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By

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ABSTRACT

THE RECOVERY OF ECOSYSTEM PROCESSES AFTER WILDFIRE IN MICHIGAN JACK PINE FORESTS

By

Zhanna Abramovsky

I investigated the recovery of ecosystem processes after wildfire in Michigan jack pine (*Pinus banksiana*) forests using a chronosequence of 11 wildfire-regenerated stands spanning 72 years. The objective of this study was to characterize recovery patterns of soil nutrients, soil carbon (C) and nitrogen (N) mineralization, as well as determine the mechanisms that drive those patterns.

Total N mineralization spiked immediately following wildfire, decreased to minimum values after about 10-15 years following wildfire, and then increased, reaching a steady state after about 40 years. Soil respiration rates declined immediately after wildfire, increased after about 10-15 years, followed by a decreasing trend after 30 years.

In Michigan jack pine forests, accumulation of the forest floor largely regulates the recovery of N mineralization. The successional pattern of annual N mineralization was driven by rapid turnover of N in the mineral soil immediately following wildfire, followed by a gradual accrual of a slow-cycling pool of N in forest floor as stands matured. Soil respiration was most likely driven by heterotrophic microbial respiration early in succession and later by both root respiration and microbial respiration. All measured ecosystem processes recovered to predisturbance levels within 40 years of wildfire.

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CHAPTER 1: Literature Review

EFFECTS OF WILDFIRE ON FOREST ECOSYSTEMS

INTRODUCTION

Understanding ecosystem dynamics is essential for predicting the response of forests to climate change and sustaining production of commercial forests. Particular attention has been given to nitrogen (N) and carbon (C) cycles because N is often the most limiting nutrient to forest productivity and C plays a vital role in global warming. Mechanisms controlling soil C cycling are of particular interest because it has been estimated that, on a global basis, soils contain 1.6 times as much C as the atmosphere (Adams et al. 1990). Because C and N cycles are tightly linked, long-term changes in C storage have the potential to influence soil fertility, forest productivity and atmospheric carbon dioxide concentrations. Disturbances such as wildfire can greatly influence C and N dynamics, yet their effects on C and N cycles are not well understood. Understanding the effects of wildfire on ecosystem dynamics in forests where wildfire is an inherent ecosystem property is essential in order to manage those forests and determine their role in global climate change.

NUTRIENT CYCLING IN FOREST ECOSYSTEMS

Researchers know a great deal more about the distribution of nutrients in forest ecosystems than how the nutrients are transferred from one nutrient pool to another. Forest floor[1] and mineral soil often contain the largest pools of C and N. In temperate forests, mineral soil and forest floor account for approximately 60 and 95% of total ecosystem C (Cole and Rapp 1981; Birdsey 1990; Grigal and Ohmann 1992) and N (Cole and Rapp 1981), respectively. Similar estimates have been reported for boreal forests (Apps et al. 1993; Morris and Miller 1994). The majority of soil organic matter (SOM) is recalcitrant and resistant to microbial degradation (Smith and Paul 1990). On an annual basis, soil microorganisms liberate only ≈10% of N bound in organic matter (calculated from Nadelhoffer et al. 1983, Zak and Grigal 1991). Net N mineralization is fundamental in regulating forest productivity (Keeney 1980, Pastor et al. 1984, Zak et al. 1989) because N is the most limiting nutrient to plant productivity.

Nitrogen

Nitrogen availability is determined by N mineralization, the conversion of organically bound N to inorganic forms by soil microorganisms. The amount of N mineralized in a given soil volume depends in part on the total amount of organic N present. In temperate and boreal forests, only a small fraction of total organic N is mineralized, suggesting that other factors are also responsible for N mineralization, such as microbial activity. Microbial activity is controlled by soil temperature and moisture, as well as the chemical composition of organic matter (Swift et al. 1979).

[1] Forest Floor is composed of freshly cast (Oi), partly decomposed (Oe), and fully decomposed (Oa) vegetative material on the soil surface.

