CARBON AND NITROGEN DYNAMICS ASSOCIATED WITH POST-WILDFIRE STAND DEVELOPMENT OF BOREAL MIXED CONIFER ECOSYSTEMS: APPLICATION OF DATA IN MODEL VALIDATION AND REFINEMENT

Michael K Hoepting

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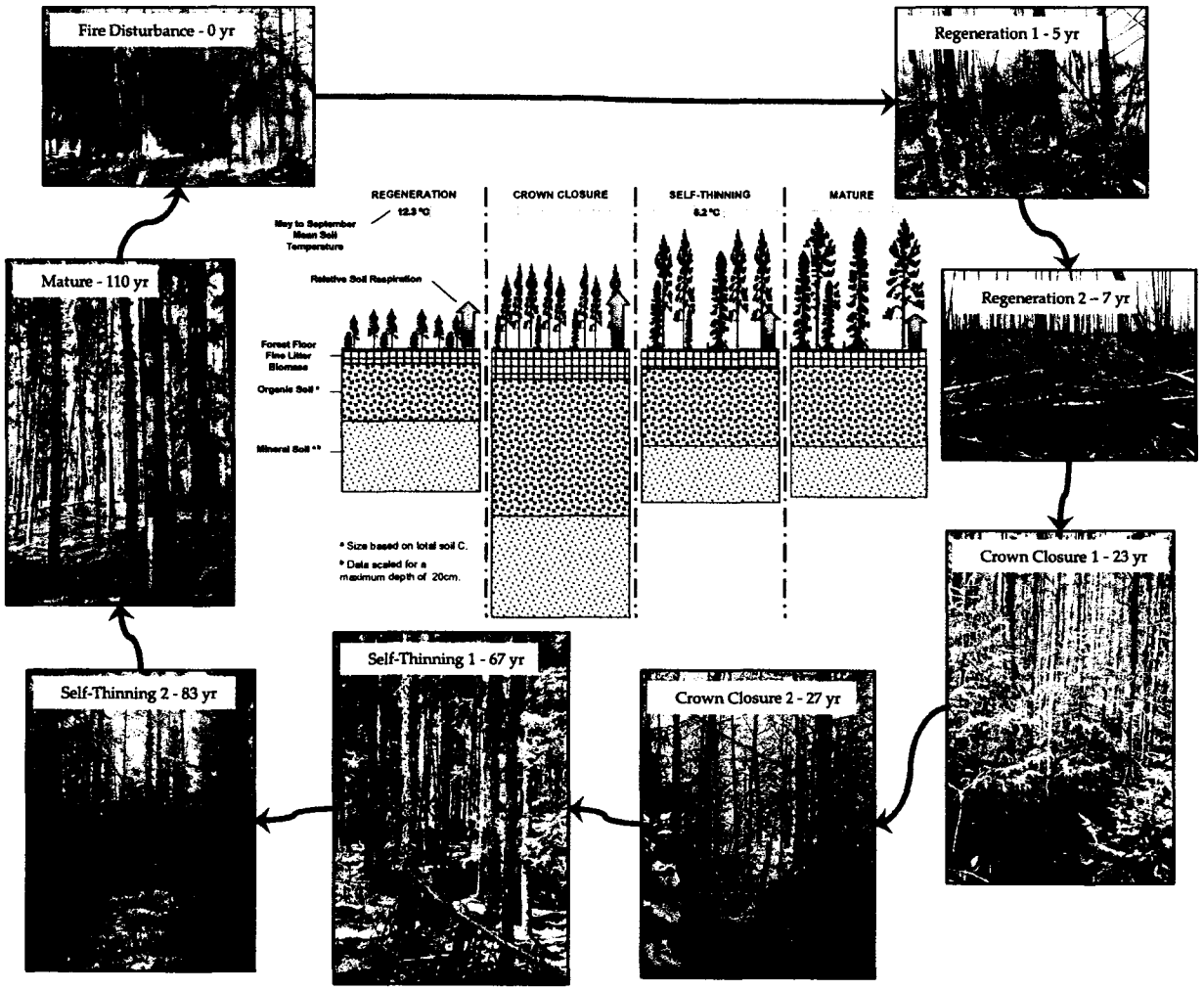

MICHAEL K. HOEPTING

Masters of Science in Forestry Thesis
Faculty of Forestry and the Forest Environment
Lakehead University
Thunder Bay, Ontario
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A CAUTION TO THE READER

This M.Sc.F. thesis has been through a semi-formal process of review and comment by at least two faculty members. It is made available for loan by the Faculty of Forestry and the Forest Environment for the purpose of advancing the practice of professional and scientific forestry.

The reader should be aware that opinions and conclusions expressed in this document are those of the student and do not necessarily reflect the opinions of either the thesis supervisor, the faculty or Lakehead University

ABSTRACT

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Key Words: carbon dynamics, nitrogen dynamics, laboratory incubations, validation, CENTURY model, boreal forest, mixed conifer

To make accurate and meaningful predictions about boreal forest ecosystem development, a strong understanding of the processes that drive change within the ecosystems in required. Once this knowledge is gained, it can be incorporated into process-based ecosystem models that can be valuable tools for both making management decisions and also guiding further research. In northwestern Ontario, various calibration and testing exercises for the CENTURY Soil Organic Matter model have been performed. However, it was identified that a validation exercise was required in order to properly evaluate the ability of the model to simulate C and N dynamics through stand development. In response to this need, this project involved the set up of a 110 year old upland mixed conifer chronosequence of fire origin from which C and N dynamics were measured (i.e. C and N pool levels and fluxes). By dividing the chronosequence into four stand development stages (regeneration, crown closure, self-thinning, and mature), it was found that pool levels were often not significantly different between stand development stages; however, N mineralization and soil respiration rates were linked to soil temperature, and substrate quality seems to decrease with time since fire disturbance.

The validation exercise employed eight different tests to evaluate the ability of the CENTURY model to simulate thirteen C and N pools, fluxes, and soil temperature calculations. The exercise was much less successful than expected. In most cases the pool levels were different and in other cases, the over time trends were very different. For example, simulated N mineralization rates increase gradually through stand development whereas real-world measured rates decreased into immobilization. It was found that growing season soil temperatures (May to September) calculated by the model were too high and thought that lowering these temperatures would result in some of the simulated pools and fluxes being more similar to the real-world data. Validation of the new lower soil temperatures was very successful; however, this success did not translate into better validation results for the other parameters. Further work with CENTURY is required before it can be relied upon to accurately simulate C and N dynamics through stand development; however, this type of work is valuable in itself because it generates new information and furthers out understanding of these forest ecosystems.

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ACKNOWLEDGEMENTS

First and foremost I would like to acknowledge the sources of funding and in-kind contributions generously provided for this project. The majority of the financial support came from the Living Legacy Trust Fund. The Centre for Northern Forest Ecosystem Research (Ontario Ministry of Natural Resources) and the Lakehead University Forest Soils Laboratory (Lakehead University) made substantial in-kind contributions through equipment and staff availability.

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[1] Co-advisor: Assistant Professor – Faculty of Forestry and the Forest Environment, Lakehead University
[2] Co-advisor: Research Scientist – Centre for Northern Forest Ecosystem Research; Adjunct Professor – Faculty of Forestry and the Forest Environment, Lakehead University
[3] Committee: Associate Professor – Faculty of Forestry and the Forest Environment, Lakehead University

1.0 INTRODUCTION

Worldwide, forests are important to people. Forested landscapes improve air and water quality, mitigate climate, provide habitat for countless species, afford humans with construction, communication (i.e. paper) and fuel materials, and are a source of food and medicinal supplies. In Canada, the forest industry is a major contributor to the economy. In 2002 alone, the forest industry contributed $29.9 billion (3%) to Canada's gross domestic product and directly employed over 360 thousand people (Canadian Forest Service 2003). Forest related tourism is also worth several billions of dollars (Canadian Forest Service 2002). Although difficult to estimate, it is certain that forests are also high in intrinsic value to the Canadian public and worldwide.

Canadian forests are under mounting pressures. One of the most obvious and negatively associated pressures comes from industrial forestry activities; particularly clear-cutting. The demand for wood is increasing worldwide and as one of the largest producers of wood products in the world, Canada's forest resources are subject to this pressure. Fortunately, forest management practices have evolved substantially in the last couple of decades, forest managers are equipped with the best available tools (e.g. GIS and models), and the management process is more publicly accountable than ever before. At the same time, public awareness of forest issues is increasing and the voices of various stakeholder groups, including preservationists, are getting louder. Other pressures that lie outside of human control are also at work. Forest fires, insect damage, and diseases affect approximately 1.6% of Canadian forests annually (Canadian Forest

Service 2002). There are also growing concerns about the potential impacts of a changing climate on Canada's forests (Canadian Forest Service 2003).

Considering the value of the resource and the number of pressures on Canadian forests, sound management is of paramount importance. Forest managers and policy makers require access to tools that assist them in making complex decisions. Models that incorporate the best available knowledge of ecosystem processes can be very helpful when attempting to predict and compare possible future forest conditions resulting from management decisions. Process-based simulation models that are built around known empirical relationships particularly show promise in this area (Kimmins 1997a).

Process-based models can also be used to complement field-based forest research activities for investigating biogeochemical cycles, and to direct the focus of research efforts. These models can be used to investigate the consequences of forest harvesting and silviculture operations, natural disturbance occurrences (*e.g.* wildfire or insect outbreaks), and/or climate change and elevated atmospheric CO_2 conditions. Building or calibrating models can provide the framework for planning of research projects that not only assist with model development but also enrich the existing scientific knowledge base.

The downside of process-based models is that they are often quite complex and their use and development require a substantial understanding of natural forest processes as well as the impacts of forest harvesting for both the developers and users. Models also require enormous amounts of data for both calibration and validation making their portability between sites somewhat more limited. These characteristics have thus far limited the use of process-based models primarily to the scientific community.

Here in Ontario, ongoing development of process-based simulation models has been strongly supported under three key science priorities by the Living Legacy Trust Fund. These science priorities included: Priority 2) Effects of Intensive Forest Management on the Environment, Priority 4) Tools and Techniques for Forest Productivity Forecasting, and Priority 12) Understanding Ecosystems. This project had two main objectives: 1) to advance our overall understanding of the dynamics (carbon and nitrogen) that occur through succession within fire-origin upland mixed conifer (jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) B. S. P.)) forest ecosystems in northwestern Ontario, and 2) to validate and further refine the CENTURY Soil Organic Matter model (Parton *et al.* 1987,1988) so as to gain greater confidence in the ability of the CENTURY model to adequately simulate the carbon and nitrogen dynamics of this ecosystem type. The CENTURY model – a process-based model – was originally developed for use in agroecosystems but has since been modified to simulate forests (Sanford *et al.* 1991; Metherell *et al.* 1993). The model tracks the flows of carbon and nutrients through various soil and aboveground pools and is recognized for the strength of its soil compartment.

For this project, a chronosequence of fire-origin upland mixed conifer sites was established to provide local estimates of biomass, and *in situ* soil carbon and nitrogen dynamics through four stages of stand development (regeneration, crown closure, self-thinning, and mature or "steady state" condition). Long-term laboratory incubations, using soils from the chronosequence sites, were also completed to investigate carbon and nitrogen dynamics under two different temperature regimes, and to be able to differentiate between site-level and substrate quality effects on pool sizes and fluxes. Even though similar data exists in the literature, it is not derived from chronosequences

spanning a complete rotation, or it is not from local sites. Therefore, it was important to collect local data in order to complete a meaningful validation. The locally derived chronosequence data was compared against simulated data obtained from modelling completed using an existing, locally calibrated version of the CENTURY model (version 5.3.2.3) as a validation exercise (statistical and qualitative). Following this exercise, refinements were made to the model to improve soil temperature calculations; a subsequent validation process was then undertaken. The process of validation, model adjustment, and subsequent validation lead to the development of suggested refinements to the calibration of the model that may improve confidence in future simulations with the CENTURY model.

This project received generous financial and in-kind contributions from the Living Legacy Trust, Ontario Ministry of Natural Resources, and Lakehead University,

2.0 LITERATURE REVIEW

In Canada, the majority of industrial forestry activities take place within the boreal forest region. The boreal forest stretches from the tip of Newfoundland across Canada to the border of the Yukon and into Alaska. It is characterized by major stand replacing disturbances that have resulted in a mosaic of predominantly even-aged stands consisting mainly of white spruce (*Picea glauca* [Moench] Voss), black spruce, balsam fir (*Abies balsamea* [L.] Mill.), jack pine, white birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) (Canadian Forest Service 2002). Wildfire has historically been the dominant disturbance regime with wind, insect, and disease damage impacting the forest to a lesser extent. In the 20th century, forest harvesting activities, particularly clearcut harvesting, has become a new dominant type of stand replacing disturbance. Of Canada's total commercial forest, approximately 0.4% is harvested annually (Canadian Forest Service 2002).

Our ability to address the challenges posed by these external and internal factors rests on the development of a better understanding of forest processes. To study the impacts of silvicultural procedures, including forest harvesting, we first need to be confident in our knowledge of the processes that take place and govern forest development under *natural* conditions. In the boreal forest, this generally means being able to predict (with some degree of certainty) how forest composition will change over time (i.e. successional development) and how forest ecosystems respond to disturbance events. Long-term site productivity is a particularly important concern and no longer

only refers to merchantable timber yields. All ecosystem processes, particularly soil processes including carbon (C) and nutrient dynamics, must be maintained for site productivity to be preserved. Sound knowledge of natural processes (e.g. disturbance processes) can be used as a benchmark against which the impacts of operational management decisions can be referenced. Tools required to describe and make predictions for complex ecosystems extend beyond traditional mensurational models and data. The use of computerized simulation models is gaining in popularity as well as necessity for managing the increasing complexity of our understanding of interactions within ecosystems.

2.1 STAND DEVELOPMENT PATTERNS AND PROCESSES IN BOREAL MIXED CONIFER STANDS

2.1.1 Species Compositional Changes and Growth Patterns

In Ontario's boreal forest, black spruce and jack pine are two of the most common and commercially important tree species. Black spruce is the backbone of the pulp and paper industry (Lamhamedi and Bernier 1994) and is also used extensively for dimension lumber. Jack pine is also very commonly used as fibre for pulp and paper and is an important source of roundwood for sawmills (Rudolph and Laidly 1990). Black spruce commonly occurs in pure and mixed stands, and tolerates a wide range of site conditions by occupying both upland and lowland sites (Viereck and Johnston 1990). This characteristic explains why black spruce is a dominant component in 10 of 28 forested ecosites and an overstory associate in 11 other ecosites (Racey *et al.* 1996; Morris 1997). Jack pine is limited to upland sites and is one of the most well adapted tree species to dry, coarse sandy sites (Rudolph and Laidly 1990). Jack pine is a

dominant component in 9 of 28 forested ecosites and an overstory associate in 6 other ecosites (Racey *et al.* 1996).

Black spruce is considered to be a pioneer species that readily establishes on sites disturbed by fire given an adequate seed source. Following fire disturbances, the semi-serotinous cones open and accelerate seed release; depending on fire intensity the open cones may release seed for up to three years (Viereck and Johnston 1990). Regeneration success of black spruce seed is primarily influenced by available seedbed. The optimal seedbed for black spruce is heavily burned microsites where the surface organic layer has burned off and mineral soil is exposed (Viereck and Johnston 1990; Lamhamedi and Bernier 1994; Miyanishi and Bajtala 1999).

Jack is also a pinoneer species and under natural conditions primarily regenerates following wildfire disturbances. Most trees have serotinous cones that are suitable for providing a large seed release following fire. Like black spruce, jack pine germinates most successfully on exposed mineral soil and the seedling survival similarly depends on microsites with exposed mineral soil (Rudolph and Laidly 1990). On upland sites, black spruce germinants are more prone to moisture stress than are jack pine (Lamhamedi and Bernier 1994).

In most cases, the future forest species composition is determined by the species that establish on the site within approximately the first five years following major disturbances, however the slower growth rates of some trees may lead to the assumption that these trees are younger (Gutsell and Johnson 1999). Black spruce is commonly an associate of jack pine on drier upland sites and may form a second stratum under the faster growing jack pine. Recruitment of both species may occur at the same time, but for the first 25-30 years the jack pine typically grows much faster than the black spruce.

Provided the site does not burn, is not harvested, or otherwise disturbed, the black spruce stratum will enter the canopy at around 80 years (depending on growth rates) and eventually dominate as the jack pine falls out of the canopy (Viereck and Johnston 1990; Rudolph and Laidly 1990; Gutsell and Johnson 1999).

Growth of young seedlings is often inhibited by competing trees or other shrub and herbaceous species. Because black spruce is shade tolerant, it will usually surpass shrub and herbaceous competition given time; although, under heavy competition, mortality may be high (Viereck and Johnston 1990; Lamhamedi and Bernier 1994). In addition to reducing the quality and quantity of light that reaches the seedlings, competition also influences water and nutrient availability, gas exchange, and soil and air temperature (Lamhamedi and Bernier 1994). Jack pine is very shade intolerant so it must outgrow competing species in order to survive. In comparison to other native conifer species within its range, and during the first twenty years, only tamarack (*Larix* spp.) grows faster (Rudolph and Laidly 1990).

As the canopy closes in mixed conifer stands of jack pine and black spruce, conditions on the forest floor change. Before canopy closure, more light reaches the ground causing warmer conditions that promote faster decomposition and nutrient cycling and allowing the growth of shrubs and herbaceous species that are shade intolerant. Given sufficient stocking, eventually crown closure occurs and the amount of light reaching the forest floor is dramatically reduced (Taylor and Adams 1995). Because of the cooler and moister ground conditions, community composition changes and an almost continuous mat of feathermosses (*Hylocomium splendens* (Hedw.) BSG., *Pleurozium schreberi* (Brid.) Mitt., *and Ptilium crista-castrensis* (Hedw.) De Not.) often develops (Taylor and Adams 1995; Lamhamedi and Bernier 1994). Mosses tend to

effectively retain nutrients (particularly phosphorus) and as a result compete with the trees for these resources (Lamhamedi and Bernier 1994). Duckert and Morris (2001) reported that on a 100-year old upland black spruce/jack pine site, 32% of total live biomass nitrogen (N) and 33% of total live biomass phosphorus was contained in the moss layer.

The productivity of black spruce (i.e. height and diameter) is mostly related to climatic conditions but at local scales, growth is influenced by soil moisture and nutrient availability with moisture regime being the most influential factor (Viereck and Johnston 1990). Mature black spruce stands often reach heights of 12 m on poor sites and 20 m on good sites with an average diameter at breast height (DBH) of about 13 cm on poor sties and 23 cm on good sites (Viereck and Johnston 1990). Mature jack pine commonly reaches heights of 17 to 20 m and DBH of 20 to 25 cm (Rudolph and Laidly 1990). Local northwestern Ontario measurements of a 110-year old black spruce stand on an upland sandy site include a mean dominant height of 19.6 m and mean DBH of 14.8 cm (Morrison *et al.* 1993), and at another local black spruce/jack pine 100-year old site a mean height of 15.1 m and mean DBH of 14.2 cm (Edgington and Morris 2001).

2.1.2 Fire Effects on Soil Carbon and Nitrogen Dynamics

Forest fires have the potential to drastically alter the physical and chemical properties of the forest floor and soil. Fire consumes a portion, or in extreme cases all, of the forest floor litter and humus resulting in a reduction in organic C, nutrients, and the insulating effect of this layer. During very hot fires, enough heat may penetrate down to the mineral soil to destroy organic matter. Further soil C may be lost by fire burning down into dead roots (Kimmins 2004). As a result, a substantial portion of the

nutrient capital on a site may be lost during a forest fire. However, under more moderate wildfire conditions, organic matter may actually increase through the addition of forest necromass. A nutrient pulse, that would be beneficial to colonizing vegetation, is often detected following fire as a result of increased litter inputs and improved conditions for decomposition (e.g. warmer soils and higher pH from ash deposition may stimulate microbial activity) (González-Pérez *et al.* 2004, Kimmins 2004). Increased decomposition and mineralization following fire, along with reduced vegetation demand for N can raise ammonium (NH_4) concentrations. Corresponding with surplus NH_4 conditions, may be increased N volatilization and nitrification rates, particularly if soil conditions are warmer and drier (Killham 1994; Waring and Schlesinger 1985). The greater mobility of nitrate (NO_3) (water soluble) can be beneficial since the NO_3 could be pulled towards the remaining live and new plant roots and help to satisfy vegetation N demands. However, NO_3 may also be lost from the site through leaching if there is insufficient uptake by vegetation (Killham 1994; Paul and Clark 1989). Carbon inputs to the forest floor increase substantially following fire as killed vegetation falls. Fine litters may be readily decomposable but a large portion of these inputs are coarse woody debris that are more resistant to decay because of their high C:N ratios. The longevity of the effects of fire on a forest site will vary with severity of the burn.

Curves have been developed to represent the biomass and soil C pools from 0 to 200 years for the five different forest disturbance types (wildfire, insect mortality, clear-cut and slash burn, clear-cut, and partial cut) simulated by the Carbon Budget Model for the Canadian Forest Sector (CBM-CFS) Kurz *et al.*(1992). Figure 2.1 shows the example curves for wildfire disturbances at a site class 3 softwood stand in the Eastern Boreal ecoclimatic province. While the quantity of C may not be the same, conceivably

the curves displayed should show the pattern of soil C dynamics that would be present in an average upland black spruce-dominated stand in northwestern Ontario. The CBM-CFS divides soil C into three pools; fast, medium, and slow. The fast pool accepts detritus less than 10 cm in diameter and has a half-life of 2 to 30 years. The medium pool accepts detritus greater than 10 cm in diameter and has a half-life of 20 to 100 years. The slow pool consists of humified organic matter and has a half-life of over 100 years (Kurz *et al.* 1992).

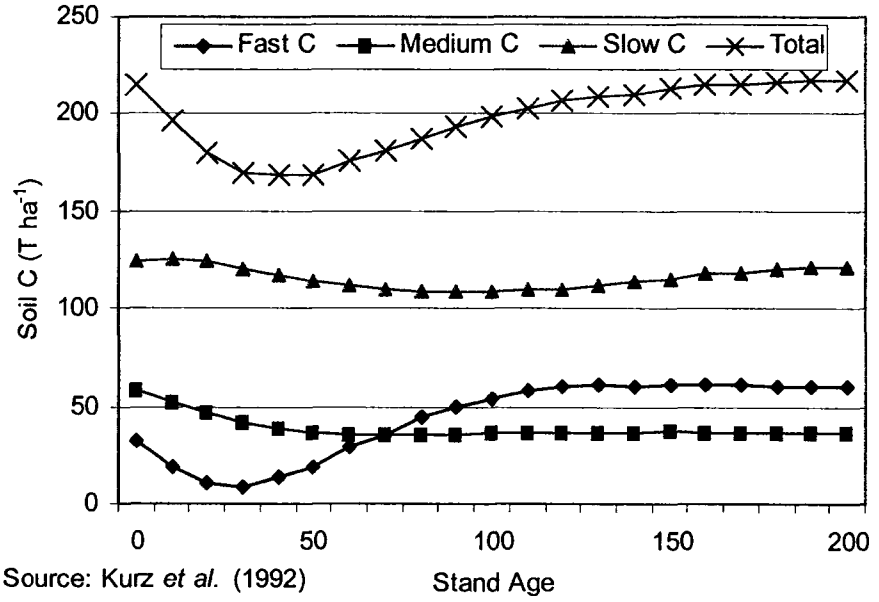

Figure 2.1 Soil carbon curves simulated by the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS) for a softwood, site class 3 forest disturbed by wildfire in the Eastern Boreal ecoclimatic province (Kurz *et al.* 1992).

The fast pool, which would consist of mainly surface residues, would be the most depleted by stand replacing wildfire disturbances and would continue to diminish for approximately 25 years because of conditions more favorable to decomposition. Around 100 years, the fast C pool should have re-stabilized at the maximum level due to

increases in litter inputs (mainly foliage) and decreasing decomposition rates. Unlike the fast C pool, the medium C pool is immediately larger following fire due to the addition of coarse woody debris. This pool slowly diminishes until stabilizing around 75 years of age. The slow C pool has a slight initial increase following fire but decreases for approximately 100 years before slowly rising. Except for the slow C pool, all pools, including the biomass C, stabilize around 100 years of age indicating that inputs are equal to transfers out of the pools (Kurz *et al.* 1992). Because soil N is linked to C, curves representing N dynamics following wildfire disturbances in the boreal forest should be similar to the C curves presented by Kurz *et al.* (1992).

Wang *et al.* (2003) assembled a chronosequence of well-drained and poorly-drained black spruce sites at the northern end of the BOREAS study area in Manitoba. The seven stands burned between 1998 and 1850. Carbon distribution was quantified for the stands and comparisons were made between the dry and wet sites. The following data is from the seven dry chronosequence sites and was sometimes estimated from figures in the paper. Live tree C increased from 1.5 T ha^{-1} at age 3 to 80 T ha^{-1} at age 151. Forest floor C started high at age three (35.4 T ha^{-1}) and dropped sharply to 4.6 T ha^{-1} at age 37 before rising gradually and stabilizing around 27 T ha^{-1} at age 71. This pattern is similar to the classic trend presented by Covington (1981), theoretical curves in Barnes *et al.* (1998), the fast soil C pool in the previous example by Kurz *et al.* (1992), observations from an "excessively drained" 72 year jack pine wildfire chronosequence in Michigan (Rothstein *et al.* 2004), and observations from a 95 year Siberian Scots pine (*Pinus sylvestris* ssp. sibirica Lebed) wildfire chronosequence in Siberia (Wirth *et al.* 2002) (Figure 2.2). One year following fire, in upland jack pine and black spruce stands in Quebec, Brais *et al.* (2000) also found reductions in forest

floor C. Concentrations were depleted by 11 and 26% in light/moderate and severe burn classes, respectively, which corresponded with dry weight losses of 41 and 60%. Smith *et al.* (2000) reported that in upland black spruce stands in Quebec, recent burns (6, 8, and 11 yr) had lower amounts of C in the organic horizon compared to old burn sites (75, 76, and 85 yr) (35 versus 50 T ha^{-1}), although the differences were not statistically significant. In other upland black spruce stands in Quebec (2, 14, and 21 yr), Simard *et al.* (2001) found that while forest floor thickness was significantly different than control stands for the three regenerating stands, only the 2-year-old site had significantly lower forest floor C (40 versus 100 T ha^{-1}) although the pools were in the other stands were lower than the corresponding controls (50 versus 70 T ha^{-1}, and 70 versus 80 T ha^{-1}). Dry weight measures of litter (L layer only) from a 12 stand jack pine chronosequence (13 to 57 years) in New Brunswick by MacLean and Wein (1977) also revealed a trend of decreasing litter mass following wildfire disturbance. This trend reversed around age 37 when litter mass started to increase again. Carbon contents of the litter were not measured.

A large flux of C in the mineral soil is not expected following a wildfire disturbance since the majority of C consumed is lost from the forest floor. Depth of burn is typically limited by oxygen supply and moisture; however, smoldering ground fires can sometimes penetrate to deeper layers and slowly consume moist organic matter and roots (Kimmins 2004). Mineral soil C may also decrease slowly over a number of years as the decomposition of root litter outpaces the addition of new root litter. Rothstein *et al.* (2004) reported relatively stable total C content in the mineral soil of a Michigan jack pine chronosequence with total mineral soil C ranging between 41.9 and 54.6 T ha^{-1} for depths of up to 100 cm. However, for a Siberian Scots pine

chronosequence, Wirth *et al.* (2002) reported soil C contents between 9.3 and 25.2 T ha^{-1} (25 cm depth), noting a small spike around 15 years followed by losses for 20 years, and then increasing again with stand age. Wirth *et al.* (2002) suggested that the spike resulted from C moving down from the surface organic layers and eventually disappearing. Again, although not significant, Smith *et al.* (2000) did report lower levels of mineral soil C in recent burns than older burns (18 versus 30 T ha^{-1}).

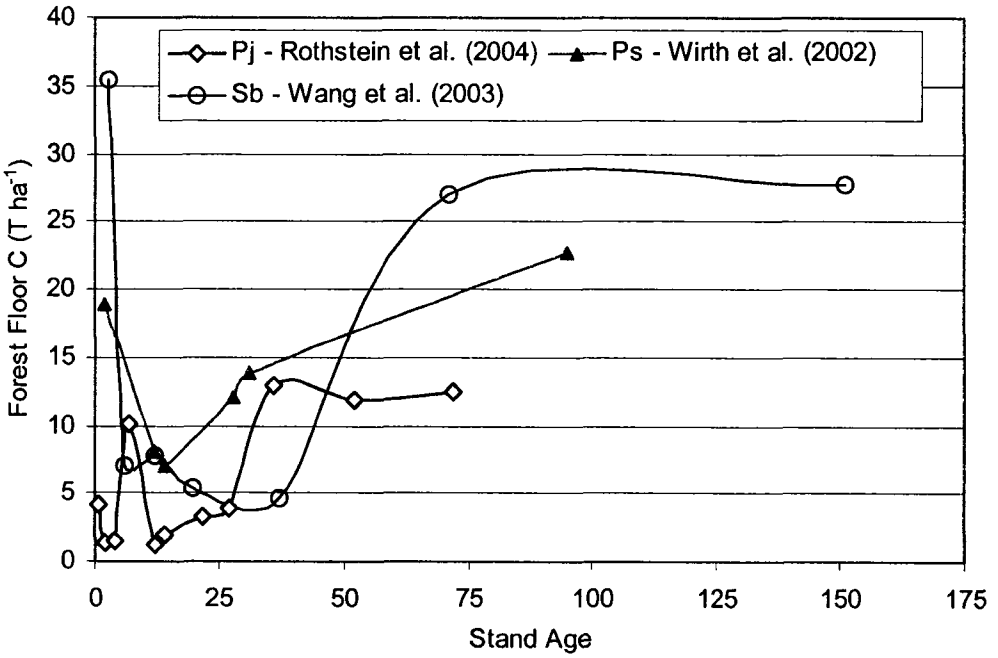

Figure 2.2 Trends from boreal forest chronosequences of forest floor carbon accumulation following stand-replacing wildfire disturbances.

Because N is intimately tied to organic C, decreasing amounts of total N are expected in the forest floor and organic horizons in the years following fire until the organic material again begins to accumulate. Wirth *et al.* (2002) found that total N in the organic layers followed a pattern similar to total C. Nitrogen in the organic layer started high and decreased for 14 years before increasing with age (382.5, 169.5, and

397.9 kg ha^{-1} at 2, 14, and 95 years, respectively). This trend was also reported by MacLean and Wein (1977) where N in the litter layer (L layer only) decreased from 184 to 63 kg ha^{-1} between 13 and 37 years after wildfire, and then rose up to 125 kg ha^{-1} by age 57; however, no trend was apparent for the F and H layers. Smith *et al.* (2000) found that organic horizon N was significantly lower at recent burns than old burns (907 versus 113.9 kg ha^{-1}). Brais *et al.* (2000) reported forest floor N content was only significantly reduced at the severely burned sites in their study (764 kg ha^{-1} in severely burned sites versus 1364 kg ha^{-1} in controls). Like forest floor C, Simard *et al.* (2001) reported that total forest floor N was only significantly lower than controls in a 2-year-old stand (1060 versus 2130 kg ha^{-1}), although N concentrations (mg g^{-1}) were significantly higher than controls in the 14, and 21-year-old.

As with mineral soil C, with the exception of extremely hot fires and when dead roots are consumed, little change in mineral soil total N reserves are expected. This is illustrated by MacLean and Wein (1977) not finding a relationship between total mineral soil N and time since fire. Mineral soil N measurements made by Brais *et al.* (2000) one year post-fire were not significantly different from the controls. Conversely, Wirth *et al.* (2002) found that total mineral N was variable throughout the Siberian Scots pine chronosequence, starting low at 399.3 kg ha^{-1} at 2 years and showing a gradual rise to 750.9 kg ha^{-1} at 95 years. Brais *et al.* (2000) reported mineral soil N contents at 69.6 kg ha^{-1} for recently burned stands and 1458 kg ha^{-1} for old burns but differences were not significant.

Despite minimal expected changes in total soil N, available N (NH_4 and NO_3) levels would be expected to be higher following fire because of potentially improved conditions for decomposition (e.g. temperature and pH) and a short-term rise in the

amount of readily decomposable materials. Smith *et al.* (2000) reported that average concentrations of available N ($NH_4 + NO_3$) over the summer months were higher in the recent burn for both the organic horizons and mineral soil, and higher in the organics than the mineral soils. Available N concentrations were 12.9 and 5.8 mg kg^{-1} for organic horizons in recent and old burns, respectively, and 1.1 and 0.7 mg kg^{-1} for mineral soil in recent and old burns, respectively. In a post-fire chronosequence of sub-boreal spruce stands dominated by hybrid white spruce (*Picea glauca x engelmannii*) in British Columbia, Driscoll *et al.* (1999) found that trends in available N (NH_4 and NO_3) were related to time since fire. In general, NH_4 concentrations were always higher in mid- and late-seral stages (50-80 years and >140 years respectively) than the early-seral (<14 years) stage for the organic (L + F + H), and mineral soil layers (A + B). However, NO_3 displayed the opposite trend by always decreasing with age. Despite the sometimes sizable differences between seral stages, there were not any significant differences for NH_4 and the only significant difference for NO_3 was that the concentration in the early and mid-seral stages was higher than the late-stage (42, 20, and 4.0 mg kg^{-1}, respectively). Brais *et al.* (1995) reported relatively stable concentrations of NH_4 detected by ion exchange resins in the organic horizons of a 231 year post-fire mixed-wood chronosequence in the southern part of the boreal forest in northwestern Quebec. Nitrate concentrations were initially high before dropping sharply and then rising gradually. It should be noted that the youngest site in the chronosequence had burned 27 years prior to measurements so the initial pulse of mineralization that may have occurred following fire would not have been detected by the study.

The pH of forest soils has been noted to be higher recently following wildfire disturbances than in mature, steady-state conditions (Brais *et al.* 2000; Simard *et al.*

2001). In the forest floor, Simard *et al.* (2001) reported that pH was significantly higher 2 and 14 years following fire (3.50 and 3.61) than in unburned stands. The pH of mineral soil was unaffected and ranged between 3.71 and 3.98. Brais *et al.* (1995) found a small but steady increase in acidity between 27 and 231 years following fire.

Following fire, the forest floor and soil conditions are often much more favorable for microbial activity and a boost in N mineralization often occurs. DeLuca *et al.* (2002) found that N mineralization was initially high but decreased with age in a Scots pine (*Pinus sylvestris* L.) chronosequence in Sweden (3-352 years). Nitrogen mineralization was determined by measuring NH_4 and NO_3 sorption to mixed bed ion exchange resins. Net ammonification decreased linearly with time since fire. Net nitrification decreased logarithmically. This is similar to Driscoll *et al.* (1999) who reported high levels of NO_3 at earlier stages of stand development. Total net N mineralization, measured as the NH_4 plus NO_3 adsorbed by the resins, declined linearly over time (Deluca *et al.* 2002). Therefore, NH_4 was produced in greater quantities than NO_3 and the ratio of NH_4 to NO_3 increased over time. Despite the lengthy chronosequence and the decreasing mineralization trends, net immobilization was never found. Smith *et al.* (2000) also used *in situ* resins to estimate N mineralization rates at recent and old black spruce burns in Quebec. Significant differences in N mineralization were only observed for NH_4 in the organic horizons with 3.7 kg ha^{-1} mineralized over the summer in the recent burn, and 13.3 kg ha^{-1} mineralized in the old burns. Net N mineralization ($NH_4 + NO_3$) was greater in the organic horizons (3.71 and 13.28 kg ha^{-1} for recent and old burns) than the mineral soil (1.55 and 3.55 kg ha^{-1} for recent and old burns), and more NH_4 was mineralized than NO_3. Small amounts of NO_3 were immobilized at the old burns in both the organic horizons (0.02 kg ha^{-1}) and mineral soil (0.12 kg ha^{-1}). Contradictory to

theory and other studies, Simard *et al.* (2001) did not find that net N mineralization was significantly different between burned and control stands for either the forest floor or mineral soil. Incomplete recovery of the microbial population following the fire disturbances was given as a possible explanation. Differences in nitrification between burned and control stands were also not significant; potentially because pH levels remained too low (pH remained below 4) for sizeable amounts of nitrification to occur. Ste-Marie and Paré (1999) reported that nitrification rates decreased with decreasing pH levels and that nitrification in conifer stands was low regardless of pH.

Fire also has the ability to directly reduce the microbial communities present in the organic layers and mineral soil. Even if only a little of the forest floor is burned, the heat may be enough to cause mortality. However, bacteria and fungal communities are able to recolonize very quickly and may even return at greater numbers than predisturbance levels because of higher pH, less microbial competition, a more prevalent food source, and better availability of nutrients. Soil fauna may take a few years to fully return to disturbed sites (Kimmins 2004). The quick response of the microbial community helps retain available N on the site as it is rapidly immobilized by the microbes. This boost in nutrition also fuels population growth which along with warmer soil temperatures and lower C:N ratios can increase decomposition rates on the site, thus triggering further nutrient turnover. Microbial biomass levels are likely to maintain these high activity levels until crown closure occurs. At this point, soil temperature decreases, moss cover increases, the quality of litter inputs decreases (i.e. more conifer needles that are more resistant to decay than herbaceous debris), and the competition for available N with vegetation will become aggressive. Despite less favorable conditions the microbial biomass may not decrease but actually continue to increase; however, it

may become less active (Dyrness *et al.* 1986) or the C:N ratios widen (Ohtonen *et al.* 1992). Vance and Chapin III (2001) reported that out of four different stand types in Alaska (birch north slope, birch south slope, aspen, black spruce), the black spruce stand had the largest microbial biomass carbon (MB-C) pool (670 kg ha^{-1}), but the lowest summer soil respiration, and net N (NH_4 and NO_3) immobilization (-0.06 μg g^{-1} d^{-1}). This site was approximately 70 years old and only the organic layers were sampled. Uchida *et al.* (1998) found that in an 80+ year old black spruce stand in Saskatchewan that despite having the largest MB-C pool (approximately 700 kg ha^{-1}), the FH layer had similar respiration rate by area (0.29 kg ha^{-1} hr^{-1}) and lower relative respiration (i.e. respired CO_2 per unit MB-C) than the other soil layers. The relative respiration rate for the FH layer was 0.44 mg CO_2 g^{-1} MB-C h^{-1} compared to 1.35, and 0.94 for the L and A horizons, respectively. The total amount of MB-C in this stand was 1670 kg ha^{-1} for a depth down to 50 cm which represented 2% of the total soil C. Total quantities of microbial biomass are related to the amount of soil organic C (Uchida *et al.* 1998; Pietikäinen *et al.* 1999).

2.1.3 Methods of Study

Scientific study of forests can be a daunting task. The longevity of forests makes investigating processes and impacts challenging since one rotation may easily be as long as a human lifetime. In agriculture, quantifying the effects of different treatments over the rotation, or even several rotations, of a crop is relatively simple. Such a study may only take a few years. A similar study on a northern forest would require centuries. There are essentially three ways to perform studies of long-term processes and effects on forests; 1) set up study sites with numerous re-measurements and track changes as they

occur; 2) study a chronosequence of sites to capture the treatment effects at different stages in time; and 3) simulate the treatment effects and their impacts through time in a modelling environment.

A long-term ecological research design typically utilize sites starting from a "time zero" state and has the advantage of tracking changes as they occur at each study location (Dyck and Cole 1994). Data can be complied to portray detailed trends through time of ecosystem processes and pools, and the data is suitable for repeated measures statistical analyses. The long-term approach can produce a very complete dataset; however, this approach requires substantial time and financial commitments that are not available to all researchers. Also, unless the replicate sites are used, which could substantially increase costs, the variability is not captured for the site type being studied.

The chronosequence approach relies on the base assumption that the only differentiating factor between sites is age or time (Dyck and Cole 1994). Basic site characteristics (e.g. climate, soils, disturbance history, etc...) are assumed to be the same. By connecting the dots, measurements made at an assemblage of sites of varying ages can be a surrogate for continuous trend data produced from a long-term study with the advantage that the data can be collected in a relatively much shorter amount of time. Therefore, long-term trend data should be available in a timelier manner and at a fraction of the cost. In reality though, the sites are never completely identical and as a result data may show more pronounced "noise" and trends may be more difficult to discern. However, because of this noise a chronosequence may actually be more representative of a particular site type because more of the natural range of variation of the site type is incorporated into the data.

Chronosequences may sometimes be hindered by not having enough sites to represent all portions of the chronosequence and by not having enough replicated sites upon which to apply rigorous statistical testing. However, if sufficient sites are available and spaced evenly, then after a single re-measurement overlap could be achieved and repeated measures made possible (Morris *pers comm.* 2006). For example, if a chronosequence was established of 20 sites that were each five years apart (e.g . 0, 5, 10, 15....95 years) and were then re-measured in five years time, a fully replicated (n = 2) chronosequence would exist that would allow greater statistical testing.

Modelling allows researchers to make comparisons between different treatment effects on a single site, often for an unlimited time span, without having to alter the real-world (RW) forest landscape. Ecosystem models use mathematical equations to emulate the "rates of transfer of material between ecosystem components" (Kimmins 1997b). When a simulation is run, the equations produce estimates of the future size of the components (or pools) within the ecosystem. Generally a model will not describe all processes within an ecosystem, just the ones that satisfy the objectives of the developers. To model all processes would require an enormous amount of scientific knowledge and computing power (Kimmins 1997b).

2.2 SIMULATION MODELLING

Kimmins (1988; 1990; 1997a; 1997b) classifies models into three categories: historical bioassay, process-based simulation, and hybrid models. Historical bioassay models are empirical models that were derived from statistical relationships that exist between data sets (Korzukhin *et al.* 1996). These models use past data to make predictions for the future under the assumption that the same conditions will be repeated.

For example, yield tables are based on measurements for a particular site type and are used to estimate the tree growth on the same site, by the same species, under the same conditions. The Sustainable Forest Management Model (Ontario Ministry of Natural Resources) is a computerized planning model that relies heavily on empirical yield tables. Historical bioassay models are often used to predict future wood supplies by foresters (Kimmins 1997b). The ability of this model type to accurately predict future yields is limited to those times similar to those under which the model was derived (Kimmins 1988; 1990).

Process-based simulation models are built using equations that are believed to describe the main ecological processes influencing forest growth and succession, changing environmental conditions, and disturbance regimes. By incorporating these variables, greater model flexibility is achieved and ecosystems can be modeled over time, and predictions can be made based on different scenarios. Because process-based models have greater flexibility and can be applied to wider ranging conditions, they also have the potential to address much more complicated situations and questions, such as those arising in forest management planning (Kimmins 1988, 1990, 1997a, 1997b; Korzukhin *et al.* 1996). Empirical relationships exist within process-based models (*e.g.* C allocation patterns and the effect of moisture on biomass production) but it is the combination of these equations that allow the greater flexibility of the predictions made by the process-based models (*e.g.* greater C allocation to roots when moisture is limiting) (Korzukhin *et al.* 1996). A disadvantage of process-based simulation models is that they are often very complex, expensive to produce and calibrate, and can be difficult to interpret (Kimmins 1988; 1990; 1997a; 1997b).

Ryan *et al.* (1996a) further categorizes process-based simulation models into physiological based models and ecosystem/tissue models. Physiologically based models are effective for analyzing the short-term reactions of plants to climate change and CO_2 enrichment. These models examine canopy level processes and interactions (e.g. effects of CO_2 on photosynthesis and water use efficiency). Ecosystem/tissue models are more suited to making long-term predictions since they consider water, C, and nutrient (especially N) flows between the soil and plants. Should a growth requirement, such as water or nutrients, become limiting, net production is consequently restricted. The CENTURY model (described in section 2.2.1) is considered a process-based simulation model in the ecosystem/tissue model category (Ryan *et al.* 1996a).

The third class of model described is the hybrid model that combines the empirical growth data of historical bioassay models with the environmental flexibility of the process-based simulation model. In many cases, in order to avoid the complexity typical of process-based models, hybrid models may exclude some of the ecological processes that are not considered essential to fulfill the objectives for the model and replace them with historical bioassay components. Unfortunately, this also reduces the flexibility of the model. The advantage of hybrids is that they, like process-based simulation models, are more adaptable than their historical bioassay counterparts, but they are still more complicated since they require much more input and calibration than the historical bioassay models (Kimmins 1988; 1990; 1997a; 1997b). Hybrids also rely on strong and often proven process-based models so the development of such models cannot be forgone. A recent example of a hybrid model is TRIPLEX (Peng *et al.* 2002a). TRIPLEX has merged components of three existing models; the forest production model from 3-PG (Landsberg and Waring 1997), the forest growth and yield

model from TREENYD3 (Bossel 1996) and the soil-carbon-nitrogen model from CENTURY 4.0 (Parton *et al* 1993).

Computer models can be very useful for providing insight into the conditions of an ecosystem far into the future, or when the actual experiments that would provide the same information are too difficult or simply impractical, as in the case of long-term forest productivity and climate change (Kimmins 2004; Ter-Mikaelian 1998). However, model output cannot, and should not, be considered to be an absolute representation of what the future will hold, even if the environmental conditions somehow occur as they have been set in the models. It should also be noted that the equations used within models are not assumed to completely describe the actual processes that they are mimicking. Instead, ecosystem models are to be used for the purpose of providing us with indications of what may happen to an ecosystem under different scenarios (Kimmins 2004; Korzukhin *et al.* 1996).

Computer models are built upon the best understanding of ecosystem processes at the time of development and may include relationships and data that were not derived specifically from the immediate intended region or site type, or even biome that the builders intended to use the model for. For example, the CENTURY model simulates forest soil C dynamics but the underlying relationships of the model were derived from grasslands data (Metherell *et al.* 1993). For this reason, it is important that once a model has been calibrated, a process called verification is carried out. Verification has two purposes, 1) to ensure that the relationships within the model are reflected accurately in the model output, and 2) to check that the model is properly calibrated. Verification ensures that the model performs as expected by comparing against data upon which the model was built (Kimmins 2004).

To further improve the precision of models, a process called validation has to be undertaken (Kimmins 2004). Validation tests a model against data that is known to be factual so as to measure the model's ability to make relatively accurate predictions. Although it is a good place to start, the data set that the model is compared against cannot be the same data set that the model was calibrated with. For true model validation, models should be tested against outside data sets with the exception of site specific calibration data (*e.g.* local climate variables and initial pool sizes) if required. In all cases, models should be constructed using the best available scientific knowledge, and be updated when new information becomes available.

2.2.1 Description of the CENTURY Soil Organic Matter Model

Numerous process-based models have been developed over the years, each with advantages and disadvantages. In most cases, models are developed with a specific objective or group of objectives in mind that will then limit the portability of the model. As a broad example, a model developed for lakes or oceans will generally have limited applicability to modelling forest dynamics. However, similar to using components of process-based models in hybrids, some models have been converted from one usage to another. The CENTURY model is one example of such a model.

The CENTURY model was originally developed as a tool for modelling the impacts on productivity and sustainability of various management regimes and climate scenarios on agroecosystems. Its usage has since been expanded from agroecosystems, to include forests and savannas (Sanford *et al.* 1991; Metherell *et al.* 1993). Sanford *et al.* (1991) derived the forest version of the CENTURY model to initially simulate hurricane effects on tropical forests in Puerto Rico. CENTURY is primarily intended to

be a "tool for ecosystem analysis, to test the consistency of data and to evaluate the effect of changes in management and climate have on ecosystems" (Hilinski 2002). Using the CENTURY model to ask research oriented questions and as a framework to carry-out research is well within the capabilities of the model. It is unlikely that the CENTURY model, in its current state, will be used in forest management. However, it is conceivable that individual components of the model (e.g. soil organic matter submodel) may be incorporated into other process-based or hybrid models that would be suitable (i.e. user friendly and widely applicable) for widespread use. Examples of such models that currently exist that have integrated CENTURY components are the process-based model CenW (Kirschbaum 1999), and the hybrid models InTEC (Chen *et al.* 2000) and the previously mentioned TRIPLEX model. All of these models are fairly recent and still in various stages of development. Further development of the CENTURY model, therefore, remains as a very relevant science priority.

In 2000, CENTURY version 5 was released. The core processes in version 5 are still the same as in previous versions with the exception of a new layered soil physical structure, and new erosion and deposition submodels. Perhaps the most important change with version 5 was to rewrite the programming code in C++ and the creation of a graphical user interface that substantially improves operability of the model. Some minor program bugs were also rectified. Calibration files from the previous version 4 can be utilized by CENTURY version 5 (Hilinski 2002).

The CENTURY model does not grow individual trees, nor does it grow stands or forests. Instead, the model tracks the flow of C, N, and optionally phosphorus (P) and sulfur (S) through various biomass and soil pools. When using CENTURY for forest simulations, the biomass include tree components only (large wood, fine branches,

leaves, coarse roots, and fine roots). The soil pools include surface and soil organic matter (SOM) pools that represent SOM at various stages of decay and different origins (Metherell *et al.* 1993; Hilinski 2002).

Biomass production (and therefore C production) in the CENTURY model is affected by temperature, growth potential of the tree species, soil moisture, leaf area index, and nutrient availability. Decomposition of organic materials is influenced by soil temperature and soil moisture, the maximum decomposition rates of individual SOM pools, and the C:N ratios of the SOM pools (Metherell *et al.* 1993; Hilinski 2002).

Refer to Appendix I for a more detailed description of the processes contained within the CENTURY model.

2.2.2 Applications of CENTURY in Modelling Forest Systems

Ryan *et al.* (1996a) reviewed seven different process-based simulation models, including the CENTURY model (version 4), in order to compare the abilities of the various models to produce growth estimates. The models were tested using two intensively studied, climatically different sites (Australia and Sweden), where four treatments had been imposed (control, fertilization, irrigation, irrigation plus fertilization). In general, the CENTURY model performed with the same accuracy as the other models; however, there were minor differences. The differences can be attributed to the varying configurations of each model, although, most model processes were used by one or more of the models (see Table 2.1).

Table 2.1 Model processes of seven process-based simulation models (Ryan *et al.* 1996a).

	Models						
Variable	BIOMASS	BIOME-BGC	CENTURY	MBL-GEM	HYBRID	PnET-CN	Q
Time step [a]	D	D/A	M	M/A	D/A	M	A
Transpiration [b]	PM	PM	PM	I	PM	WUE	---
Photosynthesis							
Model [c]	F	F/P	I	P	F	P	I
Scaling Method [d]	B	B/N	C	B/N	B/N	N	B/N
Respiration							
Model [e]	G/M	G/M	M	G/M	G/M	G/M	---
Scaling Method [f]	N	B	B	N	B	N	---
Allocation [g]	A/V	V	C	V	V	C	V
Turnover [h]	C	C	C	C	C	C	C
Leaf N [i]	I	V	V	V	I	V	V
Litter N j	---	P	P	P	---	P	C
Decomposition [k]	---	AET	LCI	LCI	---	R	M
N Mineralization [l]	---	P	P	C:N	---	C:N	P

[a] Time step: D = daily, M = monthly, A = annual.
[b] Transpiration: PM = Penman-Monteith, I = soil moisture as input, WUE = water use efficiency, --- = not simulated.
[c] Photosynthesis (model): F = Farquhar *et al.* (1980) biochemical model, P = phenonenological model, I = net primary production only.
[d] Photosynthesis (scaling method): B = biomass, N = foliar nitrogen, C = climate.
[e] Respiration (model): G = growth, M = maintenance respiration, --- = not simulated.
[f] Respiration (scaling method): B = biomass, N = tissue nitrogen, --- = not simulated.
[g] Allocation of carbon: A = allometric equations, V = variable percentage, C = constant percentage.
[h] Turnover of leaves: C = constant percentage.
[i] Leaf nitrogen: I = input, V = variable.
[j] Litter nitrogen: --- = not simulated, P = constant percentage of leaf nitrogen, C = constant.
[k] Decomposition: --- = not simulated, AET = actual evapotranspiration and lignin concentration, LCI = lignocellulose index, R = residence time for given stage, M = microbial growth rate.
[l] Nitrogen mineralization: --- = not simulated, P = proportional to decomposition, C:N = maintains constant carbon to nitrogen ratio.
Source: Ryan *et al.* (1996a)

Ryan *et al.* (1996b) then performed a second study where the same models were calibrated to run climate change scenarios. The three scenarios were 1) increased temperature (+4°C), 2) increased atmospheric CO_2 (700 ppm), and 3) increased temperature compounded with raised CO_2 levels. A 60-year simulation was run for the Australian site and 120-year simulation was run for the Swedish site, representing one rotation each, respectively. Unlike the previous study, Ryan *et al.* (1996b) found that

the output from the models varied greatly. In general, most models agreed that biomass production would increase if atmospheric concentrations of CO_2 and temperatures rise, but the models did not concur on the amount of the growth increase. The main conclusion that could be drawn from the study was that there is still a significant amount of research and model development to be done before accurate predictions can be made regarding the impacts of climate change on forests and that no one model can be favored (Ryan *et al.* 1996b).

Kelly *et al.* (1997) evaluated the ability of CENTURY to simulate soil organic matter (SOM) for seven sites across a variety of land use, climate, and treatment types. Comparisons were made against long-term datasets for each site. Only one of the sites was forested. Generally, Kelly *et al.* (1997) found that the CENTURY model performed well across the sites; although, extreme values were not captured, and the model did perform better with the grass and crop systems than with the forest system.

Kelly *et al.* (1997) documented an important constraint in the structure of CENTURY that limits the ability of the model to realistically simulate forest sites that have litter layers, in various stages of decay, overlying the mineral soil. The CENTURY model does not explicitly recognize this layer(s) and incorporates the materials into the belowground pools. Kelly *et al.* (1997) suggest that unrealistically high quantities of simulated SOM result. To counteract this, they reduced the decomposition rate of materials entering SOM pools by two-thirds in order to increase the build-up of organic debris on the forest floor and reduce the amount of SOM in belowground pools, and presented data for the surface litter plus SOM rather than just the SOM pools. Unfortunately, Kelly *et al.* (1997) did not present data from model runs prior to making these changes so that the effectiveness of these changes could not be evaluated.

In central Canada, CENTURY (version 4) simulations were tested by Peng *et al.* (1998) against observed soil organic matter data that had been collected along the boreal forest transect case study (BFTCS) (Price and Apps 1995) and also against two regional-scale empirical regression models (Schimel *et al.* 1994; Burk *et al.* 1989). Generally CENTURY correlated well with the BFTCS data ($R^2 = 0.92$) and better than either regression model; however, CENTURY did overestimate soil C by 2-8% for fine-textured soil and underestimated soil C by 5-18% for sandy soil. The mean estimate of N mineralization for all sites (3.28 g N m^{-2} yr^{-1}) was within the range estimated for each of the sites modelled. Despite results suggesting a need for further improvements in slow pool C dynamics, the basic structure of CENTURY is thought to be suitable for modelling boreal forest ecosystems. Peng *et al.* (1998) also recommended that further development of CENTURY to simulate a fluctuating fire cycle that would more realistically represent real-world conditions should be considered. Peng *et al.* (2002b) have since gone on to use CENTURY to investigate harvesting intensity and rotation length on the long-term C and N dynamics for these same BFTCS sites.

