.

TABLE 1. Frequency and mean cover of common shrub taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years $n = 92$		> 85 years $n = 54$	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Tall Shrubs					
Amelanchier spp.	Serviceberries	0.40	0.67	0.35	0.48
Alnus crispa	Green Alder	0.38	1.32	0.39	2.00
Salix spp.	Willows	0.29	0.41	0.19	0.41
Sorbus spp.	Mountain-Ashes	0.27	0.43	0.43	0.63
Corylus cornuta	Beaked Hazel	0.12	0.29	0.24	0.39
Acer spciatum	Mountain Maple	0.07	0.07	0.22	0.56
Low Shrubs					
Diervilla lonicera	Low-Bush Honeysuckle	0.49	1.62	0.65	2.00
Rosa acicularis	Wild Rose	0.38	0.68	0.37	0.63
Chimaphila umbellata	Prince's Pine	0.13	0.14	0.09	0.09
Lonicera spp.	Honeysuckles	0.12	0.17	0.22	0.26
Ericaceous Shrubs					
Vaccinium spp.	Blueberries	0.99	3.97	0.94	3.00
Gaultheria hispidula	Creeping Snowberry	0.54	1.24	0.52	1.37
Ledum groenlandicum	Labrador Tea	0.49	5.52	0.41	3.37
Arctostaphylos uva-ursi	Bearberry	0.15	0.24	0.06	0.06

STAND-TYPE II. JACK PINE - BLACK SPRUCE - FEATHERMOSS.

TABLE 2. Frequency and mean cover of common herb, fern and fern-ally taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years $n = 92$		> 85 years $n = 54$	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Maianthemum canadense	Wild Lily-of-the-Valley	0.90	2.78	0.93	1.91
Cornus canadensis	Bunchberry	0.89	4.97	0.93	4.37
Linnaea borealis	Twinflower	0.80	1.43	0.82	1.26
Clintonia borealis	Bluebead Lily	0.66	1.18	0.67	1.07
Aralia nudicaulis	Wild Sarsaparilla	0.59	1.55	0.67	1.41
Lycopodium spp.	Club Mosses	0.51	1.23	0.65	1.63
Trientalis borealis	Star Flower	0.49	0.58	0.54	0.61
Coptis trifolia	Goldthread	0.46	0.76	0.39	0.59
Goodyera repens	Rattlesnake Plantain	0.32	0.32	0.19	0.20
Aster macrophyllus	Large-leaved Aster	0.30	2.62	0.39	3.54
Rubus pubescens	Dewberry	0.28	0.42	0.32	0.41
Melampyrum lineare	Cow-Wheat	0.26	0.29	0.15	0.15
Pyrola spp.	Pyrolas	0.23	0.25	0.22	0.35
Petasites palmatus	Coltsfoot	0.23	0.32	0.24	0.31
Fragaria spp.	Strawberries	0.23	0.26	0.17	0.33
Anemone spp.	Wood Anemones	0.23	0.25	0.15	0.15
Streptopus roseus	Twistedstalk	0.21	0.26	0.35	0.37
Viola spp.	Violets	0.20	0.21	0.30	0.30
Oryzopsis spp.	Rice Grasses	0.15	0.21	0.26	0.28
Monotropa uniflora	Indian Pipe	0.11	0.11	0.24	0.24

STAND-TYPE II. JACK PINE - BLACK SPRUCE - FEATHERMOSS.

TABLE 3. Frequency and mean cover of common cryptogam taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n* = 92		> 85 years *n* = 54	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Bryophytes					
Pleurozium schreberi	Schreber's Moss	1.00	80.42	1.00	57.87
Dicranum polysetum	Broom Moss	0.99	2.83	1.00	5.46
Ptilium crista-castrensis	Plume Moss	0.75	2.72	0.76	5.06
Hylocomium splendens	Stair-Step Moss	0.55	0.79	0.61	1.72
Polytrichum spp.	Hair-Cap Mosses	0.28	0.32	0.22	0.26
Lichens					
Cladina spp.	Reindeer Lichens	0.40	0.66	0.50	0.80
Peltigera spp.	Dog Lichens	0.12	0.13	0.17	0.22

STAND-TYPE II. JACK PINE - BLACK SPRUCE - FEATHERMOSS.

TABLE 4. Species richness, diversity and evenness in younger (≤ 85 years) and older (> 85 years) stands.

	≤ 85 years *n* = 92		> 85 years *n* = 54	
	mean	s.d.	mean	s.d.
Species Richness				
All Species	24.70	9.16	27.72	9.37
Trees	3.22	1.17	3.85	1.51
Shrubs	6.02	2.84	6.57	2.62
Herbs	10.05	6.17	10.91	5.88
Cryptogams	5.40	2.15	6.39	2.84
Diversity (H)				
All Species	1.889	0.428	2.175	0.470
Trees	0.840	0.296	0.969	0.316
Shrubs	1.380	0.555	1.532	0.442
Herbs	1.785	0.724	1.964	0.630
Cryptogams	0.411	0.210	0.733	0.389
Evenness				
All Species	0.597	0.080	0.660	0.085
Trees	0.781	0.160	0.779	0.135
Shrubs	0.838	0.166	0.859	0.157
Herbs	0.870	0.113	0.895	0.127
Cryptogams	0.247	0.098	0.400	0.166

STAND-TYPE II. JACK PINE - BLACK SPRUCE FEATHERMOSS.

TABLE 5. Means and standard deviations of selected soil variables, in younger (≤ 85 years) and older (> 85 years) stands.

Variable	≤ 85 years			> 85 years		
	Mean	s.d.	*n*	Mean	s.d.	*n*
Organic Horizon Depth (cm)	**8.13**	3.31	*92*	**7.33**	2.93	*54*
Mineral Horizon Nitrogen (%)	**0.05**	0.09	*69*	**0.04**	0.05	*36*
Mineral Horizon Organic Matter (%)	**1.19**	1.00	*70*	**1.08**	0.81	*36*
Mineral Horizon pH	**5.42**	0.50	*79*	**5.26**	0.46	*45*
Organic Horizon Nitrogen (%)	**1.02**	0.30	*69*	**1.15**	0.49	*36*
Organic Horizon Organic Matter (%)	**57.11**	12.04	*69*	**56.27**	15.49	*36*
Organic Horizon pH	**4.18**	0.46	*69*	**4.21**	0.59	*36*
Total Base Saturation (%)	**69.05**	22.58	*70*	**62.69**	28.35	*36*
Total Exchangable Bases (meq/100g)	**1.28**	1.36	*70*	**1.36**	1.51	*36*

APPENDIX III

STAND-TYPE III: BLACK SPRUCE - FEATHERMOSS

STAND-TYPE III. BLACK SPRUCE - FEATHERMOSS.

TABLE 1. Frequency and mean cover of common shrub taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years $n = 111$		> 85 years $n = 142$	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Tall Shrubs					
Amelanchier spp.	Serviceberries	0.41	0.53	0.30	0.32
Sorbus spp.	Mountain-Ashes	0.26	0.34	0.42	0.59
Salix spp.	Willows	0.25	0.49	0.15	0.25
Alnus rugosa	Speckled Alder	0.17	0.96	0.14	1.03
Alnus crispa	Green Alder	0.14	0.80	0.34	2.11
Low Shrubs					
Rosa acicularis	Wild Rose	0.30	0.39	0.25	0.29
Diervilla lonicera	Low-Bush Honeysuckle	0.27	0.70	0.24	0.61
Ericaceous Shrubs					
Vaccinium spp.	Blueberries	0.88	4.05	0.92	3.58
Ledum groenlandicum	Labrador Tea	0.68	4.08	0.63	9.32
Gaultheria hispidula	Creeping Snowberry	0.60	1.54	0.74	1.72

STAND-TYPE III. BLACK SPRUCE - FEATHERMOSS.

TABLE 2. Frequency and mean cover of common herb, fern and fern-ally taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 111*		> 85 years *n = 142*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Cornus canadensis	Bunchberry	0.82	4.30	0.78	2.37
Maianthemum canadense	Wild Lily-of-the-Valley	0.77	2.25	0.67	1.27
Linnaea borealis	Twinflower	0.55	0.98	0.51	0.63
Lycopodium spp.	Club Mosses	0.50	1.20	0.50	1.27
Clintonia borealis	Bluebead Lily	0.45	0.76	0.47	0.68
Trientalis borealis	Star Flower	0.43	0.47	0.36	0.37
Coptis trifolia	Goldthread	0.40	0.78	0.35	0.49
Equisetum spp.	Horsetails	0.38	0.41	0.21	0.29
Goodyera repens	Rattlesnake Plantain	0.31	0.31	0.23	0.24
Epilobium angustifolium	Fireweed	0.23	0.23	0.10	0.10
Petasites palmatus	Coltsfoot	0.22	0.28	0.16	0.17
Aster macrophyllus	Large-leaved Aster	0.21	0.87	0.16	0.69
Aralia nudicaulis	Wild Sarsaparilla	0.18	0.27	0.31	0.65
Rubus pubescens	Dewberry	0.17	0.24	0.23	0.64
Streptopus roseus	Twistedstalk	0.16	0.16	0.21	0.21

STAND-TYPE III. BLACK SPRUCE - FEATHERMOSS.

TABLE 3. Frequency and mean cover of common cryptogam taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 111*		> 85 years *n = 142*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Bryophytes					
Pleurozium schreberi	Schreber's Moss	1.00	63.08	1.00	59.27
Ptilium crista-castrensis	Plume Moss	0.96	13.89	0.93	10.06
Dicranum polysetum	Broom Moss	0.96	3.62	1.00	4.25
Hylocomium splendens	Stair-Step Moss	0.66	3.41	0.75	7.04
Polytrichum spp.	Hair Cap Mosses	0.54	0.96	0.45	0.54
Sphagnum spp.	Peat Mosses	0.39	2.89	0.37	2.29
Ptilidium spp.	Naugehyde Liverworts	0.28	0.33	0.32	0.37
Lichens					
Cladina spp.	Reindeer Lichens	0.47	1.04	0.55	1.04
Cladonia spp.	Club Lichens	0.29	0.43	0.27	0.61
Peltigera spp.	Dog Lichens	0.25	0.28	0.35	0.45

STAND-TYPE III. BLACK SPRUCE - FEATHERMOSS.

TABLE 4. Species richness, diversity and evenness in younger (≤ 85 years) and older (> 85 years) stands.

	≤ 85 years *n = 111*		> 85 years *n = 142*	
	mean	s.d.	mean	s.d.
Species Richness				
All Species	25.15	9.11	26.03	11.09
Trees	3.08	1.16	3.13	1.28
Shrubs	5.35	2.85	5.70	2.87
Herbs	8.34	5.74	8.12	6.98
Cryptogams	8.38	3.89	9.08	4.54
Diversity (H)				
All Species	1.950	0.403	2.041	0.466
Trees	0.681	0.361	0.709	0.405
Shrubs	1.235	0.603	1.269	0.560
Herbs	1.639	0.749	1.558	0.899
Cryptogams	0.871	0.342	0.976	0.414
Evenness				
All Species	0.614	0.082	0.638	0.092
Trees	0.636	0.216	0.659	0.225
Shrubs	0.835	0.175	0.803	0.201
Herbs	0.909	0.114	0.935	0.080
Cryptogams	0.428	0.146	0.463	0.177

STAND-TYPE III. BLACK SPRUCE FEATHERMOSS.