The amount of soil organic matter is regulated by a balance between aboveground and belowground production of plant litter and decomposition of that material by soil microorganisms. When primary production exceeds decomposition, organic matter accumulates in the soil and forest floor. Because plant nutritional needs are supplied almost entirely by internal cycling rather than external sources in most forested ecosystems (Bormann and Likens 1967; Cole and Rapp 1981; Johnson and Van Hook 1989), nutrients locked up in undecomposed organic matter may have negative effects on forest productivity. This is especially evident in boreal forest ecosystems (Bormann and Sidle 1990; Pastor et al. 1987; Van Cleve and Viereck 1981; Van Cleve et al. 1983) where forest productivity declines as stands mature. In boreal forests of Alaska, forest productivity and N mineralization decline with succession (Van Cleve and Nooman 1975; Van Cleve and Viereck 1981). The decline in N mineralization is attributed to establishment of coniferous species. Coniferous litter has been found to reduce soil N availability because of its high lignin and low N content (Pastor et al. 1987). Cold temperatures and high moisture may also contribute to reduced N mineralization rates.

In boreal coniferous forests, a large proportion of N capital is contained in the forest floor (Foster and Morrison 1976, Weetman and Algar 1983). Wildfire is an integral ecosystem process in these forests because it directly mineralizes a significant fraction of the forest floor and releases the bound nutrients. The conditions that prevail after wildfire, such as warmer soil temperatures and higher cation availability (Neary et al. 1999), favor higher rates of nutrient cycling.

Because N cycling and availability often increase in boreal forests immediately following wildfire, it is considered a rejuvenating process (Tamm 1991).

Carbon

In addition to N, C is also sequestered in organic matter. The major difference between C and N is that the majority of C in the ecosystem is supplied externally through primary production and returned to the atmosphere through soil respiration. Soil respiration is defined as the soil surface flux of carbon dioxide (CO_2) produced by soil microorganisms and roots. Soil respiration is a major flux in the global C cycle, second in magnitude to gross primary productivity (GPP) (Houghton and Woodwell 1989). Rates of soil respiration have been measured in a variety of ecosystems to examine nutrient and C cycling, microbial activity and root dynamics.

Soil respiration is primarily controlled by soil temperature (Edwards 1975, for reviews see Singh and Gupta 1977, Raich and Schlesinger 1992) and moisture (Edwards 1975, Linn and Doran 1984, Raich and Schlesinger 1992). However, there is no consensus on the exact nature of the relationship between temperature, moisture and soil respiration (Lloyd and Taylor 1994). Because microclimate varies by vegetation type and time of year, CO_2 fluxes also differ among biomes and vary during the growing season (Raich and Schlesinger 1992). Other factors that influence soil respiration include soil pH, substrate (Katznelson and Stephenson 1956), rates of C inputs to soils (Trumbore et al.

1995), diffusivity (Davidson and Trumbore 1995) and organic matter (Gaarder 1957).

In recent decades, interest in the factors that control soil respiration has grown dramatically. Global climate models predict temperature increases due to the increasing CO_2 emissions into the atmosphere, potentially leading to a greenhouse effect in the near future (Houghton et al. 1990). Precipitation patterns are also expected to change and therefore may alter soil respiration rates. The relationship between temperature, moisture and soil respiration suggests increasing rates of soil respiration, which will likely lead to a positive feedback to the greenhouse effect. Land-use changes and different ecosystem management techniques, such as fertilization and forest harvesting may also lead to changes in soil respiration (Raich and Schlesinger 1992) and C storage.

The role of boreal forests in the global C cycle has been of particular interest because this ecosystem stores approximately 800 Gt of C (Apps et al. 1993). This amount of C is large enough that even small changes in C fluxes may have significant impacts on climate (Nalder and Wein 1999). Some scientists have proposed that boreal forests are a net C sink (D'Arrigo et al. 1987; Myneni et al. 2001). Whether or not this ecosystem is a long-term sink for C is uncertain. Because wildfire is an integral component of boreal forests, understanding the effect of fire on C dynamics is vital in determining whether this ecosystem can serve as a long-term sink for C.

The immediate effect of fire on the C cycle is the combustion of biomass during the burning process, releasing CO_2 into the atmosphere. Fire also converts part of the biomass into charcoal, which is an inert form of C that does not break down via decomposition. Carbon is returned to the ecosystem through the regrowth of vegetation. The net exchange of C between the atmosphere and terrestrial ecosystems after wildfire is determined by examining changes in C storage (live and dead biomass) and C losses (soil respiration) after wildfire.

EFFECTS OF FIRE ON SOIL .

Soil is an integral component of ecosystem sustainability. Soil supplies mineralizable nutrients for plant growth, serves as a habitat for soil microorganisms, provides a protective layer against erosion, helps to regulate soil temperature and moisture, and serves as a significant sink and source of C.