Price *et al.* (1999) used CENTURY (version 4) and the gap model, FORSKA2 (Prentice *et al.* 1993), to investigate climate change effects on boreal vegetation dynamics and C cycling at the same BFTCS sites as Peng *et al.* (1998). A second part of the exercise was to consider the potential of linking the two models together, thereby combining the strengths of each model (*i.e.* belowground processes of CENTURY; aboveground processes of FORSKA2) into one that would be suitable for simulating total ecosystem C dynamics at the landscape level. In comparison to the real-world BFTCS site, the relatively simple forest biomass production submodel of CENTURY overestimated biomass and also produced higher estimates than FORSKA2. An

explanation for the overestimation of biomass production by the CENTURY model given by Price *et al.* (1999) was that CENTURY does not implement any sort of regeneration delay (*e.g.* inadequate seed dispersal and seedling mortality) following stand replacing disturbances. Immediately following a disturbance, the live biomass that survived, starts growing again. FORSKA2 on the other hand, has a regeneration delay that may be unrealistically too slow and in some cases results in an underestimation of biomass production. Soil and litter C pools simulated by CENTURY were similar to real-world measurements along the transect, and the trend of C pools decreasing under warmer and drier conditions was achieved. Despite the overly simplistic biomass production model of CENTURY, the model was still able to adequately use litter provided from biomass to drive the belowground C cycling processes and predict realistic estimates of soil and litter C pools. Price *et al.* (1999) conclude that using FORSKA2 to generate aboveground biomass estimates and using the CENTURY model to generate soil and litter C estimates is a viable option for approximating "spatially-averaged ecosystem C densities". When the data was combined, in some cases the CENTURY estimates of soil and litter C were high in comparison to the data. Possible reasoning for this was that data higher in C than the target sites was used in the validation process so calibration may have been inaccurate. Both models may also not adequately simulate the disturbance effects of wildfire on forest soils. Using combined data from the model for climate change scenarios resulted in decreases in total ecosystem C at all but one of the sites. Under warmer conditions, slightly more biomass was simulated by FORSKA2 but the gains were mitigated by decreases in the soil C stocks as predicted by CENTURY. It was concluded that the greatest loss of total C

storage would occur at the northern most sites where warming conditions would likely be the greatest.

In northwestern Ontario, the CENTURY model has primarily been investigated through undergraduate thesis projects at Lakehead University, Thunder Bay. All theses used the model for a shallow, upland black spruce-dominated site in the region. Attwell (1998) worked on model calibration, Metsaranta (1999) investigated long-term forest productivity and N dynamics, Hoepting (2000) explored potential effects of climate change, and Klos (2001) focused on the effects of varying climate on respiration and net primary production.

A CNFER report by Edgington and Morris (2001) examined some of the CENTURY model calibration parameters for the local northwestern Ontario site, including initial soil C pool sizes, tree compartment death rates, allocation ratios for the tree compartments, gross and net maximum production rates, parameters controlling the impact of wild-fire disturbances, and also the duration of the scheduled equilibrium period. Calibration variables were altered with the objective being that, following an equilibrium period, pool levels be similar to the initial starting point values. Generally the large C pools (e.g. total system C, total mineral soil C) could be maintained near the initial levels but the individual components of these C pools were more variable (e.g. SOM active, slow and passive C pools). For example, after a 5000-year equilibrium period, the total C in the soil only increased by 2.3%, but the passive SOM pool (very slow turnover) increased by 54.0%. Mineral N in the soil pools increased by 20.4% with the largest build-up occurring in the slow and passive SOM pools. The build-up of N with the current calibration was unexplained by Edgington and Morris (2001) but they

suggested that further examination of decomposition, respiration and particularly N mineralization rates may help pinpoint the source of this problem.

Luckai and Larocque (2002) compared the abilities of the CENTURY model (version 4) and another process-based model, FOREST-BGC (Running and Coughlan 1988; Running and Gower 1991) to simulate the effects of climate change on the same northwestern Ontario site. Under control conditions, biomass C production for both models was similar and the relative predictions following 100 years of climate change were comparable. However, discrepancies did exist between the models in regards to the impact of rising temperatures and CO_2. Luckai and Larocque (2002) suggested that interaction effects of these two key physiological processes are not well represented within either model at the stand and soil level, and that caution should be taken when using model predictions that rely on these interactions. The greater complexity of the CENTURY soil model (five soil C pools versus one in FOREST-BGC) allowed CENTURY to more realistically simulate soil C totals from rotation to rotation. Luckai and Larocque (2002) advocate investing in model development, improvement and testing, so process-based models can be used with confidence to make forest management and policy decisions.

As can be seen from several of the works presented, the CENTURY model is a process-based model that is often chosen to investigate soil C dynamics and climate change impacts on forests. The most obvious reason for selecting the CENTURY model seems to be the detailed SOM submodel that simulates C and nutrient flows through soil compartments. One of the main criticisms of CENTURY is the rather simplistic forest production submodel; however, the litter inputs to the soil from the aboveground production still enable the soil and litter processes to be adequately simulated. Another

point that is worth noting are the efforts to use the SOM submodel of CENTURY as part of new models (e.g. CenW, InTEC, and TRIPLEX) or in tandem with another model that has greater aboveground strengths and is more spatially applicable (e.g. FORSKA2). Despite the relative success of CENTURY, the investigators do have criticisms and all suggest further work to improve the model. Soil C pools simulated by CENTURY have been shown to be sensitive to improper calibration (Price *et al.* 1999) and also to not respond accurately following fire disturbances (Peng *et al.* 1998; Price *et al.* 1999). Edgington and Morris (2001) had concerns over N build-up across all soil compartments, as well as C build-up in some of the soil compartments. From these observations, it is apparent that work with the CENTURY model should be focused on model calibration, verification, and validation for natural ecosystems. That is, before trying to use CENTURY to investigate new disturbances on forest ecosystems (e.g. harvesting or climate change scenarios), confidence in the ability of the model to replicate natural systems should first be developed.

2.2.2.1 Statistical Validation

One method of evaluating the abilities of models in general and the CENTURY model in particular that seems to be lacking in the literature is statistical validation. Statistical validation is a quantitative method of comparing model predictions to real-world data in order to credibly judge whether the former are reliable representations of reality. Several different parametric and non-parametric tests exist. A constant issue with using statistical validation is that the various tests do not always provide consistent results so it is often advised that more than one test be used (Mayer and Butler 1993; Yang *et al.* 2004).

Mayer and Butler (1993) and Yang *et al.* (2004) reviewed several common statistical tests for model validation. Parametric tests included the paired *t*-test, chi-square (χ^2) test, linear regression, simultaneous *F*-test, separate *t*-tests, novel test, and modelling efficiency. Two deviance measures – mean absolute error (MAE) and mean absolute percent error (MA%E) – were also presented by Mayer and Butler (1993). Each test provides some measure of how well the observed (i.e. real-world) and predicted (i.e. simulated) data compare. Mayer and Butler (1993) recommended the use of several tests to guide validation but also selected modelling efficiency as the best overall measure of agreement between the observed and predicted data. Yang *et al.* (2004) were generally dissatisfied with the inconsistencies between tests and suggested that the use of multiple tests could be a greater source of confusion than a benefit, and that statistical tests should not be used as the sole method of evaluating models. Despite the lack of consensus, statistical validation is an important component of model validation and helps reduce user bias in evaluating models.

2.2.3 CENTURY Model and Real-world Pool Relationships

Forest soils data is typically grouped by organic and mineral soil horizons. This is not surprising given the obvious differences between organic and mineral substrates. However, the pools that make up the CENTURY model soil compartments cannot be easily separated along these lines. After a cursory examination, it would seem that the pools labelled "surface" (i.e. surface structural, metabolic and microbe) would represent organic horizons, and the pools labelled "belowground" (i.e. belowground structural and metabolic) and "active SOM" pool that are only replenished by dead roots, would

represent organic portions of the mineral soil pool with relatively fast turnovers. The slow and passive SOM pools would also be considered part of the mineral soil pool. These assumptions within the model could be realistic for grassland, agricultural, and maybe even deciduous forest systems, but are not suitable for typical conifer-dominated boreal forest systems where a very prominent organic layer exists. In these other systems, it is reasonable to say that all of the roots occur in the mineral soil; however, in conifer-dominated boreal forests, often a significant proportion of roots exist within the surface organic layer and a large portion of the non-living soil organic C is stored there. The presence of highly decomposed and relatively stable organic material in the surface organic layer also indicates that significant components of the slow and passive SOM pools are contained there.

The lack of a distinct surface organic layer in the CENTURY model was an issue noted by Kelly *et al.* (1997). An adaptation was used that retained more materials on the surface, in the clittr(1,1) pool, and reduced the amount of materials that entered the active, slow and passive SOM pools. However, the problem with the Kelly *et al.* (1997) adaptation is that while more material does remain on the surface, it is in an unnatural undecomposed state. The presence of rooting and of active, slow and passive SOM pools in an organic layer was not dealt with.

The distribution of C and N between the CENTURY model soil pools makes calibrating and validating the model difficult. The distribution of measured total C and N to the respective calibration pools always requires estimation at some point. Very few direct measurements can be utilized without some form of transformation. Total C and N can be relatively easily measured for individual soil horizons, but dividing totals into active, slow, and passive pools requires more complex laboratory analyses (e.g.

microbial biomass and lignin concentration determinations). Model output pools also often have to be combined in order to represent real-world pools that are easily measurable (i.e. total soil C and N) for comparison of simulated and real-world data.

Because outputs for the CENTURY model pools usually do not match up well with commonly measured real-world pools, it is important for users of the model to know which combinations of CENTURY pools can be related back to the real-world measured pools, or combinations thereof. Fortunately, by grouping CENTURY model pools together, comparisons can be made between many of the soil C and N pools that can be measured for forest sites as seen in Table 2.2. These pools make up all horizons in a soil profile, although mineral soil pools are often only reported to a certain depth (e.g. 50 cm) in order to standardize reporting between sites. Some pools, like the fine and coarse dead roots, could be measured separately but in most cases it would be most practical to combine them into one pool as in Table 2.2. Broad categorizations into organic materials and mineral soils cannot be made with CENTURY model output. For this reason, most comparisons of simulated soils data must be made to total horizon measurements from actual forest sites. Surprisingly, the CENTURY model does not have a good output parameter for available N. The aminrl(1) variable is the best offered. This variable reports the available N before plant uptake, but only for the first soil layer so if more than one soil layer is used, the amount reported is too low.

Overall, the CENTURY Soil Organic Matter model is a fairly robust model that by including a large number of parameters makes it suitable for modelling various types of ecosystems worldwide. At the same time, the complexity of CENTURY (like most process-based models) makes it difficult to accurately calibrate and use efficiently. Also, the majority of relationships, equations, and parameters in the model have

originated from studies of C and nutrient dynamics in grassland and agroecosystems so caution should be exercised before accepting the default configuration of CENTURY when simulating forest ecosystems. However, the level of detail in the representation of soil C and nutrient dynamics is rarely surpassed with other process-based models so CENTURY is ideal for investigating these dynamics in boreal forest ecosystems.

Table 2.2 Measurable real-world forest floor and belowground C and N site parameters and the corresponding CENTURY model pools.

Pool Name	CENTURY Output Pools	Description of Equivalent Real-World Pool
Carbon Pools		
Total Forest Floor Fine Litter (TFFFLc)	CLITTR(1,1) [a] + WOOD1C	All fine (< 2 cm dia.) plant residues that constitute the 'L' layer.
Dead Roots (DRc)	CLITTR(2,1) [b] + WOOD3C	C in dead fine and coarse roots
Microbial Biomass and Microbial Products (MBPc x 2)	SOM1C(1) + SOM1C(2)	MB-C (organic + mineral) * 2 to 3 [c d]
Total Soil (TSc)	MBPc + SOM2C + SOM3C	Total Soil C (organic + mineral)
Total Forest Floor and Soil	TSc + TFFFLc + DRc	Total Soil C (organic + mineral) + Total Forest Floor Fine Litter + Dead Roots
Carbon Producing Pools		
Forest Floor Fine Litter and Soil	MT1C2(1) + MT2C2(1) + ST1C2(1) + ST2C2(1) + S11C2(1) + S21C2(1) + S2C2(1) + S3C2(1)	Total CO_2 Respiration from decomposition in the soil (organic + mineral) and Forest Floor Fine Litter
Total Forest Floor and Soil	RESP(1)	Total CO_2 Respiration from decomposition in the soil (organic + mineral) + Forest Floor Fine Litter + Dead Wood
Nitrogen Pools		
Total Forest Floor Fine Litter (TFFFLn)	METABE(1,1) + STRUCE(1,1) + WOOD1E(1)	All fine (< 2 cm dia.) plant residues that constitute the 'L' layer.
Dead Roots (DRn)	METABE(2,1) + STRUCE(2,1) + WOOD3E(1)	N in dead fine and coarse roots
Microbial Biomass and Microbial Products (MBPn x 2)	SOM1E(1,1) + SOM1E(2,1)	MB-N (organic + mineral) * 2 to 3 [d]
Available N	AMINRL(1)	Mineral N (NH_4 + NO_3) available for plant uptake (organic + mineral)
Total Soil (TSn)	MBPn + SOM2C + SOM3C	Total Soil N (organic + mineral)
Total Forest Floor and Soil	TSn + TFFFLn + DRn	Total Soil N (organic + mineral) + Total Forest Floor Fine Litter + Dead Roots
Nitrogen Mineralizing/Immobilizing Pools		
Total Soil	S1MNR(1,1) + S1MNR(2,1) + S2MNR(1) + S3MNR(1)	Total Soil N Mineralization (organic + mineral)
Total Forest Floor and Soil	Total Soil + METMNR(1,1) + STRMNR(1,1) + W1MNR(1) + METMNR(2,1) + STRMNR(2,1) + W3MNR(1)	Total Soil N Mineralization (organic + mineral) + Total Forest Floor Fine Litter + Dead Roots

[a] CLITTR(1,1) is equal to surface metabolic and structural C (METABC(1,1) + STRUCC(1,1)).
[b] CLITTR(2,1) is equal to belowground metabolic and structural C (METABC(2,1) + STRUCC(2,1)).
[c] "organic + mineral" indicates the sum of the measurements made for the organic (FH) and mineral soil layers excluding roots (fine roots, coarse roots) and root litter (dead fine roots and dead coarse roots).
[d] Source: Metherell *et al.* (1993)

2.3 SUMMARY

Mixed conifer stands, particularly those consisting of jack pine and black spruce, are an important source of wood fibre in northwestern Ontario. Under natural conditions these stand are often established following stand replacing wildfire disturbances. Both tree species usually regenerate at the same time; however, because of faster growth rates, the jack pine typically forms the main canopy. Eventually, as the jack pine breaks up, a shift towards black spruce occurs. In order to properly manage these stands, it is important to understand how the jack pine and black spruce develop through time and also how the soil C and N pools change in relation to stand development. A chronosequence approach to studying these changes is suitable when long-term studies are not feasible. Vegetation and soil C and N data does exist in the literature for jack pine and black spruce; however, the majority of this data is not locally derived and often from stands that have different characteristics than those in northwestern Ontario. For these reasons, this project has initiated the location and study of a fire-origin upland mixed conifer chronosequence in northwestern Ontario.

It is decreasingly acceptable to consider forest productivity only in terms of tree size and merchantable timber yields. As our understanding of forest ecology has increased, so too has the range of site characteristics that are looked upon as indicators of healthy forest ecosystems. In particular, soil C and nutrient (e.g. N) pools and fluxes are recognized as the basis upon which long-term sustainability must be measured. Our understanding of forest ecosystem dynamics is accompanied by a need for tools with which to organize and utilize this knowledge for ecosystem management. Process-based simulation models are one such tool that can be used.

Process-based simulation models have now existed for some time but having confidence in these models requires substantial calibration and validation efforts. Efforts to parameterize models for local site conditions also have the added benefit of directing forest research and expanding our knowledge base. The CENTURY model is one such process-based simulation model that has had widespread use and development.

While the CENTURY model does have some short comings and not all aspects of it may be entirely representative of upland mixed conifer forest ecosystems in northwestern Ontario, the CENTURY model is respected and has undergone valuable development locally. Therefore, further efforts will be made to validate the CENTURY model and evaluate its suitability for simulating our local sites.

3.0 MATERIALS AND METHODS

This research project was initiated with two broad objectives in mind. Specific research questions were then formulated. The two objectives and their associated research questions are as follows:

- Objective 1: To advance our understanding of C and N dynamics through stand development using a chronosequence of fire-origin upland mixed conifer sites.
    - Question 1.1: How does vegetation evolve through stand development (i.e. tree species composition, density, biomass, and ground vegetation)?
    - Question 1.2: Do environmental conditions change through stand development (e.g. soil temperature and soil moisture)?
    - Question 1.3: Do soil pools (C and N) change through stand development (i.e. totals, available N, microbial biomass C, and microbial biomass N)?
    - Question 1.4: Do soil pool fluxes change through stand development (i.e. N mineralization and soil respiration)?
    - Question 1.5: Are differences in soil pool and soil pool fluxes between stand development stages related to environmental factors (e.g. temperature) or differences in substrate quality?
- Objective 2: Evaluate how well the CENTURY model simulates local forest conditions by comparing model output with data derived from the chronosequence sites.
    - Question 2.1: Can the CENTURY model adequately simulate the changes in biomass and soil C and N pools that occur through stand development in local forest conditions?
    - Question 2.2: Does making improvements in the simulation of environmental factors (e.g. soil temperature) improve simulation of the other CENTURY model pools?

3.1 STUDY SITE LOCATION

The first task was to locate new study sites to enhance an existing chronosequence of ecosite (ES) 20, fire-origin stands. Three sites had already been located from other previous and ongoing research initiatives. These three sites were subject to stand replacing wildfire disturbances in 1996, 1936, and 1892 respectively. The 1892 site is the source of the current calibration data set for the CENTURY model. With the assistance of Duckert (CNFER – Ecosystem Impacts Forester) and historical Ontario forest fire data provided by the OMNR, several potential areas were selected for further investigation. Initial criteria for selection of these potential burn areas was limited to the year burned (to ensure representation of stand development stages), proximity to the existing chronosequence sites (mainly to ensure similar climate), and accessibility.

After potential burn areas were identified, field inspections were completed. Ideal site conditions consisted of shallow to moderately deep, coarse loamy upland soils either supporting a black spruce and/or jack pine overstory with feathermoss/tall shrub understory vegetation or having the potential for the vegetation to develop into a stand similar in composition and structure as found at the 1892 site. According to the Northwestern Ontario Terrestrial and Wetland Ecosite Classification System, these sites were classified as ES20 ecosites (Racey *et al.* 1996). Each site was also to have regenerated naturally, without anthropogenic intervention, following wildfire disturbance.

In total, 7 chronosequence sites were identified; 3 existing and 4 new. The new sites included 1998, 1980, 1976, and 1920 fire disturbances. The 1920 site was not indicated on the fire history maps but was considered to be suitable since the area had

not been logged in the past. Site location took place in the summer of 2002 and stand ages at this time were 4 (1998), 6 (1996), 22 (1980), 26 (1976), 66 (1936), 82 (1920) and 110 (1892) years old (Figure 3.1).

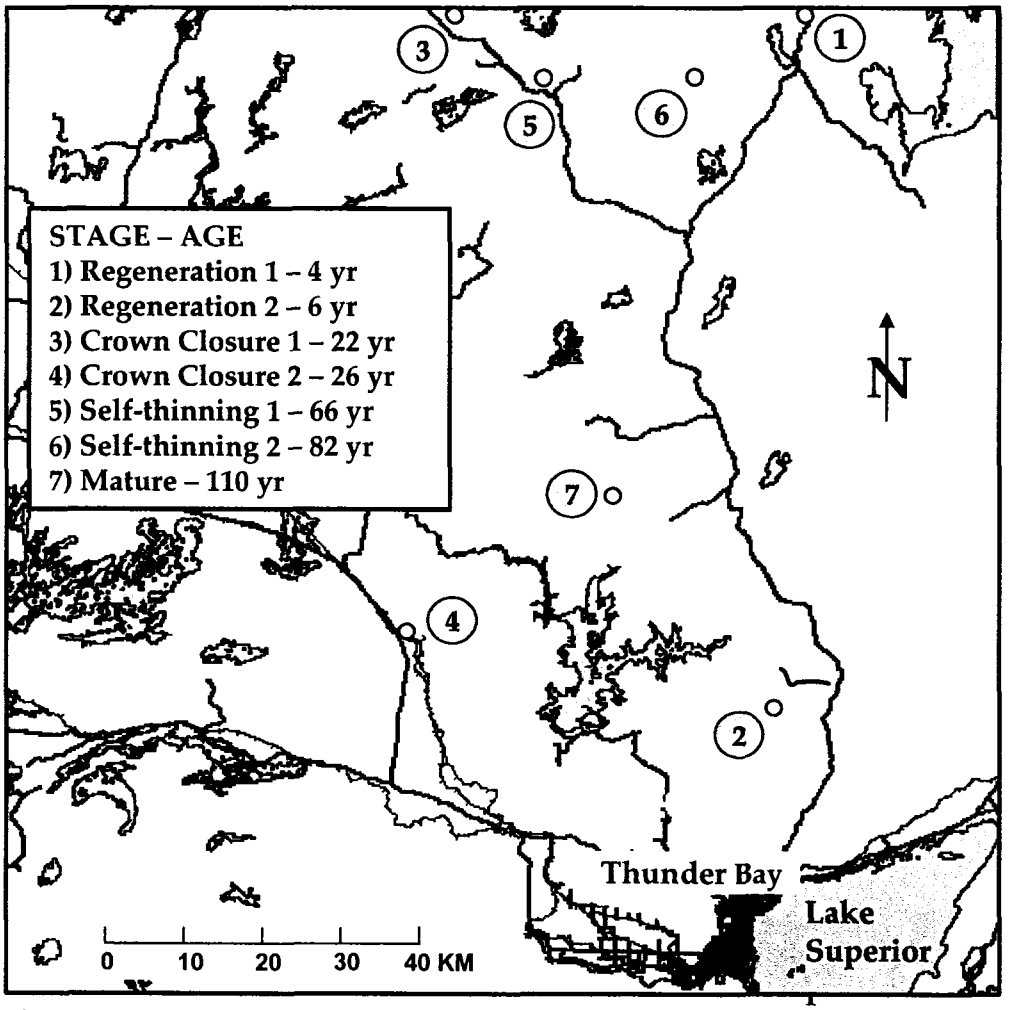

Figure 3.1 Locations of northwestern Ontario mixed conifer chronosequence study sites including the year of stand replacing wildfire disturbance and age in 2002.

The age of the sites allowed for reasonable pairings of six of the sites into three groups that were representative of different developmental stages of the chronosequence. The 4 and 6-year old sites represent the regeneration stage, recent crown closure and the onset of self-thinning is represented by the 22 and 26-year old sites, and the 66 and

82-year old sites are both undergoing self-thinning and converting from overstories dominated by jack pine to black spruce. The 110-year old site was a suitable benchmark site for a mature stand in a "steady state" condition. This site was not replicated in this study. From here on the sites will be referred to as Regen-1, Regen-2, CrwnCl-1, CrwnCl-2, SelfThin-1, SelfThin-2, and Mature, respectively.

Three plots were established at each site and located in areas that best represented the ES20 condition including appropriate soils – depth, texture, Bm layer – and vegetation. Soils had to be shallow to moderately deep, sandy to coarse-loamy in texture, and rapidly to well-drained. At the younger sites (Regen and CrwnCl), plot locations were biased towards areas where enough black spruce was present that it would eventually dominate the canopy. Only small amounts of hardwood tree species were tolerated. At the older sites (SelfThin and Mature), plots were located where there was either as much spruce as jack pine or black spruce was dominant. Plots were also located at sufficient distances from roadways and stand edges to minimize external influences. Plots were located in July and August of 2002. See Appendix II for colour photographs of each of the plots in the chronosequence.

The general plot areas were circular with a radius of 7.5 m (176.7 m^2) based on the size of tree inventory plots often used by CNFER (Duckert *pers. comm.*, July 2002). The majority of the subsequent data collection activities were carried out within the plot areas.

3.2 PROCEDURES FOR VEGETATION INVENTORIES AND QUAUNTIFICATION OF THE PHYSICAL AND CHEMICAL PROPERTIES OF THE SOIL AT CHRONOSEQUENCE SITES

3.2.1 Vegetation Inventory

In August and October of 2003, the tree species within each plot at each site were inventoried with the exception of the mature site. For the regeneration stage sites, only heights were tallied for the newly regenerated tree species within a 3 m radius (28.3 m^2) circular plot as per CNFER procedure. These plots used the centre point of the already established working plots. Diameter at breast height (DBH, 1.3 m) was tallied for live trees in the three plots at each of the remaining sites. Total height was also measured for at least three trees representing the range of DBH for each species at each site (intensive trees). At the crown closure stage sites, a 5 m plot radius (78.5 m^2) was used because of the high density of trees. At the self-thinning stage sites, 7.5 m radius plots were used for tree inventory. The various plot sizes were used in order to capture approximately 100 trees within each plot. CNFER has found that plot sizes that include approximately 100 trees adequately capture tree size variability particularly when sampling young dense stands (Duckert *pers. comm.*, 6 April 2004; Morris *pers. comm.*, 24 Nov 2004). Inventory data for the mature site was provided by CNFER from an inventory of four 50 m x 50 m (2500 m^2) plots located adjacent to the plots of the current study. This inventory was done in 1992 so the stand at that time was 100 years old (Duckert *pers. comm.*, 6 April 2004).

The following non-linear regression equation developed by Schumacher (1939) was used to estimate tree heights based on the measured DBH for each tree:

$$\text{Height (m)} = 1.3 + (C * \exp^{(-A / DBH)})$$

where C and A are regression based parameters derived from each site using the height and DBH from intensive trees measured at each site (see Appendix III). Intensive trees were those that had both the height and DBH measured; most had just DBH measured. For less frequently occurring species (*e.g.* trembling aspen, white birch, balsam fir) regional parameters were used that had been derived from measurements across all of the CNFER research sites (Duckert *pers. comm.* 26 Nov 2004). Tree heights were used to compute an average tree height for each site to be used as part of the site-level vegetation descriptions.

Dry weight of live biomass was calculated for stem wood, stem bark, live branches, foliage, cones, and roots using localized allometric equations of the form:

$$\text{Biomass} = B + C * DBH^{A}$$

where A, B, and C are regression based parameters derived from local biomass sampling. Parameters A and C were taken from Ter-Mikaelian (1997) when local data was not available (Duckert *pers. comm.* 26 Nov 2004). Once converted to carbon (assumed biomass is 50% C), the biomass pools – summed to above and belowground pools – from the chronosequence sites were compared to the equivalent CENTURY model live vegetation pools (i.e. aboveground, belowground, and total) to test the ability of CENTURY to adequately simulate biomass production. The N content of biomass was determined by applying locally derived component and tree species specific percentages provided by CNFER (Duckert *pers. comm.* 10 Dec 2004). See Appendix III for the allometric equation coefficients and nutrient percentages.

3.2.2 Air and Soil Temperature

Both air and soil temperature are vital drivers for many ecosystem processes in the real world and also in CENTURY model simulations. Temperature data was collected to address research question 1.2 and objective 2. At all sites, except the 1892 site, air and soil temperature was tracked between October 2002 and October 2003. One single channel HOBO® Pro Temperature Logger (Part # H8-030-08) was installed in one of the plots at each site to record air temperature. The units were attached to either trees or wooden stakes and situated 1 to 1.5 m above the ground. Two 4-channel HOBO® H8 Outdoor/Industrial temperature loggers were also installed at each site normally in the two plots farthest apart. Each unit had 4 separate probes (TMCx-HA wide range temperature sensors), each at the end of 6.1 m (20 ft) cables. The cables were laid out in pairs in opposite directions. On each side, a small hole was dug and one probe was pushed horizontally into the soil profile at the organic layer and mineral soil interface and one was inserted at a depth of approximately 10 cm into the mineral soil. The holes were then refilled carefully to minimize disturbance. Figure 3.2 shows the two types of temperature loggers on-site at the 1920 site, plot 1. Both the air and soil temperature recorders were scheduled to record temperature 4 times daily at 06:00, 12:00, 18:00 and 24:00. Data was downloaded to a laptop computer in May 2003, at least once during the summer and again in October 2003.

Bear inflicted damage was a concern so the soil temperature units attached to the stakes were covered by empty coffee cans and the cables on all units were covered with either fire hose or flexible plastic tubing. Even with these precautions, several HOBO units were tampered with by wildlife, some repeatedly. Units were found with the temperature probe cables disconnected from the datalogger units or the temperature

probes unearthed resulting in periods where valid data was not collected. Most HOBO damage occurred in the spring and early summer. Also, in several cases, some units stopped functioning for undetermined reasons. This most commonly occurred at various times between the initial installation (October 2002) and the first return visits in May of 2003. The malfunctioning may have been related to nearby lightening strikes (Whaley *pers. comm.* 2003).

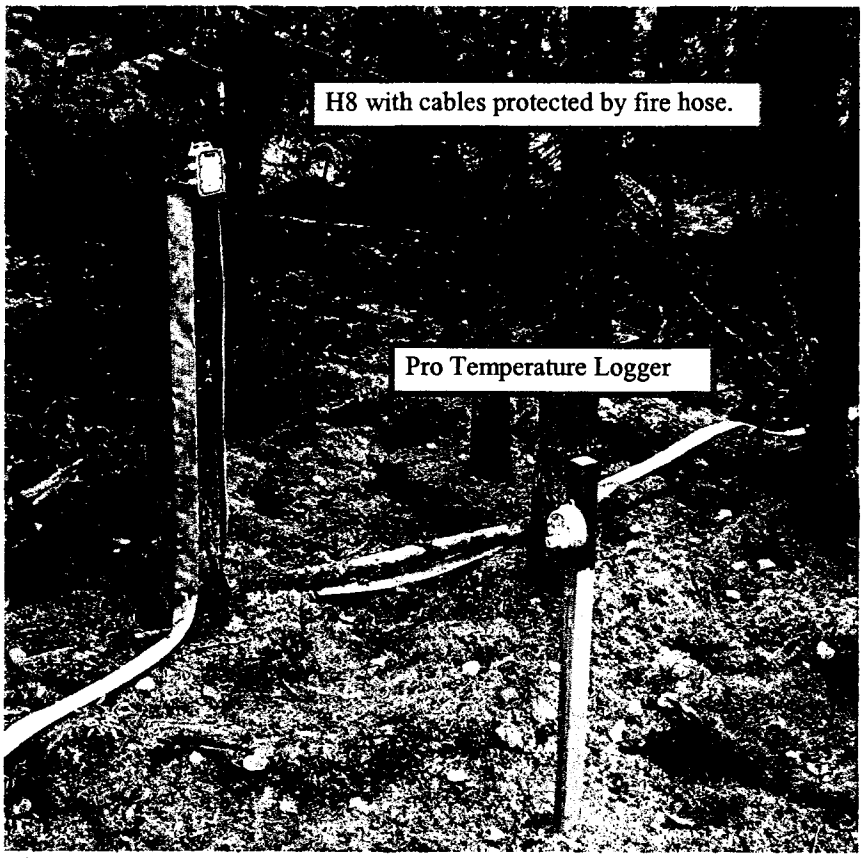

Figure 3.2 HOBO® Pro Temperature Logger (air temperature) and H8 Outdoor/Industrial External Logger (soil temperature) on-site setup at the SelfThin-2 site, plot 1.

Data from both soil temperature recorders at each site were combined and averaged to produce more complete datasets. Therefore, a maximum of 4 interface

temperature readings and 4 mineral soil temperature readings were averaged to produce one mean interface and one mineral soil temperature reading per measurement occasion for each site. To compare to the CENTURY model, the mean interface and mean mineral soil temperatures were then averaged to generate a single mean soil temperature. Monthly temperature values were generated by deriving the mean of all measurements made within each month provided temperature data was available for at least 25 days per month. Using cumulative heat sums for each site was considered but too many gaps existed in the soil temperature data to make meaningful site to site comparisons.

For the mature site, air and soil temperature data that had been collected from a location immediately adjacent to this study's plots was provided by CNFER. The data was collected between 1994 and 2002 for dates ranging between April and November of each year using a CR10 datalogger (Campbell Scientific Canada Corp., Edmonton, Alberta). Soil temperature probes were located in both closed canopy and open canopy positions at the organic and mineral soil interface. The open and closed canopy readings were averaged (Whaley *pers. comm.* 2004). Reporting of monthly temperatures was again limited to those months that had at least 25 days of data available.

3.2.3 Forest Floor Fine Litter Collections

Forest floor fine litter has relatively fast turnover and is an important contributor of nutrients to the soil. The litter quantity and quality strongly influence soil pools (research questions 1.3 to 1.5). One-time collections of surface fine litter were made at a representative location in each plot. All surface fine litter (less than 2 cm diameter) was collected from a 0.25 m^2 (0.5 m X 0.5 m) subplot in the forest floor. The F and H layer materials were not included. At many sites, live moss made picking up the litter difficult

so the top layer of live moss was also collected. Litter was stored frozen until sorting to prevent further decay of the material. Litter was thawed and sorted into the following categories: needles, woody debris, bark, cones, deciduous/herbaceous, moss, and 'decomp mix'. The decomp mix classification was given to materials that more closely resembled constituents of the F layer. The moss and decomp mix were not reported since they were not uniformly collected and were not part of the targeted litter layer. After sorting, the litter was dried in paper bags to a constant mass at 45°C and weighed. The regeneration and mature sites were each represented by three litter samples while the crown closure and self-thinning sites were each represented by two samples due to the extended amount of time required for litter sorting.

3.2.4 Soil Descriptions

Soil pits established on the Regen, CrwnCl, and SelfThin-2 sites (one per site) in August and October 2003, were used to assess soil layer depths, bulk density, slope position, soil colour, coarse fragments, rooting depth, moisture regime, and drainage class. Data for SelfThin-1 and Mature were provide by Duckert *pers comm.* (2003) and Duckert and Morris (2001), respectively. Two soil pits were located at CrwnCl-1 because of relatively wider separation between plots. Additional measures of soil depth and mineral soil bulk density (and organic layer bulk density at CrwnCl-2) were taken at representative locations throughout the plots in November 2003. Bulk density was not re-measured when soil pits were immediately adjacent to or within plots. CrwnCl-1 was not revisited due to logistical constraints and because there had been two soil pits dug at this site. Each plot was divided into NW, NE, SE, and SW quadrants (previously done), and at least two depth measures were made in each quadrant at representative and

undisturbed spots. Bulk density samples were taken from the NE quadrant. A small hole was dug and the organic layer thickness measured at opposing faces. When highly variable, another one or two faces were measured. The depth of mineral soil was measured by attempting to dig down to bedrock. However, since the CENTURY model only simulates a soil layer that is 20 cm (Metherell *et al.* 1993) and the functional rooting depth was within this 20 cm, if bedrock was not reached within 20 to 30 cm, a value of 30 cm was assigned. If depths of only 20 cm had been assigned to 20+ measures, depths of less than 20 cm would have influenced mean site depths too strongly. In total, a minimum of 8 organic layer thicknesses and 4 mineral soil depths were measured at each plot (Table 3.1). Quadrant measures were averaged to provide depths at each plot. Measures from soil pits were included with those from the closest plot. Average measures from the three plots were then averaged to provide mean site depths. Depth and bulk density measurements from the soil pit at plot 2 at CrwnCl-1 were also used for plot 3 because of the close proximity of the two plots. Additional bulk density samples were retrieved from the NE quadrant in each plot.

Table 3.1 The number of soil layer thickness measurements and bulk density samples taken at each chronosequence site by individual plots.

Site	Plot	Number of Measurements Including from Soil Pits			
		Soil Layer Thickness		Bulk Density Samples	
		Organic	Mineral	Organic	Mineral
Regen-1	1	10	5		1
	2*	9	5	1	1
	3	8	4		1
	Total	27	16	1	3
Regen-2	1	9	4		1
	2*	9	5	1	1
	3	8	4		1
	Total	26	13	1	3
CrwnCl-1	1*	1	1	1	1
	2*	1	1	1	1
	3				
	Total	2	2	2	2
CrwnCl-2	1*	11	6	2	1
	2	8	5	1	1
	3	8	5	1	1
	Total	27	16	4	3
SelfThin-1	1				
	2	Data From CNFER			
	3				
SelfThin-2	1	8	4		1
	2*	9	5	1	1
	3	8	4		1
	Total	25	13	1	3
Mature	1				
	2	Data From CNFER			
	3				

* Plots that had the soil pit within or close by.

3.2.5 Bulk Density

Bulk density is the mass of the soil particles in a specific volume of soil, and is usually expressed in grams per cubic centimetre (g cm^{-3}). Bulk density samples were collected by tapping a cylinder of known volume (28, 48 or 173 cm^3) horizontally into the soil profile until it was completely filled with soil. The cylinder was emptied into a labelled bag and brought back to the lab. Each sample was oven-dried at 105°C to a

constant weight. Bulk density was then calculated by dividing the oven dried mass by the volume of the cylinder (Culley 1993).

Bulk density corrected for coarse fragments (mainly gravel and organic debris) was also calculated for each mineral soil sample. After oven drying and weighing, the soil was passed through a 2 mm wire sieve. Fragments, whether stones or organic debris, that did not pass through the screen were washed, dried and weighed. The volume of the fragments was then determined by measuring the amount of water displaced (1 ml = 1 cm^3) when put into a graduated cylinder. The calculation of bulk density corrected for fine fraction coarse fragments was performed as follows (Culley 1993):

$$\text{Bulk Density} = \frac{\text{(oven dry soil weight – coarse fragment weight)}}{\text{(volume of cylinder – volume of coarse fragments)}}$$

3.2.6 Soil Sample Collections

Organic layer and mineral soil samples were collected from each site/plot numerous times during the study. The first collections were made at the time of plot location and establishment in July and August 2002. These samples were used for mineralization bags (procedure described in section 3.3.7) and soil texture analysis. Subsequent soil collections were made 6 times; October 2002 (T-0), May (T-1), June (T-2), July (T-3), August and early September for CrwnCl-2 (T-4), and October (T-5) of 2003. These samples were used to determine pH as well as annual means of several C and N pools (*e.g.* available N, MB-C and MB-N, total C and N) that could be compared to CENTURY model pools (research questions 1.3, 1.4 and 2.1). Samples were not collected from November 2002 to April 2003 because of site access limitations resulting

from winter conditions and because the soils would have been at or near freezing during this time so it was believed that any changes would have been minimal. It should also be noted that only a small number of samples were collected on rainy days in order to avoid excessively wet samples.

Organic and mineral soil samples were collected using a shovel or trowel from a previously undisturbed area in the same vicinity in each plot each time. Collection locations had to have sufficient but representative depths of both the organic layer materials and mineral soil. Organic materials included components of the F and H layers, and mineral soil was taken from approximately the top 10 cm of the Bm layer. Samples were put in polyethylene bags, labelled, and stored in a cooler until they were brought to the lab where they were refrigerated (approximately 4°C) until processing.

3.2.6.1 Basic Soil Sample Processing

All soil samples brought back to the lab underwent some standard processing and analysis. All samples were sieved to remove coarse fragments, large organic debris, and roots. Organic and mineral samples were passed through 4 mm and 2 mm sieves, respectively. Sieving produced relatively uniform samples for laboratory analysis. The gravimetric moisture content (% water to dry weight) was measured for all samples. Approximately 5 g of fresh organic material and 10 g of fresh mineral soil were weighed into drying tins and the weight of the tins and samples were recorded. The samples were oven dried at 105°C for a minimum of 24 hours and then re-weighed. The following equation, followed by an example calculation (T-0 organic soil at Regen-1, plot 1), was used to calculate gravimetric moisture content (Topp 1993):

$$\text{Moisture Content (\%)} = \frac{(\text{moist weight} - \text{oven dry weight})}{\text{oven dry weight}} \times 100$$

Tin weight = 1.411 g
Moist soil weight = 5.060 g
Tin + oven dry soil weight = 3.383 g
Oven dry soil weight = 3.383 – 1.411 = 1.972 g

$$MC = \frac{(5.060 - 1.972)}{1.972} \times 100 = 156.6\ \%$$

Moisture contents were required for simple descriptive purposes, and also for many calculations in other analyses. All samples were processed in field moist conditions, except when they were too wet to sieve. In these cases the materials were dried slowly at low temperatures (4 – 8°C) to minimize chemical changes. Prior to drying, a sub-sample was passed through a sieve or carefully hand sorted in order to obtain a moisture content describing the field conditions. After drying, a subsequent moisture content was determined for analytical purposes.

3.2.6.2 Soil Texture

Fractions of sand (0.05-2.00 mm), silt (0.002-0.05 mm) and clay (< 0.002 mm) (Agriculture Canada Expert Committee on Soil Survey 1987), and the resulting soil textural class, were found using an adapted Bouyoucos hydrometer method (McKeague 1978). Fifty grams of 2 mm sieved, air-dried mineral soil were placed in a dispersion cup. The cup was then filled to within 5 cm of the top with water and 10 ml of sodium hexametaphosphate [$(NaPO_3)_6$] that acts as a dispersing agent to help break apart soil microaggregates. The mixture was then stirred for 15 minutes with an electric mixer (milkshake machine). After mixing the cup was covered with plastic film and left at room temperature for 6 days. After 6 days, the contents of the cup were emptied into a 1000 ml sedimentation cylinder. The cup was rinsed several times to ensure all soil

particles were transferred to the cylinder. The volume in the cylinders was made up to 1000 ml with water while the soil hydrometer (Bouyoucos scale 0-60 g L^{-1}) was inside and the bulb below the 1000 ml mark. For each batch of textures run, one blank containing only water and 10 ml of sodium hexametaphosphate, was set up. The sedimentation cylinders were left covered overnight so the contents could equilibrate to room temperature. The following day, each cylinder was sealed with a rubber stopper and agitated. Three to four drops of amyl alcohol were added to reduce foaming if necessary, and the time was recorded after each was mixed.

The hydrometer was used to take readings in each cylinder after 30 s(econds), 40 s, 1 min(ute), 2 min, 5 min, 10 min, 1 hr, 2 hr, 4 hr, and 8 hr. Usually a 12 hr reading is also taken, but due to the low fine particle content of the soils, this reading was not necessary. The hydrometer was read at the top of the meniscus. A temperature reading of the soil solution was also taken at the same time as the hydrometer readings. The blank was treated in the same manner.

A spreadsheet developed by Meyer (*pers. comm.* 2002) was used to process the hydrometer and temperature readings, and incorporate the readings taken from the blank. Percentages of sand and clay were applied to a standard Canadian soil texture triangle to determine soil texture.

3.2.7 *In Situ* Nitrogen Mineralization Rates

In situ mineralization bags were used to estimate N mineralization rates across the chronosequence sites (research question 1.4), and make comparisons to CENTURY model outputs (research question 2.1). Separate mineralization bags containing organic layer material and mineral soil were used. Soils were collected in July and August of

2002 during plot establishment. After sieving, soils were adjusted to similar moisture contents by drying under cool conditions or by adding distilled water and thoroughly mixing. Moisture contents of 150% and 23% were chosen for organic and mineral soils, respectively. These values were the approximate means and medians of the field fresh soils at the time of sampling across all the sites. When the mean moisture content for the site was close to the moisture content desired, adjustments were not made. When the mean was not close, all or only those farthest from 150% or 23% were adjusted. In total, 11of 21 organics, and 16 of 21 mineral soils were adjusted.

Equal amounts of soil, based on dry weights, from each plot within a site were bulked to produce a uniform mixture. Moisture content was measured. Fifty grams of organic material and 150 g of mineral soil were weighed into separate polyethylene bags. The bags were sealed by twisting the tops, then folding them over and wrapping an elastic band around the loop. In total, 126 organic and 126 mineral soil mineralization bags were produced (7 sites X 3 plots X 6 planned measures = 126). One full set was refrigerated pending field installation. The other five sets were frozen. Remaining materials were saved for T-0 available N (NH_4 and NO_3) analysis.

The first installation (T-0) of mineralization bag (refrigerated set) took place between October 18 2002 and November 1 2002. In each of the 21 chronosequence plots, one organic and one mineral mineralization bag was installed. A hole was excavated in an undisturbed area near the site of the initial soil collections at each plot. One organic bag was inserted into the soil profile at the interface between the organic layer and the mineral layer. One mineral bag was inserted into the Bm layer at around 10 cm. The hole was then carefully refilled and marked.

The first set of mineralization bags were removed in May 2003, put in labelled zip-lock bags and stored in a cooler before being refrigerated back at the lab until further analysis. Bags to be used for the second set were removed from the freezer and left overnight in a refrigerator. These bags were then installed in the same pit/horizon locations. In total, five sets of mineralization bags were cycled on a 30 to 40 day basis at each site between October 2002 and October 2003.

Once returned to the lab, all samples were analyzed for moisture content and available N (NH_4 and NO_3). In some cases, the samples were very wet and were dried at cool temperatures to better facilitate microbial biomass analysis. Moisture content was determined before and after drying.

To account for possible changes in the chemical composition of the organic materials and mineral soils that had been frozen prior to field installation, the 6^{th} set of frozen mineralization bags were analyzed to represent benchmarks (T-0-Frozen) for mineralization bags installed in May, June, July, and August 2003. The T-0-Frozen samples were thawed in the lab through a combination of room and refrigerator temperatures and analyzed for available N (NH_4 and NO_3).

After analyses, the T-n (n = 1..5) chemical concentrations had the T-0 or T-0-Frozen concentrations subtracted to determine the amount of flux for the *in situ* period. Daily mineralization rate was determined by dividing the change in N over the mineralization period by the number of days in that period. Annual N mineralization rates were calculated for comparison to CENTURY output and were the daily rate multiplied by the number of days per year (daily rate * 365 days).

The CENTURY model does not have an output variable specific for monthly N mineralization rate that is directly equivalent to that measured with the *in situ*

mineralization bags; however, the model does output monthly N mineralization for each of the pools separately (e.g. mineralization for slow SOM = s2mnr(1)). A new output variable called MNLZn was calculated in order to compare monthly CENTURY model N mineralization data to the equivalent data derived at the chronosequence sites. MNLZn was equal to the total mineralization of the surface microbe (s1mnr(1,1)), soil microbe (s1mnr(2,1)), slow (s2mnr(1)), and the passive (s3mnr(1)) pools.

3.2.8 Soil Respiration

In support of research question 1.4 infra-red gas analysis (IRGA) was used to measure CO_2 evolution, and to provide an indication of microbial respiration at each of the chronosequence sites; although, it was not possible to partition between microbial and root respiration. Measurements were completed in late May 2003 (T-1), late July and early August (T-3), and early September 2003 (T-4).

Within each plot, three small representative areas were cleared of live ground vegetation. Round, Rubbermaid® plastic storage containers were pushed into the organic layer to a depth of approximately 2 cm to achieve a seal with the ground. The containers each covered a surface area of 624.6 cm^2 with a volume of 1500 cm^3. The containers were wrapped in aluminium foil to prevent excess heat from building up within the containers and to reduce the potential effects of elevated photosynthetic and microbial respiration. A small 0.635 cm hole (1/4 in.) was drilled in the top of each container to allow entrance of the IRGA sampling tube. The hole was covered with standard electrical tape to prevent the escape of gasses from within the containers.

The containers were left on site for approximately 24 hours; set up time was recorded. In May 2003 (T-1), CO_2 concentrations were measured with a CIRAS I

Differential CO_2/H_2O Infra-Red Gas Analyser (PP Systems, Amesbury, MA, USA) (Figure 3.3). Traditional cuvettes were not used to sample the gas build up in the containers. The small diameter rubber sampling hose was connected directly to the Analysis Port to measure undiluted gas from within the containers. To measure the CO_2 concentration, a hole was punched through the electrical tape and the sample hose inserted. Gas was sampled until a stable reading was achieved; approximately one minute. A measure of the ambient CO_2 concentration was made at each container location in each plot. An ambient reading consisted of achieving a stable reading while sampling air immediately adjacent to the container. Before and after measurements were made, 5000 ppm CO_2 standard gas (SCOTTY® II Analyzed Gas, cat. no. 2-3438, Supelco, Bellefonte, PA, USA) was sampled at least three times from a helium balloon as a calibration check.

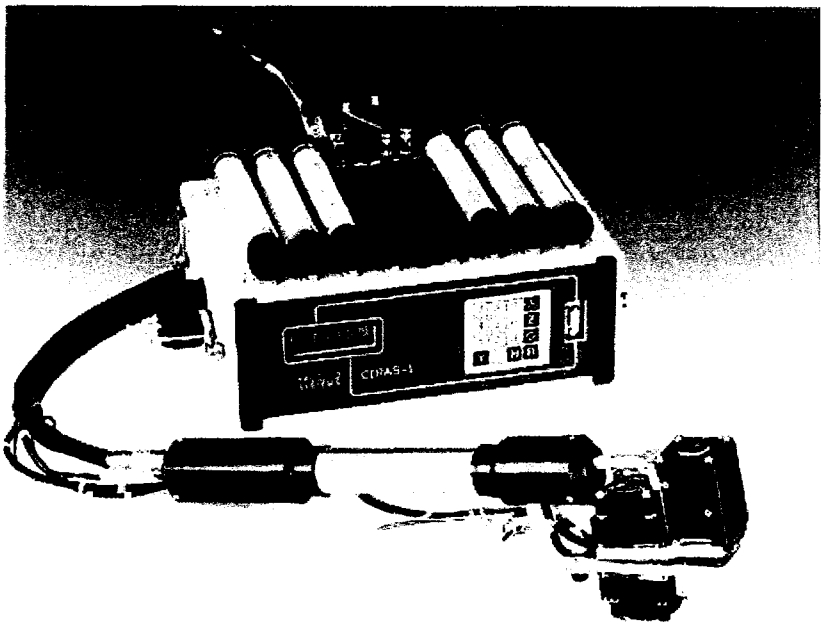

Figure 3.3 CIRAS I Differential CO_2/H_2O Infra-Red Gas Analyser (http://www.ppsystems.com/Ciras_One.html, April 12 2004).

Sampling performed in July/August (T-3) and September (T-4) was completed using a Bacharach® 2815 CO_2 Analyzer (Part No. 19-8028, Bacharach Inc., Markham, ON, Canada) (Figure 3.4). Carbon dioxide is detected by the unit using the infra-red absorption principle. This handheld unit could be directly calibrated using a standard gas (2500 ppm CO_2, part no. 24-1130, Bacharach Inc., Markham, ON, Canada) and also ambient air with the assumption that air has 340 ppm CO_2. Calibration was performed prior to measuring the first containers. Containers were set up in the same manner and in the same locations as in May. The air inside and next to the containers was sampled until steady readings were achieved which took approximately 30 to 60 seconds.

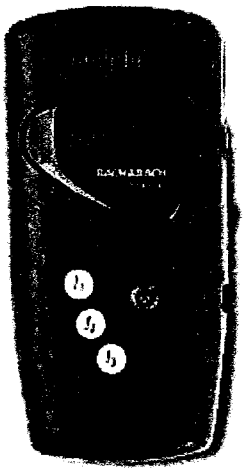

Figure 3.4 Bacharach 2815 CO_2 Analyzer (http://www.bacharach-inc.com, April 12 2004).

The concentration of CO_2 measured was converted to weight by applying the following formula:

$$C\ (mg\ m^{-3}) = C\ (ppm) * GMW / 24.45$$

where C is the concentration of CO_2, GMW is the gram molecular weight of CO_2 (44 g mol^{-1}), and 24.45 is the molar volume of air in litres at normal temperature and pressure conditions (25°C and 760 torr). Regardless of the equipment used, the following calculations were performed to generate an estimate of the CO_2 concentration flux on an hourly and area basis:

CO_2 (ppm) = container (ppm CO_2) – ambient (ppm CO_2)

CO_2 (ppm m^{-2}) = (CO_2 Evolved / 624.58 cm^2) * (10000 cm^2 / 1 m^2)

CO_2 (ppm m^{-2} hr^{-1}) = CO_2 Evolved by area / time (hr)

CO_2 (mg m^{-2} hr^{-1}) = ((Rate (ppm m^{-2} hr^{-1}) * 44) / 24.45) * (1 m^3 / 1000000 cm^3) * 1500 cm^3

To assess the relationship between MB-C, soil moisture, and soil temperature on soil respiration rates scatterplots were created with soil respiration rate (mean plot values, n = 7 sites x 3 plots x 3 measures = 63) on the y-axis and MB-C, organic material moisture content, mineral soil moisture content, and soil temperature on the x-axis. Measured moisture contents from T-1, T-3 and T-4 were used. Soil temperatures were the mean soil temperature for the chronosequence site for the 24 hours preceding the soil respiration measurement. Because data from 1994 to 2002 was used for the 110 year old site, the mean from the same measurement dates over the nine years was used. Due to missing soil temperature data, 12 of the 63 measurements could not be plotted. One MB-C value was also missing.

In summary, field measurements at chronosequence sites included vegetation inventories (tree biomass C and N), air and soil temperatures, forest floor fine litter, soil descriptions (horizon depths, mass, texture), soil moisture, total soil C and N, available N (NH_4 + NO_3), MB-C, MB-N, *in situ* N mineralization, and soil respiration.

3.3 TEMPERATURE AND MOISTURE CONTROLLED LABORATORY SOIL INCUBATIONS

Long-term laboratory incubations of organic material and mineral soils were completed to gain information on the fluxes of available inorganic N (NH_4 and NO_3), microbial carbon and nitrogen pools, and also soil respiration under controlled temperature and moisture conditions (research question 1.5). Regulating temperature and moisture conditions allowed testing for differences in soil substrate quality between the development stages. Soils from each of the 21 plots were incubated in darkness for 30 weeks at either 10 or 20°C in 1 L plastic food storage containers. Bulked soils (i.e. equal amounts of soils from three plots mixed) from the Regen-2, CrwnCl-1, and SelfThin-1 sites were incubated under the same conditions for 39 weeks in 1.5 L Rubbermaid® plastic storage containers. Two Conviron E7H growth chambers (Conviron Products Company, Winnipeg, MN, Canada) were used. Both mineral soil and the corresponding site/plot organic material were incubated in the same containers to mimic more natural conditions (*i.e.* an organic layer on top of the mineral soil). The layers were separated within the containers by a circular piece of fine Noseeum screening (*i.e.* screening that could be found on windows or tents) that partially ran up the sides of the containers to facilitate easier removal of the organic portion for sampling of the mineral soil.

