MATURE WHITE SPRUCE STANDS
IN THE MID-BOREAL UPLAND ECOREGION OF SASKATCHEWAN

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ABSTRACT

A three-stage approach was used to investigate mature white spruce (*Picea glauca* (Moench) Voss) stand types in Saskatchewan. The approach involved: 1) identification of potential stand types in a conceptual model, 2) description and quantification of stand structure and forest floor processes in selected representative stand types and 3) simulation of two stand types using the ecosystem management model, FORECAST. The computer model explored the role of nitrogen fixation in succession patterns under different disturbance regimes. White spruce stands with high-density aspen were hypothesized to have greater levels of forest floor nitrogen and greater stemwood biomass than stands with low-density aspen.

Analyses of field data on stand structure (stem densities, basal area, snag distribution, and coarse woody debris volumes) provided recognition of four distinct white spruce stand types similar to those depicted in the conceptual model. Summer season measures of nitrogenase activity and potential mineralizable nitrogen rates were greater in the spruce-aspen (*Populus tremuloides* Michx.) stand type (wS/tA), than in the spruce–balsam–fir (*Abies balsamea* (L.) Mill.) stand type (wS (bF)). Rates of microbial activity were greater in litter than in well-decayed logs or mineral soil. Greater nitrogen concentrations and nitrogen content occurred in aspen logs than in white spruce logs that had been decomposing under wS/tA stands for up to 45 years.

Nitrogen fixation rates measured in spruce litter and decaying logs were used as inputs for the FORECAST computer simulations that evaluated white spruce succession over 240 years. The simulations predicted that time between disturbances, disturbance type and disturbance severity were key determinants of stand composition over the 240-year simulation period. Computer simulated white spruce stemwood biomass was greatest in aspen-dominated stands when multiple partial harvests were introduced compared to simulations with multiple light fires. The simulated harvest disturbances deposited moderate amounts of stemwood on the forest floor over the 240-year period and did not remove forest floor matter. In contrast, multiple stand replacement fires and light fires consumed forest floor organic matter and left some stemwood on the forest floor. The increase in white spruce biomass in simulations with harvesting in comparison to simulations with fire was attributed to increased available nitrogen.
from the accumulations of litter and stemwood on the forest floor and to reduced nitrogen loss due to fire.

Results show that there are different nitrogen legacies associated with wS/tA stands, compared to wS (bF) stands. These legacies may respond differently to various forest management practices and to a range of disturbance intensities. However, the inferences from my research are limited by a single season of microbial activity measurement, by the small number of sites used to test the conceptual model and by the fact that the simulations run with FORECAST have yet to be validated.
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Chapter 1
Introduction

Forest sustainability has been described as the maintenance of forest structure, composition and process rates in a non-declining pattern of variation within the historic range of change (Kimmins 1995). In keeping with this ecological definition of sustainable forestry, recent research has focused on identifying the historic ranges of forest ecosystems, and in testing the sustainability of future stands through modeling and field experiments.

1.1 Forest Floor Nitrogen Economies in Boreal Forest Management

Species composition and changes within certain boreal stand types depend, in part, upon sufficient supplies of nutrients to realize potential stand growth. Of these nutrient pools, nitrogen has been identified as one of the factors most limiting to forest growth in some boreal and temperate forests (Myrold 1987). Because the forest floor has been identified as an important source of available nitrogen for species' growth, knowledge about nitrogen legacies found in litter layers, logs and mineral soils in different stand types of boreal forests is requisite for the development of long-term boreal forest management strategies.

Several studies have explored the growth dynamics of various boreal stand types and found benefits for white spruce (Picea glauca (Moench) Voss) from the presence of aspen (Populus tremuloides Michx.) (Kabzems and Senyk 1967, V. Lieffers, personal communication, 1999). The response of white spruce to the presence of aspen raises important questions about the sustainability of the nitrogen cycle and forest productivity if
succession pathways dependent on natural disturbance are replaced by pathways dependent on harvest regimes or if ecosystems are held in existing stand types through management strategies.

Some studies have suggested that if boreal forests are maintained as late seral stand types, available nitrogen is likely to decline (Pare and Bergeron 1996). As a result, foresters are not certain about the consequences of maintaining boreal forests as late seral stand types and what management scenarios could provide adequate nitrogen pools for future growth.

There is little quantitative information about structural attributes or nitrogen-related processes in the mature white spruce stand types of Saskatchewan’s Mid-Boreal Upland Ecoregion, but this information is required for calibration and/or validation of computer simulations of forest management alternatives applied within adaptive management strategies. Calibrated ecosystem models such as FORECAST (Kimmins et al. 1999, Seely et al. 1999), for example, can be used to produce simulations concerning stand level responses to disturbance and management practice.

1.2 Thesis Approach

I investigated mature white spruce (Picea glauca (Moench) Voss) stands using the following approach: 1) identification of stand types within a conceptual framework, 2) description and quantification of stand structure and certain soil processes for several white spruce stand types and 3) simulation of white spruce-aspen stands using the ecosystem management model, FORECAST. FORECAST was also used to investigate
the role of nitrogen fixation in stand development patterns under different fire and management regimes.

Some operational objectives of my research were to examine the role of forest floor substrates, (particularly down woody debris), in the nutrient economy of white spruce-dominated stands, and to use the model FORECAST to simulate stand biomass, decomposing mass and other characteristics with respect to nutrient economies. FORECAST simulated natural disturbance and harvesting practices that varied the presence of aspen. The latter objective was designed to emulate potential forest management actions in conjunction with natural disturbance patterns in terms of forest renewal.

The thesis consists of information syntheses followed by field research and simulation modeling. Chapter 2 describes the post-glacial distribution of white spruce and trembling aspen. Chapter 3 explores a succession framework that could be applied to boreal forests and proposes a productivity rating for white spruce-dominated stand types based on aspen presence in Saskatchewan’s Mid-Boreal Upland Ecoregion. Chapter 4 reviews the literature on microbial activity and substrate nitrogen transformations in boreal forests. Chapter 5 describes the hybrid computer model FORECAST and several other hybrid computer models.

Chapter 6 describes my objectives, hypotheses and study area. Chapter 7 reports my analysis of white spruce-dominated stand structural attributes in four stand types and the use of these attributes to describe “old growth”. Chapter 8 describes the rates of nitrogen mineralization, nitrogen fixation and CO₂ evolution found in the substrates of three white spruce stand types. Chapter 8 also investigates the role of coarse woody debris chemical
attributes that are believed to be important to forest sustainability. Chapter 9 describes the results of computer simulations involving white spruce-aspen stands that are subject to fire disturbance, as well as those that are subject to stand replacement harvesting. The influence of nitrogen fixation rates in woody debris and forest floors is explored for selected scenarios. Chapter 10 provides a summary of my research and the applications of my results in mixedwood management.
Chapter 2

Post-Glacial Distribution of Saskatchewan’s White Spruce Forests

The present-day distribution of white spruce in Saskatchewan reflects post-glacial white spruce migration, the environmental conditions associated with North American ice sheet movement, and the fire regimes of pre-recorded history. More recent climate fluctuations and human settlement have also contributed to current white spruce distribution patterns. During the retreat of the Cordilleran ice sheet between 14,000 and 7,000 BP, white spruce migrated north from warmer, mid-western forests to occupy the newly exposed till, glaciofluvial, glaciolacustrine and ice settlement landforms. These boreal forests thrived in the cooler environments created near the ice sheet (Ritchie and MacDonald 1986). Seed dispersal from the newly created forests has been attributed to strong winds that blew from the southeast in the wake of the retreating ice sheet. This resulted in fairly rapid migration rates of approximately 2 km/yr (Ritchie and MacDonald 1986).

About 11,000 BP, the open, mid-western forests found near the present US border consisted not only of white spruce but aspen, black spruce (Picea mariana (Mill.) B.S.P.), ash (Fraxinus spp.), oak (Quercus spp.), and elm (Ulmus americana L.), although the latter three species did not migrate north with white spruce because they were not adapted to the cool, wet, summers and the cold winters (Ritchie and MacDonald 1986). Plant material from the Hafichuk Ranch research site southwest of Moosejaw, Saskatchewan has confirmed the presence of white spruce and willow (Salix spp.) about 12,000 BP on mesic sites, and communities consisting of Shepherdia canadensis and Artemesia on xeric sites (Ritchie 1964).
About 10,000 BP, it is likely that the southern portion of the mid-western spruce woodlands in Saskatchewan were replaced by jack pine (*Pinus banksiana* Lamb.) oak savanna, and prairie. White spruce and lodgepole pine (*Pinus contorta* var. *latifolia*) were found in the present location of Cypress Hills National Park during this period, whereas Manitoba’s present day Riding Mountain National Park had numerous prairie plants (Thompson and Kuijt 1976, Ritchie 1983).

Warming and cooling trends continued into recorded history. The Little Ice Age that occurred from 1350-1870 AD, shifted the boreal forest treeline southward (Pielou 1991). It is assumed that the current oldest living white spruce stands in Saskatchewan are those that germinated under Little Ice Age climate regimes of cool, moist summers and cold winters.

Larsen and MacDonald (1998) used both charcoal dating and pollen analyses to investigate boreal forest composition over an 840-year period. They found that high levels of white spruce existed until 1185 AD, followed by a period of aspen dominance. White spruce abundance gradually rose again, however, over the subsequent 800-year period. According to the authors’ findings, aspen was only abundant after 1930 AD and between the years 1250 and 1550 AD, a period that includes the latter portion of the Medieval Warming Period (900-1300 AD).

2.1 Saskatchewan Boreal Forest Fire Regimes

The boreal forest fire interval, often referred to as a fire cycle, is defined as the period of time required for an area to burn that is equal in size to the area of interest (Forest Resources Development Branch 1986). Fire frequency, or the number of fires per
unit time/area, (Forest Resources Development Branch 1986), varies according to
temporal scale, geographic locale, climate, and post-European settlement activity.

Fire frequencies before 1730 AD in Kananaskis, Alberta, were approximately one
every 50 years. From 1730 to the present, the fire cycle was estimated at 90 years-a
periodicity consistent with the climate of the post-Little Ice Age (Johnson and Larsen
1991). The authors believed that human activity after 1880 in the Kananaskis Valley did
not affect the fire incidence greatly and Indian bands visited the area infrequently from
1781 to the 1840’s. In the recent study conducted in Alberta’s Wood Buffalo National
Park, charcoal abundance was used in calculating a 69-year fire cycle over 840 years
(Larsen and MacDonald 1998). In keeping with the moister climate of the Little Ice Age,
herbs and shrub abundance in this study peaked between 1350-1750 AD.

If a 50-year period is used to determine fire cycles rather than the longer periods
associated with some charcoal studies (Larsen and MacDonald 1998), there is
considerable variation in fire frequency. For example, Saskatchewan fire cycles were
estimated at 221 years using fire records between 1918 and 1979 (Thorpe 1996). Inclusion
of the 1980-1995 period in fire cycle calculations, however, would probably shorten this
cycle because there were several years after 1979 with high fire incidence (Thorpe 1996).

In northern Saskatchewan’s La Ronge area, where the forest is predominantly jack
pine rather than white spruce, fire cycles increased from 15 years in the period from 1849-
1890 AD to 39 years from 1950-1990 AD (Thorpe 1996). Although fire cycles estimated
for Prince Albert National Park Forest from 1945 to the present range from 1,745 to 645
years, the cycles were much shorter prior to the Park’s establishment. Active fire
suppression is generally believed to have contributed to these estimates.
The northern portion of Township 57 that contains Prince Albert National Park is also reported to have had a 15-year fire cycle during the 130-year interval from 1760-1890 AD (Weir 1996 in Weyerhaeuser 1997). The relatively short fire cycle found in the southern part of the National Park during this period may have been caused by increased fuel accumulation because the climate was moister and cooler during the Little Ice Age. Another important factor may have been the presence of fewer high-pressure weather systems (Weir et al. 1999).

Fire frequencies of 40-70 years are commonly cited for Saskatchewan’s Mid-Boreal Upland Ecoregion, with over 90 percent of forest losses occurring due to large fires (Thorpe 1996, Larsen and MacDonald 1998, Weir 1996 in Weyerhaeuser 1997, Rowe and Scotter 1973). Anecdotal information on traditional burning by First Nations people in Alberta and Saskatchewan has revealed that although meadows were burned frequently, less underburning may have taken place in forested locations than researchers had originally estimated (A. Leighton, personal communication 1999, Morse 1913). Based on this information, and the weather patterns assumed to have existed in the Little Ice Age, lightning strikes probably account for most of the fires started during pre-European history.

2.2 The Impact of Twentieth-Century European Settlement

In 1908-1909, an extensive exploration of the province’s central and northwest regions took place to assess the land for agricultural potential (Crean 1910). Near Meadow Lake, homesteaders began to clear land for buildings, roads and crops as early as 1907 (Diamond Jubilee Heritage Group 1995). The process of profitably disposing of timber
not required for personal use often resulted in the establishment of family-owned portable sawmills. At least 55 mills operated in the Meadow Lake area alone over an 80-year period (Diamond Jubilee Heritage Group 1995). As the Meadow Lake population grew in the 1920's and 1930's, the sawmills became larger, often employing 20-40 men (Diamond Jubilee Heritage Group 1995).

The amount of timber removed by Saskatchewan sawmill companies during the first half of the 20th century varied with the timber harvesting location and the company type. In 1932 at Greig Lake, near Meadow Lake, the Stonehoker mill removed 400,000 board feet (9,600 m$^3$) of lumber in 42 days (Stonehoker 1995). Other Meadow Lake-based camps could average 100,000 board feet (2,400 m$^3$) of lumber per year (Peters 1995).

In central Saskatchewan, the Prince Albert Lumber Company cut 258,651 logs in one timber berth during one year. During the winter of 1917-1918 it abandoned 25,308 logs in one location (Shortt 1977 in Goode et al. 1996). From 1905 to 1919, the Prince Albert Lumber Company harvested 335 million board feet (738,000 m$^3$) and employed up to 2000 men in 14 camps during the winter months (Shortt 1977 in Goode, et al. 1996).

C. H. Morse, a forestry faculty member at the University of Toronto, provided the first professional timber evaluation in Saskatchewan that led to a forest management decision which indirectly affected both the fire cycles and mature white spruce abundance near Prince Albert. He surveyed the timber berths near the present location of Prince Albert National Park and recommended that most of this area, which was largely unproductive due to fire and logging in the first decade of the century, become the Sturgeon River Forest Reserve (Morse 1913). In the Reserve, forest fires were more
closely controlled and timber companies were required to submit cutting plans (Goode et al. 1996).

Post-settlement distribution of aspen, white spruce and birch was estimated using early inventory information from the three timber berths that were located either within or adjacent to the present Prince Albert National Park boundaries (Weir and Johnson 1998). The authors reported a species change from 29% aspen composition in 1883-4 based on the timber berth inventories, to 49% aspen based on the most recent Saskatchewan Environment and Resource Management (SERM) timber inventory (1992-1994). In addition to changes in aspen dominance, the authors also reported slightly more than a 50% decrease in white spruce on burned sites from 1883-4 to the early 1990's. Sites that were logged and burned showed even greater declines in white spruce stand types. According to the authors, mixed stands with white birch decreased from 12% to <1% in approximately 115 years.

The results of past research, Saskatchewan’s logging history, and the fact that First Nations underburning may not have been as frequent as scientists once believed, add credence to the hypothesis that mature white spruce forests in Saskatchewan were more abundant during early European settlement coincident with the Little Ice Age.

2.3 Current Landscape Distribution of Boreal Forest Species

A mixedwood stand may be defined as a tree community where no single species exceeds 80% of the basal area (MacDonald 1995). In addition to white spruce and aspen, present-day Saskatchewan boreal forests consist of balsam poplar (*Populus balsamifera* L.), birch (*Betula papyrifera* Marsh.), balsam fir (*Abies balsamea* (L.) Mill.), jack pine
and black spruce. Aspen and white spruce are the most frequently encountered species in
the Mid-Boreal Upland Ecoregion, a subdivision of the Boreal Plain (Beckingham et al.
1996).

In the Mid-Boreal Upland, the Ecoregion that contains the majority of
Saskatchewan’s merchantable timber, aspen is often encountered on south-facing slopes,
and in association with white spruce on mesic sites (Padbury and Acton 1994). Balsam fir,
a dominant species in eastern Canada, diminishes in the boreal forest from east to west in
response to changes in precipitation, whereas white spruce dominance increases from east
to west (Burns and Honkala 1990).

In north-central Saskatchewan, the area occupied by mature white spruce stands
older than 60 years may be as high as 25% (D. Lorer, personal communication, 1999).
However, the area occupied by white spruce stands older than 140 years, may range from
0.01 to 0.07% in western portions of the province (Westworth and Associates 1994).
Stands older than 100 years in the Cold Lake Air Weapons Range made up 0.42% of the
area before a recent fire. (Westworth and Associates 1994). Current older white spruce
stands occupy less than 0.01% of the Cold Lake Air Weapons Range located in
Saskatchewan. The area occupied by white spruce stands more than 125 years old in the
province has been estimated to be as low as 5% of the total forest cover (R. Nesdoly,
personal communication, 1999).

During 1994, tree mortality caused by spruce adelgids (Adelges lariciatus Patch),
aspen leaf beetles (Chrysomela crotchii W. J. Brown) or large aspen tortrix (Chorist
oneura conflictana Walker) accounted for losses of approximately 133,000 m³ in
Saskatchewan (Natural Resources Canada 1994). Diseases such as western gall rust
(Endocronartium harknesii [J. P. Moore] Y. Hiratsuka) and Venturia leaf and shoot blight
(Venturia macularis (Fr.:Fr.) E. Mueller and Arx) also contribute to mortality in
Saskatchewan’s mixedwood stands.

In addition to insect and disease mortality, winds of sufficient strength to snap tree
boles also have a major influence on stand structure, composition and landscape-level
forest mosaics in Saskatchewan (J. Thompson, personal communication, 1998, S.
Navratil, personal communication, 1996). Although wind is a common disturbance factor
in Saskatchewan’s Boreal Plain forests, gap patterns created by wind have yet to be
studied.

Regeneration of aspen, white spruce, and balsam fir is contingent on seed source,
disturbance patch size, microclimate and micro-site features, as well as on above and
belowground competition. Good seed years and seed viability are important factors
contributing to the regeneration success of aspen and white spruce. Aspen, a robust
pioneer species, typically distributes large numbers of seed into openings after fire or
logging and it can sprout after light fires by means of root suckers. It can average
one million seeds per tree annually with 95% viability, whereas white spruce has both

In Saskatchewan, white spruce colonization of aspen stands can take place for 15
to 20 years after aspen establishment (Dix and Swan 1971, Kabzems et al. 1986). The
delay appears to be related to a combination of factors that include lack of available seed
sources, limited seed distribution distances, and lower spruce seed viability compared to
aspen (Kolabinski 1994). On the other hand, white spruce can establish at the same time
as aspen in cases when there is an appropriate combination of seed supply and seedbed.
The time required for aspen and white spruce to reach reproductive maturity plays an important role in post-disturbance development. White spruce is generally not reproductively mature until it reaches 30-50 years old whereas trembling aspen may produce seed at 15 years (Peterson and Peterson 1992). This sexual precocity permits aspen seedlings to establish well before white spruce. Aspen does require moist seedbeds, however, and regeneration success subsequent to seed dispersal is governed by local climate and stand microclimate (Peterson and Peterson 1992).

Aspen grows quickly in its’ early years, achieving crown closure at about 12 years, compared to white spruce that attains crown closure at approximately 20 years depending on initial stand density. Aspen suckering, with height growth rates of 2 m per year in mixedwood forests, ensures rapid establishment on suitable sites after light fires (Peterson and Peterson 1992). Suckering can occur the year following fire, and unless disturbance is frequent, no loss of vigour will occur in multiple sucker production events (S. Navratil, personal communication, 1999). Based on past studies, aspen clearly has a competitive edge compared to white spruce during establishment on mesic sites after disturbance, and particularly after fire.

In Saskatchewan, although aspen has more rapid early growth than white spruce, it has a shorter lifespan. Aspen senescence occurs between 70-100 years whereas age-related mortality in white spruce may not begin until 150 years, although white spruce more than 200 years old have been found (Thorpe and Godwin 1992).

The phenomenon of rapid early growth in aspen, particularly through suckering, may take greater advantage of the assart flush associated with ecosystem disturbance than white spruce (Peterson and Peterson 1992). Aspen photosynthesizes more efficiently than
white spruce and can absorb large amounts of nutrients during maximum canopy
development (Peterson and Peterson 1992). Moreover, aspen appears to contribute more
total nitrogen to the soil. Approximately 10% more total nitrogen (expressed as the sum of
throughfall, stem flow, litterfall, and root litter) has been reported in 25% softwood/75% hardwood stands compared to softwood-dominated stands (Gordon 1981 as cited in
Peterson and Peterson 1992). In Alberta aspen-spruce stands, the presence of aspen may contribute to a 12% increase in spruce productivity expressed as height growth or annual increment (Lieffers et al. 1996).

Since balsam fir is a minor commercial species in Saskatchewan’s boreal
mixedwood, less is known about its’ reproductive and regeneration potential in the Mid-
Boreal Upland Ecoregion compared to aspen and white spruce. It is considered to be a late-successional, fire-intolerant species and shorter-lived than white spruce. Balsam fir can be a very effective competitor for resources such as light and nutrients. Logan (1969) found that balsam fir grows best in 45% light up to age 9. This characteristic high shade tolerance may account for the higher density of balsam fir advance regeneration saplings in Saskatchewan’s Boreal Plain compared to the density of white spruce saplings.

Traditionally, balsam fir has thought to have established near parent trees because of limited seed dispersal. However, foresters have often searched without success for the parent trees of many of the balsam fir seedlings that occur in the late successional white spruce stands of Saskatchewan (C. Halland, personal communication, 1998). This lack of success in finding parent trees, and recent studies in Alberta, support the hypothesis that seed dispersal distances may be greater than originally reported (> 250 m) for the western boreal forest (Stewart et al. 1998).
Landscape models that are being developed in Alberta have adopted 1 km as the maximum distance for seed dispersal (S. Cumming, personal communication, 1999). Most anecdotes describing long distance seed dispersal involved discovery of seedlings in extremely large clearcuts where seed dispersal >1.5 km was necessary for the seedlings to be present (C. Halland, personal communication, 1998). Foresters have described seed dispersal as accompanying very strong autumn winds and it is believed that winter seed dispersal occurs when seed travels on the snow surface (J. Thompson, personal communication 1999, C. Halland, personal communication, 1998). The rationale for winter seed dispersal is that the seed encounters minimum friction on the snow surface and is propelled by the winter winds. Whether such dispersal holds true in closed stands has not been studied.

According to Beckingham et al. (1996), current mixed stands of trembling aspen and white spruce in Saskatchewan within the low bush cranberry ecosite phase have mean volumes of 290 m$^3$/ha (+ 10 m$^3$/ha), mean ages of 75.2 years, and a mean annual increment of 4.0 m$^3$/ha/yr. The mean basal area of these mixedwood stands is 17.2 (+ 1.3) m$^2$/ha for white spruce; the stand site index for white spruce is 19.8 m at 50 years. Mean white spruce densities in these stands are 677 stems/ha compared to aspen with 530 stems/ha.

Aspen’s widespread distribution on the landscape appears to be comparatively recent; white spruce has dominated the Boreal Plain landscape during most of the post-glacial period. Aspen growing rapidly in aspen-spruce cohorts may provide a “nurse tree” effect where a “nurse tree” is defined as one that contributes a positive benefit to other biota in an ecosystem. Aspen’s higher foliar and wood nitrogen content may provide a
nitrogen legacy (nitrogen inherited from prior stand development) in mixedwood litter and
down woody debris (Alban and Pastor 1993). Aspen also has a physical role as a “nurse
tree” in suppressing competing herbs and shrubs through shading. A detailed discussion of
published findings concerning the role of substrate nitrogen in potential boreal forest
growth can be found in Chapter 4 and Chapter 8.

Given the growth patterns of aspen and white spruce, and the potential positive
effect of aspen’s nitrogen legacy in Saskatchewan’s boreal forests (see Chapter 4), the
relative abundance of aspen may be a key in assessing future mixedwood forest growth in
this province. This concept is relevant to my thesis where links will be investigated
between processes and stand structure in stands with various amounts of aspen, white
spruce and balsam fir.
Chapter 3

Succession and Saskatchewan’s White Spruce Stands

In Saskatchewan, tree species distributions were compiled from early expedition notes and the diaries of fur traders and then refined through a series of geological and land surveys. The forks of the North and South Saskatchewan Rivers held tracts of jack pine and white spruce (Hector 1857, in Spry 1968). The land to the north of Green Lake village, described from canoes that plied Green Lake and the Beaver River, was covered with a thick forest of tall aspen and poplar. Between Green Lake and Fort Carlton, forests of birch, aspen, poplar and jack pine could be found (Macoun 1875). In the early 20th century, the uplands north of Anglin Lake were wooded with jack pine and a few spruce, whereas merchantable white spruce stands were located near Montreal Lake where trees ranged in diameter from 25 to 61 cm (Saint Cyr 1910).

Forest mapping and ecological classifications stemmed from the recognition of national forest regions (Fernow 1908, Halliday 1937, Rowe 1972). Although students conducted individual ecological studies at specific locations in Saskatchewan, large-scale ecological classification was not undertaken until the 1980’s. Forest inventory information collected prior to that time and up to the 1990’s did not include ecological information such as down woody debris volumes, understory plant distributions and soil profile descriptions.

Drawing upon available data at the provincial level, Kabzems et al. (1986), described the Saskatchewan mixedwood ecodistricts using a combination of forest management information, soil properties and vegetation associations. The ecodistricts
included climate, although they were based primarily on geological and physiographic properties. The ecoregions of Saskatchewan (referred to as landscapes) were refined further and published as a map (Padbury and Acton 1994, Figure 1). In 1996, vegetation associations and ecosite moisture and nutrient regimes were compiled for Saskatchewan's Mid-Boreal Upland Ecoregion (Beckingham et al. 1996). The authors combined vegetation associations, ecosite types and ecosite phases with site index information. Written descriptions of the Ecoregions were published two years later (Acton et al. 1998).

3.1 Forest Succession and Stand Development Models

Succession, which can be regarded as both a product and a process, is defined as a change in the composition of communities following natural or human disturbance that may reach a climax or stable state under a given set of environmental conditions (Whittaker 1975). Clusters of structural and process attributes that are temporally or spatially separated are known as succession types (after Whittaker 1975, Peterken 1996) and a sequence of types or stages is known as a sere (Kimmins 1997).

In keeping with the definition of succession as a process, indices of succession include a loss or gain in species richness, changes in plant biomass, and fluxes in energy and/or changes in nutrient levels (Peterken, 1996, Waring and Schlesinger 1985, Mueller-Dombois and Ellenberg 1974). Early North American ecologists recognized individual state factors that they associated with changes in succession types. For example, Cowles (1899 in Real et al. 1991) felt that parent material influenced vegetation succession;
Figure 1. Map of the Mid-Boreal Upland Ecoregion in Saskatchewan, after Padbury and Acton (1994).
Clements (1916, 1936) proposed that vegetation change occurred largely in response to climate. In documenting a comprehensive view of succession, Clements described five successional development stages: 1) exposure of bare mineral soil, 2) seed migration 3) vegetation growth 4) competition for light, space, and nutrients, and 5) climax.