The overall affects of fire on the soil system are complex because all of the components of the soil system interact to control the rate of recovery of ecosystem processes (Dunn and DeBano 1977; DeBano et al. 1998). The recovery of soil processes after a disturbance depends on SOM pools, physical and chemical soil properties, SOM quality and soil microbial community composition (Neary et al. 1999). Burning of SOM during a wildfire may result in a decrease in total nutrient and C pools through leaching, runoff, volatilization and erosion. However, burning of SOM can also lead to an increase in available pools of N by enhancing mineralization and nitrification (Neary et al. 1999) through a changing microclimate following a burn. Because temperature and moisture regulate many ecosystem processes, such as microbial activity, soil microclimate can be the most critical driving force in ecosystems (Swift et al. 1979).

In order to understand how fire-induced changes in the soil system affect soil processes, we need to understand how the physical, chemical and biological soil systems interact, which effects are transient and which are long-lasting, as well as what mechanisms control the rate of recovery of the soil system. The physical system includes soil microclimate, soil bulk density, and water-holding capacity. Soil organic matter content and quality, pH, and nutrient availability are components of the soil chemical system. The biological soil system includes microorganisms, soil fauna and plant roots.

Soil Physical System

Fire affects soil by destroying organic matter, which leads to changes in soil properties such as bulk density, porosity and water-holding capacity. The magnitude of these changes largely depends on fire severity, proportions of overstory and understory vegetation burned, forest floor consumption, heating of the soil, proportion of area burned, and the fire return interval (Wells et al. 1979).

In general, soil temperatures can remain elevated for a few minutes to an hour during prescribed fires, and for several days after a severe fire (DeBano et al. 1998). If the entire organic horizon is consumed during a fire, soil temperatures can remain elevated above normal for months to years due to solar radiation heating exposed mineral soil (Neary et al. 1999).

Decrease or removal of the overstory following wildfire allows more solar radiation to reach the soil surface and heat the soil. Blackening of the soil surface as a result of incomplete combustion of organic matter produces additional heat absorption by decreasing soil albedo (Christensen and Muller 1975). Removal of the canopy and increased solar heating may also lead to greater evaporation rates and decreased soil moisture availability.

Fire also affects soil moisture availability by changing the structure of the soil. The structure of the soil in the upper horizons results from the aggregation of mineral soil particles by organic matter. The aggregation of individual mineral particles in the soil enhances porosity. Thus, when a wildfire burns soil organic matter, soil structure can be destroyed, affecting total porosity and pore size distribution in the surface horizons of the soil. This can lead to a reduction in infiltration rates and an increase in overland flow and therefore reduced soil water availability (DeBano et al. 1998).

Alteration or destruction of soil organic matter can further decrease infiltration rates, and hence decrease soil moisture availability, by making particles water-repellent. Hydrophobic organic compounds that form in high-intensity fires cause water repellency by coating soil aggregates and preventing soil wetting. This condition forms when soil temperatures rise above 176°C during a wildfire and destroyed at temperatures above 288°C (DeBano 1981).

Soil Chemical System

Fire can reduce or completely destroy soil organic matter depending on fire severity and soil heating. The destruction of organic matter by wildfire begins at low temperatures, starting at 200°C, and is complete at 500°C (Debano et al. 1998). During combustion of organic matter, nutrients essential to plant and microbial metabolism can be lost through volatilization, ash convection, mineralization, erosion, runoff and leaching (Neary et al. 1999).

Direct loss of nutrients to the atmosphere through volatilization is temperature dependant. Nitrogen losses begin at 200°C and over half the N in organic matter can be volatilized at temperatures above 500°C. Other nutrients such as sulfur (S), potassium (K), phosphorus (P), sodium (Na), magnesium (Mg) and calcium (Ca) are lost at temperatures above 800°C, 760°C, 774°C, 880°C, 1107°C, and 1240°C, respectively (Weast 1988).

Total N decreases after wildfire, however, soil N can be made more available after a low-intensity fire due to conversion of organic nitrogen to inorganic forms such as ammonium (NH_4^+) and nitrate (NO_3^-) (Picket and White 1985). However, high-intensity fires can cause large losses of nitrogen through consumption or volatilization of NH_4^+. Furthermore, NO_3^- can be lost through leaching, denitrification, or overland flow (Neary et al. 1999). Nutrient-rich ash material remaining after fire can be lost by convection in a smoke column or surface wind transport (Neary et al. 1999). Cations from ash can also be easily lost through leaching, especially in acidic soils such as Spodosols.