TABLE 5. Means and standard deviations of selected soil variables, in younger (≤ 85 years) and older (> 85 years) stands.

Variable	≤ 85 years			> 85 years		
	Mean	s.d.	*n*	Mean	s.d.	*n*
Organic Horizon Depth (cm)	**15.60**	25.74	*111*	**13.05**	7.24	*142*
Mineral Horizon Nitrogen (%)	**0.06**	0.07	*64*	**0.07**	0.07	*73*
Mineral Horizon Organic Matter (%)	**3.29**	10.12	*64*	**2.00**	1.72	*73*
Mineral Horizon pH	**5.29**	0.65	*84*	**5.20**	0.92	*108*
Organic Horizon Nitrogen (%)	**1.06**	0.32	*63*	**1.06**	0.28	*70*
Organic Horizon Organic Matter (%)	**57.60**	11.19	*66*	**56.69**	12.34	*74*
Organic Horizon pH	**4.13**	0.72	*66*	**3.94**	0.56	*74*
Total Base Saturation (%)	**62.88**	26.85	*62*	**50.76**	27.75	*68*
Total Exchangable Bases (meq/100g)	**1.50**	1.35	*62*	**1.54**	2.80	*68*

APPENDIX IV

STAND-TYPE IV: BLACK SPRUCE - SPHAGNUM

STAND-TYPE IV. BLACK SPRUCE - SPHAGNUM.

TABLE 1. Frequency and mean cover of common shrub taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 58*		> 85 years *n = 132*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Tall Shrubs					
Alnus rugosa	Speckled Alder	0.53	7.17	0.46	6.14
Amelanchier spp.	Serviceberries	0.41	0.52	0.19	0.25
Sorbus spp.	Mountain-Ashes	0.31	0.38	0.33	0.43
Salix spp.	Willows	0.29	1.05	0.27	0.64
Cornus stolonifera	Red-Osier Dogwood	0.22	0.41	0.18	0.39
Acer spicatum	Mountain Maple	0.21	1.17	0.10	0.36
Viburnum spp.	Viburnums	0.12	0.16	0.08	0.09
Alnus crispa	Green Alder	0.10	0.66	0.07	0.20
Low Shrubs					
Ribes spp.	Gooseberries	0.41	0.76	0.22	0.32
Lonicera spp.	Honeysuckles	0.41	0.66	0.19	0.30
Rubus strigosus	Raspberry	0.41	0.53	0.23	0.57
Rosa acicularis	Wild Rose	0.38	0.41	0.20	0.21
Rhamnus alnifolia	Buckthorn	0.12	0.16	0.11	0.16
Ericaceous Shrubs					
Ledum groenlandicum	Labrador Tea	0.79	9.36	0.93	21.83
Gaultheria hispidula	Creeping Snowberry	0.74	1.45	0.90	2.87
Vaccinium spp.	Blueberries	0.71	1.24	0.86	2.13
Oxycoccus spp.	Cranberries	0.31	0.43	0.53	0.68
Chamaedaphne calyculata	Leatherleaf	0.21	0.81	0.36	2.86
Kalmia polyfolia	Bog-Laurel	0.19	0.26	0.39	0.55
Andromeda glaucophylla	Bog Rosemary			0.12	0.18

STAND-TYPE IV. BLACK SPRUCE - SPHAGNUM.

TABLE 2. Frequency and mean cover of common herb, fern and fern-ally taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 58*		> 85 years *n = 132*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Cornus canadensis	Bunchberry	0.86	2.22	0.64	1.45
Carex spp.	Sedges	0.74	6.98	0.77	6.17
Equisetum spp.	Horsetails	0.72	2.14	0.70	2.58
Lycopodium spp.	Club Mosses	0.55	3.19	0.36	1.29
Coptis trifolia	Goldthread	0.53	0.72	0.43	0.61
Linnaea borealis	Twinflower	0.53	0.83	0.42	0.54
Trientalis borealis	Star Flower	0.50	0.59	0.38	0.39
Maianthemum canadense	Wild Lily-of-the-Valley	0.48	0.67	0.45	0.67
Rubus pubescens	Raspberry	0.48	1.36	0.43	0.90
Smilacina trifoliata	False Solomon's Seal	0.47	0.83	0.68	1.73
Viola spp.	Violets	0.47	0.74	0.33	0.52
Aster macrophyllus	Large-leaved Aster	0.43	0.97	0.14	0.17
Clintonia borealis	Bluebead Lily	0.40	0.53	0.33	0.59
Galium triflorum	Bedstraw	0.38	0.40	0.16	0.17
Mitella nuda	Mitrewort	0.38	1.14	0.33	0.64
Petasites palmatus	Coltsfoot	0.35	0.43	0.33	0.48
Aralia nudicaulis	Wild Sarsaparilla	0.28	0.36	0.17	0.35
Dryopteris spp.	Wood Ferns	0.28	0.41	0.11	0.24
Fragaria spp.	Strawberries	0.26	0.35	0.11	0.14
Gymnocarpium dryopteris	Oak Fern	0.21	0.38	0.17	0.25
Pyrola spp.	Pyrolas	0.19	0.21	0.24	0.28
Calamagrostis canadensis	Marsh Reed Grass	0.19	0.21	0.21	0.61

STAND-TYPE IV. BLACK SPRUCE - SPHAGNUM.

TABLE 3. Frequency and mean cover of common cryptogam taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 58*		> 85 years *n = 132*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Bryophytes					
Pleurozium schreberi	Schreber's Moss	0.97	18.48	0.96	20.08
Sphagnum spp.	Peat Mosses	0.85	36.85	0.96	50.97
Dicranum polysetum	Broom Moss	0.79	1.91	0.88	1.73
Ptilium crista-castrensis	Plume Moss	0.74	3.35	0.71	3.56
Hylocomium splendens	Stair-Step Moss	0.57	1.22	0.59	3.22
Polytrichum spp.	Hair-Cap Mosses	0.41	0.69	0.43	0.88
Aulacomnium palustre	Ribbed Bog Moss	0.35	0.43	0.20	0.22
Drepanocladus uncinatus	Red Hook Moss	0.26	0.28	0.11	0.21
Plagiomnium spp.	Leafy Mosses	0.21	0.31	0.20	0.34
Ptilidium spp.	Naugehyde Liverworts	0.22	0.28	0.18	0.21
Rhytidiadelphus triquestris	Shaggy Moss	0.22	0.40	0.19	0.71
Brachythecium spp.	Ragged Mosses	0.21	0.31	0.05	0.05
Lichens					
Cladina spp.	Reindeer Lichens	0.31	0.34	0.40	0.52
Cladonia spp.	Club Lichens	0.26	0.45	0.18	0.29
Peltigera spp.	Dog Lichens			0.22	0.27

STAND-TYPE IV. BLACK SPRUCE - SPHAGNUM.

TABLE 4. Species richness, diversity and evenness in younger (≤ 85 years) and older (> 85 years) stands.

	≤ 85 years *n = 58*		> 85 years *n =132*	
	mean	s.d.	mean	s.d.
Species Richness				
All Species	36.12	12.60	31.58	12.31
Trees	2.98	1.41	2.30	1.30
Shrubs	8.40	3.44	7.72	2.72
Herbs	13.43	8.04	11.19	7.75
Cryptogams	11.31	5.07	10.36	4.30
Diversity (H)				
All Species	2.491	0.381	2.397	0.359
Trees	0.608	0.407	0.388	0.406
Shrubs	1.477	0.527	1.312	0.508
Herbs	2.058	0.705	1.811	0.850
Cryptogams	1.586	0.562	1.493	0.433
Evenness				
All Species	0.706	0.072	0.709	0.068
Trees	0.632	0.222	0.539	0.253
Shrubs	0.735	0.185	0.654	0.210
Herbs	0.862	0.175	0.859	0.148
Cryptogams	0.687	0.173	0.661	0.146

STAND-TYPE IV. BLACK SPRUCE - SPHAGNUM.

TABLE 5. Means and standard deviations of selected soil variables, in younger (≤ 85 years) and older (> 85 years) stands.

Variable	≤ 85 years			> 85 years		
	Mean	s.d.	*n*	Mean	s.d.	*n*
Organic Horizon Depth (cm)	**68.21**	68.87	*58*	**96.81**	69.27	*132*
Mineral Horizon Nitrogen (%)	**0.07**	0.06	*14*	**0.12**	0.15	*21*
Mineral Horizon Organic Matter (%)	**1.90**	1.51	*26*	**4.15**	5.41	*71*
Mineral Horizon pH	**5.65**	1.83	*14*	**6.00**	0.93	*22*
Organic Horizon Nitrogen (%)	**1.36**	0.45	*26*	**1.23**	0.46	*74*
Organic Horizon Organic Matter (%)	**61.69**	18.89	*26*	**63.17**	16.71	*41*
Organic Horizon pH	**5.11**	0.83	*26*	**4.83**	0.91	*74*
Total Base Saturation (%)	**79.75**	28.50	*14*	**80.83**	24.45	*20*
Total Exchangable Bases (meq/100g)	**2.08**	1.47	*14*	**2.66**	2.44	*20*

APPENDIX V

STAND-TYPE V: WHITE SPRUCE - BALSAM FIR MIXED WOOD

STAND-TYPE V. WHITE SPRUCE - BALSAM FIR MIXED WOOD.

TABLE 1. Frequency and mean cover of common shrub taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n* = 78		> 85 years *n* = 39	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Tall Shrubs					
Sorbus spp.	Mountain-Ashes	0.72	0.96	0.74	1.08
Amelanchier spp.	Serviceberries	0.65	1.09	0.51	0.85
Acer spicatum	Mountain Maple	0.54	3.42	0.74	11.26
Corylus cornuta	Beaked Hazel	0.41	3.15	0.46	3.05
Viburnum spp.	Viburnums	0.40	0.68	0.51	0.77
Cornus stolonifera	Red-Osier Dogwood	0.28	0.46	0.26	0.82
Alnus rugosa	Speckled Alder	0.24	1.99	0.18	4.44
Prunus spp.	Cherries	0.14	0.24	0.18	0.59
Salix spp.	Willows	0.14	0.14	0.05	0.05
Alnus crispa	Green Alder	0.13	0.45	0.05	0.23
Low Shrubs					
Diervilla lonicera	Low-Bush Honeysuckle	0.76	3.53	0.54	1.39
Rosa acicularis	Wild Rose	0.62	0.69	0.44	0.51
Ribes spp.	Gooseberries	0.47	0.74	0.46	0.64
Lonicera spp.	Honeysuckles	0.27	0.36	0.36	0.54
Rubus strigosus	Raspberry	0.26	0.63	0.13	0.15
Ericaceous Shrubs					
Vaccinium spp.	Blueberries	0.67	1.10	0.51	0.92
Gaultheria hispidula	Creeping Snowberry	0.28	0.35	0.31	0.31
Ledum groenlandicum	Labrador Tea	0.15	0.19	0.18	0.31

STAND-TYPE V. WHITE SPRUCE - BALSAM FIR MIXED WOOD.