As ecologists tested various facets of the Clementsian view of succession, other successional hypotheses arose that acknowledged the variable or stochastic nature of succession, the partitioning of limited resources and the role of life histories. Egler (1954), for example, investigated the particular successional patterns associated with species arrival times. Based on the assumption that plants have certain threshold levels of nutrient and light requirements, Tilman (1988) proposed that competition for available light and nutrients controls plant community development.

One weakness of single pathway or “linear” succession models is that researchers tend to substitute space for time (the chronosequence approach) and assume that the stands differ only in their growth not in their origins or disturbance patterns (Picket et al. 1987). The “linear” model lacks the dynamic elements of divergence and convergence that may be found in evolving forests.

Succession models that attempt to overcome the weaknesses of the single pathway approach are referred to as multiple pathway models, where a pathway is defined as a temporal pattern of ecosystem change. Originally, the multiple pathway approach presented three independent development patterns describing the effects of colonizers entering an ecosystem. This approach recognized the role of stress gradients, differential growth rates, and plant adaptive characteristics that might influence successional patterns (Drury and Nisbet 1973, Connell and Slatyer 1977).
Work with early multiple pathway models initiated several avenues of research related to the probability of particular species replacement. The stand type was considered a function of the degree of disturbance. Noble and Slatyer (1977) declared that the method of species arrival, the conditions under which species established and grew to maturity, and the time to reach critical stages in life history were important factors governing stand development. The authors also believed that the size, growth rate and mortality of species controlled stand composition.

Cattelino et al. (1979) applied the multiple pathway approach in a fire-prone environment. In this application, the authors integrated life history characteristics with long and short inter-fire cycles to produce a conceptual model that would eliminate some species given short fire cycles and increase the ability of others to persist if fire cycles were lengthened. Declining stem densities were used to illustrate the disappearance of aspen in the absence of fire. The ability of species to seed into disturbed areas, or in the case of aspen, to sprout after fire, governs the competitive advantage that species can retain into the mature stage of the stand.

In a comprehensive model, (Oliver 1981), combined autogenic competition, structural attributes, and regeneration mechanisms as factors influencing succession. Oliver also recognized the role of seed crop cycles and the activity of seed predators. In this model, stand response to disturbance intensity and size reflected functional processes such as growth and mortality, increasing stand biomass, and changes in age class distribution. Other stand processes included: changes in species diversity, stand structure and size differentiation within species.
Oliver’s (1981) model proposed four spatially explicit stages: 1) Stand Initiation 2) Stem Exclusion 3) Understory Re-initiation and 4) Old Growth. Each stage has a number of characteristics. For example, stand initiation or regeneration involves the recruitment of a new generation of individuals until all available space is occupied. At the stem exclusion stage, it is assumed that no new recruitment occurs. As light diminishes due to crown closure, patches of herbaceous and shrub cover typical of early stages slowly disappear (Peterken 1996).

With this particular model, the scale of application determines whether it is classified as a succession model or a stand structure (development) model. In stand structure classification, the stands represented by the model can be one of several different structural stages within a sere (Kimmins 1997).

3.2 Past Applications of Succession and Development Models

Attribute-oriented models have been applied to the boreal forests of Saskatchewan and Alberta. These models consist of steady state or climax models based on stand age, stand structure models and models based on successional pathway development. A model consisting of four development stages was developed for Prince Albert National Park within the Mid-Boreal Upland Ecoregion by Thorpe and Godwin (1992). The study described four stand types (the average age of stands is in brackets):

1) aspen-spruce stands (100 years) with dense balsam fir regeneration,
2) white spruce stands (150 years) with balsam fir in the seedling and sapling layer,
3) white spruce stands (190 years) with advance balsam fir and
4) balsam fir-dominated stands with white spruce veterans (200 years).

This study is a very useful guide to the composition of Saskatchewan’s mature white spruce forests in the Prince Albert National Park, but it cannot easily be extrapolated to the Mid-Boreal Upland Ecoregion because of differences in fire frequencies. The mean ages of the four stands in the park were much greater than the majority of mature white spruce stands in northwestern Saskatchewan. In the northwest portion of the Mid-Boreal Upland Ecoregion, for example, the oldest spruce-dominated stands are about 130 years old (R. Nesdoly, personal communication, 1997). Furthermore, there appears to be a greater abundance of balsam fir in the Prince Albert National Park sites than elsewhere in the Mid-Boreal Upland Ecoregion.

The Prince Albert Model Forest, also located in the Mid-Boreal Upland Ecoregion, has adopted Oliver’s (1981) model to describe both individual structural stages and broader successional stages in a series of chronosequence studies. The studies explain differences in biomass, understory vegetation, snags, and debris volumes on sites of burned and clear-cut origin (Thrasher-Huag 1997, Sulistoyowati 1998). According to Sulistoyowati (1998), Oliver’s stand initiation stage was associated with the establishment of trembling aspen. “Old growth” stands occurred when trembling aspen had senesced.

Kabzems et al. (1986), encompassing a much larger geographic area, introduced the concept of understory re-initiation, or the third stage of Oliver’s model, in white spruce stands at about 100-120 years where aspen had already been lost from the canopy. Unfortunately Oliver’s developmental stages do not adequately describe the successional pathways in the Mid-Boreal Ecoregion in its entirety where the mosaic of stand types are more appropriately described by a multiple pathway model reflecting the different
successional pathways that result from fire interacting with stand composition and other
disturbance. These stand types may represent the outcomes of different succession
pathways rather than a chronosequence of seral stages within a single dominant pathway.

In characterizing Alberta boreal mixedwoods, a multiple pathway decision tree
model was developed by Lieffers et al. (1996). It was based on seed sources and
disturbance, where disturbance was defined as a change to the forest floor. This model
was used as a vehicle for discussions about silvicultural treatments and harvesting in
mixedwood natural stands. Although the authors briefly discussed the impact of fire and
insects as agents of disturbance, they did not mention wind, disease and senescence as
other potential factors. They described the nature of ‘stand history”, but only seed
presence or absence was depicted in the multi-pathway figure as a subset of the important
disturbance agents. In reviewing published conceptual models, the multiple pathway
approach to stand development appears to be the most applicable to Saskatchewan’s
forests, as long as it accounts for all disturbance mechanisms.

3.3 A Succession Framework for Mid-Boreal Upland Stands

Based on studies in Saskatchewan cited previously, fire frequency, intensity,
severity and spread largely determine future mixedwood stand development. In addition to
the disturbance phenomena, the potential for seed dispersal from surrounding trees, the
distance and time of year that seed disperses, seed viability, seed bed conditions and
competition from herbs should be considered in the construction of a conceptual model
involving stand development. Finally, the ideal conceptual model should be as simple as
possible in representing ecosystems and the factors inherent to ecosystem integrity if it is
to be useful as a potential tool for forest managers, but complex enough to be a realistic representation.

Figure 2 presents a multi-pathway model of succession and a series of stand types that theoretically exist in the Mid-Boreal Upland Ecoregion. The model consists of several stands that potentially differ from each other according to a number of stand attributes such as structure, the density of main canopy stems, growth rates, soil processes and nutrient dynamics. However, because the stand outcomes are the focus of interest, only the effect of seed and disturbance factors are depicted in the model. Mortality and the subsequent creation of canopy gaps are linked to both allogenic phenomena (disturbances external to the stand) such as fire, local wind damage and insect infestation, and to autogenic (within stand) phenomena such as senescence. Senescence is defined as a deterioration process linked to the natural life span of boreal tree species. The solid bi-directional arrows depicted in Figure 2 indicate that stands may undergo minor disturbances more than once. The encompassing dotted arrow represents fire as the major stand replacement phenomenon. Seed continues to enter stands as stands grow and experience disturbance.

The Conceptual Model Assumptions and Limitations: Based on Saskatchewan's records of fire cycles, this model assumes that mature white spruce stand development followed earlier seral stages and that white spruce has remained dominant. The model also assumes that initial development has been the result of stand-replacing fire, wind, disease and/or insect disturbances. The current stand types however, are the result of several smaller-scale fire, wind, disease and insect disturbances acting within a relatively
Figure 2. A succession framework for white spruce stands in the Mid-Boreal Upland Ecoregion of Saskatchewan.
similar age group. Severe fire is part of this model only by virtue of the fact that it causes stand replacement. According to Peterson and Peterson (1992), moderately intense fires will kill the cambium as well as remove needles and leaves from canopies, whereas light fires will result in aspen sprouting. Sprouting as a regeneration phenomenon is depicted in the model.

One limitation of my approach is that seed source is designated only by presence or absence of seed in keeping with the decision tree format. Disturbance gradations are not depicted, nor are the interactions of factors shown that control development. The flow chart detail is limited by the dimensions of the page. As a result, all processes and interactions cannot be shown in detail. In order to present a model at an appropriate scale, the “potential regeneration” factors have been summed into two categories: 1) the presence or absence of seed and 2) seed dispersal distance. In the proposed model, aspen sprouting has been separated from seed germination because, according to the research cited earlier, stands could have different early growth dynamics when they originate from sprouting compared to stands that are established from seed. The seed dispersal figures represent the farthest distance seed could potentially travel (Figure 2). Because of the research in Saskatchewan forests on seed dispersal in mature natural stands, expert opinion has been used (C. Halland, personal communication 1998, J. Thompson, personal communication, 1999).

A Productivity Rating: A potential site productivity rating has been assigned to the stand outcomes in the conceptual model (Figure 2). Among the factors that could influence productivity, the rating system is based on published literature that suggests that aspen litter and large woody debris contain either a higher content or concentration of
nitrogen than white spruce debris. Consequently, aspen debris is considered to have a higher quality in terms of creating nitrogen reserves than debris from coniferous species growing on similar sites (Stump and Binkley 1993, Alban and Pastor 1993). According to the results of modeling, aspen occupancy in boreal mixedwood stands can lead to greater total biomass production (Wang et al. 1995).

3.4 The Stands of Mid-Boreal Upland Model

In Figure 2, I portrayed only white spruce, trembling aspen and balsam fir-dominated pathways because of the current low incidence of other species on mesic sites such as balsam poplar (*Populus balsamifera* L.) willow (*Salix* spp.), and birch in the Mid-Boreal Upland Ecoregion. The acronyms representing the dominant species are similar to those commonly used on forest cover maps by both the Saskatchewan Environment and Resource Management Branch (SERM) and recognized by Saskatchewan forest companies. The letters refer to a main canopy species and the major sub-canopy species: wS-white spruce, tA-trembling aspen and bF-balsam fir. Brackets indicate the presence of a species in the sub-canopy or a species with a minor main canopy presence. In the model, these respective outcomes are depicted as, for example: wS (tA), and wS (wS). In terms of aspen regeneration, both suckering and seed germination will lead to a widely-spaced spruce-aspen cohort with younger aspen shown in Figure 1 as wS-(tA).

A spruce-aspen stand type (wS/tA) has been initially chosen to undergo structural and functional change (Figure 2). This type was chosen because fire-origin stand types are frequent on the Saskatchewan forest landscape. The starting conditions however, can have a wide range of aspen and spruce percent cover, as well as a wide range of structure
and age classes. These variations, together with the spatial role of landscape pattern (control for seed sources) as well as the diversity and magnitude of subsequent disturbances, can lead to the different outcomes.

This thesis will involve research related to the following mature stand types illustrated in the model: wS/tA, a white spruce-aspen cohort, wS (tA), a white spruce stand type with minor aspen, and wS (bF), a white spruce stand type with advance regeneration of balsam fir. A fourth stand type that includes balsam fir as a dominant canopy (bF/wS), does not appear in the model but is the subject of research. Specific hypotheses and objectives concerning these composition types are outlined in Chapter 5.
Chapter 4

Forest Floor Processes and Saskatchewan’s White Spruce Stands

Of the physical and chemical attributes that comprise forest ecosystems, soil properties have been recognized as the least renewable and the most susceptible to change due to forest management (Kimmins 1996). Computer models such as FORECAST predict long-term declines in forest growth under certain management regimes that cause nutrient losses to exceed nutrient replacements and cause reductions in nutrient availability (Wei et al. 1997). Modeling exercises and field experiments have demonstrated that low rates of biomass retention after harvesting can reduce microbial activity, and modify nitrogen legacies (Harmon et al. 1986, Morris et al. 1997). Based on mass balance calculations in Idaho forests, replacement of nitrogen losses after harvesting was estimated to take 250-270 years. Using the same mass balance calculations, the replenishment of nitrogen removed in bole wood harvesting in Montana was estimated to take 135-150 years (A. Harvey, personal communication, 1999, Jurgensen et al. 1996).

The greatest sources of nitrogen in forest ecosystems are soil and forest floor organic matter. For example, total nitrogen input to the forest floor from rainfall, aspen throughfall and aspen litterfall in the central Saskatchewan boreal forest was 2.7, 2.1, and 40.1 kg/ha respectively, during the 1995 season (Huang 1996). Because microbiially-derived nitrogen (nitrogen fixation and/or mineralizable nitrogen) has been found to be a key factor in determining stand growth, forest scientists have investigated microbial fluxes within forest ecosystems by measuring nitrogen fixation (Hendricksen 1990), monitoring CO2 evolution rates (Malik and Hu 1997), and by measuring nitrogen mineralization rates (Flanagan and
Van Cleve 1983). To date, however, these three indices of microbial activity have not been measured simultaneously within litter, logs and mineral soils within Saskatchewan’s Mid-Boreal Upland Ecosystem as part of nitrogen budget investigations.

4.1 Litter Layers and Woody Debris Quality

*Litter layers:* Litter quality may be defined as the chemical components and/or physical characteristics of fine foliar debris that could nurture forest stands. Forest floor litter quality appears to be a function of tree species. Forest leaf litter has greater proportions of sugars, amino acids, and greater cellulose to lignin ratios than fallen logs. Forest litter usually has higher N concentrations, greater respiration rates and greater nitrogenase activity rates than fallen logs (Peterson and Peterson 1992, Hope and Li 1997, Sollins 1982, Sollins et al. 1987). One Alaskan field study confirmed that substrate nitrogen availability rates (g/m²/yr) measured as nitrogen mineralized were lower in white spruce-dominated stands compared to aspen stands (Flanagan and Van Cleve 1983). This study interpreted the finding to be the result of relatively high amounts of lignin and phenolics measured in white spruce litter compared to aspen litter (characteristics believed to slow microbial activity). The Alaskan study found strong correlations (r=0.95) between fungal biomass and N mineralized.

As an extension of the Alaskan field studies, computer simulations with the hybrid model LINKAGES and a series of different Alaskan stand types predicted that available nitrogen rates in boreal white spruce stands would decline significantly from early to late succession stand types (Pastor et al. 1987). The major assumption of the model used by Pastor et al. (1987) was that spruce litter contained more recalcitrant material and consequently mineralized more slowly than aspen litter. This assumption, tested in
Colorado forests, confirmed that net nitrogen mineralization was highly correlated with litter quality and varied with changes in species composition (Stump and Binkley 1993). Litter composition was also believed to account for species differences in the rates of mass loss. Aspen leaf litter lost 62% of its’ mass in 6 months whereas spruce needle litter lost 43% of its’ mass in the same time period (Stump and Binkley 1993).

In a field study conducted near Green Lake, Saskatchewan, Gross (1946) examined the nitrogen fractions of mor forest floors under aspen, spruce, birch, and jack pine stands. Nitrogen concentration was slightly higher in the F and H layers of aspen-dominated stands than spruce-dominated stands. In a more recent Saskatchewan study, Xiao (1987) found consistently higher N, S, and P in the L, F, and H layers under pure aspen stands compared to coniferous stands.

**Fallen Logs:** The amounts of woody detritus in Saskatchewan’s Boreal Plain can be up to 60 Mg/ha (Halliwell et al. 1995); this is less than is commonly found in Canadian west coast forests. Although the role of detritus in Saskatchewan’s Mid-Boreal Upland Ecoregion has not been investigated before, it is believed that the decomposition rates are relatively rapid compared to Pacific coast woody debris. In white spruce logs measured over 14 years, mass loss ranged from 38% (±18%) in Alberta to 61% in Minnesota respectively (Laiho and Prescott 1999, Alban and Pastor 1993). According to decomposition simulations, 95% decomposition had occurred in white spruce logs after 35 to 42 years and aspen logs reached 95% decomposition in 38 years respectively (Laiho and Prescott 1999, Alban and Pastor 1993).

The relationships of nitrogen and cellulose contents to rates of fallen log decomposition have been explored in Pacific coast forests (Means, et al. 1985, Sollins...
1982), but these aspects of decomposition have not been documented for Saskatchewan’s Mid-Boreal Upland Ecoregion. In Alberta, however, higher nitrogen content has been found in aspen logs than in white spruce logs (Peterson and Peterson 1992). In Minnesota, Alban and Pastor (1993) reported higher initial N concentration in fallen aspen boles than in fallen spruce boles and the N concentration declined with decomposition: On the other hand, nitrogen content increased with decomposition in both species. The Minnesota results represent a common pattern of N with respect to decomposition rates. It is often assumed that increases in nitrogen content are due to asymbiotic nitrogen fixation or to the transfer of N due to fungal hyphae, whereas a decrease in concentration may be the result of changes to wood density (Sollins et al. 1987).

The physical properties of decaying logs have been used as a basis for decay classes (Triska and Cromack 1980, Hope 1987). These field classifications have wide ranging forest management uses because they can supply general estimates of wildlife habitat, forest floor moisture retention and nutrient cycling (Harmon et al. 1986). The visual or tactile decomposition state of fallen logs is often associated with particular levels of successional development (Spies et al. 1988). As a result, it is desirable to examine both the chemical and physical properties of logs at several temporal scales in white spruce over a range of stand types as part of addressing sustainable forestry issues.

4.2 Processes in Litter Layers, Fallen Logs and Mineral Soils

Respiration Rates: Since carbon dioxide is created when microbes decompose plant polymers, CO₂ evolution is considered a general index of microbial activity. Mineral soil samples from aspen-dominated stands may have greater microbial respiration than soil
samples from coniferous-dominated stands (Bauhus et al. 1998). Alaskan aspen stands studied for two years had peak soil respiration in June and July of both years, whereas white spruce stands attained the highest seasonal soil respiration in July only (Schlentner and Van Cleve 1984). The authors attributed their results to the openness of leafless Alaskan aspen stands in spring that could permit higher debris and mineral soil temperatures to occur earlier in the season. This condition is thought to account for the differences in respiration rates.

*Mineralizable Nitrogen Rates:* The amount of net inorganic nitrogen measured before and after incubation is significantly correlated with microbial biomass nitrogen; anerobic incubations conducted in the laboratory that kill sample microbial biomass populations that develop aerobically are considered rates of potential nitrogen mineralization (Myrold 1987). Low net mineralization has been attributed to effective immobilization by microbial biomass when microbes compete with plants for nitrogen. In North Sweden, for example, the N pool sizes for both microbes and total plants measured on a sub-arctic heath were the same (Jonasson et al. 1999).

Nitrogen mineralization rates have been successfully used to distinguish different ecosystem types and successional stages but N mineralization has not been shown as significantly different with respect to the topographic position of stands (Vitousek et al. 1982, Wally et al. 1996). In Alaska, the amount of N mineralized in boreal forests declined from deciduous-dominated stands to coniferous-dominated stands (Van Cleve et al. 1993). In a recent study of N transformation rates in old growth Douglas-fir forests, well-decayed boles had greater potential mineralization rates than mineral soil in both summer and winter (Hart 1999).
Nitrogenase Activity Rates: Asymbiotic nitrogen fixation, or the amount of dinitrogen fixed by the microbial enzyme nitrogenase (Roskoski 1980, Silvester 1982), is considered a small but important contribution to coniferous forest ecosystem nitrogen budgets (Hendrickson 1990). Nitrogenase activity has been found to vary within coniferous forest litter, fallen woody debris, and mineral soil for a range of forest types with and without anthropogenic disturbance (Dawson 1983, Heath et al. 1988, Cushon and Feller 1989). Symbiotic nitrogen fixation in forest floor substrates may contribute up to 308 kg/ha (Marschner 1986) compared to asymbiotic nitrogen fixation which can contribute an average of 1 kg/ha/yr N in ecosystem types on the Pacific coast. However, nitrogen fixation rates are highly variable depending on the debris species and substrate type. In northern temperate (hardwood) forests, asymbiotic N fixation rates in litter, logs and mineral soil ranged from 4.7 to 14.1 kg/ha/yr (Todd et al. 1975).

Successional stand types and associated differences in organic matter quality can influence nitrogenase rates. In Alaska, the greater nitrogenase activity rates found in willow sites than in white spruce stands (Weber et al. 1981, 1984), might be due to the anaerobic conditions of the early stage willow stand. According to the authors, the nitrogen-fixing capability of cyanobacteria in moss within white spruce stands might explain the fact that in mature Alaskan white spruce stands, moss accounts for 24% of the ecosystem productivity (Weber et al. 1981, 1984).

In Ontario, aspen logs produced greater than 1000 nmol/day of nitrogenase activity when incubated at 30 °C with 75 % saturation (Hendricksen 1991). Rates over 500 nmol/day occurred under field temperatures with the same level of saturation. These results indicate that aspen logs may be a major nitrogen sources in white spruce-aspen stands of the Mid-
Boreal Upland Ecoregion. Higher amounts of cellulose found in aspen logs compared to spruce logs may account for higher overall nitrogen fixation in aspen debris because the cellulose comprises a carbon source that is relatively easy for microbes to break down and some microbes can degrade cellulose.

The relative nitrogen activity rates in litter, log and mineral soils in Saskatchewan may resemble those in some Oregon Douglas-fir stands, where nitrogenase activity rates were greater in litter than in logs or mineral soil (Hope et al. 1997). Conversely, the order could be similar to that in Idaho and Montana stands where logs had higher rates of nitrogen fixation than litter (Jurgensen et al. 1996).

The importance of litter, logs and soils in supplying nitrogen for future stand growth will also depend upon the substrate mass. In Saskatchewan boreal forests, litter layers are relatively thin, and the mass of logs may be only 60 Mg/ha (Halliwell et al. 1995). Recent studies of boreal aspen and coniferous stands have shown that forest soils have different spatial and temporal microbial biomass patterns according to soil depth (Scheu and Parkinson 1995). In mature and old growth Douglas-fir stands on the Pacific coast, nitrogen fixation and nitrogen mineralization rates declined with depth in forest mineral soils, litter layers and within logs (Hart 1999, Hope et al. 1997). As a result, the depth of the litter, log and mineral soil substrates should be taken into consideration when evaluating process rates.

4.3 Substrate Moisture and Temperature in Relation to Microbial Processes

A substantial body of literature has confirmed that microbial activity rates in litter layers and fallen logs are sensitive to microclimate (Meentemeyer and Berg 1986, Moore 1986, Clarholm et al. 1981, Sollins et al. 1987). A recent Saskatchewan study of aspen litter
and grass decomposition rates reported that moisture and temperature had greater effects on litter decomposition rates than did litter quality (Kochy and Wilson 1997). Schmidt et al. (1998) found that an increase in temperature of 2°C either increased or tended to increase net mineralization but that there were no positive correlations between the two variables. The authors believed that this result was due to greater immobilization that occurred concurrently with greater mineralization.

When mature 75-year-old stands and 450-year-old Douglas-fir stands were compared in Oregon temperate forests, lower litter, log and mineral soil respiration levels occurred in the 450-year-old stands. These stands were not only cooler in early spring when temperatures were relatively low, but the three substrate moisture contents were lower in August when day temperatures were relatively high (Hope et al. 1997). In the Oregon study, logs tended to be moister later in the summer season than the LFH layers.

Seasonal substrate moisture and temperature have been found to have an effect on the nitrogenase activity of Boreal Plain forests. In an Alberta boreal forest study with drier and wetter habitats, the drier habitats occupied by jack pine had less nitrogen fixation measured as nitrogenase activity than did the moister sites occupied by larch and black spruce. There were greater populations of nitrogen-fixing Azotobacter and Azospirillum on the larch-black spruce site than on the jack pine site. Nitrogenase activity under larch stands was as high as 26 μmole/day (Florence and Cook 1984).

Similar findings were reported in a comparison of substrate nitrogen fixation rates for Ontario mixedwood, hardwood and jack pine stands; the jack pine stand had 40-70 times less nitrogen-fixing bacteria during the growing season than the other two stand types (Hendricksen 1990). Nitrogen fixation in the Ontario boreal mixedwood stands responded
positively to autumn precipitation (Hendricksen 1990). In Alaska, where the summer seasonal temperatures and precipitation are different than in Ontario, higher nitrogenase activity levels occurred in July and early August than in late August and September (Klingensmith and Van Cleve 1993).

In studies of Colorado meadow communities conducted during the winter, microbial activity continued in soil that was not frozen and both soil inorganic nitrogen pools and microbial biomass nitrogen increased until snow melt (Brooks et al. 1998). These findings, together with those of an Alberta study by Lousier and Parkinson (1976), suggest that microbial activity in boreal forests may take place in fall, winter and early spring. Nitrogen mineralization in the Saskatchewan Boreal Plain could be relatively high during narrow time intervals closely related to snowmelt.

4.4 Questions Related to Substrate Microbial Activity

Since studies in Colorado have shown that net N mineralization in litter is greater in aspen stands than in lodgepole pine stands (Stump and Binkley 1993), the amounts of available nitrogen may be higher in Saskatchewan aspen-dominated stands than in conifer-dominated stands. Although aspen logs in other locations have been found to have higher cellulose and higher nitrogenase activity, rates of mineralized nitrogen (available nitrogen) may or may not be higher than that found in Saskatchewan spruce logs. If mature Saskatchewan stands with forest floors composed predominantly of aspen litter are found to have higher nitrogen availability than stands with predominantly coniferous litter, then a productivity rating system could be formulated for mature white spruce succession stand types based on aspen occupancy.
According to published literature, the open stand structure found in Saskatchewan's aspen stands during spring may generate higher ground temperatures compared to temperatures found in white spruce-dominated stands. This condition may lead to greater potential mineralizable nitrogen rates, greater respiration rates, and greater nitrogenase activity rates in aspen-dominated mid-to-late stand types than to white spruce stands. Due to the composition of leaf litter compared to needle litter, it is likely that stands with aspen litter will have greater rates of microbial activity.
Computer modeling can overcome limitations of traditional research strategies by extending inferences in time and space. Computer models may be used at the outset of a forest management project to assess the sensitivity of simulated ecosystems to a range of processes or to explore long-term development of selected stands under a variety of assumptions about site-specific processes.

Computer models may be classified as: 1) empirical (based exclusively on data analyses and mathematical relationships), 2) succession/developmental, where models may be both empirical and processed-based (hybrid), and 3) exclusively process or mechanism-based. The latter group may have reduced stand data inputs but represent more below-ground processes than the other types (Peng and Smith, unpublished 1999).