Wildfire produces a layer of charcoal from woody vegetation. Charcoal is potentially important in forests where plants belong to the Ericaceae family are present (Wardle et al. 1998, Pietikainen et al. 2000). Ericaceous plants produce secondary metabolites, such as phenolics, which retard nutrient cycling, tree seedling growth (Zackrisson et al. 1997), mycorrhizal functioning (Nilsson et al. 1993) and soil biological processes (Wardle and Lavelle 1997). Zackrisson et al. (1996) demonstrated that charcoal could adsorb significant amounts of phenolics, resulting in their deactivation. Furthermore, this study showed that charcoal could maintain high sorptive capacity for about a century after wildfire. The study also showed that experimental heating could reactivate charcoal at temperatures above 450°C.

Soil Biological System

The least understood component of soil processes is the microbial community. Soil microorganisms play a vital role in soil fertility and primary production by driving organic matter turnover through the processes of mineralization and immobilization. Soil microbes transform organic matter to inorganic forms, making nutrients available for plant uptake. Microbial composition is related to their function in soil because taxonomic groups of soil organisms vary in their function in soil processes. Wildfire has direct effects on microbial community composition (Vazquez et al. 1993) because heating tolerance differs between fungi and bacteria (Wells 1979), but our understanding of the significance of those changes on ecosystem processes is lacking. Sustainable forest management will require an understanding of the function of different soil taxonomic groups and their role in the recovery of soil and ecosystem processes after disturbance.

Soil microbial activity can be limited by soil microclimate, as well as substrate quality and quantity. Conifers produce poor-quality litter that has high carbon: nitrogen ratios and is not easily decomposed (Pastor et al. 1987). Fire can modify decomposition rates by removing organic substrate, changing the chemical composition of the remaining substrate, and by altering the physical, chemical and biological characteristics of the soil environment (Neary et al. 1997). High temperatures during fire can destroy or damage microbes, whereas higher than normal temperatures associated with changing microsite climate may temporarily enhance microbial activity. Soil desiccation as a result of decreased infiltration rates may also inhibit the ability of microbes to recover after fire and recolonize the site (Neary et al. 1999).

Soil microorganisms are most abundant in organic horizons and the top 1-2 cm of mineral soil, where heating from wildfire will have the greatest effect. Soil heating can have damaging or lethal effects on soil organisms depending on fire severity. Fungi and bacteria vary in their tolerance of heating. The lethal temperature for bacteria is 210°C in dry soil and 110°C in wet soil, whereas the lethal temperature for fungi in dry and wet soil is 155°C and 100°C, respectively (Dunn and DeBano 1977). Spores and other resting forms of microbes can tolerate higher temperatures than actively growing microbes.

There are a wide variety of microbial responses to fire, even in the same ecosystem. The composition of recolonizing soil microbes can be different after wildfire than before wildfire due to differential responses of soil microbes to heating temperatures. Vazquez et al. (1993) reported findings from an Atlantic *Pinus pinaster* forest and observed a 16-fold increase in aerobic heterotrophic bacteria, a 2-fold increase in acidophilic bacteria, and a decrease in cyanobacteria, fungi and algae one month after wildfire. Overall, microbial populations increased 25-fold, but returned to pre-fire abundance within one year of burning. Increases in microbial populations may have resulted from improved fire-induced substrate quality, more favorable environmental conditions or a combination of the two factors. Zackrisson et al. (1996) demonstrated that artificially made charcoal could enhance microbial biomass in humus. Therefore, severely burned sites, where charcoal forms, may be an important habitat for recolonizing microorganisms. Fonturbel et al. (1995) found no effect on microbial abundance after a prescribed burning treatment in a *Pinus pinaster* forest. The effect of fire may also depend on the frequency of burning. Hossain et al. (1995) found that burning 2-3 times per year reduced microbial biomass, but biomass increased at 7-year burning intervals.

The effects of fire on soil microorganisms vary widely. Overall, bacteria seem to be favored over fungi, but the effect is temporary (Vazquez et al. 1993). The response of soil microbes to fire depends on fire severity, charcoal presence and activation, changes in microclimate, and fire frequency.

DISTURBANCE RECOVERY AND FIRE RETURN INTERVAL

Frequency of disturbance may play a significant role in whether that disturbance has a positive or a negative effect on ecosystem processes. With increasing disturbance frequency, a greater proportion of the forest is found in younger age classes. The question to consider is whether those forests have recovered from the previous disturbance before the next disturbance event. If not, what are the possible consequences on ecosystem processes if the time interval is too short to allow the ecosystem to recover? What factors control the rate of recovery?