TABLE 2. Frequency and mean cover of common herb, fern and fern-ally taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n* = 78		> 85 years *n* = 39	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Cornus canadensis	Bunchberry	0.96	4.58	0.82	4.59
Clintonia borealis	Bluebead Lily	0.91	2.21	0.85	1.18
Maianthemum canadense	Wild Lily-of-the-Valley	0.90	1.78	0.80	1.39
Aralia nudicaulis	Wild Sarsaparilla	0.87	3.01	0.74	1.82
Trientalis borealis	Star Flower	0.80	0.81	0.80	0.82
Linnaea borealis	Twinflower	0.78	1.37	0.85	1.39
Rubus pubescens	Dewberry	0.76	2.22	0.64	2.13
Lycopodium spp.	Club Mosses	0.74	2.59	0.59	1.39
Viola spp.	Violets	0.74	1.27	0.62	1.08
Streptopus roseus	Twistedstalk	0.72	0.83	0.80	0.85
Aster macrophyllus	Large-leaved Aster	0.65	1.53	0.36	1.41
Coptis trifolia	Goldthread	0.62	0.76	0.56	1.03
Galium triflorum	Bedstraws	0.51	0.56	0.56	0.67
Petasites palmatus	Coltsfoot	0.49	0.51	0.41	0.46
Pyrola spp.	Pyrolas	0.46	0.62	0.31	0.41
Carex spp.	Sedges	0.44	0.69	0.33	0.67
Equisetum spp.	Horsetails	0.44	0.89	0.36	0.41
Fragaria spp.	Strawberries	0.44	0.44	0.36	0.39
Mitella nuda	Mitrewort	0.44	1.13	0.56	1.39
Dryopteris spp.	Wood Ferns	0.41	0.78	0.23	0.54
Anemone spp.	Wood Anemones	0.40	0.41	0.33	0.36
Oryzopsis spp.	Rice Grasses	0.35	0.37	0.26	0.26
Goodyera repens	Rattlesnake Plantain	0.33	0.33	0.15	0.15
Actaea rubra	Baneberry	0.32	0.33	0.33	0.33
Mertensia peniculata	Virginia Bluebells	0.26	0.31	0.41	0.62
Gymnocarpium dryopteris	Oak Fern	0.24	0.27	0.44	0.59
Cinna latifolia	Wood Reed Grass	0.23	0.23	0.18	0.18
Moneses uniflora	One-Flower Wintergreen	0.22	0.23	0.21	0.21
Schizachne purpureus	Purple Oatgrass	0.22	0.27	0.18	0.74
Calamagrostis canadensis	Marsh Reed Grass	0.21	0.31	0.28	0.36
Luzula spp.	Wood Rushes	0.21	0.21	0.13	0.13

STAND-TYPE V. WHITE SPRUCE - BALSAM FIR MIXED WOOD.

TABLE 3. Frequency and mean cover of common cryptogam taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 78*		> 85 years *n = 39*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Bryophytes					
Pleurozium schreberi	Schreber's Moss	0.97	29.97	1.00	20.90
Dicranum polysetum	Broom Moss	0.87	2.18	0.85	2.00
Ptilium crista-castrensis	Plume Moss	0.85	3.39	0.80	4.36
Hylocomium splendens	Stair-Step Moss	0.62	1.73	0.72	5.87
Rhytidiadelphus triquestris	Shaggy Moss	0.50	2.89	0.56	7.44
Brachythecium spp.	Ragged Mosses	0.47	5.77	0.54	2.39
Drepanocladus uncinatus	Red Hook Moss	0.47	1.04	0.62	0.90
Plagiomnium spp.	Leafy Mosses	0.45	2.32	0.44	0.82
Ptilidium spp.	Naugehyde Liverworts	0.35	0.36	0.39	0.41
Polytrichum spp.	Hair-Cap Mosses	0.32	0.39	0.26	0.39
Thuidium spp.	Fern Mosses	0.22	0.33	0.18	0.18
Hypnum spp.	Pig-Tail Mosses	0.21	0.31	0.26	0.39
Lichens					
Cladonia spp.	Club Lichens	0.39	0.60	0.41	0.74
Peltigera spp.	Dog Lichens	0.28	0.30	0.46	0.56

STAND-TYPE V. WHITE SPRUCE - BALSAM FIR MIXED WOOD.

TABLE 4. Species richness, diversity and evenness in younger (≤ 85 years) and older (> 85 years) stands.

	≤ 85 years *n = 78*		> 85 years *n = 39*	
	mean	s.d.	mean	s.d.
Species Richness				
All Species	41.19	40.85	39.59	11.82
Trees	3.82	3.79	3.82	1.07
Shrubs	8.03	7.99	7.56	3.70
Herbs	19.30	19.15	16.85	6.77
Cryptogams	10.05	10.06	11.36	5.85
Diversity (H)				
All Species	2.539	2.672	2.536	0.322
Trees	0.958	0.340	0.961	0.273
Shrubs	1.680	0.455	1.450	0.667
Herbs	2.643	0.437	2.488	0.496
Cryptogams	1.294	0.299	1.453	0.361
Evenness				
All Species	0.688	0.871	0.698	0.063
Trees	0.720	0.201	0.749	0.169
Shrubs	0.847	0.166	0.746	0.240
Herbs	0.910	0.107	0.912	0.115
Cryptogams	0.582	0.123	0.619	0.117

STAND-TYPE V. WHITE SPRUCE - BALSAM FIR MIXED WOOD.

TABLE 5. Means and standard deviations of selected soil variables, in younger (≤ 85 years) and older (> 85 years) stands.

Variable	≤ 85 years			> 85 years		
	Mean	s.d.	*n*	Mean	s.d.	*n*
Organic Horizon Depth (cm)	**8.60**	8.70	*78*	**10.82**	7.82	*39*
Mineral Horizon Nitrogen (%)	**0.04**	1.10	*33*	**0.07**	0.05	*17*
Mineral Horizon Organic Matter (%)	**1.56**	2.54	*33*	**1.90**	1.91	*17*
Mineral Horizon pH	**5.40**	5.92	*55*	**5.53**	0.82	*28*
Organic Horizon Nitrogen (%)	**1.31**	2.27	*32*	**1.36**	0.22	*17*
Organic Horizon Organic Matter (%)	**60.84**	59.99	*33*	**62.39**	10.15	*17*
Organic Horizon pH	**4.89**	5.65	*33*	**4.95**	0.60	*17*
Total Base Saturation (%)	**81.10**	79.79	*32*	**83.66**	11.40	*16*
Total Exchangable Bases (meq/100g)	**3.14**	4.16	*32*	**2.24**	1.89	*16*

Appendix VI

Stand-Type VI: Trembling Aspen

STAND-TYPE VI. TREMBLING ASPEN.

TABLE 1. Frequency and mean cover of common shrub taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 130*		> 85 years *n = 66*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Tall Shrubs					
Corylus cornuta	Beaked Hazelnut	0.75	11.23	0.62	7.11
Acer spicatum	Mountain Maple	0.72	13.41	0.70	13.24
Amelanchier spp.	Serviceberries	0.63	1.87	0.67	1.53
Cornus stolonifera	Red-Osier Dogwood	0.51	1.62	0.42	1.68
Viburnum spp.	Viburnums	0.45	1.40	0.56	1.08
Sorbus spp.	Mountain-Ashes	0.42	0.57	0.68	1.05
Prunus spp.	Cherries	0.35	0.99	0.29	0.53
Alnus rugosa	Speckled Alder	0.21	1.92	0.36	6.23
Salix spp.	Willows	0.20	0.38	0.09	0.30
Alnus crispa	Green Alder	0.19	1.75	0.18	1.50
Low Shrubs					
Diervilla lonicera	Low-Bush Honeysuckle	0.79	6.95	0.76	4.42
Rosa acicularis	Wild Rose	0.65	0.95	0.52	0.61
Ribes spp.	Gooseberries	0.54	0.88	0.59	0.94
Lonicera spp.	Honeysuckles	0.53	0.82	0.56	0.92
Rubus strigosus	Raspberry	0.35	1.15	0.29	1.20
Ericaceous Shrubs					
Vaccinium spp.	Blueberries	0.47	0.71	0.42	0.79
Gaultheria hispidula	Wintergreen	0.05	0.05	0.15	0.15
Ledum groenlandicum	Labrador Tea	0.05	0.06	0.14	0.30

STAND-TYPE VI. TREMBLING ASPEN.

TABLE 2. Frequency and mean cover of common herb taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 130*		> 85 years *n = 66*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Aralia nudicaulis	Wild Sarsaparilla	0.95	5.90	0.88	4.91
Maianthemum canadense	Wild Lily-of-the-Valley	0.94	1.72	0.92	1.39
Aster macrophyllus	Large-leaved Aster	0.91	11.47	0.82	8.17
Streptopus roseus	Twistedstalk	0.84	1.50	0.83	1.24
Rubus pubescens	Dewberry	0.83	2.04	0.85	3.11
Cornus canadensis	Bunchberry	0.79	1.88	0.89	3.21
Clintonia borealis	Bluebead Lily	0.77	1.75	0.88	2.46
Viola spp.	Violets	0.75	1.09	0.85	1.36
Galium spp.	Bedstraws	0.75	0.86	0.74	0.85
Trientalis borealis	Star Flower	0.68	0.70	0.77	0.83
Lycopodium spp.	Club Mosses	0.55	1.63	0.58	1.61
Pyrola spp.	Pyrolas	0.53	0.88	0.47	0.80
Mitella nuda	Mitrewort	0.52	1.22	0.70	2.29
Fragaria spp.	Strawberries	0.51	0.55	0.47	0.62
Actaea rubra	Baneberry	0.49	0.52	0.47	0.47
Anemone spp.	Wood Anemones	0.48	0.49	0.47	0.67
Linnaea borealis	Twinflower	0.48	0.77	0.64	0.94
Petasites palmatus	Coltsfoot	0.43	0.53	0.50	0.70
Oryzopsis spp.	Rice Grasses	0.39	0.52	0.41	0.46
Carex spp.	Sedges	0.38	0.87	0.47	1.24
Equisetum spp.	Horsetails	0.33	0.37	0.33	0.49
Coptis trifolia	Goldthread	0.32	0.35	0.41	0.49
Lathyrus spp.	Peavines	0.32	0.42	0.17	0.20
Dryopteris spp.	Wood Ferns	0.25	0.33	0.33	0.49
Pteridium aquilinum	Bracken Fern	0.25	1.29	0.20	0.64
Epilobium angustifolium	Fireweed	0.22	0.30	0.18	0.18
Sanicula marilandica	Snakeroot	0.21	0.25	0.11	0.12
Athyrium felix-femina	Lady Fern	0.20	0.49	0.26	0.67
Gymnocarpium dryopteris	Oak Fern	0.20	0.25	0.27	0.41
Mertensia paniculata	Virginia Bluebells	0.19	0.22	0.42	0.64
Cinna latifolia	Wood Reed Grass	0.17	0.17	0.21	0.21
Calamagrostis canadensis	Marsh Reed Grass	0.15	0.44	0.26	0.33
Goodyera repens	Rattlesnake Plantain	0.05	0.05	0.27	0.27

STAND-TYPE VI. TREMBLING ASPEN.