In terms of meeting either scientific or operational objectives, empirical models are often considered more relevant in the descriptive or characterization stage of knowledge accumulation, whereas simulation models (including process and hybrid models) are usually employed as explanatory tools in research (Korzukhin et al. 1996). The most desirable computer models to evaluate stand development should be easy to operate and the model's function (mechanisms and algorithms) should be easily understood.
5.1 Computer Model Types

Site index (tree height in relation to age) and growth and yield models (models that express yield in biomass in relation to age) are common methods of predicting forest growth. Although the data demands and complexity of these models are less than hybrid models, they are not necessarily useful for forest ecosystem research because they are not ecosystem-based. The models function according to a series of mathematical relationships based on inventory data, and below ground and many community processes are not represented.

One limitation of exclusively data-driven models when used for ecosystem studies is that empirical field studies have found poor relationships between site index and soil chemistry. Edmonds and Chappell (1994), among others, reported low correlations between soil nitrogen (kg/ha) and site index in Douglas-fir. This finding may be due in part to the asymptote in tree height commonly experienced after trees reach maturity and/or the high variation in soil nitrogen content expressed on a per hectare basis.

Site index and growth and yield models do not explicitly represent key ecosystem processes. Because the models do not include the causes of change in forest ecosystems, they may have low explanatory powers. They also cannot make accurate predictions under significantly changed growing conditions. Growth and yield models cannot, for example, account for changes in site quality that may be due to changes in either biochemical or biogeochemical properties (Kimmins et al. 1999, Battagilia et al. 1998). Based on this evidence, neither growth and yield models nor site index have been adopted as key analytical tools in this thesis either to characterize Saskatchewan’s Mid-Boreal Upland
Ecoregion stand types, or to explore the effect of aspen on white spruce-aspen stand growth.

Ecosystem process-based simulation models can explore hypotheses about forest behavior and function. Some ecosystem simulation models such as SORTIE, are based entirely on competition for light while models such as LINKAGES and FORECAST, are based on both above-ground light competition and below-ground factors. Because of the desire for balanced ecosystem representation in research situations, simulation models used in examination of succession and/or development usually contain an integration of both above and below-ground forest ecosystem characteristics.

Examples of Hybrid Computer Models: Most hybrid models do not provide measures of statistical probability for the occurrence of any single stand type because the outcomes are simulated deterministically. These models can still evaluate succession and development in a systematic fashion, however, and permit qualitative comparisons of the outcomes (Kimmins personal communication 1999). Hybrid models' representation of certain aspects of succession, particularly regeneration, has been criticized (Makipaa et al. 1998). Independent regeneration models permit examination of regeneration processes in greater detail.

CENTURY is a biogeochemical model that focuses on below ground changes in carbon, nitrogen, phosphorus, and sulphur for a variety of plant systems. It was designed for grasslands but has been extended to savannas and forests. CENTURY is based on climate, soil texture, plant productivity, decomposition and management submodels (Peng et al. 1998). The forest types are divided into pure coniferous and pure deciduous stands. The forest submodel divides trees into components consisting of leaves,
fine roots, coarse roots, branches and large wood. Appropriate carbon and nutrient levels are assigned using a fixed allocation scheme (Metherell et al. 1993). Gross production is driven by a maximum gross production rate that is modified by soil moisture, soil temperature and live leaf area index.

The organic matter submodel creates three pools of organic matter: active, slow and passive. Above and below biotic residues are partitioned into structural and metabolic pools as a function of nitrogen to lignin ratios. The organic matter decomposition rates are modified by soil moisture, soil temperature and may be increased by cultivation.

Because the design of CENTURY is weighted toward analysis of carbon pools, it does not incorporate specific forest management strategies for the evaluation of a variety of future forest values. It calculates soil moisture and temperature changes based on a monthly time step. As a result, it may not be able to adequately capture nutrient fluxes that are responses to soil moisture and temperature changes (B. Seely, personal communication 2000). Based on the above limitations, this model lacks the full potential to act as a decision support tool for sustainable forest management. The model has been employed to simulate central Canadian boreal forest responses to global climate change based on the assumption that large tracts of the boreal forest are homogeneous. It has also been modified to examine carbon budgets in urban, forest and agricultural environments in the Lower Fraser Valley (S. Ames, personal communication, 2000).

LINKAGES, a non-spatially explicit stand level model that consists of production, climate and decomposition components, has been used to analyze soil processes in eastern US hardwood forests (Pastor and Post, 1985, Pastor et al. 1987). The
model includes representation of soil nitrogen and water availability. Like the CENTURY model, one advantage of LINKAGES compared to nonhybrid models, is that it represents the feedback between species growth and nitrogen availability.

This model has been used with Alaskan boreal forest chronosequences and in British Columbia. Keenan (1993) selected this model to examine the growth and regeneration patterns of coastal redcedar (*Thuja plicata* Donn) - western hemlock (*Tsuga heterophylla* [Raf] Sarge) stands with and without windthrow disturbance on northern Vancouver Island. In the LINKAGES model, saplings are established at a user-specified rate and growth is modified according to available light, soil moisture, and soil nutrients. Exogenous tree mortality is simulated by killing a small portion of the trees each year so that only 1% of the trees reach the potential maximum age.

In LINKAGES, tree growth is a function of diameter (Keenan 1993). Within-stand mortality takes place according to a threshold of reduced incremental diameter growth. Light levels are calculated from the allometric relationship of diameter and foliage biomass. Available moisture is calculated from the climate component (Keenan 1993). The proportion of the growing season that falls below field moisture capacity is used to limit diameter growth (Keenan 1993).

The model's use as a decision support tool in sustainable forestry is less effective than some other hybrid models because forest management practices such as burning or partial harvesting have not been incorporated into the design. Keenan (1993) commented on the use of slashburning as a potential management tool but did not demonstrate its' effect on regeneration in northern Vancouver Island forests.
5.2 The FORECAST Model

FORECAST is superior to other hybrid simulation models for certain applications because it has been designed specifically to make long-term stand-level projections about the sustainability of forest ecosystems. The major differences between FORECAST and other hybrid computer models are that it does not assume that historical bioassay data can be used directly in predicting future events. Below-ground processes are represented. The FORECAST model permits the examination of outcomes based on changes to growth regulating factors over time. FORECAST represents trees, shrubs, herbs and mosses. It simulates nutrient cycling and nutrient control of growth as well as light competition. Unlike most mathematical models, the FORECAST model produces graphic representations of the changes in a wide variety of structural and process attributes, natural disturbance and management practices.

Like most ecosystem models, the data requirements for FORECAST are extensive. Data are required on height, stand density, stem size frequencies, biomass accumulations, foliar nutrient concentrations, and litter biomass and decomposition rates. Soil properties and the nitrogen transformations within litter and down woody debris are an essential part of the empirical dataset that must be supplied for sites. However, FORECAST has the option of running exclusively as an above-ground light competition model if desired, which reduces the data requirements (Kimmins et al. 1999).

The model examines the consequences of different management or natural disturbance scenarios starting from a variety of user-specified starting states. These states represent the outcome of historical disturbance regimes for the forest ecosystem of interest. Because no confidence intervals or probabilities can be attached to FORECAST
outputs, the model is considered a trend evaluator with the potential to compare different outcomes rather than as a direct predictor of the effects of various management scenarios on successional patterns (Kimmins et al. 1990).

5.3 The General Function of FORECAST

The model creates growth indices for each species as if it were occupying the site alone; these indices drive plant production according to available light and below-ground nutrient resources (Kimmins 1993). Plant growth is expressed as total net primary productivity (TNPP). TNPP is described as the sum of the change in biomass plus the sum of the tissues lost as litterfall plus mortality at each time step (Kimmins 1993). TNPP is used with estimates of foliar nitrogen and simulated shading to produce shade-corrected nitrogen efficiency (SCFNE).

The potential nutrients required for plant growth are calculated from the predicted new biomass times the expected concentration of nutrients in the new biomass. The amount of nutrients available from internal cycling within plants is subtracted from the predicted nutrient demand for new growth to yield a net nutrient demand. Actual plant growth is based on whether the net nutrient demand required for plant growth can be satisfied. Potential available nutrients to meet the demand are calculated in part from the percent of fine root biomass in relation to total potential soil occupancy by fine roots. If nutrient availability is greater than uptake demand, growth can increase. If nutrient uptake demand is greater than nutrient availability, competition results and growth is limited to what is possible at the given level of available nutrients.
Forest floor temporal changes are part of FORECAST’s representation of ecosystem function. Down woody debris decays at rates provided in the input file. All stems entering the forest floor are subjected to a size-dependent mass loss rate.

The timing of seedling establishment is user specified; there is no simulation of seed dispersion or assignment of probabilities for seed germination. The user also defines the intensity and frequency of forest management treatments such as fertilization, commercial thinning, pruning and underburning. The intensity of fires is defined by the consumption of forest floor material. Using the growth and nutrient indices, FORECAST can simulate species growth for as long a time-span as the data permits. The model can simulate runs up to 240 years but the model will not permit the simulation of plant growth for longer than is described by the input data. Inevitably, as with any model, the believability of predictions with FORECAST is reduced with increasing time in the future (J. P. Kimmins, personal communication 1998).

5.4 Nitrogen Transformations Represented in FORECAST

The model can recognize up to five nutrients but has generally focused on nitrogen, with the possible addition of phosphorous, and potassium. The availability of nutrients for plant growth is calculated from the balance of nutrient inputs and outputs from the ecosystem, the circulation of nutrients within the system and net amount available from internal cycling within the plant. The total soil nutrient pool is estimated from the sum of nutrients in organic matter, nutrients held on exchange sites, and net nutrient inputs from N fixation, weathering, precipitation and seepage (Kimmins 1993).

Since nitrogen has been considered one of the factors most limiting plant growth (Myrold 1987), and since foliar nitrogen appears to be one of the best predictors of NPP,
nitrogen transformations are central to the function of FORECAST. Nitrogen may come from precipitation, mineral weathering and seepage as geochemical inputs whereas geochemical outputs may occur as nitrogen immobilization, volatilization and as part of removal of harvested materials (Kimmins 1993).

Litter is defined as above and below-ground dead plant material in the form of leaves, bark, branches, and coarse and fine roots. An increase in nitrogen content in one of these substrates is interpreted as nitrogen immobilization from the “available N pool” or from N fixation, and a decrease in content is interpreted as nitrogen mineralization (Kimmins et al. 1999). The change in the net nitrogen for each time step in each substrate is expressed as kg/ha/yr. The simulation of nitrogen mineralization depends on the nitrogen concentrations for fresh litter and the changes over time in concentration and weight loss in forest floor litter, including roots.

In addition to these inputs, rates of symbiotic nitrogen fixation may be defined by the user. Asymbiotic nitrogen fixation may also be specified in the model for any one of the decomposing litter types. Alternatively, where no data are available, nitrogen fixation may be estimated from published values and entered in the model as a single rate.

5.5 Initial Ecosystem Conditions in FORECAST

The condition of an ecosystem in the present reflects past growth patterns, management treatments and natural disturbances. The ECOSTATE file defines present values for trees, shrubs and mosses at the start of a simulation run. The initial ecosystem condition is created by running the ECOSTATE file containing these components several times without nutrient feedback so that the system is forced to develop as it has in the
past. While the ecosystem accumulates forest floor litter and coarse woody debris, it establishes values for forest floor and below-ground nutrient contents as well as soil organic matter. FORECAST has proven to be very sensitive to initial conditions of the ECOSTATE file and care must be taken to insure that this file is a realistic representation of the ecosystem of interest (Kimmins et al. 1999).

5.6 The Limitations of the FORECAST Model

There are several assumptions and constraints associated with the FORECAST model. The most notable assumptions are that: 1) historical bioassay information used in creating the starting state and growth driving function provides the best estimate of growth production for unchanged conditions, 2) empirical data that reflect growth, allocation and turnover (litterfall) is the best base for predicting future growth, 3) the initial stand state is accurately defined, 4) the methods used to estimate process rates produce acceptable estimates (Morris et al. 1997) and finally, 5) that these estimates forecast the effect of changes in growth conditions or stand growth with acceptable accuracy.

The empirical data incorporated into the model from localities other than the area of interest are assumed to accurately represent the growth patterns of the area of interest. Since FORECAST is not a spatially explicit model, the responses of individual trees to above and below-ground resource competition, including below-canopy light and below-ground nutrients, cannot be simulated but are derived from empirical inputs. Since there is no regeneration sub-model in FORECAST and trees must be “planted” to simulate regeneration, the user bases the number of regenerating trees on values from prior research. Coppicing and sprouting can be simulated based on data inputs. Since no
allowance has been made for seasonal climate effects in FORECAST, the effects of short-
term or long-term climate change cannot be simulated. Inferences from FORECAST runs
must be restricted to single regions with homogeneous climate.

The representations of soil processes are relatively simplistic but more complex
than most other hybrid models. There is no representation of soil horizons or soil mixing
(Kimmins et al. 1999). The available nitrogen calculated in the model from nitrogen
inputs may not resemble field measures of available nitrogen since the model calculates an
annual rate and field measures are based on hourly or daily rates.
Chapter 6
Research Strategies and the Study Area

One objective of my thesis was to investigate the structural and process characteristics of selected mature white spruce stands. Mistik Management Ltd., a forest company operating in the Mid-Boreal Upland Ecoregion, recognized that different mature white spruce types could exist in their management areas and these types might require different management practices. The company wished to identify various white spruce stand types and understand their potential long-term sustainability under harvesting and natural disturbance regimes. My thesis followed a series of inductive strategies (information synthesis, observation, and hypothesis generation) and deductive strategies (experiments) stemming from these goals.

*Inductive Strategies:* Literature provided a theoretical base for the potential existence of different mature white spruce types and determined the processes that were likely to contribute to their formation (Chapters 2-4). A conceptual model of stand succession was necessary in order to graphically depict the synthesis of succession and stand information and provide context for hypothesis generation concerning the white spruce stand types. It also provided the framework for the future exploration of white spruce stand sustainability through computer modeling. Because the potential sustainability of mature white spruce stands was of interest to Mistik Management Ltd., a productivity rating system was introduced into the conceptual model (Figure 2). This rating system depended on the forest floor nitrogen "levels" created by the presence of aspen.
The purpose of the conceptual model was to prepare for an exploration of the white spruce stand types derived from selected successional pathways. This exploration was conducted by means of field experiments and later by computer modeling. Computer modeling was used to investigate the long-term simulated growth patterns of aspen-white spruce stands and the contribution of N fixation in decaying logs to the nitrogen economy of these mixedwood stands.

Field observations confirmed the presence of the white spruce types on the landscape as they were represented in the conceptual model. Once the existence of the mature white spruce stand types had been verified, then testable hypotheses were posed concerning the differences that existed in the white spruce types and whether different levels of productivity occurred according to the presence or absence of aspen.

These hypotheses led to a series of experiments. Selected results from the experiments were used later to test for the sustainability of a white spruce-aspen type with the computer model, FORECAST.

6.1 Hypotheses

Four null hypotheses were created from selected research questions related to the white spruce stands of the Mid-Boreal Upland Ecoregion:

1) mature mid-to-late seral stand types in the Mid-Boreal Upland, such as those depicted in the conceptual model are not statistically different in key structural and process attributes-particularly the structural attribute of age (Chapter 7, Chapter 8),
2) there is no statistically significant difference in the levels of forest floor respiration, nitrogenase activity or mineralizable nitrogen among selected stand types or among log and mineral soil substrate types.

3) there is no difference in the effects of simulated stand replacement harvesting compared to the effects of simulated natural disturbance on white spruce-aspen stands when these disturbance agents are introduced at 60-year, 80-year and 120-year intervals using the model FORECAST (Chapter 9) and,

4) there is no difference in simulated white spruce-aspen stand growth over 240 years when simulated nitrogen fixation from logs and nitrogen fixation from litter is introduced in the model FORECAST.

**Deductive Strategies:** The use of stand field characteristics and litter, log and mineral soil nitrogen attributes was designed to address the null hypothesis that the stand types were similar. The modeling and field experiments evaluated forest floor and mineral soil nitrogen properties as indicators of differences in stand type productivity. Computer modeling was considered as a means to examine long-term changes in selected white spruce stand types.

The process study and modeling objectives were:

1) to analyze certain chemical attributes of boreal aspen and white spruce logs over a range of residence times (Chapter 8) to determine total N content and possible N accrueement.

2) to simulate aspen-white spruce cohort growth over periods of 60, 80 and 120 years using selected nitrogen data extrapolated over time to determine if stand biomass was reduced according to the substrate N type (Chapter 9).
6.2 Study Area

Two Canadian boreal Ecozones are present in Saskatchewan: the Boreal Shield and Boreal Plain. The Boreal Shield is located in the northeastern and northcentral portion of the province. The Shield Ecozone is typified by bedrock outcroppings, glaciofluvial deposits, lakes, and little topographic relief. The low-lying peatlands of the Boreal Shield are often perennially frozen. The Boreal Plain, situated directly south of the Boreal Shield, consists of lowlands and gently undulating hills composed of glaciofluvial, glaciolacustrine and morainal deposits. The Boreal Plain often has taller white spruce forests than the Boreal Shield (Padbury and Acton 1994).

The Boreal Plain consists of a number of Ecoregions (Figure 1). Both the Mid-Boreal Lowland Ecoregion and the Boreal Transition Region border the Mid-Boreal Upland Ecoregion. The Boreal Transition Region consists of contiguous aspen stands with scattered spruce interspersed with farmland. The Mid-Boreal Lowland has elevations less than 400 m and is dominated by wetlands (Padbury and Acton 1994).

Saskatchewan’s Mid-Boreal Upland Ecoregion extends from east of Candle Lake and the Torch River to the Alberta border (Figure 1, p 23). The northeastern border is situated at Wapawekka Lake northeast of La Ronge and extends west to the Alberta border near the Clearwater River. The southern border extends from slightly north of Prince Albert to the Cold Lake Air Weapons Range at the Alberta border. The Ecoregion comprises 10 million hectares or 16% of the province. Elevation differences are commonly 2-50 m in much of the Ecoregion although total elevation may reach 900 m in hillier locales.
There are three forest companies operating in the Mid-Boreal Upland Ecoregion. Weyerhaeuser Canada Ltd. operates in the central portion of the province from the Prince Albert vicinity to slightly east of Green Lake. Mistik Management Ltd.'s holdings extend from east of Highway 155 to the Alberta border, and SaskFor McMillan Ltd. (recently purchased by Weyerhaeuser Canada Ltd.) operates in the eastern portion of the Mid-Boreal Upland Ecoregion. In addition, the provincial government manages several parks in the Ecoregion including Meadow Lake Provincial Park to the west of Meadow Lake and Candle Lake Provincial Park which is situated on the western, southern and southeastern portions of Candle Lake. Finally, a significant portion of Saskatchewan’s Mid-Boreal Upland lies within the boundaries of Prince Albert National Park.

In the Mid-Boreal Upland Ecoregion, glaciation and subsequent glaciofluvial action have resulted in a wide variety of landforms including moraine, kame, kettle, esker and ice settlement types. Glacial deposits at least 100 m thick overlie bedrock that is either mudstone and shale from the Upper Cretaceous Riding Mountain Formation or sandstone and siltstone of the Manville and Lower Colorado group of the Lower Cretaceous Age (Acton et al. 1998). The soil texture of the Ecoregion, derived primarily from these glaciofluvial, morainal and/or glaciolacustrine materials, is often silty or sandy loam, although greater amounts of clay deposition can occur. The soils of the Mid-Boreal Upland are classified as Organic, Gray Luvisols or Brunisols (Beckingham et al. 1996, Acton et al. 1998).

At the landscape level, soil drainage, reflective of soil properties, can be an important factor governing tree species distribution. Trembling aspen grow on well aerated silts, clays and loamy tills, whereas white spruce grow well on moist or deep
sandy loams; balsam fir can grow on a range of sites but is often found on moist sandy loams (Beckingham et al. 1996). Low bush cranberry is an indicator of mesic sites in the Mid-Boreal Upland Ecoregion (Beckingham et al. 1996). Common plant community types within this ecosite type are green alder and feathermoss.

The soils where mid-to-late succession stand types were chosen in the Ecoregion were variants of Degraded Eutric Brunisols similar to either the Bodmin Association with Btj or Bm horizons, or the Pine Association with Bm horizons (Rostad and Ellis 1972, Crossen et al. 1970). The search for research sites in the low bush cranberry ecosystem type ranged from Candle Lake and Prince Albert National Park, north to Buffalo Narrows. Sites were also examined in the more southwesterly extremities of the Ecoregion, slightly south of Meadow Lake and within Meadow Lake Provincial Park. All sample plots were located in mesic low bush cranberry ecosites with Brunisolic soils within the Mid-Boreal Upland.

The climate of the Ecoregion is characterized by long, cold winters and relatively short summers with temperatures ranging from −40 °C to 32 °C (Table 1). There is an average frost-free period of 80-100 days in the southern portion of the region and 70 days in the northern region. July and August are generally the warmest months (Beckingham et al. 1996). Waskesui, Saskatchewan, has been considered a typical climate station for the Mid-Boreal Upland Ecoregion. Based on data from this station, total mean precipitation is 456 mm annually, with the majority falling as rain. Mean annual snowfall is 147 cm and mean temperature range is 18 °C in January to 16.3 °C in July (Table 1).
Table 1. Mean monthly temperature, rainfall and snowfall for Meadow Lake, Green Lake, and Waskesui Lake, Saskatchewan for 1962-1990 (Environment Canada 1994).

<table>
<thead>
<tr>
<th></th>
<th>May</th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Meadow Lake Measurements: 1977 – 1990</strong></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Monthly temperature (°C)</td>
<td>10.4</td>
<td>16.7</td>
<td>15.2</td>
</tr>
<tr>
<td>Monthly rainfall (mm)</td>
<td>44.0</td>
<td>83.1</td>
<td>63.4</td>
</tr>
<tr>
<td>Monthly snowfall (cm)</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Green Lake Measurements: 1962 – 1990</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Monthly temperature (°C)</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Monthly rainfall (mm)</td>
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<td>76.0</td>
<td>0</td>
</tr>
<tr>
<td>Monthly snowfall (cm)</td>
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<td>0</td>
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<tr>
<td><strong>Waskesui Lake Measurements 1977 – 1990</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Monthly temperature (°C)</td>
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<td>16.3</td>
<td>15.0</td>
</tr>
<tr>
<td>Monthly rainfall (mm)</td>
<td>37.9</td>
<td>79.7</td>
<td>57.5</td>
</tr>
<tr>
<td>Monthly snowfall (cm)</td>
<td>1.9</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

ND= No Data.
Chapter 7

Stand Structure in Saskatchewan's Mid-Boreal Upland Ecoregion

This chapter addresses differences in selected stand characteristics such as age, down woody debris, regeneration patterns, and basal area among stand types. Since the stand structure characteristics that I selected for measurement are often used to separate “mature” and “old growth” white spruce stands, I explored the validity of these attributes as “old growth” descriptors.

Mid-Boreal Upland Ecoregion foresters refer to white spruce stands as “old growth” where aspen is senescing from the canopy, when the stand structure is “park like”, or when white spruce are taller than the average. In Alberta, “old growth” white spruce forests have been characterized as stands having trees >18 m tall, or stands with canopy gaps. Older white spruce forests typically have both abundant conifer regeneration, and a range of decay in snags and logs (Fairbarns 1991).

Age has been declared insufficient as a characterization of “old growth” coniferous forests (Franklin et al. 1981, Timoney and Robinson 1996). In Alberta and British Columbia, scientists have used stand characteristics such as multi-storied canopies with two or more species, tree diameter, and the abundance of saplings to describe “old growth” (Lee et al. 2000, Timoney and Robinson 1996, Stelfox 1995). Stands have also been typified by understory plant associations, the density of main canopy species, basal area, snags with particular decay classes, and the numbers and volumes of decaying logs (Twolan-Strutt and Walsh 1996, Thrasher-Huag 1997 and Sulistiyowati 1998).
Early studies of white spruce stand structure carried out at Candle Lake, Saskatchewan, found that balsam fir was significantly associated with white spruce and black spruce, whereas aspen was associated with all species except balsam fir (Swan 1966). The author concluded that balsam fir did not demonstrate pioneer behavior at Candle Lake. However, Swan’s research took place in only one location of the Mid-Boreal Upland Ecoregion and the study did not consider the proximity of seed source as a factor in successional development on mesic sites. Some stands near Candle and Waskesui Lakes are composed almost exclusively of balsam fir; mixed stands of aspen and balsam fir can be found near Waskesui Lake. Based on published literature (Stelfox 1995), representative stand attributes such as basal area and coarse woody debris volumes may or may not have potential to characterize mature or “old growth” white spruce stands.

7.1 Research Objectives

The objectives of this study were to: 1) test for differences in the structural characteristics of four of the stand types described in the conceptual model (Figure 2); and 2) examine specific descriptors of ‘old growth” for mature white spruce stands in the Mid-Boreal Ecoregion. The research focused on differences in both living and non-living stand attributes.

7.2 Methods I. Field Sampling Approach

The study of the stand types representing multiple successional pathways employed a stratified sampling approach based on a technique known as ‘subjective sampling without preconceived bias’ (Mueller-Dombois and Ellenberg 1974, Beckingham
et al. 1996). This representative sampling design has been applied to plant communities
where vegetation types are selected according to some recognized category that
constitutes a null hypothesis (Poore 1962). The sites were representative of certain white
spruce mid-to-late seral stand types (Figure 2) and conformed to the ecosite classification
used by Beckingham et al. (1996).

7.3 Methods II. Stand Selection

The final plots selected for measurement from the pool of potential sites were
screened during field reconnaissance to ensure homogeneous site conditions and lack of
identifiable anthropogenic disturbance. The result was that the final selection was
representative, rather than random. The plots chosen for measurement were replicated as
uniformly as possible in the southeastern, central and northwestern portions of the
Ecoregion. The plot dimensions used in this study, 400 m$^2$, have been found satisfactory
in describing natural forest stand variability (Walmsley et al. 1980).

Due to limited time and human resources, a minimum of five plot replicates were
selected in four stand types or successional stages. The four mid-to-late succession stand
types selected for structural characterization were:

a) white spruce-aspen, (wS/tA),
b) widely spaced white spruce with minor aspen (wS (tA));
c) white spruce with advance balsam fir (wS/bF), and,
d) balsam fir-dominant with white spruce veterans (bF/wS).

The spruce-aspen stand type (wS/tA), is one of the most common types featured
on the Saskatchewan boreal landscape. The (wS (tA)) or white spruce with minor aspen
type is characterized by large diameter spruce trees with both younger and/or older aspen or white spruce in gaps. Because balsam fir is not a commercial species in Saskatchewan's Boreal Plain, the successional relationships and development patterns of the two balsam fir types chosen for research (wS/bF and bF/wS) have not been the subject of intensive study in the past. The bF/wS type, consisting of decadent white spruce veterans and abundant balsam fir in the main canopy, represents the most mature white spruce stand type selected for study. Plots were located north and east of Prince Albert, Prince Albert National Park, Candle Lake Provincial Park, north and south of Green Lake, south and west of Meadow Lake, Meadow Lake Provincial Park, and just south of Buffalo Narrows.