Covington (1981) documented the recovery of forest floor following clear cutting in northern hardwoods. Figure 1 illustrates an initial decrease in forest floor early in secondary succession, followed by an asymptotic increase. Covington (1981) attributed the initial decrease in forest floor to a decline in plant production and increase in decomposition rates, followed by accumulation of forest floor when plant production exceeded the rate of decomposition. By year 64, the forest floor had recovered to within 5% of predisturbance levels. Can one expect the same rate and pattern of forest floor recovery if a 50-year-old stand is cut and what are the possible consequences on productivity of as subsequent regenerating stand? These issues have important implications for forest management strategies.

What about natural disturbances, such as wildfire? Climate change models predict a change in climate in boreal forest ecosystems that will favor greater fire activity (Flannigan and Van Wagner 1991). During the 1980s, the warmest decade in recent history, the area of boreal forests burned increased dramatically (*in* Stocks et al. 1996). This may result in a significant decrease in the ability of these forests to store C, and raises the possibility of positive feedbacks to global climate change from increased fire activity.

Rotation age and fire return interval are the keys to understanding the benefits and damage a disturbance can cause to an ecosystem. Long disturbance return intervals may lead to sequestration of nutrients essential to plant growth, thereby limiting plant productivity. A disturbance return interval that is too short may also lead to a decrease in plant productivity because the inputs to the ecosystem between disturbance events are not high enough to replace losses (Aber and Melillo 1991).

JACK PINE ECOSYSTEM

One of the most fire-prone ecosystems is one that is dominated by jack pine (*Pinus banksiana* L.). Jack pine is an early successional, short-lived, shade-intolerant tree species, and a significant component of North American boreal forests. It grows on droughty, nutrient-poor, sandy soils (Cayford and McRae 1983), where most other species struggle to survive because of low nutrient availability and drought stress. Jack pine forests are extremely prone to fire because their foliage is highly combustible and the tree density is usually high enough to spread the fire through the tree crowns (Rowe and Scotter 1973). One characteristic that makes jack pine ideally suited for post-fire regeneration is serotinous cones. Seeds are enclosed in the serotinous cones and the cone scales are held together with a bonding resin that melts at about 50ºC (Cameron 1953). Forest fires provide the necessary heat to melt the resin and open the cones to begin seed germination. Jack pine stands are predominantly maintained by wildfire, even-aged, and are typically less than 100 years old. Even though jack pine is predominantly found in the boreal forest, the southern extent of this species is in the temperate zone, in northern Lower Michigan.

Jack pine in Michigan is of extreme interest because it is home to the Kirtland's Warbler (*Dendroica kirtlandii* Baird), an endangered species. The Kirtland's warbler is an endangered songbird whose breeding range and nesting habitat are very narrow and limited to young jack pine stands of northern Lower Michigan (Walkinshaw 1983). Management of Kirtland's warbler habitat requires the creation of early-successional jack pine stands through clear-cutting and/or prescribed burning.

MANAGEMENT IMPLICATIONS

Understanding the recovery patterns of ecosystem processes and the factors controlling these patterns is fundamental to sustain the production of commercial forests and manage for wildlife habitat. Management of forests for wood production is often based on expected rates of productivity. However, productivity depends on soil fertility and changes with stand age (Ryan et al. 1997). Management activities that alter nutrient supply in the soil could affect forest production, rotation ages, sustainability, and other aspects of forest management. Sustainability problems are likely to occur when the post-harvest replenishment of nutrients is less than what is required to reestablish pre-harvest biomass production rates. Understanding the effects of natural disturbances on ecosystems and comparisons with different management techniques may provide great insight into the proper management of forests, as well as further our knowledge of benefits and costs of ecosystem management.

RATIONALE

The overall affects of fire on ecosystem processes are complex because all the components of the system interact to control nutrient and C cycling. Pools of labile nutrients in soil organic matter are of vital importance not only because they control ecosystem productivity, but also because these pools can respond to changing soil moisture and temperature resulting from climate change. For this reason, we need to understand which effects are transient and which are long-lasting, as well as what mechanisms control the rate of ecosystem recovery.

The objective of this study is to examine how ecosystem processes, both belowground and aboveground, recover after wildfire and determine what are the main factors that limit and drive those processes. In this study I will investigate the recovery of ecosystem process in the jack pine ecosystem of northern Lower Michigan. The results of this project will provide important baseline information on the maximum rotation age required for sustainable management of northern Lower Michigan jack pine forests.