TABLE 3. Frequency and mean cover of common cryptogam taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years n = 130		> 85 years n = 66	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Bryophytes					
Pleurozium schreberi	Schreber's Moss	0.77	1.79	0.83	3.20
Plagiomnium spp.	Leafy Mosses	0.64	0.73	0.61	1.00
Dicranum polysetum	Broom Mosses	0.46	0.75	0.62	1.20
Drepanocladus uncinatus	Red Hook Moss	0.45	0.61	0.58	0.85
Brachythecium spp.	Ragged Mosses	0.42	0.83	0.55	0.92
Ptilium crista-castrensis	Plume Moss	0.34	0.35	0.64	1.09
Rhytidiadelphus triquestris	Shaggy Moss	0.30	0.58	0.59	1.91
Hylocomium splendens	Stair-Step Moss	0.29	0.37	0.47	2.02
Callicladium haldanianum	Shiny-Leaf Moss	0.25	0.29	0.24	0.30
Ptilidium spp.	Naugehyde Liverworts	0.20	0.20	0.32	0.32
Hypnum spp.	Pig-Tail Mosses	0.17	0.21	0.21	0.30
Polytrichum spp.	Hair-Cap Mosses	0.15	0.17	0.20	0.20
Lichens					
Peltigera spp.	Dog Lichens	0.35	0.35	0.38	0.46
Cladonia spp.	Club Lichens	0.32	0.48	0.30	0.52

STAND-TYPE VI. TREMBLING ASPEN.

TABLE 4. Species richness, diversity and evenness in younger (≤ 85 years) and older (> 85 years) stands.

	≤ 85 years *n =130*		> 85 years *n = 66*	
	mean	s.d.	mean	s.d.
Species Richness				
All Species	38.37	9.65	42.62	10.35
Trees	3.87	1.23	4.14	1.12
Shrubs	8.97	3.12	9.09	3.09
Herbs	18.83	5.50	20.36	5.55
Cryptogams	6.70	4.66	9.03	6.01
Diversity (H)				
All Species	2.531	0.424	2.601	0.358
Trees	0.903	0.380	1.038	0.261
Shrubs	1.530	0.515	1.545	0.465
Herbs	2.406	0.543	2.522	0.437
Cryptogams	1.583	0.711	1.775	0.805
Evenness				
All Species	0.698	0.094	0.697	0.072
Trees	0.681	0.216	0.754	0.139
Shrubs	0.716	0.207	0.722	0.198
Herbs	0.831	0.160	0.848	0.125
Cryptogams	0.958	0.066	0.913	0.121

STAND-TYPE VI. TREMBLING ASPEN.

TABLE 5. Means and standard deviations of selected soil variables, in younger (≤ 85 years) and older (> 85 years) stands.

Variable	≤ 85 years			> 85 years		
	Mean	s.d.	*n*	Mean	s.d.	*n*
Organic Horizon Depth (cm)	**8.16**	5.14	*131*	**9.08**	4.60	*65*
Mineral Horizon Nitrogen (%)	**0.08**	0.08	*66*	**0.07**	0.06	*21*
Mineral Horizon Organic Matter (%)	**2.61**	5.92	*66*	**1.71**	1.49	*21*
Mineral Horizon pH	**5.49**	0.92	*88*	**5.86**	0.96	*39*
Organic Horizon Nitrogen (%)	**1.44**	0.33	*65*	**1.47**	0.30	*21*
Organic Horizon Organic Matter (%)	**55.56**	10.90	*65*	**54.82**	9.56	*21*
Organic Horizon pH	**5.65**	0.69	*66*	**5.31**	0.51	*21*
Total Base Saturation (%)	**82.54**	20.39	*66*	**86.69**	16.76	*20*
Total Exchangable Bases (meq/100g)	**3.12**	2.68	*66*	**2.45**	1.42	*20*

APPENDIX VII

STAND-TYPE VII: BIRCH - TREMBLING ASPEN MIXED WOOD

STAND-TYPE VII. BIRCH - TREMBLING ASPEN MIXED WOOD.

TABLE 1. Frequency and mean cover of shrub taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 65*		> 85 years *n = 31*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Tall Shrubs					
Amelanchier spp.	Serviceberries	0.77	2.55	0.81	1.87
Alnus crispa	Green Alder	0.68	7.20	0.52	5.26
Corylus cornuta	Beaked Hazelnut	0.55	10.17	0.55	7.23
Sorbus spp.	Mountain Ashes	0.49	0.65	0.42	0.77
Salix spp.	Willows	0.40	0.72	0.32	0.74
Acer spicatum	Mountain Maple	0.34	1.40	0.42	1.74
Prunus spp.	Cherries	0.26	0.40	0.19	0.42
Viburnum spp.	Viburnums	0.22	0.59	0.39	0.84
Cornus stolonifera	Red-Osier Dogwood	0.19	0.66	0.19	0.65
Alnus rugosa	Speckled Alder	0.09	1.12	0.16	0.65
Low Shrubs					
Diervilla lonicera	Low-Bush Honeysuckle	0.92	12.59	0.71	7.55
Rosa acicularis	Wild Rose	0.54	0.75	0.48	0.74
Lonicera spp.	Honeysuckles	0.32	0.46	0.19	0.19
Rubus strigosus	Raspberry	0.28	0.46	0.29	0.58
Ribes spp.	Gooseberries	0.26	0.43	0.39	0.65
Chimaphila umbellata	Prince's Pine	0.15	0.15	0.13	0.13
Ericaceous Shrubs					
Vaccinium spp.	Blueberries	0.92	3.28	0.87	7.45
Ledum groenlandicum	Labrador Tea	0.25	2.69	0.36	3.13
Gaultheria hispidula	Creeping Snowberry	0.14	0.15	0.29	0.29

STAND-TYPE VII. BIRCH - TREMBLING ASPEN MIXED WOOD.

TABLE 2. Frequency and mean cover of herb, fern and fern-ally taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n* = 65		> 85 years *n* = 31	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Maianthemum canadense	Wild Lily-of-the-Valley	0.94	2.06	1.00	1.84
Cornus canadensis	Bunchberry	0.91	5.59	0.97	4.74
Aralia nudicaulis	Wild Sarsaparilla	0.86	4.49	0.94	4.10
Clintonia borealis	Bluebead Lily	0.86	2.28	0.90	2.52
Lycopodium spp.	Club Mosses	0.82	3.62	0.77	3.03
Aster macrophyllus	Large-leaved Aster	0.74	10.89	0.65	5.32
Trientalis borealis	Starflower	0.65	0.69	0.55	0.55
Linnaea borealis	Twinflower	0.59	0.75	0.74	0.90
Rubus pubescens	Dewberry	0.57	0.88	0.52	1.13
Streptopus roseus	Twistedstalk	0.54	0.59	0.61	0.68
Fragaria spp.	Strawberries	0.48	0.65	0.32	0.36
Oryzopsis spp.	Rice Grasses	0.42	0.59	0.55	0.58
Galium triflorum	Bedstraw	0.42	0.49	0.36	0.45
Viola spp.	Violets	0.39	0.54	0.42	0.71
Pyrola spp.	Pyrolas	0.39	0.51	0.42	0.61
Epilobium angustifolium	Fireweed	0.39	0.43	0.36	0.36
Coptis trifolia	Goldthread	0.34	0.45	0.23	0.26
Melampyrum lineare	Cow-Wheat	0.32	0.34	0.19	0.19
Dryopteris spp.	Wood Ferns	0.28	0.29	0.26	0.32
Pteridium aquilinum	Bracken Fern	0.23	1.49	0.23	0.84
Equisetum spp.	Horsetails	0.23	0.28	0.13	0.29
Anemone canadensis	Canada Anemone	0.23	0.23	0.23	0.23
Petasites palmatus	Coltsfoot	0.23	0.23	0.29	0.45
Lathyrus spp.	Peavines	0.22	0.34	0.16	0.23
Apocynum androsaemifolium	Dogbane			0.23	0.23

STAND-TYPE VII. BIRCH - TREMBLING ASPEN MIXED WOOD.

TABLE 3. Frequency and mean cover of cryptogam taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 65*		> 85 years *n = 31*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Bryophytes					
Pleurozium schreberi	Schreber's Moss	0.92	4.31	0.94	9.77
Dicranum polysetum	Broom Moss	0.79	1.79	0.84	1.74
Ptilium crista-castrensis	Plume Moss	0.40	0.68	0.55	2.10
Plagiomnium spp.	Leafy Mosses	0.26	0.32	0.32	0.42
Polytrichum spp.	Hair-Cap Mosses	0.26	0.29	0.39	0.48
Hypnum spp.	Pig-Tail Mosses	0.23	0.25	0.13	0.19
Brachythecium spp.	Ragged Mosses	0.22	0.32	0.29	0.58
Drepanocladus spp.	Red Hook Mosses	0.14	0.15	0.26	0.36
Hylocomium splendens	Stair-Step Moss	0.12	0.14	0.48	0.84
Ptilidium spp.	Naugehyde Liverworts	0.12	0.12	0.19	0.23
Rhytidiadelphus triquestrus	Shaggy Moss			0.36	0.48
Lichens					
Cladonia spp.	Club Lichens	0.20	0.35	0.39	0.68
Cladina spp.	Reindeer Lichens	0.17	0.25	0.26	0.32
Peltigera spp.	Dog Lichens	0.15	0.17	0.36	0.39

STAND-TYPE VII. BIRCH - TREMBLING ASPEN MIXED WOOD.

TABLE 4. Species richness, diversity and evenness in younger (≤ 85 years) and older (> 85 years) stands.