Based on published literature, the living structure attributes selected to describe these four types were: basal area, main canopy stem density, sapling density, and regeneration (trees < 2 m). The non-living structural measurements taken during this study involved coarse woody debris linear density, coarse woody debris volumes, and snag numbers.

7.4 Methods III. Measurement of Living Stand Attributes

Site characteristics recorded at each plot included elevation, aspect, location, micro-topography, organic matter distribution over the plot, stand initiating factors, and ecosystem moisture and nutrient regimes (Walmsley et al. 1980). The location of all stems, including snags, were mapped within the 400 m$^2$ plot boundaries. All trees within the plot were identified by species and measured for dbh. Percent cover and frequency of understory species were noted in each plot and used as indicators to verify the mesic moisture regime and the mesotrophic nutrient regime (Walmsley et al. 1980, Beckingham
et al. 1996). I recorded tree heights, diameters and tree pathology within variable radius prism plots established at the center of each 400 m² plot. Tree ages were determined using a 1.3m boring height on representative individuals from each crown class in each prism plot. The core rings were counted to obtain the mean age for each tree, and the count results were adjusted to obtain total age based on the intervening rings from the germination point to the 1.3m boring height (Walmsley et al. 1980). British Columbia boring height adjustment tables were used in the absence of boring height adjustment tables for Saskatchewan. At least two trees of each species in the dominant and codominant layers were bored to obtain tree ages. Basal areas were calculated using equations in Husch et al. (1972).

Saplings were defined as trees 2-10 m in height and less than 10 cm in diameter. Sapling species, diameter and height were recorded for each plot. For trees < 2 m, defined as seedlings, I recorded the diameter at the root collar, height, and substrate upon which the seedling had germinated. Four subplots of 4x5 m, usually located on the plot or immediately adjacent to it, were used to assess the < 2 m trees. For trees in this category, age estimates were determined by counting the living and dead whorls of branches on each stem. This age estimate method was tested for accuracy by cutting sample trees, counting the rings and then comparing ring-counted ages to age estimates obtained by counting branch whorls. A regression analysis showed a close data fit between ring counted ages and whorl age estimates. This technique was used for white spruce and balsam fir seedlings.

A 1 m³ soil pit in the center of each plot provided data on soil physical properties. Soil profile descriptions included horizon depths, color, coarse fragments, textural classes
using hand texturing, soil consistence, root abundance and root distribution (Canadian Soil Survey Committee 1978, Walmsley et al. 1980). Samples collected from each soil horizon were transported to the laboratory where sub sampling took place in preparation for laboratory analyses. The laboratory sub samples were used to verify the soil field texture classes and obtain nitrogen concentration estimates for the forest floor horizons.

7.5 Methods IV. Measurement of Non-Living Stand Attributes

The snag species were recorded for each standing dead stem. Snag decay levels were classified according to a modified six-stage classification (Thomas et al. 1979). Snag Class 1 consisted of complete boles that had retained small branches and bark whereas snags in Class 6 were very friable short boles or stumps <2 m tall. I made visual estimates of the distance from the snag to the nearest neighbour main canopy living tree (Stelfox 1995).

A modified transect method was employed to measure coarse woody debris volumes in boles greater than 10 cm in diameter lying on the forest floor. Three 50 m transects were established with randomly selected orientations that radiated from the center of each plot at the soil pit location. The transect random orientation and 50 m length tested favourably against three transects of 30 m length and preset orientation that form a triangle. There were no differences in the volume estimated (using a t test) among the 3 transects of 30 m when transects were oriented at 45 degree angles on each plot, and the volumes estimated by three 50 m transects with random orientation.

The methods for determining fallen log volumes were initially designed for evaluations of residual material in clearcut sites (Warren and Olsen 1964). The log
orientation in residual studies in clearcuts can be biased by the felling techniques employed on the site since felling is often conducted with the same orientation. In the natural stands that I selected, where many factors contribute to treefall, I could not detect an orientation bias in decayed boles on the forest floors. However, I assessed the orientation of each log associated with plot transects as a check. My choice of transect method followed Brown (1971) who suggested that if the log orientation is random then the choice of sampling plane should be random. Log volumes were calculated by measuring both the perpendicular and transect diameters to overcome diameter bias and then dividing by the length of the line. The calculations followed van Wagner (1978).

In addition to volume measures and orientation, other log attributes were assessed including species, log decay class, butt end diameter and bark retention. Fallen log decay classes were assigned according to a modified version of Triska and Cromack (1980). Decay class modifications were necessary because the appearance of certain class attributes in Saskatchewan boreal forest logs did not coincide with the same class attributes found in Pacific coast logs where down woody debris classifications have been applied frequently. In Saskatchewan boreal forests, for example, bark was visible on boles that were well decayed in relation to other decay attributes occurring in the logs. This bark retention trait was useful in identifying the species of decay class 5 logs (Triska and Cromack 1980).

In Saskatchewan, newly fallen white spruce boles are often suspended above the ground by their branches. Based largely on visual and anecdotal information, the reason that this phenomenon occurs is related to the retention of sound lower branches at maturity. The boles have a lower weight-to-surface area ratio that permits a greater degree
of suspension compared to the heavier conifer logs found in Pacific Coast forests. It is not
known whether the length of time that logs are without ground contact in Boreal Plain
forests modifies decomposition processes compared to coastal species.

7.6 Methods V. Statistical Analyses

Single factor ANOVA, MANOVA and other multivariate analyses were employed
with discrete, continuous and categorical data, respectively, to determine if any statistical
differences existed in the structural attributes with respect to the four stand types. Based
on published literature, the structural attributes of most interest as indicators of particular
mid-to-late succession stand types were basal area and coarse woody debris volumes
(Stelfox 1995). In cases of continuous data, such as basal area and down woody debris
volumes, least square comparisons were undertaken to detect differences in attributes
related to the individual types. However, much of the structural data related to stand
measures was discrete data and consequently analyzed by Chi Square and by categorical
modeling. Continuous data were log-transformed when they had non-normal distribution
(Kleinbaum and Kupper 1978). Statistical analyses were carried out using Statistical
Analysis Systems (SAS Institute Inc. 1989). A probability value \( p \leq 0.05 \) or \( t \leq 0.05 \) was
accepted as evidence of significant statistical differences among white spruce stand types
and stand attributes.

7.7 Results-Stand Structural Analyses

There were commonalities among several of the stand types selected for intensive
study within the framework of a multiple pathway approach. In all but the most decadent
type, (bF/wS), a type with widely scattered veteran white spruce, charcoal was found at the interface of the mineral soil and litter layer. In all stand types except the most decadent type there was no visual evidence of strong soil podzolization. Stand characteristics are depicted in Figures 3, 4 and 5 and in Tables 2, 3, 4 and 5.

A. wS/tA stand type. In aspen-spruce (wS/tA) types, (aged approximately 60 to 115 years), the senescing aspen displayed dead tops, conks, cracks and fissures typical of decadent trees. The white spruce-aspen stands usually had fairly homogeneous canopies and were characterized by abundant herbaceous species on the forest floor.

B. wS (tA) stand type. This type, (aged approximately 80-120 years), contained very few mature aspen in the canopy but had scattered younger aspen, birch, balsam fir or white spruce saplings in canopy gaps. There were fewer herbs on the forest floor in this type compared to the wS/tA.

C. wS (bF) stand type. The white spruce-advance balsam fir successional type (aged approximately 100-130 years) consisted of multi-storied canopies in stands with three tree species present: white spruce, aspen and balsam fir. Moss species (Hylocomium splendens (Hedw.) B.S.G. Pleurozium schreberi (Brid.) Mill. Polytrichum commune Hedw.) dominated the forest floor within this type.

D. bF/wS stand type. This type had a multi-storied canopy with a few, tall, large diameter white spruce veterans (aged approximately 130-180 years). The highest incidence of balsam fir regeneration was found in this type whereas aspen regeneration was similar to that in the white spruce-aspen type (wS/tA). Veteran aspen of approximately 130 years were extremely rare and only one was found in close proximity...
to the plots. Some stands contained scattered large-diameter birch approximately 260 years old and young birch saplings.

The bF/wS stands reflected some classic old growth characteristics previously defined by researchers working in Pacific coast forests (Spies et al. 1988). Among these traits were frequent large gaps, dense regeneration in openings and mild mound and pit topography. The forest floor under these stands consisted of conifer needles, twigs, cones and some forbs; there was little herbaceous or moss cover.

Age: In addition to the simple linear treatment of age and volume, and age and stand type, age was also analyzed in the context of the multiple pathway model (Figure 2) described earlier. When statistical analyses was conducted on data from the stand types by species, neither the ages of individual white spruce nor aspen trees were significantly different between the white spruce-aspen stand type (wS/tA), and the white spruce with minor aspen stand type (wS (tA)), (Table 2). The white spruce in the wS (bF) succession stand type was slightly (but significantly) older than the spruce in the two white spruce-aspen types wS/tA and wS (tA). However, aspen and white spruce canopy trees in the bF/wS type, where balsam fir was dominant, were substantially older than the same species in the other three stand types (Figure 3).

Main Canopy Tree Densities: In the wS/tA type, the mean densities of the two main canopy tree species were quite similar (425 stems/ha for aspen compared to 397 stems/ ha for white spruce). In the wS (bF) type, there were similar numbers of white spruce stems in the main canopy as in the (wS (tA)) type. The balsam fir canopy density
Table 2. Differences in age between white spruce and trembling aspen stand types of the Mid-Boreal Upland Ecoregion, Saskatchewan. Mean total age (yrs) and standard error (SE). Bold face values indicate p ≤ 0.05.

<table>
<thead>
<tr>
<th>Stand Type</th>
<th>Species</th>
<th>Mean Age (SE)</th>
<th>wS/tA tA</th>
<th>wS/tA wS</th>
<th>wS (tA) tA</th>
<th>wS (tA) wS</th>
<th>wS (bF) tA</th>
<th>wS (bF) wS</th>
<th>bF/wS tA</th>
<th>bF/wS wS</th>
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<tbody>
<tr>
<td>wS/tA</td>
<td>tA</td>
<td>100 (8.2)</td>
<td>--</td>
<td>.44</td>
<td>.76</td>
<td>.48</td>
<td>.65</td>
<td>.21</td>
<td>&lt;.00</td>
<td></td>
</tr>
<tr>
<td>wS/tA</td>
<td>wS</td>
<td>92 (7.1)</td>
<td>--</td>
<td>.41</td>
<td>.08</td>
<td>.33</td>
<td>.02</td>
<td>&lt;.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>wS (tA)</td>
<td>tA</td>
<td>105 (18.5)</td>
<td>--</td>
<td>.92</td>
<td>.90</td>
<td>.64</td>
<td>.06</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>wS (tA)</td>
<td>wS</td>
<td>107 (3.8)</td>
<td>--</td>
<td>.95</td>
<td>.44</td>
<td>&lt;.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>wS (bF)</td>
<td>tA</td>
<td>108 (17.3)</td>
<td>--</td>
<td>.76</td>
<td>.08</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>wS (bF)</td>
<td>wS</td>
<td>113 (6.5)</td>
<td>--</td>
<td>--</td>
<td>.01</td>
<td></td>
<td></td>
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</tbody>
</table>

wS = white spruce  
tA = trembling aspen
in the multi-strata type, wS (bF), was approximately 300 stems/ha. In the bF/wS type, the
density of the main canopy white spruce was lower than in the wS/tA type (< 200
stems/ha), whereas balsam fir main canopy density was over 400 stems/ha.

*Main Canopy Heights:* Main canopy heights were very similar for all successional
types; no further analyses involving dominant species tree heights was undertaken.
Moreover, since the ages of the white spruce were essentially similar in three of the white
spruce-dominated stand types, the relationship of height over age (site index) was not
calculated or utilized as a discriminating characteristic for these stands.

*Basal Area:* Least Square Means with transformed data indicated that canopy basal
area differed significantly between species (aspen and white spruce) within stand type
(p≤0.00). The wS/tA white spruce type had considerably larger total basal area compared
to the wS (bF) type (Figure 3). The white spruce in the widely spaced stand type, (wS
(tA)), had significantly greater total basal area than the white spruce in the (wS (bF)) stand
type (p≤0.05). Lower basal areas occurred in the bF/wS type (t≤0.01) than in the other two
stand types (Figure 3, Table 3).

*Sapling Numbers/ha:* In the wS/tA type, although the total sapling numbers/ha were
the lowest of the four stand types, slightly higher densities of aspen saplings (trees 2-10 m in
height), occurred than white spruce saplings. In the wS (tA) type, the mean total number of
saplings was greater than in the wS/tA and white spruce occurred more frequently (217
aspen and 320 white spruce stems/ha, respectively). The wS (bF) type had a mean of 1700
white spruce saplings/ha and 1242 balsam fir saplings/ha, respectively. In the bF/wS type,
the balsam fir saplings ranged in age from 80-115 years. Mean sapling density for white
Figure 3. Mean age (A) and mean live basal area for each tree species (B) with standard error bars in four white spruce stand types in Saskatchewan. The lack of an error bar in (A) denotes the presence of a single tree. Basal area standard errors were too small to be displayed.
spruce was much lower (313 stems/ha) in this type compared to balsam fir sapling density (1102 stems/ha).

*Sapling Diameters:* Chi Square tested the expected distribution of sapling diameters by species and by stand type. The null hypothesis assigned the same diameter in each of four stand types for each species. Chi Square statistics revealed statistically significant differences in sapling diameter among stand types (Table 4).

*Regeneration:* Regeneration, which consisted of aspen, spruce and balsam fir, was quite low within both the wS/tA and wS (tA) stand types. The difference between the two stand types occurred in species distribution, rather than total regeneration numbers. Balsam fir seedlings averaged only 19 stems/ha in the wS/tA stands compared to 65 stems/ha in the wS (tA) stand types. In the wS/bF stand type, white spruce regeneration numbers were low (17 stems/ha), but the stand type contained 1692 balsam fir seedling stems /ha. Aspen seedling numbers were lower in the wS (bF) stands than in the other three stand types. In the bF/tA stand type, mean spruce regeneration was 256 stems/ha while mean balsam fir regeneration was over 6000 stems /ha (Figure 4). Spatial distribution of the regeneration was not collected in the field due to time constraints.

*Snag Numbers/ha and Snag Classes:* Analysis of variance showed that snag species did not differ significantly by stand type since there was a significant species by stand type interaction (Table 4). Aspen was the most frequent species of snag found in all stages except the most decadent stand type, bF/wS. In the wS/tA stand type, the mean number of aspen snags (240 stems/ha) was more than three times the number of white spruce snags. Aspen snags occurred more often as intact boles with bark and small branches (Snag Class1) in the wS/tA type than in the other three stages. Dead trees in
Snag Class 2 (complete boles without small branches) and Snag Class 6 (boles with little bark < 2 m in height) were also found more often in wS/tA than in the other stand types. The numbers of aspen and white spruce snags were much lower in the bF/ wS stand type than in the other three types. Like the wS/tA stand type, the majority of snags were in Snag Class 1, (sound boles and intact fine branches). This lower snag number was partially due to the lower total density of stems in this stage compared to the other types.

The log-transformed distance from the snags to the nearest living main canopy bole was significantly different by type (p≤0.02). As might be expected, the nearest neighbor tree species was not as important as the distance to the nearest living main canopy tree when snags were used to determine if differences existed among types.

Coarse Woody Debris Volumes: The characteristics of down woody debris within various stand types may depend on stem competition, disturbance patterns and the diameter of the stems at mortality. Log-transformed coarse woody debris volumes differed significantly among stand types (p≤0.00). When the four types were compared, the wS/tA type had significantly less coarse woody debris volume than the wS (tA) type (p≤0.03), and the lowest volume of the four types (Figure 5b).

7.8 Results-Soil and Organic Matter Descriptions

Within the wS/tA type, thin Ah soil horizons were more frequent than Ae horizons and were almost always underlain by Bm horizons. Based on selected sub sampling of the forest floor horizons, mean nitrogen concentration in the L and F horizons was 1.05% and 1.30%, respectively. Mean N concentration was lowest in the B horizons (0.06 %). The
Table 3. Comparisons of basal area in white spruce stand types in the Mid-Boreal Upland Ecoregion. Mean basal area (m²/ha) and standard error (SE). Bold face values indicate p ≤ 0.05.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Mean basal area (m²/ha)</th>
<th>SE</th>
<th>wS/tA</th>
<th>wS(tA)</th>
<th>WS/bF</th>
<th>bF/wS</th>
</tr>
</thead>
<tbody>
<tr>
<td>wS/tA</td>
<td>58.2</td>
<td>5.5</td>
<td>--</td>
<td>&lt;.001</td>
<td>.001</td>
<td>.546</td>
</tr>
<tr>
<td>wS/tA</td>
<td>57.4</td>
<td>4.5</td>
<td>&lt;.001</td>
<td>--</td>
<td>.055</td>
<td>.005</td>
</tr>
<tr>
<td>wS/bF</td>
<td>46.1</td>
<td>3.5</td>
<td>.001</td>
<td>.046</td>
<td>--</td>
<td>.165</td>
</tr>
<tr>
<td>bF/wS</td>
<td>45.4</td>
<td>2.7</td>
<td>.544</td>
<td>.005</td>
<td>.165</td>
<td>--</td>
</tr>
</tbody>
</table>

Table 4. Sapling species, sapling height (m), and sapling dbh (cm), in white spruce and trembling aspen stand types. A. Descriptive statistics: sapling mean ht (m), diameter (cm), and standard error (SE). B. Chi Square statistics for diameter by stand type and sapling species. Bold face values indicates significance at p≤0.05.

A.  

<table>
<thead>
<tr>
<th>Stand Type</th>
<th>Species</th>
<th>Mean Ht.(m)</th>
<th>SE</th>
<th>Mean Dbh (cm)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>wS/tA</td>
<td>tA</td>
<td>2.5</td>
<td>.1</td>
<td>1.3</td>
<td>.1</td>
</tr>
<tr>
<td></td>
<td>wS</td>
<td>4.4</td>
<td>.3</td>
<td>4.9</td>
<td>.4</td>
</tr>
<tr>
<td>wS(tA)</td>
<td>tA</td>
<td>3.5</td>
<td>1.2</td>
<td>2.7</td>
<td>.4</td>
</tr>
<tr>
<td></td>
<td>wS</td>
<td>3.7</td>
<td>.4</td>
<td>3.6</td>
<td>.3</td>
</tr>
<tr>
<td>bF/wS</td>
<td>tA</td>
<td>N/A</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>wS</td>
<td>4.0</td>
<td>.3</td>
<td>4.9</td>
<td>.5</td>
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</table>
Table 4. (con’t).

<table>
<thead>
<tr>
<th>Statistic</th>
<th>d.f</th>
<th>Chi Square value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chi-Square</td>
<td>9</td>
<td>192</td>
<td>&lt;0.00</td>
</tr>
<tr>
<td>Likelihood Ratio Chi-Square</td>
<td>9</td>
<td>206</td>
<td>&lt;0.00</td>
</tr>
</tbody>
</table>

B.

Figure 4. Mean regeneration by species for four white spruce stand types in Saskatchewan. Individual regeneration means displayed due to wide range in seedling density.
wS/tA and bF/wS types (the latter type with main canopy balsam fir) differed considerably. The coarse woody debris volumes were higher in the bF/wS type ($p \leq 0.00$) than the other stand type. The wS/tA and wS (bF) types were not significantly different in coarse woody debris volumes, although this outcome occurred for very different reasons. Coarse woody debris volumes in the bF/wS type were the highest of the four selected types (Figure 5b), because the boles were greater in diameter and length than in the other types.

*Coarse Woody Debris Piece Numbers (Linear Density):* The stand types differed in the numbers of decayed boles (measured as numbers of debris pieces/transect length) found on the forest floor as well as the volumes/ha of decayed material. Overall linear density varied by stage ($p \leq 0.01$). The white spruce-aspen type (wS/tA) had significantly more down boles/transect than the white spruce with minor aspen type ($p \leq 0.05$). However, coarse woody debris linear density in the white spruce-aspen (wS/tA) type was not different statistically from either the wS (bF) type or from the bF/wS type. The white spruce with minor aspen type (wS (tA)), had considerably fewer boles than the bF/wS type ($p \leq 0.01$).

Relatively low coarse woody debris volumes but high linear densities were typical of the wS (bF) type because most dead stems were from small diameter balsam fir that had succumbed to competition. Although the causes for the number of boles on the forest floor were quite different, the total numbers of fallen decaying boles were similar in the advance balsam fir regeneration type and the scattered white spruce veteran type ($p \leq 0.89$).
Figure 5. Mean snag density by species (A)-no error bars indicate only one group of snags was present. Total coarse woody debris volume (B) for four white spruce stand types in Saskatchewan.
Table 5. Snag characteristics for four stand types in the Mid-Boreal Upland Ecoregion.
A. Descriptive statistics of snag distributions by stand type: snag numbers, mean distance to nearest tree (m), and standard error (SE). B. Analyses of variance (ANOVA) by snag species and stand type for distance to nearest tree. Bold face values indicate significance at p ≤ 0.05. d.f. = degrees of freedom.

### A.

<table>
<thead>
<tr>
<th>Stand Type</th>
<th>Snag N</th>
<th>Snag Mean Distance (m)</th>
<th>SE</th>
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<tr>
<td>wS/tA</td>
<td>107</td>
<td>4.3</td>
<td>.4</td>
</tr>
<tr>
<td>wS(tA)</td>
<td>30</td>
<td>3.0</td>
<td>.5</td>
</tr>
<tr>
<td>wS(bF)</td>
<td>60</td>
<td>3.5</td>
<td>.4</td>
</tr>
<tr>
<td>bF/wS</td>
<td>34</td>
<td>3.0</td>
<td>.2</td>
</tr>
</tbody>
</table>

### B.

<table>
<thead>
<tr>
<th>Statistic</th>
<th>d.f</th>
<th>SS</th>
<th>Mean Square</th>
<th>F value</th>
<th>p value</th>
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<tbody>
<tr>
<td>Stand Type</td>
<td>3</td>
<td>5.29</td>
<td>1.76</td>
<td>0.79</td>
<td>0.51</td>
</tr>
<tr>
<td>Species</td>
<td>2</td>
<td>1.09</td>
<td>1.09</td>
<td>0.24</td>
<td>0.79</td>
</tr>
<tr>
<td>Stand Type x Species</td>
<td>2</td>
<td>17.14</td>
<td>8.57</td>
<td>3.76</td>
<td><strong>0.03</strong></td>
</tr>
</tbody>
</table>
Effective rooting depth varied from 14-21 cm. An estimated 85% of the plot surface in this stage was composed of organic matter. It should be emphasized that the soil analysis values reported here are strictly descriptive, since the data were too few for statistical analysis. The soil profile characteristics for the white spruce with minor aspen (wS (tA)) type were Ae horizons beneath mor humus types, and Bm or Bmj horizon development. At Candle Lake, Ck horizons could be found beneath both white spruce with minor aspen and advance balsam fir types. Ck denotes the presence of carbonate; the horizon will effervesce with the addition of dilute HCl (The Canadian System of Soil Classification 1978). Mean N concentrations in the L and F horizons were in 1.14 and 1.43% respectively. The average effective rooting depth within this type was 16 cm. The estimated organic matter cover of the ground surface was 68% for the wS (tA) plots.

Soil profile characteristics typical for the advance balsam fir (wS (bF)) type, are represented by plots located on Highway 155 north of Green Lake, approximately 3.0 km south of the Aubichon Junction. In these plots, soil profiles had Ae horizons underlying mor humus. As in the wS/tA and wS (tA) types, the mineral soil horizons were classified as Bm. The mean concentration of N was 1.36 and 1.62 % in L and F horizons, respectively. Mean effective rooting depth was 20 cm. An estimated 75% of the plot surface was composed of organic matter (including moss).

In the bF/wS type, the soil profiles had more strongly developed Ae horizons (6-12 cm) compared to the other types, where Ae horizons averaged only 4-8 cm in depth. Visually, there appeared to be greater amounts of iron deposition (designated as Bf) in the soil profiles; the effective rooting depth was highly variable, ranging from 11 to 60 cm.
Within the bF/wS type, mean concentration of N in the mineral soil Bm horizons was .91% which was higher than that of the Ws (tA) type where total mean N in the Bm horizon was only .44%. This difference may be due to organic matter translocation, which appears to be greater in the most decadent stand type than in the white spruce-aspen stand type. It is likely that some balsam fir dominated stands have not undergone fire disturbance for at least 180-200 years, the age of the oldest trees.

To summarize, as single variables the selected stand density descriptors were significantly different in value for two or more stand types. Total basal area, sapling height, the distribution and species of snags, coarse woody debris volumes and coarse woody debris linear densities were all helpful in characterizing the four mid-to-late white spruce succession stand types. The analysis of data did not always yield statistically significant outcomes. However, coarse woody debris volume was significantly different in three out of four stand types.

7.9 Discussion

A broad definition of “old growth” that has found favour in British Columbia includes forests that have particular structural, compositional and functional characteristics. In an analysis of structural “old growth” attributes in 12 British Columbia biogeoclimatic zones, different clusters of traits were associated with different zones, but age and basal area have been considered strong “old growth” factors (Wells et al. 1998). Conversely, the simple linear regression of age with stand type demonstrated that a chronosequence single pathway approach to characterizing white spruce succession was not useful.
The strong relationships of age and "old growth" described in the Wells et al. (1998) study may reflect the relatively low frequency of stand replacement fires in some BC biogeoclimatic zones compared to that in the boreal forest. In white spruce stands at Candle Lake, Saskatchewan, Swan (1966) found that the age of the main canopy species in upland stand types did not differ by more than 15 years. Analysis of stands conducted in my current study showed that the mean ages of three of the four selected mid-to-late white spruce stand types were also quite similar. In the Mid-Boreal Upland Ecoregion, age appears less important as an attribute of mid-to-late succession stand types.

Since white spruce basal area, sapling height and diameter, coarse woody debris volumes and the number of fallen logs occurred from one stand type to another, it is evident that the four types selected for study were structurally distinct. In this study, white spruce species basal areas were quite similar to those in Beckingham et al. (1996) for the wS/tA and wS (bF) types. The white spruce of the widely spaced stage, wS (tA), however, had greater basal areas than the aspen–white spruce phases reported by Beckingham et al. (1996). My stem densities for white spruce in the white spruce-balsam fir type (wS (bf), were much lower than Beckingham et al. (1996) reported for aspen-spruce stands. The exclusive choice of mature stands in this study might account for the lower densities due to aspen and white spruce senescence in these stands.

In this study, the stands displaying the greatest amounts of down woody debris were those that had visual evidence of other "old growth" characteristics that are accepted in coastal forests, such as abundant regeneration and large gaps.