CHAPTER 2

THE RECOVERY OF ECOSYSTEM PROCESSES AFTER WILDFIRE IN MICHIGAN JACK PINE FORESTS

ABSTRACT

I investigated the recovery of ecosystem processes after wildfire in Michigan jack pine (*Pinus banksiana*) forests using a chronosequence of 11 wildfire-regenerated stands spanning 72 years. The objective of this study was to characterize recovery patterns of soil nutrients, soil carbon (C) and nitrogen (N) mineralization and aboveground biomass as well as determine the mechanisms that drive those patterns.

In situ N and C mineralization were measured monthly during the 2002-growing season. Multiple regression analysis was used to determine the important factors controlling N and C mineralization. To determine seasonal effects, N mineralization and soil respiration were analyzed using analysis of variance.

Annual N mineralization rates spiked to 3564 mg N/m^2 1 year following wildfire, decreased to a minimum 325 mg N/m^2 after about 8 years then began to increase, reaching a steady state of 1284 after about 44 years. Rates of N mineralization increased with increasing forest floor mass and decreasing C: N ratios. Generally, soil respiration rates decreased after wildfire, began to increase after about 10-15 years, and then declined after 30 years. Soil respiration declined with increasing soil moisture and increased with increasing

temperature and forest floor moisture. Forest floor and soil N and C pools as well as C: N ratio increased with succession, whereas temperature decreased. Soil and forest floor became more acidic as stands matured. Understory vegetation reached a peak 7 years after wildfire and then decreased.

In this jack pine chronosequence, accumulation of forest floor largely regulates the recovery of N mineralization. The initial spike in N mineralization immediately following wildfire was driven by rapid turnover of N in the mineral soil. The recovery of N mineralization to predisturbance levels was driven by a gradual accrual of forest floor. Soil respiration was most likely driven by microbial heterotrophic respiration early in succession and later by both root respiration and microbial respiration. All measured ecosystem processes recovered to predisturbance levels within 40 years of wildfire.

INTRODUCTION

The response of forest ecosystems to wildfires has been studied extensively, including studies of vegetation succession (Bergeron and Dubuc 1989; De Grandpré et al. 1993), soil microbial activity (Bissett and Parkinson 1980; Sharma 1981; Tiwari and Rai 1977; Vázquez et al. 1993; Widden and Parkinson 1975), soil chemistry (Austin and Baisinger 1955; Bauhus et al. 1993; Dunn et al. 1979; Dyrness et al. 1989; Kutiel and Naveh 1987) and soil respiration (Weber 1990). However, most studies of soil processes have focused on the immediate affects of fire on soil chemistry and microbial activity and long-term studies are uncommon. Furthermore, numerous studies on the effects of fire on soil chemistry are conducted using prescribed burns (Ahlgren and Ahlgren 1965; Giovannini and Lucchesi 1997; Lynham et al. 1997). To study the recovery of soil processes after wildfire requires following the same burn for several decades, a method unlikely to be undertaken. Instead, scientists have used chronosequences of stands regenerated at different times to study succession (Bormann and Sidle 1990; DeLuca et al. 2002; Krause 1998; Pare et al. 1993). Because meeting the assumptions of a chronosequences is often problematic, these studies are uncommon. At the same time, more studies on the long-term effects of wildfire on ecosystem processes are needed to build better predictive models of climate change and make more informed forest management decisions.

Wildfire is the most common agent of disturbance in boreal forest ecosystems. In boreal forests, decomposition rates decrease through succession leading to low nutrient availability and accumulation of forest floor (Bormann and Sidle 1990; Pastor et al. 1987; Van Cleve and Viereck 1981; Van Cleve et al. 1983). Nitrogen mineralization rates in boreal forests of Alaska decline during the course of succession (Van Cleve and Viereck 1981; Van Cleve et al. 1983) and net N immobilization rates increase in mature stands (Van Cleve and Nooman 1975; Van Cleve and Viereck 1981). These trends with succession are often attributed to decreasing substrate quality and a changing soil microclimate that slows down microbial activity. DeLuca et al. (2002) also observed a decrease in N mineralization along a 352-year fire chronosequences in northern Sweden. In contrast, Brais et al. (1995) reported no change in N mineralization over 231 years of succession in the southern boreal forest of Canada. In boreal forests, a large proportion of the total ecosystem N capital is stored in the forest floor and can range from 7.8 % in jack pine (*Pinus banksiana*) to as much as 72.4 % in black spruce (*Picea mariana*) (Morris and Miller 1994). Thus, wildfire plays a positive role in these systems by rapidly mineralizing the nutrients sequestered in the forest floor and creating post-fire conditions that stimulate microbial activity and therefore increasing N mineralization rates (see review by Neary et al. 1999).