The soils used were collected in October 2002 and sieved as before. Moisture contents of the soils were adjusted in the same manner and to the same target levels as the mineralization bag materials (150% for organic materials and 23% for mineral soils). At the onset (T-0), the organics were between 141.0 and 164.3% (mean of 148.5%), and the mineral soils were between 20.9 and 26.5% (mean of 22.8%).

The amount of soil available for the incubations was a concern, so rather than removing a full set of containers at every sampling point, samples were repeatedly removed from containers for moisture content, available N, MB-C, and MB-N determinations (Repeated Measures Approach). Approximately, 50 g of fresh organic material and 250 g of fresh mineral soil was used in each container. For the bulked incubations, approximately 125 g of fresh organic material and 250 g of fresh mineral soil was used in each container. Two repetitions of each temperature-site-plot combination resulted in a total of 84 individual plot containers (2 temperatures X 7 sites X 3 plots X 2 reps = 84) and 12 bulked soil containers (2 temperatures X 3 sites X 2 reps = 12). Because of the number of containers, set up was completed over two days.

In order to maintain the desired moisture contents during the incubation, the containers were weighed on a weekly basis and distilled water was added with a spray bottle to return the moisture contents to the initial levels. As expected, the 10°C incubations required less water than the 20°C incubations. On average, the amount of water added to each container at each watering was 0.7 g for the 10°C treatment, 2.5 g for the 20°C treatment, 1.7 g for the 10°C bulked treatment, and 4.8 g for the 20° bulked treatment. It should be noted that more water was required earlier on in the incubations particularly for the 10°C incubations. The target weight of each container to achieve the desired moisture content was calculated based on moisture content samples that were taken each time the incubating soil was sampled.

During the incubation the container lids were placed loosely on top of the containers so gas exchange could still occur but excessive moisture loss was prevented. Approximately every second day, all lids were removed and the containers were vented for a few minutes. This prevented CO_2 from building up to toxic levels within the

containers. The containers remained inside the growth chambers while venting took place. During venting, the container positions within the growth chambers were also rotated to remove the potential effects of localized conditions within the growth chambers. See Figure 3.5 for a timeline displaying venting, moisture adjustments, and other sampling occasions (described below).

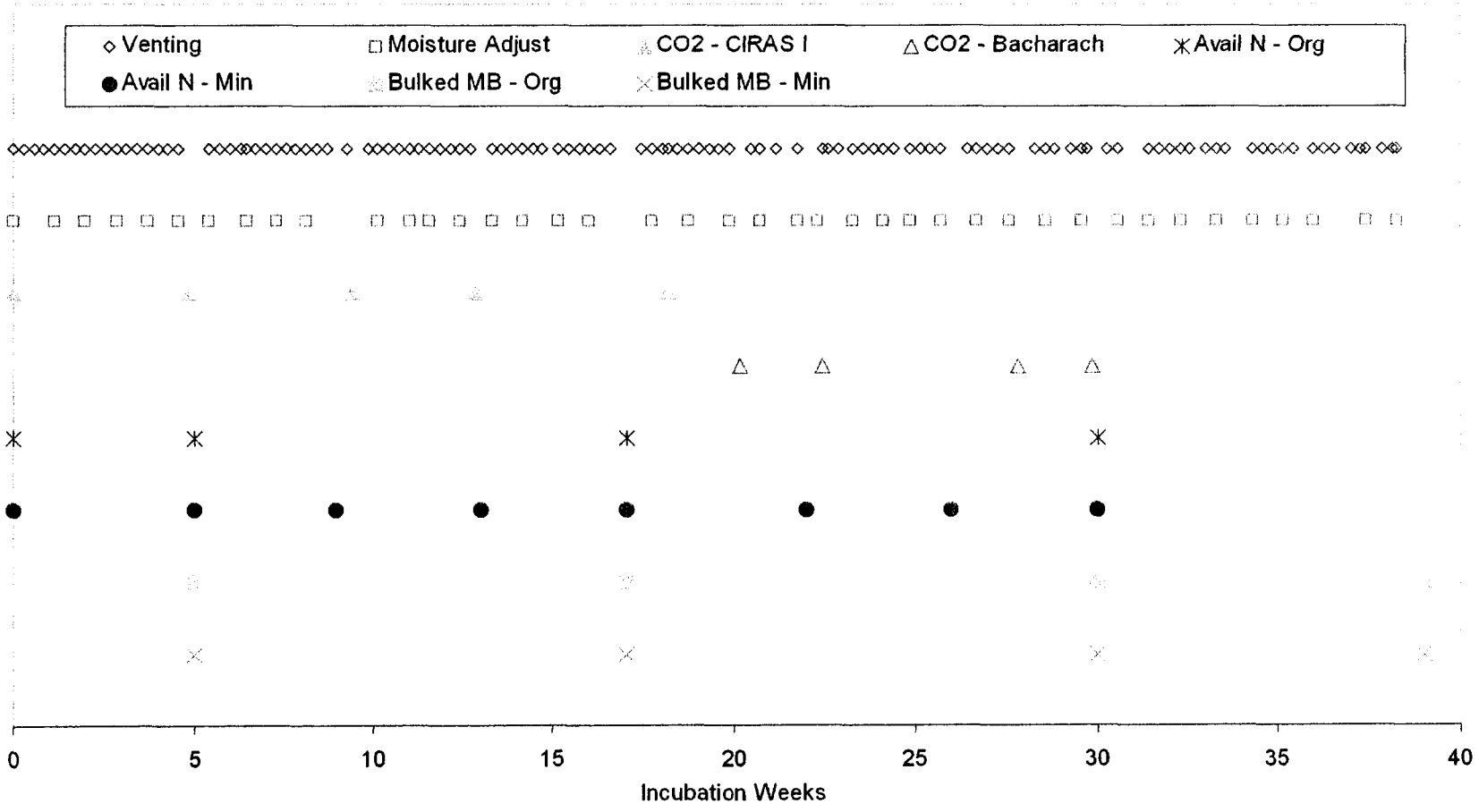

Figure 3.5 Timeline of events/sampling during the 30 and 39-week (bulked soils) temperature controlled laboratory incubations.

3.3.1 Carbon and Nitrogen Sampling

As per the timeline in Figure 3.5, incubating soils were sampled for available N (30-week incubations), and MB-C and MB-N (39-week bulked soil incubations) determinations. Sampling was done every 4^{th} or 5^{th} week depending on scheduling and, in total, took place 7 times over the 30-week incubations and 4 times over the 39-week incubations. Organic soils incubated for 30 weeks were limited to available N sampling at the T-0, T-1, T-4, and T-7 occasions (0, 5, 17, and 30 weeks, respectively) due to the limited material available. Sampling for MB-C and MB-N determinations was completed at the T-1, T-4, T-7, and T-9 (5, 17, 30, and 39 weeks, respectively) occasions for both organic and mineral soils.

3.3.2 Soil Respiration Indices

Indices of soil respiration were measured in a similar way as previously described for the on-site measurements. In total, 8 measures were made for the 30-week incubations (Figure 3.6). The day before sampling, the containers were vented and lids with a 0.635 cm (1/4 in.) hole covered with electrical tape were snapped on to prevent gas exchange and trap evolved CO_2. The containers remained sealed for approximately 24 hours prior to gas sampling. Empty containers (sealed after being in the growth chambers) were used as blanks and measures of the ambient air within each chamber. Two 1 L containers were used for each temperature treatment.

The first 4 measurements were made using the CIRAS I and the remaining measures were made with the Bacharach 2815 CO_2 Analyzer. Initially, it was expected that some of the containers may have had CO_2 concentrations greater than the capacity of the CIRAS I (Luckai *pers. comm.* April 2003). To counteract this, the sample hose

was split with one fork drawing ambient air from a large bag. This approach stabilized the readings and standardized the air being used to dilute the sample, since within the room the CO_2 concentration varied with time of day. Prior, during, and after sampling with the CIRAS I, standard gas (5000 ppm CO_2) was sampled to check the calibration of the unit. Measurements made on the 126^{th} and 127^{th} incubation days were not diluted with ambient air. Readings never exceeded the concentration of standard gas.

To measure the CO_2 concentration in the containers, the sample hose was inserted through the hole in the container lids to between one half and two thirds of the distance to the soil surface. Approximately one minute was required per container to achieve a stable reading. The blank containers were mixed in evenly during sampling as were an additional 10 standard gas readings. After sampling from a container, it would be left open briefly to vent and then the lid would be rested on top again. Sampling with the Bacharach was done in the same way except that the standard measurements were not completed. The unit was calibrated with ambient air (outdoors) and the 2500 ppm CO_2 calibration gas. The time at which each container was sampled was recorded to calculate the total time with a sealed lid. The duration was either rounded to the nearest 1/4 hour or the 1/12 hour.

Through a series of manipulations, the measured CO_2 concentrations were converted into the mass of CO_2 evolved per kg of dry weight soil in the container per day (mg CO_2 kg^{-1} d^{-1}). Due to sampling diluted air with the CIRAS I, the measurements had to be scaled up based on the readings of the 5000 ppm standard gas. The three readings of the standard gas made prior to sampling of the containers and one standard gas reading made after each batch of containers were averaged. The ratio of the measured standards to 5000 ppm was used to scale the container CO_2 readings. After

subtracting the appropriate blank, the concentrations were divided by the number of hours the containers were sealed, followed by the calculated dry-weight of the combined organic and mineral soil in the container, and finally, ppm CO_2 was converted to weight in mg. A sample calculation is below.

1980, 10°C, plot 1, rep 1 diluted container reading = 782 ppm CO_2
Dry mass of soil (organic + mineral) = 221.7 g
Diluted initial standards = 2076, 2090, 2013 ppm CO_2
Diluted within run standard = 2072 ppm CO_2
Diluted blank reading = 527 ppm CO_2
Duration = 27 hours
Container = 1 L = 1000 cm^3

Sample corrected for standards = (782 * 5000) / average (2076, 2090, 2013, 2072) = 1895.5 ppm
Subtract blank = 1895.5 – [(527 * 5000) / average (2076, 2090, 2013, 2072)] = 618.1 ppm
CO_2 evolved (ppm kg^{-1} dry soil hr^{-1}) = 618.1 ppm / [221.7 g (1 kg / 1000 g)] / 27 hr
= 103.3 ppm CO_2 kg^{-1} hr^{-1}
CO_2 evolved (mg kg^{-1} dry soil d^{-1}) = (103.3 * 44) / 24.45) * (1 m^3 / 1000000 cm^3) *
1000 cm^3 * 24 hr = 4.5 mg kg^{-1} dry soil d^{-1}

The readings taken with the Bacharach CO_2 analyzer were manipulated to the same end expression but without needing to scale the readings based on the readings of the standard gas. Only the blanks were subtracted, followed by converting to a per kg dry soil and per day value.

3.4 LABORATORY ANALYSES

This study involved extensive soils analyses including pH, total C, total N, available N (NH_4 + NO_3), MB-C, and MB-N. Specific laboratory procedures are described below.

3.4.1 Soil pH

All organic layer and mineral soil monthly collections (n = 252) and mineralization bag (n = 224) samples underwent pH analysis. Soil pH determination

followed the procedure by Hendershot *et al.* (1993). Sieved (2 mm mineral; 4 mm organic) soils were air-dried and then ground with a mortar and pestle to a consistent aggregate (approximately 30 seconds). Ten grams of mineral soil were weighed into 30 ml glass extraction jars and 20 ml of 0.01 *M* $CaCl_2$ was used to make a 1:2 soil to solution ratio. For organics, 2 g of material and 20 ml of 0.01 *M* $CaCl_2$ was used to make a 1:10 soil to solution ratio. The jars were capped and hand-shaken vigorously to completely mix the solution. After one hour, pH was measured using an Accumet® Research AR20 pH/conductivity meter (cat. no. 13-636-AR20C, Fisher Scientific, Pittsburgh, PA, USA)with an Accumet® Research 3-in-1 Combination Electrode (cat. no. 13-620-530, Fisher Scientific, Pittsburgh, PA, USA).

Individual pH measures were converted to the concentration of hydrogen ions (H^+) in the solution based on the following formula by Sorensen (1909):

$$pH = - \log_{10}[H^+]$$

Site means for each measurement occasion were then determined and these means were converted back to pH using the same formula.

3.4.2 Total Carbon and Nitrogen

Total C and N was determined for T-0, T-1, T-3, and T-5 organic material and for T-0 mineral soil monthly collections (n = 105); T-0, T-1, T-2, and T-5 organic material and T-0 mineral soil mineralization bags (n = 105). Sieved (2 mm mineral; 4 mm organic) soils were air-dried and then ground with a mortar and pestle to a consistent aggregate (approximately 30 s). Samples of approximately 2 g for mineral and 0.5 g for organic were burned by high temperature oxygen combustion in a LECO®

CNS2000 macro element analysis furnace (Leco Corporation, St. Joseph, MI, USA) to determine total C and N.

3.4.3 Microbial Biomass Carbon and Nitrogen

The chloroform fumigation extraction (0.5 *M* K_2SO_4) method, described by Voroney *et al.* (1993), was used for quantification of MB-C and MB-N the mineral and organic soils. Exposure to the chloroform kills and lyses microbial cells, releasing the cell contents into the extracting solution. Microbial biomass extractions were completed for monthly collections, T-0 and T-0-Frozen *in situ* mineralization bags, T-1, T-4, T-7 and T-9 bulked organic soil incubations, and T-1, T-4 and T-7 bulked mineral soil incubations. These numbers do not include and blanks or quality control samples.

Approximately 20 g of field-moist mineral soil, or 5 g of field-moist organic material, was weighed into 100 ml glass jars. One blank (*i.e.* empty jar) and one quality control sample was used for approximately every 10 samples. The quality control samples were mineral and organic soils that were used every time to detect if there were large differences between batches. In each batch, half of the jars were extracted immediately and the other half was fumigated for 24 hours prior to extraction. Blanks were used in all batches of extractions.

The glass sample jars were placed into heavy walled desiccators. A 100 ml beaker containing a few boiling chips and 40 ml of ethanol-free chloroform ($CHCL_3$) (code 3004-2, Caledon Laboratories Ltd., Georgetown, ON, Canada) was placed in the centre of each desiccator. A vacuum was applied until the chloroform boiled for 2 minutes. The desiccators were sealed while still under vacuum to allow the chloroform vapour to infiltrate the soil and kill the microbes. The desiccators were covered with a

garbage bag and left in darkness at room temperature for a period of 24 hours. After the 24 hours, desiccators were opened and the chloroform beaker removed. The residual chloroform fumes were removed by evacuating the desiccator 4 times for 2 minutes each for mineral samples, and 5 times at 2 minutes each for organic samples (Luckai *pers comm.* 2002). All procedures involving the chloroform were performed under a fume hood.

Forty ml of 0.5 *M* K_2SO_4 was added to each jar to achieve a soil to extractant ratio of 1:2.5 for mineral samples and 1:20 for organic samples. To account for the high variability of soil moisture and maintain the desired soil to extractant ratios, either the mass of soil or the amount of extracting solution used was altered based on measured moisture contents.

The capped jars were placed on a horizontal shaker at 160 rpm for one hour. After shaking, the slurry was immediately filtered through VWR 696 glass microfiber filter papers (11 cm dia., cat. no. 28333-133, VWR Scientific Products, West Chester, PA, USA) into plastic vials. Extractions were usually frozen unless they could be analyzed within a few days, in which case they were stored in a refrigerator.

Extracts were analyzed using the Technicon Instruments AutoAnalyzer® II (Pulse Instrumentation (1992) Ltd., Saskatoon, SK) for total extractable C (Industrial Method No. 455-76W/A) and dissolved N (organic and inorganic) (Method No. G-086-93 A). Organic carbon is oxidized to CO_2 by sulphuric acid, potassium persulfate, and ultraviolet light. The CO_2 is dialyzed through a silicon rubber membrane into a weakly buffered phenolphthalein indicator solution. The decrease in colour of the phenolphthalein solution indicates the concentration of CO_2 in the solution. Inorganic and organic N is oxidized to nitrate by acidic and basic reagents, and exposure to UV

radiation. The nitrate is further reduced to nitrite by potassium persulfate and a hydrazine sulphate solution containing a copper catalyst. The concentration of nitrite is revealed by the development of pink colouration with a sulfanilamide and *N*-(1-naphthyl)-ethylene diamine solution (Voroney *et al.* 1993; Bran+Luebbe Method No. G-086-93 A). The colour intensity of the solution is proportional to the total soluble N concentration (Voroney *et al.* 1993).

Determination of microbial carbon and microbial nitrogen was simply the subtraction of unfumigated values from fumigated values. The calculations required to determine MB-C and MB-N are from Voroney *et al.* (1993), and are as follows:

Weight of soil sample (oven-dry weight equivalent) taken for microbial biomass measurements (MS):

MS (g) = (soil wet weight (g) * 100) / (100 + soil water content (%))

Total volume of solution in the extracted soil (VS) (assumes 1 g of water = 1 ml):

VS (ml) = soil wet weight (g) – soil oven-dry weight (g) + extractant volume (ml)

Total weight of extractable C and N in the fumigated (O_F) and non-fumigated (O_{UF}) soil samples:

OC_F, OC_{UF} ($\mu g\ g^{-1}$ soil) = extractable C ($\mu g\ ml^{-1}$) * [VS (ml) / MS (g)]

ON_F, ON_{UF} ($\mu g\ g^{-1}$soil) = extractable N ($\mu g\ ml^{-1}$) * [VS (ml) / MS (g)]

Microbial biomass C and N in the soil (MB-C, MB-N):

MB-C ($\mu g\ g^{-1}$ soil) = $(OC_F - OC_{UF}) / k_{EC}$

where: $k_{EC} = 0.25 \pm 0.05$ and represents the efficiency of extraction of microbial biomass C.

MB-N ($\mu g\ g^{-1}$ soil) = $(ON_F - ON_{UF}) / k_{EN}$

where: $k_{EN} = 0.18 \pm 0.04$ and represents the efficiency of extraction of microbial biomass N.

T-0 monthly collection and T-0 mineralization bag extractions were analyzed at the University of Guelph (Guelph, ON); the remainder were analyzed at the Forest Soils Laboratory at Lakehead University, Thunder Bay, ON.

3.4.4 Available Nitrogen

The method described by Kalra and Maynard (1991) was used to extract inorganic N (NH_4 and NO_3) from mineral and organic soils. Extractions were completed for monthly collections, *in situ* mineralization bags, and T-0 to T-7 for the 30 week laboratory incubations.

Approximately 10 g of field-moist mineral soil or 5 g of field-moist organic material was weighed into 60 ml glass jars. One blank and one quality control sample were used for approximately every 10 samples. Forty ml of 2 *M* KCL was added to each jar resulting in 1:5 and 1:20 soil:extractant ratios for mineral and organic samples, respectively. The higher ratio was used for the organics because of the typically greater N concentrations. The K^+ and Cl^- ions displace the NH_4 ions and bring them into the solution. Nitrate is water soluble so it easily becomes mixed with the 2 *M* KCl solution.

The capped jars were placed on a horizontal shaker at 160 rpm for one hour. After shaking, the slurry was immediately filtered through Fisher P5 (11 cm dia., cat. no. 09-801C, Fisher Scientific, Pittsburgh, PA, USA) filter paper into plastic vials. Extractions were usually frozen unless they could be analyzed within a few days, in which case they were stored in a refrigerator.

A 0.5 *M* K_2SO_4 solution is also a suitable extracting solution for available N and was used instead of 2 *M* KCl for laboratory incubation analyses in order to use less sample material and improve laboratory efficiency since these extracts could also be used for MB-C and MB-N extractions. For mineral soil incubation samples, a soil to extractant ratio of 1:2.5 was used (10 g fresh : 20 ml 0.5 *M* K_2SO_4) since this ratio was also used for microbial biomass extractions. Organic samples were extracted in a 1:20 solution (4 g fresh : 32 ml 0.5 *M* K_2SO_4).

To confirm that available N extractions using 2 *M* KCl and 0.5 *M* K_2SO_4 produced similar results, non-fumigated 0.5 *M* K_2SO_4 microbial biomass monthly collections or mineralization bag extractions were analyzed for available N and compared to corresponding available N 2 *M* KCl extractions. The relationship between the two extraction procedures was very strong (Appendix IV).

Both the 2 *M* KCl and 0.5 *M* K_2SO_4 extractions were analyzed for NH_4 and NO_3 concentrations using a Technicon Instruments AutoAnalyzer® II (Pulse Instrumentation (1992) Ltd., Saskatoon, SK). The T-0 monthly collection and T-0 mineralization bag extractions were analyzed at the University of Guelph, Guelph, ON, using a TRAACS 800 AutoAnalyzer. The remainder were analyzed at the Forest Soils Laboratory at Lakehead University, Thunder Bay, ON.

Data produced by the AutoAnalyzer is presented in micrograms per ml ($\mu g\ ml^{-1}$) and had to be corrected for blanks and scaled based on the dry weight of the samples extracted and the volume of extracting solution used. The calculations provided in Kalra and Maynard (1991) do not account for the water present in the soil samples. Instead calculations provided by Voroney *et al.* (1993) for microbial biomass were used and are as follows:

Weight of soil sample (oven-dry weight equivalent) taken for microbial biomass measurements (MS):

MS (g) = (soil wet weight (g) * 100) / (100 + soil water content (%))

Total volume of solution in the extracted soil (VS) (assumes 1 g of water = 1 ml):

VS (ml) = soil wet weight (g) – soil oven-dry weight (g) + extractant volume (ml)

Total concentration of NH_4 and NO_3 in the soil samples (odw) after direct subtraction of blanks:

NH_4 ($\mu g \cdot g^{-1}$ soil) = [NH_4 ($\mu g \cdot ml^{-1}$) – blank] * [VS (ml) / MS (g)]

NO_3 ($\mu g \cdot g^{-1}$ soil) = [NO_3 ($\mu g \cdot ml^{-1}$) – blank] * [VS (ml) / MS (g)]

3.5 STATISTICAL ANALYSES

The chronosequence sites were grouped into stand development stages in order to simplify the complex dataset and allow for easier comparisons to other published data. Grouping chronosequence sites into stand development stages also allowed individual sites to be treated as replicates so the stages could be statistically compared. The mature stage was not testable because there was only one chronosequence site. Statistical analyses were performed on the following data sets: forest floor fine litter, total soil C and N, available N, MB-C and MB-N, N mineralization, and soil respiration.

Having three stand development stages with two replications allowed tests, albeit with low statistical power. Tests with 2 degrees of freedom (df) for the numerator term and 3 df for the denominator ($F_{2,3(\alpha = 0.05)} = 9.55$) coupled with data that exhibited a high degree of variability resulted in relatively high probabilities of accepting the null hypothesis of equal means when it should have been rejected (Type II errors). However, when differences were found to be statistically significant there was a high degree of confidence in the results. The chronosequence approach in general, does not lend itself to producing powerful statistical tests because adding replicates often means adding several sites (in this study at least three) which can be a prohibitive cost. Adding another replicate to the three stand development stages would have improved the one-way ANOVA test statistic to $F_{2,6(\alpha = 0.05)} = 5.14$. A more efficient improvement would have been to replicate the Mature stand development ($F_{3,4(\alpha = 0.05)} = 6.59$). It should be noted that even if a test does not detect significant differences, a trend may still be apparent in the data which could provide useful guidance for future work.

Data Desk® 6.0 (Data Description Inc., Ithaca, NY) was used to perform all ANOVA tests and Microsoft® Excel was used for regression analyses. Prior to

performing ANOVA, the normality and heterogeneity of variance were evaluated for each data set with normal probability plots and dotplots of the raw data and residuals. Transformations were performed as required. Log transformations were the most common. When significant differences were observed ($\alpha = 0.05$), Bonferroni post hoc tests were used.

3.5.1 Chronosequence Soil Pools, *In Situ* Nitrogen Mineralization and CO_2 Respiration ANOVA

Annual means for total soil C, total soil N, available N, MB-C, MB-N, and *in situ* N mineralization rates were calculated as follows: 1) values from the three plots in each site were averaged for each measurement time (T-0 to T-5), 2) these values were then averaged to produce annual means ($n = 6$), and 3) values from the two sites in each stand development stage grouping ($n = 2$) were then averaged to produce an overall mean for each stage. Nitrogen mineralization rates were scaled up from approximately 345 days of data to 365 days in order to produce annual mineralization rates. The standard error of the mean for each stage used the two annual means from the sites. Because there was only one replicate of the mature site, the annual stage mean was the average of the six measurement times and standard error was not calculated. Summary statistics (i.e. means and standard error) for forest floor fine litter were calculated in the same manner as other pools except that for four chronosequence sites, means were based on two, rather than three plots (CrwnCl-1, CrwnCl-2, SelfThin-1, and SelfThin-2).

The use of developmental stage groupings provided site replication and therefore degrees of freedom for one-way ANOVA ($\alpha = 0.05$) in order to test for differences between the Regeneration, Crown Closure, and Self-Thinning stages for measures of soil

chemical properties (forest floor fine litter, total soil C, total soil N, available N, MB-C, MB-N, and *in situ* N mineralization rate).

$Y_{ij} = \mu + G_i + \varepsilon_{(i)j}$

$i = 1, 2, 3;\ j = 1, 2$

Y_{ijk} = the measure of soil chemical properties for the i^{th} Group and the j^{th} replicate

μ = the grand mean of the measures of chemical properties

$\varepsilon_{(i)j}$ = the random effect of the ij^{th} treatment combination

The $\varepsilon_{(ij)}$ is assumed to be IID $N(0, \sigma^2)$.

Carbon dioxide respiration measurements were analyzed using repeated measures procedures. Respiration measurements were made on three occasions (T-1, T-2, and T-4) so deriving annual means was not applicable. The linear model and estimated mean squares (EMS) table (Table 3.2) are presented below. For this type of analysis, "Site" was included as a separate term in the model rather than providing replication (as in the one-way ANOVA procedures previously described) and refers to the two chronosequence sites within each stand development stage group. Site is nested within the stand development stage "Group" which prevents the Group x Site interactions from being tested. The CO_2 respiration data did not require transformation.

$Y_{ijk} = \mu + G_i + S_{(i)j} + M_k + GM_{ik} + SM_{(i)jk} + \varepsilon_{(ijk)}$

$i = 1, 2, 3;\ j = 1, 2;\ k = 1, 2, 3$

Y_{ijk} = the rate of CO_2 evolution at the i^{th} Group, the j^{th} Site within the Group, and the k^{th} measurement occasion

μ = the grand mean of the CO_2 evolution rate measurements

G_i = the fixed effect of the stand development stage grouping

$S_{(i)j}$ = the random effect of the Site within Group

M_k = the fixed effect of the Measurement occasion

GM_{ik} = the interaction of the i^{th} Group and the k^{th} Measurement occasion

$SM_{(i)jk}$ = the interaction of the j^{th} Site within Group and the k^{th} measurement occasion

$\varepsilon_{(ijk)}$ = the random effect of the ijk^{th} treatment combination

The $\varepsilon_{(ijk)}$ is assumed to be IID $N(0, \sigma^2)$.

Table 3.2 Estimated Mean Squares (EMS) table for the repeated measures ANOVA of CO_2 respiration data from chronosequence sites.

	3 F i	2 R j	6 F k	DF	EMS
G_i	0	2	3	2	$3\sigma^2_S + 6\Phi(G)$
$S_{(i)j}$	1	1	3	3	$3\sigma^2_S$
M_k	3	2	0	2	$\sigma^2_{SM} + 6\Phi(M)$
GM_{ik}	0	2	0	4	$\sigma^2_{SM} + 2\Phi(GM)$
$SM_{(i)jk}$	1	1	0	6	σ^2_{SM}
$\varepsilon_{(ijk)}$	1	1	1	0	na

3.5.2 Statistical Analyses for Laboratory Incubations

Statistical analyses for the laboratory incubations were performed separately for data from organic samples and mineral soil samples. Listed in Table 3.3 are the testable measurements made, the measurement occasions when measurements were made, and the type of analyses performed. The total available N mineralized was the total of the mineralized N between measurement occasions (*e.g.* T-2 – T-1 = x) and is an indicator of the mineralization potential of the soils. Analysis of the actual amounts of available N mineralized between measurement occasions allows for comparison of the trend of mineralization for each soil. Measures of MB-C and N from the 39-week bulked soil incubations quantified MB changes during the incubations and point in time

measurements of CO_2 respiration from the 30-week incubations were used to gauge microbial activity during the incubations.

Table 3.3 Measurements from laboratory incubations on which statistical analyses were performed.

Testable Measurements	Measurement Occasions	Type of Analyses
Organic Material		
Total Available N Mineralized	T-7	Split-plot
Available N Mineralized Between Measurements	T-1, T-4, T-7	Split-plot with Repeated Measures
Bulked Organic Material		
Individual Measurements of MB-C	T-1, T-4, T-7, T-9	Graphical
Individual Measurements of MB-N	T-1, T-4, T-7, T-9	Graphical
Mineral Soil		
Total Available N Mineralized	T-7	Split-plot
Available N Mineralized Between Measurements	T-1 to T-7	Split-plot with Repeated Measures
Bulked Mineral Soil		
Individual Measurements of MB-C	T-1, T-4, T-7	Graphical
Individual Measurements of MB-N	T-1, T-4, T-7	Graphical
CO_2 Respiration		
Non-bulked Soils	T-1 to T-7	Split-plot with Repeated Measures

The laboratory incubations generated a substantial amount of data. However, to analyze the data at the level of stand development stages considerable summarizing was required. For each measurement occasion during the 30-week incubations, plot averages were calculated for each temperature, site, and replicate combination to allow ANOVA. This reduced the data from 72 to 24 numbers for the Regen, CrwnCl, and Self-Thin sites (6 sites X 3 plots X 2 temps X 2 reps = 72; 6 sites X 2 temps X 2 reps = 24). The mature stage was excluded because there were no replicate sites. For presentation purposes, means for the stand development stages were derived by averaging the two incubation

replicates and then the two chronosequence sites in each stage. Bulked soils data was summarized by averaging temperature replicates (3 sites X 2 temps X 2 reps = 12).

Split-plot designs were required because of the use of separate temperature-controlled growth chambers. Technically, four growth chambers should have been used – one for each temperature x repetition combination – but only two were available and it was assumed that using two would not have an effect on the results. Split-plot designs result in whole plot error (ω) and a restriction on randomization (δ). The two temperature replicates allow a test on "Temperature" using whole plot error. These factors enter the linear model following "Temperature". The two replicate stands within each stand development stage result in degrees of freedom for experimental error (ε). However, since soils from only one chronosequence site were used for the bulked soil incubations, there was no replication for stand development stage and an estimate for experimental error could not be made. As with the repeated measures ANOVA for CO_2 respiration, "Site" was included as a nested factor, but because of the split-plot design, "Site" was nested within "Temperature" and whole plot error as well as "Group". Repeated measures ANOVA was not possible for the bulked soils because only one site was represented for each stand development stage. Changes of MB-C and N over the duration of the 39-week incubations had to be examined using qualitative graphical methods.

Three different linear models and EMS tables were required to describe the ANOVA tests presented in Table 3.3. The following linear model was used for tests on total available N mineralized and total mineralization rate for organic and mineral soils. Table 3.4 is the associated EMS table.

$Y_{ijkl} = \mu + T_i + \omega_{(i)j} + \delta_{(ij)} + G_k + TG_{ik} + \omega G_{(i)jk} + \varepsilon_{(ijk)l}$

$i = 1, 2;\ j = 1, 2;\ k = 1, 2, 3;\ l = 1, 2$

Y_{ijkl} = measurements for the i^{th} Temperature, the j^{th} whole plot error within Temperature, the k^{th} Group, and the l^{th} replicate

μ = the grand mean of the measurements

T_i = the fixed effect of the incubation Temperature

$\omega_{(i)j}$ = the random effect of whole plot error within Temperature

G_k = the fixed effect of Group

TG_{ik} = the interaction of the i^{th} Temperature and the k^{th} Group

$\omega G_{(i)jk}$ = the interaction of the j^{th} whole plot error within Temperature and the k^{th} Group

$\varepsilon_{(ijk)l}$ = the random effect of the $ijkl^{th}$ treatment combination

The $\varepsilon_{(ijk)l}$ is assumed to be IID $N(0, \sigma^2)$.

Table 3.4 Estimated Mean Squares (EMS) table for the total available N mineralized and total N mineralization rate for organic and mineral soils during laboratory incubations.

	2 F i	2 R j	3 F k	2 R l	DF	EMS
T_i	0	2	3	2	1	$\sigma^2 + 6\sigma^2_{\delta} + 6\sigma^2_{\omega} + 12\Phi(T)$
$\omega_{(i)j}$	1	1	3	2	2	$\sigma^2 + 6\sigma^2_{\delta} + 6\sigma^2_{\omega}$
$\delta_{(ij)}$	1	1	3	2	0	$\sigma^2 + 6\sigma^2_{\delta}$
G_k	2	2	0	2	2	$\sigma^2 + 2\sigma^2_{\omega G} + 8\Phi(G)$
TG_{ik}	0	2	0	2	2	$\sigma^2 + 2\sigma^2_{\omega G} + 4\Phi(TG)$
$\omega G_{(i)jk}$	1	1	0	2	4	$\sigma^2 + 2\sigma^2_{\omega G}$
$\varepsilon_{(ijk)l}$	1	1	1	1	12	σ^2

The following linear model was used for ANOVA on available N mineralized between measurements for organic soils. Table 3.5 is the associated EMS table.

$$Y_{ijklm} = \mu + T_i + \omega_{(i)j} + \delta_{(ij)} + G_k + TG_{ik} + \omega G_{(i)jk} + S_{(ijk)l} + M_m + TM_{im} + \omega M_{(i)jm} + GM_{km} + TGM_{ikm} + \omega GM_{(i)jkm} + SM_{(ijk)lm} + \varepsilon_{(ijklm)}$$

$i = 1, 2;\ j = 1, 2;\ k = 1, 2, 3;\ l = 1, 2;\ m = 1, 2, 3$

Y_{ijklm} = measurements for the i^{th} Temperature, the j^{th} whole plot error within the i^{th} Temperature, the k^{th} Group, the l^{th} Site within Temperature, whole plot error and Group, the m^{th} Measurement occasion

μ = the grand mean of the available N measurements

T_i = the fixed effect of the incubation Temperature

$\omega_{(i)j}$ = the random effect of whole plot error within Temperature

$\delta_{(ij)}$ = the random effect of restriction on randomization

G_k = the fixed effect of Group

TG_{ik} = the interaction of the i^{th} Temperature and the k^{th} Group

$\omega G_{(i)jk}$ = the interaction of the j^{th} whole plot error within Temperature and the k^{th} Group

$S_{(ijk)l}$ = the random effect of Site within Temperature, whole plot error and Group

M_m = the fixed effect of Measurement occasion

TM_{im} = the interaction of Temperature and Measurement occasion

$\omega M_{(i)jm}$ = the interaction of whole plot error and Measurement occasion

GM_{km} = the interaction of Group and Measurement occasion

TGM_{ikm} = the interaction of Temperature, Group and Measurement occasion

$\omega GM_{(i)jkm}$ = the interaction of whole plot error, Group and Measurement occasion

$SM_{(ijk)lm}$ = the interaction of Site and Measurement occasion

$\varepsilon_{(ijklm)}$ = the random effect of the $ijkl^{th}$ treatment combination

The $\varepsilon_{(ijklm)}$ is assumed to be IID $N(0, \sigma^2)$.

Table 3.5 Estimated Mean Squares (EMS) table for available N mineralized between measurements for organic soils during laboratory incubations.

	2 F i	2 R j	3 F k	2 R l	3 F m	DF	EMS
T_i	0	2	3	2	3	1	$\sigma^2 + 3\sigma^2_S + 18\sigma^2_\delta + 18\sigma^2_\omega + 36\Phi(T)$
$\omega_{(ij)}$	1	1	3	2	3	2	$\sigma^2 + 3\sigma^2_S + 18\sigma^2_\delta + 18\sigma^2_\omega$
$\delta_{(ij)}$	1	1	3	2	3	0	n/a
G_k	2	2	0	2	3	2	$\sigma^2 + 3\sigma^2_S + 6\sigma^2_{\omega G} + 24\Phi(G)$
TG_{ik}	0	2	0	2	3	2	$\sigma^2 + 3\sigma^2_S + 6\sigma^2_{\omega G} + 12\Phi(TG)$
$\omega G_{(ij)k}$	1	1	0	2	3	4	$\sigma^2 + 3\sigma^2_S + 6\sigma^2_{\omega G}$
$S_{(ijk)l}$	1	1	1	1	3	12	$\sigma^2 + 3\sigma^2_S$
M_m	2	2	3	2	0	2	$\sigma^2 + \sigma^2_{SM} + 6\sigma^2_{\omega M} + 24\Phi(M)$
TM_{im}	0	2	3	2	0	2	$\sigma^2 + \sigma^2_{SM} + 6\sigma^2_{\omega M} + 12\Phi(TM)$
$\omega M_{(ij)m}$	1	1	3	2	0	4	$\sigma^2 + \sigma^2_{SM} + 6\sigma^2_{\omega M}$
GM_{km}	2	2	0	2	0	4	$\sigma^2 + \sigma^2_{SM} + 2\sigma^2_{\omega GM} + 8\Phi(GM)$
TGM_{ikm}	0	2	0	2	0	4	$\sigma^2 + \sigma^2_{SM} + 2\sigma^2_{\omega GM} + 4\Phi(TGM)$
$\omega GM_{(ij)km}$	1	1	0	2	0	8	$\sigma^2 + \sigma^2_{SM} + 2\sigma^2_{\omega GM}$
$SM_{(ijk)lm}$	1	1	1	1	0	24	$\sigma^2 + \sigma^2_{SM}$
$\varepsilon_{(ijklm)}$	1	1	1	1	1	0	n/a

The following linear model was used for ANOVA on available N mineralized between measurements for mineral soils and CO_2 respiration measurements. Table 3.6 is the associated EMS table.

$$Y_{ijklm} = \mu + T_i + \omega_{(ij)} + \delta_{(ij)} + G_k + TG_{ik} + \omega G_{(ij)k} + S_{(ijk)l} + M_m + TM_{im} + \omega M_{(ij)m} + GM_{km} + TGM_{ikm} + \omega GM_{(ij)km} + SM_{(ijk)lm} + \varepsilon_{(ijklm)}$$

$i = 1, 2;\ j = 1, 2;\ k = 1, 2, 3;\ l = 1, 2;\ m = 1..7$

Y_{ijklm} = measurements for the i^{th} Temperature, the j^{th} whole plot error within the i^{th} Temperature, the k^{th} Group, the l^{th} Site within Temperature, whole plot error and Group, the mth Measurement occasion

μ = the grand mean of the available N OR CO_2 respiration measurements

T_i = the fixed effect of the incubation Temperature

$\omega_{(ij)}$ = the random effect of whole plot error within Temperature

$\delta_{(ij)}$ = the random effect of restriction on randomization

G_k = the fixed effect of Group

TG_{ik} = the interaction of the i^{th} Temperature and the k^{th} Group

$\omega G_{(i)jk}$ = the interaction of the j^{th} whole plot error within Temperature and the k^{th} Group

$S_{(ijk)l}$ = the random effect of Site within Temperature, whole plot error and Group

M_m = the fixed effect of Measurement occasion

TM_{im} = the interaction of Temperature and Measurement occasion

$\omega M_{(i)jm}$ = the interaction of whole plot error and Measurement occasion

GM_{km} = the interaction of Group and Measurement occasion

TGM_{ikm} = the interaction of Temperature, Group and Measurement occasion

$\omega GM_{(i)jkm}$ = the interaction of whole plot error, Group and Measurement occasion

$SM_{(ijk)lm}$ = the interaction of Site and Measurement occasion

$\varepsilon_{(ijklm)}$ = the random effect of the $ijkl^{th}$ treatment combination

The $\varepsilon_{(ijklm)}$ is assumed to be IID $N(0, \sigma^2)$.

Table 3.6 Estimated Mean Squares (EMS) table for available N mineralized between measurements for mineral soils and CO_2 respiration measurements during laboratory incubations.

	2 F i	2 R j	3 F k	2 R l	8 F m	DF	EMS
T_i	0	2	3	2	7	1	$\sigma^2 + 7\sigma^2_S + 42\sigma^2_\delta + 42\sigma^2_\omega + 84\Phi(T)$
$\omega_{(i)j}$	1	1	3	2	7	2	$\sigma^2 + 7\sigma^2_S + 42\sigma^2_\delta + 42\sigma^2_\omega$
$\delta_{(ij)}$	1	1	3	2	7	0	n/a
G_k	2	2	0	2	7	2	$\sigma^2 + 7\sigma^2_S + 14\sigma^2_{\omega G} + 56\Phi(G)$
TG_{ik}	0	2	0	2	7	2	$\sigma^2 + 7\sigma^2_S + 14\sigma^2_{\omega G} + 28\Phi(TG)$
$\omega G_{(i)jk}$	1	1	0	2	7	4	$\sigma^2 + 7\sigma^2_S + 14\sigma^2_{\omega G}$
$S_{(ijk)l}$	1	1	1	1	7	12	$\sigma^2 + 7\sigma^2_S$
M_m	2	2	3	2	0	6	$\sigma^2 + \sigma^2_{SM} + 6\sigma^2_{\omega M} + 24\Phi(M)$
TM_{im}	0	2	3	2	0	6	$\sigma^2 + \sigma^2_{SM} + 6\sigma^2_{\omega M} + 12\Phi(TM)$
$\omega M_{(i)jm}$	1	1	3	2	0	12	$\sigma^2 + \sigma^2_{SM} + 6\sigma^2_{\omega M}$
GM_{km}	2	2	0	2	0	12	$\sigma^2 + \sigma^2_{SM} + 2\sigma^2_{\omega GM} + 8\Phi(GM)$
TGM_{ikm}	0	2	0	2	0	12	$\sigma^2 + \sigma^2_{SM} + 2\sigma^2_{\omega GM} + 4\Phi(TGM)$
$\omega GM_{(i)jkm}$	1	1	0	2	0	24	$\sigma^2 + \sigma^2_{SM} + 2\sigma^2_{\omega GM}$
$SM_{(ijk)lm}$	1	1	1	1	0	72	$\sigma^2 + \sigma^2_{SM}$
$\varepsilon_{(ijklm)}$	1	1	1	1	1	0	n/a

3.6 CENTURY MODEL SIMULATIONS USED FOR COMPARISONS

The CENTURY Soil Organic Matter model, version 5.3.2.3 was used for all simulations executed for this project. The calibration settings used for the model were made available by Edgington and Morris (*pers comm.* 2002). These settings represented the most progress to date with calibrating the CENTURY model, version 4, for upland black spruce-dominated sites in northwestern Ontario and are the end point of work by Edgington and Morris (2001). Version 5 of the CENTURY model can utilize the calibration files from version 4.

It should be noted that while C and N pools can be set as part of model calibration to describe a simulation start point for a site, they will change during the course of the simulation. Other parameters that describe the site, such as soil texture, the ranges of C:N ratios allowed for organic matter in pools, and variables that are parameters in model equations (e.g. many fix.100 file variables), do not change during a simulation and will have a more profound effect on the model calibration than initial pool levels, particularly if an equilibrium period is utilized. The equilibrium period allows the model pools to gravitate towards modal site conditions representative of the physical site parameters and the parameters that influence model equations. Since no two forest sites are identical many parameters could be derived for each site used for calibration; however, the model user must pick either one site or mean values from a series of sites (e.g. a chronosequence) to populate the calibration parameters for a particular site type. Soil texture, for example, may vary between sites within the same site type but soil texture (which influences decomposition rates) is only set once in the model.

When possible, local data from a 100-year old site was used for calibration as this was the most comprehensive data set available for the local ES20 site classification. This site actually represents the same stand as the 110-year old site used in this project; however, the data that the initial calibration has been based upon was colleted in 1992. See Edgington and Morris (2001) for a more detailed explanation of model calibration. The files used for calibration are located in Appendix V (site.100, tree.100, trem.100, fire.100, and fix.100). See either Metherell *et al.* (1993) or Hilinski *et al.* (2002) for definitions of the model variables.

For the purpose of comparing simulation results to the chronosequence data, a CENTURY model run called Unaltered was executed. The Unaltered run represented the initial configuration of the model. Scheduling of events in the model is controlled in the Site Management window. Two blocks were created for the Unaltered simulation. Because the model was calibrated with data from a 100-year old stand, the model was started at year 100. Growth was initiated in the month of May. In August a Burn event and a Tree Removal event were scheduled to represent a catastrophic forest fire that would return the stand to an early successional status. This was the first management block. The second management block was the equilibrium period that was used to stabilize the model pools. Following the suggestion by Edgington and Morris (2001), a 5000-year equilibrium period was to be used prior to implementing trials with the model. Because only natural, steady state conditions were desired for this project, CENTURY was only run until year 5000. Tree growth each year was initiated in May and stopped in September, except every 100th year when a Burn and Tree Removal event was also scheduled to restart stand development, as previously described for block 1.

The final rotation (years 4900 to 5000) was used as the Unaltered rotation for comparing simulated trends to real-world chronosequence measurements.

Data was collected from the suite of chronosequence sites with the purpose of using the data to validate the current local calibration of the CENTURY model. Some of the chronosequence data collected was not suitable or intended (e.g. soil physical descriptions) for the validation exercise. Table 3.7 shows the datasets that were selected for the validation exercise as well as their corresponding CENTURY model pools.

Annual means for each chronosequence pool (Table 3.7) were derived by averaging the individual measurements from each chronosequence site (T-0 to T-5). The comparable simulated values were derived by averaging the pool levels for the simulated months that corresponded with the RW measurements. Therefore, rather than a simulated annual mean being based on 12 months, the annual means were typically based on 6 months. Measures from the 110-year old site (Mature) were compared to data from simulated years 98 and 99 because simulations were set to run for 100 years. Biomass was a one-time measure at the chronosequence sites so the calculated biomass C and N were compared to one simulated month for each stand age. Monthly means soil temperatures were computed a full year for each chronosequence site when sufficient data existed.

Table 3.7 Measured real-world forest floor and belowground soil temperature, and C and N site parameters with the corresponding CENTURY model pools.

Pool Name	CENTURY Output Pools	Description of Equivalent Real-World Pool
Soil Temperature (STemp)	STEMP	Directly measured soil temperatures
Carbon Pools		
Aboveground Live Biomass (BIOcAB)	FBRCHC + RLEAVC + RLWODC	Calculated C in the aboveground live tree pools
Belowground Live Biomass (BIOcBL)	CROOTC + FROOTC	Calculated C in the belowground live tree pools
Total Live Biomass (BIOcTL)	FRSTC	Calculated C in the total live tree pool
Microbial Biomass and Microbial Products (MBPc)	SOM1C(1) + SOM1C(2)	MB-C (organic + mineral) * 2 [a] [b]
Total Soil (TSc)	MBPc + SOM2C + SOM3C	Total Soil C (organic + mineral)
Nitrogen Pools		
Aboveground Live Biomass (BIOnAB)	FBRCHE(1) + RLEAVE(1) + RLWODE(1)	Calculated N in the aboveground live tree pools
Belowground Live Biomass (BIOnBL)	CROOTE(1) + FROOTE(1)	Calculated N in the belowground live tree pools
Total Live Biomass (BIOnTL)	FRSTE(1)	Calculated N in the total live tree pool
Microbial Biomass and Microbial Products (MBPn)	SOM1E(1,1) + SOM1E(2,1)	MB-N (organic + mineral) * 2 [b]
Available N (AvailN)	AMINRL(1)	Mineral N (NH_4 + NO_3) available for plant uptake (organic + mineral)
Total Soil (TSn)	MBPn + SOM2C + SOM3C	Total Soil N (organic + mineral)
Nitrogen Mineralizing/Immobilizing Pools		
Total Soil (MNLZn)	S1MNR(1,1) + S1MNR(2,1) + S2MNR(1) + S3MNR(1)	Total Soil N Mineralization (organic + mineral)

[a] "organic + mineral" indicates the sum of the measurements made for the organic (FH) and mineral soil layers excluding roots (fine roots, coarse roots) and root litter (dead fine roots and dead coarse roots).
[b] Source: Metherell *et al.* (1993)

3.7 COMPARISON OF CHRONOSEQUENCE DATA TO CENTURY MODEL SIMULATIONS – STATISTICAL VALIDATION

Based on recommendations by Mayer and Butler (1993) five types of statistical validation methods were employed to evaluate the performance of the CENTURY model. These methods included deviance measures, paired *t*-tests ($\alpha = 0.05$), linear regression, a simultaneous *F*-test, and modelling efficiency (EF). The two deviance

measures used were mean absolute error (MAE) and mean absolute percent error (MA%E). The formulas for the deviance measures and modelling efficiency are:

$$\text{MAE} = \left(\sum |y_i - \hat{y}_i|\right)/n,$$

$$\text{MA\%E} = 100\left[\sum \left(|y_i - \hat{y}_i|/|y_i|\right)\right]/n, \text{ and}$$

$$\text{EF} = 1 - \sum (y_i - \hat{y}_i)^2 / \sum (y_i - \bar{y})^2$$

where y_i are observed real-world values, $\hat{y}_i$ are simulated values for the same points in time, $\bar{y}$ is the mean of observed values, and n is the number of pairs (observed and simulated). To test for slope = 1 and intercept = 0 from the linear regression the simultaneous F-test was used ($\alpha = 0.05$). Calculation of the F statistic was performed using the following equation:

$$F = \frac{n(b_0 - 0)^2 + 2\sum \hat{y}_i (b_0 - 0)(b_1 - 1) + \sum \hat{y}_i{}^2 (b_1 - 1)^2}{2\sum (y_i - \tilde{y}_i)^2 / (n-2)}$$

where b_0 is the y intercept coefficient, b_1 is the slope coefficient, $\tilde{y}_i$ is the predicted value from $y_i = b_o + b_1 \hat{y}_i$. The degrees of freedom for the F statistic are 2 for the numerator and $n - 2$ for the denominator.

When examining the results of the statistical tests it is important to understand the meaning of the numbers. The MAE is in the same units as the data whereas MA%E is a relative value. Both methods are a measure of the difference between the real-world and simulated data and smaller numbers indicate better model performance than larger numbers. Kleijnen (1987) recommended that for MA%E an upper limit of 10% be used to accept a model; however, Mayer and Butler (1993) suggest that setting an absolute limit is impractical and that the real value of deviance measures are to rank different

models. Paired *t*-tests simply compare the means of the observed and simulated values and determine whether the means are significantly different. Different means would indicate that the simulated data is different enough from the RW data that the model should be re-evaluated or re-calibrated. Linear regression seeks to quantify the extent to which a response variable (*y*, real-world) is influenced by a predictor variable (*x*, simulated). For model validation, the stronger the relationship between the RW and simulated data the better. As with any regression, a high R^2 (coefficient of determination, $1 \geq R^2 \geq 0$) is desired. Model validation also requires that the line of best fit, described by the linear model ($y_i = b_o + b_1 x$), to have a slope = 1 and a y-intercept = 0. In this situation model output would perfectly replicate real-world data ($y = \hat{y}$). The simultaneous *F*-test is used to test whether the slope =1 and the y-intercept = 0. Like the R^2 calculation, modelling efficiency is an indicator of goodness of fit; however, the modelling efficiency is a measure of the variation explained by the $y = \hat{y}$ line rather than the linear model. Modelling efficiency has a maximum of 1 (best) and a theoretical limit of negative infinity. A model achieving a modelling efficiency of less than zero should not be accepted (Mayer and Butler 1993).

4.0 RESULTS AND DISCUSSION

4.1 CHRONOSEQUENCE SITE DESCRIPTIONS AND MEASUREMENTS

A suite of seven upland sites in various stages of development following wildfire disturbance were located in the Thunder Bay area of northwestern Ontario. These seven sites formed the chronosequence from which all of the data for this study were collected, nd subsequently, compared to output from the CENTURY model for validation purposes. The following measurements made at each site describe the physical (*e.g.* vegetation, soil) and chemical (*e.g.* soil C and available N) properties, as well as estimates of C and N fluxes (soil respiration and N mineralization, respectively). Summarized data, including statistical analyses when applicable, are presented for each parameter. The majority of the data was summarized to the stand development stage level (i.e. regeneration, crown closure, self-thinning, and mature). To view the raw data and statistical analyses refer to Appendix VI and VII. At the end of this section there is a summary (4.1.13) to synthesize the data presented.

4.1.1 Vegetation Inventories

Vegetation inventories confirm that the chronosequence sites are suitable ES20s (Figure 4.1). By density, jack pine was initially the dominant tree species in the chronosequence giving way to black spruce after the crown closure stage. Trace amounts of white birch and trembling aspen were present throughout the chronosequence. While staying steady until the crown closure stage, stem density

dropped linearly through the self-thinning and mature stages. Little mortality or recruitment occurred over the first 30 years. Mean tree height and DBH were almost directly proportional and increased linearly over time. DBH was not measured at the regeneration stage sites because most trees were not yet tall enough.

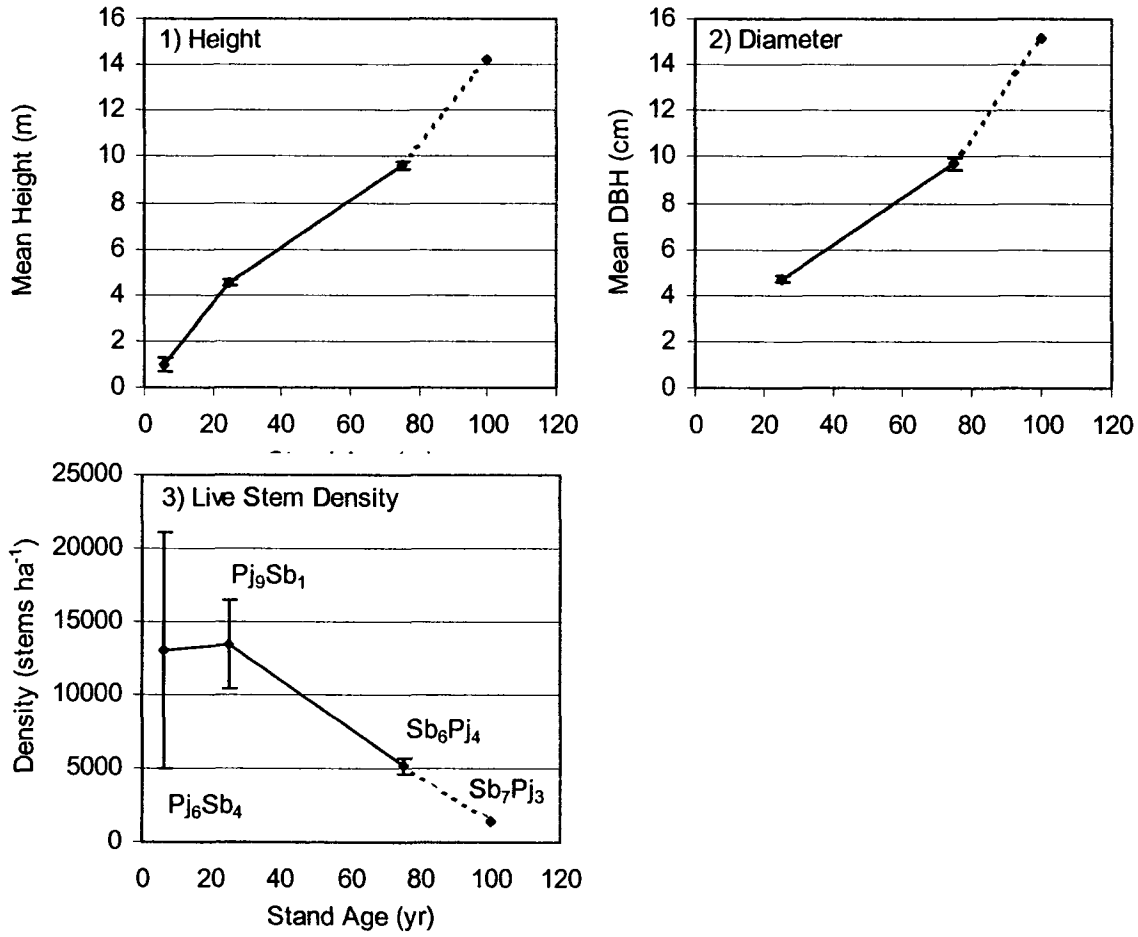

Figure 4.1 Mean height, DBH, and stem density of live trees across the stand development stages with standard error bars.