Snags may have limited use as late succession stage descriptors in Saskatchewan's Boreal Plain because there is a fairly rapid transfer of snags to the forest floor up to 16-20
years after tree death (Sulistyowati 1998). In a recent Alberta study of snags within permanent sample plots, snags comprised up to 8.2% of the canopy in older aspen stands. The fall-down rates of the snags were 9-21% of the total snags/year (Lee 1998). My results showed that fewer snags occurred in the most decadent white spruce-dominated stands because most of the veterans had fallen already.

In Pacific coast Douglas-fir chronosequences, Spies et al. (1988) reported a U shaped curve due to high volumes of down woody debris in both the youngest and oldest stands. Although younger stages of white spruce development were not examined during my research, there was a considerable increase in down woody debris volume within the bF/wS or most decadent stage. It is assumed that the fire-generated debris had become humus in most wS/tA stands.

Siitonen et al. (2000) examined managed mature and mesic old growth Norway spruce (Picea abies L. Karst.) forests in southern Finland. In over-mature forests, coarse woody debris volumes reached a mean of 111 m$^3$/ha (70-184 m$^3$/ha). Seventy percent of this volume was logs; 24% of the logs consisted of trunks > 40 cm. Decay class three logs were dominant. The authors concluded that the best plan to maintain structural diversity was to retain “old growth” characteristics in the form of snags, logs and large living trees.

Analyses of “old growth” attributes in BC’s Sub-boreal Spruce Zone determined that the number of large logs was an important “old growth” criterion, but other density-dependent structural attributes could correlate poorly with “old growthness” (Kneeshaw and Burton 1998). In Saskatchewan basal area, although statistically significant, is not a good descriptor of “old growth” since different combinations of stem density and tree diameter in the four stand types resulted in similar basal areas. Some researchers believe
that only non-stand density-related variables should be used as predictors of differences in
successional types because structural criteria can often be inferred from stand selection
criteria (Lee in Stelfox 1995).

Lee (personal communication, 1999), like Siitonen (2000), suggested that removal
of down woody debris would likely decrease species biodiversity in mature mixedwood
stands and that the selection of harvesting alternatives should seek to perpetuate the input
of snags and down woody debris. The choice of down woody debris as an effective
der descriptor of “old growth”, is, therefore, appropriate for several reasons that could be
helpful in evaluating forest sustainability.
Chapter 8

White Spruce Stand Processes

This chapter addresses microbial activity in litter layers, logs and mineral soil in late succession stands as well as changes in cellulose, nitrogen concentrations and nitrogen content in coarse woody debris. Differences in nitrogen concentration and in content between white spruce and aspen fallen logs may be important in sustaining white spruce-aspen stands because aspen and white spruce appear to have different nitrogen uptake efficiencies (Peterson and Peterson 1992) where nitrogen uptake efficiency is defined as the capability of a plant to utilize available nitrogen. If aspen woody debris contains greater nitrogen content than white spruce fallen boles, this potential nitrogen pool might sustain aspen more favourably than white spruce given aspen’s more efficient nitrogen uptake (Peterson and Peterson 1992).

Studies in both boreal and temperate ecosystems have reported declines in microbial activity rates from younger to older stands due to differing litter quality, microclimate, and microbial populations (Ryan et al. 1997, Schlentner and Van Cleve 1985, Chang and Trofymow 1996). This trend suggests that mature white spruce stand types that do not have aspen may have lower rates of microbial activity including lower rates of nitrogenase activity and available nitrogen.

8.1 The Nitrogen Economies of Boreal Forest Floors

In southwest Alberta, aspen and lodgepole pine litter had C/N ratios were 37.5 compared to 71.9 for lodgepole pine respectively (Scheu and Parkinson 1995). In Saskatchewan, litter from aspen stands had higher total NH$_4$-N, and higher exchangeable
Ca, Mg, and K than jack pine/black spruce stands (Xiao 1987). Macronutrients in aspen litter released faster than those in oak, birch or pine litter (Bockheim et al. 1991). Pare and Bergeron (1996) describe net mineralization and nitrification measured with aerobic incubations as higher under birch and aspen than under white spruce stands. These results indicate that the different mixes of tree species in Saskatchewan’s white spruce-dominated stands might affect the microbial nitrogen economies of litter layers and woody debris according to the canopy composition.

8.2 Research Goals

The objectives of this study were to: 1) establish whether significant differences in microbial activity (represented by potential mineralizable nitrogen, nitrogenase activity and CO₂ evolution) existed within several Saskatchewan white spruce stand types, and 2) assess the differences in cellulose content, nitrogen concentration and nitrogen content within a chronosequence of down woody debris.

8.3 Definitions of Forest Floor and Mineral Soil

This study involved measurements in three substrates: forest floor, well-decayed logs and the mineral soil beneath both litter layers and logs. For the purposes of the study, forest floor was defined as encompassing L, F, and H horizons (Canadian Soil Survey Committee 1978). In mature white spruce stands, L horizons tend to occupy the upper 4 cm whereas F and H layers occupy the lower 4 cm. The forest floor layers of wS/tA plots were classified as mors primarily because the F and H horizons, averaged > 2 cm (Green et al. 1993). The forest floors from the plots classified as wS (bF) and wS/bF stand types respectively, were
also described as mors because, among other characteristics, the F layer was > 2 cm and Ah horizons were not present. No further refinements to the classification of the forest floors in Saskatchewan stands were recorded because of time constraints.

Well-decayed logs were defined as logs that could be distinguished from the forest floor but had litter accumulations on the sides of the log and were very friable. According to fallen log classifications for temperate climates, well-decayed logs are in complete contact with the ground, lack structural integrity, have a minimum amount of bark and lack large branches. Based on a modified version of the U.S. Pacific coast classification, the logs chosen for this study were associated with decay class 4-5 boles (Triska and Cromack 1980).

Mineral soils were defined as naturally occurring, unconsolidated material subject to soil-forming processes. Mineral soil horizons were distinguished from litter layers according to the Canadian Soil Classification System that defines mineral soil horizons as those layers with 17 percent or less organic matter. Ah horizons, therefore, were classified as mineral soil (Canadian Soil Survey Committee 1978).

8.4 Methods I. Measures of Microbial Activity

Respiration rates, rates of nitrogen mineralized and nitrogenase activity rates were selected as indices of potential microbial activity.

1) The amount of CO₂ released (respired) during enzymatic breakdown of organic carbon has often been used as a general index of microbial activity (Zibilske 1994).

2) The amount of net potential mineralizable nitrogen (NH₄⁺) has been defined as the amount of ammonium produced during decomposition that is
extractable by strong KCl solutions following anaerobic incubations (Bundy et al. 1994, Hart et al. 1994). Net mineralizable nitrogen has been used to describe differences in successional types, and site types along toposequences (Walley et al. 1993).

3) Nitrogenase activity rates have been defined as the accumulation of nitrogenase over time where nitrogenase, a nitrogen-fixing enzyme, is responsible for the reduction of dinitrogen to ammonia. Nitrogen fixation can be estimated by a technique known as “acetylene reduction” whereby levels of acetylene are reduced to ethylene by the enzyme nitrogenase. These rates of conversion are compared to amounts of actual nitrogen fixed, determined by tracer studies (Silvester et al. 1982, Hendricksen 1990, 1991).

8.5 Methods II. Sites and Stands Chosen for Study

Replicated sites were located south of Meadow Lake, north of Green Lake and in Prince Albert National Park. The stand types selected for process measurement consisted of the spruce-aspen type wS/tA, the spruce-balsam fir type (wS (bF)) and the balsam fir type, (bF/wS). Only three of the four white spruce types described in Chapter 7 were chosen for the process study because of difficulties in gathering samples and conducting replicated short-term in situ incubations in geographically dispersed sites. Incubations are discussed in the appendices and later in this chapter. The need to overcome variability in nitrogen-related measurements within substrate types and by depth limited the number of types and plots that could be successfully compared in a single season. Since the fourth
type, wS (tA), containing white spruce with minor aspen with senescing aspen, was sampled in 1998 rather than 1997, it was not included in the analyses.

The white spruce-aspen type, (wS/tA), was characterized by a rich herbaceous cover with very little moss, relatively low volumes of down woody debris, and minor amounts of needle litter. In contrast, the white spruce-balsam fir type (wS (bF)), had forest floors with little herbaceous cover but a relatively high percentage of moss, and a very dense sub-canopy of white spruce and balsam fir saplings. Mortality associated with self-thinning in this sub-canopy type generated abundant small diameter down woody debris. Slightly higher volumes of down woody debris were found in the wS (bF) type than in the wS/tA type. The third type, bF/wS, had a forest floor that consisted of scattered herbs and forbs with relatively deep layers of coniferous needles, twigs and well decayed wood. The bF/wS stands were typified by abundant regeneration in large gaps between main canopy trees.

8.6 Methods III. Research Design

Two investigations explored forest floor and mineral soil changes over time. The first experiment addressed microbial activity in forest floor, logs and mineral soils over one season, and the second measured the nitrogen concentrations and cellulose content in woody debris with different residence times on the forest floor.

Experiment 1. Microbial Activity: The experimental design for the respiration, mineralizable nitrogen and nitrogenase study was a stratified randomized block type with whole plot (substrate) and subplot effects (depth). The whole plot had a factorial design (that tested for differences among logs, litter and mineral soil) and the subplot had a one-way
treatment structure that tested for the influence of depth on CO₂ evolution, nitrogenase activity and nitrogen mineralized (SAS Institute Inc. 1987, Peterson 1985). Two replicated plots were chosen in each of the three types located within the Mid-Boreal Upland Ecoregion. Each plot contained three randomly chosen blocks consisting of four substrates: litter (LFH) layers, well-decayed logs, mineral soil beneath logs and mineral soil beneath forest floor.

Mineral soil sampling took place at two depths, 0-4 and 4-8 cm. LFH sampling took place from 8-4 cm and from 4 to 0 cm. Mineral soils, logs and litter are referred to as substrates. Substrate is defined as a surface upon plants and animals live. Two depths were sampled within each substrate type because published literature, (Chapter 4), has reported changes in N concentration, N content and microbial activity rates with increasing soil and litter layer bulk densities; the substrate bulk densities usually increase with depth. The two mineral soil substrates were referred to as Litter Soil and Log Soil. The mineral soil under litter layers and logs, respectively, were separated to address speculation about soil development under decayed logs that might be different than under litter layers and therefore N content in soils directly beneath logs might be different than soil N beneath forest floor. Rates of potential mineralized nitrogen, nitrogenase activity rates and substrate respiration rates were measured in replicated samples from litter layers, log and mineral soil substrates during May, July and late August of 1997. Well-decayed logs could not be identified by species, particularly in the wS/tA type; this accounted for choice of both log species for the measurement of microbial process rates. In this study, each log was checked to ensure similar length, decay level, and diameter. The forest floor litter layers were
assessed to ensure that they were representative of forest floors for the stand type of interest. The subplots were checked to ensure that they all had similar micro-topography.

Experiment 2. A retrospective design was chosen to assess the nature of coarse woody debris in Mid-Boreal Upland spruce and aspen stands because of time limitations and because only short-term funding was available for the project. Suitable long-term retrospective research sites were found that had homogeneous site characteristics. The log decay field research took place in a Canadian Forest Service white spruce stand-release trial (wS/tA) that had been established in 1952 and in an adjacent Demonstration Forest maintained by the Saskatchewan Foresters Association. These sites were approximately 2.5 and 4.0 km, respectively, from the town of Candle Lake.

The two research locations have similar elevation and micro-topography. The stands at both locations were mesic mixedwood types on sandy loam soils where aspen was senescing from the canopy (wS/tA). The cutting of selected trees from the plots took place when the stands were approximately 40 years old.

At the Demonstration Forest, individual white spruce trees were removed from the canopy in 1953 (Aschim unpublished document, 1983), and both white spruce and aspen boles were cut and left on the ground in 1986-1988 (C. Halland, personal communication, 1997). On the Canadian Forest Service research site, selected white spruce and aspen boles were felled in 1973 within selected plots (C. Halland, personal communication, 1997) and aspen boles were felled in 1952, during the establishment of the stand release research trial (Yang 1995). All boles with intact branches and foliage had been left where they had fallen.
Since felling additional live trees at these two sites to provide fresh log material was not permitted, samples were obtained in 1997 from freshly cut aspen and white spruce logs provided by Mistik Management Ltd. Samples were taken from a 30-35 year-old stand on a site with undulating terrain located 42 km north of Meadow Lake on the Stewart Lake Road near Highway 903. The second site was approximately 43 km south of Meadow Lake on the Burness Road. Samples were taken from recent blowdown in a 50-year-old stand.

The experimental design for this project consisted of two simple random replicated plots in both the Demonstration Forest and an adjacent 1952 Canadian Forest Service Stand Release Trial that represented different log residence times. Two plots were established for each residence time, except for the 1997 interval. Each plot contained 15 randomly chosen logs of each species.

The chemical attributes that were measured in the logs were cellulose percent and nitrogen concentration. The study of nitrogen concentration and cellulose in fallen logs had a 2X4 factorial structure (two species and four times since felling). Other characteristics that were collected but not reported here included wood density, log color, bark retention, hardness, and surface litter accumulation following the methods of Triska and Cromack (1980).

8.7 Methods IV. Specific Sampling Techniques in Microbial Processes

_Nitrogenase Activity:_ The acetylene reduction technique assumes a linear relationship between ethylene produced (nitrogenase levels) and the acetylene reduced. The ratio of nitrogenase to actual nitrogen fixed has been established as a 3:1 ratio for coastal
forests (Silvester et al. 1982) but this ratio has not been determined for Saskatchewan boreal forests. As a result, variations in nitrogenase activity rates from one successional stand type to another are reported here as ethylene production rates.

Several field incubation techniques have been used to measure CO₂ evolution and nitrogenase activity. These techniques involve trapping the gas produced by microbial activity over set lengths of time. Long-term installations of soda lime blocks have been used to trap CO₂ evolved in mineral soil where the amount of CO₂ was measured as a change in the dry weight of the soda lime (Zibilske 1994). This method, however, has been reported as unreliable (Ewel et al. 1987). In the Appalachians, one researcher used a chamber attached to the top of fallen logs to measure CO₂ produced in woody residue on harvested sites (Mattson et al. 1987). This technique has limitations because it is not able to accurately estimate the extent of CO₂ diffusion from the substrate not enclosed by the chamber. Consequently, the technique also has limited application to studies of CO₂ release from litter and mineral soil.

Another approach to measuring gas evolution consists of a series of field incubations where small samples are destructively removed and enclosed in single, portable, incubation chambers (Sollins et al. 1987). This technique has five advantages:

1) both the sample size and the head-space of the chamber can be accurately measured,

2) sampling can be repeated as many times as desired over a season provided destructive sampling is done with care,

3) in situ substrate incubations can be performed at substrate temperatures,
4) Gas samples for estimations of both nitrogenase and CO₂ evolution rates can be taken directly from the chamber and stored in Vacutainers for several months until the samples are analyzed, and,

5) The technique can be applied equally to LFH layers, log and mineral soil samples, although logs may be more susceptible to destruction as mentioned previously.

*Procedures for Sample Incubation:* A metal coring device was used to extract a 216-cm³ sample at each of two 4 cm depths in forest floor litter layers, decayed logs and mineral soil. Compression of the material inside the coring device is a common concern. However, careful standardized extraction techniques can ensure that compression will be uniform from plot to plot and with depth throughout the sampling interval. Forest floor litter layers and mineral soil samples were placed in labeled 500 ml Mason wide mouth canning jars and used for CO₂ evolution, nitrogen fixation and moisture content measurements. Each jar had a rubber septum in the lid for extraction of gas samples at the initiation and termination of 5-hour incubation periods. The jars were incubated on the plots at ambient soil temperatures. Before each incubation period, the head-space of each sample jar was flushed by means of a bicycle pump to remove any accumulation of CO₂ or natural ethylene and to restore the natural levels of O₂. The final values for microbial activity were expressed on a dry weight basis. This expression of values was chosen to be compatible with the prior findings of other scientists. In a study of microbial activity in litter layers, logs and mineral soil at the H. J. Andrew Forest (Hope et al. 1997), values were expressed on a volume basis. This expression did not change the relative difference
in amounts of activity. The very small amounts of activity in mineral soil compared to relatively large amounts in LFH layers may account for this finding.

*CO₂ Evolution Field Procedures:* Measurement of substrate respiration followed a slightly modified version of Sollins (1982). Published studies were used to determine the length of the incubation period. In an Oregon study, respiration rates were constant up to four hours using an initial one-hour resting period and unsieved mineral soil samples (Griffiths et al. 1990). In preliminary tests conducted at the H. J. Andrews Forest and Mary’s Peak near Corvallis, Oregon, we found respiration rates constant up to six hours (Hope et al. 1997). Based on these studies, a five-hour sampling period was selected.

Preliminary tests with roots from Douglas-fir ecosystems showed that roots found within the 216 cm³ samples did not produce sufficient CO₂ to be detected by gas chromatography with this size of incubation chamber (Hope unpublished 1997). Roots were retained within the sample, since roots are considered an inherent part of litter, log and soil substrates. Substrate moisture contents were measured on all samples according to the protocol described later in the text.

*CO₂ Evolution Laboratory Analysis:* The CO₂ evolved was stored in sterile vials known as Vacutainers. These vials were desirable to use because they were portable and under vacuum. The vials had minimal leakage (determined by prior tests) and samples could be stored up to three months.

Net CO₂ evolved was measured on a Hewlett Packard 5730A gas chromatograph fitted with a thermal conductivity detector. The column was packed with Poropak R; the carrier gas was helium. Gaseous 0.5 ml samples were injected into the column from the Vacutainer. Flow rates were 0.05 ml/sec. Net amounts of CO₂ evolved during the five-hour
incubation period were calculated by subtracting the sample taken at the beginning and end of the 5-hour period. The CO$_2$ evolved during the incubation period was divided by the sample dry weight and incubation period to express the final amounts as μmol·g$^{-1}$·h$^{-1}$.

**Nitrogenase Activity Field Procedures:** Nitrogenase activity was measured using a modified form of the acetylene reduction assay (Sollins 1982). In order to simulate the higher atmospheric levels of nitrogen present in the interior of woody material and within mineral soil, an aliquot of nitrogen gas was introduced into the head-spaces of the incubation jars at the start of the incubation period. The amount of nitrogen used was equal to 10% of the head-space (Li personal communication 1998). Five-hour incubations had been found to be successful in previous respiration and nitrogenase activity studies (Hope et al. 1997).

Commercially generated acetylene was filtered to remove impurities before being transferred to a portable air bladder fitted with a stopcock. The air bladder was selected as an appropriate container because it could be carried to the field sites. During filtering, the gas passed sequentially through distilled water, sodium dioxide and a desiccant before entering the air bladder. Usually a sulphuric acid filter is used to purify acetylene, but this step was not considered necessary because of the high initial purity of the commercial acetylene. In the field, 50 ml of acetylene was withdrawn from the air bladder with a large syringe fitted with a needle, and then inserted into the head-space of the incubation jars at the start of the incubation period. Head-space gases were withdrawn from the septum in the top of the jar at the beginning and end of the 5-h incubation period using a 20 ml syringe and placed in Vacutainers.
Nitrogenase Activity Laboratory Methods: The total amount of ethylene taken at the start of the incubation was used as the control. Net amounts of ethylene were calculated by subtracting the initial value of ethylene at the start of the incubation period from the incubated level.

Ethylene was measured on a Hewlett Packard 5890 gas chromatograph fitted with a flame ionization detector and a stainless steel column 3mm outer diameter packed with Poropak R on 80-100 Chromosorb W. The oven temperatures were 45 to 50 °C. Flow rate was 40 ml min⁻¹. Acetylene served as the standard (McNabb and Geist 1979). Samples of 0.25 ml were injected into the GC from the Vacutainers. Ethylene standards were used to calibrate the machine.

Mineralizable Nitrogen Field Methods: The measurement compared samples that had been incubated for 7 days with those that had no incubation. Representative litter samples were collected randomly from the surface of the 400 m² plot. Two samples of bulk log and mineral soil were extracted from the same excavation locations and depths that were used in the collection of nitrogenase activity and respiration samples. Samples were transported to the laboratory in plastic bags and samples were stored in a cold room for a maximum of 2 days before processing.

Mineralizable Nitrogen-Laboratory Analyses: Mineralizable nitrogen (ammonium concentration) was determined by a KCl extraction and incubation method (Waring and Bremner 1964). In the laboratory, two sub samples were taken from each of the two bulk samples. Mineral soil samples were sieved through a 2mm sieve so that results could be based on a < 2mm soil fraction. Net mineralizable nitrogen in the samples was assessed by subtracting the ammonium prior to, and after, a 7-day incubation period. Thirty ml of 2N
KCl solution was added to the first sample and these samples were shaken for 1 hour before being filtered into vials using Whatman # 40 filter paper. Fifteen ml of distilled H₂O, was added to the second sample before the receptacles were incubated at 40 °C for 7 days. Care was taken to completely submerge all samples to ensure anaerobic conditions. When the samples were removed following the incubation period, an additional 15ml of 4 N KCl was added to the samples. These samples were treated in the same manner as the first samples.

Following filtering, the solutions were processed on an autoanalyzer. Autoanalysis procedures were conducted on a Technicon Auto Analyzer II Segmented Flow System by Envirotest Ltd. of Saskatoon, Saskatchewan. Hypochlorite was added to the ammonium to form indophenol blue. The levels of ammonium were determined colorimetrically by autoanalysis at 600 nm. After processing on the Auto Analyzer, the initial amount of mineralizable nitrogen (as ammonium concentration) was subtracted from the amount accumulated after incubation. Final values for mineralizable nitrogen were converted to μg/g/h⁻¹.

Gravimetric moisture contents were determined for each sample so that the net amount of ammonium could be expressed on a dry weight basis. Samples were dried at 105 °C for 72 h. Net amounts of nitrogen mineralized were then expressed on an hourly rate of ammonium produced per sample per dry weight. Final values were converted to micromoles/g/h.
In Saskatchewan's Boreal Plain, the smaller diameters and the inherent species differences in lignin and cellulose composition (wood quality) may affect nitrogen transformation rates within CWD compared to logs in Pacific coast ecosystems. Cellulose and lignin proportions have been found to be moderately good indicators of log decay levels in prior studies (Lambert et al. 1980, Means et al. 1985, Hope 1987). Change in cellulose within logs over time has also been found to be an acceptable index of decay, and a better descriptor of log decay class than mass loss (Hope 1987).

To test for temporal changes in wood cellulose percent, the horizontal center of the log length was chosen as most representative of the log decay class assigned to each log. The amount of sampling necessary to describe inherent variability within entire log length would have been both costly and labour intensive. Thirty logs of each species, within three cutting periods, (1952-1953, 1973, and 1986) and 12 logs of each species taken from the 1997 cutting period, were measured for density, cellulose percent, nitrogen concentration and nitrogen content. All logs were selected for the same approximate original diameter of 45-50 cm.

**Laboratory Measurement of Cellulose, Nitrogen Concentration and Nitrogen Content:**

Residence interval is defined as the length of time that a log has lain on the ground. Replicated sub samples from the sapwood and heartwood were ground using a Wiley mill in preparation for estimates of lignin and cellulose. Lignin and cellulose evaluations followed a modified protocol in Van Soest (1991). In the current study, the acid detergent fiber and neutral detergent fiber were determined by placing multiple samples in a filter bag with a pore size of 40 microns. Residual matter determinations were made by drying a
representative sample of 1 g at 100 °C in a forced air oven until a constant mass was achieved.

An estimate of nitrogen concentration in the wood samples was determined by the Kjeldahl method (Bremner 1994). The samples were digested with sulphuric acid and the ammonium produced was analyzed with a Lachat Quikchem Automatic Flow Injection Ion Analyzer using a salicylate-hypochlorite colorimetric method. The work was conducted in the Soil Science Department of the University of British Columbia, Vancouver, BC.

Nitrogen content was calculated from the N concentrations, the wood density of the logs sampled at Candle Lake and the volumes of the down woody debris found on wS/tA stand types. Values were expressed as kg/N/ha. The residence times of the plots at Candle Lake were linked to the decay levels of the stand type plots through the Triska and Cromack (1980) log decay classification system.

8.9 Methods VI. Substrate Moisture and Temperature Data

I recorded air and substrate temperatures during sample collections. Substrate temperatures were measured at each depth at the time of sample removal on each plot by means of a dial probe thermometer. Air temperatures were taken at the ground surface. Readings were taken between 0900 a.m.–1200 p.m. This temporal window was kept as narrow as possible because of the potential for temperature increases to affect microbial activity. As mentioned previously, for potential mineralizable nitrogen rate determinations, bulk samples from each substrate were collected in the field and taken to the laboratory for incubation under controlled temperatures. Substrate moisture contents
were calculated gravimetrically using fresh sub samples from the bulk samples. Measurements were conducted within 12 hours of the field incubations. The moisture content samples were dried at 105°C for 72 h.

8.10 Methods VII. Data Analyses

Repeated measures ANOVA (SAS Institute Inc. 1989) was used to analyze differences in forest floor, log and mineral soil microbial respiration, nitrogenase activity and mineralizable nitrogen. The effect of succession type and seasonal sampling at the two depths 0-4, and 4-8 cm, was addressed separately because of potential autocorrelation in the data. It was necessary to examine the two depths separately, because it was expected that microbial activity would change with forest floor and mineral soil depth.

Pearson Product Moment correlations were used to investigate differences in association among respiration, nitrogen fixation and mineralizable nitrogen according to type, substrate and sampling date. Least Square Means procedures were used to examine significant interactions between processes and substrate type for each seasonal sampling interval. During analyses, log transformations of the data were necessary because of non-normal distribution of residuals (Kleinbaum and Kupper 1978).

Statistical Analyses of Coarse Woody Debris for Nitrogen Concentration and Cellulose Content: Analysis of variance (ANOVA) was conducted to determine differences in nitrogen concentration expressed as percent and cellulose percent by species according to the years of residence that the logs had been on the forest floor.
8.11 Results-Microbial Activity

Rates of potential mineralizable nitrogen and nitrogenase activity measured in 1997 tended to be lower in May than in July (Figures 6-8). In most cases, the substrate type (litter layers, logs and mineral soil), accounted for variation in microbial respiration, nitrogenase activity and mineralized nitrogen. Mineral soil microbial activity rates were lower during all three sampling dates compared to the rates in litter layers and logs.

CO$_2$ Evolution Rates: In keeping with the general trends found in litter microbial activity, respiration rates were lower in May than in either July or August. The highest rates generally occurred during August. Different successional types had different patterns in microbial activity. Total mean forest floor respiration in May was greater in the wS/tA type than in the wS (bF) or bF/wS type. The highest total mean litter layer respiration in July and August occurred in the wS (bF) type (Figure 6). There was very little difference in respiration rates in logs among the three types during May, but in July there was greater respiration in the wS (bF) type. The highest respiration rate in the bF/wS type for logs occurred during August whereas the highest rate produced in wS (bF) logs was in July (Figure 6).