	≤ 85 years *n = 65*		> 85 years *n = 31*	
	mean	s.d.	mean	s.d.
Species Richness				
All Species	33.92	7.45	37.00	9.31
Trees	4.46	1.19	4.52	1.71
Shrubs	8.82	2.78	9.23	3.06
Herbs	15.09	4.36	15.68	5.81
Cryptogams	5.55	3.91	7.58	4.34
Diversity (H)				
All Species	2.547	0.315	2.718	0.332
Trees	0.971	0.379	1.125	0.323
Shrubs	1.468	0.467	1.615	0.443
Herbs	2.105	0.480	2.301	0.432
Cryptogams	1.311	0.738	1.440	0.669
Evenness				
All Species	0.728	0.079	0.758	0.067
Trees	0.650	0.185	0.783	0.113
Shrubs	0.687	0.182	0.744	0.165
Herbs	0.787	0.158	0.854	0.102
Cryptogams	0.871	0.179	0.786	0.217

STAND-TYPE VII. BIRCH - TREMBLING ASPEN MIXED WOOD.

TABLE 5. Means and standard deviations of selected soil variables, in younger (≤ 85 years) and older (> 85 years) stands.

Variable	≤ 85 years			> 85 years		
	Mean	s.d.	*n*	Mean	s.d.	*n*
Organic Horizon Depth (cm)	**7.26**	4.82	*65*	**7.90**	3.08	*31*
Mineral Horizon Nitrogen (%)	**0.07**	0.05	*42*	**0.09**	0.07	*19*
Mineral Horizon Organic Matter (%)	**1.65**	1.12	*44*	**2.84**	4.05	*19*
Mineral Horizon pH	**5.19**	0.58	*55*	**5.28**	0.64	*27*
Organic Horizon Nitrogen (%)	**1.31**	0.34	*40*	**1.30**	0.30	*20*
Organic Horizon Organic Matter (%)	**58.26**	14.45	*44*	**63.10**	12.28	*20*
Organic Horizon pH	**5.01**	0.57	*44*	**5.13**	0.77	*20*
Total Base Saturation (%)	**76.31**	18.76	*44*	**77.03**	20.25	*17*
Total Exchangable Bases (meq/100g)	**2.14**	2.79	*44*	**2.04**	1.61	*17*

Appendix VIII

Stand-Type VIII: Red Pine

STAND-TYPE VIII. RED PINE.

TABLE 1. Frequency and mean cover of shrub taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 18*		> 85 years *n = 44*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Tall Shrubs					
Amelanchier spp.	Serviceberries	0.67	1.22	0.48	0.71
Alnus crispa	Green Alder	0.50	1.22	0.34	1.02
Salix spp.	Willows	0.44	0.44	0.21	0.23
Corylus cornuta	Beaked Hazelnut	0.39	4.89	0.50	4.59
Acer spicatum	Mountain Maple	0.22	2.67	0.48	1.46
Prunus spp.	Cherries	0.22	0.67	0.09	0.11
Shepherdia canadensis	Buffalo Berry	0.17	0.22	0.05	0.05
Sorbus spp.	Mountain-Ashes	0.06	0.06	0.39	0.48
Cornus stolonifera	Red-Osier Dogwood	0.06	0.17	0.16	0.57
Low Shrubs					
Diervilla lonicera	Low-Bush Honeysuckle	0.94	3.56	0.77	3.30
Chimaphila umbellata	Prince's Pine	0.72	0.72	0.64	0.68
Rosa acicularis	Wild Rose	0.33	0.72	0.32	0.50
Lonicera spp.	Honeysuckles	0.33	0.33	0.30	0.50
Rubus strigosus	Raspberry	0.22	0.22	0.09	0.09
Juniperus communis	Juniper	0.11	0.17	0.11	0.50
Ericaceous Shrubs					
Vaccinium spp.	Blueberries	0.94	2.56	0.93	5.23
Gaultheria procumbens	Wintergreen	0.39	0.89	0.11	0.18
Gaultheria hispidula	Creeping Snowberry	0.17	0.22	0.39	0.50
Arctostaphylos uva-ursi	Bearberry	0.22	0.78	0.25	2.00
Epigaea repens	Trailing Arbutus	0.11	0.11	0.09	0.09
Ledum groenlandicum	Labrador Tea	0.06	0.06	0.14	0.16

STAND-TYPE VIII. RED PINE.

TABLE 2. Frequency and mean cover of herb, fern and fern-ally taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 18*		> 85 years *n = 44*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Maianthemum canadense	Wild Lily-of-the-Valley	1.00	2.39	0.93	2.23
Aralia nudicaulis	Wild Sarsaparilla	0.83	1.17	0.89	2.00
Lycopodium spp.	Club Mosses	0.67	1.83	0.59	1.25
Cornus canadensis	Bunchberry	0.61	1.17	0.73	2.14
Aster macrophyllus	Large-leaved Aster	0.56	3.89	0.39	2.64
Oryzopsis spp.	Rice Grasses	0.44	0.78	0.43	0.64
Linnaea borealis	Twinflower	0.44	0.72	0.84	1.75
Melampyrum lineare	Cow-Wheat	0.44	0.44	0.21	0.21
Clintonia borealis	Bluebead Lily	0.33	0.61	0.48	0.71
Lathyrus spp.	Peavines	0.33	0.44	0.18	0.27
Polypodium vulgare	Rock Polypody	0.33	0.39	0.27	0.36
Fragaria spp.	Strawberries	0.33	0.33	0.21	0.25
Viola spp.	Violets	0.28	0.33	0.14	0.14
Trientalis borealis	Starflower	0.28	0.28	0.25	0.25
Pteridium aquilinum	Bracken Fern	0.22	0.61	0.14	0.25
Agropyron spp.	Wheat Grasses	0.22	0.22	0.02	0.02
Anemone canadensis	Canada Anemone	0.22	0.22	0.05	0.05
Corallorhiza spp.	Coral Root	0.22	0.22		
Streptopus roseus	Twistedstalk	0.22	0.22	0.18	0.18
Pyrola spp.	Pyrolas	0.17	0.17	0.36	0.48
Goodyera repens	Rattlesnake Plantain	0.17	0.17	0.25	0.25
Rubus pubescens	Dewberry	0.17	0.17	0.25	0.25
Apocynum androsaemifolium	Dogbane	0.17	0.22	0.21	0.30

STAND-TYPE VIII. RED PINE.

TABLE 3. Frequency and mean cover of cryptogam taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 18*		> 85 years *n = 44*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Bryophytes					
Dicranum polysetum	Broom Moss	1.00	7.11	0.98	6.52
Pleurozium schreberi	Schreber's Moss	0.94	17.67	0.98	25.52
Hylocomium splendens	Stair-Step Moss	0.33	0.33	0.32	0.52
Ptilium crista-castrensis	Plume Moss	0.28	0.33	0.32	0.75
Plagiomnium spp.	Leafy Mosses	0.17	0.17	0.14	0.14
Polytrichum spp.	Hair-Cap Mosses	0.17	0.17	0.25	0.25
Lichens					
Cladina spp.	Reindeer Lichens	0.72	1.89	0.36	0.59
Cladonia spp.	Club Lichens	0.28	0.39	0.14	0.18
Peltigera spp.	Dog Lichens	0.28	0.39	0.23	0.32

STAND-TYPE VIII. RED PINE.

TABLE 4. Species richness, diversity and evenness in younger (≤ 85 years) and older (> 85 years) stands.

GROUPVIII	≤ 85 years *n = 18*		> 85 years *n = 44*	
	mean	s.d.	mean	s.d.
Species Richness				
All Species	28.83	6.25	27.36	7.96
Trees	4.72	1.45	5.18	1.66
Shrubs	7.89	2.03	7.66	3.13
Herbs	10.44	3.71	9.39	3.82
Cryptogams	5.78	2.29	5.14	2.44
Diversity (H)				
All Species	2.482	0.394	2.294	0.407
Trees	0.994	0.430	1.040	0.372
Shrubs	1.702	0.294	1.649	0.393
Herbs	2.010	0.472	1.920	0.582
Cryptogams	1.213	0.443	1.009	0.558
Evenness				
All Species	0.741	0.092	0.699	0.087
Trees	0.641	0.214	0.654	0.174
Shrubs	0.843	0.137	0.855	0.151
Herbs	0.883	0.088	0.907	0.110
Cryptogams	0.736	0.187	0.658	0.264

STAND-TYPE VIII. RED PINE.

TABLE 5. Means and standard deviations of selected soil variables, in younger (≤ 85 years) and older (> 85 years) stands.

Variable	≤ 85 years			> 85 years		
	Mean	s.d.	*n*	Mean	s.d.	*n*
Organic Horizon Depth (cm)	**5.78**	2.94	*18*	**6.82**	2.79	*44*
Mineral Horizon Nitrogen (%)	**0.07**	0.05	*16*	**0.05**	0.04	*36*
Mineral Horizon Organic Matter (%)	**3.46**	4.99	*16*	**1.53**	1.18	*36*
Mineral Horizon pH	**5.47**	0.43	*16*	**5.39**	0.51	*39*
Organic Horizon Nitrogen (%)	**0.96**	0.23	*17*	**1.01**	0.26	*36*
Organic Horizon Organic Matter (%)	**63.20**	11.14	*17*	**59.55**	9.58	*36*
Organic Horizon pH	**4.66**	0.45	*17*	**4.64**	0.54	*36*
Total Base Saturation (%)	**75.83**	15.70	*16*	**78.11**	17.71	*36*
Total Exchangable Bases (meq/100g)	**1.14**	0.59	*16*	**1.30**	0.90	*36*

APPENDIX IX

STAND-TYPE IX: WHITE PINE

STAND-TYPE IX. WHITE PINE.

TABLE 1. Frequency and mean cover of shrub taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 14*		> 85 years *n = 30*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Tall Shrubs					
Corylus cornuta	Beaked Hazelnut	0.79	10.14	0.63	5.90
Acer spicatum	Mountain Maple	0.71	6.29	0.70	15.07
Amelanchier spp.	Serviceberries	0.71	2.00	0.50	0.77
Alnus crispa	Green Alder	0.50	1.64		
Cornus stolonifera	Red-Osier Dogwood	0.43	1.43	0.17	1.67
Sorbus spp.	Mountain Ashes	0.29	0.29	0.37	0.53
Salix spp.	Willows	0.21	1.36	0.13	0.23
Prunus spp.	Cherries	0.14	0.86	0.17	0.20
Viburnum spp.	Cranberries	0.07	0.71	0.17	0.33
Low Shrubs					
Diervilla lonicera	Low-Bush Honeysuckle	0.71	6.29	0.53	1.03
Rubus strigosus	Raspberry	0.64	5.79	0.27	0.27
Lonicera spp.	Honeysuckles	0.57	0.93	0.60	0.87
Rosa acicularis	Wild Rose	0.43	0.57	0.37	0.63
Chimaphila umbellata	Princes's Pine	0.29	0.29	0.40	0.60
Ribes spp.	Gooseberries			0.20	0.27
Juniperus communis	Juniper			0.17	1.27
Ericaceous Shrubs					
Vaccinium spp.	Blueberries	0.50	2.29	0.63	1.43
Gaultheria procumbens	Wintergreen	0.29	0.43	0.03	0.03
Arctostaphylos uva-ursi	Bearberry			0.13	0.33

STAND-TYPE IX. WHITE PINE.