Calculations of live tree biomass reveal that biomass (and C and N) peaked at the self-thinning stage (Figure 4.2). Biomass was not calculated for the regeneration stage because height and DBH was not collected and it would be expected that the biomass at

this stage would be lower than the others because of the relatively shorter stem heights and smaller diameters. The higher stem density at the self-thinning sites more than compensated for having lower mean height and DBH than the mature site. Carbon to N ratios were steady through the crown closure, self-thinning, and mature stages, fluctuating between 369 and 388. The small differences are likely a factor of varying species compositions between stages. The C and N fractions used in calculations were species specific but not age specific.

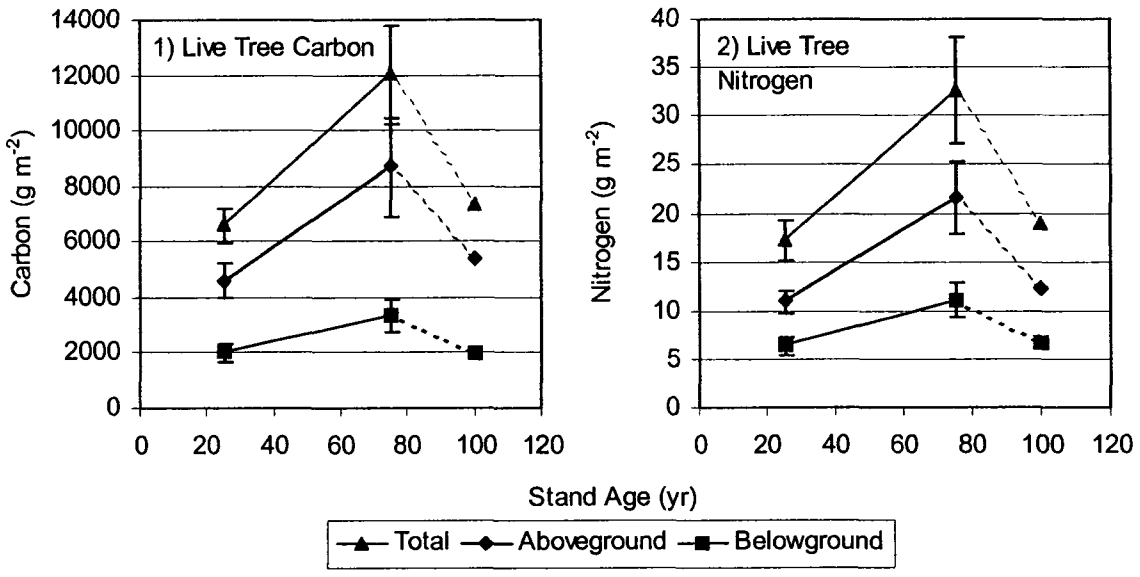

Figure 4.2 Calculated carbon and nitrogen in live tree biomass across the stand development stages with standard error bars.

Ground vegetation at the sites showed a distinctive trend of progressing from herbaceous plants at the younger sites to moss dominance at the older sites. The regeneration stage sites had sporadic ground vegetation with substantial portions of exposed duff. CrwnCl-1 also had sparse ground vegetation due to the high density of the trees and an almost continuous mat of needles overlying the F layer. Quantitative

measurements of percent coverage of ground vegetation species are not available; however, Table 4.1 does show lists of the common species noted at each site.

Table 4.1 Ground vegetation species present at chronosequence sites.

Chronosequence Site	Species Name
Regen-1	Sporadic distributions of: - fireweed (*Epilobium angustifolium* L.) - grasses (*Carex* spp.) - bunchberry (*Cornus canadensis* L.) - various mosses - blueberry (*Vaccinium* spp.) - labrador tea (*Ledum groenlandicum* Oeder) - wild red raspberry (*Rubus idaeus* L. var. *strigosus* (Michx.) Maxim.) - alder (*Alnus* spp.) - willow (*Salix* spp.)
Regen-2	Sporadic distributions of: - fireweed - bunchberry - grasses - wild red raspberry - various mosses
CrwnCl-1	Patchy distributions of: - laborador tea - Schreber's moss (*Pleurozium schreberi* (Brid.) Mitt.) - plume moss (*Ptilium crista-astrensis* (Hedw.) De Not.) - stair-step moss (*Hylocomium splendens* (Hedw.) BSG.)
CrwnCl-2	- sporadic ground pine (*Lycopodium obscurum* L.) - extensive blueberry - extensive labrador tea - patchy Schreber's moss, plume moss, and stair-step moss - patchy alder
SelfThin-1	Extensive mat of Schreber's moss, plume moss, and stair-step moss
SelfThin-2	Extensive mat of Schreber's moss, plume moss, and stair-step moss
Mature	- extensive mat of Schreber's moss, plume moss, and stair-step moss Sporadic amounts of: - sweet coltsfoot (*Petasites palmatus* (Ait.) Gray.) - bunchberry - twinflower (*Linnaea borealis* L.) - prickly wild rose (*Rosa acicularis* Lindl.) - labrador tea - ground cedar (*Lycopodium complanatum* L.) - stuff clubmoss (*Lycopodium annotinum* L.)

4.1.2 Forest Floor Fine Litter

Forest floor fine litter collections were summarized by grouping the sorted materials into foliage/herbaceous and fine woody debris groupings for each stand development stage. The combined litter pools were the lowest during the regeneration stage (Figure 4.3); however, significant differences between stages were not found through ANOVA. A sharp rise occurred between the regeneration and crown closure stages (308 to 642 g m^{-2}) after which the amount of litter on the forest floor declined with age to 417 and 362 g m^{-2} for the self-thinning and mature stages, respectively. Very little conifer foliage litter was recovered at the regeneration stage sites, but there was some herbaceous debris from the early-establishment herbs and shrubs present on the sites. The fine woody litter at the regeneration sites mainly originated from the pre-fire trees. At crown closure, the majority of forest floor litter was conifer needles, particularly at CrwnCl-1, and fine woody litter was at the lowest point of the chronosequence. The amount of fine woody litter clearly started to increase after the crown closure stage. Increased tree mortality and self-pruning following the crown closures stages are likely the cause of the increase of woody litter pools. In addition, the contribution of needle litter to the total litter dropped in the self-thinning and mature stages. This may be partially attributed to the greater difficulty of recovering all the needles, particularly black spruce needles, because of the thick moss layers at the sites. The regeneration and crown closure sites had less moss and black spruce making collecting and sorting the litter easier. Also, Morrison (2003) found that jack pine needle litter underwent greater mass loss when incorporated into the feathermoss layer of a 70-year old self-thinning stand, so the reduced levels of foliage litter at the older chronosequence sites may also be attributable to faster decomposition. Presumably,

black spruce needles and other types of litter would also decompose faster when incorporated into the moss layer. Live tree biomass also decreased with age which would have reduced foliage litter inputs; however, Wang *et al.* (2003) did not find that forest floor C pools were related to litterfall rates.

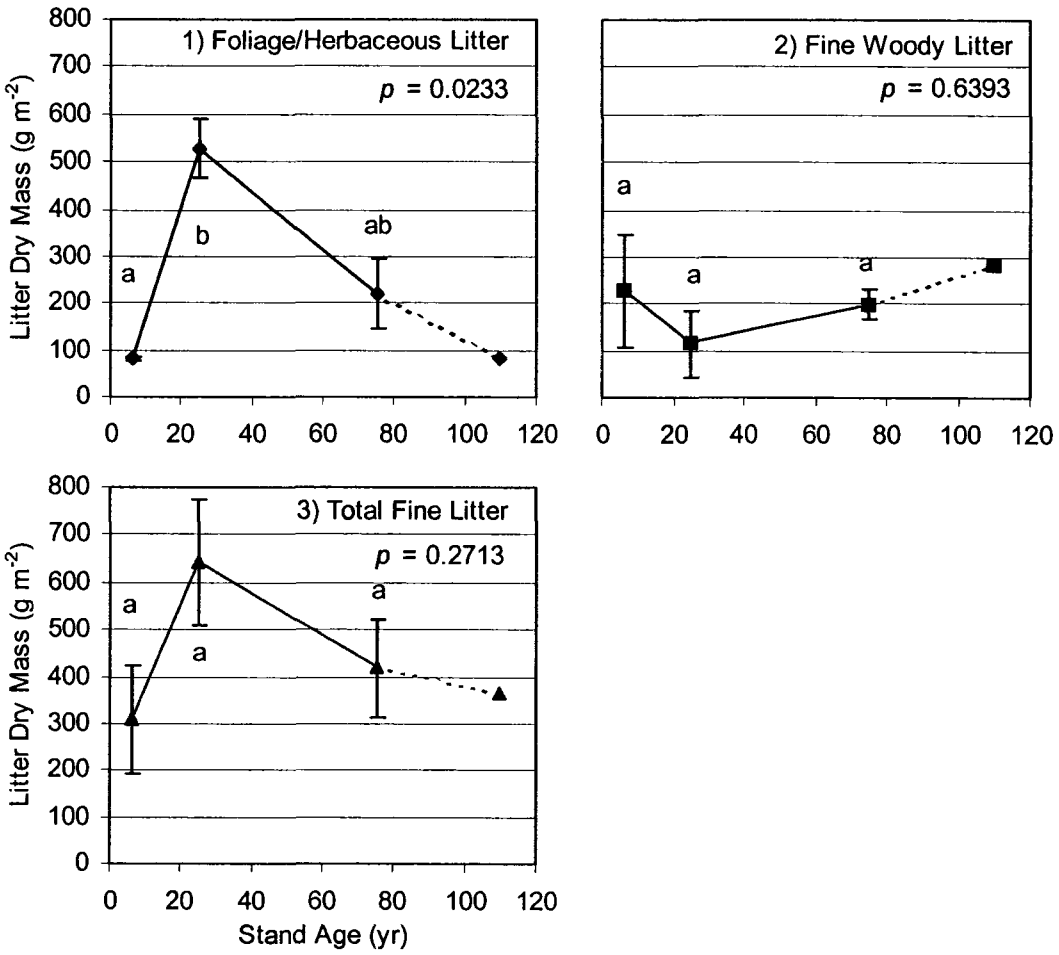

Figure 4.3 Dry mass of measured forest floor 1) foliage/herbaceous, 2) fine woody, and 3) total fine litter with standard error bars for stand development stages and ANOVA results.

The spike of foliage/herbaceous litter at the crown-closure sites can be attributed to the dense spacing of the trees and the resulting 'lifting' of the live crown. Particularly

at CrwnCl-1, the density of the trees has reduced the amount of light available to lower branches and consequently, these branches are dying, thus resulting in substantial deposits of needles to the forest floor. The only significant difference between stages resulted from this spike. While the crown closure stage was significantly higher than the regeneration stage, the regeneration stage and self-thinning stages were not significantly different.

The trend of fine woody litter accumulation appears quite realistic. Following disturbance, large amounts of debris from the previous stand would be deposited on the forest floor, followed by a period of rapid tree growth with little competition and therefore little self-pruning of branches. As the forest matures, self-pruning and self-thinning increase which results in greater amounts of woody litter.

Overall, the chronosequence sites have much lower quantities of fine litter than the jack pine sites of MacLean and Wein (1977). For all sites, the dry mass of litter ranged between 1935 and 7727 kg ha^{-1} (Regen-2 and CrwnCl-1, respectively), whereas MacLean and Wein (1997) reported amounts of between 6340 and 19370 kg ha^{-1} from their 57-year chronosequence. Without quantification of litterfall, it is difficult to determine whether the differences are the result of less litterfall over time, greater decomposition rates, or sampling discrepancies.

4.1.3 Soil Physical Descriptions

Table 4.2 displays horizon depths, bulk densities, coarse fragments, volume, dry mass, and soil textures of organic and mineral soils for each chronosequence site. Mineral soil depths on all sites were relatively shallow at around 20 cm on average. A discontinuous Ae horizon was noted on several sites but has not been presented because

only the Bm layer was sampled for chemical characteristics. The organic layer thickness overall ranged from a 5.3 cm average at Regen-2 to an average of 10.7 cm at the CrwnCl-1. Following crown closure, organic layer thickness remained relatively stable. Thinner layers at the regeneration stage sites were expected considering they were recently burned and have had minimal fresh litter inputs. Bulk density of the organic layer does not appear to follow any trend with age. Chronosequence site values fell within a range of 0.077 to 0.155 g cm^{-3} (Regen-2 and Regen-1, respectively). Mineral soil bulk densities appeared to be fairly consistent and ranged between 0.752 g cm^{-3} (CrwnCl-2) and 1.110 g cm^{-3} (CrwnCl-1). Regen-2 had the lowest mass of organic materials at 40.5 Mg ha^{-1} resulting from the lowest thickness and bulk density. The mass of the organic layer was almost half that of the next lowest site (SelfThin-2) and not even a third as heavy as the chronosequence site with the greatest organic layer mass (CrwnCl-1). In all cases, the ranges of physical characteristics across the sites allow them to be classified as ES20s.

For modelling purposes, on those sites with mean mineral soil depths greater than 20 cm, soil mass was calculated to a maximum depth of 20 cm to more closely replicate the 20 cm simulation depth setting in the CENTURY model (edepth in fix.100). Similarly, nutrient volumes in the mineral soil were only calculated for up to 20 cm depths. The Bm layers for the regeneration and crown-closure sites were adjusted and set to 20 cm. The thicknesses of organic layers were not altered.

Table 4.2 Volume and mass of organic and mineral soil layers for chronosequence sites and volume and mass of mineral soil truncated to a maximum of 20 cm depth to mimic the 20 cm simulation layer thickness setting in the CENTURY model. Standard error of plot means presented in parentheses where available.

	Organic Layer				Bm Mineral Soil							
	Site Means				Site Means						Mineral Depths Set To a Max of 20 cm	
		Bulk					Bulk	Percent				
Chronosequence Sites	Thickness (cm)	Density (g cm^{-3})	Volume (m^3 ha^{-1})	Mass (Mg ha^{-1})	Soil Texture	Thickness (cm) [a]	Density [b] (g cm^{-3})	Large CF [c] (%)	Volume [d] (m^3 ha^{-1})	Mass (Mg ha^{-1})	Volume (m^3 ha^{-1})	Mass (Mg ha^{-1})
Regen-1	6.1 (0.6)	0.155	609.4	94.2 (8.5)	Loamy Sand	22.2 (2.6)	1.07 (0.03)	20.0	1778	1982 (136)	1600	1637 (52)
Regen-2	5.3 (0.6)	0.077	528.2	40.5 (4.5)	Sand	25.1 (1.3)	1.07 (0.10)	10.0	2258	2397 (121)	1800	1929 (185)
CrwnCl-1	10.7 (1.7)	0.141 (0.004)	1066.7	149.2 (27.8)	Sand	36.0 (3.0)	1.11 (0.16)	25.0	2700	3725 (1536)	1500	1944 (754)
CrwnCl-2	10.1 (1.0)	0.105 (0.021)	1014.2	102.2 (10.2)	Silty Sand	22.4 (2.6)	0.75 (0.06)	0.0	2242	1709 (329)	2000	1450 (155)
SelfThin-1	10.1	0.098	1010.0	99.0	Silty Sand	18.6	0.96	3.0	1804	1735	1804	1735
SelfThin-2	8.9 (1.0)	0.085	890.8	75.8 (8.4)	Silty Sand	15.0 (2.7)	0.87 (0.08)	5.0	1427	1278 (339)	1427	1270 (332)
Mature	8.3	0.098	830.0	81.3	Silty Loam	16.6	1.04	--	1660	1726	1660	1726

[a] Partial estimates, includes 20+ measures as 30 cm to balance depths less than 20 cm.

[b] Bulk density adjusted for fine coarse fragments = (soil - CF) / (vol cylinder - vol CF).

[c] 3.0 % for 1920 site suggested by Duckert (*pers comm.* 26 Nov 2004); large CF at 1892 already accounted for.

[d] Volume adjusted for large coarse fragment percentage of the soil.

4.1.4 Measured Air and Soil Temperatures at Chronosequence Sites

Temperature curves including monthly maximum and minimum ranges are presented in Figure 4.4 for each stand development stage. The data for the mature site is an average from years 1994 to 2002 that was collected by CNFER at their study area immediately adjacent to the plots established for this study. Missing values indicate that fewer than 25 days of data were available, except at the mature site where data was not collected through the winter. Datalogger malfunctions and damage caused by wildlife to the dataloggers were the main cause of lost temperature data.

Despite variations in the canopy cover present between the chronosequence sites, air temperatures over the measurement period were almost identical at each stand development stage and will be presented from this point forward as the mean of all site data. Air temperatures fluctuated around the monthly means by as much as 10°C and as little as 2°C. The greatest fluctuations occurred in the spring months (May and June) with the least in the fall and winter months. Open canopy conditions allowed greater air temperature fluctuations in the regeneration stage sites than in the crown-closure, self-thinning, or mature stage sites.

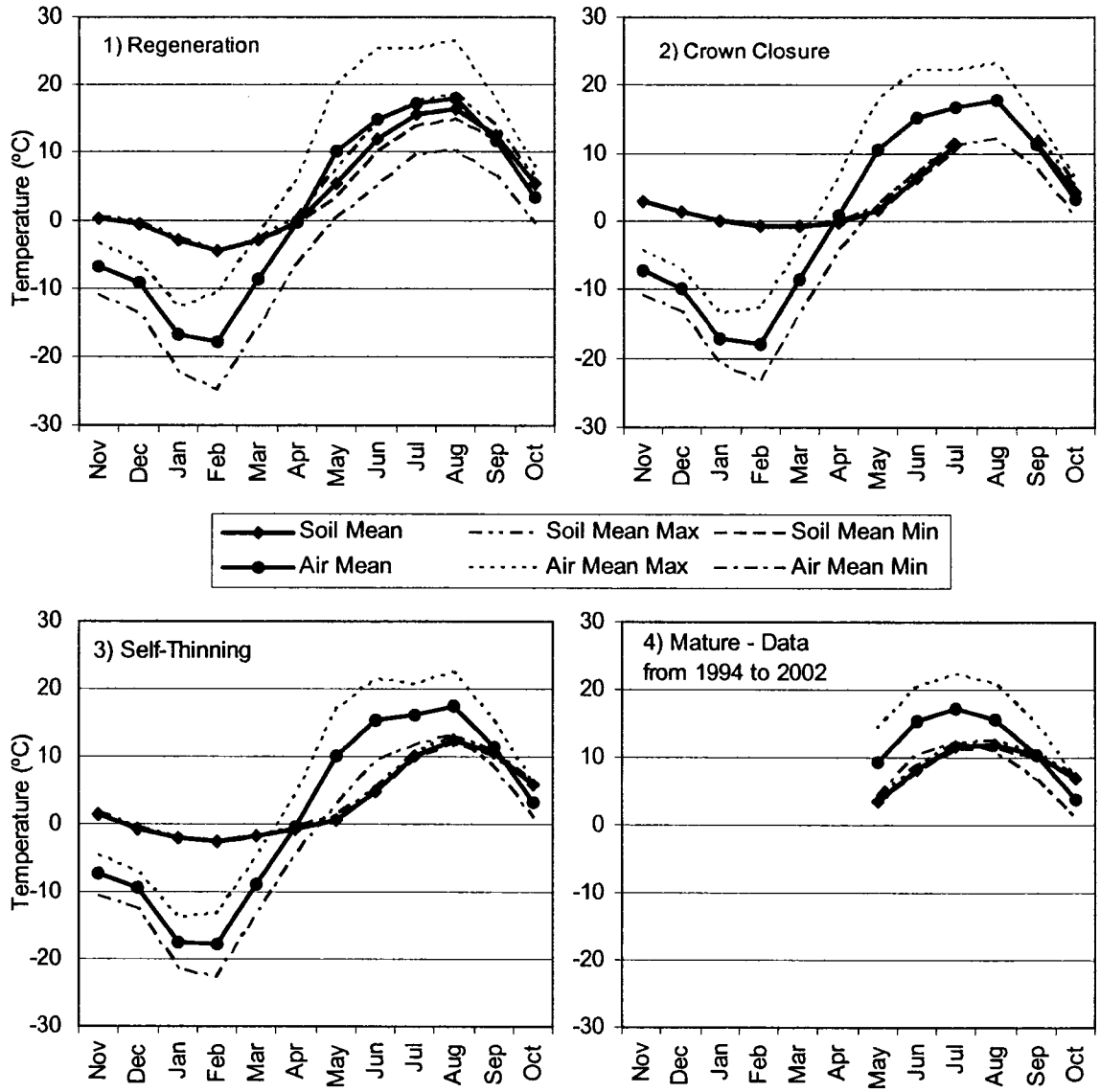

Figure 4.4 Mean monthly air and soil temperatures including ranges recorded between November 2002 and October 2003 at chronosequence sites in stand development stage groupings.

Soil temperatures were more variable than air temperatures between the development stages but did follow identifiable patterns. Temperatures for the regeneration stage were higher in the growing season months and lower in the winter months than the other three stages. Although there were some gaps, the soil temperature

curves for the crown-closure, self-thinning, and mature stages appeared to be almost identical. Fluctuations in soil temperature were very small but most pronounced for the regeneration stage indicating that soil heating and cooling occurs more quickly at these sites. From April to August, soil temperature increases lagged behind rising air temperatures by as much as 4.8°C for the regeneration stage (May 2003), and 10.4°C for the older stages (June 2003 for self-thinning). It should be noted that these temperature lags are greater than the programmed 2.0°C temperature lag that the CENTURY model uses in calculations of soil temperatures indicating a weakness with the model. Summing growing degree days through the growing season would more clearly reveal the cumulative effect of the lags between sites; however, too many gaps in the data were present to permit these calculations (see Appendix V, Table A6 and A7 for monthly temperatures at individual chronosequence sites). The insulating effect of snow cover was apparent during the winter months when air temperatures were much lower than soil temperatures which only went a few degrees below freezing. Overall, the differences between the stand development stages probably coincide with the onset of crown closure of the regenerating trees and also increasing amounts of insulation provided by a live-moss layer. In the absence of crown closure and a continuous moss layer, regeneration stage sites are exposed to harsher temperature conditions driven by greater air and soil temperature extremes and fluctuations.

4.1.5 Soil Moisture

Gravimetric moisture content measurements (i.e. ratio of water in the soil relative to dry soil expressed as a percentage) were made on each occasion that soils were

sampled at the chronosequence sites (T-0 to T-5) (Figure 4.5). The primary reason for calculating moisture contents was to use the values in chemical analyses; however, some trends were observed that were worth reporting. Regeneration sites had the lowest moisture contents at almost all measurement occasions for both organic and mineral soils most likely because of greater sun and wind exposure, and also quickly draining sandy soils. The crown closure stage had the highest mineral soil moisture contents. The mature stage site had the highest moisture contents in the organic layer. Seasonally, the highest moisture contents were found in the month of May (T-1) for organic and mineral soils, and the lowest in June (T-2) for organics.

The relatively high moisture content of mineral soils in the crown closure stage was mainly because of the CrwnCl-2 site which had a mean moisture content of 59%. These soils are silty sands that are able hold water well in the more abundant pore space. Also, small basins in the bedrock may have restricted drainage from some areas of the site thereby elevating the moisture content in the soil (personal observation). CrwnCl-1 had a lower mean moisture content at 24% because of the quicker draining sandy soils.

The mature site had the highest organic layer moisture content. The moisture contents of the two sites in the self-thinning stage were not very similar as can be seen by the wider standard error bars in Figure 4.5. The mean moisture content for SelfThin-2, at 245%, was actually very similar to the mature site at 250%. The reason for the differences may have been in the species of moss present. All three sites had continuous mats of moss cover; however, in addition to feathermosses, SelfThin-2 and the Mature site had sporadic occurrences of sphagnum moss that holds moisture more effectively than feathermoss.

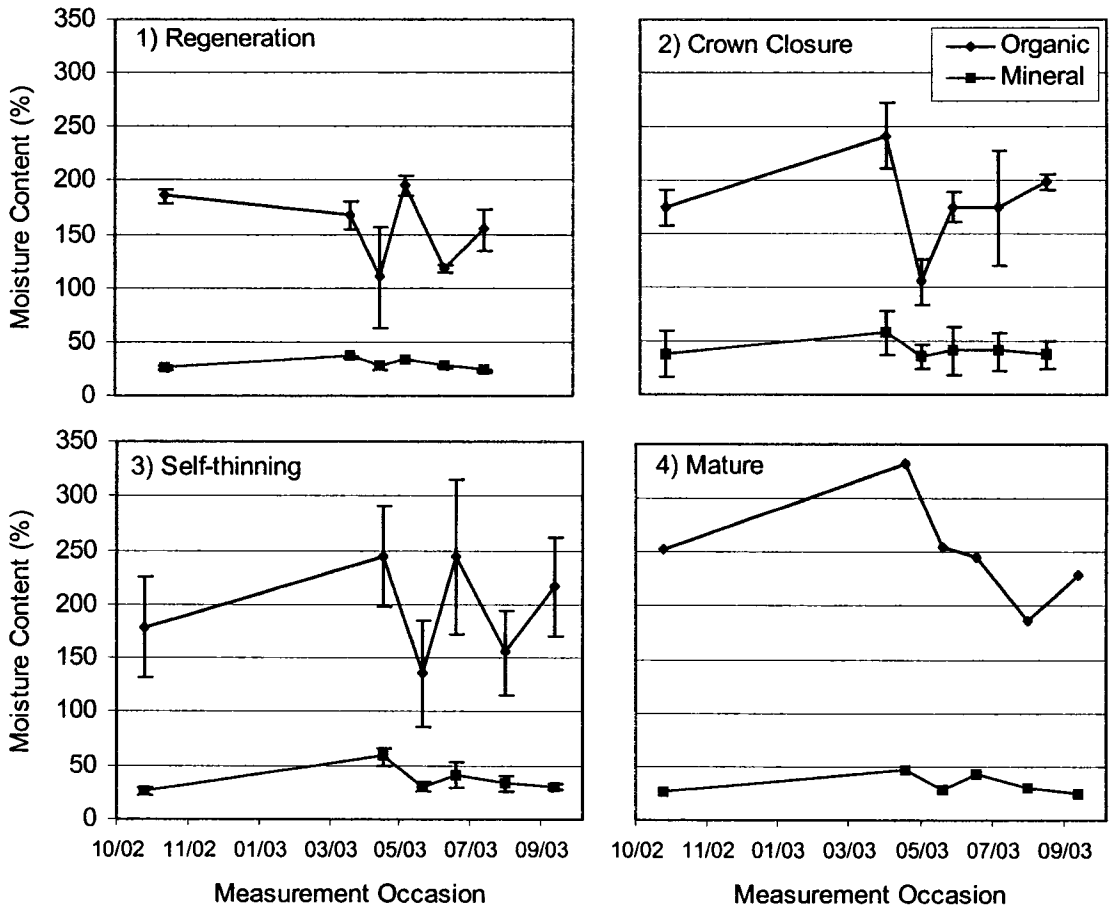

Figure 4.5 Mean monthly gravimetric moisture contents for organic and mineral soils, with standard error bars, for each stand development stage. Error bars not possible for the mature stage because the site was not replicated.

Mineral soil moisture contents peaked in the spring most likely because extra moisture was present following the snow melt. Seasonally, organic soils were more variable as would be expected because of greater exposure to sun and wind. Very little rainfall occurred between T-1 and T-2 (personal observation) which explains the low moisture contents recorded for the T-2 measurement occasion.

4.1.6 Soil pH

Mean pH values over the six measurement occasions were stable through time and similar between sites. For mineral soils, mean annual pH ranged between 4.3 and 4.4 for the four stand development stages. Organic soils were slightly more variable but also stable over time and between development stages, with the exception of the regeneration stage that had a mean annual pH of 3.9 versus 3.2, 3.1, and 3.1 for the crown-closure, self-thinning, and mature stages, respectively. The higher pH of organic soils at the regeneration stage sites may be indicative of the greater amounts of higher quality litter (i.e. foliage and herbaceous materials) relative to more acidic litter fractions such as conifer needles. Ash deposition following fire disturbances may also have affected soil acidity.

4.1.7 Total Soil Carbon and Nitrogen

Measurements of mineral soil total soil C and N were only available for the T-0 (October 2002) measurement occasion because of equipment difficulties. Total C and N were determined for the T-0, T-1, T-3, and T-5 organic layer samples. These measurements were averaged to create an annual mean for each site. Examination of the organic data, revealed that seasonal fluctuations were very minimal so it was judged that the T-0 mineral soil measurements would adequately describe the sites.

Mean annual measurements of total soil C and N for the stand development stages often had high variation between the chronosequence sites and very few significant differences were found between stages (Figures 4.6 and 4.7). The total C in the combined organic and mineral soil (up to 20 cm depth) for the crown closure sites

was the only significantly different stage. Separately, the crown closure stage had greater amounts of total C in the organic and mineral soil than did the other stages but only when added together did the difference become significant. ANOVA did not find any significant differences between stages for total soil N. The mature stage was not included in the ANOVA because replicate sites were not available, but the total C and N amounts measured for the mature stage were similar to the other stand development stages.

Overall, the total C and N trends observed from the chronosequences sites are fairly similar to the findings of other authors. For mineral soil, Rothstein *et al.* (2004) and Smith *et al.* (2000) found no effect of wildfire or stand age on C levels. The organic layer is generally believed to decline following fire and gradually return to pre-disturbance levels over the course of stand development (Kurz *et al.* 1992; Rothstein *et al.* 2004; Wirth *et al.* 2002; Bhatti *et al.* 2002). Organic layer carbon values are within the ranges presented by Morrison *et al.* (1993), Smith *et al.* (2000), and Simard *et al.* (2001).

Higher total C levels (organic + mineral) in the crown closure stage were mainly related to the larger mass of the organic layer. Both CrwnCl-1 and CrwnCl-2 had more material in their organic layers than any of the other chronosequence sites so despite relatively average concentrations of C, totals were higher than at other sites. The mean concentration of C in the organic layer for the crown closure stage was 41.1% which was well within the range of 36.9 to 42.7% for the other stages (Table 4.3).

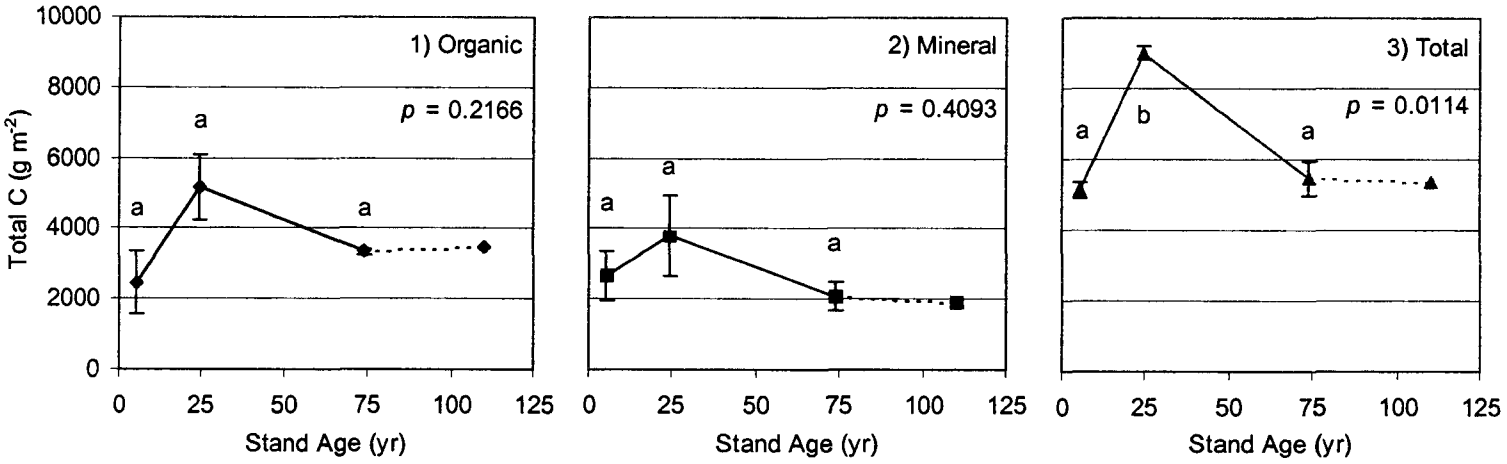

Figure 4.6 Annual means of total soil carbon for stand development stages with standard error bars.

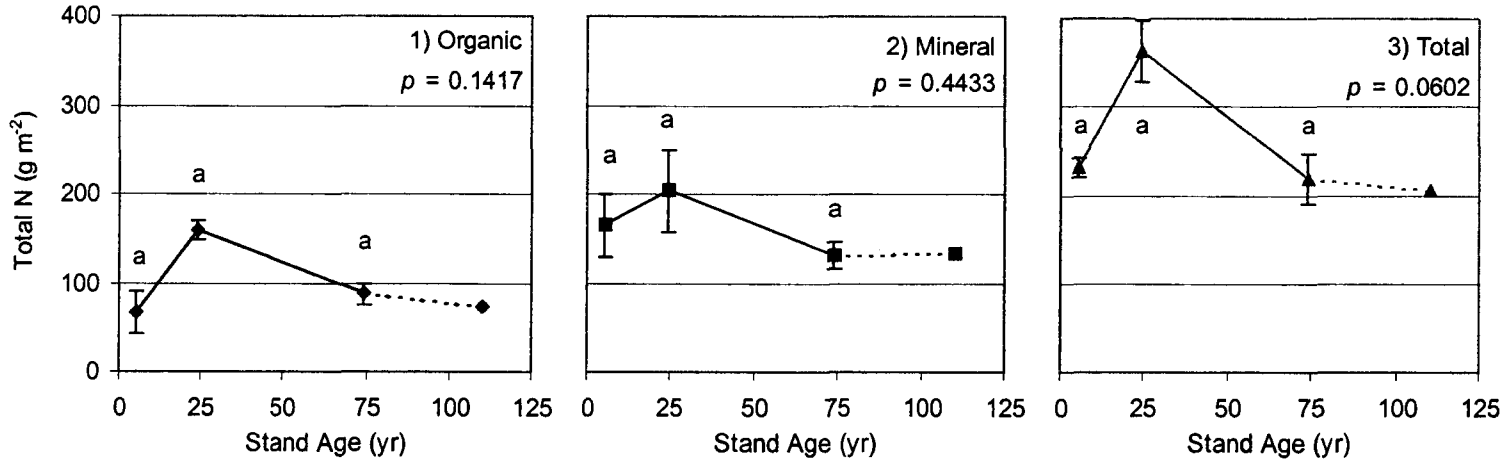

Figure 4.7 Annual means of total soil nitrogen for stand development stages with standard error bars.

Table 4.3 Concentrations of total carbon and nitrogen and C:N ratios based on masses at each stand development stage.

	Stand Development Stage			
	Regeneration	Crown Closure	Self-Thinning	Mature [a]
Organic		-------- % --------		
Total C	36.9	41.10	39.15	42.67
	(1.09)	(0.41)	(4.37)	
Total N	1.00	1.29	0.99	0.89
	(0.03)	(0.16)	(0.01)	
Mineral				
Total C	1.47	2.44	1.34	1.09
	(0.25)	(1.09)	(0.09)	
Total N	0.09	0.13	0.09	0.08
	(0.01)	(0.05)	(0.00)	
	C:N Ratio Based on C and N Masses ($g\ m^{-2}$)			
Organic	37.1	32.5	38.5	48.1
Mineral	16.1	18.7	15.8	14.1
Total	22.1	24.8	24.9	26.0

[a] Only one site measured so statistical analyses were not possible.
Numbers in parentheses indicate the standard error of the mean.

Mean concentrations of C from all stand development stages were 40.0 and 1.59% for the organic and mineral soils, respectively. A mineral soil measurement of 3.52% C at CrwnCl-2 inflated the mean for the crown-closure stage to 2.44%. CrwnCl-1 had a mineral soil C fraction of only 1.35%. The mean concentrations of N were 1.04% and 0.10% for the organic and mineral soils, respectively. Again, a high measurement at CrwnCl-2 of 1.8% drove up the mean for the crown-closure stage.

Concentrations of C and N in the organic and mineral soils at the chronosequence sites were similar to values presented by other authors. Smith *et al.* (2000) reported C concentrations of 39.2 and 34.6% in organic horizons at a recent and old burn, respectively, and 1.57 and 2.26% for mineral soils in the same stands. Nitrogen concentrations at the recent and old burn sites were 1.0% in the organic horizons (both sites) and 0.05 and 0.08% in the mineral soils. MacLean and Wein

(1977) reported an average N concentration in the organic layer of 0.81% within a range of 0.55 to 1.11%. Driscoll *et al.* (1999) reported a range of 1.5 to 1.8% total soil N for the forest floor (L, F and H) and from 0.10 to 0.20% in the mineral horizons (A and B).

Carbon to N ratios across the stand development stages were in a fairly tight range. For the organic and mineral soil combined, the range was 22.1 to 26.0. For the organic layers, the C:N ratios for the regeneration, crown closure, and self-thinning stages were 37.1, 32.5, and 38.5, respectively. The ratio for the mature site was higher at 48.1. For the mineral soil the C:N ratios ranged between 14.1 and 18.7.

As seen in Figure 4.7 and by the close range of C:N ratios, total soil N generally follows a pattern similar to total soil C over stand development. Therefore, a decrease in organic layer N was expected for the regeneration stage which did occur but not at a significant level, and total N in the mineral soil remained relatively stable. The levels of total N in the organic layer are similar to those reported by Smith *et al.* (2000), Simard *et al.* (2001), and Duckert and Morris (2001). For the mineral soil, the total N levels found by this study were often higher than those reported from other studies; however, part of this may be because of different depths sampled. For example, Smith *et al.* (2000) reported total N of 85.1 and 113.9 g m^{-2} for recent and old burns, lower than the 131 to 203 g m^{-2} range found with this study. However, the pools calculated by Smith *et al.* (2000) were only for a depth of 10 cm; whereas ours were for a depth of up to 20 cm.

4.1.8 Available Inorganic Nitrogen from Fresh Soils

No significant differences (at $\alpha = 0.05$) in the mean annual amount of inorganic N available for plant uptake were detected between the stand development stage

groupings (Figure 4.8). These findings were similar to studies by MacLean and Wein (1977) and Driscoll *et al.* (1999). The value from the mature stage fell within the ranges produced by the other stages. Ranges across the stand development stages were 0.086 to 0.209 g m^{-2} for organics, 0.127 to 0.481 g m^{-2} for mineral, and 0.248 to 0.599 g m^{-2} for the organic and mineral soil combined. The majority of the available N was located in the mineral soil with the exception of the self-thinning stage where approximately equal amounts were in the organic and mineral soil. While greater concentrations were found in the organic layers, the substantially larger mass of the mineral soil compensated for lower concentrations. Available N may also be utilized more rapidly by plants and microbes in the organic layers since rooting is prevalent (especially black spruce) in the organic layers and concentrations of microbes are higher (see Section 4.1.9). Although not significant, it appears that available N decreases with stand age in the mineral soil which may be related to fewer organic inputs to the mineral soil resulting from more rooting taking place in the organic layer as the organic layer thickens and becomes moister. Uptake is also likely to increase through time due to the demands of trees and increasingly prolific moss layers.

The standard error of the mean for mineral soil in the crown closure stage (0.175 g m^{-2}) was quite large because of the large difference between CrwnCl-1 and CrwnCl-2 (0.215 and 0.566 g m^{-2}, respectively). Large differences were also found in the concentration of available N at the two sites (CrwnCl-1 at 8.812 μg g^{-1} and CrwnCl-2 at 30.928 μg g^{-1}). Similarly, CrwnCl-2 also had higher concentrations of total N in the mineral soil at 0.175% compared to 0.082% at CrwnCl-1. Higher levels of available N

at CrwnCl-2 were therefore a result of different chemistry rather than mineral soil mass which is actually greater at CrwnCl-1.

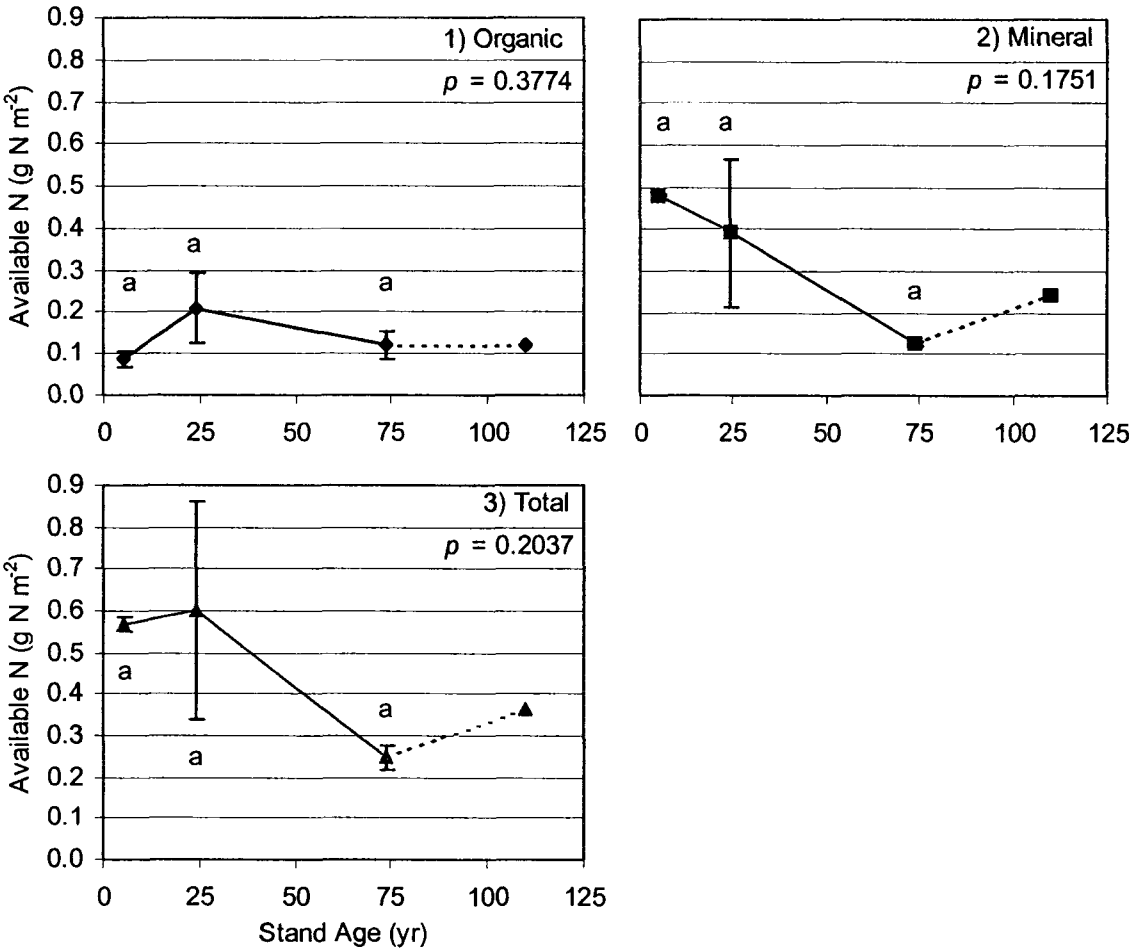

Figure 4.8 Annual means of available N (NH_4 + NO_3) for stand development stages with standard error bars and ANOVA results.

The majority of available N at all the chronosequence sites was in the form of NH_4. Nitrate never contributed more than one third to the total available N (Appendix VI). Nitrate levels were the highest for mineral soil at the regeneration development stage sites. These warmer soils (section 4.1.4), with presumably less plant uptake, would result in creating conditions that were conducive to greater nitrification and thus

higher levels of NO_3 (Paul and Clark 1989). Driscoll *et al.* (1999) also reported higher amounts of NO_3 in the organic horizons at the early-seral stage. The mid- and later-seral stages had successively lower amounts of NO_3.

4.1.9 Microbial Biomass Carbon and Nitrogen

Microbial biomass C and N pools were both higher in the organic horizons for all stand development stages except the regeneration stage (Figure 4.9 and 4.10). For this stage the mineral soil had slightly more MB-C and MB-N. For the mature stage, MB-C and MB-N was within the range from other stages. Microbial biomass C and N pools in the mineral soil were steady across development stages. Fluctuations in the organic layer – mirrored in the totals – had the lowest levels in the regeneration stage, highest at crown closure, with declines as the stands matured.

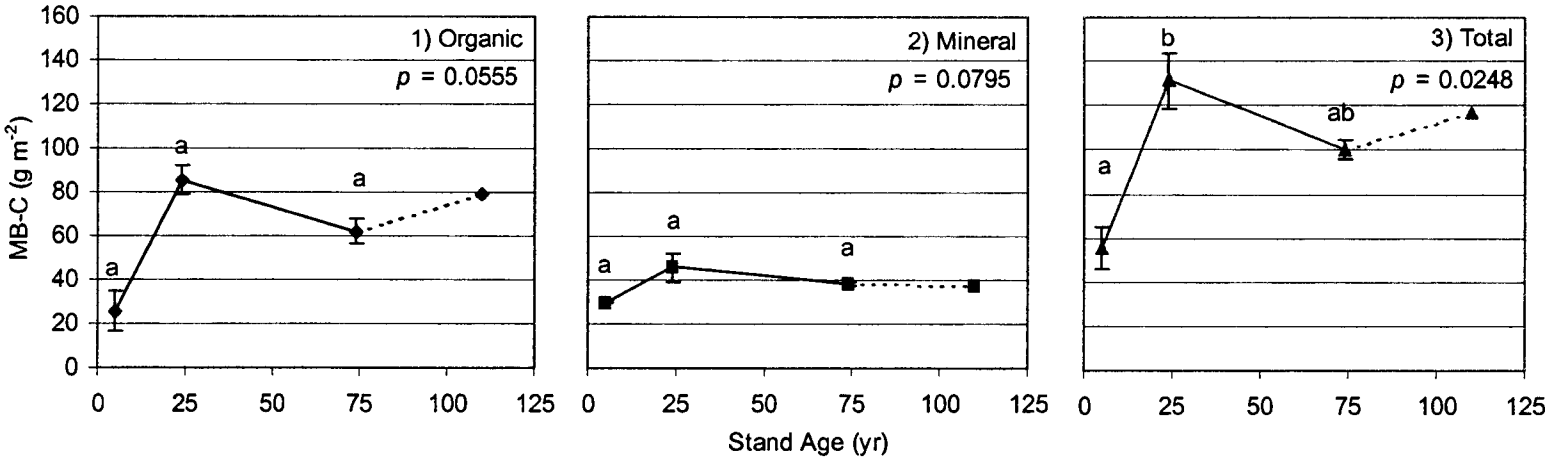

Figure 4.9 Annual means of microbial biomass carbon for stand development stages with standard error bars.

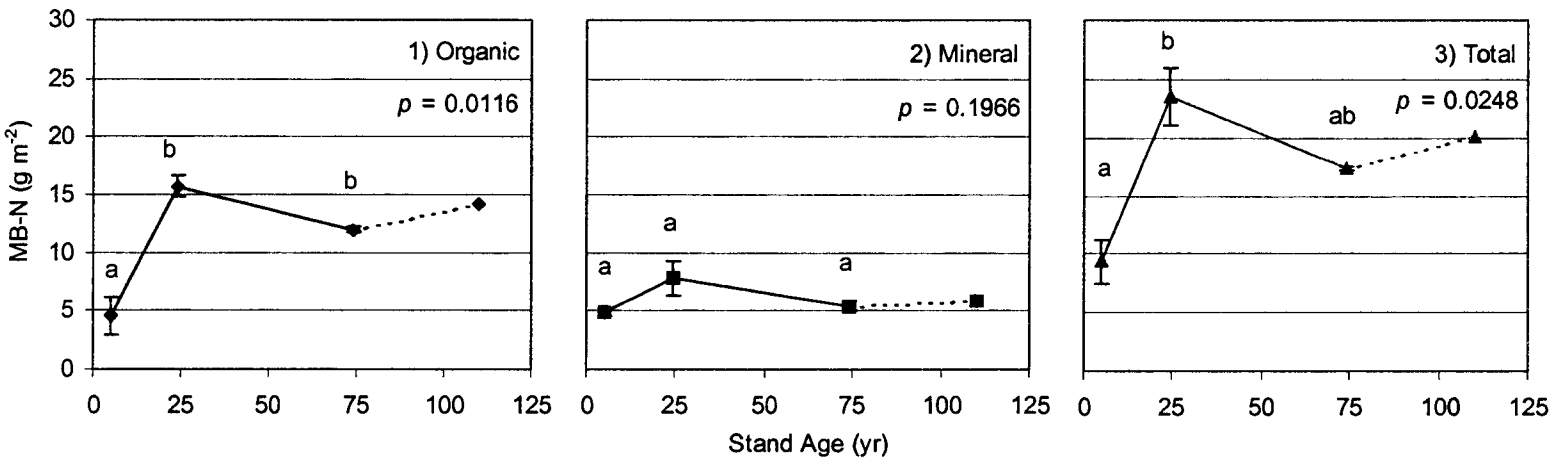

Figure 4.10 Annual means of microbial biomass nitrogen for stand development stages with standard error.

The most prominent MB trend appears to be that pools in the organic layer are reduced during fire disturbances or during the regeneration stage but recover to levels as high as or higher than pre-fire conditions in the crown closure stage. After the crown closure stage, levels remain relatively stable. Either fire or the post-fire conditions have an apparent effect on MB. Measurements revealed that concentrations (i.e. $\mu g\ g^{-1}$) of MB-C and MB-N were lowest in the regeneration stage (Table 4.4). Following the regeneration stage, in organic soils, MB concentrations increased with time, and in mineral soils, MB concentrations peaked at the crown closure stage. Site-level measures (i.e. $g\ m^{-2}$) were primarily influenced by the concentrations rather than the masses of soil at each site. Low concentrations in the regeneration stage may be the result of lower soil moisture in both the organic and mineral horizons (Killham 1994) and in the type of litter inputs to the soil. Forest floor fine litter collections revealed that fine woody litter was more prevalent than more easily degradable foliage/herbaceous litter at the regeneration stage. Also, due to less live plant biomass on the sites, easily consumable fine root litter and root exudates would not be available to the same extent as in the later stand development stages.

The highest levels of MB-C and MB-N were always in the organic layer soils except at the regeneration stage where pool sizes were equal with those in the mineral soil. Because no significant differences were detected, it seems that MB in the mineral soil was either not significantly affected by wildfire disturbance or stand development stage, or the MB pool had sufficient time to recover to pre-disturbance levels.

Table 4.4 Mean annual microbial carbon and microbial nitrogen soil concentrations, and C:N ratios from stand development stages.

	Stand Development Stage			
	Regeneration	Crown Closure	Self-Thinning	Mature [a]
Organic		-------- μg g^{-1} --------		
MB-C	3801	7181	7271	9765
	(140)	(1828)	(1543)	
MB-N	672	1319	1380	1743
	(21)	(318)	(201)	
Mineral				
MB-C	168	304	267	215
	(15)	(71)	(41)	
MB-N	27.3	51.4	37.6	34.3
	(3.8)	(15.8)	(3.6)	
	C:N Ratios C:N Ratio Based on C and N Masses (g m^{-2})			
Organic	5.6	5.5	5.2	5.6
Mineral	6.2	5.9	7.0	6.3
Total	5.9	5.6	5.8	5.8

[a] Only one site measured so statistical analyses were not possible.
Numbers in parentheses indicate the standard error of the mean.

Uchida *et al.* (1998) also reported higher amounts of MB-C in the organic layer soils; however, Pietikäinen *et al.* (1999) reported the opposite for Scots Pine sites in Finland with approximately only 25% of MB-C in the organic horizons. The difference may be partially explained by the thickness of the organic horizons. For the total of the L, F, and H horizons, Pietikäinen *et al.* (1999) reported a thickness of 5.4 cm; whereas, the average across all the chronosequence sites for this study was 8.5 cm, not including the litter layer. Therefore, even if concentrations of MB-C were equal between studies (concentrations not reported by Pietikäinen *et al.* (1999)), site-level MB-C would differ. Amounts of total MB-C were generally within the range of 78.5 to 167 g m^{-2} presented by other authors (Pietikäinen *et al.* 1999 and Uchida *et al.* 1998, respectively) and 21.7 to 67 g m^{-2} for organic soil only (Pietikäinen *et al.* 1999 and Vance and Chapin III 2001, respectively).

The C:N ratios of the MB pools were quite stable across the stand development stages (Table 4.4). For the organic horizons the C:N range was between 5.2 and 5.6. For the mineral soils the C:N ratio was 5.9 to 7.0. The MB C:N ratios for the combined organic and mineral soils were 5.6 to 5.9. The C:N ratio of bacterial microbes has a tight range of 3:1 to 5:1 and fungi have wider ranges of between 4.5:1 to 15:1 (Paul and Clark 1989). Therefore, the majority of MB measured from the chronosequence is most likely fungi rather than bacteria which is logical given the relatively low pH conditions at these sites. The lower the C:N ratio, the better nourished the MB population; therefore, because the overall ratios are just under 6.0 (i.e. near the low end of the C:N range for fungi), the MB populations in this chronosequence site are in good supply of N. Since the MB does not seem to be limited by N supply, then MB population growth must be limited by easily consumable organic materials. Vance and Chapin III (2001) found that microbial respiration in Alaskan forest soils (including black spruce) responded most rapidly to labile C (sucrose) additions rather than N, or C and N additions.