The accumulation of forest floor C and N depends on the balance between primary production and decomposition. The source of forest floor is the littefall and mortality of understory and overstory plants. The factors that control the rate of production are complex (Ryan et al. 1997) and include nutrient, light and water availability. Decomposition is controlled mainly by temperature, moisture, and quality of the organic matter. Accumulation of forest floor occurs when the rate of litter production exceeds the rate of decomposition. The balance between production and decomposition may shift throughout succession and may lead to loss of forest floor early in succession and accumulation of forest floor as stands mature (Covington 1981).

The accumulation of forest floor in boreal forests plays an important role in global carbon (C) cycling because it stores vast quantities of C. Nitrogen and C cycles are tightly linked in terrestrial ecosystems (Bolin and Cook 1983; Melillo and Gosz 1983), consequently, ecosystem C storage may be constrained by the availability of N (Townsend and Rastetter 1996). In boreal forest ecosystems, soil respiration (CO_2 flux) is a large component of total C flux and it has been hypothesized that CO_2 flux changes during forest succession following wildfire (*in* Wang et al. 2002). Soil respiration is a cumulative flux of microbial respiration and plant root respiration. The rate of soil respiration is controlled largely by soil temperature (Edwards 1975, for reviews see Singh and Gupta 1977, Raich and Schlesinger 1992), moisture (Edwards 1975, Linn and Doran 1984, Raich and Schlesinger 1992) and substrate quantity (Trumbore et al. 1995). Because all these factors change throughout the course of succession following wildfire, it is reasonable to hypothesize that soil respiration rates change as well.

The objective of this study was to characterize the recovery of C and N cycling after wildfire in Michigan jack pine forests and to determine the main factors controlling those patterns. Specifically, the goal was to determine the pattern in C and N mineralization, changes in microclimate and vegetation accumulation. I hypothesized the following:

1) Soil temperature will decrease with succession.

Rationale: Soil temperature will be high after wildfire due to greater soil heating associated with removal of the forest canopy and blackening of the soil surface causing decreased soil albedo. Soil temperature will decrease as the canopy closes.

2) Soil moisture will decrease with succession.

Rationale: Soil moisture depends primarily on plant transpiration and evaporation. Immediately following wildfire, loss of vegetation will reduce transpiration. Concurrently, higher soil temperature (Hypothesis 1) will lead to greater evaporation rates. Decrease in transpiration will be more than increase in evaporation, resulting in higher soil moisture. Soil moisture will decrease with succession as plants reestablish and leaf area increases, resulting in greater moisture loss via transpiration.

3) Organic matter quality will decrease with succession.

Rationale: Organic matter quality will decrease due to increasing inputs of poor-quality coniferous litter from jack pine. As soil microorganisms exhaust more labile sources of C and N, recalcitrance of organic matter will increase.

4) Substrate quantity will increase with succession.

Rationale: Litter inputs will increase as plant production increases with stand age, whereas decomposition of organic matter will decrease due to less favorable microclimate (Hypothesis 1 & 2) for heterotrophs and decreasing organic matter quality (Hypothesis 3).

5) Net N mineralization rates will initially increase with succession and then decrease.

Rationale: Nitrogen mineralization is partly dependant on the quantity of organic N. Nitrogen mineralization will be low early in succession because of the limited amount of organic N remaining after wildfire. Nitrogen mineralization will increase as organic matter accumulates with succession (Hypothesis 4) and then decrease as organic matter quality decreases (Hypothesis 3).

6) Soil respiration will increase with succession.

Rationale: Root respiration will increase with vegetation recovery. Concurrently, microbial respiration will increase with greater accumulation of organic matter (Hypothesis 4).

MATERIALS AND METHODS

Site Description and Selection

All study sites were located in the Highplains District (8) of Region II of northern Lower Michigan (44°30'N, 84°30'W) (Albert *et al.* 1986). This region is characterized by a cold climate (MAT = 6.7°C) and a short growing season (*ca.* 115 days) from May through September. The average temperature during the growing season is 16.9°C (Albert *et al.* 1986). Soils in the Highplains District form on glacial outwash and are dominated by excessively well-drained, acidic sands of the Grayling series (Typic Udipsamments) (Werlein 1998). Jack pine (*Pinus banksiana)* is the dominant tree species in the outwash plains often co-occurring with northern pin oak (*Quercus ellipsoidalis*). The fire cycle for jack pine forests in the in the Highplains District is *ca.* 30 years (Ryel 1981; Simard and Blank 1982).