TABLE 2. Frequency and mean cover of herb, fern and fern-ally taxa, in younger (≤85 years) and older (>85 years) stands.

Species	Common Name	≤ 85 years *n = 14*		> 85 years *n = 30*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Aster macrophyllus	Large-leaved Aster	0.86	13.14	0.53	2.20
Aralia nudicaulis	Wild Sarsaparilla	0.86	9.21	0.87	1.67
Oryzopsis spp.	Rice Grasses	0.79	0.86	0.53	1.03
Cornus canadensis	Bunchberry	0.71	2.79	0.67	1.43
Lycopodium spp.	Club Mosses	0.64	1.86	0.47	1.27
Clintonia borealis	Bluebead Lily	0.57	1.21	0.53	0.77
Streptopus roseus	Twistedstalk	0.50	0.64	0.40	0.40
Linnaea borealis	Twinflower	0.50	0.57	0.77	1.03
Pyrola spp.	Pyrolas	0.50	0.57	0.37	0.50
Rubus pubescens	Dewberry	0.43	0.57	0.43	0.57
Trientalis borealis	Starflower	0.43	0.43	0.50	0.50
Pteridium aquilinum	Bracken Fern	0.36	2.07	0.07	0.10
Fragaria spp.	Strawberries	0.36	0.43	0.37	0.50
Viola spp.	Violets	0.36	0.36	0.30	0.30
Lathyrus spp.	Peavines	0.29	0.43	0.27	0.30
Actaea rubra	Baneberry	0.29	0.29	0.07	0.07
Anemone canadensis	Canada Anemone	0.29	0.29		
Galium triflorum	Bedstraws	0.21	0.21	0.27	0.47
Mitella nuda	Mitrewort	0.21	0.21	0.17	0.23
Moneses uniflora	One-Flower Wintergreen	0.21	0.21	0.07	0.07
Maianthemum canadense	Wild Lily-of-the-Valley	0.93	3.79	0.90	2.37
Polypodium vulgare	Rock Polypody	0.14	0.14	0.57	0.83
Coptis trifolia	Goldthread	0.14	0.14	0.23	0.40

STAND-TYPE IX. WHITE PINE.

TABLE 3. Frequency and mean cover of cryptogam taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 14*		> 85 years *n = 30*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Bryophytes					
Pleurozium schreberi	Schreber's Moss	0.71	2.64	0.87	7.80
Dicranum polysetum	Broom Moss	0.64	2.00	0.87	3.93
Drepanocladus uncinatus	Red Hook Moss	0.29	0.29	0.20	0.20
Brachythecium spp.	Ragged Moss	0.21	0.29	0.07	0.07
Callicladium haldanianum	Shiny-Leaf Moss	0.21	0.21		
Hypnum spp.	Pig-Tail Mosses	0.21	0.21	0.23	0.27
Polytrichum spp.	Hair-Cap Mosses	0.21	0.21	0.30	0.33
Ptilium crista-castrensis	Plume Moss	0.21	0.21	0.40	0.53
Lichens					
Cladina spp.	Reindeer Lichens	0.21	0.21	0.30	0.93
Cladonia spp.	Club Lichens			0.20	0.23
Peltigera spp.	Dog Lichens	0.14	0.14	0.17	0.20

STAND-TYPE IX. WHITE PINE.

TABLE 4. Species richness, diversity and evenness in younger (≤ 85 years) and older (> 85 years) stands.

	≤ 85 years *n = 14* mean	s.d.	> 85 years *n = 30* mean	s.d.
Species Richness				
All Species	30.43	7.41	29.00	7.31
Trees	5.00	1.41	4.57	1.89
Shrubs	7.64	2.53	7.03	2.81
Herbs	13.00	3.94	11.50	4.70
Cryptogams	4.79	3.12	5.90	3.27
Diversity (H)				
All Species	2.392	0.219	2.336	0.470
Trees	1.109	0.312	1.022	0.414
Shrubs	1.445	0.294	1.426	0.533
Herbs	1.979	0.528	2.166	0.580
Cryptogams	1.236	0.806	1.454	0.682
Evenness				
All Species	0.707	0.036	0.698	0.119
Trees	0.700	0.142	0.717	0.180
Shrubs	0.738	0.113	0.763	0.225
Herbs	0.784	0.169	0.928	0.072
Cryptogams	0.941	0.105	0.875	0.187

STAND-TYPE IX. WHITE PINE.

TABLE 5. Means and standard deviations of selected soil variables, in younger (≤ 85 years) and older (> 85 years) stands.

Variable	≤ 85 years			> 85 years		
	Mean	s.d.	*n*	Mean	s.d.	*n*
Organic Horizon Depth (cm)	**6.07**	1.73	*12*	**8.53**	4.70	*32*
Mineral Horizon Nitrogen (%)	**0.09**	0.06	*5*	**0.10**	0.09	*20*
Mineral Horizon Organic Matter (%)	**2.53**	2.13	*5*	**3.06**	3.12	*20*
Mineral Horizon pH	**5.04**	0.36	*8*	**5.48**	0.52	*23*
Organic Horizon Nitrogen (%)	**1.16**	0.24	*5*	**1.16**	0.27	*23*
Organic Horizon Organic Matter (%)	**58.18**	8.68	*5*	**58.92**	11.90	*23*
Organic Horizon pH	**4.63**	0.34	*5*	**5.07**	0.55	*23*
Total Base Saturation (%)	**75.73**	30.83	*5*	**80.40**	19.66	*20*
Total Exchangable Bases (meq/100g)	**2.13**	1.30	*5*	**1.86**	1.03	*20*

APPENDIX X

STAND-TYPE X: BIRCH - TALL SHRUB MIXED WOOD

STAND-TYPE X. BIRCH - TALL SHRUB MIXED WOOD.

TABLE 1. Frequency and mean cover of shrub taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 26*		> 85 years *n = 17*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Tall Shrubs					
Acer spicatum	Mountain Maple	1.00	51.23	0.71	19.24
Corylus cornuta	Beaked Hazelnut	0.77	7.15	0.24	0.88
Sorbus spp.	Mountain Ashes	0.73	1.12	0.71	0.82
Amelanchier spp.	Serviceberries	0.62	0.92	0.77	0.94
Viburnum spp.	Viburnums	0.23	0.39	0.24	0.29
Alnus crispa	Green Alder	0.19	0.77	0.12	1.00
Cornus stolonifera	Red-Osier Dogwood	0.12	0.50	0.06	0.06
Alnus rugosa	Speckled Alder	0.12	0.19	0.06	0.41
Sambucus pubens	Elderberry			0.12	0.12
Low Shrubs					
Diervilla lonicera	Low-Bush Honeysuckle	0.81	4.77	0.41	2.24
Lonicera spp.	Honeysuckles	0.46	0.85	0.18	0.29
Ribes spp.	Gooseberries	0.42	0.54	0.29	0.35
Rosa acicularis	Wild Roses	0.23	0.23	0.12	0.12
Rubus strigosus	Raspberries	0.12	0.15	0.12	0.12
Ericaceous Shrubs					
Vaccinium spp.	Blueberries	0.58	1.12	0.65	1.88

STAND-TYPE X. BIRCH - TALL SHRUB MIXED WOOD.

TABLE 2. Frequency and mean cover of herb, fern and fern-ally taxa, in younger (≤85 years) and older (>85 years) stands.

Species	Common Name	≤ 85 years *n = 26*		> 85 years *n = 17*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Clintonia borealis	Bluebead Lily	1.00	2.31	1.00	3.47
Cornus canadensis	Bunchberry	0.96	1.77	0.94	4.77
Maianthemum canadense	Wild Lily-of-the-Valley	0.96	1.46	0.88	3.82
Streptopus roseus	Twistedstalk	0.96	1.42	0.71	1.12
Aralia nudicaulis	Wild Sarsaparilla	0.92	3.54	0.94	2.65
Lycopodium spp.	Club Mosses	0.85	4.77	0.94	16.59
Trientalis borealis	Starflower	0.81	0.81	0.82	0.88
Aster marcophyllus	Large-leaved Aster	0.73	3.46	0.41	3.88
Viola spp.	Violets	0.73	1.27	0.35	0.41
Rubus pubescens	Dewberry	0.69	1.23	0.24	0.29
Linnaea borealis	Twinflower	0.62	0.62	0.53	0.82
Gymnocarpium dryopteris	Oak Fern	0.46	0.46	0.53	0.59
Coptis trifolia	Goldthread	0.42	0.42	0.12	0.12
Drypoteris spp.	Wood Ferns	0.39	1.27	0.71	1.35
Anemone spp.	Anemones	0.39	0.42	0.06	0.06
Galium triflorum	Bedstraw	0.39	0.39	0.18	0.18
Mitella nuda	Mitrewort	0.35	0.50	0.18	0.41
Pyrola spp.	Pyrolas	0.35	0.46	0.24	0.24
Carex spp.	Sedges	0.31	0.58	0.35	0.35
Goodyera repens	Rattlesnake Plantain	0.31	0.31	0.12	0.18
Osmunda spp.	Royal Ferns	0.19	0.62	0.18	0.41
Pteridium aquilinum	Bracken Fern	0.19	0.58		
Actaea rubra	Baneberry	0.19	0.19	0.12	0.12
Cinna latifolia	Wood Reed Grass	0.19	0.19	0.06	0.06
Mertensia paniculata	Virginia Bluebells	0.19	0.19	0.06	0.06
Oryzopsis spp.	Rice Grasses	0.19	0.19		
Petasites spp.	Coltsfoot	0.15	0.15	0.12	0.12
Trillium cernuum	Trillium	0.15	0.15		
Monotropa uniflora	Indian-Pipe	0.12	0.12	0.35	0.35
Calamagrostis canadensis	Marsh Reed Grass	0.12	0.12	0.24	1.06

STAND-TYPE X. BIRCH - TALL SHRUB MIXED WOOD.

TABLE 3. Frequency and mean cover of cryptogam taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years n = 26		> 85 years n = 17	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Bryophytes					
Dicranum polysetum	Broom Mosses	0.89	2.42	0.82	2.24
Pleurozium schreberi	Schreber's Moss	0.89	3.85	0.71	0.94
Ptilium crista-castrensis	Plume Moss	0.65	0.69	0.65	0.65
Plagiomnium spp.	Leafy Mosses	0.58	1.04	0.18	0.35
Drepanocladus uncinatus	Red Hook Moss	0.54	0.58	0.59	0.71
Hypnum spp.	Pig-Tail Mosses	0.46	0.92	0.29	0.29
Polytrichum spp.	Hair-Cap Mosses	0.46	0.50	0.53	0.53
Brachythecium spp.	Ragged Mosses	0.39	0.54	0.65	1.12
Callicladium haldanianum	Shiny-Leaf Moss	0.39	0.42	0.35	0.35
Ptilidium spp.	Naugehyde Liverworts	0.39	0.39	0.53	0.59
Hylocomium splendens	Stair-Step Moss	0.31	0.39	0.24	0.35
Rhytidiadelphus triquestrus	Shaggy Moss	0.23	1.15	0.24	0.77
Lichens					
Cladonia spp.	Club Lichens	0.23	0.42	0.59	1.06
Peltigera spp.	Dog Lichens	0.23	0.23	0.12	0.12

STAND-TYPE X. BIRCH - TALL SHRUB MIXED WOOD.