The MB-C pool accounted for between 1.04 and 2.29% of the total soil carbon pool (see Section 4.1.7) as seen in Table 4.5. Fractions of MB-N ranged between 2.92 and 19.63%. Both MB-C and MB-N fractions increased through the stand development stages with smallest fractions in the regeneration stage and the highest in the mature stage. Fractions were generally similar between organic and mineral horizons for MB-C, however, MB-N fractions of the total mineral soil N pool were 1/5 to 1/2 lower than in the organic horizon.

Table 4.5 Microbial carbon and microbial nitrogen fractions of the total soil pools of carbon and nitrogen.

	Stand Development Stage			
	Regeneration	Crown Closure	Self-Thinning	Mature
MB-C	-------- % of Soil Total Carbon --------			
Organic	1.04	1.65	1.85	2.29
Mineral	1.12	1.20	1.83	1.98
Total	1.08	1.46	1.84	2.18
MB-N	-------- % of Soil Total Nitrogen --------			
Organic	6.80	9.84	13.69	19.63
Mineral	2.92	3.84	4.15	4.44
Total	4.03	6.48	7.96	9.77

The lower fractions at the regeneration stage are indicative of lower MB concentrations. These data suggest that as stand development progresses, increasing proportions of the total soil C and N pools have been consumed and incorporated into the living microbial population. Fluctuations in the microbial population could then translate quickly into the release or immobilization of C and N.

4.1.10 *In Situ* Nitrogen Mineralization Rates

As explained in Section 3.2.7, two sets of T-0 mineralization bags (unfrozen and frozen) were measured to calibrate possible differences because the T-1's were placed in the ground unfrozen whereas T-2 to T-5 mineralization bags were frozen (for storage) and then thawed prior to field installation. Frozen storage increased the concentration of available N in all samples except mineral soils from the regeneration stage sites (Table 4.6). Increases ranged from 2 to 40x; therefore, it was prudent to have measured both T-0's. Concentration of MB-C and MB-N tended to decrease in frozen organic samples, but was variable in frozen mineral samples (data not presented). The large increases in

available N in organic samples could have been due to lyses of the soil microbes during freezing.

Table 4.6 Concentrations of available nitrogen (NH_4 and NO_3) between T-0 (Oct 2002) and T-0-Frozen mineralization bag benchmarks.

Chronosequence	Mineral		Organic	
Site	T-0 (Oct 2002)	T-0-Frozen	T-0 (Oct 2002)	T-0-Frozen
		----- $\mu g\ g^{-1}$ -----		
Regen-1	4.2	3.5	29.5	55.5
Regen-2	3.9	4.0	49.9	92.4
CrwnCl-1	0.9	2.0	72.2	131.4
CrwnCl-2	1.6	7.6	47.9	153.8
SelfThin-1	0.1	1.3	22.5	109.0
SelfThin-2	0.1	2.2	50.8	215.9
Mature	0.0	1.6	3.5	137.7

Although mean annual available N mineralization rates did not differ significantly between stand development stages, there was a definite downward trend (Figure 4.11). Simard *et al.* (2001) also did not find significant changes in net N mineralization between recently burned and mature reference stands. Overall, the decrease was almost linear and mineralization switched to immobilization during the self-thinning stage (e.g. SelfThin-1 mineralized N whereas SelfThin-2 immobilized N). In comparison to mineral soil, the organic layer mineralized larger amounts of N over a longer period of time (i.e. immobilization did not begin until the mature stage).

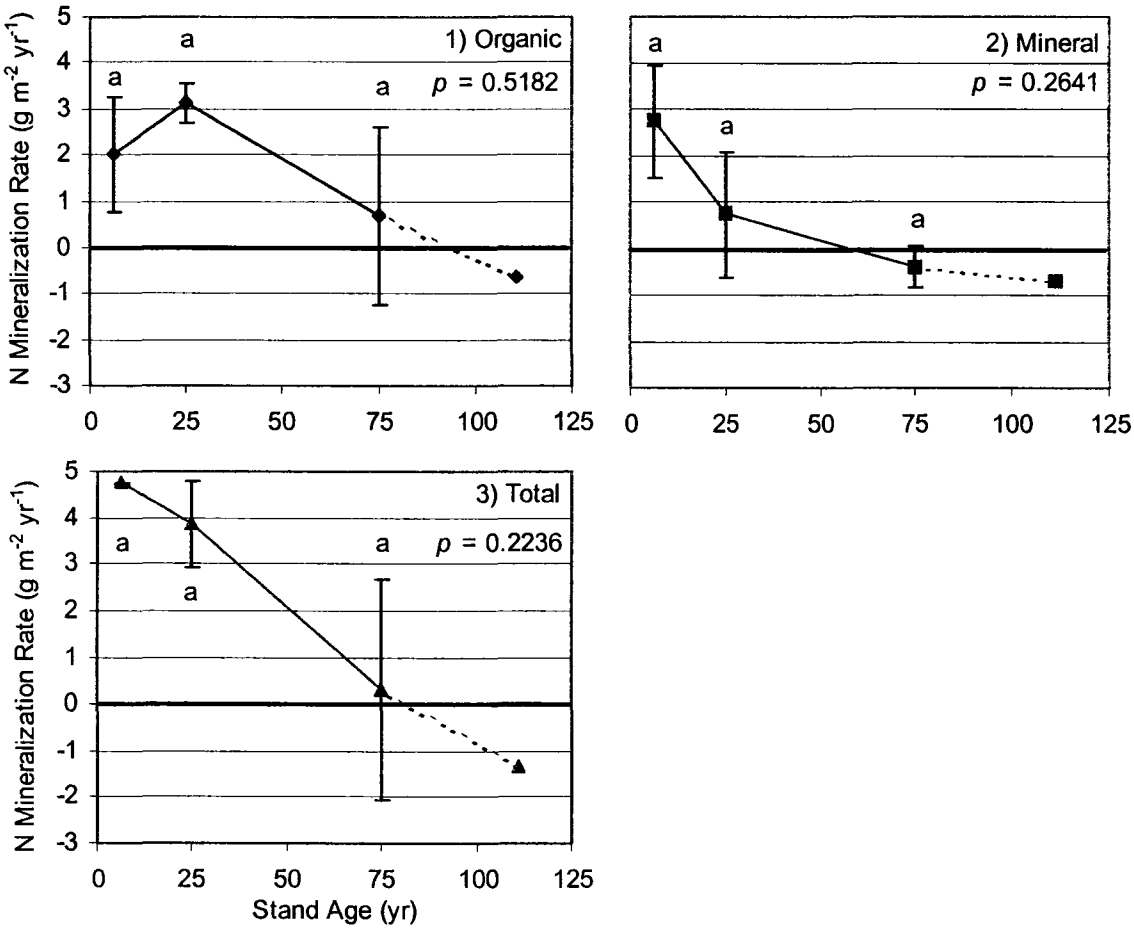

Figure 4.11 Mean annual nitrogen ($NH_4 + NO_3$) mineralization rates for stand development stages with standard error bars and ANOVA results.

Decreasing N mineralization rates over time were observed by Deluca *et al.* (2002), although not to the point of net immobilization. Binkley *et al.* (1994), using two different *in situ* mineralization bag experiments, found net immobilization and near zero mineralization in a 200 year old Alaskan white spruce stand. However, increasing net N mineralization was found by Smith *et al.* (2000) for black spruce stands in Quebec and by Idol *et al.* (2003) for a hardwood chronosequence in Indiana. Considering that total soil N concentrations, available N, and soil temperatures were lower at the later development stage sites than the earlier stages, it is not surprising that N mineralization

rates decreased. Also, on the forest floor, quantities of woody litter increased, and foliage/herbaceous litter decreased with stand age resulting in reduced substrate quality. Woody litter tends to have higher C:N ratios, therefore greater amounts of N would be required by the microbial community to consume these materials. Driscoll (1999) suggested that lower decomposition rates, primarily related to low soil temperatures at later stages, could increase the size of the potentially mineralizable N pool. For example, dead moss may be a large sink for readily mineralizable N that could be a sizeable source of N under warmer conditions. Combined, all of the above factors could lead to reduced N mineralization and even immobilization as observed in the local chronosequence.

Nitrogen mineralization rates were found to be positively related to soil temperature. In a linear regression of individual mineralization rates (total soil) from each individual measurement period and the mean soil temperature (where available) for the same periods, a significant relationship was not found ($R^2 = 0.0589$; $p = 0.2225$; n = 27). However, when only the two mineralizing stages (regeneration and crown closure) were included, a significant linear relationship between N mineralization and soil temperature was found ($R^2 = 0.6375$; $p = 0.0006$; n = 14) (Figure 4.12). Through a meta-analysis, Rustad *et al.* (2001) reported that net N mineralization increased with increasing mean soil temperatures ($R^2 = 0.30$; $p < 0.0678$).

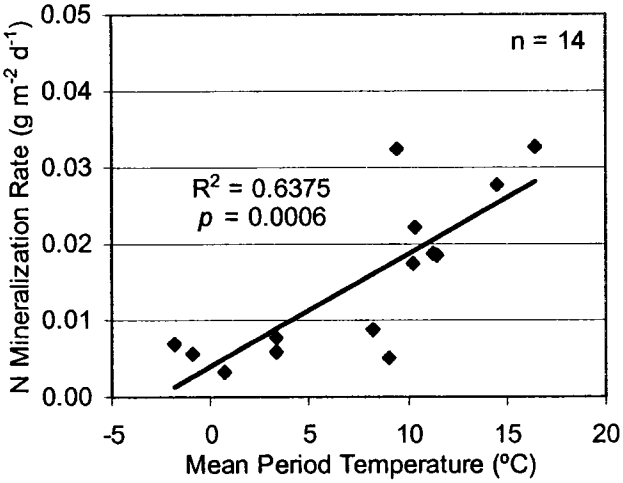

Figure 4.12 Relationship between nitrogen mineralization rate for each measurement period and the mean soil temperature of that period for regeneration and crown closure stand development stages.

Nitrogen mineralization rates at the older chronosequence sites were not related to soil temperature. On an Alaskan white spruce site, Paré and Van Cleve (1993) also did not find a soil temperature relationship with N mineralization rates except when a bladed site was included in the analysis. They suggested that on the 14 year old regenerating sites that were not bladed, the soil temperature variation was not substantial enough to significantly affect N mineralization rates. Similarly, in this study a significant relationship was not found when all the stand development stages were included of which the crown closure, self-thinning, and mature stages all had very similar soil temperatures. A significant relationship between soil temperature and N mineralization rates however was found when data from the two stages that had more widely differing soil temperatures (i.e. regeneration and crown closure) were used in the regression.

Under natural field conditions, immobilization of available N through plant uptake, particularly by moss, may be an important factor but for this study it can be ruled out as a factor because root excluding buried bags were used. Microbial biomass was also not likely a factor affecting N mineralization at the older sites since the mature stage MB-C and MB-N levels were generally similar to those from other stages. Therefore, substrate quality must be the most influential factor driving N mineralization at the later stage sites. Higher proportions of woody litter present with greater C:N ratios and lignin contents slow decomposition at these sites. The later stage sites should have greater proportions of more recalcitrant organic material in the organic and mineral horizons (i.e. more materials in the later, slower stages of decomposition). The finer texture soils at these sites (Table 4.2) also bind to and protect the materials from microbial attack (Haynes 1986).

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4.1.11 Soil Respiration

Three measurements of soil respiration made at the chronosequence sites provided evidence of seasonal trends. Using repeated measures ANOVA, measurements made in late May 2003 were found to be significantly ($p = 0.0007$) lower than measurements made in early August and early September of 2003 (Figure 4.13). Neither the interaction between stand development stage group and time of measurement, nor the stand development stage factor were found to be significant ($p = 0.1756$ and 0.0820, respectively). Higher rates can be attributed to microbial respiration, root respiration or both, because root exclusion procedures were not used. Root respiration has been found to account for between 50 and 80% of CO_2 respired (Uchida *et al.* 1998 and Bowden *et*

al. 1993. Assuming root respiration is related to live root biomass, only a small fraction of soil respiration should originate from root respiration in the regeneration stage since less live root biomass exists at this stage given that trees are small and shrub and herbaceous vegetation was not that prevalent at these sites.

Seasonal fluctuations of soil respiration have been noted by other authors. Similar to this study, Pietikäinen *et al.* (1999) found the lowest rates in May and the maximum rates achieved in late summer months at three boreal mixed wood stands in Finland. Schlentner and Van Cleve (1985) found that respiration rates peaked in late June and July in Alaskan aspen, birch and black spruce stands, and in July for white spruce. The decline in respiration rates after the peaks was associated with increasing moisture contents and decreasing temperatures. Moister and cooler soils in the spring could also then explain lower measures of soil respiration made in May for this study.

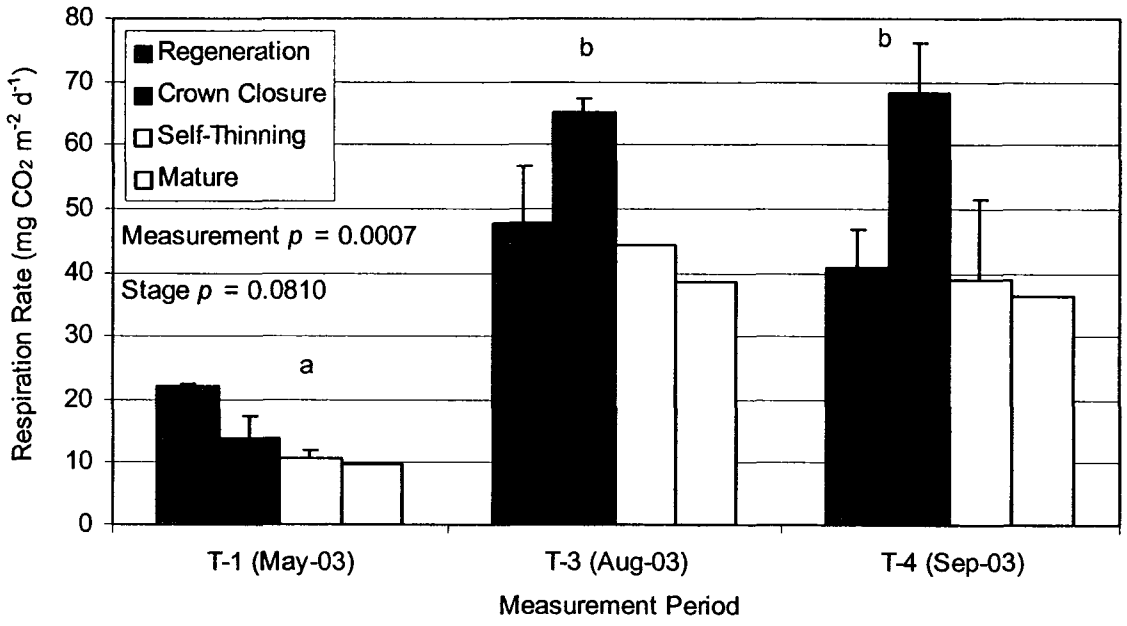

Figure 4.13 Soil respiration rates measured at chronosequence sites grouped in stand development stages with standard error bars.

The ANOVA did not detect significant differences between the stand development stage groupings, despite that measures from the crown closure stage were higher at both the August and September measurement occasions. The higher respiration levels may be attributed to a greater amount of root respiration resulting from the higher stem densities of the trees (mainly at CrwnCl-1) and thick root mat from ground vegetation at CrwnCl-2 (extensive labrador tea and blueberry).

Linear regression revealed that soil respiration measured at the sites of this study appears to be primarily driven by soil temperature rather than the size of the microbial population or moisture content (Figure 4.14). A relationship was not found with MB-C ($R^2 = 0.0069$; $p = 0.5217$; n = 61) and very low coefficients of determination (R^2) were found for organic gravimetric moisture content ($R^2 = 0.0697$; $p = 0.0366$; n = 63), and mineral soil gravimetric moisture content ($R^2 = 0.0755$; $p = 0.0293$; n = 63). The moisture content relationships can confidently be disregarded because of the wide variation in the measurements as seen in panel 2 and 3 of Figure 4.14. However, mean soil temperature from the 24 hours preceding the soil respiration measurement accounted for 49% of the variation in the soil respiration measurements ($R^2 = 0.4907$; $p = <0.0000$; n = 51). These results are in agreement with a meta-analysis by Rustad *et al.* (2001) that reported that soil respiration rates are higher in warmer soils.

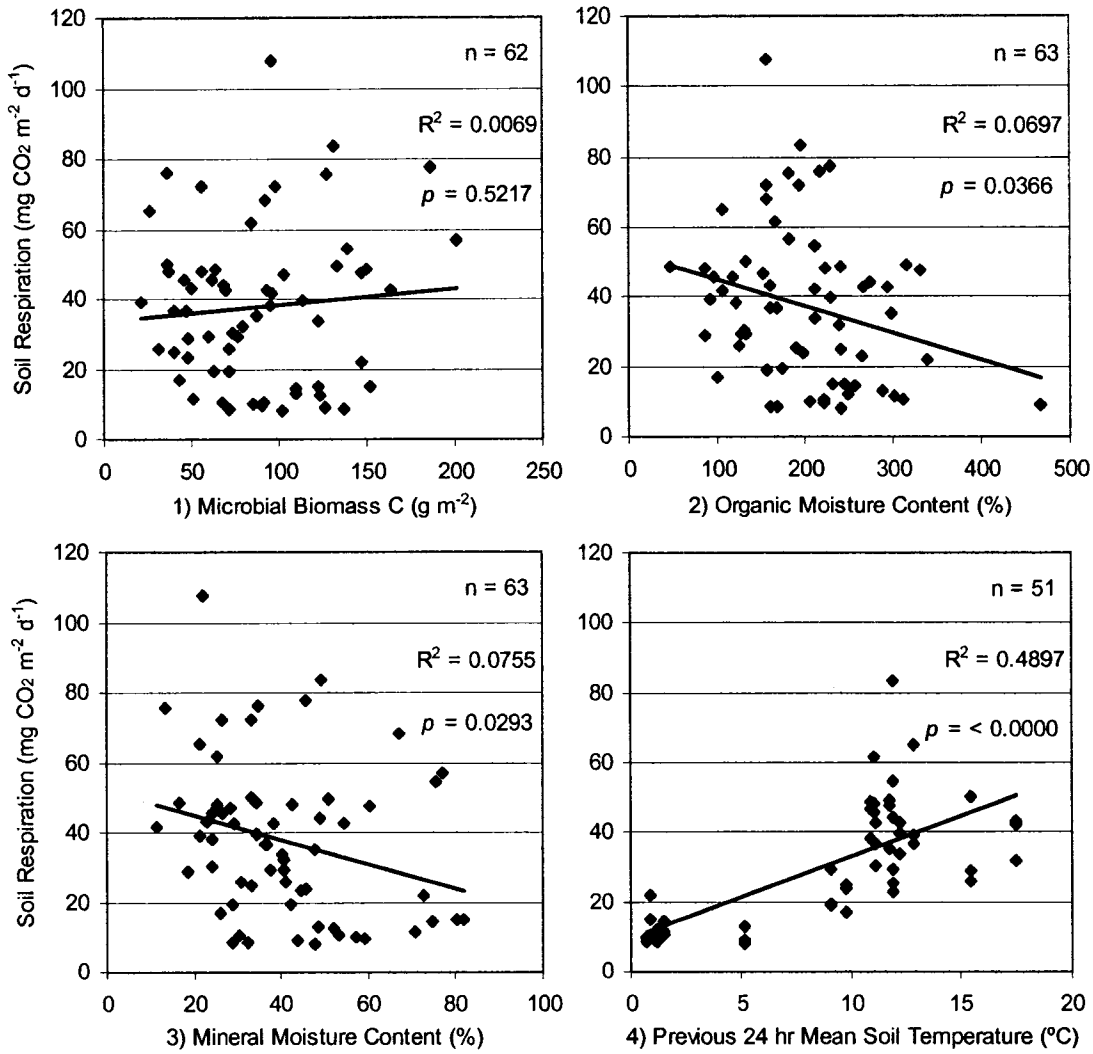

Figure 4.14 Scatterplots of 1) total soil microbial biomass carbon, 2) organic layer gravimetric moisture content, 3) mineral soil gravimetric moisture content, and 4) soil temperature against soil respiration plot means from chronosequence sites.

4.1.12 Laboratory Soil Incubations

Aerobic laboratory incubations of organic and mineral soils were performed to investigate soil C and N fluxes under controlled conditions (temperature and moisture) and to help explore differences in substrate quality between the development stages. As stated previously, the statistical analysis did not include the mature stand development stage due to a lack of replicate sites. Available N (NH_4 and NO_3) and soil respiration measures presented are from the 30 week incubations and the MB-C and MB-N data is from the 39 week bulked soil incubations. The 39th week measure for the mineral soil was excluded due to problems with these data. For consistency, data for the bulked soil incubations are presented under the development stage headings even though only one site for each stage was represented. Data tables and ANOVA summaries can be found in Appendices VII and VIII, respectively.

4.1.12.1 Available Nitrogen

For organic materials, the most available N was mineralized from the crown closure and self-thinning stages (Figure 4.15). The mature stage mineralized the least N over the incubation. For mineral soils, the concentration of available N decreased with age of the stand development stages (Figure 4.16). However, ANOVA revealed there was a significant interaction effect of temperature and stand development stage on the total amount of available N mineralized for both organic and mineral soils ($p = 0.0003$ and $p = 0.0004$, respectively) (Figure 4.17). For each stage, more N was mineralized at 20°C than at 10°C; however, the pattern of increase in the regeneration stage soils was different than that of the crown closure and self-thinning stage soils. While mineralizing

roughly the same concentrations at 10°C, the regeneration stage organic soils mineralized 2/3 more N at 20°C than 10°C, but the crown closure and self-thinning stage soils mineralized 2.5-3 times more N at 20°C than 10°C. In contrast, regeneration stage mineral soils mineralized double the amount of N than the other stages at 20°C. Mineral soils were significantly different at all stages at 10°C (Regen > CrwnCl > SelfThin) (Figure 4.16 panel 3). These results indicate that recently burned soils have different N responses to temperature than do those under more mature stands. Some insight can be obtained by considering the individual means for NH4 and NO3 (Figures 4.15 and 4.16 for organic and mineral soils, respectively).

The differences between groups may be primarily related to NO_3 production. The regeneration stage soils had higher concentrations of NO_3 than any of the other development stage groups. For all stages, the quantity of available N increased over the duration of the incubations. Nitrate concentrations in the organic soils were negligible, except after week 5 in the regeneration stage organic soils. By the 30^{th} week, NO_3 made up the majority of the available N in the regeneration stage organic soils. The higher levels of nitrification may have been attributable to larger pre-existing nitrifier populations in the regeneration stage organic soils. Nitrification in turn reduced the concentrations of NH_4.

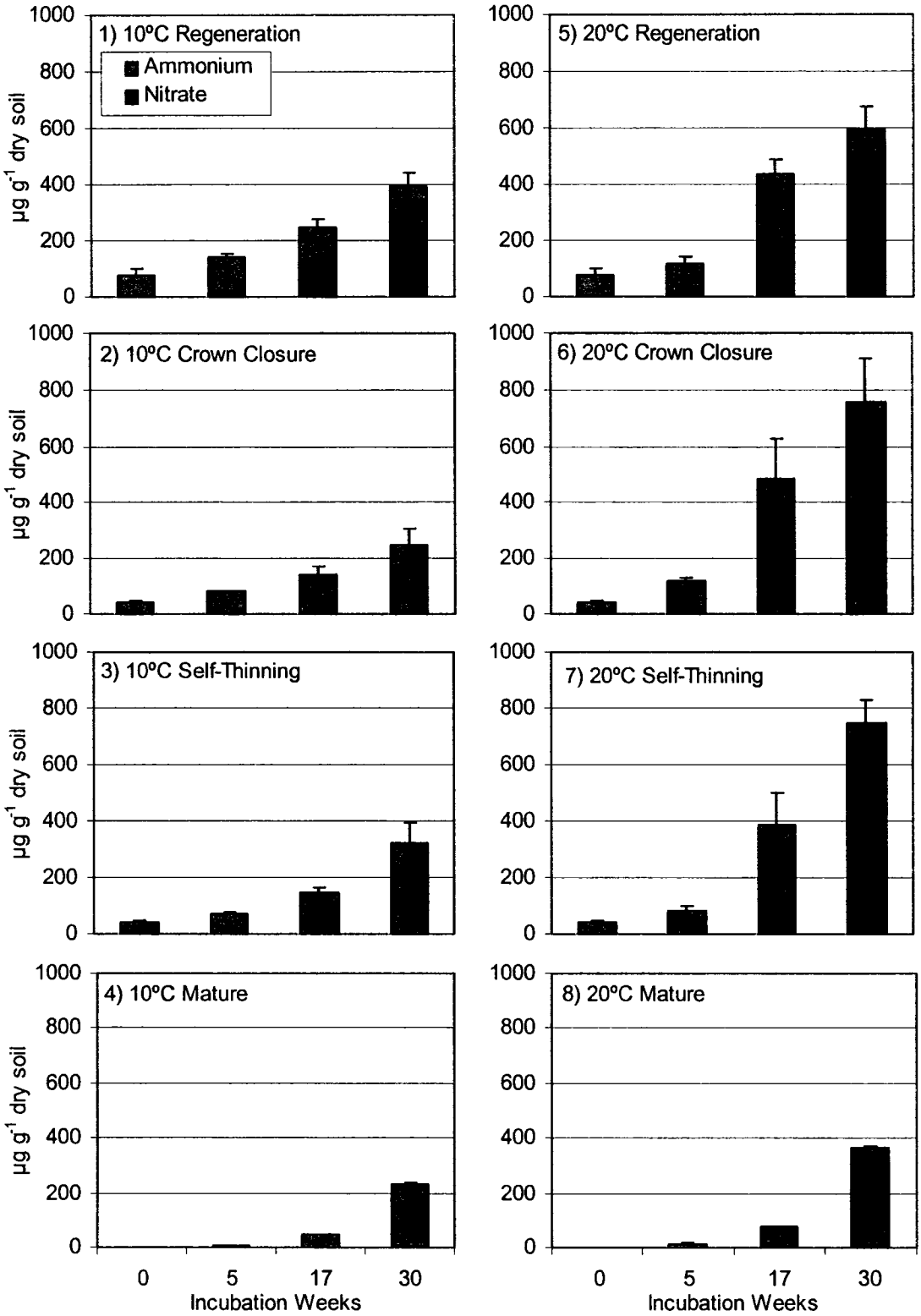

Figure 4.15 Ammonium and nitrate concentrations during 30 week laboratory incubations of organic materials for stand development stages with standard error bars for total concentrations.

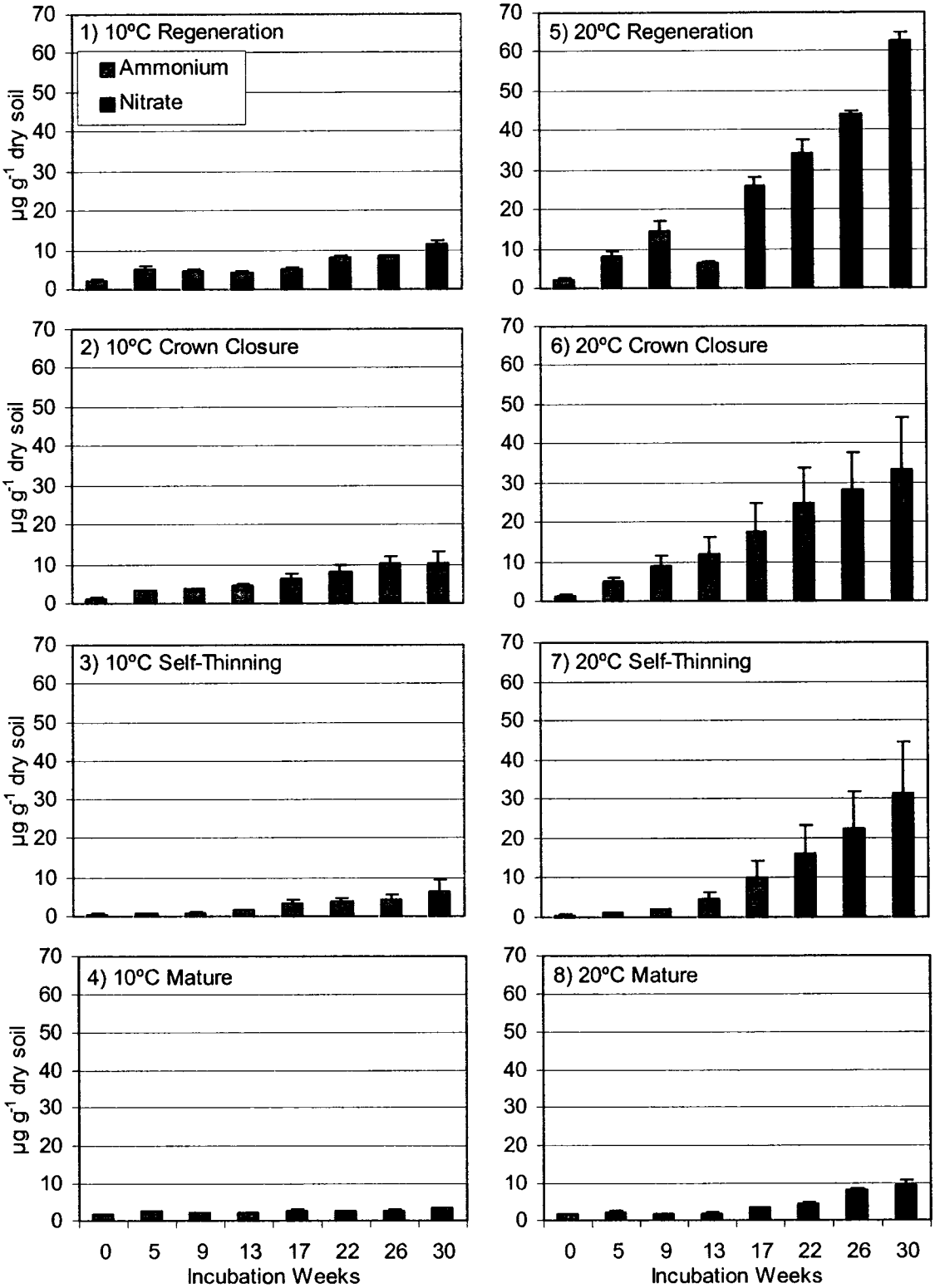

Figure 4.16 Ammonium and nitrate concentrations during 30 week laboratory incubations of mineral soils for stand development stages with standard error bars for total concentrations.

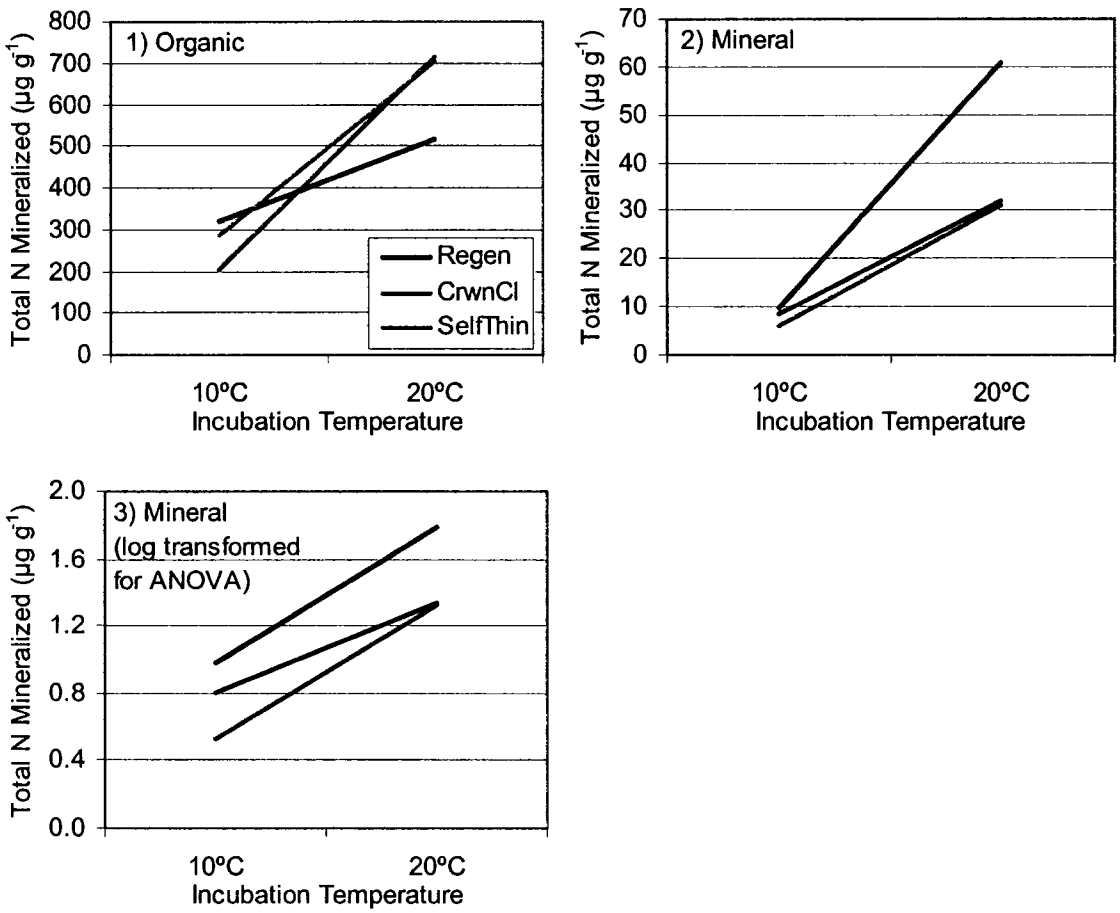

Figure 4.17 Interaction plots displaying significant ($p \leq 0.05$) group x temperature interactions for total N mineralized during 30 week laboratory incubations for 1) organic and 2 & 3) mineral soils.

The lower levels of total N mineralized in the 20°C regeneration stage organic soils when compared to the other stages may also be attributed to nitrification because a portion of N that was mineralized, and subsequently converted to NO_3, may have leached through the organic layer into the mineral soil thus artificially lowering the values for the organics. The potential for leaching of NO_3 was higher in the 20°C incubations because more water was added at each moisture adjustment occasion in order to maintain the target gravimetric moisture contents. However, NO_3 leaching does

not fully explain the differences between the regeneration and other stages as the difference is approximately 200 $\mu g\ g^{-1}$ and the total concentration of N in the 20°C regeneration stage mineral soil was only 62.3 $\mu g\ g^{-1}$. Therefore, clearly a substrate effect does exist on the temperature response of N mineralization in the regeneration stage soils. This could be an important consideration of simulation modelling.

As noted above, leached NO_3 from the organic layer may have artificially inflated the total N mineralized in the regeneration stage mineral soils at both temperatures. In the mineral soil of the other development stage groups, the majority of NO_3 was probably produced within the mineral soils rather than entering from the above organic because the amount of NO_3 started low with the concentration of NH_4 increasing but at week 17 the NH_4 concentration peaked and NO_3 started to rise. Between week 22 and 26, NO_3 surpassed NH_4 in the mineral soils of the crown closure and self-thinning stages. Without incubating organic and mineral soils separately, it is difficult to determine the origin and fate of mobile nutrients such as NO_3. The mature stage soils were not included in statistical analyses but for both temperatures showed less than average available N concentrations for the organic and mineral soils; however, a positive response to temperature was observed for both the organic and mineral soils.

Repeated measures ANOVA for the amounts of N mineralized between each measurement occasion resulted in significant 3-way interactions (temperature x group x measurement) for both organic and mineral soils ($p = 0.0002$ and p □0.0001, respectively). In all but a few cases, the most N was always mineralized in soils incubated at 20°C but the levels and order of groups differed with each measurement occasion. These results indicate that N mineralization does not occur at steady rates

even when environmental conditions are controlled (i.e. temperature, gravimetric moisture content).

4.1.12.2 Microbial Biomass Carbon and Nitrogen

Figures 4.18 and 4.19 show the concentrations of MB-C and MB-N in the organic and mineral soils at 10° and 20°C over the duration of the 39 week bulked soil incubations. In the organic materials, the concentrations of MB-C were, on average, the lowest in the regeneration stage soils for both the 10° and 20°C incubations and decreased over time, except for a relatively high measure at week 5 in the 10°C incubations. Absolute values for MB-C and MB-N concentrations in the crown closure and self-thinning stages were very similar. However, the trend by the 39th week was upwards at 10°C but downwards at 20°C. Unlike available N, higher concentrations of MB-C were not observed in the warmer conditions. Based on individual samples, the C:N ratios during the incubations indicate well nourished microbial populations with means of 6.5 (2.9 to 16.1) for the 10°C soils and 5.2 (1.9 to 14.6) for the 20°C soils and no apparent shifts overtime.

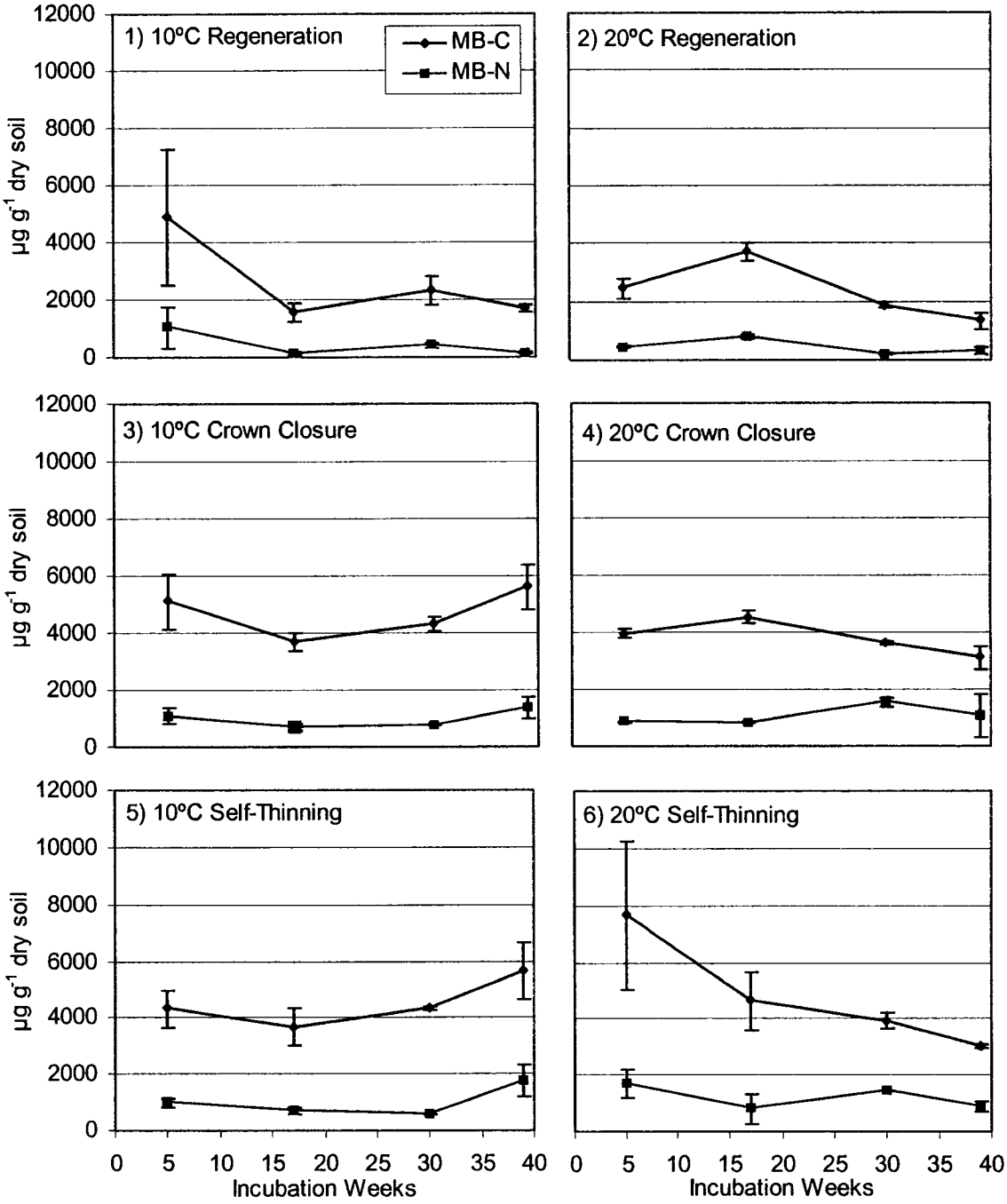

Figure 4.18 Concentrations of microbial carbon and nitrogen during 39 week incubation of bulked organic materials for stand development stages with standard error bars.

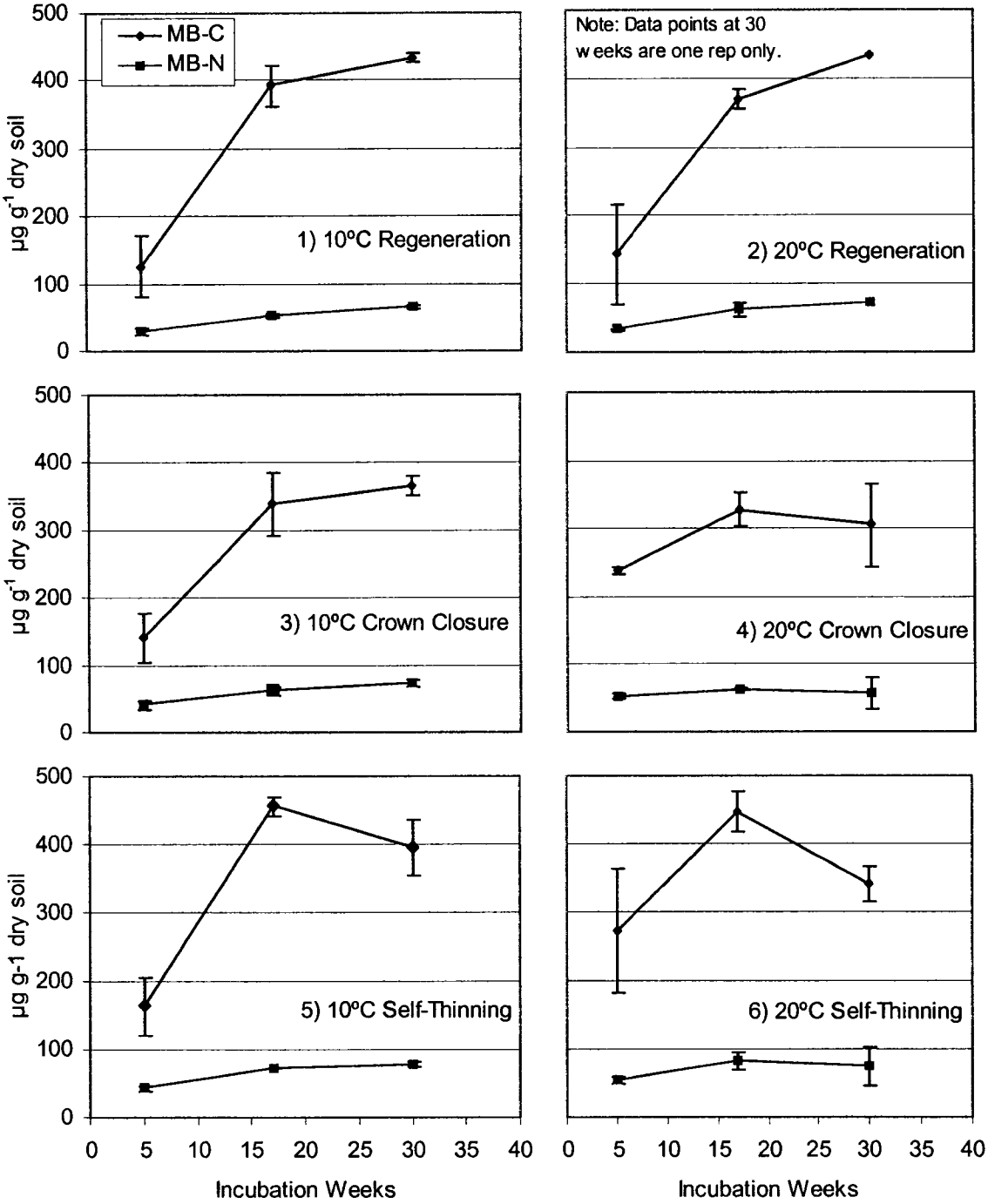

Figure 4.19 Concentrations of microbial carbon and nitrogen during 39 week incubation of bulked mineral soil for stand development stages with standard error bars.

Initially it appears that some consistencies exist between some of the temperature x group treatment combinations in the organic MB measures. The curves of the 10°C regeneration stage appear similar to the 20°C self-thinning stage curves. The 10°C crown closure and self-thinning stage curves appear similar, and the 20°C regeneration and crown closure stage curves appear similar. However, it is difficult to make conclusive statements about these apparent similarities for a few reasons, 1) there is no apparent reason why the similarities would exist (particularly the regeneration and self-thinning stage pairings), 2) relatively high variation was evident for some measurements (e.g. 10°C regeneration stage, week 5) which reduces the confidence in the reported MB data, and 3) statistical comparisons were not possible.

Temperature and stand development stage had little effect on microbial biomass in the bulked mineral soils (Figure 4.19). Microbial carbon displayed similar trends and concentrations between stand development stages and at both temperatures. For each soil, concentrations rose between weeks 5 and 17, and levelled off thereafter. Changes in MB-N occurred at lower magnitudes than MB-C which is reflected in the larger C:N ratios for weeks 17 and 30. The average C:N ratios across temperatures were 4.2, 6.0, and 5.6 for week 5, 17, and 30, respectively.

Three scenarios may explain the mineral soil MB trends. Firstly, at temperatures warmer than normal field conditions, the microbial population expanded but the N supply was insufficient to maintain the original nutrition levels so MB-N did not rise parallel to MB-C. Secondly, the initial T-0 concentrations were actually similar to those at T-4 and T-7 but due to soil manipulations (e.g. storage, mixing, drying/wetting, etc.), a portion of the population died and concentrations dropped to the T-1 level. At this

point the remaining microbes could then feed on those that died and the populations rebounded. Thirdly, with conditions different from those experienced in the field, a shift in the microbial population may have occurred that resulted in a population (characterized by wider C:N ratios) that was better adapted to the incubating conditions. This third scenario may be the most plausible because as seen in the 30 week incubation available N measurements, the supply of N increased through time indicating that the microbial populations should not have been N-limited.

As in the organic soils, the C:N ratios of the mineral soils also indicated well nourished microbial populations with means of 5.3 (3.1 to 5.8) for the 10°C soils and 5.2 (2.2 to 7.2) for the 20°C soils.

4.1.12.3 Soil Respiration

Soil respiration measurements using IRGA were made 8 times during the 30 week laboratory incubations. When possible, measurements were made the day before sampling of the regeneration and crown closure stage soils, and two days before sampling of the self-thinning and mature stage soils. Respiration measurements were reported as concentrations scaled to the dry mass of soils in each container and in the absence of live roots were essentially an index indicating microbial activity in the combined organic and mineral soils.

For each stand development stage, CO_2 release from the 20°C incubations exhibited more fluctuation over time and was always greater than the corresponding measures from the 10°C incubations (Figure 4.20). Repeated measures ANOVA found the 3-way interaction of temperature, group and measurement occasion to be significant

($p = 0.0005$). Interaction plots confirm that a greater amount of CO_2 was respired from the warmer soils and that the self-thinning stage measurements were always the lowest at both temperatures (Figure 4.21). The 3-way interaction was significant because, from measurement to measurement, neither the regeneration stage, nor the crown closure stage consistently respired more than the other.

Interestingly, for each temperature and stage combination, measurements of CO_2 release often exhibited similar fluctuations at each measurement occasion. For example, the third measurement revealed a decline in respiration for all stages and both temperatures; although most apparent in the 20°C incubations. This common decline was then followed by a sharp increase in respiration recorded at both temperatures and all stages for the fourth measurement. These consistencies across the treatments suggest that the measurements may have been confounded by outside factors. Most likely, from measurement to measurement, the analytical equipment responded differently, despite calibration of the equipment with a standard concentration CO_2 gas. However, we can still safely conclude that more CO_2 is respired from warmer soils.

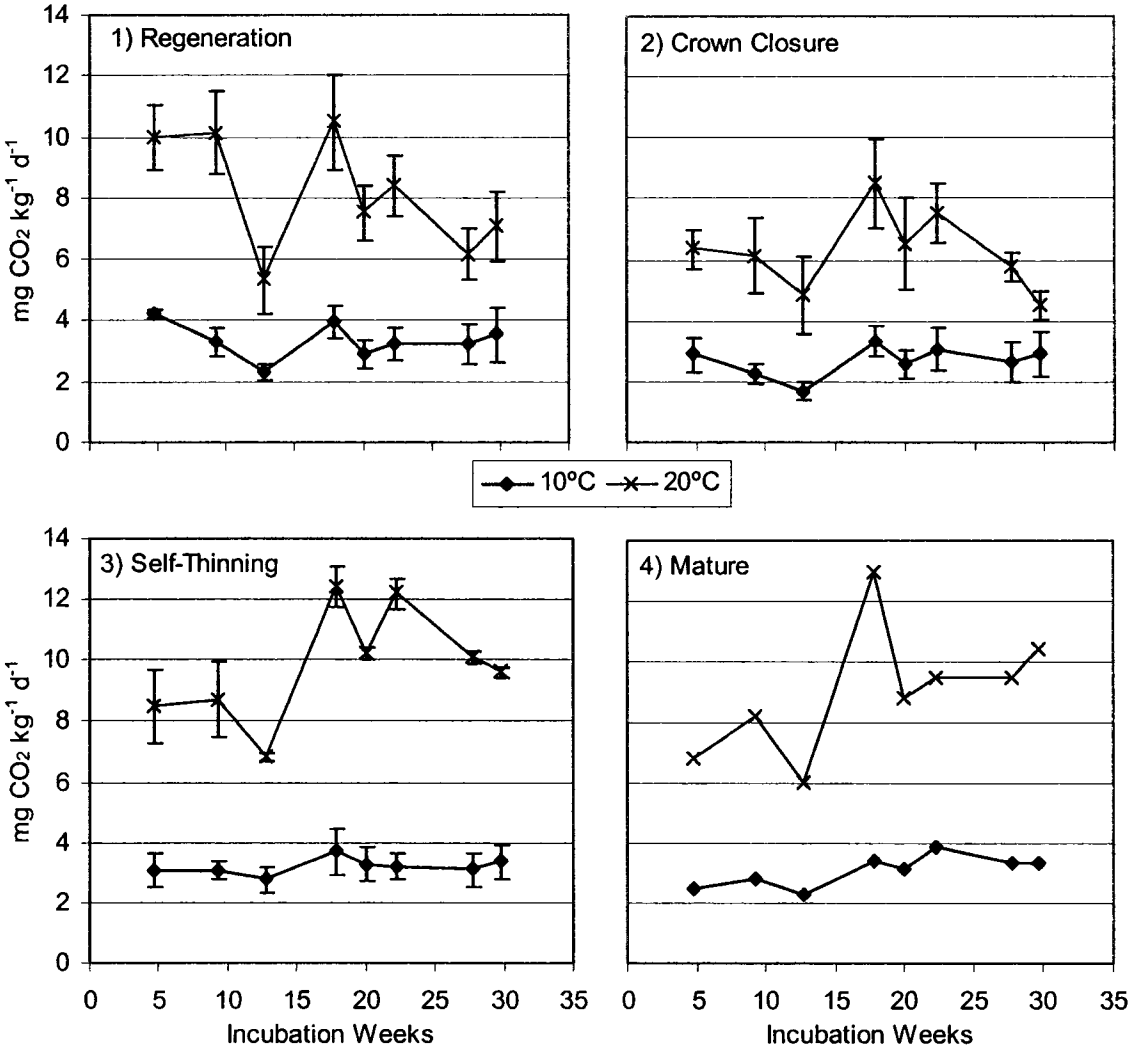

Figure 4.20 Soil respiration measurements by stand development stage from organic and mineral soils incubated at 10° and 20°C for 30 weeks.

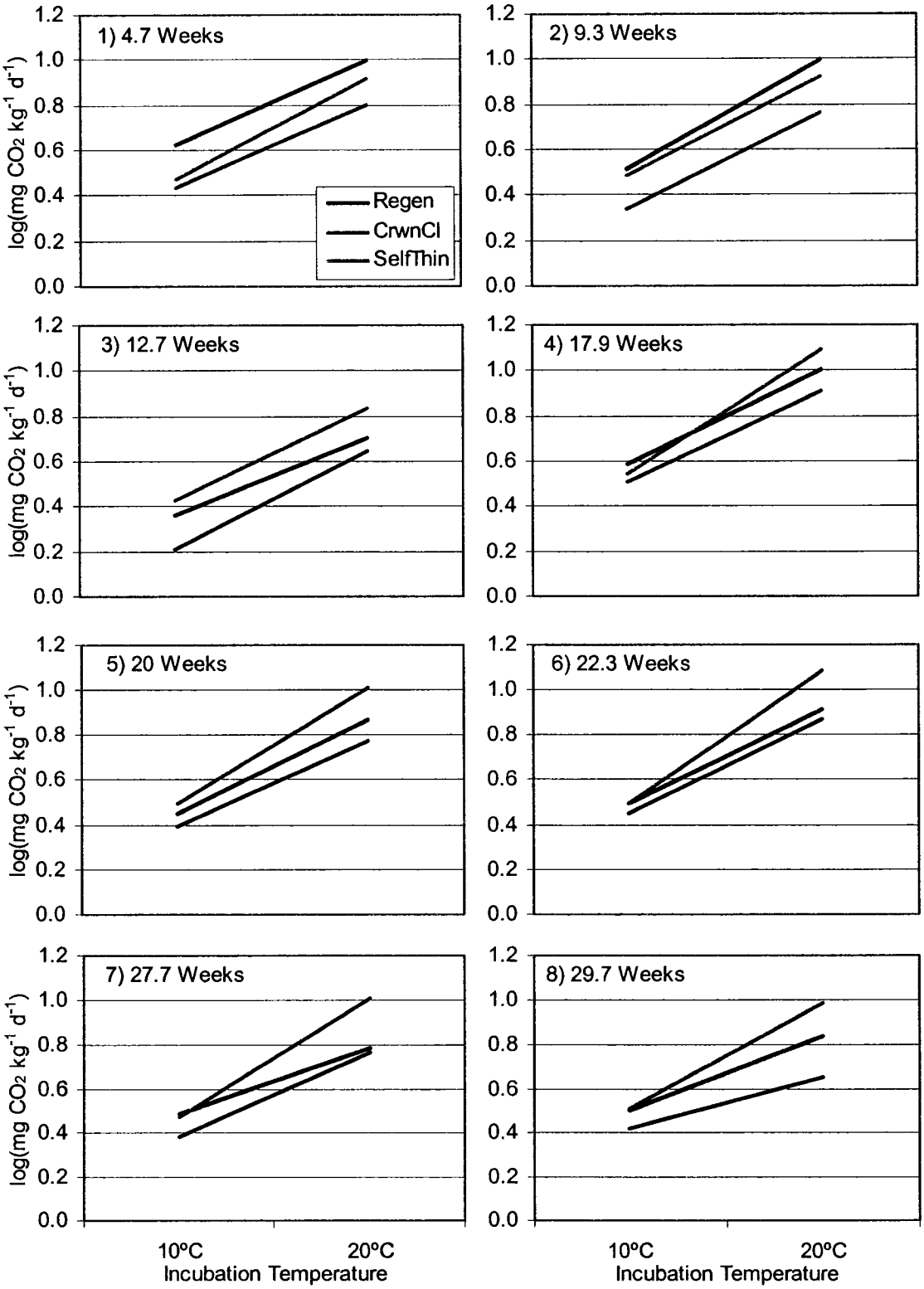

Figure 4.21 Interaction plots displaying significant ($\alpha = 0.05$) group by temperature by measurement occasion interactions for soil respiration during 30 week laboratory incubations.