Microbial respiration rates at 8-4 and 0-4 cm differed by stand type from one seasonal sampling date to another. At these depths, rates were in the order of LFH layers > logs > mineral soil (Figure 6). At the lower depths in both organic and mineral soil substrates (4-0, and 4-8 cm respectively), the respiration rates among stand types over the season were, in general, not significantly different and litter layers, logs and mineral soil had marginally different respiration rates within single succession types. At the second depth, July was the
Figure 6. Mean substrate respiration rates (µg/g/h) of litter, logs, and mineral soil in three mid-to-late seral stand types of white spruce in Saskatchewan. Standard error bars are presented for each type. Bar graphs represent the means of two depths-includes L, F and H. Log Soil=Soil under logs; Litter Soil=Soil under litter.
only month with consistently significant differences in stand types by substrate, \((p \leq 0.0001,\) Table 6, 7). The main effects of either stand type or substrate alone were not significant.

*Potential Nitrogen Mineralization Rates:* Published literature suggested that higher nitrogen mineralization rates could exist in early spring on sites with aspen, compared to mid summer rates (Chapter 4). Because of significant interaction terms (Tables 8, 9) substrate type and stand type alone only accounted for variation in N mineralization in May and August (Table 8) and in analyses of lower substrate layers, no significant differences in mineralized N occurred due to substrate or stand type alone (Table 9). July rates were significantly different among substrates within successional types. Potential N mineralization rates in litter layers were higher in the wS (bF) stand type during May.

Within logs, the potential mineralization rates were higher in August than the other two months (Figure 7). In August, logs in the wS/tA type not only had warmer temperatures than in May, but the mean moisture contents of logs were higher in wS/tA plots than the log moisture contents in the bF/wS type. In a trend that was similar to the distribution pattern of respiration rates, potential mineralization rates diminished within the lower sampling depth compared to surface depths (8-4, and 0-4 cm). In terms of substrate type, seasonal potential mineralization expressed on a per gram basis, was greatest in litter followed by logs and mineral soils.

*Nitrogenase Activity Rates:* Ethylene production rates in August were by far the lowest of all three sampling dates (Figure 8). When the three types were compared, the rates were considerably higher in the wS/tA type than the wS (bF) or bF/wS types over all sampling periods. Like the other two processes, nitrogenase rates differed significantly
Table 6. Analysis of variance (p values) of log-transformed CO$_2$ evolution rates at LFH 8-4 cm and mineral soil 0-4 cm depths. Three sampling dates in 1997. Bold face values indicate significance at p≤0.05. d. f.= degrees of freedom.

<table>
<thead>
<tr>
<th></th>
<th>d. f.</th>
<th>May</th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stand Type</td>
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<td>.5206</td>
<td>.0001</td>
<td>.1183</td>
</tr>
<tr>
<td>Substrate</td>
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<td>.0001</td>
<td>.0001</td>
<td>.9674</td>
</tr>
<tr>
<td>Stand Type x</td>
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<td>.0044</td>
<td>.0001</td>
<td>.6708</td>
</tr>
<tr>
<td>Substrate</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 7. Analysis of variance (p values) of log-transformed CO$_2$ evolution rates at LFH 4-0 cm and mineral soil 4-8 cm depths. Three sampling dates in 1997. Bold face values indicate significance at p≤0.05. d. f.= degrees of freedom.

<table>
<thead>
<tr>
<th></th>
<th>d. f.</th>
<th>May</th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
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<td>.8924</td>
<td>.0001</td>
<td>.2271</td>
</tr>
<tr>
<td>Substrate</td>
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<td>.0001</td>
<td>.0001</td>
<td>.0001</td>
</tr>
<tr>
<td>Stand Type x</td>
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<td>.0001</td>
<td>.0001</td>
<td>.0364</td>
</tr>
<tr>
<td>Substrate</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 8. Analysis of variance (p values) of mineralizable nitrogen rates at LFH 8-4 cm and mineral soil 0-4 cm depths. Three sampling dates in 1997. Bold face values indicate significance at $p \leq 0.05$. d. f. = degrees of freedom.

<table>
<thead>
<tr>
<th></th>
<th>d. f.</th>
<th>May</th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stand Type</td>
<td>2</td>
<td>.0027</td>
<td>.0356</td>
<td>.1082</td>
</tr>
<tr>
<td>Substrate</td>
<td>2</td>
<td>.0001</td>
<td>.0001</td>
<td>.0001</td>
</tr>
<tr>
<td>Stand Type x Substrate</td>
<td>5</td>
<td>.1696</td>
<td>.0037</td>
<td>.5177</td>
</tr>
</tbody>
</table>

Table 9. Analysis of variance (p values) of mineralizable nitrogen at LFH 8-4 cm and mineral soil 4-8 cm depths. Three sampling dates in 1997. Bold face values indicate significance at $p \leq 0.05$. d. f. = degrees of freedom.

<table>
<thead>
<tr>
<th></th>
<th>d. f.</th>
<th>May</th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stand type</td>
<td>2</td>
<td>.0010</td>
<td>.4943</td>
<td>.0962</td>
</tr>
<tr>
<td>Substrate</td>
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<td>.0001</td>
<td>.0001</td>
<td>.0001</td>
</tr>
<tr>
<td>Stand Type x Substrate</td>
<td>5</td>
<td>.0001</td>
<td>.0336</td>
<td>.0199</td>
</tr>
</tbody>
</table>
Figure 7. Potential mineralizable nitrogen rates (µg/g/h) of litter, logs, and mineral soil in three mid-to-late seral stand types of white spruce in Saskatchewan. Standard error bars are presented for each type. Bar graphs represent the means of two depths—includes L, F and H. Log Soil = Soil under logs; Litter Soil = Soil under litter.
Figure 8. Mean nitrogenase activity rates (µg/g/h) of litter, logs, and mineral soil in three mid-to-late seral stand types of white spruce in Saskatchewan. Standard error bars are presented for each type. Bar graphs represent the means of two depths-includes L, F and H. Log Soil=Soil under logs; Litter Soil=Soil under litter.
according to substrate type within different stand types at upper litter layers and upper soil depths (Table 10). However, substrate alone was a significant factor in explaining variation in nitrogenase activity at lower substrate depths (Table 11); the sequence was LFH layers>logs>mineral soils (Figure 8). When the upper litter layer was compared to the upper mineral soil, nitrogenase activity rates differed significantly within the three different stand types as well as by sampling month (p≤ 0.001, Table 10).

Substrate Moisture and Temperature: To some degree, canopy density may account for the differences in seasonal substrate moisture and temperature. In May, very little difference existed in below-canopy air temperatures between Meadow Lake plots and the plots north of Green Lake (Table 12). Substrate moisture contents, however, were generally lower in wS (bF) litter layers during May than in the more open canopies of the ws/tA plots at Meadow Lake. The greater moisture contents found during May in the litter and logs at the Meadow Lake wS/tA plots, compared to the wS (bF) plots, might be due to less canopy interception on the Meadow Lake plots (Table 12). In both wS/tA and wS (bF) types, most of the substrate moisture contents declined over the summer season. The bF/wS plots at Waskesui Lake tended to have lower May moisture contents than the other two locations. Although litter samples were drier in the bF/wS plots than the other two sites in May, soil samples were moister.

In August, forest floor moisture contents at the Meadow Lake plots were much lower than July values. At Waskesui Lake, forest floor moisture contents declined to less than one half of July values. However, air temperatures ranged from 15 to 19 °C during August. These factors may account for the considerable decline in microbial activity during August.
Table 10. Analysis of variance (p values) for log-transformed nitrogenase activity rates at LFH 8-4 cm and mineral soil 0-4 cm depths. Three sampling dates in 1997. Bold face values indicate a significance of p<0.05. d. f.=degrees of freedom.

<table>
<thead>
<tr>
<th></th>
<th>d. f.</th>
<th>May</th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stand Type</td>
<td>2</td>
<td>.0018</td>
<td>.0001</td>
<td>.1626</td>
</tr>
<tr>
<td>Substrate</td>
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<td>.0001</td>
<td>.0001</td>
<td>.0188</td>
</tr>
<tr>
<td>Type x Substrate</td>
<td>6</td>
<td>.0110</td>
<td>.0001</td>
<td>.2773</td>
</tr>
</tbody>
</table>

Table 11. Analysis of variance (p values) for log-transformed nitrogenase activity rates at LFH 4-0 cm and mineral soil 4-8 cm depths. Three sampling dates in 1997. Bold face values indicate a significance of p<0.05. d.f.=degrees of freedom.

<table>
<thead>
<tr>
<th></th>
<th>d.f.</th>
<th>May</th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stand Type</td>
<td>2</td>
<td>.3610</td>
<td>.3249</td>
<td>.3198</td>
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<tr>
<td>Substrate</td>
<td>3</td>
<td>.0026</td>
<td>.0001</td>
<td>.0014</td>
</tr>
<tr>
<td>Type x Substrate</td>
<td>6</td>
<td>.2000</td>
<td>.2002</td>
<td>.0724</td>
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</table>
Table 12. Mean below-canopy air temperature, mean substrate temperature (°C), and mean substrate moisture content (%) for LFH, logs and mineral soils. Meadow Lake (wS/tA), Green Lake (wS (bF)) and Waskesui Lake (bF/wS) sites by sampling month, 1997.

<table>
<thead>
<tr>
<th>Sampling Int. 9 a.m. to 12 p.m.</th>
<th>May</th>
<th>July</th>
<th>Aug.</th>
</tr>
</thead>
<tbody>
<tr>
<td>LO</td>
<td>LS</td>
<td>LI</td>
<td>MS</td>
</tr>
<tr>
<td>MEADOW LAKE wS/tA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Air temp.</td>
<td>13.1</td>
<td>12.9</td>
<td>13.3</td>
</tr>
<tr>
<td>Substrate temp.</td>
<td>7.1</td>
<td>4.5</td>
<td>6.2</td>
</tr>
<tr>
<td>Moisture content</td>
<td>355</td>
<td>90</td>
<td>204</td>
</tr>
<tr>
<td>GREEN LAKE wS (bF)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Air temp.</td>
<td>13.9</td>
<td>13.5</td>
<td>13.7</td>
</tr>
<tr>
<td>Substrate temp.</td>
<td>6.9</td>
<td>2.1</td>
<td>6.5</td>
</tr>
<tr>
<td>Moisture content</td>
<td>294</td>
<td>97</td>
<td>130</td>
</tr>
<tr>
<td>WASKESUI LAKE bF/wS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Air temp.</td>
<td>16.9</td>
<td>16.8</td>
<td>17.0</td>
</tr>
<tr>
<td>Substrate temp.</td>
<td>9.5</td>
<td>4.1</td>
<td>8.2</td>
</tr>
<tr>
<td>Moisture content</td>
<td>215</td>
<td>193</td>
<td>112</td>
</tr>
</tbody>
</table>

Legend: LO=logs, LS=soil beneath logs, LI=LFH, MS=soil beneath LFH. Moisture content percent = (wet weight-dry weight/dry weight) x100. ND= no data. Air temp=ground-level air temperature.

8.12 Results-Woody Debris Nitrogen Concentrations, Cellulose Content, and Nitrogen Content

The mean nitrogen concentration in fallen logs differed between tree species except for sound logs. Sound aspen logs had nitrogen concentrations of 0.041 % whereas
the nitrogen concentration in white spruce logs was 0.045 %. Nitrogen concentration increased significantly over the 45-year residence time (Table 13, p<0.0001). In aspen logs, nitrogen concentration increased approximately 25 times from 6 months after felling to 45 years after felling. In white spruce logs, nitrogen concentration increased approximately 6 times the initial amount from 6 months after felling to 45 years after felling. The greatest increase in nitrogen concentration percent in both species occurred between 12 and 25 years; the greatest N increase in trembling aspen logs occurred between 12 and 45 years.

Cellulose levels declined at different rates in aspen and white spruce logs (p<0.001). Cellulose levels in sound aspen logs (6 months after felling) were slightly higher (60%) than in spruce logs (50%). Cellulose declined by 28 % in aspen and by 35 percent in white spruce over the 45-year residence period (Table 14). Like nitrogen concentration, cellulose concentration in both aspen and spruce log declined most rapidly between 12 and 25 years.

The results of converting nitrogen concentrations to N content (g/ha) showed that for tA/wS sites, the N contents were greater for tA logs than wS logs for all decay classes. N content in tA logs increased substantially in decay class 4-5 logs, following the pattern of N concentration increase depicted in Table 13 whereas it did not increase in wS logs classified as decay class 4-5. The N content of white spruce logs decreased from 5 kg/ha (decay class 2) to 4 kg/ha in decay class 4-5 whereas N content in trembling aspen logs increased from 39 kg/ha in decay class 2, to 101 kg/ha in decay classes 4-5 respectively. Because experimental logs were located only in wS/tA stands rather than in wS (bF) or bF/wS stands, results have only been reported for this stand type.
Table 13. Differences in nitrogen concentration of trembling aspen and white spruce logs with 0.5 to 45 years of residence in the Mid-Boreal Upland Ecoregion. Mean nitrogen concentration and standard error (SE). ANOVA results expressed as p values. Bold face values indicate significance at p ≤ 0.05.

<table>
<thead>
<tr>
<th>Log Res. (years)</th>
<th>Species</th>
<th>Mean Conc. N (SE)</th>
<th>.5/tA</th>
<th>.5/wS</th>
<th>12/tA</th>
<th>12/wS</th>
<th>25/tA</th>
<th>25/wS</th>
<th>45/tA</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5</td>
<td>tA</td>
<td>0.041 (.002)</td>
<td>--</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>0.5</td>
<td>wS</td>
<td>0.045 (.001)</td>
<td>0.9465</td>
<td>--</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>tA</td>
<td>0.279 (.028)</td>
<td>0.0003</td>
<td>0.0003</td>
<td>--</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>12</td>
<td>wS</td>
<td>0.065 (.006)</td>
<td>0.6982</td>
<td>0.7458</td>
<td>0.0009</td>
<td>--</td>
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<tr>
<td>25</td>
<td>tA</td>
<td>0.653 (.153)</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
<td>--</td>
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<td></td>
</tr>
<tr>
<td>25</td>
<td>wS</td>
<td>0.339 (.027)</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.3582</td>
<td>0.0001</td>
<td>0.0001</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>45</td>
<td>tA</td>
<td>1.028 (.092)</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
<td>--</td>
</tr>
<tr>
<td>45</td>
<td>wS</td>
<td>0.279 (.023)</td>
<td>0.0002</td>
<td>0.0003</td>
<td>0.9984</td>
<td>0.0008</td>
<td>0.0001</td>
<td>0.3511</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

45/tA = trembling aspen logs with 45-year residence times
45/wS = white spruce logs with 45-year residence times
Table 14. Differences in cellulose concentration between trembling aspen and white spruce logs in the Mid-Boreal Upland Ecoregion by years of residence. Mean cellulose concentration, and standard error (SE). ANOVA results expressed as p values. Bold face values are significant at p≤ 0.05.

<table>
<thead>
<tr>
<th>Log Res. (years)</th>
<th>Species</th>
<th>Cellulose (%) (SE)</th>
<th>.5/tA</th>
<th>.5/wS</th>
<th>12/tA</th>
<th>12/wS</th>
<th>25/tA</th>
<th>25/wS</th>
<th>45/tA</th>
</tr>
</thead>
<tbody>
<tr>
<td>.5 tA</td>
<td>59.9 (0.87)</td>
<td>--</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>.5 wS</td>
<td>50.0 (0.49)</td>
<td>.0014</td>
<td>--</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12 tA</td>
<td>45.6 (1.56)</td>
<td>.0001</td>
<td>.1518</td>
<td>--</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12 wS</td>
<td>42.7 (3.15)</td>
<td>.0001</td>
<td>.0022</td>
<td>.0974</td>
<td>--</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>25 tA</td>
<td>27.8 (3.76)</td>
<td>.0001</td>
<td>.0001</td>
<td>.0001</td>
<td>.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>25 wS</td>
<td>30.0 (1.32)</td>
<td>.0001</td>
<td>.0001</td>
<td>.0001</td>
<td>.0001</td>
<td>.6999</td>
<td>--</td>
<td></td>
<td></td>
</tr>
<tr>
<td>45 tA</td>
<td>31.1 (.72)</td>
<td>.0001</td>
<td>.0001</td>
<td>.0001</td>
<td>.0025</td>
<td>.2723</td>
<td>.4992</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>45 wS</td>
<td>15.0 (1.64)</td>
<td>.0001</td>
<td>.0001</td>
<td>.0001</td>
<td>.0001</td>
<td>.0001</td>
<td>.0001</td>
<td>.0001</td>
<td></td>
</tr>
</tbody>
</table>

45/tA = trembling aspen logs with 45-year residence times
45/wS = white spruce logs with 45-year residence times
8.13 Discussion

My data suggest that for the Mid-Boreal Upland Ecoregion in Saskatchewan both structural and functional differences exist by stand type, and that there are seasonal variations in forest floor processes with different canopy compositions. The respiration, nitrogenase and mineralizable nitrogen rates differed by substrate type. The potential mineralization pattern is similar to that found in a Quebec study where net N mineralized was greater under aspen than under spruce in younger stands, and nitrogen reserves declined significantly with time since fire (Pare and Bergeron 1996).

The relative differences in substrate nitrogen mineralization rates found in this study were somewhat similar to Hart’s (1999) substrate rates for Oregon old growth Douglas-fir; mineralization rates for fallen logs were approximately 60 percent of rates for forest floors. Modeling the biomass production of white spruce-aspen stands through computer simulation would permit an examination of long-term growth trends in response to nitrogen fixation from litter and logs only as well as from both litter and logs. Reports from FORECAST simulation runs document such variables as litter biomass, and nitrogen uptake by spruce and aspen.

The literature (Chapter 4) confirmed that mixedwood logs and litter can have relatively high values for nitrogenase activity. My hourly rates were greater than the rates of 26 moles/day found in Alberta (McNabb et al. 1979). My high nitrogenase values might be due to the addition of nitrogen gas to the incubation chamber. Li (personal communication 1999) has reported at least 10% increases in nitrogenase activity rates in Douglas-fir substrates using this method. Although controls were run to account for endogenous ethylene
produced, it is also possible that true natural endogenous levels were higher than the tests reflected.

The 3:1 ratio of ethylene produced to nitrogen fixed that has been calculated for Oregon Douglas-fir forests by Silvester et al. (1982) is one of the few ratios available for nitrogenase conversion. Current work with nitrogen tracers by Feller (personal communication 1999) in BC’s ESSF zone has yielded different ratios for those forests. In future, nitrogen tracers could be used to verify the ratio of ethylene produced by nitrogenase activity and determine the actual amounts of nitrogen fixed for Saskatchewan Mid-Boreal Upland Ecoregion substrates.

Based on the literature, decomposition rates in aspen and white spruce fallen logs appear much more rapid on my study sites than in logs on the Oregon Pacific coast. Intense periods of microbial activity are necessary to provide such rates within the very short summer season typical of the Mid-Boreal Upland Ecoregion. If Mid-Boreal Upland microbial populations are very effective captors of nitrogen as Saskatchewan research has suggested (Walley et al. 1996), then an additional nitrogen source and relatively high levels of cellulose within fresh litter or logs might result in an increase in microbial activity.

Microbial activity process rates are related to seasonal substrate temperatures and substrate moisture content (Schlenter and Van Cleve 1985, Witkamp 1969, Bonan and Van Cleve 1992). At least two authors have suggested (Chapter 4) that flushes of microbial activity could occur in early spring. During the course of collecting samples, I found relatively high activity rates in May when temperatures were slightly above 0 °C. The intensity of the spring activity may be related to substrate moisture contents. Summer precipitation in Saskatchewan occurs in June and early July rather than in August. The
pattern of seasonal decline documented in this study may be the result of mortality in microbial populations. In Oregon, I found flushes of nitrogen mineralization associated with spring and fall precipitation events that followed dry intervals. Although I did not investigate the specific occurrence of precipitation events with microbial activity decreases or increases in Saskatchewan, the amounts of nitrogen fixed and mineralized declined in August during periods of low precipitation.

The seasonal variation in forest floor processes reflected in this study warrants further investigation since the processes were only measured during the summer months. Measurement throughout the year for all three indices within all stand types would be useful to gain more accurate estimates of annual contributions of these processes since studies have reported N fixation at below-freezing temperatures (Chapter 4).

In my study sites, the patterns of nitrogen and cellulose loss suggest that intense fixation of nitrogen in tA logs 12-45 years after treefall. However, without appropriate conversion rates the specific amount of nitrogen fixation cannot be defined. Nitrogen concentration in spruce logs changed from .041% to .28 % over 45 years. Aspen nitrogen concentration changed from .045% to 1.028 % in the same time period. Other scientists have reported similar findings for hardwood sites. In Minnesota, the nitrogen concentrations in aspen logs increased 23% over the average residence period of 14-17 years (Alban and Pastor 1993).

On wS/tA sites, it appears that N is accruing in individual tA logs. Studies conducted in a number of forest ecosystems have reported increases in either nitrogen content (kg/ha) or nitrogen concentrations associated with increasing decay levels in coarse woody debris (Arthur and Fahey 1990, Sollins et al. 1987). In the latter study,
when wood density and N concentration were plotted, N concentration declined initially with density but leveled off at log decay class 4. This change from reduced levels to a pattern of nondecline was interpreted to mean that nitrogen had been accrued in logs by means of nitrogen fixation, insect colonization, and/or hyphal translocation. In Saskatchewan, this topic requires further exploration in aspen and white spruce stands and in stands with white spruce and balsam fir.

We do not know the total contribution of nitrogenase activity in litter, log and mineral soil to long term stand growth patterns in Saskatchewan Mid-Boreal mixedwood sites, nor can we assess the result of high or low levels of nitrogenase on the total nitrogen economy. However, stand level modeling with the hybrid model FORECAST permits comparisons of stand level response to different N levels under a series of disturbance intensities. The role of nitrogenase activity (converted to nitrogen fixation) can be traced independently of the other nitrogen sources. Chapter 9 addresses the question of long term changes to the nitrogen economy of one boreal forest mixedwood type and its’ effect on stand biomass production over 240 years under various disturbance regimes.
Chapter 9

Computer Simulations of White Spruce-Aspen Stand Types

This chapter addresses white spruce sustainability over 240 years and the potential role of nitrogen fixation from forest floors (including woody debris) in the production of stemwood biomass. Computer simulation can be used to examine the relationships of aspen and white spruce in boreal forests over long periods of time. Hybrid ecosystem simulation models, such as FORECAST (Kimmins et al. 1999), can overcome some limitations of short-term field measurements of forest structure and studies that focus on single processes. FORECAST simulates succession using yearly time steps subject to the effects of single or multiple natural disturbances and different harvesting regimes.

When FORECAST was calibrated with Douglas-fir data, whole-tree harvesting implemented at 40-year rotations over a 240-year period depleted both the active soil nitrogen pool and organic matter pool. Stem-only harvesting at 80-year intervals maintained a higher level of soil N and tree growth compared to 40-year rotations with either stem only or whole tree harvesting (Morris et al. 1997). When Wang et al. (1995) modeled the growth of northern BC aspen and white spruce stands using FORECAST and a 120–year rotation over 240 years, mixed stands of aspen and white spruce grown together yielded greater total biomass than white spruce grown alone. In simulations of lodgepole pine forest ecosystems, Wei et al. (1999 unpublished) found that 120-year rotations of stem-only harvesting and light fire could sustain net primary production. As rotations became longer, observed differences between harvesting and wildfire disturbance became less apparent.
To date, white spruce or aspen growth has not been monitored extensively in response to different quantities and distribution of slash after harvesting in the Mid-Boreal Upland Ecoregion. Based on my field measures of process rates and published literature (Jurgensen et. al. 1996), it is possible that nitrogen fixed in litter layers and coarse woody debris may be important to the nitrogen economy of these forests but there is no empirical evidence of the long-term effect of harvest removal and slash retention in the forests. Because such evidence will not be available for many decades, ecological process-based ecosystem management simulation modeling can provide an estimate of what these inputs might do. In Chapter 8, there was evidence that total nitrogen content in aspen logs could reach 101 kg/ha. However, only a portion of this amount, when mineralized, would potentially contribute to total nitrogen uptake in white spruce-aspen mixedwood stands over 240 years; precipitation could be a significant source of nitrogen for stand growth.

9.1 Objectives

In Chapter 7 and 8, I examined differences in aspen-white spruce stands using structural and process field data. In this chapter, I explored changes to aspen and white spruce stemwood biomass, forest floor and nitrogen economies in response to fire and harvesting. As an independent experiment, I addressed the effect of nitrogen fixation on cumulative stemwood biomass, litter biomass and nitrogen uptake. The goals of this chapter were:

1) to examine simulations of different aspen densities in white spruce stands when the stands were subject to fire and harvesting disturbance over a 240-year period and,
2) to examine the growth of computer-simulated white spruce stands over 240 years subject to specific amounts of nitrogenase activity from litter layers and logs.

For the purposes of this modeling exercise, litterfall components originally composed of foliage were called litter layers; boles decomposing on the forest floor were defined as logs. The biomass production of white spruce stemwood was used as a major response variable in experiments related to the above objectives.

In Experiment 1, FORECAST was used to compare the effect of several disturbance types, disturbance frequencies and stand stem densities on stemwood biomass, coarse woody debris and total nitrogen content. In Experiment 2, FORECAST was used to compare the effect of different sources of nitrogen fixed on stemwood biomass subject to the two different aspen densities and disturbances.

9.2 Methods I. Modeling Experimental Design

Harvesting, one of the two selected disturbance types, was based on the current practices employed by forest companies in Saskatchewan’s western Mid-Boreal Upland Ecoregion. Harvesting mixedwoods in this area, and specifically the treatment of logging slash, varies according to stand species composition and age (Table 15) but the amount of slash left on sites, or piled and burned at the roadside has not been quantified.

Because there were no appropriate datasets available to calibrate FORECAST for balsam fir stand types, only the aspen-white spruce cohort (tA/wS) stand type or white spruce with minor aspen stand type (wS(tA)) could be simulated. The wS (wS) stand type depicted in Figure 2 involves regeneration of white spruce under canopies of white spruce
and could not be successfully simulated with the version of FORECAST that I used. A
detailed description of the current structure and function of the FORECAST model can be
found in Kimmins et al. (1999) and has been described briefly in Chapter 5.

Experiment 1. I used a factorial approach to examine the impact of both variation
in aspen density and variation in disturbance in simulated mixedwood stands. The design

Table 15. Current harvest practices in the Mid-Boreal Upland Ecoregion (R.
Nesdoly, K. Johnson, personal communication, 2000).

<table>
<thead>
<tr>
<th>Species</th>
<th>Approximate Harvest Age</th>
<th>Slash Treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pure aspen</td>
<td>80</td>
<td>Slash left on site</td>
</tr>
<tr>
<td>Pure spruce</td>
<td>90-140</td>
<td>Slash burned at roadside</td>
</tr>
<tr>
<td>Mixedwoods</td>
<td>80-120</td>
<td>Slash left on site or burned at roadside</td>
</tr>
</tbody>
</table>

consisted of a 2X2X2 combination (two rotation lengths of 60 or 80 years; two initial
aspen densities of 50,000 or 8,000 stems/ha respectively and two disturbance types
consisting of fire and harvesting). Initial white spruce densities of 3,600 stems/ha were
applied to all treatments. In all other respects, the simulated stands were identical.