TABLE 4. Species richness, diversity and evenness in younger (≤ 85 years) and older (> 85 years) stands.

	< 85 years *n = 26*		> 85 years *n = 17*	
	mean	s.d.	mean	s.d.
Species Richness				
All Species	37.65	10.42	32.71	6.68
Trees	3.77	1.18	3.47	1.01
Shrubs	7.38	2.62	5.18	2.01
Herbs	17.00	5.73	13.12	4.59
Cryptogams	9.50	4.53	10.94	5.43
Diversity (H)				
All Species	2.344	0.257	2.151	0.340
Trees	0.836	0.309	0.866	0.177
Shrubs	0.887	0.331	1.029	0.468
Herbs	2.439	0.430	1.891	0.618
Cryptogams	1.933	0.747	2.102	0.872
Evenness				
All Species	0.653	0.065	0.619	0.076
Trees	0.652	0.203	0.744	0.140
Shrubs	0.452	0.142	0.676	0.248
Herbs	0.876	0.089	0.744	0.207
Cryptogams	0.905	0.167	0.968	0.059

STAND-TYPE X. BIRCH - TALL SHRUB MIXED WOOD.

TABLE 5. Means and standard deviations of selected soil variables, in younger (≤ 85 years) and older (> 85 years) stands.

Variable	≤ 85 years			> 85 years		
	Mean	s.d.	*n*	Mean	s.d.	*n*
Organic Horizon Depth (cm)	**7.35**	3.64	*26*	**13.41**	7.92	*17*
Mineral Horizon Nitrogen (%)	**0.05**	0.02	*8*	**0.05**		*1*
Mineral Horizon Organic Matter (%)	**1.18**	0.57	*8*	**1.21**		*1*
Mineral Horizon pH	**5.26**	0.47	*20*	**5.04**	1.44	*6*
Organic Horizon Nitrogen (%)	**1.32**	0.43	*7*	**1.37**	0.04	*2*
Organic Horizon Organic Matter (%)	**59.99**	6.89	*8*	**56.81**	8.56	*2*
Organic Horizon pH	**5.06**	0.52	*8*	**5.44**	1.61	*2*
Total Base Saturation (%)	**75.77**	21.58	*8*	**100.00**		*1*
Total Exchangable Bases (meq/100g)	**1.26**	1.02	*8*	**0.64**		*1*

APPENDIX XI

STAND-TYPE XI: BALSAM POPLAR

STAND-TYPE XI. BALSAM POPLAR.

TABLE 1. Frequency and mean cover of shrub taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 17*		> 85 years *n = 20*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Tall Shrubs					
Cornus stolonifera	Red-Osier Dogwood	0.71	16.88	0.45	5.45
Alnus rugosa	Speckled Alder	0.53	7.18	0.50	8.05
Amelanchier spp.	Serviceberries	0.53	1.41	0.40	0.50
Acer spicatum	Mountain Maple	0.47	12.82	0.65	9.60
Salix spp.	Willows	0.47	1.24	0.10	0.10
Corylus cornuta	Beaked Hazelnut	0.35	3.41	0.25	4.00
Sorbus spp.	Mountain-Ashes	0.35	0.65	0.50	0.90
Viburnum spp.	Viburnums	0.29	1.35	0.65	2.50
Rhamnus alnifolia	Buckthorn	0.29	0.29	0.15	0.25
Prunus spp.	Cherries	0.24	1.35	0.20	0.85
Alnus crispa	Green Alder	0.12	0.29	0.15	0.25
Sambucus spp.	Elderberries	0.12	0.18		
Low Shrubs					
Ribes spp.	Gooseberries	1.00	2.41	0.90	1.70
Rosa acicularis	Wild Rose	0.71	1.12	0.80	0.85
Rubus strigosus	Raspberry	0.65	3.88	0.60	1.95
Lonicera spp.	Honeysuckles	0.59	1.12	0.60	1.00
Diervilla lonicera	Low-Bush Honeysuckle	0.12	0.18	0.25	1.30
Taxus canadensis	Canada Yew	0.12	0.12	0.05	0.05
Ericaceous Shrubs					
Gaultheria hispidula	Creeping Snowberry	0.29	0.35	0.05	0.05
Ledum groenlandicum	Labrador Tea	0.24	0.41	0.10	0.30
Vaccinium spp.	Blueberries	0.24	0.29	0.15	0.35

STAND-TYPE XI. BALSAM POPLAR.

TABLE 2. Frequency and mean cover of herb, fern and fern-ally taxa, in younger (≤85 years) and older (>85 years) stands.

Species	Common Name	≤ 85 years n = 17		> 85 years n = 20	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Rubus pubsecens	Dewberry	0.94	5.06	0.95	4.25
Galium triflorum	Bedstraw	0.94	1.29	0.85	1.30
Mitella nuda	Mitrewort	0.88	3.65	0.95	3.85
Aralia nudicaulis	Wild Sarsaparilla	0.82	6.12	0.80	4.40
Aster macrophyllus	Large-leaved Aster	0.82	3.82	0.80	2.35
Viola spp.	Violets	0.82	1.65	0.95	2.00
Petasites spp.	Coltsfoot	0.77	1.35	0.80	0.95
Carex spp.	Sedges	0.71	4.77	0.55	3.90
Actaea rubra	Baneberry	0.71	1.06	0.80	0.80
Fragaria spp.	Strawberries	0.65	2.12	0.50	1.00
Equisetum spp.	Horsetails	0.65	2.06	0.70	7.05
Maianthemum canadense	Wild Lily-of-the-Valley	0.65	0.82	0.80	0.80
Mertensia paniculata	Virginia Bluebells	0.59	1.06	0.75	1.15
Trientalis borealis	Starflower	0.59	0.59	0.75	0.75
Streptopus roseus	Twistedstalk	0.53	2.35	0.75	0.95
Cornus canadensis	Bunchberry	0.53	1.41	0.40	0.80
Athyrium felix-femina	Lady Fern	0.53	1.12	0.35	1.00
Calamagrostis canadensis	Marsh Reed Grass	0.47	4.24	0.25	0.30
Clintonia borealis	Twinflower	0.41	1.24	0.65	0.65
Gymnocarpium dryopteris	Oak Fern	0.41	0.88	0.55	0.55
Dryopteris spp.	Wood Ferns	0.41	0.53	0.40	0.75
Anemone canadensis	Canada Anemone	0.41	0.47	0.40	0.40
Epilobium angustifolium	Fireweed	0.35	0.41	0.10	0.10
Linnaea borealis	Twinflower	0.35	0.35	0.35	0.70
Cinna latifolia	Wood Reed Grass	0.29	0.41	0.50	0.50
Pyrola spp.	Pyrolas	0.29	0.41	0.35	0.50
Bromus spp.	Brome Grasses	0.29	0.35	0.25	0.35
Coptis trifolia	Goldthread	0.29	0.29	0.25	0.25
Lathyrus spp.	Peavines	0.29	0.29	0.20	0.20
Asarum canadense	Wild Ginger	0.24	1.65	0.15	0.15
Lycopodium spp.	Club Mosses	0.24	0.47	0.25	0.30
Solidago spp.	Goldenrods	0.24	0.29		
Botrychium spp.	Grape Ferns	0.24	0.24	0.45	0.45
Circaea alpina	Enchanter's Nightshade	0.18	0.24	0.40	0.75

STAND-TYPE XI. BALSAM POPLAR.

TABLE 3. Frequency and mean cover of cryptogam taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years *n = 17*		> 85 years *n = 20*	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Bryophytes					
Pleurozium schreberi	Schreber's Moss	0.71	2.29	0.85	5.65
Brachythecium spp.	Ragged Moss	0.53	1.18	0.65	1.90
Plagiomnium spp.	Leafy Moss	0.53	0.71	0.80	1.60
Drepanocladus uncinatus	Red Hook Moss	0.47	0.71	0.60	0.75
Dicranum polysetum	Broom Mosses	0.41	0.77	0.75	1.15
Hylocomium splendens	Stair-Step Moss	0.35	1.29	0.60	1.75
Ptilium crista-castrensis	Plume Moss	0.29	0.47	0.70	0.80
Sphagnum spp.	Peat Mosses	0.24	1.41		
Rhytidiadelphus triquestrus	Shaggy Moss	0.24	0.88	0.50	1.00
Ptilidium spp.	Naugehyde Liverworts	0.24	0.29	0.45	0.45
Polytrichum spp.	Hair-Cap Mosses	0.24	0.29	0.25	0.25
Hypnum spp.	Pig-Tail Mosses	0.18	0.24	0.20	0.20
Eurhynchium spp.	Beaked Mosses	0.18	0.18	0.35	0.35
Climacium dendroides	Common Tree Moss	0.12	0.18	0.25	0.25
Callicladium haldanianum	Shiny-Leaf Moss	0.12	0.12	0.35	0.55
Lichens					
Peltigera spp.	Dog Lichens	0.35	0.41	0.40	0.40
Cladonia spp.	Club Lichens	0.24	0.59	0.45	0.70

STAND-TYPE XI. BALSAM POPLAR.

TABLE 4. Species richness, diversity and evenness in younger (≤ 85 years) and older (> 85 years) stands.

	< 85 years *n = 17*		> 85 years *n = 20*	
	mean	s.d.	mean	s.d.
Species Richness				
All Species	45.76	10.58	47.20	11.36
Trees	4.41	1.54	4.35	1.09
Shrubs	9.82	2.58	8.65	3.41
Herbs	22.29	5.36	22.70	8.08
Cryptogams	9.24	8.58	11.50	5.61
Diversity (H)				
All Species	2.717	0.402	2.717	0.410
Trees	0.889	0.433	1.103	0.260
Shrubs	1.512	0.607	1.398	0.562
Herbs	2.532	0.343	2.545	0.427
Cryptogams	1.729	0.810	2.097	0.642
Evenness				
All Species	0.714	0.092	0.708	0.077
Trees	0.609	0.190	0.772	0.149
Shrubs	0.661	0.243	0.666	0.212
Herbs	0.827	0.126	0.834	0.141
Cryptogams	0.943	0.098	0.896	0.143

STAND-TYPE XI. BALSAM POPLAR.

TABLE 5. Means and standard deviations of selected soil variables, in younger (≤ 85 years) and older (> 85 years) stands.