4.1.12.4 Laboratory Incubations Summary

Measurements of available N in the 30 week incubations show that N mineralization in the chronosequence soils is affected by both the temperature of the soils and stand development stage. Not unexpectedly, N mineralization occurs at a greater rate in the warmer soils. Overall, considering the organic and mineral soils together, the crown closure and self-thinning stage soils have the greatest potential for available N release, particularly under warmer soil conditions. In general, the organic soils had much greater mineralization potential than did mineral soils. If the organic and mineral soils are considered separately, the regeneration stage soils mineralized the most N in the mineral soils at both temperatures and also in the 10°C organics.

The organic regeneration stage soils clearly had the greatest nitrification potential. The greatest concentrations of NO_3 in mineral soil were also in the regeneration stage soils; however, because of the experimental setup (i.e. organic over mineral soil in each container) it was difficult to determine whether the NO_3 in the mineral soil was produced there or leached down from the organic layer above. In a real-world setting, as long as the N remained within the rooting zone it should not matter to the trees whether the N is in the organic or mineral horizons. The greater potential for nitrification in the regeneration stage soils could be because at the chronosequence sites where the soils originated there is less vegetation and therefore less NH_4 uptake, so a more prolific nitrifier community could have become established. With the presence of more vegetation at the other stages there would be a stronger demand for the NH_4 and it would be rapidly immobilized so a smaller nitrifier community would likely be supported. Therefore, the incubated regeneration stage soils, with a greater initial

population of nitriers, and an absence of N uptake could produce NO_3 sooner than the other stages. These results show that from a nutrient conservation perspective, under conditions of minimal plant uptake, there is the potential for N to be lost from regeneration stage soils through leaching of NO_3.

Through the use of a similar methodology and soils, incubations by Luckai (2004) also revealed that soils recently disturbed by wildfire (5 years) behaved differently than those from established stand conditions (50 and 110 year). It was found that soils from the 5-year old burn site produced greater amounts of both NH_4 and NO_3 than the other soils, although from this study only the 10°C regeneration stage soils produced greater amounts of NH_4. As with this study, only small amounts of NO_3 were produced by the older stage soils. Luckai (2004) also found that the presence of an organic layer overtop of the incubating mineral soils definitely resulted in greater amounts of available N in both the organic and mineral layer.

Over 12 week incubations, Smith *et al.* (1998) found that NH_4 concentrations were consistently higher than NO_3 in recent burns with NO_3 concentrations near zero. In contrast to this study and the work by Luckai (2004), Smith *et al.* (1998) reported peak available N concentrations 2 weeks into the incubation; however, they postulated that this was a result of rapid release of N from lysed microbes following thawing of the soils. The soils used in this experiment were not stored in a frozen state so this result would not have been expected.

Measures of MB-C and MB-N concentrations did not produce clear trends, nor did they appear to be related to available N mineralization or soil respiration. Increased microbial activity (but not quantity), as indicated by higher soil respiration

measurements, was likely the main driver behind higher available N concentrations in soils incubated at 20°C which is in agreement with Vance and Chapin III (2001). Luckai (2004) also did not find that MB-C was influenced by stand age and that soil respiration was not related to MB-C or any N measurement. Conversely, Smith *et al.* (1998) reported CO_2 was released from organic material in a similar pattern as NH_4 release and that weekly means of CO_2 release were positively related to NH_4 concentrations. The laboratory incubation results of this study are presented in confidence given that the soils used had similar origins as those used by Luckai (2004). Differences between the studies were likely due to natural variation.

4.1.13 Summary Discussion of Field Studies and Laboratory Incubations

Although not significantly different from the other stages, the annual N mineralization rate was the highest for the regeneration stage and the mean annual amount of available N was nearly the highest. The controlled temperature and moisture conditions in the laboratory incubations confirmed that this was related to the actual soil from the regeneration stage sites and not site conditions. Greater amounts of available N were mineralized over the 30 week incubation from the regeneration stage soil in all but the 20°C organic material indicating that substrate quality is indeed better in this stage although the temperature response was not as great as for the crown closure or self-thinning stages. Field data for the regeneration stage soils showed that the majority of available N was in the mineral soils which also mineralized the most N (by area and concentration). That the majority of N mineralization occurs in the mineral soil is strictly a function of soil mass since concentration ($\mu g\ g^{-1}$) based measures of available

N and N mineralization rates were much greater in organic soils from all sites. The exception was the self-thinning stage where approximately equal amounts of available N were measured in the organic and mineral horizons.

In the field, microbial biomass was influenced by stand development stage with the lowest MB-C and MB-N levels and concentrations observed in the regeneration stage, particularly in the organic horizons. In the 39-week aerobic incubations, the regeneration stage soils also had the lowest concentration of MB-C and MB-N. No relationships incubation temperature were found. Interestingly, the greatest amounts of N were mineralized from the soils with the least MB so a relationship between MB and available N does not appear to exist. There may be a stronger relationship of MB-C and MB-N to litter inputs and moisture controls than revealed by soil temperature and N pool levels and fluxes which should be investigated further.

Microbial activity in the field, as indexed by CO_2 evolution, was influenced by soil temperature but not MB-C pool size. Laboratory aerobic incubations also supported the positive relationship between CO_2 evolution and soil activity. Again, no relationship with MB-C was evident. There does appear to be a relationship between CO_2 evolution and N mineralization. In the laboratory incubations, greater respiration rates were measured in the 20°C soils which is also where the highest levels of available N (and N mineralization rates) were found. Also, as previously reported, N mineralization rates decreased through the chronosequence and a slight downward trend of soil respiration was also found (although not significant) which may have been more pronounced had root respiration been separated from the soil respiration. The highest CO_2 evolution rates in the field were measured in the crown closure stage but these soils respired the

least CO_2 in the incubations suggesting that much of the CO_2 measured in the field was actually root respiration. The two downward trends of N mineralization and soil respiration suggest that microbial activity is positively related to N mineralization.

Overall, the data presented from the chronosequence sites generally fell within ranges reported in other studies. Differences can be attributed to natural variation within upland black spruce-dominated sites in northwestern Ontario. The chronosequence approach assumes that the basic characteristics of all sites are the same (*e.g.* soil texture, soil depth, climate, disturbance history); however, this is impossible to achieve because of differences in the physical characteristics of the sites and their disturbance histories. The data set would be strengthened through the inclusion of additional chronosequence sites of varying ages to fill gaps in the existing chronosequence. The strength of statistical analyses would also be increased through the addition of a greater number of replicated sites.

The data collected from the chronosequence sites was beneficial in two ways. Firstly, the data provided local estimates of several important C and N pools and pool fluxes. The estimates contribute to our knowledge base of these upland black spruce-dominated systems in northwestern Ontario. The literature provides comparable measures from similar sites but mainly from sites in different geographic regions where important factors such as climate and fire cycle may differ. Secondly, these estimates can now be used for local validation of the CENTURY model.

4.2 CENTURY MODEL VALIDATION

The ability of the CENTURY model to simulate C and N dynamics for local mixed conifer sites in northwestern Ontario was assessed using the data presented in Section 4.1 and statistical validation procedures. These tests included: deviance measures, paired *t*-tests, linear regression, the simultaneous *F*-test, and modelling efficiency (see Section 3.7 for a description of the tests). Observed (RW) and simulated (CENT) levels were compared for soil temperatures from May to September, tree biomass C and N, total soil C and N, MB-C and N, available N, and N mineralization pools (Table 4.7). With the exception of soil temperature, all other data analyzed were annual means for each chronosequence site. Soil temperature data is presented for only the months of May to September because simulated soil temperature data through the winter months is believed to be flawed (see Section 4.1.4) and the most comprehensive data set could be compiled for the RW soil temperatures for this time period.

Overall, the results of the model validation exercise were much less successful than expected. With the current calibration, the CENTURY model most adequately simulated live tree aboveground biomass N (BIOn-AB) (Figure 4.22 and 4.23). The MAE, slope, y-intercept, *t*-test, and simultaneous *F*-test were acceptable (or not significant). However, the MA%E was above the 10% threshold at 24.4% and the modelling efficiency was relatively low at 0.28. Validation of the belowground and total live tree biomass N pools was less successful. While the over time trends of biomass C accumulation were similar to N, the validations were less successful (Figure 4.24 and 4.25). The biomass C pools all had very high y-intercepts and negative modelling efficiencies. The belowground biomass C and N pools both had significant *t*-tests.

Table 4.7 Results of the CENTURY model validation exercise comparing observed and simulated soil temperature, and carbon and nitrogen pools.

	Number of Data Pairs	Deviance Measures MAE	MA%E	Paired *t*-test *	Linear Regression R^2	Slope	Intercept	Simultaneous *F*-test † *	Modelling Efficiency
STemp (May to September)									
	28	4.00	109.0	0.0000	0.79	1.13	-5.7	0.0000	-0.15
Carbon Pools									
BIOc-AB	7	1976.6	30.5	0.3188	0.24	0.56	3460.1	0.5048	-0.19
BIOc-BL	7	1386.8	53.0	0.0186	0.17	0.75	1673.4	0.0958	-2.97
BIOc-TL	7	3202.8	34.9	0.1406	0.22	0.59	5155.4	0.3324	-0.62
TSc	7	2242.7	30.7	0.0247	0.78	-9.48	45328.0	0.0015	-1.91
MBPc x 2	7	43.6	26.2	0.7112	0.25	1.60	-103.5	0.0010	0.20
Nitrogen Pools									
BIOn-AB	7	3.6	24.4	0.8153	0.29	1.14	-2.8	0.9684	0.28
BIOn-BL	7	4.4	51.1	0.0181	0.23	1.06	4.2	0.0970	-2.64
BIOn-TL	7	6.1	22.7	0.3337	0.27	1.11	1.6	0.1869	0.05
TSn	7	110.5	38.6	0.0086	0.35	-15.37	2585.9	0.0135	-2.62
MBPn x 2	7	21.6	57.2	0.0034	0.05	2.78	-1.18	0.0202	-3.53
AvailN	7	0.2	37.1	0.6015	0.20	0.47	0.22	0.4510	-0.11
MNLZn	7	4.7	234.3	0.0291	0.56	-1.32	11.51	0.0022	-4.11

* *p*-value; significant if < 0.05

† *F*-test for slope = 1 and intercept = 0

BIOc-AB = aboveground biomass carbon
BIOc-BL = belowground biomass carbon
BIOc-TL = total biomass carbon
TSc = total soil carbon
MBPc x 2 = carbon in microbial biomass and microbail products
BIOn-AB = abovegoround biomass nitrogen
BIOn-BL = belowground biomass nitrogen
BIOn-TL = total biomass nitrogen
TSn = total soil nitrogen
MBPn x 2 = nitrogen in microbial biomass and microbial products
AvailN = nitrogen available for uptake
MNLZn = annual nitrogen mineralization rate

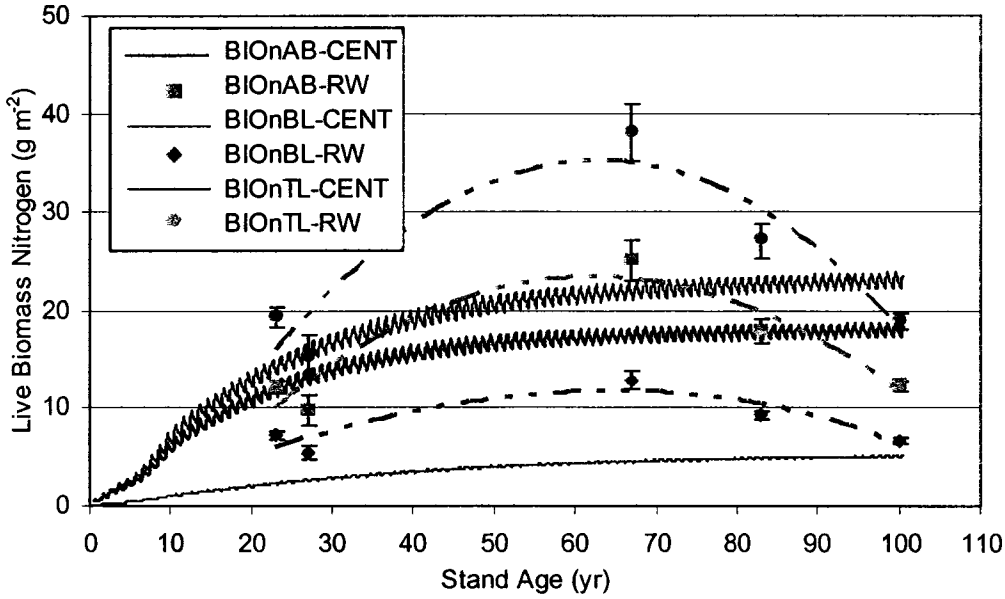

Figure 4.22 Observed (RW) with 3rd order polynomial trend line (— · ·) and simulated (CENT) aboveground (AB), belowground (BL) and total (TL) tree live biomass nitrogen (BIOn).

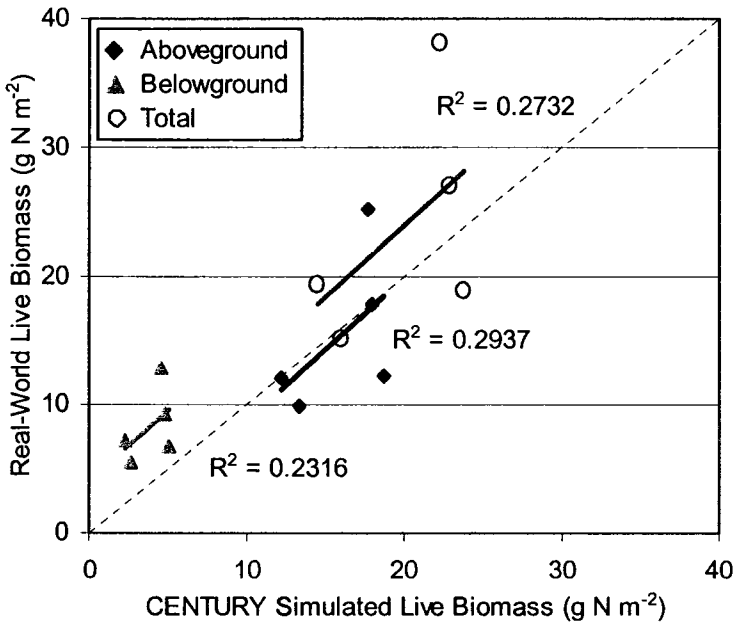

Figure 4.23 Observed versus simulated live tree biomass nitrogen.

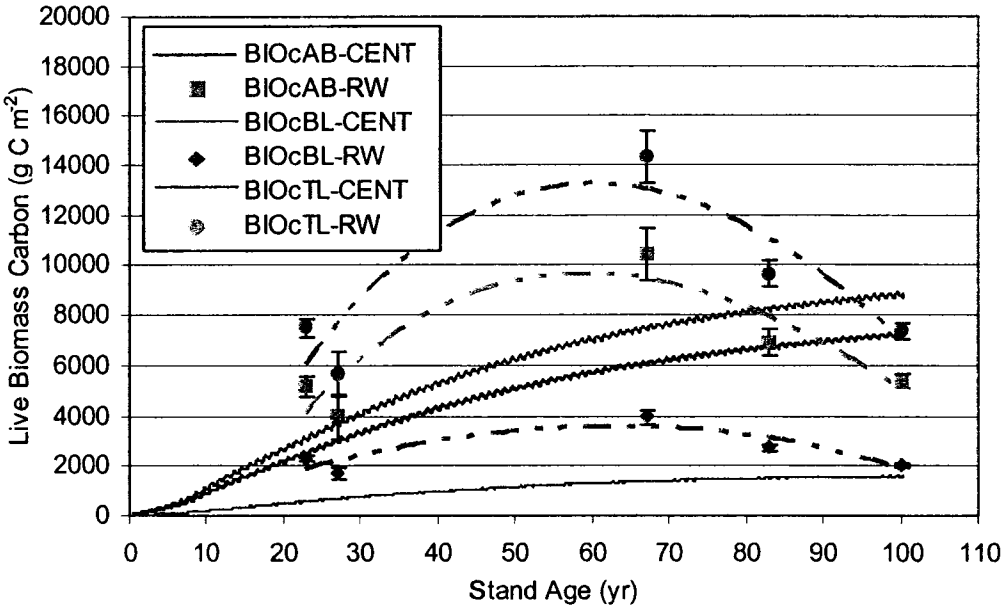

Figure 4.24 Observed (RW) with 3rd order polynomial trend line (— · ·) and simulated (CENT) aboveground (AB), belowground (BL) and total (TL) tree live biomass carbon (BIOc).

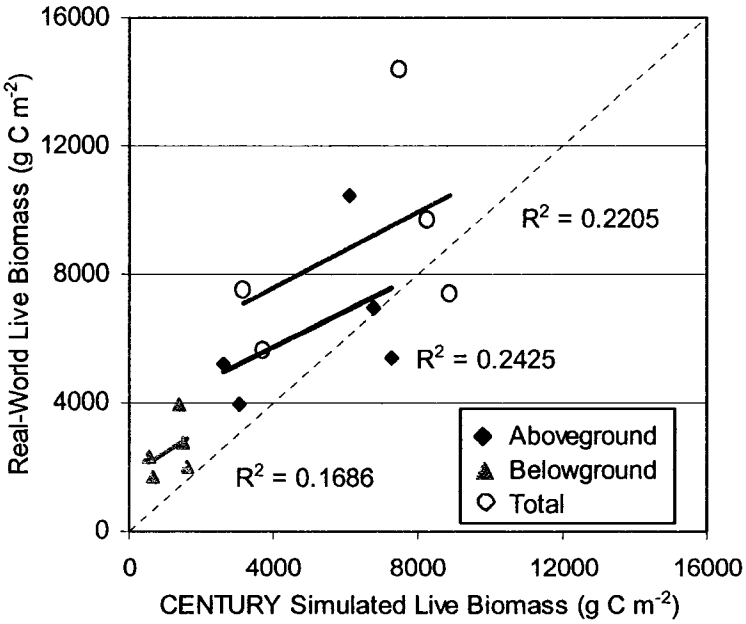

Figure 4.25 Observed versus simulated live tree biomass carbon.

For all statistical validation calculations, measures of deviance were typically high. The exception was AvailN which had an MAE of 0.18 g m^{-2}; however, this was because the quantities of AvailN are low naturally. By looking at the MA%E, unacceptable deviance still existed for AvailN (37.13%). Paired *t*-tests rejected the similarity of the observed and predicted values for STemp, BIOc-BL, TSc, BIOn-BL, TSn, MBPn x 2 and MNLZn. From the linear regression, R^2 values were generally low with 10 of 13 pools below 0.50. The line of best fit often deviated greatly from the desired $y = x$ trend, as revealed by examining the slope and y-intercept coefficients. This deviation lead to the rejection of slope =1 and y-intercept = 0 for 6 of 13 parameters by the simultaneous *F*-tests. Modelling efficiency was perhaps the most convincing statistic for rejecting the simulated data from the CENTURY model. Negative values could not be accepted and 10 of the 13 calculations produced negative results. The three pools that were positive (MBPc x 2, BIOn-AB, and BIOn-TL), were only slightly above zero at 0.20, 0.28, and 0.05, respectively.

Weaknesses in the tests were most apparent with the simultaneous *F*-tests where several tests did not identify significant differences despite seemingly large slope and y-intercept deviations from the 1 and 0 targets. For example, despite the BIOc-AB pool having a slope of 0.56 and a y-intercept of 3460 the test did not reject that slope = 1 and y-intercept = 0 ($p = 0.5048$) (Figure 4.25). The number of data pairs affects the outcome of this test. Soil temperature, for example, with 28 data pairs had a significant simultaneous *F*-test with a slope of 1.13 and y-intercept of -5.7. The remaining pools used 7 data pairs representing annual means for each chronosequence site, and even large coefficients did not always lead to significant tests. The MA%E calculations for

STemp and MNLZn were strongly influenced by some infrequently occurring low values within the respective RW datasets that caused very high measures of deviance (> 100%) so this measure was not particularly useful on these parameters. The RW data tended to have much larger ranges compared to the simulated data. This resulted in nearly vertical linear model slopes as found for TSc (Figures 4.26 and 4.27). The CENTURY model TSc had a range of under 1000 g m^{-2} over 100 years, but the data from the chronosequence sites had a range of over 4000 g m^{-2} which resulted in an almost vertical line of best fit which meant a significant simultaneous *F*-test and a negative modelling efficiency.

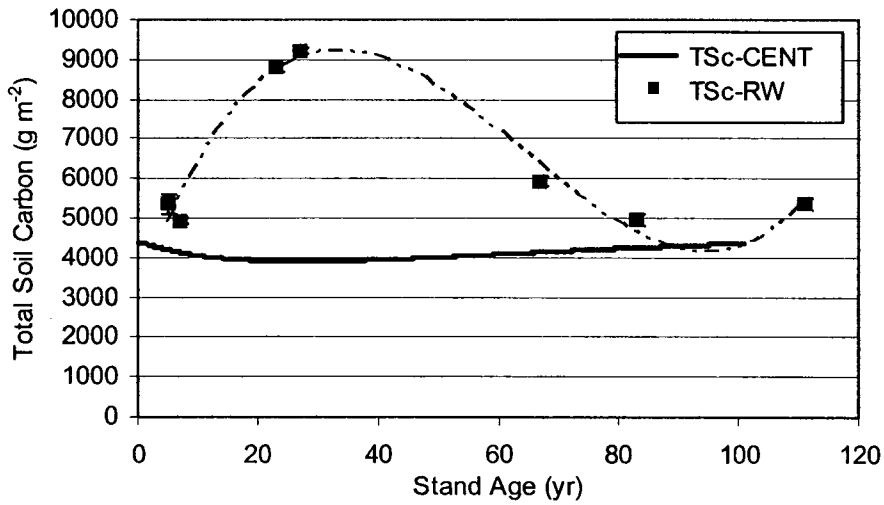

Figure 4.26 Annual observed (RW) with 3rd order polynomial trend line (— · ·) and monthly simulated (CENT) total soil carbon.

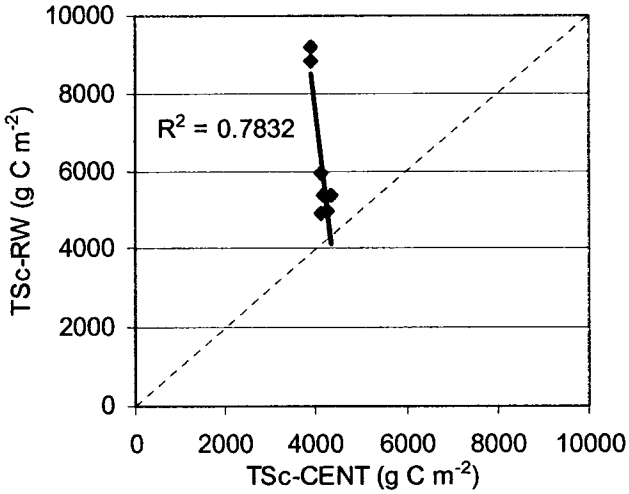

Figure 4.27 Annual observed (RW) versus simulated (CENT) total soil carbon.

Ironically, despite the negative results of the statistical validation, some of the RW data actually did appear to be fairly similar to CENTURY model simulations. For example, in the later stages of stand development MBPc was very similar for both data sources but the annual MBPc-RW x 2 means from the Regen and CrwnCl sites differed substantially (Figure 4.28). However, for MBPn x 2, simulated levels were much lower than RW levels (Figure 4.29). These results are due to a large difference in the C:N ratios of the simulated and measured MB pools. The C:N ratios for simulated pools increased from 13.2 to 15.6 compared to the RW C:N ratios that remained stable between 5.5 and 6.1 across the chronosequence. Adjustments to CENTURY to reduce the C:N ratios of the microbial pools (surface microbe and active SOM pools) may resolve this discrepency. In the CENTURY model user manual, Metherell (1993) states that the microbial pool in the model should be equivalent to approximately 2 to 3 times the measured live microbial pool. This was the reason for doubling the MB-C and MB-N pools measured at the chronosequence sites for comparison to CENTURY data.

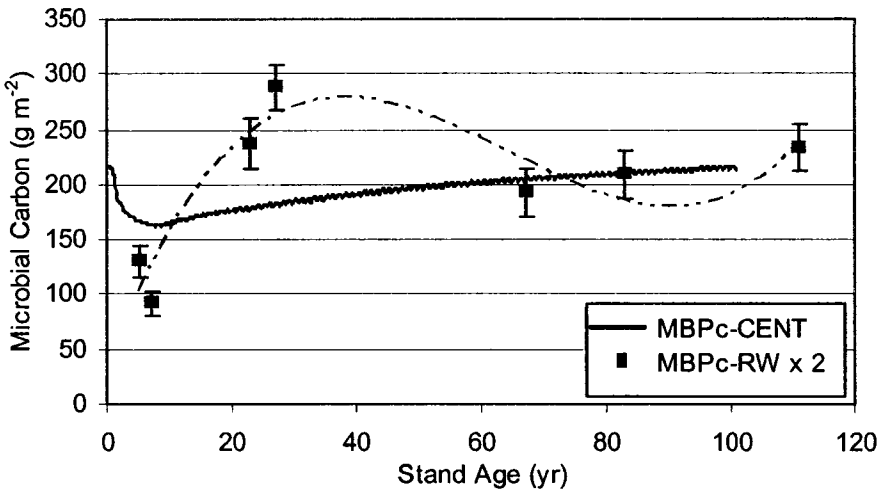

Figure 4.28 Annual observed (RW) with 3rd order polynomial trend line (— · ·) and monthly simulated (CENT) microbial biomass and microbial products carbon.

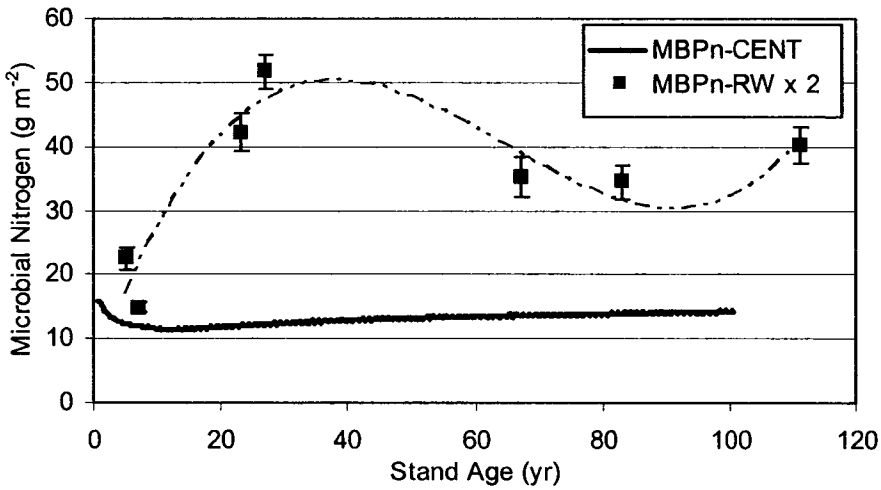

Figure 4.29 Annual observed (RW) with 3rd order polynomial trend line (— · ·) and monthly simulated (CENT) microbial biomass and microbial products nitrogen.

AvailN was another pool where RW and simulated levels did not appear to differ too substantially, particularly if the CrwnCl-2 data point was omitted (Figure 4.30), but the statistical tests indicated otherwise. As seen in Figure 4.31, directly comparing

mean annual available N data revealed bias towards the CENTURY simulated data and therefore unsuccessful validation of the ability of the CENTURY model to simulate available N.

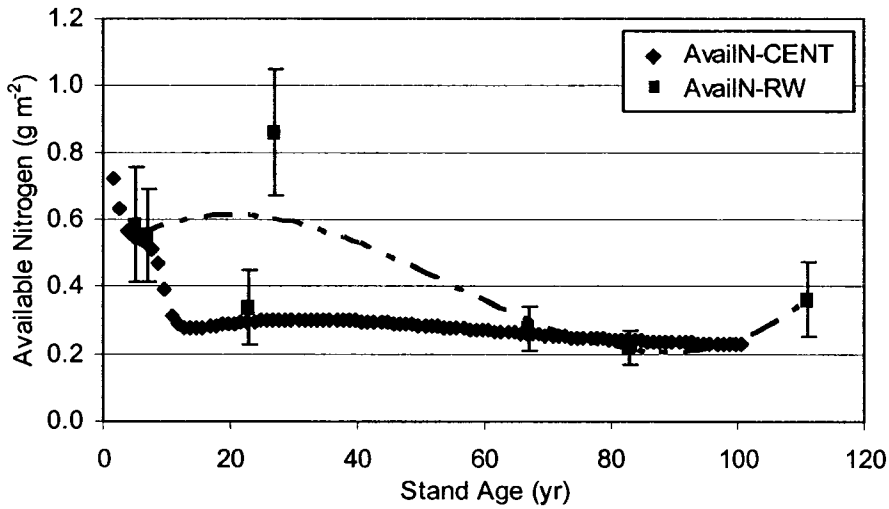

Figure 4.30 Observed (RW) with 3rd order polynomial trend line (— · ·) and simulated (CENT) annual available nitrogen.

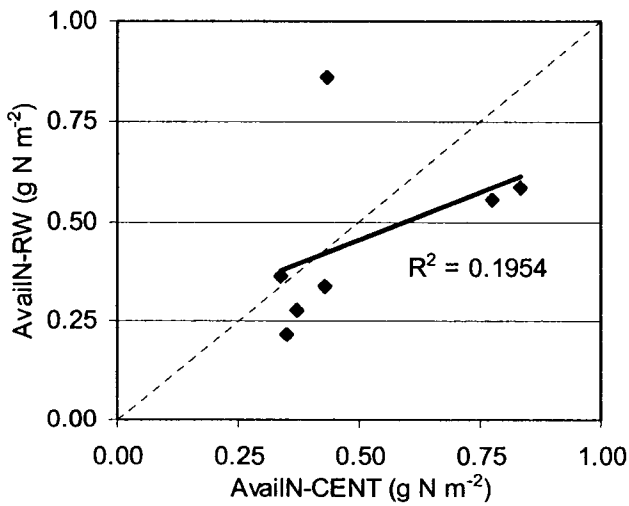

Figure 4.31 Annual observed (RW) versus simulated (CENT) available nitrogen.

With the exception of MBPc, simulated C levels were always lower than RW measures (Figures 4.24 and 4.26). The CENTURY model calibration needs to be altered to increase C in the biomass and the soil. Simulated N also needs to be raised in several pools including belowground tree biomass, total tree biomass, MBPn, and total soil N (Figures 4.22, 4.29 and 4.32). Simulated available N, however, needs to be lowered slightly. The trend of increasing N mineralization rates over time needs to be reversed for MNLZn to be more similar to RW measures (Figure 4.33).

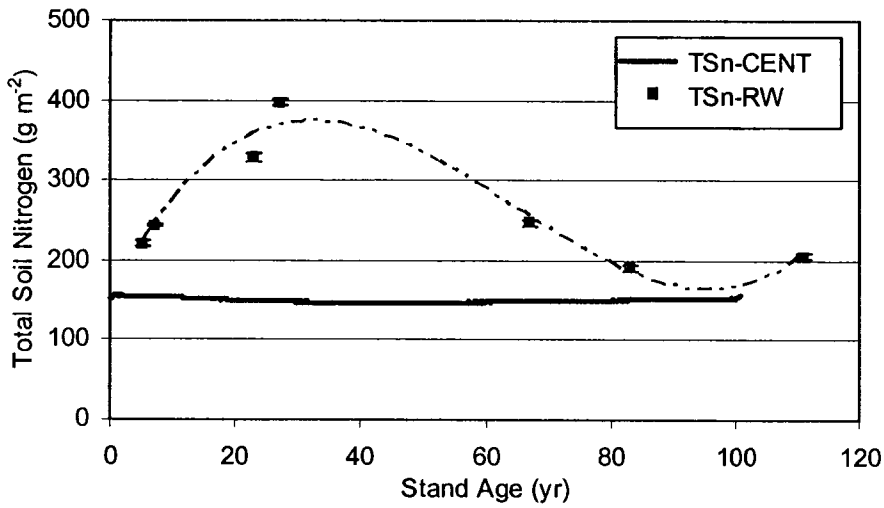

Figure 4.32 Annual observed (RW) with 3rd order polynomial trend line (— · ·) and monthly simulated (CENT) total soil N.

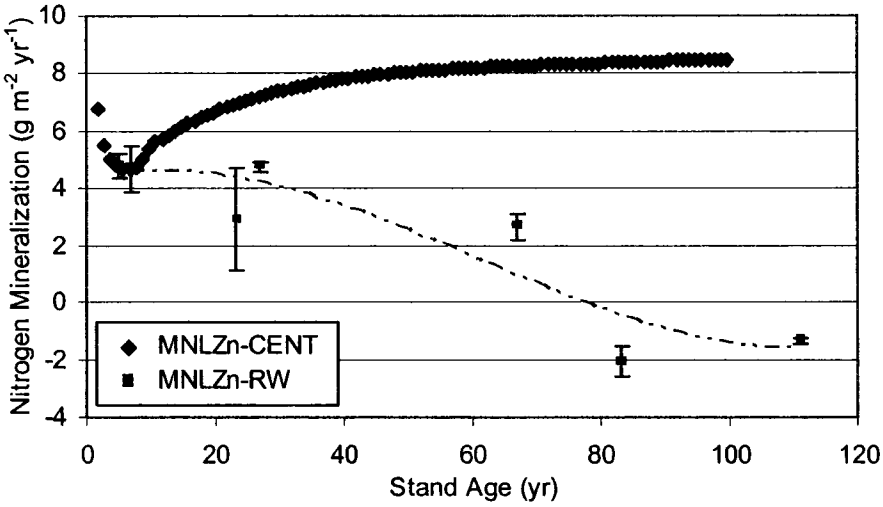

Figure 4.33 Observed (RW) with 3rd order polynomial trend line (— · ·) and simulated annual N mineralization rates.

The trends displayed by CENTURY simulations over time are the greatest concern with the model. The current local calibration of the CENTURY model was achieved by manipulating initial pool levels and the equilibrium period in order to make the model reach target pool levels at the end of a 100-year rotation. This exercise was relatively successful; however, this validation exercise has shown that while some end point targets have been met, the trends through the stand development stages have not correlated well with RW measures. Microbial biomass C is a good example of a case where RW and simulated data matched well towards the end of the simulated 100-year rotation but differed over the first 30 years (Figure 4.28).

The live biomass C and N pools also provide good examples of differing trends over time (Figures 4.22 and 4.24). Biomass measurements were not made for the Regeneration chronosequence sites. Each carbon and nitrogen pool peaked at the SelfThin-1 site and declined towards the Mature site. The CENTURY model live

biomass C and N curves increased progressively until the end of the 100-year rotation. Overall, the CENTURY model biomass C and N data was almost always lower and did not reflect the rapid accumulation toward the self-thinning stage followed by a decline towards maturity. Based on these findings, the CENTURY model would be unable to realistically model shorter rotations for such scenarios as shorter fire intervals or short rotation forest harvesting. Longer rotation scenarios would also be flawed because biomass continues to increase where it should decline.

As seen in Figure 4.33, two radically different trends of annual N mineralization rates resulted from the chronosequence site measures and the CENTURY model simulation. A steady decline towards immobilization was found by the RW measures; however, the simulated rate dropped sharply through the first seven years and then rose through the remainder of the rotation. Because mineralization is essentially a by-product of organic matter decomposition in the CENTURY model, decomposition rates need to be curbed to reverse the trend of simulated N mineralization. Laboratory incubations showed that in cooler soils CO_2 evolution (and presumably decomposition) and N mineralization was lower than in warmer soils. The soil C and N pools could potentially increase with a reduction in decomposition rates which could help rectify some of the disparities between the simulated and RW total soil C and N pool levels. The laboratory incubations revealed that MB levels were unaffected by soil temperature but the microbial pools in the CENTURY model are primarily regulated by decomposition rates, so with slow decomposition these pools would likely increase as well. Theoretically, tree biomass production would be reduced if less N mineralization occurred and more N was tied up in unavailable SOM pools. If N available for

production were to become more limited, that could induce a decline in production earlier in the 100-year rotation and the shape of the live biomass C and N curves could become more similar to those derived from the chronosequence data.

Simulated soil temperatures for the months of May to September were on average 1.5°C higher than the mean RW temperatures from the regeneration stage sites, but were on average 4.8°C higher than the mean measured soil temperatures from crown closure, self-thinning, and mature sites (Figure 4.34). The winter months are excluded because during the winter, soil activity should be at or near zero and there are concerns regarding the ability of the CENTURY model to realistically simulate temperatures below freezing. The crown closure, self-thinning, and mature stage data were combined because soil temperatures were found to be equivalent across these periods (Section 4.1.4). To reduce simulated soil temperatures, the four fix.100 file variables that are used in the calculation of soil temperature (elitst, pmntmp, pmxbio, and pmxtemp) could be adjusted.

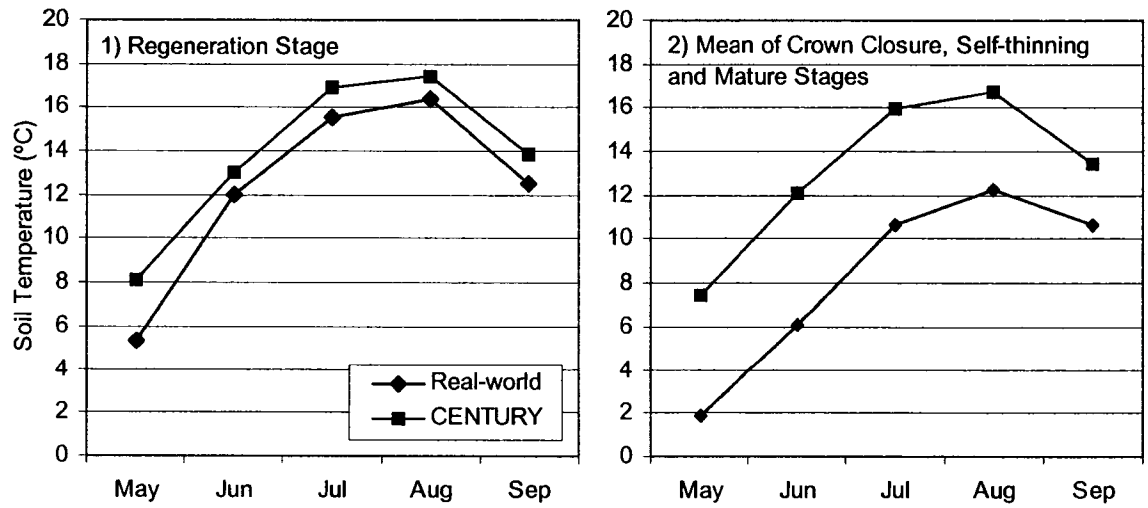

Figure 4.34 Comparison of real-world and CENTURY simulated May to September monthly soil temperature data.

4.2.1 Adjustment of Soil Temperature Simulated by the CENTURY Model and Evaluation of the Effects on Model Performance

Soil temperature is one of the main drivers of decomposition in the CENTURY model; therefore, ensuring that soil temperatures are simulated realistically is an important first step in model refinement and adaptation to conditions in northwestern Ontario. By lowering the mean growing season simulated soil temperatures (May to September) by approximately 1.5°C during the regeneration stage years and by approximately 5°C during the following stages, a lowering of decomposition rates was expected to occur that would help rectify some of the discrepancies between model output and RW measures of soil C and N pools and N mineralization rates. Two of the four fix.100 file variables that are used for calculation of soil temperatures were altered to generate the lower soil temperatures. The new calibration is referred to as RWSim and the old calibration is referred to as Unaltered. The soil temperature calculations were recreated in a spreadsheet. Calculation variables that required data simulated data were populated with Unaltered data from years representing the regeneration and mature stages. New values were determined by adjusting the soil temperature fix.100 file variables until the calculated soil temperatures were similar to the RW temperatures. Table 4.8 shows the changes made to the soil temperature calculation variables and Table 4.9 contains the measured, Unaltered, and RWSim soil temperatures for May to September. The RWSim soil temperature curves are presented in Figure 4.35.

Table 4.8 Changes made to the CENTURY model variables that are used in soil temperature calculations to produce the RWSim calibration.

Variables	Unaltered	RWSim	Variable Definitions
Elitst	0.40	-0.04	effect of litter on soil temperature relative to live biomass
Pmxbio	600.0	no change	maximum dead biomass level for soil temperature calculation
Pmntmp	-0.0035	no change	effect of biomass on minimum surface temperature
Pmxtmp	0.004	-0.0117	effect of biomass on maximum surface temperature

Table 4.9 Soil temperature effects of the RWSim calibration in comparison to measured and Unaltered soil temperatures for the months of May to September.

	Regeneration Stage			Mean of Crown Closure to Mature		
	Measured	Unaltered	RWSim	Measured	Unaltered	RWSim
	----- Soil Temperatures (°C) -----					
May	5.3	8.1	5.7	1.8	7.4	2.7
June	12.0	13.0	10.6	6.1	12.1	7.4
July	15.6	16.8	14.2	10.4	15.9	11.2
August	16.3	17.4	14.4	12.2	16.7	12.0
September	12.5	13.8	10.5	10.6	13.4	8.7
Mean	12.3	13.8	11.1	8.2	13.1	8.4

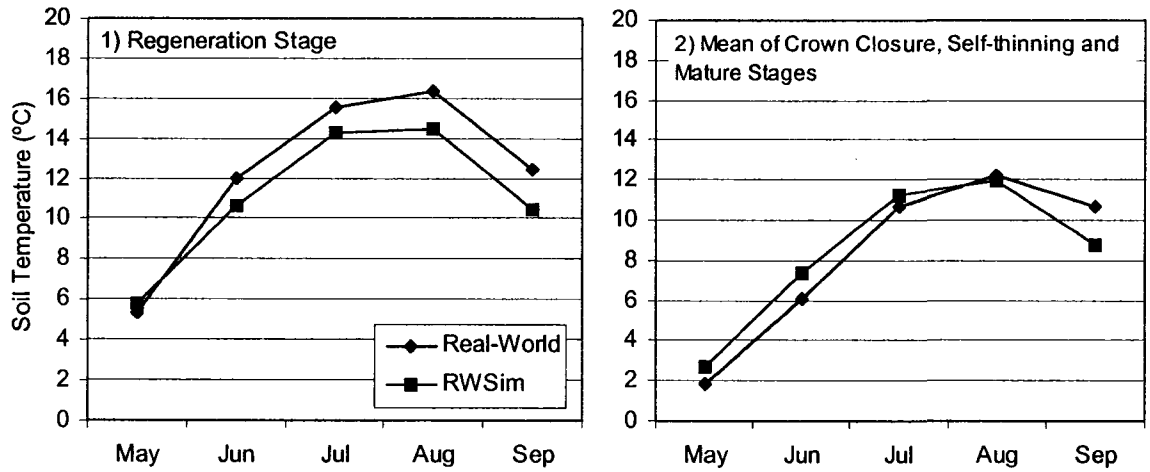

Figure 4.35 Comparison of real-world and RWSim (CENTURY Model) simulated monthly May to September soil temperature curves.

The RWSim calibration was successful at lowering mean growing season soil temperatures by 2.7°C for the regeneration stage and by 4.7°C for the remaining stages. Although not a perfect match to the RW measured soil temperatures, a sizeable improvement over the Unaltered calibration (Figure 4.34) was achieved.

Statistical validation analyses were re-run using CENTURY model data simulated by the RWSim calibration (Table 4.10). Validation results were very good for soil temperature (Figure 4.36). Mean absolute error was low at 1.22°C, the *t*-test was not significant, linear regression produced an R^2 of 0.88 with a slope of 1.12 and a y-intercept of -1.0, the simultaneous *F*-test was not significant, and most convincing was the modelling efficiency calculated at 0.97. However, MA%E was still greater than 10% at 30.3% but this deviance measure is susceptible to infrequent low RW measures. For example, the May soil temperature was only 0.63°C which made this month account for approximately 10% of the total MA%E.

Table 4.10 Results of the CENTURY model validation exercise using the RWSim calibration comparing observed and simulated soil temperature, and carbon and nitrogen pools.

	Number of Data Pairs	Deviance Measures MAE	MA%E	Paired *t*-test *	Linear Regression R^2	Slope	Intercept	Simultaneous *F*-test †*	Modelling Efficiency
STemp (May to September)									
	28	1.22	30.3	0.7322	0.88	1.12	-1.0	0.3084	0.97
Carbon Pools									
BIOc-AB	7	2032.9	31.2	0.2767	0.24	0.57	3478.4	0.4762	-0.25
BIOc-BL	7	1413.4	54.1	0.0175	0.17	0.76	1680.3	0.0920	-3.09
BIOc-TL	7	3271.9	35.5	0.1236	0.22	0.60	5180.3	0.3108	-0.70
TSc	7	1408.7	17.1	0.1377	0.71	-7.76	45549.4	0.0103	-0.78
MBPc x 2	7	56.4	37.6	0.1411	0.35	1.28	-100.9	0.0026	0.02
Nitrogen Pools									
BIOn-AB	7	3.5	23.3	0.9313	0.30	1.14	-2.5	0.9868	0.29
BIOn-BL	7	4.5	51.9	0.0173	0.23	1.09	4.1	0.0936	-2.73
BIOn-TL	7	6.2	22.6	0.2880	0.27	1.13	1.7	0.1807	0.00
TSn	7	71.2	22.6	0.0482	0.38	-16.86	3475.3	0.0459	-1.22
MBPn x 2	7	18.3	46.3	0.0070	0.08	2.70	-9.1	0.0352	-2.51
AvailN	7	0.3	54.5	0.2373	0.17	0.32	0.3	0.1052	-1.05
MNLZn	7	4.5	na	0.0359	0.56	-1.32	11.2	0.0026	-3.78

* *p*-value; significant if < 0.05

† *F*-test for slope = 1 and intercept = 0

BIOc-AB = aboveground biomass carbon

BIOc-BL = belowground biomass carbon

BIOc-TL = total biomass carbon

TSc = total soil carbon

MBPc x 2 = carbon in microbial biomass and microbail products

BIOn-AB = abovegoround biomass nitrogen

BIOn-BL = belowground biomass nitrogen

BIOn-TL = total biomass nitrogen

TSn = total soil nitrogen

MBPn x 2 = nitrogen in microbial biomass and microbial products

AvailN = nitrogen available for uptake

MNLZn = annual nitrogen mineralization rate

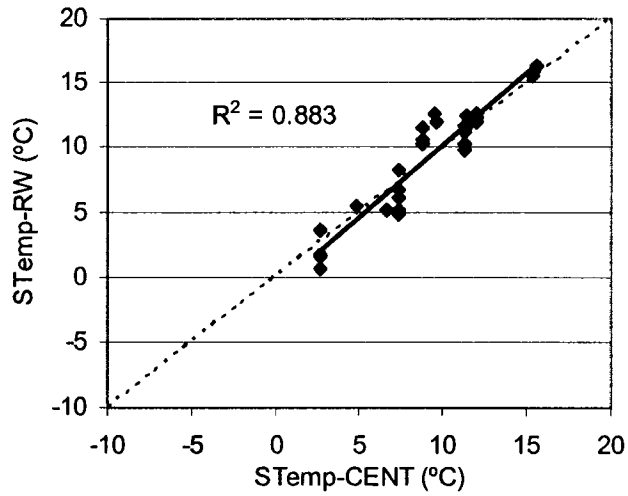

Figure 4.36 Observed (RW) versus CENTURY model simulated (CENT) monthly (May to September) soil temperatures using the RWSim calibration.

According to the validation statistics, however, the effect of lower soil temperatures on the C and N pools was marginal. The RWSim calibration resulted in only 5 of the 12 parameters (not including soil temperature) having deviance measures that were lower than the Unaltered calibration. Total soil C was the only pool where the *t*-test became non-significant, and the results of linear regression showed very little change which was reflected in an unchanged number of pools with significant simultaneous *F*-tests. Modelling efficiency calculations were similar with 9 of 12 calculations producing negative values and the highest modelling efficiency being only 0.29.

Table 4.11 contains the 100-year means of the C and N pools used in the validation exercise generated by the Unaltered and RWSim model calibrations. When directly comparing the data from the two simulations, it is clear that soil temperature is an important driver of processes within the CENTURY model. Changes in the mean

pool levels ranged between a drop of -4% to and increase of 26%. The greatest increases were found in the microbial and soil C and N pools (23 – 26%). The mean annual N mineralization rate was lowered by 4%. The live tree biomass C pools were minimally affected by the lower soil temperatures and only dropped by 2 to 3%. As expected, decomposition rates were lower with the RWSim calibration which was reflected in the substantially larger soil C and N pools. The MBPc and MBPn pools increased in the same proportions as the increases in the total soil C and N pools and did not exhibit any change in C:N ratios. Curiously, annual average available N levels increased (18%) while N mineralization rates decreased. This may be related to decreased demand for N for decomposition that outweighed reduced mineralization of N; however, greater amounts of available N should then have translated into increased biomass production which was not the case, assuming that biomass production is being limited by N supply. It may also be that the output variable aminrl(1) is not actually representative of the amount of N that is available for plant uptake.

It was found that processes in the CENTURY model are sensitive to soil temperatures and that by reducing soil temperatures with the RWSim calibration, increases were achieved in the soil C and N pools and the N mineralization rates were reduced. However, the trends exhibited by these pools over time were the same as those from the Unaltered calibration which explains why the validation exercise again had poor results. Figure 4.37 shows the RWSim, Unaltered, and RW trends for all pools (except for the biomass pools) and it is clear that the levels simply shifted up or down on the y-axes. Figures of the biomass pools were not included because the differences were

barely distinguishable. So while N mineralization did decrease, the simulated trend still increases with time rather than decreasing over time as the RW measures revealed.

Table 4.11 CENTURY model simulated 100-year mean pool sizes for Unaltered and RWSim calibrations.

	Unaltered	RWSim	Change
	----- ($g\ m^{-2}$) -----		(%)
Carbon Pools			
BIOc-AB	4525	4412	-2%
BIOc-BL	1013	987	-3%
BIOc-TL	5538	5399	-2%
TSc	4080	5021	23%
MBPc	194	241	24%
Nitrogen Pools			
BIOn-AB	14.3	13.9	-2%
BIOn-BL	3.5	3.4	-2%
BIOn-TL	17.8	17.3	-2%
TSn	150	189	26%
MBPn	13.0	16.4	26%
AvailN	0.44	0.52	18%
	----- ($g\ m^{-2}\ yr^{-1}$) -----		
MNLZn	7.57	7.29	-4%

Soil temperature does seem to be an important driver within the CENTURY model, but the simulated data trends suggest that the model structure is resistant to change. It was expected that N mineralization would decrease with lower soil temperatures but this occurred only marginally. It is likely that the proportion of the SOM pools that decomposed at each monthly time-step was lower but because the pool sizes had increased the actual quantity of N mineralized remained similar to previous levels thereby leading the N mineralization rates decreasing by only 4% on average. Investigations into production limitations in CENTURY were performed as background work for this project. Through these investigations it was found that while biomass

production is usually limited by N availability, a substantial portion of N requirements (sometimes over 50%) were met by the retranslocated N pool resulting from needle mortality. Therefore, even if the available N pool in the soil were decreased, the impact on biomass production could be buffered by the retranslocated N pool which increases the resistance of the CENTURY model to change resulting from reduced nutrient availability in the soil.

Another factor that may influence the ability of CENTURY to change pool trends is the setting of the C:N ratios for the five tree biomass compartments. In both the Unaltered and RWSim calibrations the cerfor(1..2,1..5) variables (tree.100 file) that set the maximum and minimum C:N ratios of tree biomass are set at fixed ratios (i.e. maximums are the same as minimums). This was done so that initial calibration of the model would be easier (Morris *pers comm.* 2002). If these ratios were allowed to float between reasonable maximums and minimums, then the nutrient concentration of the biomass would likely decrease through stand development as the available N pool declined. In turn, the quality of litter would decrease (higher C:N ratios) which could have a negative impact on decomposition and further reduce the N supply. Under these conditions it is likely that at some point during stand development N mineralization rates in the CENTURY model would start to decrease rather increase for the entire 100 years as they do with the current calibration.