The use of combined log and litter fixation in Experiment 1 represented the accepted
view of nitrogen fixation contributions to the nitrogen economy. A conversion factor of
3:1 (moles of ethylene to moles of nitrogen fixed) from the published literature was used
for litter layers and logs because a conversion rate for the Mid Boreal Upland was not
available (see Chapter 8). The sensitivity of FORECAST to different nitrogen conversion
rates is shown in Appendix 1. Results showed that if the conversion rate is assumed to be
3 or more, the change in cumulative stemwood biomass over 240 years is relatively low. If
the conversion rate is truly lower than 3, the amount of potential nitrogen fixed is greater and there may be an effect in the amount of simulated stemwood biomass produced during the run. Interim disturbances of mild harvesting and light fires were applied to simulate stand-maintaining disturbance every 15-20 years. Research design summaries are provided in Tables 16 and 17.

*Experiment 2:* The 120-year disturbance simulations were used to explore the effect of N fixation on stand growth. The design consisted of a 2X2X4 factorial treatment (2 aspen densities, fire or harvesting replacement disturbances, and 4 fixation treatments). The fixation treatments consisted of N from litter only, logs only, a combination of litter and logs and a control with no fixation. Only litter, log and no fixation are presented here due to technical difficulties with the combined substrate runs; Experiment 1 was conducted satisfactorily with combined substrate nitrogen fixation. Research design details for Experiment 2 are given in Table 18.

9.3 Methods II. The Saskatchewan White Spruce-Aspen Calibration Dataset

A representative dataset for low, medium and high quality sites for both white spruce and aspen in the study area was supplied by B. Seely and C. Welham (personal communication 2000). The dataset consisted of soil, tree, plant (herb and shrub), and bryophyte components. However, the dataset lacked individual forest floor component N fixation rates; these were supplied from the literature and from my measurements (Chapter 8). The published sources of some of the other major variables used in the mixedwood dataset are given in Appendix 2.
To determine the amounts of nitrogen fixed in each simulation, the hourly rate of nitrogen fixed was adjusted to reflect a daily rate based on a theoretical average of 10 h of fixation/day. Ten hours was based on the fact that many growing season nights are cool; frosts typically occur in April and early May, and can occur in mid-August. The daily rate was multiplied by the number of days/year (160) in which nitrogen fixation might be possible.

Table 16. Experiment 1. Sixty and 80-year simulation designs with fire and harvest disturbances. Stem reductions after first and second disturbance respectively. All simulations conducted over 240 years.

<table>
<thead>
<tr>
<th>Stand Replacement (years)</th>
<th>Initial Aspen stems</th>
<th>Initial Spruce stems</th>
<th>Natural Disturbance (years)</th>
<th>Harvest Disturbance (years)</th>
<th>Stem Reduction</th>
</tr>
</thead>
<tbody>
<tr>
<td>60</td>
<td>50,000</td>
<td>3,600</td>
<td>Light fire, 35, 55</td>
<td>Light harvest, 35, 55</td>
<td>Aspen: 1,100; 550 Spruce: 1,000, 600</td>
</tr>
<tr>
<td>60</td>
<td>8,000</td>
<td>3,600</td>
<td>Light fire, 35, 55</td>
<td>Light harvest, 35, 55</td>
<td>Aspen: 1,100; 500 Spruce: 1,000, 600</td>
</tr>
<tr>
<td>80</td>
<td>50,000</td>
<td>3,600</td>
<td>Light fire, 55, 68</td>
<td>Light harvest, 55, 68</td>
<td>Aspen: 1,100; 500 Spruce: 1,000, 600</td>
</tr>
<tr>
<td>80</td>
<td>8,000</td>
<td>3,600</td>
<td>Light fire, 55, 68</td>
<td>Light harvest, 55, 68</td>
<td>Aspen: 1,100; 500 Spruce: 1,000, 600</td>
</tr>
</tbody>
</table>
Table 17. Experiment 2. One hundred and twenty-year simulation designs-fire disturbance. Sources of nitrogen fixation in mixedwood stands. Light fires applied to remove spruce and aspen differentially.

<table>
<thead>
<tr>
<th>Initial Aspen Stems</th>
<th>Initial Spruce Stems</th>
<th>Multiple Light Fires (Years):</th>
<th>Nitrogen Fixed</th>
</tr>
</thead>
<tbody>
<tr>
<td>50,000-high</td>
<td>800</td>
<td>Spruce-45, 80, 115; Aspen-35, 55, 80, 105, and 115</td>
<td>None, Litter, Log, Litter and Log</td>
</tr>
<tr>
<td>800-low</td>
<td>800</td>
<td>Spruce-45, 80, 115; Aspen-35, 55, 80, 105, and 115</td>
<td>None, Litter, Log, Litter and Log</td>
</tr>
</tbody>
</table>

Table 18. Experiment 2. One hundred and twenty-year simulation designs-harvesting disturbance. Sources of nitrogen fixation in mixedwood stands. Mild wind/harvesting applied to remove white spruce and aspen differentially.

<table>
<thead>
<tr>
<th>Initial Aspen Stems</th>
<th>Initial Spruce Stems</th>
<th>Multiple Light Winds/Harvesting (Years):</th>
<th>Nitrogen Fixed</th>
</tr>
</thead>
<tbody>
<tr>
<td>50,000-high</td>
<td>800</td>
<td>Spruce-45, 68, 80, 105, 115; Aspen-35, 55, 80, 105, and 115</td>
<td>None, Litter, Log, Litter and Log</td>
</tr>
<tr>
<td>800-low</td>
<td>800</td>
<td>Spruce-45, 68, 80, 105, 115; Aspen-35, 55, 80, 105, and 115</td>
<td>None, Litter, Log, Litter and Log</td>
</tr>
</tbody>
</table>

Expected based on temperatures above 5 °C, but excludes those periods when substrate moisture contents might be either too high or too low for optimum fixation. The 160-day period corresponds to spring, summer and early fall seasons in Saskatchewan.
An aspen-white spruce management file calling for stand-replacing fires at 80, 160 and 240 years was used in the setup stage of FORECAST modeling to create an initial ecosystem state with a forest floor nitrogen legacy for the subsequent simulations. In this setup file scenario, spruce regeneration was simulated to occur after the 80-year interval fires, while aspen was programmed to resprout (sucker) after fires.

9.4 Methods III. Simulation Scenarios for Experiments 1 and 2

The 60 and 80-year replacement interval simulations involved either initial high aspen densities of 50,000 stems/ha or initial low aspen densities of 8,000 stems/ha. These levels represented a variation in aspen regeneration density around an assumed average of 30,000 stems/ha, although the literature suggests that much higher initial aspen densities can occur (Kabzems et al. 1986). White spruce starting densities were maintained at 3600 stems/ha.

Since the post-harvest slash levels have not been quantified on sites in the Mid-Boreal Upland Ecoregion, it was necessary to establish a starting point for simulating potential amounts of organic matter within the forest floor. Simulations with FORECAST compared the retention of 5% and 50% of the harvested stemwood biomass on the forest floor. Leaving 50% of simulated stemwood on the forest floor after harvesting yielded greater stemwood biomass production than simulations with 5% retention of harvested stemwood. Since one objective of the computer simulations was to determine if a particular level of stemwood bole retention in the forest floor would lead to non-declining yields over time (sustainable forestry), the former stemwood retention level (50%) was represented as slash and a potential nitrogen pool for the Experiment 1 study. The choice
was not linked to whether or not a company would leave such an amount of debris. Experiment 2 addressed the question of whether fallen logs deposited by wind during stand development affected stemwood biomass production when harvesting removed 95% of the material. This design was a more realistic simulation in terms of forest practice.

For each simulation, FORECAST generates reports on nitrogen inputs, nitrogen losses and a wide variety of other stand characteristics including stemwood biomass, canopy height, litterfall and nitrogen uptake. However, only output immediately relevant to my thesis will be reported here.

In constructing the Experiment 1 series of FORECAST simulations, a stand-replacing fire disturbance interval of 60 years was chosen to represent the minimum fire interval in the western and southern reaches of the Mid-Boreal Upland Ecoregion (R. Nesdoly, personal communication, 2000). The interval of 80 years was chosen because it is close to the maximum fire interval for this region (65-75 years-Chapter 2). It is also a common age for harvesting mixedwood stands in Saskatchewan (R. Nesdoly, personal communication, 2000).

The disturbance interval of 120 years was chosen because it represents the typical age of aspen and white spruce mixedwood stands in the Mid-Boreal Upland Ecoregion in the absence of a more frequent fire interval (Chapter 3). Mature white spruce may be harvested when it reaches this age although relatively few intact stands remain in the Ecoregion.

In Experiment 2, each 120-year disturbance scenario was run with litter and log nitrogenase activity separately, from a series of modified soil data files. The objective of
Experiment 2 was to determine if forest floor nitrogen fixation was an important factor in simulated white spruce-aspen stand biomass production.

9.5 FORECAST Results-Experiment 1

In 60-year simulations, stemwood biomass production was highest in the first rotation with the possible exception of harvested high-density aspen scenarios (Figures 9,10). This pattern of variation may have been due to the presence of a debris legacy and accompanying residual nitrogen pool derived from the ECOSTATE file (this file is described in Chapter 5). The legacy curve is labeled in Figures 11 and 12.

Reductions in stemwood biomass associated with mild harvesting or light fire took place at 35 and 55 years. All scenarios resulted in a decrease in white spruce stemwood biomass over 240 years. These scenarios will be described in detail according to the sequence of stand replacement intervals (60, and 80 years respectively).

1. Stemwood biomass in scenarios with 60-year replacement intervals:

A. Disturbance Effects. White spruce stemwood biomass accumulation declined over the sequence of 60-year stand replacement fires and harvests (Figures 9,10). The stemwood biomass accumulations in white spruce declined more rapidly than the stemwood biomass accumulations in aspen with both disturbance types. However, declines were less marked in harvested stand simulations than in the fire disturbance simulations.

B. Density Effects. The simulations with high-density aspen retained
Figure 9. Experiment 1. Stemwood biomass (t/ha) in simulated high-density aspen-white spruce over 240 years. A. Stand replacement fire at 60-year intervals. B. Stand replacement harvesting at 60-year intervals. The simulation incorporates light fires or mild harvesting at 35 and 55 years respectively.
Figure 10. Experiment 1. Stemwood biomass (t/ha) in simulated low-density aspen-white spruce over 240 years. A. Stand replacement fire at 60-year intervals. B. Stand replacement harvesting at 60-year intervals. The simulation incorporates light fires or mild harvesting at 35 and 55 years respectively.
aspen dominance; the low-density aspen simulations maintained white spruce dominance. In high aspen-density simulations (Figure 9, 10), the aspen stemwood biomass increased rapidly until harvested or lightly burned at age 35. In low-density aspen stands, simulations with fire resulted in gradual increases in aspen stemwood biomass. Although there was a gradual decline in aspen density relative to spruce in high-density simulations with harvesting, the decline in stand biomass was less than fire-disturbed stands. The increase in aspen biomass in fire-disturbed scenarios may have been due to the ability of aspen to take greater advantage of the assart flush than white spruce (Figure 9, 10).

2. Nitrogen in deadwood in scenarios with 60-year replacement intervals: The definition of deadwood within FORECAST includes both standing dead and fallen deadwood (coarse woody debris) where decomposition has not yet begun (B. Seely, personal communication 2000). When a tree dies, the biomass is transferred to one of several decomposition types that include sapwood, heartwood, and foliar litter. Nitrogen fixation in these substrates commences when they begin to decompose. Figure 11 and Figure 12 depict the total nitrogen in kg/ha over time found in aspen and white spruce deadwood for simulations with 60-year stand replacement intervals.

A. Disturbance Effects. As might be expected, the simulations of replacement fire over 240 years produced less deadwood total nitrogen than simulations of replacement harvesting because of the progressive decline in living stemwood biomass. Each successive white spruce
Figure 11. Experiment 1. Simulated total nitrogen (kg/ha) in dead woody debris in high-density aspen-white spruce over 240 years. A. Stand replacement fire at 60-year intervals. B. Stand replacement harvesting at 60-year intervals. The simulation incorporates light fires or mild harvesting at 35 and 55 years respectively.
Figure 12. Experiment 1. Simulated total nitrogen (kg/ha) in dead woody debris in low-density aspen-white spruce over 240 years A. Stand replacement fire at 60-year intervals. B. Stand replacement harvesting at 60-year intervals. The simulation incorporates light fires or mild harvesting at 35 and 55 years respectively.
nitrogen peak is lower than the previous one in the fire disturbance type. This trend is less evident in the harvested disturbance type.

B. Density Effects. Simulations with high aspen density have greater total nitrogen from aspen deadwood than from white spruce deadwood. In simulations with low-density aspen and stand replacement harvesting, total nitrogen from aspen deadwood rose slowly over the simulation period relative to white spruce total nitrogen (Figure 12).

3. Decomposing litter and log mass in scenarios with 60-year replacement intervals:
Decomposing litter and log mass from the FORECAST aspen-white spruce simulations are depicted in Figures 13 and 14 respectively.

A. Disturbance Effects. Simulated fire reduced the amounts of both white spruce and aspen litter and log mass, particularly aspen and white spruce litter compared to the litter and log mass in harvesting scenarios. Aspen heartwood and spruce heartwood were greater in the harvesting scenarios than in the fire disturbance scenarios (Figures 13,14).

B. Density Effects. There was greater aspen litter and aspen log mass than white spruce litter and log mass in high-density aspen scenarios compared to low-density scenarios (Figures 13,14). In both the high-density scenarios (Figure 13), aspen heartwood peaks were dominant over white spruce peaks after the initial legacy of white spruce mass declined (the initial white spruce log mass was a legacy from the Ecostate file). The low-density scenarios differed according to disturbance type. Low aspen density harvesting simulations
Figure 13. Experiment 1. Changes in the mass (t/ha) of six forest floor components in simulated aspen-white spruce stand types over 240 years. A. High-density aspen-white spruce with replacement fire at 60-year intervals. B. High-density aspen-white spruce with replacement harvesting at 60-year intervals. Spsap-white spruce sapwood, sphart-white spruce heartwood, split-white spruce litter, assap-aspen sapwood, ashart-aspen heartwood and aslit-aspen litter.
Figure 14. Changes in the mass (t/ha) of six forest floor components in simulated aspen-white spruce stand types over 240 years. A. Low-density aspen-white spruce with replacement fire at 60-year intervals. B. Low-density aspen-white spruce with replacement harvesting at 60-year intervals. Spsap-white spruce sapwood, sphart-white spruce heartwood, split-white spruce litter, assap-aspen sapwood, ashart-aspen heartwood and aslit-aspen litter.
(Figure 14) had the following descending order for total decomposing mass: 1) white spruce heartwood 2), aspen heartwood and, 3) white spruce litter. In the fire simulation, however, the descending order was: 1) White spruce heartwood 2) aspen heartwood and, 3) aspen sapwood.

The rise over time in aspen and white spruce heartwood decomposing mass depicted in the FORECAST simulation figures can be explained in the following manner. When a tree dies and becomes standing or down woody debris, the heartwood that initially undergoes decomposition is small. As insects, disease, and fungi penetrate the log, the undecomposed mass is transformed into decomposed mass. This phenomenon is shown in Figure 13 and 14 as an increase in decomposing heartwood mass. Once the log’s entire heartwood is involved in the decomposed process, mass loss leads to a decline in total heartwood decomposing mass. The differences in the shape of the aspen decomposing heartwood mass as compared to the white spruce heartwood mass reflects the more rapid invasion of organisms into aspen wood.

4. Stemwood biomass in scenarios with 80-year replacement intervals:

In 80-year stand replacement simulations, stand disturbance and initial stand density were important factors in controlling stand development over 240 years (Figures 15,16).

A. Disturbance Effects. Greater peak stemwood biomass occurred in the 80-year stand replacement simulations compared to the 60-year replacement simulations. Compared to the fire replacement simulations, harvesting scenarios had higher peak white spruce stemwood biomass
Figure 15. Experiment 1. Stemwood biomass simulations (t/ha) in high-density aspen-white spruce over 240 years. A. Stand replacement fire at 80-year intervals. B. Stand replacement harvesting at 80-year intervals. The simulation incorporates light fires or mild harvesting at 35 and 55 years respectively.
Figure 16. Experiment 1. Stemwood biomass simulations (t/ha) in low-density aspen-white spruce over 240 years. A. Stand replacement fire at 80-year intervals. B. Stand replacement harvesting at 80-year intervals. The simulation incorporates light fires or mild harvesting at 35 and 55 years respectively.
values than aspen stemwood biomass values.

B. Density Effects. Based on FORECAST-generated reports, greater total aspen and white spruce biomass was found in low-density fire-driven aspen stands than in high-density aspen stands with the same fire disturbance. This finding was due to the much greater total white spruce biomass production over 240 years in low-density stands with 80-year replacement disturbance compared to the scenarios with 60-year replacement disturbance.

5. Nitrogen in deadwood with 80-year replacement intervals:

A. Disturbance Effects. The pattern of deadwood total nitrogen in these scenarios was similar to the 60-year replacement interval scenarios; both aspen and white spruce total nitrogen declined with successive fires and harvesting scenarios (Figure 17, 18). In fire disturbance simulations, the rate of decrease in white spruce total nitrogen appeared greater compared to aspen total nitrogen.

B. Density Effects. Low-density aspen stands produced similar amounts of aspen and white spruce total nitrogen. High-density aspen simulations with harvesting and fire respectively had much more distinctive aspen peaks and lower white spruce total nitrogen than the low-density aspen simulations (Figures 17, 18).
Figure 17. Experiment 1. Simulated total nitrogen (kg/ha) in dead woody debris in high-density aspen-white spruce over 240 years. A. Stand replacement fire at 80-year intervals. B. Stand replacement harvesting at 80-year intervals. The simulation incorporates light fires or mild harvesting at 35 and 55 years respectively.
Figure 18. Experiment 1. Simulated total nitrogen (kg/ha) in dead woody debris in low-density aspen-white spruce over 240 years. A. Stand replacement fire at 80-year intervals. B. Stand replacement harvesting at 80-year intervals. The simulation incorporates light fires or mild harvesting at 35 and 55 years respectively.
Figure 19. Experiment 1. Changes in litter and log decomposition mass (t/ha) in simulated aspen-white spruce stand types over 240 years. A. High-density aspen-white spruce with replacement harvesting at 80-year intervals. B. Low-density aspen-spruce with replacement harvesting at 80-year intervals. Spsap-white spruce sapwood, sphart-white spruce heartwood, split-white spruce litter, assap-aspen sapwood, ashart-aspen heartwood and aslit-aspen litter.
6. Decomposing mass with 80-year replacement intervals:

Low-density harvesting simulation yielded larger mass amounts of both white spruce and aspen heartwood than was found in the high-density scenario (Figure 19). The pattern of greater white spruce heartwood may have been due to increased overall biomass production in the main canopy of white spruce stands in the absence of high aspen competition.

7. Nitrogen fixation in simulated stands with 80-year replacement intervals:

High-density aspen-white spruce stands with harvesting produced N fixation amounts of 381 kg/ha over 240 years whereas high-density aspen stands with fire disturbance yielded 377 kg/ha N fixed respectively. Simulated low-density white-aspen spruce stands with harvesting generated 379 kg/ha nitrogen fixation whereas low-density aspen–white spruce stands with multiple fire disturbances generated 377 kg/ha of N. These values are equivalent to approximately 1.5 kg/ha/yr.

Table 19 presents comparisons of the amounts of total nitrogen (kg/ha) lost through fire or transferred from live trees to the forest floor due to harvesting. The table values indicate that stand replacement harvesting yielded more nitrogen (kg/ha) as a result of slash left on the ground than scenarios where nitrogen was removed by stand replacement fire. Since the original design called for retention of 50% of the stemwood to be left as debris, this result was not unexpected. Nitrogen content (kg/ha) of aspen slash is generally higher than the nitrogen content of white spruce slash whereas nitrogen lost from aspen biomass due to fire is generally lower than the loss from white spruce (Table 19). Unfortunately, the computer model findings in Experiment 1 cannot currently be confirmed or refuted because, to the best of my knowledge, there are no long-term field
studies in Saskatchewan dealing with slash treatments and potential nutrient benefits to mixedwood stands.

9.6 FORECAST Disturbance and Density Simulation Results-Experiment 2.

Experiment 2 simulations explored three questions: 1) whether stand disturbance and initial aspen stem density affected the relationship of aspen and white spruce over two 120-year rotations, 2) whether nitrogen fixation from logs or from litter had any effect on simulated stand characteristics compared to no nitrogen fixation and, 3) whether simulated nitrogen uptake was affected by deposition of logs on the forest floor from wind events compared to simulations without wind events.

Table 19. Experiment 1. Representative amounts of nitrogen (kg/ha) lost as “fire” or left as slash in simulated aspen and white spruce stand types. Replacement fire losses at 80, 160 and 240 years: Simulated light burns every 45 and 68 years within each 80-year period. Output from FORECAST summary reports.

<table>
<thead>
<tr>
<th>Year</th>
<th>N (kg/ha) and mass (t/ha) lost in replacement burn</th>
<th>Aspen (light fire/mild harvesting) kg/ha N</th>
<th>White spruce (light fire/mild harvesting) kg/ha N</th>
</tr>
</thead>
<tbody>
<tr>
<td>80</td>
<td>Mass: 74.4</td>
<td>Yr. 45 “fire”: 12.6</td>
<td>Yr. 45-“fire”: 7.7</td>
</tr>
<tr>
<td></td>
<td>Nitrogen: 258.6</td>
<td>Yr. 45-slash: 51.5</td>
<td>Yr. 45-slash: 10.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Yr. 68-“fire”: 4.0</td>
<td>Yr. 68-“fire”: 18.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Yr. 68-slash: 17.7</td>
<td>Yr. 68-slash: 26.7</td>
</tr>
<tr>
<td>160</td>
<td>Mass: 57.5</td>
<td>Yr. 125-“fire”: 12.6</td>
<td>Yr. 125-“fire”: 4.5</td>
</tr>
<tr>
<td></td>
<td>Nitrogen: 210.3</td>
<td>Yr. 125-slash: 56.4</td>
<td>Yr. 125-slash: 6.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Yr. 148-“fire”: 4.4</td>
<td>Yr. 148-“fire”: 10.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Yr. 148-slash: 19.9</td>
<td>Yr. 148-slash: 14.8</td>
</tr>
<tr>
<td>240</td>
<td>Mass: 53.9</td>
<td>Yr.205-“fire”: 12.0</td>
<td>Yr. 205 “fire”: 3.9</td>
</tr>
<tr>
<td></td>
<td>Nitrogen: 198.4</td>
<td>Yr. 205-slash: 55.5</td>
<td>Yr. 205 slash: 5.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Yr. 228-“fire”: 4.3</td>
<td>Yr. 228“fire”: 9.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Yr. 228-slash: 19.6</td>
<td>Yr. 228 slash: 13.1</td>
</tr>
</tbody>
</table>
In the latter simulation (wind events vs no wind events Appendix 2), greater nitrogen uptake was assumed to enhance forest sustainability.

The factorial experiment (Tables 17, 18) evaluated differences in stemwood biomass, nitrogen uptake, litter biomass and litterfall due to fire or harvesting disturbance simulated with 120-year rotations. Simulations compared the effects of no nitrogen fixation, litter N fixation or log N fixation. Unfortunately, the individual contribution of N fixation by species of log (that is, from aspen logs and spruce logs separately) could not be compared because of the nature of FORECAST model output. Although white spruce and aspen decomposing mass can be separated in FORECAST and nitrogenase activity can be assigned to key time intervals, the version of FORECAST that I used does not report or graph changes in substrate nitrogenase activity by species. The current version of FORECAST does, but it was not available for my thesis work.

1. Stemwood biomass from scenarios with 120-year replacement intervals:

A. Disturbance Effects. In Experiment 1 with 60 and 80 replacement intervals, stand simulations with high-density aspen and fire disturbance favoured aspen dominance. Contrary to the results of Experiment 1, the simulations with 120-year replacement intervals and mild interim disturbances yielded dominant white spruce stemwood biomass values that were constant from one 120-year period to another (Figure 20).

B. Density Effects. Low-density aspen with harvesting yielded low amounts of aspen stemwood biomass in response to the initial starting densities and the two disturbance types. In high-density aspen scenarios, harvesting regimes reduced
Figure 20. Experiment 2. Stemwood biomass (t/ha) in a simulated low-density aspen-white spruce stand over 240 years. A. Stand replacement fire at 120-year intervals. B. Stand replacement harvesting at 120-year intervals. Disturbances at intermediate years represent light fires (A) or wind (B).
Figure 21. Experiment 2. Simulated total nitrogen (kg/ha) in dead woody debris in low-density aspen-white spruce over 240 years. A. Stand replacement fires at 120-year intervals. B. Stand replacement harvesting at 120-year intervals. Disturbances at intermediate years represent light fires (A) or wind (B).
aspen biomass production in favour of white spruce (results not presented in
this chapter).

2. *Nitrogen in deadwood with 120-year replacement intervals*: In keeping with the lower
starting aspen stem density (Tables 17, 18), total nitrogen from aspen deadwood (standing
dead trees and logs) in low-density aspen succession scenarios was considerably less than
the total nitrogen from white spruce deadwood (Figure 21).

Simulations with fire resulted in relatively low levels of both aspen and white
spruce total nitrogen after the nitrogen decline from the legacy mass. In simulations with
harvesting as the replacement disturbance, total nitrogen was considerably higher over the
240-year period in white spruce deadwood than in aspen deadwood.

3. *Changes in decomposing mass with 120-year replacement intervals*: In scenarios with
fire disturbance, the accumulations of both white spruce and aspen decomposing mass
were relatively small after the loss of the white spruce mass legacy originating from the
Ecostate file. Because the white spruce legacy contributes a high mass to the
simulations, the first rotation in the simulations may not always be typical of natural
stand conditions.

A. Disturbance Effects: As expected, litter and sapwood for both species had much
higher accumulations in scenarios with replacement harvesting than in scenarios
with replacement fire (Figures 22, 23). In the case of the scenario with 120-year
stand replacement fire disturbance, there was a smaller pulse of white spruce
heartwood mass at 120 years than when the stand was subjected to simulated
replacement harvesting. This result was linked to the differences in disturbance
Figure 22. Experiment 2. Changes in litter and log decomposition mass (t/ha) in simulated aspen-white spruce stand types over 240 years. A. High-density aspen-white spruce with replacement fires at 120-year intervals. B. High-density aspen-white spruce with replacement harvesting at 120-year intervals. Spsap-white spruce sapwood, sphart-white spruce heartwood, split-white spruce litter, assap-aspen sapwood, ashart-aspen heartwood and aslit-aspen litter.
Figure 23. Experiment 2. Changes in litter and log decomposition mass (t/ha) in simulated aspen-white spruce stand types over 240 years. A. Low-density aspen-white spruce with replacement fires at 120-year intervals. B. Low-density aspen-white spruce with replacement harvesting at 120-year intervals. Spsap-white spruce sapwood, sphart-white spruce heartwood, split-white spruce litter, assap-aspen sapwood, ashart-aspen heartwood and aslit-aspen litter.
types, initial stand densities and the consequent nitrogen accumulation pattern from forest floor substrates and precipitation.