Variable	≤ 85 years			> 85 years		
	Mean	s.d.	*n*	Mean	s.d.	*n*
Organic Horizon Depth (cm)	**18.24**	22.23	*13*	**17.25**	11.77	*24*
Mineral Horizon Nitrogen (%)	**0.14**	0.11	*6*	**0.11**	0.08	*7*
Mineral Horizon Organic Matter (%)	**5.05**	5.19	*6*	**1.89**	1.16	*9*
Mineral Horizon pH	**6.82**	0.72	*10*	**7.09**	0.79	*17*
Organic Horizon Nitrogen (%)	**1.20**	0.54	*5*	**1.15**	0.53	*8*
Organic Horizon Organic Matter (%)	**53.31**	14.18	*6*	**55.47**	11.02	*8*
Organic Horizon pH	**6.22**	0.59	*6*	**6.00**	0.59	*8*
Total Base Saturation (%)	**99.32**	0.91	*6*	**97.97**	1.70	*9*
Total Exchangable Bases (meq/100g)	**3.42**	1.00	*6*	**3.96**	0.62	*9*

APPENDIX XII

STAND-TYPE XI: BLACK ASH

STAND-TYPE XII. BLACK ASH

TABLE 1. Frequency and mean cover of shrub taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years $n = 9$		> 85 years $n = 15$	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Tall Shrubs					
Acer spicatum	Mountain Maple	0.89	16.11	0.87	13.67
Alnus rugosa	Speckled Alder	0.78	10.33	0.47	4.60
Corylus cornuta	Beaked Hazelnut	0.78	5.33	0.40	1.33
Prunus spp.	Cherries	0.78	1.89	0.47	0.67
Cornus stolonifera	Red-Osier Dogwood	0.67	0.78	0.53	1.07
Viburnum spp.	Viburnums	0.56	2.00	0.07	0.13
Amelanchier spp.	Serviceberries	0.44	0.44	0.27	0.33
Salix spp.	Willows	0.33	0.33	0.13	0.13
Sorbus spp.	Mountain-Ashes	0.11	0.11	0.27	0.27
Sambucus pubens	Elderberry			0.13	0.20
Low Shrubs					
Ribes spp.	Gooseberries	1.00	2.11	0.80	1.33
Rubus spp.	Raspberries	0.67	2.33	0.53	0.53
Lonicera spp.	Honeysuckles	0.56	0.78	0.20	0.20
Rhamnus alnifolia	Buckthorns	0.22	0.22		
Taxus canadensis	Canada Yew	0.22	0.22	0.07	0.33
Diervilla lonicera	Low-Bush Honeysuckle	0.11	0.11		

STAND-TYPE XII. BLACK ASH

TABLE 2. Frequency and mean cover of herb, fern and fern-ally taxa, in younger (≤85 years) and older (>85 years) stands.

Species	Common Name	≤ 85 years n = 9		> 85 years n = 15	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Carex spp.	Sedges	1.00	18.11	0.93	8.60
Galium triflorum	Bedstraw	1.00	4.89	0.93	1.40
Rubus pubescens	Dewberry	1.00	3.11	0.93	1.73
Viola spp.	Violets	1.00	2.78	0.87	1.93
Athyrium felix-femina	Lady Fern	0.78	4.56	0.80	5.47
Equisetum spp.	Horsetails	0.78	2.67	0.47	0.80
Aster macrophyllus	Large-leaved Aster	0.78	2.33	0.87	1.40
Mitella nuda	Mitrewort	0.78	2.00	0.87	2.33
Circaea alpina	Enchanter's Nightshade	0.78	0.89	0.60	1.00
Streptopus roseus	Twistedstalk	0.78	0.78	0.33	0.33
Asarum canadense	Wild Ginger	0.67	4.11	0.13	0.20
Caltha palustris	Marsh Marigold	0.67	2.89	0.53	1.80
Dryopteris spp.	Wood Ferns	0.67	2.33	0.67	2.00
Fragaria spp.	Strawberries	0.67	0.78	0.27	0.27
Impatiens capensis	Touch-Me-Not	0.56	2.00	0.20	1.33
Calamagrostis canadensis	Marsh Reed Grass	0.56	0.78	0.47	3.47
Cirsium arvense	Canada Thistle	0.56	0.67		
Cinna latifolia	Wood Reed Grass	0.56	0.56	0.33	1.40
Maianthemum canadense	Wild Lily-of-the-Valley	0.56	0.56	0.33	0.33
Trientalis borealis	Starflower	0.56	0.56	0.47	0.47
Trillium cernuum	Trillium	0.56	0.56	0.40	0.40
Thalictrum spp.	Meadow Rue	0.44	3.67		
Aralia nudicaulis	Wild Sarsaparilla	0.44	1.00	0.53	1.00
Solidago spp.	Goldenrod	0.44	0.56	0.07	0.07
Bromus spp.	Brome Grasses	0.33	0.67	0.13	0.13
Lycopus uniflorus	Water-Horehound	0.33	0.56	0.20	0.20
Botrychium spp.	Grape Ferns	0.33	0.33	0.07	0.07
Gymnocarpium dryopteris	Oak Fern	0.33	0.33	0.53	0.60
Glyceria spp.	Manna Grass	0.33	0.33	0.20	0.20
Actaea rubra	Baneberry	0.33	0.33	0.13	0.13
Clintonia borealis	Twinflower	0.33	0.33	0.33	0.33
Geum aleppicum	Yellow Avens	0.33	0.33	0.13	0.13
Petasites spp.	Coltsfoots	0.33	0.33	0.13	0.13
Matteuccia struthiopteris	Ostrich Fern	0.22	2.89	0.13	2.33
Thelypteris phegopteris	Long Beech Fern	0.22	0.33	0.13	0.33
Schizachne purpurascens	Purple Oat Grass	0.22	0.33	0.07	0.07
Anemone canadensis	Canada Anemone	0.22	0.33	0.07	0.07
Pyrola spp.	Pyrolas	0.22	0.33		
Lycopodium spp.	Club Mosses	0.22	0.22	0.13	0.13
Epilobium angustifolium	Fireweed	0.22	0.22	0.07	0.07
Polygonum sagittatum	Arrow-Leaved Tear-Thumb	0.22	0.22	0.07	0.07
Scutellaria epilobiifolia	Skull Cap	0.22	0.22	0.20	0.20
Taraxacum officinale	Dandelion	0.22	0.22	0.07	0.07
Onoclea sensibilis	Sensitive Fern	0.11	0.78	0.33	3.27

STAND-TYPE XII. BLACK ASH

TABLE 3. Frequency and mean cover of cryptogam taxa, in younger (≤ 85 years) and older (> 85 years) stands.

Species	Common Name	≤ 85 years n = 9		> 85 years n = 15	
		Frequency	Mean Cover (%)	Frequency	Mean Cover (%)
Bryophytes					
Climacium dendroides	Common Tree Moss	0.89	1.67	0.47	4.73
Plagiomnium spp.	Leafy Mosses	0.78	1.89	0.93	6.87
Thuidium spp.	Fern Mosses	0.56	1.22	0.47	0.93
Calliergon spp.	Water Mosses	0.33	4.44	0.07	0.07
Brachythecium spp.	Ragged Mosses	0.33	1.44	0.13	0.40
Hypnum spp.	Pig-Tail Mosses	0.33	0.33	0.20	0.33
Pleurozium schreberi	Schreber's Moss	0.33	0.33	0.33	1.00
Campylium spp.	Star Moss	0.22	0.22	0.00	0.00
Drepanocladus spp.	Red Hooked Mosses	0.22	0.22	0.07	0.07
Mnium spp.	Mniums	0.22	0.22	0.07	0.47
Rhizomnium spp.	Round Mosses	0.11	0.89	0.27	0.40
Conocephalum conicum	Snake Liverwort	0.11	0.11	0.20	0.27
Rhodobryum roseum	Rose Moss	0.11	0.11	0.27	0.27
Rhytidiadelphus spp.	Shaggy Moss	0.11	0.11	0.27	0.27
Sphagnum spp.	Peat Mosses	0.11	0.11	0.20	0.67
Lichens					
Peltigera spp.	Dog Lichens	0.22	0.22	0.40	0.40

STAND-TYPE XII. BLACK ASH

TABLE 4. Species richness, diversity and evenness in younger (≤ 85 years) and older (> 85 years) stands.

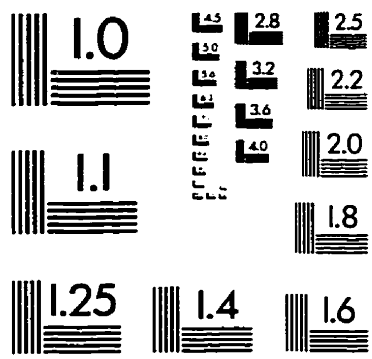
	< 85 years *n = 9*		> 85 years *n = 15*	
	mean	s.d.	mean	s.d.
Species Richness				
All Species	49.44	11.16	36.60	11.73
Trees	4.11	1.17	4.40	1.18
Shrubs	9.22	2.77	6.13	2.33
Herbs	29.11	5.84	20.87	7.86
Cryptogams	7.00	4.36	5.20	2.04
Diversity (H)				
All Species	2.752	0.317	2.471	0.368
Trees	0.678	0.392	0.834	0.279
Shrubs	1.547	0.491	1.181	0.435
Herbs	2.794	0.419	2.575	0.480
Cryptogams	1.497	0.734	1.279	0.603
Evenness				
All Species	0.708	0.056	0.693	0.064
Trees	0.485	0.279	0.574	0.159
Shrubs	0.715	0.194	0.677	0.204
Herbs	0.833	0.112	0.862	0.106
Cryptogams	0.859	0.147	0.777	0.253

STAND-TYPE XII. BLACK ASH.

TABLE 5. Means and standard deviations of selected soil variables. in younger (≤ 85 years) and older (> 85 years) stands.

Variable	≤ 85 years			> 85 years		
	Mean	s.d.	*n*	Mean	s.d.	*n*
Organic Horizon Depth (cm)	**20.00**	29.94	*9*	**55.00**	65.24	*15*
Mineral Horizon Nitrogen (%)	**0.21**	0.16	*4*	**0.50**	0.49	*7*
Mineral Horizon Organic Matter (%)	**3.21**	1.92	*4*	**9.28**	14.95	*7*
Mineral Horizon pH	**6.12**	0.55	*7*	**5.99**	0.66	*10*
Organic Horizon Nitrogen (%)	**2.16**	0.04	*3*	**1.81**	0.63	*7*
Organic Horizon Organic Matter (%)	**60.99**	4.85	*3*	**60.24**	11.93	*7*
Organic Horizon pH	**6.55**	0.12	*3*	**5.95**	0.32	*7*
Total Base Saturation (%)	**92.24**	11.31	*4*	**93.52**	10.44	*6*
Total Exchangable Bases (meq/100g)	**6.96**	7.11	*4*	**3.90**	1.06	*6*

IMAGE EVALUATION TEST TARGET (QA-3)



150mm

6″

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