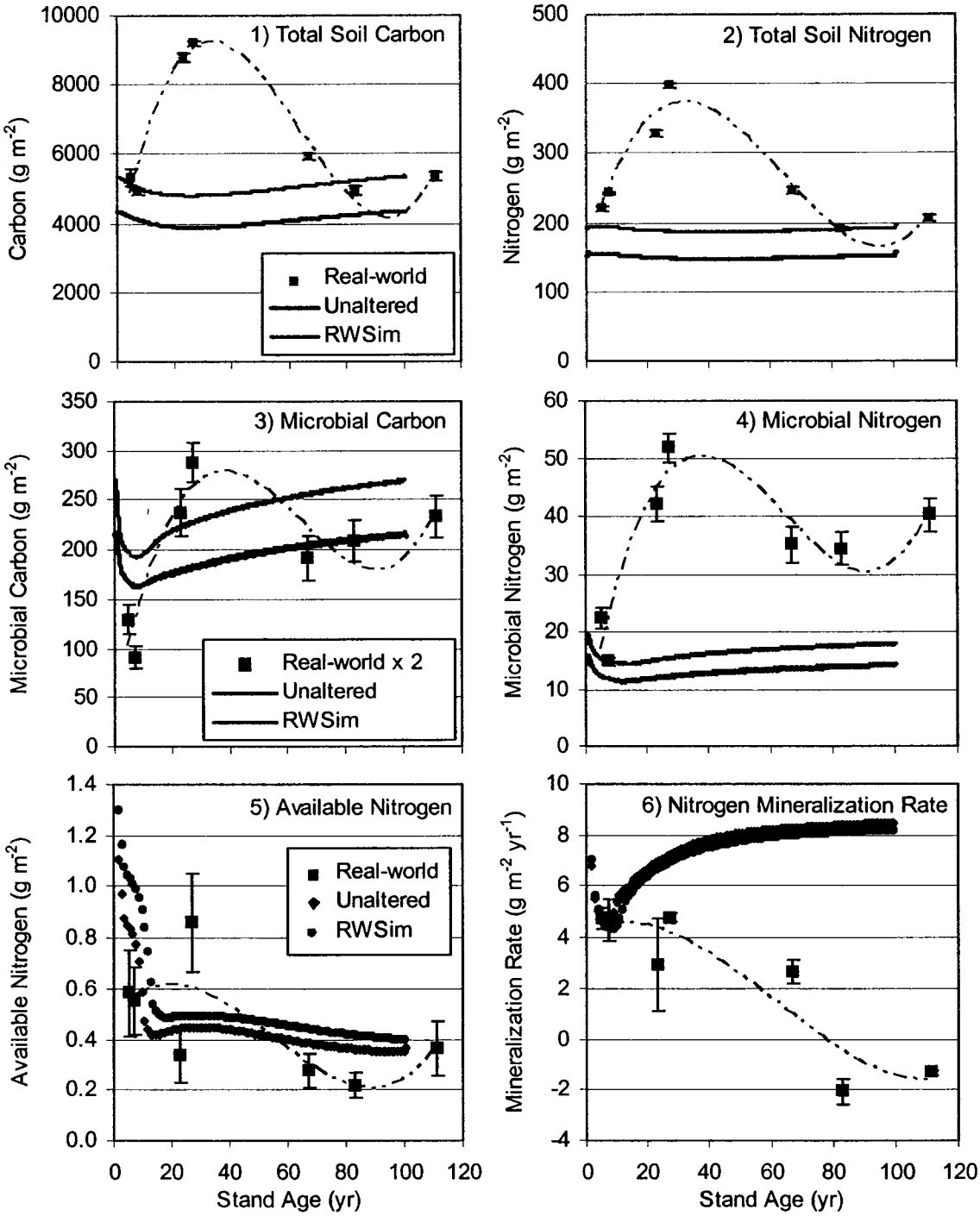

Figure 4.37 Major pool levels from the Unaltered and RWSim CENTURY model simulations and the corresponding real-world measures with 3rd order polynomial trend line (— · ·).

While the alterations to the CENTURY model with the RWSim calibration did not produce the desired results across all pools, having validated soil temperatures is one important step to improving confidence in the model and also shows that changes can be made to CENTURY to better reflect local site conditions. However, further work is clearly needed in other areas of the model. At this point it is not possible to determine whether the CENTURY model is capable of adequately simulating the C and N dynamics that exist in northwestern Ontario forests, or if the parameterization of the model has yet to reach the necessary level of refinement.

A logical place to continue with model refinement would be to change the cerfor(1..2,1..5) variables to allow the C:N ratios of tree biomass compartments to float within set ranges rather than being restricted to fixed C:N ratios, as previously discussed. Another logical place to continue with model refinement would be to ensure that the C:N ratios governing flows between the soil pools are adequately configured. For example, C:N ratios for the simulated microbial pools were between 13 and 16, whereas the C:N ratios from the RW microbial pools were between 5.6 and 6.1. The CENTURY model ratios are controlled by four fix.100 file variables that set the maximum and minimum ratios for material entering the surface and soil microbial pools. The variables for the surface microbial pool are pcemic(1,1) and pcemic(2,1), and the variables for the soil microbial pool are varat1(1,1) and varat1(2,1). Currently both sets have maximum C:N ratios of 16 and minimums of 8. Lowering the ratios would have the effect of requiring more N to be immobilized by decomposing material so that it could enter these pools, thus potentially restricting decomposition, mineralization, and eventually placing a restriction on biomass production.

Another area of the CENTURY model that should be investigated is the water submodel. Like temperature, soil moisture is an important model driver. Soil moisture can limit biomass production and SOM decomposition. Flows of C between soil pools are regulated by set decomposition rates. At each time step, these rates are scaled by the variable defac that is calculated monthly by the model based on soil temperature and soil moisture. Locally, soil moisture relations in the CENTURY model have not yet been investigated.

The CENTURY model is equipped with a microcosm option that allows model users to run CENTURY in essentially closed systems with constant soil temperature and moisture conditions (Metherell *et* al. 1993; Hilinski 2002). Microcosm simulations are ideal for simulating the dynamics of litter bags or laboratory incubations. Using the microcosm option would be a good way of testing the ability of CENTURY to model short-term dynamics. This option has not been attempted locally.

4.2.2 General Evaluation of the CENTURY Model

The above are two possible routes to improving the CENTURY model and one means of further testing and refining the model. However, there are inherent characteristics of the model that are of concern. Firstly, while the structure of the SOM submodel may have a sound scientific foundation, the pool divisions (e.g. active, slow and passive) are not easily understood by the layperson, nor are two of them easily quantifiable (slow and passive SOM) . These pool divisions make both calibrating the model and understanding the model output difficult. The forest floor and soil found in boreal stands are not divided into easily measurable groupings of materials that coincide

with the metabolic, structural, microbe, slow, or passive pools of CENTURY. A forest, particularly a boreal coniferous forest, normally has at least one distinct organic horizon with one or more distinct mineral soil horizons below. Different mineral soil layers can be simulated with CENTURY but a distinct organic horizon cannot. This is a second area of concern. The microbe pool and litter pools are segregated into surface and soil pools but none of the root litter enters the surface pool even though in boreal forests, often a large portion of the root mat exists within the surface organic horizons. The organic horizons also contain substantial proportions of materials in mid to late stages of decay that would fall into the definitions for the slow and passive SOM pools, but the CENTURY model considers those pools to be exclusively in the mineral soil. The challenge with calibrating and evaluating model output is that field data is typically related directly to specific soil horizons and is not separated into the pools the CENTURY model uses. The parameterization manual (Parton *et al.* 2001) does provide a method for calculating initial pool levels based on horizon descriptions; however, the average person could have difficulty determining whether the resulting distributions make sense for the sites that they are attempting to model.

A third area of concern with the CENTURY model is the way in which soil temperatures are calculated; specifically the size and timing of the lag that is imposed when air temperatures rapidly increase or decrease from month to month. The soil temperature data from the chronosequence sites displayed a lag greater than the 2°C lag that has been programmed into the model. This lag should either be adjustable by the user through a fix.100 file variable or allowed to float based on aboveground biomass levels and the magnitude of the month to month air temperature change. The other issue

with the lag is that it is imposed after soil temperatures are set to zero in months when the model determines that snow is present. This results in soil temperatures of either +2 or -2°C in some winter months. These issues need to be resolved especially since soil temperature is one of the main drivers of decomposition in the CENTURY model.

There are also aspects of the CENTURY model that are worthy of acknowledgement. The model as a whole is respected by the scientific community and has been utilized worldwide. CENTURY has the added flexibility of being able to simulate agro-ecosystems (as originally developed) and savannas. The SOM submodel in particular is highly regarded and has been incorporated directly or been the basis for the soil portion of other process-based models and hybrid models.

A major advantage of the CENTURY model is that almost all parameters within the model can be changed by the user. While this potentially adds to the complexity of using the model, it also dramatically increases the flexibility and adaptability of the model. Fortunately the CENTURY model developer (Natural Resource Ecology Laboratory (NREL), Colorado State University) has provided a good user manual for the model that also lists and defines all variable that the user can change. The source code for the model has also been made available and is very helpful when trying to understand the intricacies of the CENTURY model.

The CENTURY model has been in a continual state of development. NREL continues to release updated versions of the model to fix "bugs" and make improvements. The release of version 5, with a graphical user interface, was a substantial improvement over the command line version 4. As well as further

development of the CENTURY model, NREL has also been very helpful in providing support for model users.

5.0 CONCLUSIONS

The first objective of this project was to quantify C and N stores for above and belowground pools and also soil N mineralization rates for upland mixed conifer sites of wildfire origin in the Thunder Bay region of northwestern Ontario. A chronosequence of seven sites between 4 and 110 years old was selected. The sites fell into four broad stand development stage groupings of regeneration, crown closure, self-thinning, and mature in order to 1) characterize pool changes by the specific stages, and 2) to facilitate statistical analyses. The second objective of the project was to use the chronosequence data collected to validate the output of the CENTURY model which had been previously calibrated for this local site type. The calibration had been based on achieving end-of-rotation pool levels (100 years) but having chronosequence data allowed for early and mid-rotation comparisons to be made between the simulated and real-world data. The use of statistical validation procedures removed bias in the comparisons. Five research questions were associated with Objective 1 and two research questions were addressed under Objective 2 (see Section 3.0).

Question 1.1 addressed vegetation changes through stand development. A criteria for site selection was the tree species composition, so through stand development, the tree species composition changed from jack pine dominated to black spruce dominated stands. The live tree biomass C and N pools peaked at the self-thinning stage despite the trees having lower mean height and dbh than at the mature stage. As stands matured the lower vegetation shifted from pioneer, sun tolerant species

(e.g. fireweed and raspberry) to shade tolerant and continuous mats of feathermosses. The combination of tree and lower vegetation changes were reflected in the types and quantities of forest floor fine litter present at the four stages of stand development. The largest amount of litter mass was present at the crown closure stage and was in the form of foliage/herbaceous litter. Despite producing the greatest quantity of litter overall, the crown closure stage had the least fine woody litter presumably because at this stage little tree mortality occurs.

In regards to research Question 1.2, environmental conditions definitely changed between the regeneration stage and the mature stage but were not always different at every stage. Soil temperatures at the regeneration stage displayed greater variability and were overall higher in the growing season months (May to September). Once crown closure occurred, soil temperatures fluctuated seasonally in the same manner through to stand maturity because of shading and insulation from the forest floor and moss. Air temperature, however, was essentially the same at all stand development stages. Soil moisture during the sampling months (May to October) was variable but did appear to increase slightly through stand development which would most likely have been related to soil temperature and, at later stages, an increasing abundance of sphagnum mosses. Overall, it can be concluded that as mixed conifer stands mature, the soil conditions become cooler and moister which could have nutrient cycling implications.

Research question 1.3 asked whether soil C and N pools changed through stand development. Statistical analyses did not find many differences between stand development stages for total soil C and N, available N, or MB-C and MB-N. When significant differences were detected, the crown closure stage was most commonly

found to differ from the other stages. With the exception of available N, the regeneration stage often had the lowest pool levels indicating an influence of the recent wildfire disturbance. Interpretation of the data is challenging because the mass of organic and mineral horizons (i.e. dry mass) strongly influenced the amounts reported. The crown closure stage sites had the largest organic and mineral soil horizon masses. Therefore, with average concentrations applied to the soil masses (i.e. $\mu g\ g^{-1}$ applied to g m^2) the crown closure stage pools would be higher than the other stages. These site to site differences result in high levels of variation throughout a chronosequence that can only be constrained by increased site replication. However, due to the substantial resources required to have a highly replicated chronosequence, it may be more prudent to consider the site totals (i.e. g m^2) in conjunction with the nutrient concentrations (i.e. $\mu g\ g^{-1}$) in order to better interpret data that may be highly variable.

Stand development stage did not significantly (statistically) affect annual N mineralization rates or soil respiration (summer) rates (Research Question 1.4). However, despite these findings, it is difficult to ignore the trend of N mineralization rates decreasing into immobilization over time. It was likely the between site variation (i.e. differences between Selfthin-1 and Selfthin-2) that prevented ANOVA from detecting significant differences between the stages.

The results presented by this study clearly show that N mineralization and soil respiration rates are related to soil temperature (Research Question 1.5). Significant positive linear relationships were found for *in situ* N mineralization rates and soil respiration. The temperature controlled aerobic laboratory incubations also clearly showed greater N mineralization and soil respiration in the 20°C than in the 10°C soils.

Surprisingly, microbial biomass pools could not be linked to soil respiration. Therefore, the size of the microbial pool cannot be used to predict microbial activity and subsequently decomposition. The microbial pools were also unaffected by soil temperature as revealed by similar pool levels in the 10 and 20°C laboratory incubations.

Substrate quality (Research Question 1.5) was found to be the highest in the regeneration stage soils. This was revealed by the greatest N mineralization rate and high levels of available N at the chronosequence sites and in the laboratory incubations. The mature stage appeared to have the lowest substrate quality as revealed by immobilization rather than N mineralization and the lowest soil respiration determined by field measures, and the lowest N mineralization and soil respiration measured in the laboratory incubations. Microbial biomass pools were not related to substrate quality because levels were similar for all stand development stages so other factors must have been influential (e.g. soil moisture).

Data collected from the chronosequence sites and laboratory incubations generally fell within ranges reported in the literature. However, developing a more extensive chronosequence data set to reduce variation in the data and increase the strength of statistical tests would be beneficial.

Given that the CENTURY model has been tested and endorsed by numerous authors for a variety of different ecosystems, it was anticipated that a local calibration of the CENTURY model would 1) adequately simulate the natural processes of stand and soil development following wildfire disturbances for upland mixed conifer stands in northwestern Ontario and 2) pass a variety of statistical validation tests (Research Question 2.1). This exercise was less successful than expected. The CENTURY model

pools did not compare well with the chronosequence data and most tests failed. Simulated data lack the variability of RW data and produce very gradual trends over time. Validation tests confirmed a lack of agreement between RW and CENTURY values. Two main problems were deemed responsible. First, RW data were much more variable than simulated data. So even in cases were no significant differences were detected between stages, RW data still did not compare well with simulated data and validation failed (e.g. AvailN and TSn). Secondly, very different trends were projected by the simulations than were revealed by the RW data (e.g. N mineralization rates). The exercise certainly showed that no single test is best for validation. Eight tests were used and at no point were all tests in agreement. One of the most strict and easiest to interpret tests was modelling efficiency which was only above zero for 3 out of 13 tests (max of 1, < 0 unacceptable).

The aforementioned issue of data variability may partially be an artefact of the chronosequence approach used to collect the data. The main underlying assumption of a chronosequence is that differences between sites are the result of time since disturbance. In practice, it is almost impossible to meet this assumption and, in the case of this study, some of the basic physical properties of the sites (e.g. soil texture, mineral soil depth and bulk density) differed as can be seen in Table 4.2. These site to site differences no doubt contributed to variability in the data and the difficulty in some cases of identifying clear trends over time. However, the data are still meaningful because the sites represent the range of variation possible within an ES20 classification. In a simulated forest these physical properties do not change overtime so data produced by the CENTURY model are less variable and create smooth gradual trends over time. Therefore, it is of no

surprise that "messy" real-world data do not always coincide well with model output. However, given the fixed time restraints and resources, a long-term study using one site was not feasible so the chronosequence approach was required.

Because temperature was found to influence several pool levels, as determined by chronosequence measures and laboratory incubations, and also is an influential driver of processes within the CENTURY model, efforts were made to improve the simulation of soil temperatures (Research Question 2.2). The subsequent validation of the growing season soil temperatures (May to September) was very successful; however, these results did not carry through to the C and N pools. Reduced soil temperatures were found to cause systematic increases or decreases in pools in the expected direction but not changes in the trends displayed by the pools over the duration of 100 years. For example, N mineralization rates, although lower, still continued to increase gradually over time rather than decrease as the RW rates did.

With the current calibration, the CENTURY model does not adequately simulate C and N dynamics over 100 years of stand development for upland mixed conifer sites of fire origin in northwestern Ontario. Some suggestions were made to further investigate and make changes to the model. These include 1) checking the C:N ratios of the SOM pools, 2) investigating the influence of soil moisture in the model, and 3) using the microcosm option to test the model against short-term laboratory incubation experiments. Following these suggestions should help future model users to improve model output and/or gain a better understanding of the feedback mechanisms within the model and the sensitivity of the individual parameters. These suggestions could also be used as a framework for further laboratory and field-based research. Further clarifying

the relationship of CENTURY model terminology and pool definitions to RW measurable pools would significantly improve the operability of the model.

Developing and working with process-based ecosystem models has two equally important benefits. Firstly, a working model is a very powerful predictive tool that can be used to guide management decisions for day to day operations (e.g. harvest and silvicultural effectiveness) and also to give us insight into the future that can be used for decision making at the strategic level (e.g. moderating the affects of climate change). Secondly, model building and refinement can be a framework for investigating ecosystem processes. To build and improve models we need information and if that knowledge does not currently exist or, as in the case of this study, the information is not available for a specific geographic location, then new data needs to be generated. Despite the criticisms of the CENTURY model that arose from this endeavour, continued work towards further refinement will lead to a better understanding of forest soil dynamics and eventually a model that could be used to investigate practical, operational questions (e.g. long-term forest productivity, silviculture, climate change impacts, carbon storage, etc...) using a science-based ecosystem approach.

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6.0 APPENDICES

APPENDIX I

CENTURY MODEL MECHANICS

The CENTURY model, like most other process based models, is quite complex. For this reason, only a basic description of the structure and technical background of the model will be provided. Parton *et al.* (1987, 1988, 1993, 2001), Sanford *et al.* (1991), Metherell *et al.* (1993), and Hilinski (2002) provide more detailed descriptions of the CENTURY modelling environment.

The CENTURY model simulates the flows and cycling of C and nutrients (N), phosphorus (P), and sulfur (S) between above and below ground pools for terrestrial ecosystems. By examining these pools after a simulation has been executed, it is possible to interpret the effect of management and climatic scenarios upon the ecosystem (Metherell *et al.* 1993).

The rate and direction of movement for each of the C and nutrient flows is generated by a separate submodel within the CENTURY environment. Another major component of the CENTURY model is the plant production submodel. When modelling grassland ecosystems, the grassland/crop production submodel is used. Forest ecosystems require the forest production submodel, and savanna ecosystems utilize a combination of both the grassland/crop and forest production submodels. Each plant production submodel uses the same SOM submodel. There is also a water-budget submodel that tracks water flows into (e.g. precipitation), within (e.g. soil water), and out (e.g. leaching) of the ecosystem. Other components of CENTURY include systems that are used for scheduling events (e.g. fire or harvesting disturbances) during the simulation and modules that can change the management options (Metherell *et al.* 1993).

According to Metherell *et al.* (1993), the major variables required to run the CENTURY model are those describing local climate, plant and soil chemical composition, and site specific descriptors. These variables include:

(1) monthly average maximum and minimum air temperature;
(2) monthly precipitation;
(3) lignin content of plant material;
(4) plant N, P, and S content;
(5) soil texture;
(6) atmospheric and soil N inputs; and
(7) initial C, N, P, and S levels.

Other important variables include the maximum gross forest production (prdx(3)), maximum net forest production (prdx(4)), ratio of live sapwood to total stem wood which controls respiration (sapk), initial nutrient and C pool levels, and C to element ratios. If suitable data is not available within a CENTURY file, estimations from existing literature can be used for most inputs (Metherell *et al.* 1993). Model calibration can be aided by referring to the CENTURY Parameterization Workbook contained within Parton *et al.* (2001).

The forest production submodel determines the amount of production (g biomass m^{-2}) and the distribution pattern of C and nutrients within the trees (Figure A1.1). Live tree C is divided into foliage, fine branches, fine roots (< 2mm in diameter), large wood (or stemwood, > 10cm in diameter), and coarse roots. The amount of newly produced C and nutrients distributed to each individual tree component is usually constant, but can be altered to reflect the point in time when the forest changes from juvenile to mature. Once living tree material dies, it passes into the SOM submodel at decay rates specific to the type of material (Metherell *et al.* 1993).

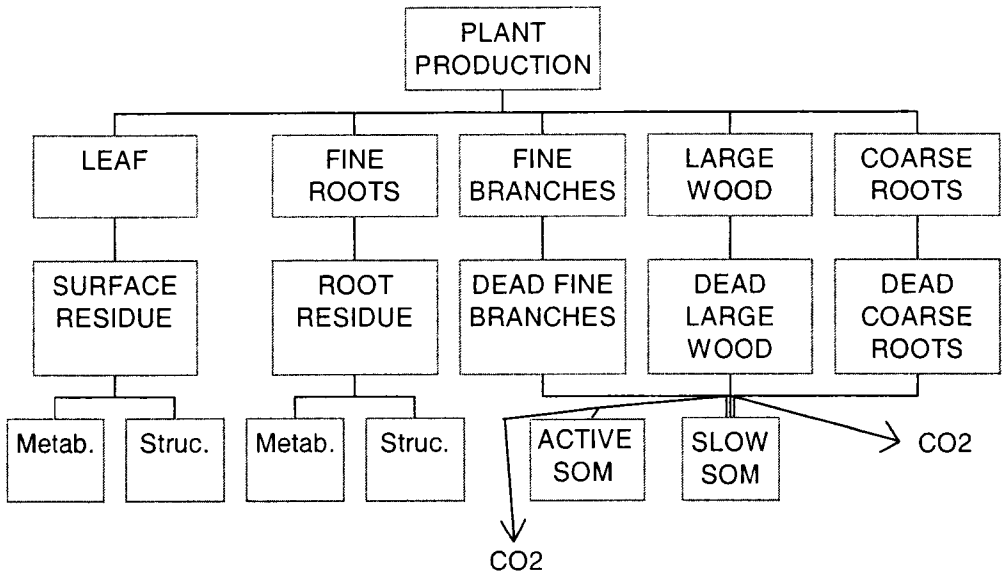

Figure A1.1 The CENTURY forest production submodel including carbon allocations and initial pathways of dead materials (adapted from Metherell *et al.* 1993).

The CENTURY model places five constraints on the amount of production possible each month. These include: species specific maximum monthly production, temperature, moisture, leaf area index (LAI), and nutrient availability. The effect of nutrient availability is implemented after the effects of temperature, moisture and LAI are applied. Atmospheric CO_2 concentration is an optional factor that can be applied to influence production.

The SOM submodel acts as the basic component of the CENTURY model for simulating the flows and pools of C and nutrients throughout the simulated ecosystem. Figure A1.2 shows the partitioning and flows of C, and where C is added and lost within CENTURY. The nutrients N, P, and S have similar pools and flows as C, but the nutrients have different avenues for entering and exiting the system. For example, C is added to the system through net primary production (NPP), whereas N is gained through atmospheric deposition, weathering of parent material, and potentially through symbiotic

fixation, non-symbiotic fixation, and fertilization (Metherell *et al.* 1993). The theory is that N is bonded to C, so as the C moves from pool to pool, the N follows. Decomposition of the organic matter releases the N in proportion to the C:N ratio of the material being decomposed (Parton *et al.* 1987, 1988).

At each monthly time-step, a set fraction of each of the live tree compartments dies based on parameter settings in the tree.100 file; leafdr(1-12) for fraction of leaves that die each month, and wooddr(2-5) for fraction of fine roots, fine branches, large wood, and coarse roots that die each month. Larger, more catastrophic events can also be scheduled (e.g. fire or harvesting) that result in greater quantities of live C dying or removed from the system (Metherall *et al.* 1993; Hilinski 2002).

Upon death, leaves enter the surface litter (or residue) pool and fine roots enter the belowground litter pool. Each of these litter pools are then divided into structural and metabolic pools as a function of the lignin:N ratios of the debris. Structural pools are slow to decay and have high, fixed, user-set C:N ratios. The lignin portions of the structural pools are eventually passed on to the slow SOM pool while the cellulose portion is passed on to the surface microbe or active SOM pool. Metabolic pools represent quickly decomposable sources of C and N, and have much shorter turnover times than the structural pools. The products of the metabolic pools are directed to the surface microbe and active SOM pools (Parton *et al.* 1987 and 1994).

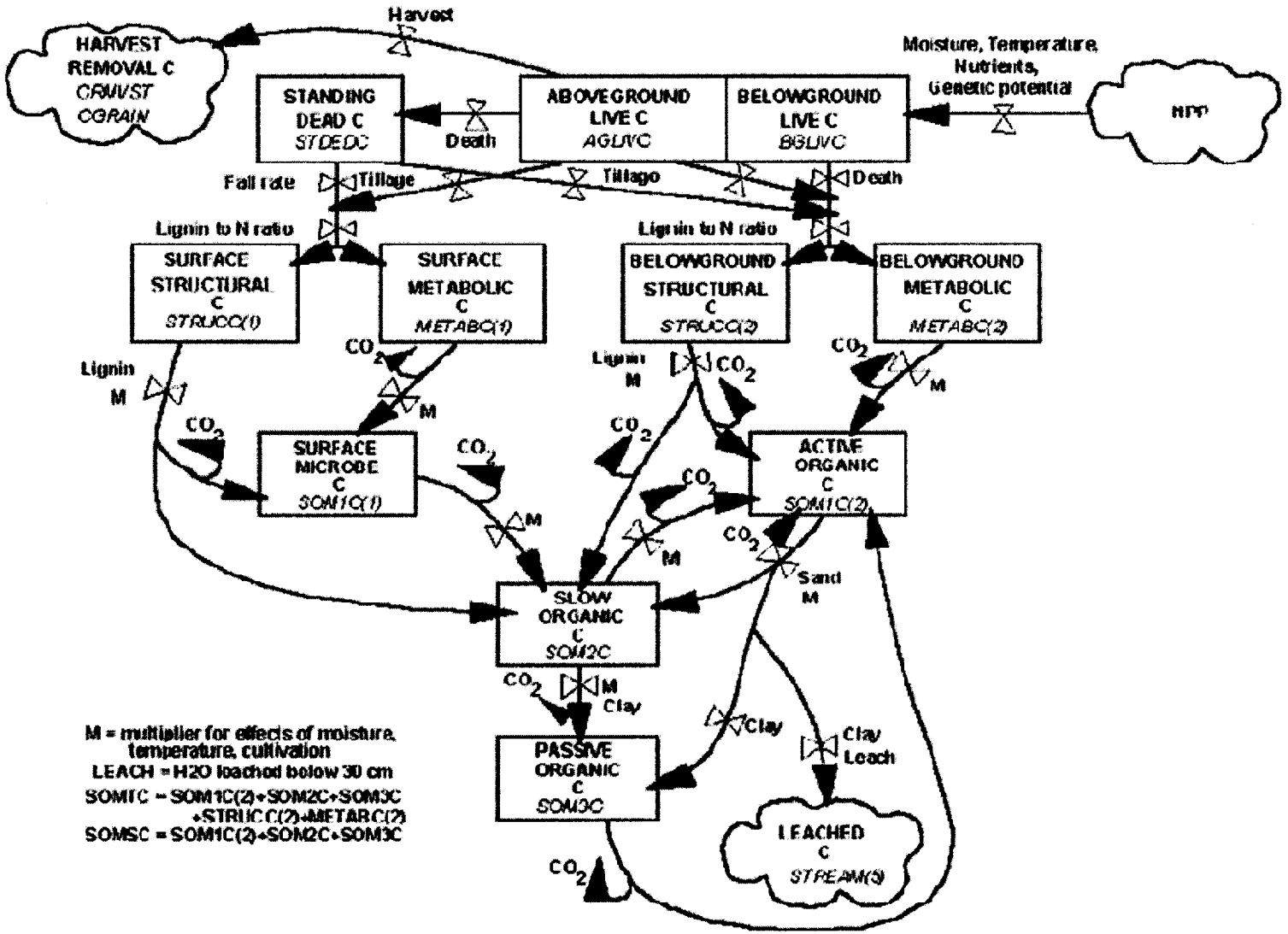

Figure A1.2 Carbon pools and flows within the CENTURY model (Metherell *et al.*

Dead fine branches, large wood and coarse roots enter respective dead wood pools for each. Materials in the dead wood pools bypass the structural and metabolic pools. As they decay, dead fine branch and large woody materials are subdivided into surface microbial and slow SOM pools. Dead coarse roots pass into the active and slow SOM pools. The lignin fractions, since they are more resistant, enter the slow SOM pool and the non-lignin fractions enter the surface microbial and active SOM pools (Metherall *et al.* 1993; Hilinski 2002). Materials entering or residing in the structural, metabolic, and dead wood pools do not undergo any actual decomposition. It is only once the material exits these pools that weight loss occurs.

As part of the movement of materials from pool to pool, C is released as CO_2 representing microbial respiration (a by-product of decomposition) and is lost from the system. The amount of CO_2 released is a set fraction of the total C moving from pool to pool. For most of the transfers, the fraction of C lost as CO_2 is around 55%.

Each pool has a maximum decay rate that is the starting point for determining the flow of C out of each pool during each monthly time-step. The highest rates are for the two metabolic pools, followed by the surface and soil active SOM pools, then the structural pools, then the slow SOM pool, and finally the passive SOM pool. Carbon flows from the active SOM and slow SOM pools are also influenced by soil temperature, moisture, and texture (Parton *et al.* 1987, 1988, and 1994; Metherall *et al.* 1993; Hilinski 2002).

Given the controls on the amount of materials that flow between pools during each time-step (i.e. C:N ratios, soil texture, maximum decomposition rates, soil temperature, and soil moisture), SOM pool levels should stay at fairly stable fractions of the total SOM during simulations. The active SOM pool that includes live microbial

biomass and microbial products can be estimated as 2 – 3 times the live microbial biomass and should account for approximately 2 to 4% of the total SOM C (Metherall *et al.* 1993). Presumably, this fraction should be distributed between the active SOM and surface microbe pools. Metherall *et al.* (1993) also suggests that another 50 – 60% of the total SOM C should be accounted for in the slow SOM pool with lignin fractions contributing 40% of this amount (Elliott and Cambardella 1992), and stabilized microbial products comprising the remaining 10 to 20%. The passive SOM pool which represents very physically and chemically protected SOM that is very resistant to decay typically contributes between 30 and 40% to the total soil SOM C with the levels being greater with high clay content soils (Metherall *et al.* 1993).

The inclusion of N dynamics makes the CENTURY model a powerful tool for investigating/predicting N fluxes in real-world situations. Nitrogen is widely considered to be one of the most limiting nutrients in boreal forest systems (Foster and Morrison 1983) and concern exists regarding potential reductions in long-term site productivity resulting from N deficiencies caused by forest harvesting activities (Gordon 1983; Foster *et al.* 1995). As mentioned previously, N is intimately linked to C in both the CENTURY environment and real world, and N concentrations/availability can be a limiting factor for both production and decomposition.

In CENTURY, mineral N availability can limit C production because all C produced requires minimum amounts of N (i.e. a maximum C:N). The amount of N per unit of C produced is a constraint set in the CENTURY model. When insufficient N is available for the calculated potential production, the production is limited to the amount of N available. The quantity of N available for uptake by plants is regulated by the fraction of mineral N available for uptake (favail[N] a fix.100 parameter), the biomass of

fine roots, the amount of mineral N available including mineralization and losses (e.g. volatilization) for the current month, and the amount of N that had accumulated via retranslocation. Retranslocated N accounts for a substantial portion of the available N pool each month particularly since this pool is only drawn upon for production (i.e. no losses through other process like volatilization). The majority of the remaining mineral N that is available for production comes from mineralization. Atmospheric deposition – a user defined amount – is another source of mineral N. In cases when there is excess N following production allocations, the N returns to the available pool with minor amounts leached or volatilized depending on fix.100 file settings for the fleach(1-3) and vlosse variables (Metherall *et al.* 1993; Hilinski 2002). The settings for our local northwestern Ontario black spruce-dominated system make these losses very small.

Mineralization of N occurs in the CENTURY model during the movement of materials from pool to pool in the SOM submodel. As C is released as CO_2 through decomposition, a proportion of N equal to the amount of N relative to the amount of C (N:C ratio) of the source pool is mineralized and enters the available N pool. However, not every decomposition flow results in a net mineralization of N for each flow. Since different C:N ratios exist between pools, additional N may be required from the available N pool in order to lower the C:N ratio of the materials moving to be equal to the C:N ratio of the destination pool. The adsorption of mineral N into decomposing materials is how the CENTURY model represents N immobilization. Should insufficient N be available, decomposition is either limited or not allowed to proceed (Parton *et al.* 1987 and 1988; Metherall *et al.* 1993; Hilinski 2002). Carbon flows from the dead fine branches, dead large wood, dead coarse roots, structural, and slow SOM

pool typically result in N immobilization. The surface microbe and active SOM pools (lowest C:N ratios) are the greatest sources of mineralized N.

Temperatures (air and soil) are very important factors influencing processes within CENTURY. Air temperature limits live C production calculations, and affects maintenance respiration in aboveground compartments. Soil temperatures influence maintenance respiration for roots and is also a main driver (along with moisture) influencing decomposition flows. Maximum and minimum monthly air temperatures are entered by the user and are averaged to provide monthly air temperatures. Alternatively, the user can create a weather data file that contains maximum and minimum monthly air temperatures that can change through time so the same temperatures are not used for each year of a simulation. Using a weather data file is particularly good for recreating historical climate conditions. Monthly precipitation levels are also entered by the user and can also be entered as part of a weather data file (Metherell *et al.* 1993).

Soil temperatures are simulated monthly based on simple equations by Parton (1984) that incorporate air temperatures, leaf C, surface litter C, the presence of snow, and four adjustable fix.100 file variables (elitst, pmxbio, pmxtemp, and pmntemp) that control the effect of canopy and surface litter on soil temperature. A maximum and minimum soil temperature are calculated and then averaged to give the mean monthly soil temperature (stemp). The new soil temperature is set to 0°C if snow is present. A lag is also incorporated that takes into account slower changes in soil temperature relative to air temperature. When the air temperature of the current month is greater than ±2°C of the air temperature from the previous month, a lag of ±2°C is imposed on the newly calculated soil temperature. An increase in month to month air temperature of

over 2°C causes a lag of -2°C, that prevents the soil temperature from rising faster than it would in the real world. A decrease of over 2°C in air temperature causes a lag of +2°C. The lag calculation was a new addition to version 5 of the CENTURY model (Hilinski 2002).

We have concerns in two areas regarding soil temperature calculations. Firstly, the lag is applied after zeroing of the temperature due to snow; therefore, if a lag is needed, the soil temperature is forced to either +2 or -2°C. As a result the soil temperatures could potentially be calculated to be abnormally high (+2°C) during some of the coldest months of the year. Second, the size of the lag cannot be controlled by the model user without changing programming code and this lag may be greater in forest soils where there is greater shading and soil insulation provided by the moss and organic layers than in a grassland system; the source for the equations.

APPENDIX II

PHOTOGRAPHS OF CHRONOSEQUENCENE SITE PLOTS

Figure A2.1 and A2.2 Regen-1 Site - 4 year old (1998 wildfire) – Plot 1 and Plot 2.

Figure A2.3 Regen-1 Site - 4 year old (1998 wildfire) – Plot 3.

Figure A2.4 Regen-1 Site - 4 year old (1998 wildfire) – soil pit.

Figure A2.5 Regen-2 Site - 6 year old (1996 wildfire) – Plot 1.

Figure A2.6 Regen-2 Site - 6 year old (1996 wildfire) – Plot 2.

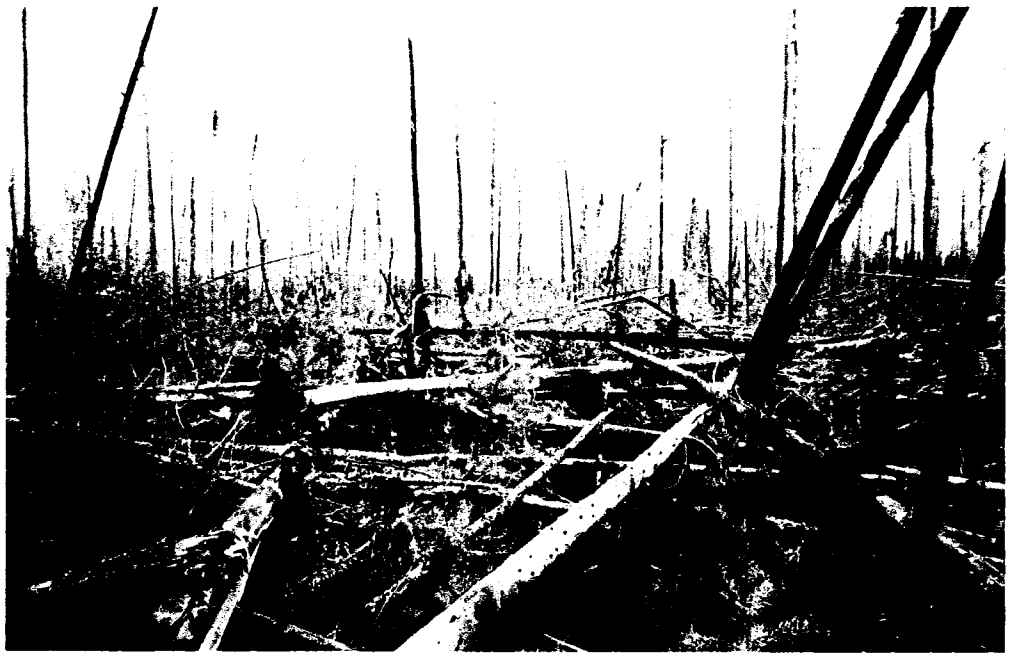

Figure A2.7 Regen-2 Site - 6 year old (1996 wildfire) – Plot 3.

Figure A2.8 Regen-2 Site - 6 year old (1996 wildfire) – Soil Pit.

Future A2.9 CrwnCl-1 Site - 22 year old (1980 wildfire) – Stand Edge.

Figure A2.10 and A2.11 CrwnCl-1 Site - 22 year old (1980 wildfire) – Plot 1 and Plot 2.

Figure A2.12 CrwnCl-1 Site - 22 year old (1980 wildfire) – Plot 3.

Figure A2.13 CrwnCl-2 Site - 26 year old (1976 wildfire) – Stand Edge.

Figure A2.14 CrwnCl-2 Site - 26 year old (1976 wildfire) – Plot 1.

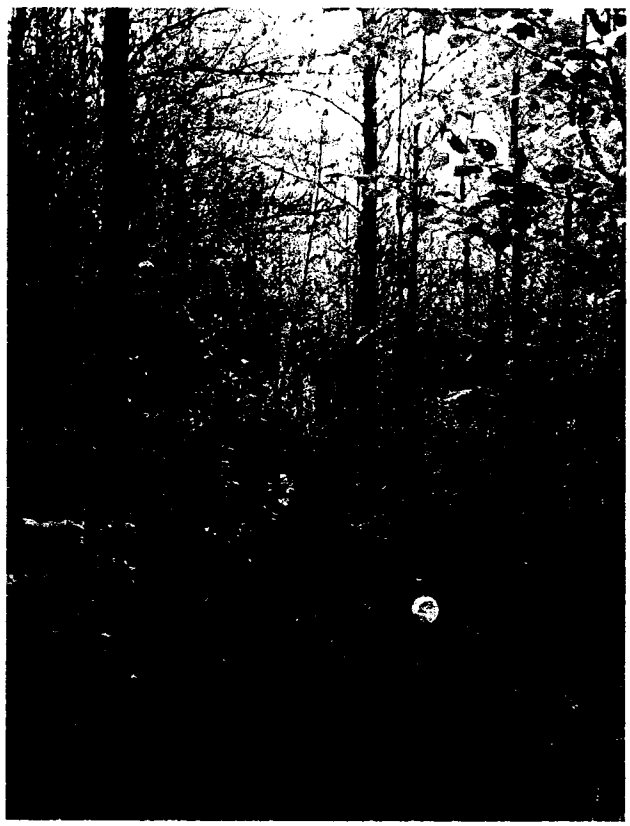

Figure A2.15 CrwnCl-2 Site - 26 year old (1976 wildfire) – Plot 2.

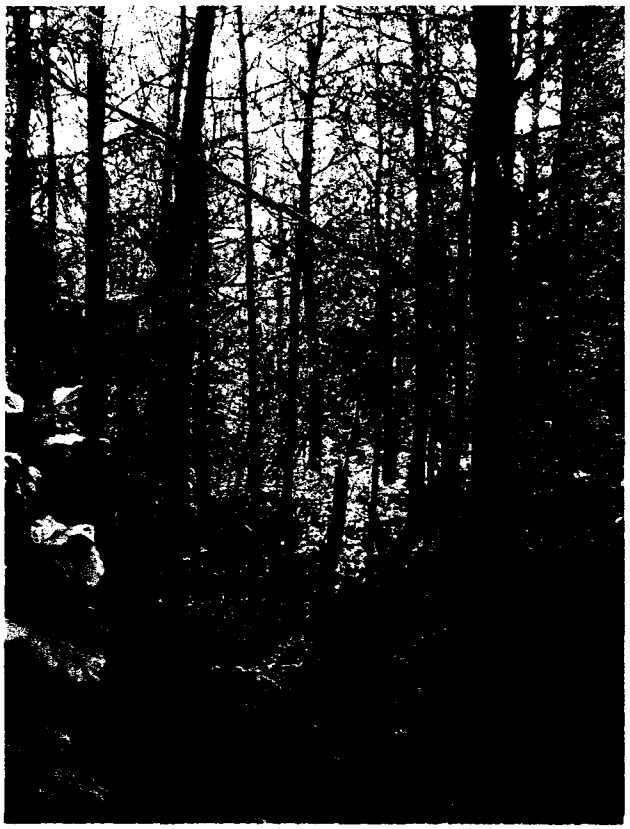

Figure A2.16 CrwnCl-2 Site - 26 year old (1976 wildfire) – Plot 3.

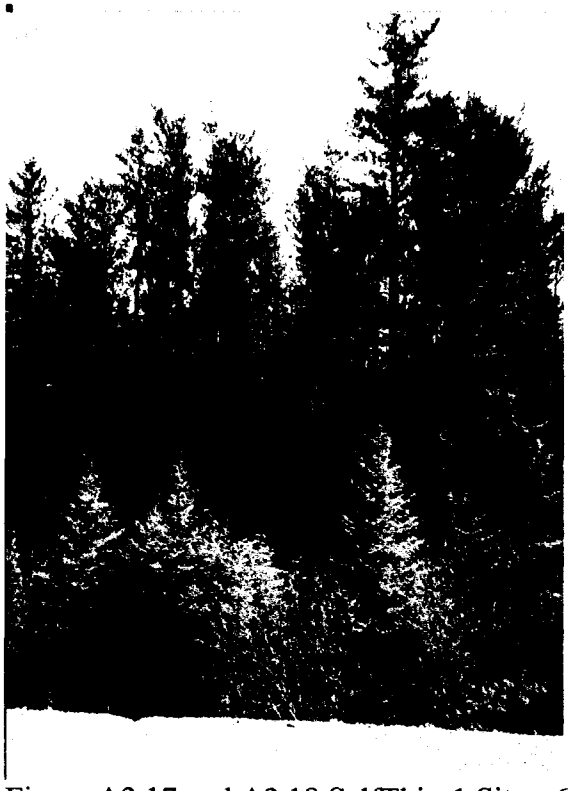

Figure A2.17 and A2.18 SelfThin-1 Site - 66 year old (1936 wildfire) – Stand Edge and Plot 1.


Figure A2.18 and A2.19 SelfThin-1 Site - 66 year old (1936 wildfire) – Plot 2 and Plot 3.

Figure A2.20 SelfThin-2 Site - 82 year old (1920 wildfire) – Stand Edge.

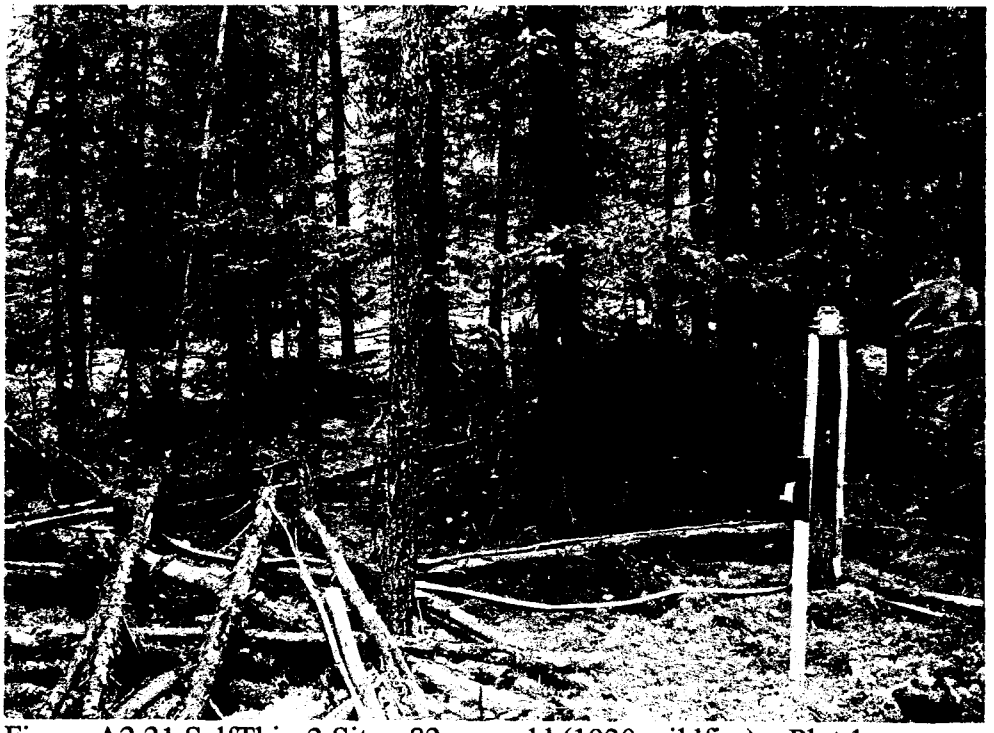

Figure A2.21 SelfThin-2 Site - 82 year old (1920 wildfire) – Plot 1.

Figure A2.22 SelfThin-2 Site - 82 year old (1920 wildfire) – Plot 2.

Figure A2.23 SelfThin-2 Site - 82 year old (1920 wildfire) – Plot 3.

Figure A2.24 SelfThin-2 Site - 82 year old (1920 wildfire) – Soil Pit.

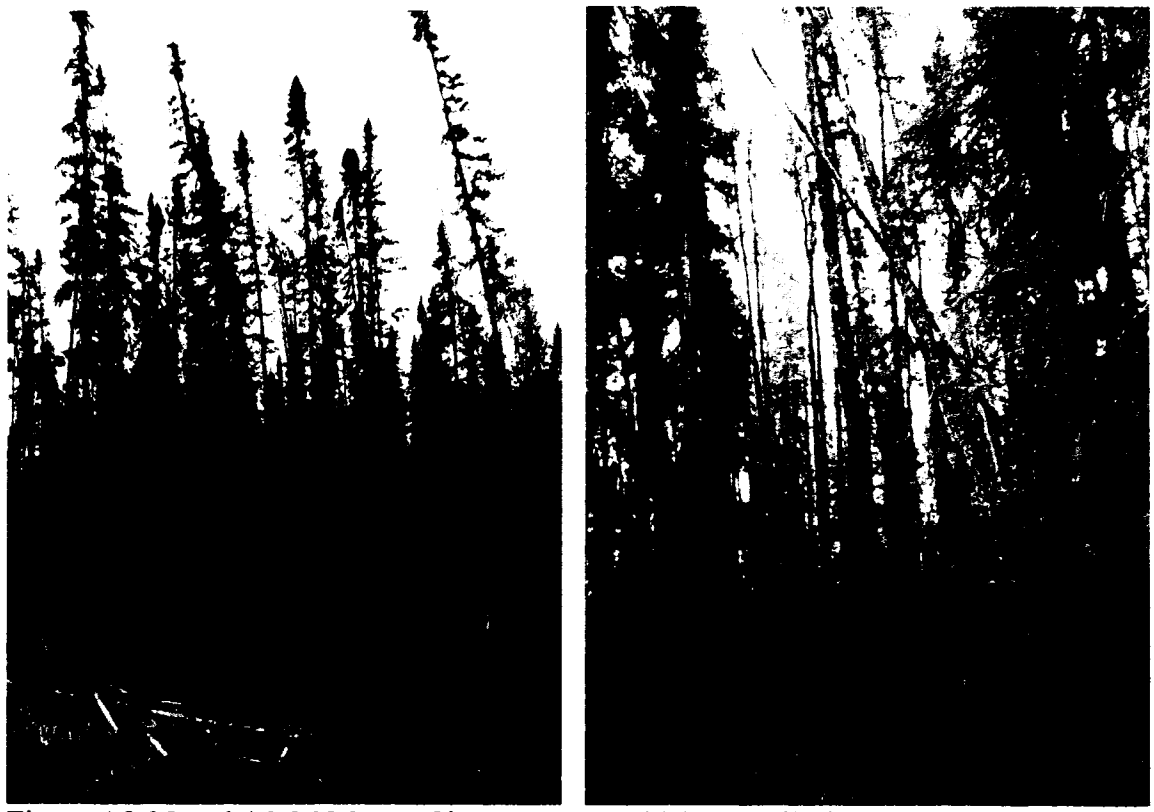

Figure A2.25 and A2.26 Mature Site - 110 year old (1892 wildfire) – Stand Edge and Plot 1.

Figure A2.27 and A2.28 Mature Site - 110 year old (1892 wildfire) – Plot 2 and Plot 3.

APPENDIX III

PARAMETERS USED IN ALLOMETRIC HEIGHT AND BIOMASS EQUATIONS, AND NUTRIENT PERCENTAGES

Table A3.1 Coefficients for allometric non-linear equation used estimate tree heights based on measured diameter at breast height (DBH).

Chronosequence Site and Tree Species	Coefficients [a]	
	A	C
Black Spruce	9.947119	25.20132
Jack Pine	9.69717	24.72861
Balsam Fir	6.66	15.44446
Larch	9.69717	24.72861
Trembling Aspen	7.040925	21.54889
White Birch	8.048699	22.14323

[a] Height (m) = $1.3 + (C*\exp^{(-A / DBH)})$

Table A3.2 Coefficients for allometric non-linear equation used to estimate biomass for tree components based on measured diameter at breast height (DBH) and percentage nitrogen for each component.

Component and Tree Species	Coefficients [a]			Percentage Nitrogen
	A	B	C	
Stem Wood				
Black Spruce	2.941	3.49	0.015	0.044950
Jack Pine	2.236943	0	0.1359444	0.047226
Balsam Fir	2.1491	0	0.0606	0.067033
Larch	2.393	0	0.0731	0.079968
Trembling Aspen	2.199	0	0.1714	0.070588
White Birch	2.33	0	0.1171	0.070588
Stem Bark				
Black Spruce	2.247	0.017	0.016	0.247015
Jack Pine	2.68196	0	0.0050741	0.201133
Balsam Fir	2.124	0	0.0114	0.392857
Larch	2.68196	0	0.0050741	0.318681
Trembling Aspen	2.552	0	0.0108	0.416667
White Birch	2.015	0	0.0407	0.416667
Live Branches				
Black Spruce	1.812	0.627	0.011	0.37022
Jack Pine	2.931628	0	0.001041	0.299574
Balsam Fir	2.0964	0	0.069	0.365922
Larch	2.055	0	0.0776	0.232675
Trembling Aspen	2.695	0	0.0065	0.493976
White Birch	2.5073	0	0.0117	0.493976
Foliage				
Black Spruce	1.256	0.287	0.071	0.799143
Jack Pine	1.882059	0	0.017637	0.843174
Balsam Fir	1.7853	0	0.1336	0.879310
Larch	1.979	0	0.0061	0.993506
Trembling Aspen	2.0261	0	0.0114	2.416667
White Birch	1.9505	0	0.0132	2.416667
Cones				
Black Spruce	3.520928	0	6.85E-05	0.285423
Jack Pine	3.520928	0	6.85E-05	0.221139
Balsam Fir	3.520928	0	6.85E-05	0.271191
Larch	3.520928	0	6.85E-05	0.271191
Trembling Aspen	n/a	n/a	n/a	n/a
White Birch	n/a	n/a	n/a	n/a
Roots				
Black Spruce	2.02789	0	0.107127	0.176575
Jack Pine	2.02789	0	0.107127	0.155616
Balsam Fir	2.02789	0	0.107127	0.197143
Larch	2.02789	0	0.107127	0.155616
Trembling Aspen	2.02789	0	0.107127	0.234211
White Birch	2.02789	0	0.107127	0.234211

[a] Dry Biomass (kg) = $B + C * DBH^A$

APPENDIX IV

COMPARISONS OF 2 *M* KCl EXTRACTIONS AND 0.5 *M* K_2SO_4 EXTRACTIONS

The comparison of available N soil extractions with 2 *M* KCl and 0.5 *M* K_2SO_4 showed a very strong, nearly 1:1 relationship for combined organic and mineral available N ($R^2 = 0.9785$) and the organics separately ($R^2 = 0.9616$). The relationship was not quite as strong for the mineral soils but still sound ($R^2 = 0.8942$).

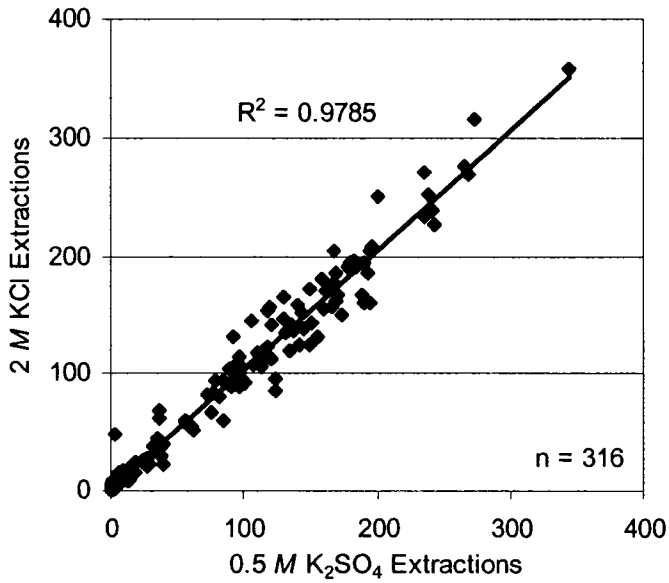

Figure A4.1 Total available N ($NH_4 + NO_3$) concentration (μg g-1) in combined organic and mineral soil using two different extracting solutions.

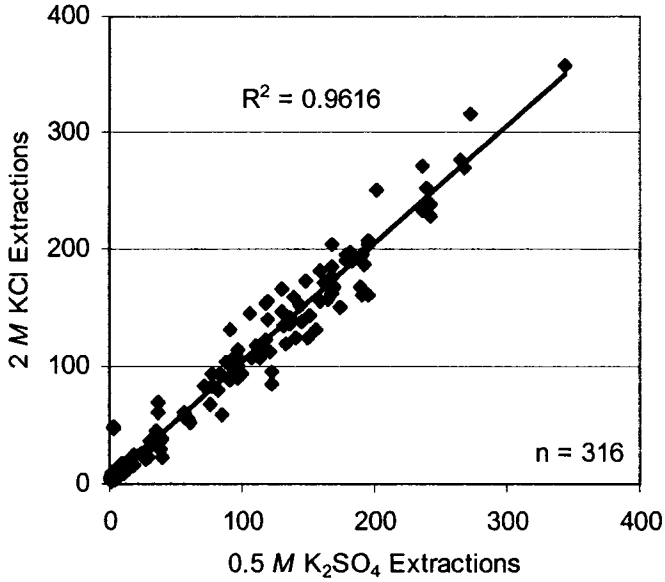

Figure A4.2 Total available N (NH_4 + NO_3) concentration (μg g^{-1}) in organic materials using two different extracting solutions.