B. Density Effects: There is little difference between high density and low aspen-density fire replacement simulations in terms of decomposing mass (Figures 22-23). This suggests that simulated fire at the 120-year interval destroyed a major portion of the nitrogen pool. However, the high-density aspen scenario with harvesting produced quite a different pattern of mass accumulation from the low-density harvesting scenario.

9.7 Experiment 2. Simulation Results Involving N Fixation

Each 240-year simulation was run with either no nitrogen fixation, fixation from litter or fixation from logs; in each case both seepage and nitrogen from precipitation were also contributors to stemwood biomass, litter biomass and to nitrogen uptake. Results indicated that N fixation from litter or logs was very similar to the control treatment (Tables 20, 21, Appendices 1, 3). In keeping with the findings of Experiment 1, there were differences in nitrogen uptake and litter biomass by species according to the disturbance regimes and stand density.

The lack of response to litter, or log nitrogen fixation by simulated stemwood biomass and litter biomass over 240 years may be the result of assumptions inherent to the structure of the FORECAST model and/or to our lack of knowledge about nitrogen processes in Saskatchewan boreal forests. Specifically, the results may be due to lack of long-term data related to seasonal nitrogen inputs for Mid-Boreal Upland forests and the lack of sensitivity of the nitrogen conversion rates expressed as yearly inputs.
Table 20. FORECAST simulations in low-density aspen-white spruce stands with wind at years: 55, 68, 80 and 115 in white spruce and 35, 68, 105 and 115 in aspen. Replacement harvesting at 120 and 240 years with 95% removal of harvested material. Data from FORECAST summary reports.

<table>
<thead>
<tr>
<th>Substrate Type</th>
<th>Species</th>
<th>Total Net Biomass Production (t/ha)</th>
<th>Total Litterfall (t/ha)</th>
<th>Total Nitrogen Uptake (kg/ha)</th>
<th>Total Nitrogen Content in Litterfall (kg/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No Fixation</td>
<td>Aspen</td>
<td>2342</td>
<td>1772</td>
<td>5812</td>
<td>4902</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>1449</td>
<td>875</td>
<td>4983</td>
<td>4172</td>
</tr>
<tr>
<td>Log N fixation</td>
<td>Aspen</td>
<td>2347</td>
<td>1776</td>
<td>5836</td>
<td>4919</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>1456</td>
<td>880</td>
<td>5004</td>
<td>4191</td>
</tr>
<tr>
<td>Litter Fixation</td>
<td>Aspen</td>
<td>2349</td>
<td>1777</td>
<td>5842</td>
<td>4923</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>1458</td>
<td>881</td>
<td>5009</td>
<td>4196</td>
</tr>
</tbody>
</table>

Table 21. FORECAST simulations in high-density aspen-white spruce stands. Nitrogen fixation effects. Periodic wind at years 55, 68, 80 and 115 in white spruce and 35, 68, 105 and 115 in aspen. Replacement harvesting at 120 and 240 years with 95% removal of material. Data from FORECAST summary reports.

<table>
<thead>
<tr>
<th>Substrate Type</th>
<th>Species</th>
<th>Total Net Biomass Production (t/ha)</th>
<th>Total Litterfall (t/ha)</th>
<th>Total Nitrogen Uptake (kg/ha)</th>
<th>Total Nitrogen Content in Litterfall (kg/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No N fixation</td>
<td>Aspen</td>
<td>3138</td>
<td>2307</td>
<td>8111</td>
<td>6760</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>1287</td>
<td>786</td>
<td>4415</td>
<td>3714</td>
</tr>
<tr>
<td>Log N fixation</td>
<td>Aspen</td>
<td>3139</td>
<td>2307</td>
<td>8125</td>
<td>6772</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>1287</td>
<td>786</td>
<td>4416</td>
<td>3715</td>
</tr>
<tr>
<td>Litter N fixation</td>
<td>Aspen</td>
<td>3139</td>
<td>2306</td>
<td>8120</td>
<td>6765</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>1290</td>
<td>788</td>
<td>4427</td>
<td>3724</td>
</tr>
</tbody>
</table>
Using high-density aspen stands with fire disturbance and litter fixation only as an example, FORECAST reported that the level of nitrogen fixed was approximately 39% of the combined nitrogen from precipitation, seepage and nitrogen fixation over 240 years. Nitrogen input from seepage was 120 kg/ha over 240 years whereas nitrogen input via precipitation was estimated at 960 kg/ha or 4 kg/ha/yr.

My field data suggested potential fixation rates of 8 kg/ha/yr or greater using an assumed 3:1 conversion rate for nitrogen fixation in litter. There are several reasons why discrepancies occurred between my nitrogenase field data and FORECAST calculations of log and litter N fixation. A variety of published sources were used in FORECAST to describe N fixation rates in various humus types. I had measured nitrogenase activity at two depths in litter, in mineral soil and in decay class 4-5 logs. As a result, it was necessary to find fixation data for other log decay classes; the data sources did not come from the Mid-Boreal Upland Ecoregion. Moreover, there are wide fluctuations from year to year in nitrogen fixation rates measured in the field and there are no relevant studies of more than one year's duration in similar stands. In the Mid-Boreal Upland, seasonal measurements of nitrogenase activity that were taken in 1998 in a white spruce-aspen cohort type were only two thirds of the 1997 figures.

FORECAST classifies decay class 4-5 logs as humus; the relatively high levels of nitrogen content found in well-decayed aspen logs (Chapter 8) are assigned to the humus category. Thus, the ultimate benefit of simulated logs to the system may be masked by structure of FORECAST decomposition classes since the period of greatest nitrogen accumulation in aspen logs occurs when the logs are classified as humus.
Appendix 1 (Tables 22-25) involved tests of stemwood biomass sensitivity to nitrogen fixation conversion rates. When conversion rates were reduced from 3.0 to 0.2, Table 25 showed that a simulated increase of approximately 300 kg/ha of nitrogen fixation in 240 years yielded only a few additional tons of stemwood biomass. Mineralization and fixation rates may be subject to daily or weekly precipitation events and temperature changes (Chapter 4, Chapter 8) over a growing season. Seasonal estimates may be more suitable in representing boreal forest nitrogen fluxes.

In measures of seasonal nitrogen supply rate in aspen LFH layers, Huang and Schoenau (1997) found that \( \text{NH}_4^+ \) supply reached its maximum during May, was quite high in July and decreased to a minimum in September. From the same study, N return from aspen litter in autumn was calculated as 28-40 kg/ha and 2 kg/ha originated from precipitation (Huang 1996, Huang and Schoenau 1997). An autumn return of 28 kg/ha nitrogen released from litter when assumed to be steady over 240 years could potentially yield 6720 N kg/ha. Simulated high-density aspen stands using FORECAST (Table 21) yielded a value of total nitrogen from litter over 240 years of 6765 kg/ha. Huang and Schoenau (1997) estimated that the maximum nitrogen uptake by roots occurred in mid-summer based on two-week measurement intervals. Based on the work of these authors as well as my own work, it is possible that the effective nitrogen fixation period in boreal forests spans approximately 100 days rather than a year and that fixation might be more appropriately expressed as kg/ha/annual quarter.

In terms of the long-term importance of logs to mixedwood stands, Appendix 3 addressed the effect of aspen and white spruce logs left periodically in low-density aspen stands. The simulations involved stand replacement fires. Comparisons of simulations
without wind events (Table 27) and with wind events (Table 28) in which logs were deposited on the forest floor, showed that greater stemwood biomass production, greater litterfall, and greater nitrogen uptake took place in stands with wind events. This finding may be related to the additional nitrogen contributed to the humus layer from well-decayed wood. In these simulations, total nitrogen uptake increased approximately 14% when logs were left during each 180-year period. I interpreted this finding as a long-term benefit from stemwood left on the forest floor.

9.8 Results Summary and General Discussion

The FORECAST simulation results differed according to the amount of stemwood retained on site after fire or harvesting, initial stem densities and the replacement disturbance frequency. Depending on the combination of these factors, the amount of cumulative aspen biomass compared to white spruce biomass changed over 240 years. This finding generally supports a multiple pathway approach to boreal forest succession such as that shown in the conceptual model (Figure 2).

The variation in potential N fixation between the surface of decomposing aspen and white spruce logs and the center is not known. Consequently, more fieldwork may be necessary to examine the N fixation in sapwood and heartwood for both species. Brunner et al. (unpublished 1998) documented higher amounts of nitrogenase activity in sapwood than heartwood for amabilis fir (Abies amabilis) and western hemlock CWD on Vancouver Island.

Due to time constraints, nitrogenase activity-N fixation ratios could not be calculated specifically for my study sites. As a result, it would be helpful to investigate N
fixation rates on xeric, mesic and hygric sites to establish the relationship between labeled N uptake and measures of nitrogenase activity. Furthermore, most field studies measure single summer seasonal rates and a more comprehensive study is required to incorporate year round monitoring over several years.

Although a number of factors may contribute to poor white spruce growth in dense aspen stands, the literature (Chapter 2), indicated that white spruce was a poor competitor for nitrogen in high-density aspen stands. This finding was supported in the FORECAST model simulations of aspen and white spruce stands that were subject to fire or harvesting. The phenomenon of efficient N uptake attributed to aspen probably permits it to capture the flush of nitrogen available after fire (the assart flush) during the species early years of development (Peterson and Peterson 1992).

Simulations with FORECAST confirmed that disturbance frequency was important to the stand outcomes of succession over 240 years. With longer intervals between disturbances (120 years compared to 60 years), greater amounts of standing biomass were produced and in harvested scenarios, greater amounts were deposited on the forest floor as a nitrogen pool than in fire scenarios. These findings were similar to the conclusions of Wang et al. (1995).

In the simulations with the FORECAST model and datasets representing Saskatchewan boreal forests, regardless of the disturbance interval, simulated replacement fires did not result in the same levels of stemwood biomass as simulated harvesting. The removal of nitrogen as part of FORECAST 's nitrogen budget calculations during simulated fires as well as the representation of nitrogen inputs in the form of nitrogen fixation and nitrogen in precipitation may account for these differing conclusions.
The conclusions that scientists reach about forest sustainability in boreal forests may depend upon the methods that have been used to test their hypotheses concerning sustainability, and their choice of temporal and spatial scales. Jurgensen et al. (1996) used mass balance calculations at a single point in time to determine the effect of N fixation from litter and logs on Idaho and Montana forests. The authors found that it took approximately 150-250 years to replace nitrogen lost as a result of harvesting.

In the mixedwood stand development simulated with FORECAST over 240 years, fire appeared to favour the eventual dominance of aspen, whereas harvesting disturbance weighted the relationship of aspen and white spruce toward the perpetuation of white spruce dominance. Of the disturbance types that were simulated, harvesting in low-density stands where within-stand competition was reduced provided greater coarse woody debris on the forest floor than fire disturbances. It also produced greater standing white spruce biomass than fire disturbances. This outcome suggests that there may be some benefit in simulating light disturbance in Saskatchewan’s dense aspen-white spruce stands.

The hypothesis advanced by Man and Lieffers (1999), that aspen presence improved the total productivity of white spruce stands, depends on the rotation length, disturbance type and disturbance severity. Simulations with FORECAST showed that high-density aspen stands with harvesting produced the greatest overall biomass. This may have been because simulated interim disturbance of high-density aspen left large amounts of aspen debris on the forest floor that produced a greater nitrogen pool than that accumulated during replacement fire scenarios.
Chapter 10
Sustainable Forest Management in Canadian Boreal Forests

Saskatchewan Forest Resource Management regulations (1999) state that company management plans must describe the predicted future structure and composition of mixedwood forests in a license area. To explore the implications of this mandate in my thesis, three approaches were used: 1) identification in a conceptual model of white spruce outcomes from succession, 2) accumulation of greater knowledge about current boreal forest structures and processes that could provide a reasonable base for making predictions about future boreal forest stand types and 3) simulation of succession outcomes with FORECAST.

Forest managers operating in the Boreal Plain forests have been concerned about the combined effects of natural disturbance and harvesting practices at various temporal and spatial scales on future forest successional pathways. In keeping with this view, the goals of this thesis were:

A. to test for differences in stand types through the collection of field information on stand structural attributes and stand processes and,
B. to engage in computer simulations of potential future white spruce-aspen stand types based upon the current stand structure and process information.

My thesis characterized representative mature white spruce stands using a conceptual model as a framework and examined some aspects of the role of litter and coarse woody debris in the nitrogen economy of these stands. The role of aspen was investigated as a potential beneficial element in the nitrogen economy of Saskatchewan boreal forests because
numerous field studies had suggested the positive influence of this species (Peterson and Peterson 1992).

Computer simulations were used to examine the differences and similarities between stand types. Modeling took place using the hybrid model FORECAST with the following boreal forest stand types: wS(tA)–low-density aspen-white spruce stands and tA/wS–high-density aspen-white spruce stands. The simulations were not designed, however, to resemble the characteristics of my field stand types but to have the same species composition with greater or lesser aspen densities. The computer model provided some insight into the effects of harvesting over 240 years on stand biomass compared to the effects of disturbance due to fire.

10.1 Summary of Thesis Findings

The conceptual model (Figure 2) proposed that, based on current empirical data (Lieffers et al. 1996), white spruce stands with high-density aspen occupancy might be different in terms of nitrogen economy than white spruce stands with low-density aspen. Once the theoretical combinations of white spruce stand types had been established, fieldwork verified that such stands existed. Structural characteristics were measured in selected stand types that resembled the stand types presented in the conceptual model.

To determine indices of microbial activity associated with aspen in mature white spruce stands compared to stands without aspen, a subset of the stands shown in Figure 2 became sites for process studies. The results from my studies showed that white spruce stands with different structural attributes (particularly with and without aspen) had different litter, log and mineral soil potential available nitrogen, microbial respiration and
nitrogenase activity rates (Chapter 8). Field investigations documented lower coarse
woody debris in the wS/tA type than the bF/wS white spruce type (Chapter 7). Harvesting
options or natural disturbance events were simulated with the model FORECAST over a
240-year period.

10.2 Conclusions

The conclusions of my thesis research are that:

1) The four mature white spruce stand types characterized in this thesis are
distinct entities (Chapter 7, Chapter 8). Based on differences in stand structure
and stand processes, white spruce stand types are better described by a multi-
pathway conceptual model of succession than by a linear model of succession.
Down woody debris volumes in these stands vary among stand types but age, a
common characteristic used to separate seral stages in linear succession, was
not statistically significant among several of the stand types that I studied
(Chapter 7). Different disturbance frequencies and types changed the species
densities in white spruce-aspen computer simulations over 240 years (Chapter
9). The fact that disturbance influenced FORECAST outcomes is compatible
with multi-pathway succession principles.

2) Woody debris levels appear to be important to the N economy of the aspen-
white spruce stands that have been investigated with FORECAST simulations
(Chapter 9). However, due to rapid decomposition, the gradual accumulation
of debris in field situations does not necessarily result in large inventories
except in the most decadent stands.
3) Nitrogen fixation in litter and woody debris may be greater in the study area than previously thought, given the relatively high nitrogenase activity that was found in litter and logs during one season of measurement (Chapter 8). However, nitrogen fixation as presented in FORECAST simulations over 240 years does not increase stemwood biomass production nor substantially change nitrogen uptake. Seasonal measurements of available nitrogen and estimates of microbial biomass changes during the summer might be helpful in understanding nitrogen transformation rates and potential effects on stemwood growth in white spruce-aspen stands.

4) The hypothesis represented in the conceptual model, i.e., that increased aspen occupancy increases total potential benefits for white spruce, is generally supported for the white spruce-aspen stands based on both field measures and computer simulations. Nitrogenase activity tended to be higher in wS/tA stands (Chapter 8) and FORECAST simulations with high-density aspen produced more total deadwood nitrogen and greater nitrogen uptake than low-density aspen stands (Chapter 9). In comparisons of simulations that featured wind events with scenarios without wind events, the scenarios with wind events had greater nitrogen uptake and greater biomass production (Chapter 9).

10.3 Forest Sustainability, Future Research Needs and the Mid-Boreal Upland Ecoregion

In my study, there was very little difference in potential mineralizable nitrogen rates among the four different stand types (Chapter 8); the approach involved anaerobic laboratory studies that are considered to represent microbial biomass nitrogen levels (Myrold 1987). A
field seasonal study that would measure microbial biomass, nitrogen availability (NH₄⁺) and nitrate (NO₃), within four or more white spruce stand types could determine if a decline in available nitrogen existed in stands with balsam fir compared to stands with white spruce and aspen. Nitrogen-related measures should be conducted during the summer combined with measures of substrate temperature and moisture content.

The role of green alder as a source of symbiotic nitrogen fixation should also be explored in these white spruce stands. Recent work in Alaska has found that sites with alder under balsam poplar had higher overall nitrogen levels than white spruce stands, and the differences were attributed to symbiotic nitrogen fixation by alder (R. Ruess personal communication 2000).

To establish whether logs on harvested sites truly have a nutrient benefit, an adaptive management research design could be implemented that would include different slash level treatments monitored over 30 years. N¹⁵ tracers could be used to determine when increases in nitrogen uptake occur and establish whether uptake rates are different between aspen and white spruce. Again, temperature may be factor limiting regeneration success and could be monitored concurrently.

A significant limitation to our understanding of Saskatchewan boreal mixedwoods is lack of spatially explicit information, particularly process information, and the lack of a landscape level perspective of succession. A combined landscape and spatially explicit stand model could simulate existing forest mosaics at landscape scales over long temporal periods in Boreal Plain forests. Attempts are currently underway at UBC’s Faculty of Forestry, Vancouver, BC to link stand and landscape models (J. P. Kimmins personal communication, 1999, B. Seely personal communication 1999).
10.4 Scientific Questions Related to Saskatchewan's Boreal Ecoregions

Perhaps as important as the definition of "old growth" in Saskatchewan's Mid-Boreal Upland Ecoregion, is how scientists and forest managers will identify the stands that are most likely to become "old growth", and the rate at which this phenomenon is likely to develop. A clearer understanding of white spruce-aspen stand growth dynamics, including the recognition of decadence characteristics and a better knowledge of the natural rates of change in all major successional pathways, would improve the identification of candidate potential future "old growth" stands. It would also be helpful in the design of management interventions in younger stands conducted to accelerate their transition to "old growth" stand conditions.

Research questions about the regeneration processes associated with small natural disturbances in mature boreal forests in Saskatchewan have not received much attention. Late seral stands usually have a low incidence of regeneration (Lieffers et al. 1996). This condition may be due to a combination of factors such as lack of an appropriate seedbed, poor seed dispersal or competition for light or nutrients (Chapter 2). Yet aspen and white spruce seedlings do grow in mature spruce stands (wS/tA, wS(tA)).

It is possible that the northeastern portions of Saskatchewan (the Churchill River Plain) will be harvested in the near future. The Churchill Plain is part of the larger Boreal Shield Ecozone that encompasses about 20% of Canada's landmass. To date, little or no research has occurred with respect to the development of white spruce stands in this Ecozone. However, foresters have noted visual differences in the Churchill Plain stands from those located elsewhere in Saskatchewan (T. Ryan, personal communication 1999). As a result, it may not be possible to apply findings from the Mid-Boreal Upland
Ecoregion to the Churchill Plain, yet predicting the future sustainability of stands in the Churchill Plain Ecoregion may be even more crucial than in the Mid-Boreal Ecoregion because of the more northerly climate.

The studies reported here indicate that mixtures of aspen and white spruce growing together could result in increased stand biomass production. Further ecological research and the use of appropriate computer models is necessary in northcentral and northern Saskatchewan in order to fully understand the future development of a range of younger, mature and older successional types on mesic, xeric and hygric sites. The approach used here to characterize forest ecosystems subject to frequent fire (a conceptual framework, descriptions of structure and process, and use of a hybrid model to test for future forest sustainability) could be applied to other ecosystem types.


Sulistiyowati, H. 1998. Structure of mixedwood boreal forest along chronosequences after
fire or clearcutting in southern Saskatchewan. MSc Thesis. Dept. of Crop Science
and Plant Ecol. Univ. of Sask., Saskatoon, SK. 161 pp.

Swan, J. M. A. 1966. The phytosociology of upland vegetation at Candle Lake,


Thompson, L. S. and J. Kuijt. 1976. Montane and subalpine plants of the Sweetgrass Hills,

Thorpe, J. 1996. Fire history and it's application to management of Saskatchewan forests.


disturbances in the southern boreal forest of Saskatchewan. MSc. Thesis. University
Sask., Saskatoon, SK. 130 pp.


Timoney, K. P., and A. L. Robinson. 1996. Old growth spruce and balsam popular forests
of the Peace River Lowlands, Wood Buffalo National Park, Canada: Development,


Appendix 1.

Table 22. Research designs for sensitivity to nitrogenase activity from different substrates in high-density aspen stands. Stand replacement fires at 120 and 240 years. Aspen partially harvested to 4,100, 2,100, 900, 840 and 700 stems/ha. White spruce partially harvested to 480, 350, 200 and 111 stems/ha respectively.

Conversion Factors

<table>
<thead>
<tr>
<th></th>
<th>Logs</th>
<th>.1</th>
<th>.3</th>
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<td>2.0</td>
<td>3.0</td>
<td>4.5</td>
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</table>

Table 23. High-density aspen with white spruce stand simulations. Changes in total net biomass production, litterfall, nitrogen uptake and nitrogen fixed/time step over 240 years due to different nitrogenase conversion rates. Response to nitrogenase activity conversion rates with litter only.

<table>
<thead>
<tr>
<th>N Conversion Rate</th>
<th>Species</th>
<th>Total Net Biomass Production (t/ha)</th>
<th>Total Litterfall (t/ha)</th>
<th>Total Nitrogen Uptake (kg/ha)</th>
<th>Total Nitrogen Fixed (kg/ha)</th>
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<tr>
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<td>3072</td>
<td>2227</td>
<td>7864</td>
<td>705</td>
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</table>
Table 24. High-density aspen with white spruce stand simulations. Changes in total net biomass production, litterfall, nitrogen uptake and nitrogen fixed/time step over 240 years due to different nitrogenase conversion rates. Response to nitrogenase activity conversion rates with logs only.

<table>
<thead>
<tr>
<th>N Conversion Rate</th>
<th>Species</th>
<th>Total Net Biomass Production (t/ha)</th>
<th>Total Litterfall (t/ha)</th>
<th>Total Nitrogen Uptake (kg/ha)</th>
<th>Total Nitrogen Fixed (kg/ha)</th>
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Table 25. High-density aspen with white spruce stand simulations. Changes in total net biomass production, litterfall, nitrogen uptake and nitrogen fixed/time step over 240 years due to different nitrogenase conversion rates. Response to nitrogenase activity in high-density aspen stands with litter and logs.

<table>
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<th>N Conversion Rates</th>
<th>Species</th>
<th>Total Net Biomass Production (t/ha)</th>
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<th>Total Nitrogen Uptake (kg/ha)</th>
<th>Total Nitrogen Fixed (kg/ha)</th>
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### Appendix 2.


<table>
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<th>Data type</th>
<th>Units</th>
<th>Calibrated</th>
<th>Source</th>
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<tr>
<td>Tree age associated with individual tree biomass max.</td>
<td>Year</td>
<td>Yes</td>
<td>Hope this thesis, Halliwell et al. 1997</td>
</tr>
<tr>
<td>Stand age at canopy closure, large root biomass, medium root biomass,</td>
<td>Mg/ha</td>
<td>Yes for</td>
<td>Peterson and Peterson 1992</td>
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<tr>
<td>small root biomass, proportion of independent mortality (no units)</td>
<td></td>
<td>medium Roots only</td>
<td></td>
</tr>
<tr>
<td>Average top height, top height of shortest live tree, average height</td>
<td>Meters</td>
<td>Yes</td>
<td>Peterson and Peterson 1992; Wang et al. 1995</td>
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<tr>
<td>of canopy bottom</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Photosynthetic light saturation</td>
<td>% max.</td>
<td>Yes</td>
<td>Modified after Barber et al. 1987, Taiz and Zeiger 1991</td>
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<tr>
<td>Curve defining shading as % maximum foliage biomass</td>
<td>% max. shading</td>
<td>Yes</td>
<td>Estimated</td>
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<td>Nutrient concentration in foliage</td>
<td>%</td>
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<td>Pastor and Bockheim 1984</td>
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<tr>
<td>Potential declines in aspen vigor over sprouting events</td>
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<td>Not</td>
<td>B. Seely personal communication, 1999</td>
</tr>
<tr>
<td>Root mortality and light reaching the forest floor</td>
<td>% max. shading</td>
<td>Not</td>
<td>B. Seely personal communication, 1999</td>
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<tr>
<td>Litter and log mass loss (Saskatchewan)</td>
<td>g/cm(^3)</td>
<td>Not</td>
<td>Hope this thesis, Laiho and Prescott 1999, and Alban and Pastor 1993</td>
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<tr>
<td>Litter decomposition – additional references</td>
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<td>Prescott 1995, Trofymow et al. 1995, Prescott et al. ND</td>
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<tr>
<td>N fixation information for logs and litter</td>
<td>kg/ha/yr</td>
<td>Not</td>
<td>Empirical data, and Hope this thesis</td>
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# Appendix 3.

Table 27. FORECAST simulations. Low-density aspen in simulated aspen-white spruce stands. No interim harvesting or wind disturbance. Replacement fires at 120 and 240 years. Mild fires at 35, 55, 68, 80, 105 and 115 years.

<table>
<thead>
<tr>
<th>Substrate Type</th>
<th>Species</th>
<th>Total Net Biomass Production (t/ha)</th>
<th>Total Litterfall (t/ha)</th>
<th>Total Nitrogen Uptake (kg/ha)</th>
<th>Total Nitrogen Content in Litterfall (kg/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No fixation</td>
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<td>4068</td>
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<td>Spruce</td>
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<td>819</td>
<td>4771</td>
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<tr>
<td>Log fixation</td>
<td>Aspen</td>
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<td>4071</td>
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<td>Spruce</td>
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</tbody>
</table>

Table 28. FORECAST simulations. Low-density aspen and white spruce stands. Stand replacement fires at 120 and 240 years. Wind events at 35, 68 80, 105 and 115 years in aspen. Wind events at 55, 68, 80 and 115 years in spruce. Materials placed on forest floor.

<table>
<thead>
<tr>
<th>Substrate Type</th>
<th>Species</th>
<th>Total Net Biomass Production (t/ha)</th>
<th>Total Litterfall (t/ha)</th>
<th>Total Nitrogen Uptake (kg/ha)</th>
<th>Total Nitrogen Content in Litterfall (kg/ha)</th>
</tr>
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<tr>
<td>No fixation</td>
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<td>5983</td>
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<td>1386</td>
<td>840</td>
<td>4753</td>
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</tr>
<tr>
<td>Log fixation</td>
<td>Aspen</td>
<td>2424</td>
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<tr>
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<td>Spruce</td>
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