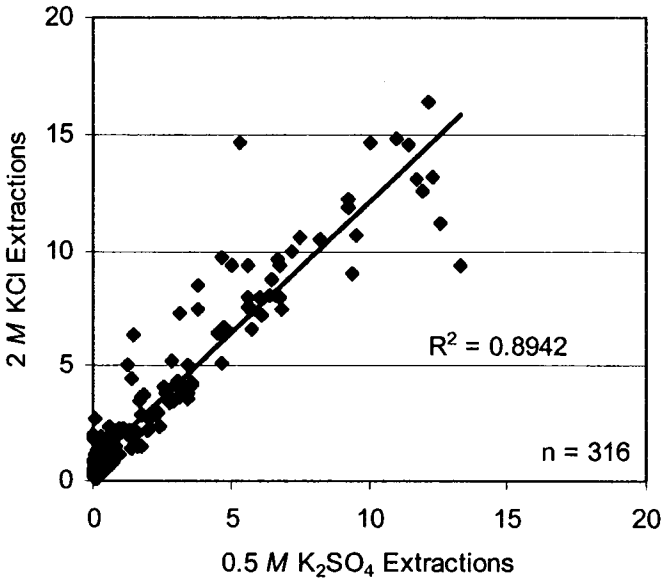

Figure A4.3 Total available N (NH_4 + NO_3) concentration (μg g^{-1}) in mineral soil using two different extracting solutions.

APPENDIX V

'UNALTERED' CALIBRATION PARAMETERS USED TO RUN THE CENTURY SOM MODEL

SITE.100 File
TB7 Workbook
*** climate parameters

1.80000	'PRECIP(1)'
1.7	'PRECIP(2)'
2.7	'PRECIP(3)'
4.3	'PRECIP(4)'
7.0	'PRECIP(5)'
8.2	'PRECIP(6)'
7.5	'PRECIP(7)'
9.0	'PRECIP(8)'
8.3	'PRECIP(9)'
5.4	'PRECIP(10)'
5.8	'PRECIP(11)'
3.4	'PRECIP(12)'
2.3	'PRCSTD(1)'
1.3	'PRCSTD(2)'
1.7	'PRCSTD(3)'
0.80000	'PRCSTD(4)'
1.00000	'PRCSTD(5)'
1.80000	'PRCSTD(6)'
2.60000	'PRCSTD(7)'
2.90000	'PRCSTD(8)'
2.30000	'PRCSTD(9)'
1.40000	'PRCSTD(10)'
1.40000	'PRCSTD(11)'
1.70000	'PRCSTD(12)'
0.00000	'PRCSKW(1)'
0.00000	'PRCSKW(2)'
0.00000	'PRCSKW(3)'
0.00000	'PRCSKW(4)'
0.00000	'PRCSKW(5)'
0.00000	'PRCSKW(6)'
0.00000	'PRCSKW(7)'
0.00000	'PRCSKW(8)'
0.00000	'PRCSKW(9)'
0.00000	'PRCSKW(10)'
0.00000	'PRCSKW(11)'
0.00000	'PRCSKW(12)'
-21.3	'TMN2M(1)'
-19.5	'TMN2M(2)'
-11.6	'TMN2M(3)'
-3.3	'TMN2M(4)'
2.6	'TMN2M(5)'
7.2	'TMN2M(6)'
11	'TMN2M(7)'
10	'TMN2M(8)'
5.1	'TMN2M(9)'
-0.1	'TMN2M(10)'
-7.4	'TMN2M(11)'
-16.7	'TMN2M(12)'
-8.9	'TMX2M(1)'
-6.2	'TMX2M(2)'
0.2	'TMX2M(3)'
8.7	'TMX2M(4)'
15.7	'TMX2M(5)'
20.5	'TMX2M(6)'
24.4	'TMX2M(7)'
22.9	'TMX2M(8)'
17.3	'TMX2M(9)'
10.8	'TMX2M(10)'
2	'TMX2M(11)'
-6.0	'TMX2M(12)'

*** site and control parameters

0.00000	'IVAUTO'
1.00000	'NELEM'
49.07	'SITLAT'
89.25	'SITLNG'
0.42	'SAND'
0.52	'SILT'
0.06	'CLAY'
0.98	'BULKD'
3.00000	'NLAYER'
1.00000	'NLAYPG'
1.00000	'DRAIN'
0.30000	'BASEF'
0.40000	'STORMF'
1.00000	'SWFLAG'
0.20000	'AWILT(1)'
0.20000	'AWILT(2)'
0.20000	'AWILT(3)'
0.20000	'AWILT(4)'
0.20000	'AWILT(5)'
0.20000	'AWILT(6)'
0.20000	'AWILT(7)'
0.20000	'AWILT(8)'
0.20000	'AWILT(9)'
0.30000	'AWILT(10)'
0.30000	'AFIEL(1)'
0.30000	'AFIEL(2)'
0.30000	'AFIEL(3)'

SITE.100 File (continued)

```
0.30000     'AFIEL(4)'
0.30000     'AFIEL(5)'
0.30000     'AFIEL(6)'
0.30000     'AFIEL(7)'
0.30000     'AFIEL(8)'
0.30000     'AFIEL(9)'
0.00000     'AFIEL(10)'
5.3         'PH'
1.00000     'PSLSRB'
3.00000     'SORPMX'
*** external nutrient input parameters
0.00070     'EPNFA(1)'
0.00360     'EPNFA(2)'
-0.90000    'EPNFS(1)'
0.01500     'EPNFS(2)'
0.00000     'SATMOS(1)'
0.00000     'SATMOS(2)'
0.00000     'SIRRI'
*** organic matter initial values
595.848     'SOM1CI(1,1)'
0.00000     'SOM1CI(1,2)'
199.138     'SOM1CI(2,1)'
0.00000     'SOM1CI(2,2)'
3075.502    'SOM2CI(1)'
0.00000     'SOM2CI(2)'
635.456     'SOM3CI(1)'
0.00000     'SOM3CI(2)'
47.86       'RCES1(1,1)'
0           'RCES1(1,2)'
0           'RCES1(1,3)'
39.59       'RCES1(2,1)'
0           'RCES1(2,2)'
0           'RCES1(2,3)'
37.01       'RCES2(1)'
0           'RCES2(2)'
0           'RCES2(3)'
28.21       'RCES3(1)'
0           'RCES3(2)'
0           'RCES3(3)'
129.056     'CLITTR(1,1)'
0.00000     'CLITTR(1,2)'
31.8000     'CLITTR(2,1)'
0.00000     'CLITTR(2,2)'
143.7       'RCELIT(1,1)'
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0           'RCELIT(1,3)'
352         'RCELIT(2,1)'
0           'RCELIT(2,2)'
0           'RCELIT(2,3)'
6478        'AGLCIS(1)'
0.00000     'AGLCIS(2)'
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0.00000     'AGLIVE(2)'
0.00000     'AGLIVE(3)'
1619        'BGLCIS(1)'
0.00000     'BGLCIS(2)'
4.6         'BGLIVE(1)'
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SITE.100 File (continued)

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TREE.100 File

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TREE.100 File (continued)

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APPENDIX VI

RAW SITE-LEVEL DATA FROM CHRONOSEQUENCE SITES

Table A6.1 Live tree biomass data from chronosequence sites.

Chronosequence Site	Density (stem ha^{-1})	Mean Height (m)	Mean DBH (cm)	Live Aboveground Biomass	Carbon [a]	Nitrogen
				-------- g m^{-2} --------		
Regen-1	21103 (5518)	0.7 (0.3)	no est.	no est.	no est.	no est.
Regen-1	4951 (1871)	1.3 (0.13)	no est.	no est.	no est.	no est.
CrwnCl-1	16510 (1478)	4.4 (0.24)	4.6 (0.19)	10382 (497)	5191 (249)	12.11 (0.65)
CrwnCl-2	10356 (945)	4.6 (0.43)	4.8 (0.39)	7928 (1350)	3964 (675)	9.77 (1.58)
SelfThin-1	5621 (349)	9.8 (0.57)	10.0 (0.64)	20849 (1605)	10425 (802)	25.20 (2.06)
SelfThin-2	4565 (197)	9.4 (0.25)	9.4 (0.14)	13834 (770)	6917 (385)	17.81 (1.22)
Mature	1359 (32)	14.2 (0.22)	15.1 (0.25)	10724 (446)	5362 (223)	12.25 (0.47)

[a] Carbon fraction estimated as 50% of biomass.

[b] Inventory within four 2500 m^2 plots (50 m x 50 m).

Table A6.2 Dry weights of forest floor litter made from 50 cm x 50 cm collections.

Chronosequence Site	Plot	Dry Litter Subdivisions (g/m²)					
		Conifer Needles	Woody Debris	Bark	Cones	Deciduous/ Herbaceous	Total
Regen-1	1	0.8	87.9	118.1	34.3	158.2	399
	2	1.6	68.4	33.4	92.7	51.6	248
	3	0	361.7	41.6	203.0	17.6	624
	Average	0.8	172.7	64.4	110.0	75.8	424
	Percent	0.2	40.8	15.2	26.0	17.9	100
Regen-2	1	0	17.7	14.6	0.0	141.5	174
	2	0	70.0	9.1	8.6	105.5	193
	3	0	185.0	10.0	9.7	8.7	213
	Average	0.0	90.9	11.2	6.1	85.2	194
	Percent	0.0	47.0	5.8	3.2	44.1	100
CrwnCl-1	1	664.4	114.6	12.9	102.6	12.1	906
	2	500.5	89.8	21.6	26.7	0.4	639
	3	no est.	no est.	no est.	no est.	no est.	no est.
	Average	582.4	102.2	17.2	64.6	6.2	773
	Percent	75.4	13.2	2.2	8.4	0.8	100
CrwnCl-2	1	no est.	no est.	no est.	no est.	no est.	no est.
	2	314.6	23.6	0	13.9	143.5	496
	3	442.5	42.7	0	6.8	33.0	525
	Average	379	33	0	10	88	510
	Percent	74.2	6.5	0.0	2.0	17.3	100
SelfThin-1	1	324.8	87.3	53.2	5.8	28.1	499
	2	222.5	192.5	119.9	0.0	11.6	546
	3	no est.	no est.	no est.	no est.	no est.	no est.
	Average	274	140	87	3	20	523
	Percent	52.3	26.8	16.5	0.6	3.8	100
SelfThin-2	1	no est.	no est.	no est.	no est.	no est.	no est.
	2	96.8	76.6	25.3	29.2	11.5	239
	3	175.9	124.2	53.3	26.4	4.1	384
	Average	136	100	39	28	8	312
	Percent	43.7	32.2	12.6	8.9	2.5	100
Mature	1	75.9	138.8	91.0	121.5	4.3	431
	2	112.7	135.1	23.2	75.5	3.3	350
	3	38.1	179.3	73.9	9.7	4.7	306
	Average	76	151	63	69	4	362
	Percent	20.9	41.7	17.3	19.0	1.1	100

Table A6.3 Mean monthly air temperatures recorded at chronosequence sites from November 2002 to October 2003.

	Chronosequence Sites							
	Regen-1	Regen-2	CrwnCl-1	CrwnCl-2	SelfThin-1	SelfThin-2	Mature *	All Sites
	---------- Degrees Celsius ----------							
Nov-02	-7.3	-6.6	-8.0	-6.7	-7.7	-7.3		-7.2
Dec-02	-9.4	-9.4	-10.3	-9.3	-9.9	-9.2		-9.6
Jan-03	-17.1	-16.7	-18.1	-16.1	-17.8	-17.3		-17.2
Feb-03	-18.0		-19.0	-17.0		-18.0		-18.0
Mar-03	-8.7		-9.3	-7.9		-9.0		-8.7
Apr-03	-0.3		0.1	1.4		-0.5		0.2
May-03	10.1		10.4	10.3		10.0	9.2	10.0
Jun-03	15.0	14.9	15.5	14.9	15.0	15.5	15.3	15.1
Jul-03	17.0	17.2	16.5	16.8	16.2		17.0	16.8
Aug-03	17.6	18.1	17.3	17.9	17.4		15.6	17.3
Sep-03	11.5	12.0	10.9	11.5	11.3	11.5	10.4	11.3
Oct-03	3.3	3.5	2.7	3.5	2.9	3.2	3.8	3.3
Mean Growing Season ^	14.2	15.6	14.1	14.3	15.0	12.3	13.5	14.1

* Mean data from 1994 - 2002; winter months not recorded.

^ May to Sep mean soil temperatures.

Table A6.4 Mean monthly soil temperatures - interface and mineral readings combined – recorded at chronosequence sites from November 2002 to October 2003.

	Chronosequence Sites							
	Regen-1	Regen-2	CrwnCl-1	CrwnCl-2	SelfThin-1	SelfThin-2	Mature *	All Sites
	---------- Degrees Celsius ----------							
Nov-02	0.6	-0.1		2.8	0.9	1.8		1.2
Dec-02	-0.3	-0.7		1.4	-0.7			-0.1
Jan-03	-3.2	-2.6		0.0	-2.2			-2.0
Feb-03	-6.0	-3.3		-0.8	-2.7			-3.2
Mar-03	-4.0	-2.2		-0.8	-2.0			-2.2
Apr-03	-0.9	-0.1		-0.2	-0.7			-0.5
May-03	5.2	5.4	1.7	1.4	0.6		3.5	3.0
Jun-03	12.0	12.0	5.9	6.6	5.0	4.7	8.2	7.8
Jul-03	15.6			11.1	10.2	9.7	11.5	11.6
Aug-03	16.3				12.6	12.2	11.9	13.2
Sep-03	12.3	12.6		11.4	10.2	10.6	10.2	11.2
Oct-03	5.5	5.4	5.5	2.9	5.3	6.3	6.8	5.4
Mean Growing Season ^	12.3	10.0	3.8	7.6	7.7	9.3	9.0	9.4

* Mean data from 1994 - 2002; winter months not recorded.

^ May to Sep mean soil temperatures.

Table A6.5 Gravimetric moisture content determinations for organic and mineral soils at chronosequence sites.

Chronosequence Site	Measurement Occasion T-0 Oct-02	T-1 May-03	T-2 Jun-03	T-3 Jul-03	T-4 Aug-03	T-5 Oct-03	Annual Mean
Organic							
Regen-1	192.4	154.9	63.2	204.1	115.0	134.2	144.0
	(22.0)	(12.0)	(9.7)	(23.1)	(14.3)	(46.8)	(3.3)
Regen-1	178.6	180.0	156.7	186.2	122.1	174.0	166.3
	(21.1)	(41.7)	(37.0)	(34.3)	(23.6)	(39.0)	(26.7)
CrwnCl-1	157.2	210.6	82.6	160.4	120.6	206.1	156.2
	(6.1)	(25.8)	(14.3)	(27.7)	(36.4)	(36.2)	(21.9)
CrwnCl-2	191.2	271.7	126.8	189.1	227.7	191.5	199.6
	(17.8)	(34.1)	(15.0)	(21.3)	(23.6)	(19.3)	(8.3)
SelfThin-1	132.0	198.4	86.7	171.5	116.3	171.1	146.0
	(6.6)	(16.1)	(15.5)	(35.6)	(25.2)	(35.7)	(15.7)
SelfThin-2	225.2	290.6	184.5	315.1	194.0	261.8	245.2
	(12.9)	(17.0)	(27.6)	(9.2)	(40.1)	(25.3)	(3.9)
Mature	252.9	332.0	253.4	245.3	186.3	228.0	249.7
	(22.8)	(68.8)	(29.3)	(25.4)	(41.3)	(38.6)	(9.6)
Mineral							
Regen-1	24.4	37.3	24.6	34.0	27.5	24.0	28.6
	(1.8)	(4.3)	(3.0)	(5.6)	(4.5)	(4.2)	(3.7)
Regen-1	27.6	35.1	28.9	33.9	26.4	22.8	29.1
	(2.4)	(5.8)	(3.0)	(5.4)	(5.0)	(3.6)	(4.0)
CrwnCl-1	16.2	37.1	24.4	19.4	21.9	23.2	23.7
	(2.5)	(7.5)	(3.4)	(6.9)	(2.8)	(4.0)	(2.4)
CrwnCl-2	59.2	78.2	46.8	63.4	58.0	50.4	59.3
	(5.7)	(2.8)	(1.9)	(9.1)	(8.7)	(9.6)	(5.4)
SelfThin-1	21.3	49.8	25.4	29.1	25.8	27.0	29.7
	(3.0)	(8.7)	(2.2)	(3.0)	(0.4)	(3.5)	(2.2)
SelfThin-2	28.6	66.2	34.5	53.1	41.1	32.6	42.7
	(2.9)	(6.5)	(8.0)	(3.8)	(2.1)	(3.3)	(3.1)
Mature	24.9	46.7	27.2	43.1	30.0	23.9	32.6
	(0.8)	(1.5)	(1.4)	(5.9)	(3.6)	(3.3)	(1.1)

Table A6.6 Organic and mineral soil pH measures at chronosequence sites.

Chronosequence Site	Measurement Occasion T-0 Oct-02	T-1 May-03	T-2 Jun-03	T-3 Jul-03	T-4 Aug-03	T-5 Oct-03	Annual Mean
Organic							
Regen-1	3.6	3.6	4.3	4.0	5.0	4.1	4.1
Regen-1	3.7	3.6	4.1	3.4	4.0	3.2	3.6
CrwnCl-1	3.2	3.2	3.2	3.3	3.4	3.2	3.2
CrwnCl-2	3.1	3.3	3.2	3.4	3.3	3.0	3.2
SelfThin-1	3.4	3.4	3.4	3.6	3.5	3.5	3.4
SelfThin-2	2.8	2.8	2.9	3.0	2.6	2.7	2.8
Mature	2.9	3.2	3.2	3.1	3.2	3.1	3.1
Mineral							
Regen-1	4.2	4.1	4.1	4.2	4.5	4.6	4.3
Regen-1	4.3	4.3	4.1	4.1	4.7	4.2	4.3
CrwnCl-1	4.1	3.8	4.2	4.5	4.6	4.3	4.3
CrwnCl-2	4.4	4.2	4.3	4.1	4.6	4.0	4.3
SelfThin-1	4.4	4.7	4.6	4.6	5.1	4.9	4.7
SelfThin-2	4.1	4.0	4.0	4.1	4.4	4.2	4.1
Mature	4.6	4.0	4.0	4.1	4.8	4.5	4.3

Table A6.7 Total carbon and nitrogen measured at chronosequence sites for organic and mineral soils.

	Chronosequence Site						
	Regen-1	Regen-2	CrwnCl-1	CrwnCl-2	SelfThin-1	SelfThin-2	Mature
Organic				-------- g m^{-2} --------			
Total C	3371	1567	6113	4263	3442	3274	3471
	(246)	(64)	(115)	(73)	(115)	(142)	(133)
Total N	90.7	42.4	170.6	148.3	99.7	74.9	72.2
	(4.1)	(0.9)	(5.8)	(4.3)	(4.1)	(3.0)	(4.8)
C:N Ratio	37.1	37.0	35.8	28.8	34.5	43.7	48.1
Mineral							
Total C	1971	3345	2682	4933	2481	1680	1879
	(no est.) [a]	(no est.)	(no est.)	(no est.)	(no est.)	(no est.)	(no est.)
Total N	130	201	157	249	147	116	133
	(no est.)	(no est.)	(no est.)	(no est.)	(no est.)	(no est.)	(no est.)
C:N Ratio	15.2	16.7	17.0	19.8	16.9	14.5	14.1
Total Soil							
Total C	5342	4912	8796	9196	5923	4953	5350
	(246)	(64)	(115)	(73)	(115)	(142)	(133)
Total N	221	243	328	397	247	191	206
	(4.1)	(0.9)	(5.8)	(4.3)	(4.1)	(3.0)	(4.8)
C:N Ratio	24.2	20.2	26.8	23.1	24.0	26.0	26.0
Organic				-------- % --------			
Total C (%)	36	38	41	42	35	44	43
	(2.5)	(1.8)	(0.9)	(0.6)	(1.2)	(1.7)	(1.6)
Total N (%)	0.97	1.03	1.13	1.45	1.01	0.98	0.89
	(0.04)	(0.02)	(0.04)	(0.04)	(0.04)	(0.04)	(0.06)
Mineral							
Total C	1.22	1.73	1.35	3.52	1.43	1.26	1.09
	(no est.)	(no est.)	(no est.)	(no est.)	(no est.)	(no est.)	(no est.)
Total N	0.08	0.10	0.08	0.18	0.08	0.09	0.08
	(no est.)	(no est.)	(no est.)	(no est.)	(no est.)	(no est.)	(no est.)

[a] One sampling occasion measured so standard error calculations were not possible.

Table A6.8 Available nitrogen (NH_4 and NO_3) measured at chronosequence sites for organic and mineral soils.

	Chronosequence Sites						
	Regen-1	Regen-2	CrwnCl-1	CrwnCl-2	SelfThin-1	SelfThin-2	Mature
Organic	-------- g m^{-2} --------						
NH_4	0.085	0.067	0.114	0.286	0.151	0.083	0.117
	(0.019)	(0.016)	(0.044)	(0.087)	(0.062)	(0.027)	(0.047)
NO_3	0.019	0.002	0.011	0.008	0.004	0.004	0.003
	(0.013)	(0.001)	(0.006)	(0.003)	(0.002)	(0.002)	(0.002)
$NH_4 + NO_3$	0.104	0.068	0.125	0.294	0.155	0.087	0.121
	(0.029)	(0.017)	(0.040)	(0.089)	(0.061)	(0.027)	(0.046)
Mineral							
NH_4	0.376	0.309	0.128	0.513	0.080	0.093	0.206
	(0.142)	(0.101)	(0.065)	(0.153)	(0.021)	(0.028)	(0.106)
NO_3	0.122	0.167	0.028	0.045	0.043	0.037	0.036
	(0.045)	(0.044)	(0.011)	(0.011)	(0.019)	(0.013)	(0.012)
$NH_4 + NO_3$	0.498	0.476	0.156	0.558	0.123	0.130	0.242
	(0.165)	(0.126)	(0.107)	(0.150)	(0.028)	(0.032)	(0.100)
Total Soil							
NH_4	0.461	0.375	0.242	0.799	0.231	0.177	0.324
	(0.144)	(0.114)	(0.076)	(0.188)	(0.064)	(0.052)	(0.119)
NO_3	0.140	0.169	0.039	0.054	0.046	0.040	0.039
	(0.053)	(0.044)	(0.010)	(0.009)	(0.018)	(0.012)	(0.013)
$NH_4 + NO_3$	0.602	0.544	0.280	0.852	0.278	0.217	0.363
	(0.171)	(0.137)	(0.112)	(0.191)	(0.066)	(0.053)	(0.110)

Table A6.9 Microbial carbon and microbial nitrogen measured at chronosequence sites for organic and mineral soils.

	Chronosequence Sites						
	Regen-1	Regen-2	CrwnCl-1	CrwnCl-2	SelfThin-1	SelfThin-2	Mature
	-------- g m^{-2} --------						
Organic							
MB-C	34.6	16.5	79.3	92.0	56.7	67.4	79.4
	(3.7)	(0.9)	(8.4)	(13.3)	(7.1)	(6.8)	(9.7)
MB-N	6.1	2.9	14.8	16.6	11.7	12.2	14.2
	(0.7)	(0.2)	(1.0)	(2.2)	(1.2)	(0.9)	(1.7)
C:N Ratio	5.6	5.7	5.4	5.5	4.9	5.5	5.6
Mineral							
MB-C	30.1	29.1	39.4	52.0	39.3	37.1	37.2
	(4.7)	(4.8)	(6.6)	(7.8)	(5.5)	(5.8)	(5.1)
MB-N	5.1	4.5	6.3	9.3	5.9	5.0	5.9
	(0.4)	(0.3)	(0.8)	(0.9)	(0.8)	(0.6)	(0.6)
C:N Ratio	5.9	6.4	6.2	5.6	6.7	7.4	6.3
Total Soil							
MB-C	64.7	45.7	118.6	144.0	95.9	104.5	116.6
	(7.4)	(5.3)	(11.6)	(9.8)	(11.1)	(10.7)	(10.4)
MB-N	11.2	7.5	21.1	25.9	17.6	17.2	20.1
	(0.9)	(0.4)	(1.5)	(1.3)	(1.6)	(1.3)	(1.4)
C:N Ratio	5.8	6.1	5.6	5.6	5.5	6.1	5.8

Table A6.10 Nitrogen ($NH_4 + NO_3$) mineralized from organic materials in situ mineralization bags at chronosequence sites.

Chronosequence Sites		Measurement Occasion					
		T-1 Oct '02 - May '03	T-2 May '03 - June '03	T-3 June '03 - July '03	T-4 July '03 - Aug '03	T-5 Aug '03 - Oct '03	Total
		------- Nitrogen Mineralized (g m^{-2}) -------					
Regen-1		0.59	-0.01	0.57	0.89	1.01	3.04
		(0.05)	(0.17)	(0.09)	(0.25)	(0.07)	(0.37)
	Days	195	33	28	42	43	341
Regen-2		0.55	0.09	0.05	-0.05	0.08	0.72
		(0.08)	(0.02)	(0.11)	(0.04)	(0.03)	(0.23)
	Days	205	32	29	42	43	351
CrwnCl-1		0.92	0.45	0.38	0.99	0.61	3.35
		(0.28)	(0.15)	(0.08)	(0.58)	(0.23)	(1.24)
	Days	200	35	26	42	43	346
CrwnCl-2		0.27	-0.25	0.02	1.69	0.87	2.61
		(0.21)	(0.23)	(0.10)	(0.41)	(0.27)	(0.41)
	Days	211	27	31	48	37	354
SelfThin-1		0.89	-0.12	-0.03	1.13	0.63	2.50
		(0.02)	(0.04)	(0.04)	(0.19)	(0.15)	(0.01)
	Days	205	36	25	42	43	351
SelfThin-2		0.71	-0.18	-0.52	-0.29	-0.94	-1.22
		(0.13)	(0.22)	(0.18)	(0.24)	(0.23)	(0.67)
	Days	209	33	28	43	42	355
Mature		0.39	0.06	-0.57	-0.16	-0.32	-0.59
		(0.03)	(0.06)	(0.09)	(0.09)	(0.12)	(0.18)
	Days	197	33	28	40	45	343

Table A6.11 Nitrogen ($NH_4 + NO_3$) mineralized from mineral soils in situ mineralization bags at chronosequence sites.

Chronosequence Sites		Measurement Occasion					
		T-1 Oct '02 - May '03	T-2 May '03 - June '03	T-3 June '03 - July '03	T-4 July '03 - Aug '03	T-5 Aug '03 - Oct '03	Total
		------- Nitrogen Mineralized (g m^{-2}) -------					
Regen-1		0.75	0.18	0.20	0.48	-0.20	1.41
		(0.03)	(0.28)	(0.14)	(0.31)	(0.22)	(0.18)
	Days	195	33	28	42	43	341
Regen-2		0.56	0.95	1.19	0.38	0.71	3.79
		(0.40)	(0.10)	(0.17)	(0.27)	(0.36)	(0.68)
	Days	205	32	29	42	43	351
CrwnCl-1		0.21	-0.25	-0.16	-0.28	-0.10	-0.59
		(0.08)	(0.09)	(0.09)	(0.11)	(0.24)	(0.45)
	Days	200	35	26	42	43	346
CrwnCl-2		0.42	0.45	0.51	0.68	-0.05	2.02
		(0.06)	(0.23)	(0.42)	(0.48)	(0.44)	(0.41)
	Days	211	27	31	48	37	354
SelfThin-1		0.08	-0.11	-0.11	-0.15	0.33	0.04
		(0.01)	(0.02)	(0.03)	(0.01)	(0.43)	(0.45)
	Days	205	36	25	42	43	351
SelfThin-2		0.07	-0.23	-0.21	-0.22	-0.21	-0.80
		(0.02)	(0.05)	(0.05)	(0.06)	(0.05)	(0.19)
	Days	209	33	28	43	42	355
Mature		0.12	-0.20	-0.21	-0.20	-0.18	-0.67
		(0.01)	(0.04)	(0.01)	(0.04)	(0.04)	(0.12)
	Days	197	33	28	40	45	343

Table A6.12 Total Nitrogen ($NH_4 + NO_3$) mineralized from in situ mineralization bags (organic and mineral soils) at chronosequence sites.

Chronosequence Sites		Measurement Occasion					
		T-1 Oct '02 - May '03	T-2 May '03 - June '03	T-3 June '03 - July '03	T-4 July '03 - Aug '03	T-5 Aug '03 - Oct '03	Total
		------- Nitrogen Mineralized (g m^{-2}) -------					
Regen-1		0.75	0.18	0.20	0.48	-0.20	1.41
		(0.03)	(0.28)	(0.14)	(0.31)	(0.22)	(0.18)
	Days	195	33	28	42	43	341
Regen-2		0.56	0.95	1.19	0.38	0.71	3.79
		(0.40)	(0.10)	(0.17)	(0.27)	(0.36)	(0.68)
	Days	205	32	29	42	43	351
CrwnCl-1		0.21	-0.25	-0.16	-0.28	-0.10	-0.59
		(0.08)	(0.09)	(0.09)	(0.11)	(0.24)	(0.45)
	Days	200	35	26	42	43	346
CrwnCl-2		0.42	0.45	0.51	0.68	-0.05	2.02
		(0.06)	(0.23)	(0.42)	(0.48)	(0.44)	(0.41)
	Days	211	27	31	48	37	354
SelfThin-1		0.08	-0.11	-0.11	-0.15	0.33	0.04
		(0.01)	(0.02)	(0.03)	(0.01)	(0.43)	(0.45)
	Days	205	36	25	42	43	351
SelfThin-2		0.07	-0.23	-0.21	-0.22	-0.21	-0.80
		(0.02)	(0.05)	(0.05)	(0.06)	(0.05)	(0.19)
	Days	209	33	28	43	42	355
Mature		0.12	-0.20	-0.21	-0.20	-0.18	-0.67
		(0.01)	(0.04)	(0.01)	(0.04)	(0.04)	(0.12)
	Days	197	33	28	40	45	343

Table A6.13 Soil respiration rates measured at chronosequence sites.

Chronosequence Sites	Measurement Occasion		
	T-1 May-03	T-3 Aug-03	T-4 Sep-03
	-------- mg CO_2 m^{-2} day^{-1} --------		
Regen-1	22.6	39.1	34.8
	(11.5)	(14.2)	(20.3)
Regen-1	21.9	56.5	46.9
	(10.8)	(30.5)	(26.1)
CrwnCl-1	10.4	63.0	76.1
	(4.9)	(34.5)	(46.0)
CrwnCl-2	17.3	67.4	60.6
	(8.4)	(21.8)	(13.5)
SelfThin-1	9.2	44.4	51.7
	(3.9)	(15.8)	(15.2)
SelfThin-2	12.1	44.1	25.9
	(3.5)	(15.7)	(11.5)
Mature	9.9	38.6	36.4
	(2.5)	(13.2)	(11.5)

APPENDIX VII

STATISTICAL ANALYSES SUMMARY TABLES FOR CHRONOSEQUENCE SITE DATA

Table A7.1 Summary of ANOVA for forest floor fine litter collections at chronosequence stand development stages.

Source [a]	df [b]	Mean Squares [c]	Probability [d]
Foliage/Herbaceous			
Data Transformed?		No	
Treatment [e]	2	104689	0.0233
Error	3	6204	
Fine Woody			
Data Transformed?		No	
Treatment	2	6998	0.6393
Error	3	13423	
Total Litter C			
Data Transformed?		No	
Treatment	2	57657	0.2713
Error	3	27734	

[a] Source of variation.

[b] Degrees of Freedom.

[c] Mean squares are the sum of squares divided by the corresponding df.

[d] Probability - reject hypothesis of equal means when less than alpha level ($\alpha = 0.05$).

[e] For this table treatment refers to the stand development stage groupings.

Table A7.2 ANOVA summary for measured soil carbon and nitrogen pools at chronosequence stand development stages.

		Total Soil Carbon		Total Soil Nitrogen		Available Nitrogen		Microbial Carbon		Microbial Nitrogen	
Source [a]	df [b]	Mean Squares [c]	Probability [d]	Mean Squares	Probability	Mean Squares	Probability	Mean Squares	Probability	Mean Squares	Probability
Organic											
Data Transformed?		Yes: log		Yes: log		No		Yes: log		No	
Treatment [e]	2	0.060	0.2166	0.086		0.008	.3774	0.165	0.0555	64.601	0.0116
Error	3	0.023		0.021		0.006		0.019		2.32	
Mineral Soil											
Data Transformed?		No		No		No		Yes: log		No	
Treatment [e]	2	1545800	0.4093	2580.56		0.068	0.1751	0.017	0.0795	4.961	0.1966
Error	3	1266080		2388.99		0.021		0.003		1.689	
Organic + Mineral											
Data Transformed?		Yes: log		Yes: log		Yes: log		No		No	
Treatment [e]	2	0.0362	0.0114	0.0290		0.083	0.2037	2927.58	0.0245	100.851	0.0248
Error	3	0.0013		0.0035		0.029		179.823		6.251	

[a] Source of variation.

[b] Degrees of Freedom.

[c] Mean squares are the sum of squares divided by the corresponding df.

[d] Probability - reject hypothesis of equal means when less than alpha level ($\alpha = 0.05$).

[e] For this table treatment refers to the stand development stage groupings.

Table A7.3 Summary of ANOVA for total annual nitrogen mineralization from *in situ* mineralization bags at chronosequence stand development stages

Source of Variation	df [a]	Mean Squares [b]	Probability [c]
Organic			
Data Transformed?		No	
Treatment [d]	2	3.000	0.5182
Error	3	3.637	
Mineral Soil			
Data Transformed?		No	
Treatment	2	4.986	0.2641
Error	3	2.326	
Organic + Mineral			
Data Transformed?		No	
Treatment	2	11.057	0.2236
Error	3	4.300	

[a] Degrees of Freedom.

[b] Mean squares are the sum of squares divided by the corresponding df.

[c] Probability - reject hypothesis of equal means when less than alpha level ($\alpha = 0.05$).

[d] For this table treatment refers to the stand development stage groupings.

Table A7.4 Summary of repeated measures ANOVA for soil respiration for soils at chronosequence stand development stages.

Source of Variation	df [a]	Mean Squares [b]	Probability [c]
Data Transformed?		No	
Group	2	501.31	0.0810
Site	3	76.96	no test
Msr	2	2505.26	0.0007
Group*Msr	4	183.23	0.1769
Site*Msr	6	80.77	no test
Error	0		

[a] Degrees of Freedom.

[b] Mean squares are the sum of squares divided by the corresponding df.

[c] Probability - reject hypothesis of equal means when less than alpha level ($\alpha = 0.05$).

APPENDIX VIII

RAW DATA FROM TEMPERATURE AND MOISTURE CONTROLLED ANAEROBIC LABORATORY INCUBATIONS

Table A8.1 Ammonium and nitrate mineralized in organic soils during 30-week anaerobic laboratory incubations.

	Stand Development Stage	Measurement Occasion T-1 0-5 Weeks	T-4 5-17 Weeks	T-7 17-30 Weeks	Total 30 Weeks
			------- NH_4 ($\mu g\ g^{-2}$) -------		
Ammonium - 10°C	Regen	36.87	1.03	30.91	68.81
		(3.97)	(8.79)	(40.25)	(44.98)
	CrwnCl	36.64	61.10	102.58	200.32
		(4.21)	(32.57)	(28.08)	(62.95)
	SelfThin	27.77	75.63	177.66	281.05
		(3.56)	(12.55)	(49.82)	(65.25)
	Mature	1.10	42.49	180.66	224.25
		(0.19)	(0.65)	(9.10)	(8.64)
Ammonium -20°C	Regen	26.60	127.35	9.49	163.45
		(7.49)	(35.95)	(36.82)	(62.38)
	CrwnCl	76.21	364.27	239.03	679.52
		(13.17)	(128.90)	(20.97)	(141.14)
	SelfThin	41.11	302.47	336.95	680.53
		(13.58)	(97.27)	(45.98)	(72.37)
	Mature	11.49	61.26	277.56	350.31
		(1.84)	(0.66)	(10.20)	(9.02)
			------- NO_3 ($\mu g\ g^{-2}$) -------		
Nitrate - 10°C	Regen	22.67	107.79	117.33	247.80
		(10.25)	(35.25)	(29.82)	(19.74)
	CrwnCl	0.00	0.00	2.63	2.63
		(0.00)	(0.00)	(1.53)	(1.53)
	SelfThin	0.00	0.00	0.99	0.99
		(0.00)	(0.00)	(0.84)	(0.84)
	Mature	0.00	0.00	5.47	5.47
		(0.00)	(0.00)	(0.23)	(0.23)
Nitrate -20°C	Regen	12.09	190.87	150.03	352.99
		(3.49)	(37.88)	(12.36)	(35.29)
	CrwnCl	0.00	2.64	29.55	32.19
		(0.00)	(1.54)	(16.99)	(18.53)
	SelfThin	0.00	0.30	24.54	24.84
		(0.00)	(0.30)	(8.18)	(8.39)
	Mature	0.00	0.00	10.64	10.64
		(0.00)	(0.00)	(0.05)	(0.05)

Table A8.2 Total nitrogen ($NH_4 + NO_3$) mineralized in organic soils during 30-week anaerobic laboratory incubations.

Stand Development Stage	Measurement Occasion			
	T-1	T-4	T-7	Total
	0-5 Weeks	5-17 Weeks	17-30 Weeks	30 Weeks
10°C Incubations	------- N ($\mu g\ g^{-2}$) -------			
Regen	59.54	108.82	148.24	316.61
	(6.32)	(43.73)	(18.76)	(63.77)
CrwnCl	36.64	61.10	105.21	202.95
	(4.21)	(32.57)	(29.47)	(64.44)
SelfThin	27.77	75.63	178.65	282.05
	(3.56)	(12.55)	(50.16)	(65.63)
Mature	1.10	42.84	185.77	229.72
	(0.19)	(0.29)	(8.51)	(8.40)
20°C Incubations				
Regen	38.70	318.22	159.53	516.44
	(4.45)	(73.06)	(35.40)	(97.50)
CrwnCl	76.21	366.92	268.58	711.71
	(13.17)	(130.43)	(25.86)	(159.51)
SelfThin	41.11	302.76	361.49	705.37
	(13.58)	(97.48)	(37.93)	(79.25)
Mature	11.49	61.26	288.20	360.95
	(1.84)	(0.66)	(10.25)	(9.08)

Table A8.3 Ammonium and nitrate mineralized in mineral soils during 30-week vanaerobic laboratory incubations.

	Stand Development Stage	Measurement Occasion T-1	T-2	T-3	T-4	T-5	T-6	T-7	Total
		5 weeks	4 weeks	4 weeks	4 weeks	5 weeks	4 weeks	4 weeks	30 weeks
		------- NH_4 ($\mu g\ g^{-2}$) -------							
Ammonium - 10°C	Regen	1.009	-0.364	-0.524	0.089	-0.369	-0.142	-0.323	-0.625
		(0.216)	(0.127)	(0.152)	(0.139)	(0.174)	(0.149)	(0.109)	(0.160)
	CrwnCl	1.727	0.238	1.046	1.916	1.009	1.128	-0.663	6.401
		(0.190)	(0.219)	(0.411)	(0.728)	(0.759)	(0.217)	(0.880)	(3.147)
	SelfThin	0.105	0.180	0.689	1.647	-0.427	-1.477	-0.370	0.346
		(0.048)	(0.051)	(0.407)	(0.786)	(0.449)	(0.492)	(0.238)	(0.185)
	Mature	0.359	-0.221	-0.092	-0.260	-0.357	-0.210	0.207	-0.573
		(0.021)	(0.029)	(0.068)	(0.146)	(0.153)	(0.168)	(0.022)	(0.061)
Ammonium -20°C	Regen	0.449	0.756	-0.728	-1.198	-0.357	-0.150	0.336	-0.891
		(0.300)	(0.188)	(1.143)	(0.632)	(0.155)	(0.078)	(0.148)	(0.166)
	CrwnCl	3.320	3.252	3.872	3.634	-0.318	-2.033	-1.228	10.500
		(1.030)	(2.238)	(2.116)	(2.149)	(0.653)	(2.159)	(0.928)	(4.815)
	SelfThin	0.625	0.536	2.589	3.415	1.044	1.267	0.553	10.029
		(0.267)	(0.294)	(1.365)	(2.000)	(1.176)	(0.810)	(0.825)	(5.192)
	Mature	-0.159	-0.787	0.260	-0.076	1.107	-0.338	-0.475	-0.467
		(0.249)	(0.247)	(0.106)	(0.192)	(0.746)	(0.117)	(0.772)	(0.059)
		------- NO_3 ($\mu g\ g^{-2}$) -------							
Nitrate - 10°C	Regen	2.150	-0.247	0.012	0.708	3.549	0.351	3.631	10.155
		(0.060)	(0.119)	(0.072)	(0.273)	(0.621)	(0.115)	(0.292)	(0.751)
	CrwnCl	0.169	0.037	-0.173	0.113	0.524	0.845	0.650	2.164
		(0.065)	(0.050)	(0.020)	(0.092)	(0.085)	(0.118)	(0.315)	(0.201)
	SelfThin	0.022	0.112	-0.110	0.120	0.919	1.715	2.916	5.694
		(0.022)	(0.092)	(0.063)	(0.069)	(0.244)	(1.039)	(1.555)	(2.715)
	Mature	0.484	-0.024	0.046	0.891	0.180	0.417	0.357	2.351
		(0.025)	(0.041)	(0.023)	(0.055)	(0.091)	(0.131)	(0.047)	(0.023)
Nitrate -20°C	Regen	5.688	5.267	-7.271	20.841	8.380	10.172	18.434	61.511
		(0.647)	(1.775)	(1.707	(1.646)	(4.415)	(2.902)	(2.486)	(1.900)
	CrwnCl	0.290	0.475	-0.765	2.062	7.272	5.819	6.257	21.409
		(0.020)	(0.056)	(0.072)	(0.328)	(2.840)	(2.047)	(3.780)	(8.787)
	SelfThin	0.036	0.283	0.134	2.206	4.658	5.147	8.423	20.886
		(0.026)	(0.164)	(0.102)	(0.653)	(3.386)	(3.362)	(3.495)	(8.185)
	Mature	0.690	0.479	-0.153	1.446	-0.186	4.292	1.800	8.367
		(0.072)	(0.044)	(0.088)	(0.022)	(0.007)	(0.000)	(1.461)	(1.287)

Table A8.4 Total nitrogen ($NH_4 + NO_3$) mineralized in mineral soils during 30-week anaerobic laboratory incubations.

	Stand Development Stage	Measurement Occasion							
		T-1	T-2	T-3	T-4	T-5	T-6	T-7	Total
		5 weeks	4 weeks	4 weeks	4 weeks	5 weeks	4 weeks	4 weeks	30 weeks
		------- N ($\mu g\ g^{-2}$) -------							
10°C Incubations	Regen	3.159	-0.611	-0.513	0.797	3.180	0.209	3.308	9.530
		(0.275)	(0.071)	(0.184)	(0.316)	(0.746)	(0.057)	(0.391)	(0.906)
	CrwnCl	1.896	0.274	0.873	2.028	1.533	1.973	-0.012	8.565
		(0.139)	(0.267)	(0.403)	(0.756)	(0.694)	(0.236)	(1.179)	(3.311)
	SelfThin	0.127	0.292	0.579	1.767	0.492	0.238	2.546	6.041
		(0.069)	(0.139)	(0.470)	(0.722)	(0.221)	(0.610)	(1.380)	(2.896)
	Mature	0.844	-0.244	-0.046	0.631	-0.178	0.207	0.564	1.778
		(0.046)	(0.070)	(0.045)	(0.202)	(0.063)	(0.037)	(0.069)	(0.038)
20°C Incubations	Regen	6.137	6.023	-7.999	19.643	8.023	10.023	18.770	60.620
		(0.935)	(1.708)	(2.609)	(2.183)	(4.427)	(2.891)	(2.582)	(1.776)
	CrwnCl	3.611	3.727	3.107	5.696	6.954	3.787	5.028	31.909
		(1.012)	(2.185)	(2.144)	(2.476)	(2.216)	(0.739)	(4.358)	(13.588)
	SelfThin	0.660	0.819	2.722	5.621	5.702	6.414	8.977	30.915
		(0.255)	(0.140)	(1.404)	(2.643)	(4.536)	(3.130)	(4.153)	(13.371)
	Mature	0.531	-0.308	0.107	1.370	0.921	3.954	1.325	7.900
		(0.321)	(0.203)	(0.194)	(0.215)	(0.753)	(0.117)	(0.689)	(1.228)

Table A8.5 Microbial carbon and microbial nitrogen concentrations in organic soils during the 39-week anaerobic laboratory incubations.

	Stand Development Stage	Measurement Occasion T-1 5th week	T-4 17th week	T-7 30th week	T-9 39th week
10°C Incubations			------- MB-C (μg g^{-2}) -------		
Microbial Carbon	Regen	4868	1552	2298	1693
		(2365)	(315)	(514)	(127)
	CrwnCl	5102	3673	4295	5620
		(990)	(305)	(241)	(776)
	SelfThin	4328	3666	4359	5641
		(660)	(664)	(62)	(1006)
			------- MB-N (μg g^{-2}) -------		
Microbial Nitrogen	Regen	1033	118	410	153
		(705.5)	(38.7)	(99.2)	(56.1)
	CrwnCl	1091	682	779	1392
		(266.3)	(141.7)	(45.1)	(381.3)
	SelfThin	976	699	582	1753
		(130.1)	(148.7)	(4.3)	(568.5)
20°C Incubations			------- MB-N (μg g^{-2}) -------		
Microbial Carbon	Regen	2450	3698	1883	1332
		(364)	(305)	(106)	(294)
	CrwnCl	3959	4524	3638	3095
		(171)	(226)	(47)	(388)
	SelfThin	7649	4638	3911	3025
		(2614)	(1045)	(297)	(52)
			------- MB-N (μg g^{-2}) -------		
Microbial Nitrogen	Regen	438	796	213	305
		(33.3)	(65.3)	(16.5)	(103.6)
	CrwnCl	844	840	1555	1075
		(24.9)	(44.4)	(155.2)	(754.7)
	SelfThin	1696	789	1460	863
		(488.0)	(542.9)	(8.6)	(177.3)

Table A8.6 Microbial carbon and microbial nitrogen concentrations in mineral soils during the 39-week anaerobic laboratory incubations.

	Stand Development Stage	Measurement Occasion			
		T-1	T-4	T-7	T-9
		5th week	17th week	30th week	39th week
10°C Incubations			------- MB-C ($\mu g\ g^{-2}$) -------		
Microbial Carbon	Regen	125.4	393.1	433.1	na
		(45.5)	(30.0)	(7.0)	
	CrwnCl	140.0	339.1	365.6	na
		(36.8)	(47.4)	(14.6)	
	SelfThin	163.5	455.9	394.3	na
		(42.9)	(14.1)	(40.8)	
			------- MB-N ($\mu g\ g^{-2}$) -------		
Microbial Nitrogen	Regen	28.4	51.7	64.9	na
		(5.1)	(2.3)	(2.6)	
	CrwnCl	40.7	61.7	72.6	na
		(7.2)	(5.9)	(5.0)	
	SelfThin	42.8	72.5	77.9	na
		(3.5)	(0.5)	(4.1)	
20°C Incubations			------- MB-N ($\mu g\ g^{-2}$) -------		
Microbial Carbon	Regen	143.2	369.1	432.6	na
		(72.9)	(14.3)	(na *)	
	CrwnCl	238.1	327.1	305.2	na
		(5.1)	(24.5)	(60.8)	
	SelfThin	273.1	447.1	340.7	na
		(91.0)	(30.2)	(25.9)	
			------- MB-N ($\mu g\ g^{-2}$) -------		
Microbial Nitrogen	Regen	33.3	61.8	72.9	na
		(1.4)	(11.3)	(na *)	
	CrwnCl	52.9	62.7	57.8	na
		(4.6)	(1.4)	(23.7)	
	SelfThin	54.8	81.7	74.2	na
		(5.3)	(12.1)	(28.6)	

* One rep so standard error not possible.

Table A8.7 Soil respiration measurements made during the 30-week anaerobic laboratory incubations.

	Stand Development Stage	Measurement Occasion							
		T-1 4.7 weeks	T-2 9.3 weeks	T-3 12.7 weeks	T-4a 17.9 weeks	T-4b * 20.0 weeks	T-5 22.3 weeks	T-6 27.7 weeks	T-7 29.7 weeks
		------- CO_2 respired (mg CO_2 kg^{-1} d^{-1}) -------							
10°C Incubations	Regen	4.2	3.3	2.3	3.9	2.9	3.2	3.2	3.5
		(0.1)	(0.4)	(0.3)	(0.5)	(0.5)	(0.5)	(0.6)	(0.9)
	CrwnCl	2.9	2.2	1.7	3.3	2.6	3.1	2.6	2.9
		(0.6)	(0.3)	(0.3)	(0.5)	(0.5)	(0.7)	(0.7)	(0.7)
	SelfThin	3.1	3.1	2.8	3.7	3.3	3.2	3.1	3.4
		(0.6)	(0.3)	(0.4)	(0.7)	(0.6)	(0.5)	(0.5)	(0.6)
	Mature ^	2.5	2.8	2.3	3.4	3.1	3.9	3.4	3.3
		(0.0)	(0.1)	(0.0)	(0.0)	(0.1)	(0.0)	(0.3)	(0.3)
20°C Incubations	Regen	10.0	10.1	5.3	10.5	7.5	8.4	6.2	7.1
		(1.1)	(1.4)	(1.1)	(1.6)	(0.9)	(1.0)	(0.8)	(1.1)
	CrwnCl	6.4	6.1	4.8	8.5	6.5	7.5	5.8	4.5
		(0.6)	(1.2)	(1.3)	(1.5)	(1.5)	(0.9)	(0.4)	(0.5)
	SelfThin	8.5	8.7	6.8	12.4	10.2	12.2	10.1	9.6
		(1.2)	(1.2)	(0.1)	(0.7)	(0.2)	(0.5)	(0.2)	(0.2)
	Mature ^	6.8	8.2	6.0	12.9	8.8	9.5	9.5	10.4
		(0.6)	(0.1)	(0.0)	(0.1)	(0.1)	(0.4)	(0.9)	(1.7)

* First measurement with the Bacharach 2815 CO2 analyzer – originally used as a trial run.

^ n = 2 for standard error calculations. For other stages n = 4.

APPENDIX IX

STATISTICAL ANALYSES SUMMARY TABLES FOR TEMPERATURE AND MOISTURE CONTROLLED ANAEROBIC LABORATORY INCUBATIONS

Table A9.1 Summary of ANOVA for total nitrogen mineralized during 30 week laboratory incubations of organic and mineral soils from stand development stages.

		Total N Mineralized	
Source [a]	df [b]	Mean Squares [c]	Probability [d]
Organic			
Data Transformed?		No	
Temp	1	854157	0.0020
WP [e]	2	1677	no test
Rest [f]	0	no est.	
Group	2	11927	0.0045
Temp*Group	2	50893	0.0003
WP*Group	4	426.9	0.9999
Error	12	53335	
Mineral Soil			
Data Transformed?		Yes: log	
Temp	1	3.0200	0.0002
WP	2	0.0006	no test
Rest	0	no est.	
Group	2	0.4343	≤ 0.0001
Temp*Group	2	0.0481	0.0004
WP*Group	4	0.0005	1.0000
Error	12	0.2463	

[a] Source of variation.

[b] Degrees of Freedom.

[c] Mean squares are the sum of squares divided by the corresponding df.

[d] Probability - reject hypothesis of equal means when less than alpha level ($\alpha = 0.05$).

[e] WP = whole plot error associated with the split-plot experimental design.

[f] Rest = restriction on randomization associated with the split-plot experimental design.

Table A9.2 Summary of repeated measures ANOVA for nitrogen mineralized between measurement occasions during 30 week laboratory incubations of organic and mineral soils from stand development stages.

		Organic			Mineral Soil	
Source [a]	df [b]	Mean Squares [c]	Probability [d]	df	Mean Squares	Probability
Organic						
Data Transformed?		No			No	
Temp	1	284718	0.0020	1	939.255	0.0001
WP [e]	2	556	no test	2	0.131	no test
Rest [f]	0	no est.		0	no est.	
Group	2	3976	0.0045	2	94.995	0.0003
Temp*Group	2	16965	0.0003	2	69.498	0.0006
WP*Group	4	142	0.9999	4	0.886	0.9994
Site	12	17778	no test	12	54.933	no test
Msr	2	199570	0.0001	6	131.315	0.001
Temp*Msr	2	84279	0.0007	6	79.754	0.0083
WP*Msr	4	1137	0.9832	12	15.751	0.2574
Group*Msr	4	13657	≤ 0.0001	12	55.406	≤ 0.0001
Temp*Group*Msr	4	3893	0.0020	12	43.760	≤ 0.0001
WP*Group*Msr	8	331	1.0000	24	4.380	0.9972
Site*Msr	24	12005		72	12.439	
Error	0			0	0.000	

[a] Source of variation.

[b] Degrees of Freedom.

[c] Mean squares are the sum of squares divided by the corresponding df.

[d] Probability - reject hypothesis of equal means when less than alpha level ($\alpha = 0.05$).

[e] WP = whole plot error associated with the split-plot experimental design.

[f] Rest = restriction on randomization associated with the split-plot experimental design.

Table A9.3 Summary of repeated measures ANOVA for soil respiration measurements made during 30 week laboratory incubations of organic and mineral soils from stand development stages.

		CO2 Evolution	
Source [a]	df [b]	Mean Squares [c]	Probability [d]
Data Transformed?		Yes: log	
Temp	1	8.4927	0.0004
WP	2	0.0037	no test
Rest	0	no est.	
Group	2	0.4043	0.0002
Temp*Group	2	0.0693	0.006
WP*Group	4	0.0029	0.9995
Site	12	0.1954	
Msr	7	0.1215	≤ 0.0001
Temp*Msr	7	0.0110	0.0071
WP*Msr	14	0.0024	0.9381
Group*Msr	14	0.0163	≤ 0.0001
Temp*Group*Msr	14	0.0063	0.0005
WP*Group*Msr	28	0.0015	0.9997
Site*Msr	84	0.0050	
Error	0		

[a] Source of variation.

[b] Degrees of Freedom.

[c] Mean squares are the sum of squares divided by the corresponding df.

[d] Probability - reject hypothesis of equal means when less than alpha level ($\alpha = 0.05$).

[e] WP = whole plot error associated with the split-plot experimental design.

[f] Rest = restriction on randomization associated with the split-plot experimental design.