In May of 2002 I established a chronosequence of 11 wildfire-regenerated stands of jack pine, which burned in years 2001, 2000, 1998, 1995, 1990, 1988, 1980, 1975, 1966, 1950, and 1930. I used fire maps from the Michigan Department of Natural Resources (DNR) and the United States Department of Agriculture-Forest Service (USDA-FS), along with USDA-FS fire reports, to identify fire locations for stands dating back to 1966. All of these stands originated from recorded fires greater than 200 acres. The two stands older than 36 years were selected using USDA-FS compartment maps followed by field surveys to validate that stands were even-aged jack pine with no evidence of planting (tree rows or furrows). I made the assumption that even-aged, unplanted jack pine forests in this region must be of wildfire origin. Jack pine's extreme shade intolerance and dependence on wildfire for regeneration (Cayford and McRae 1983), together with the high frequency of wildfires in this area, suggests that any other scenario of stand establishment is unlikely. For all fires, I used field observations to eliminate areas that showed evidence of planting, salvage logging (where possible), or that were less than 90% jack pine basal area. However, the presence of cut tree stumps at the stand that originated in 1975 does suggest that it was salvaged after the fire. I included this stand in the chronosequence because it was the only stand in that age class. All of the study sites were located within a 23 km radius (Figure 2).

At each site I identified an area (between 1 and 2.5 ha) of uniform terrain with no evidence of human disturbance, hereafter referred to as a stand. Stand borders were located at least 20 meters away from the nearest road. All soil and vegetation sampling was conducted along 3 parallel, 60-m transects beginning at stratified random points along the long axis of the stand.

Net Nitrogen Mineralization

Net N mineralization was measured using an *in situ* closed core method (Raison et al., 1987). Soil sampling was conducted *ca.* monthly throughout the 2002 growing season (May 20-November 11). Monthly soil samples were collected from 3 points along each transect. Points were randomly located within each 20-m increment along the transect, and at a random distance between 1 and 5 meters from the transect. At each sample point, two 5.08-cm inside diameter, PVC cores were driven 10 cm into the soil. Each soil core was sharpened at the penetrating end of the pipe to facilitate insertion. One PVC core was removed immediately for the time zero determination of soil NH_4^+- and NO_3^-- N concentrations, whereas the second core of each pair was capped on top with duct tape to prevent leaching and retrieved at the next sampling date. Each soil sample was separated into mineral (A horizon) and forest floor (O_e +O_a horizons) components. The three cores from each transect were composited into one mineral soil sample and one organic soil sample, yielding a final sample size of 3 for each stand.

All soil cores were kept on ice in coolers for transport to the laboratory, stored in a refrigerator at 4°C, and analyzed within 48 hours. Mineral soil was moist sieved to <4 mm and homogenized. The organic soil was homogenized and roots were removed by hand. In instances where there was an inadequate amount of sample for analysis, the organic samples from all three transects were composited. A 20-g and a 5-g subsample from the mineral and organic soil, respectively, were shaken with 50 mL of 2 M potassium chloride (KCl) for 1 hour to extract NH_4^+- and NO_3^-- N. The extracts were poured through Whatman #2 filter paper and stored frozen until analysis for inorganic nitrogen using an Alpkem Flow Solution IV Auto-Analyzer (OI Analytical, College Station, TX). An additional soil subsample was oven dried at 105°C to determine gravimetric soil moisture. Net N mineralization rates were calculated on an oven-dry basis as the increase in inorganic NH_4^+- and NO_3^-- N between the two time periods, then scaled to an areal basis using mineral soil bulk density and organic soil mass per unit area (mg N/m^2).

Soil Respiration

Soil respiration was measured monthly during the 2002 growing season using the soda lime technique (Edwards 1982; Kabwe 2002). Two sample points were randomly located along each transect (stratified within each 30 m increment). Approximately 20 g of soda lime was added to a 5.08-cm diameter metal tin fitted with a gastight lid. The containers were heated uncovered for 48 hr at 105°C to remove moisture and transferred into the field in airtight tupperware containers with mesh packets of Drierite desiccant (calcium sulfate). At time 0 in the field, the open tin was sprayed with deionized water to activate the soda lime. The tin was then placed on a plastic stand inside an inverted, white plastic bucket 20.3-cm in diameter pushed 1 cm into the soil. The container dimensions and amount of soda lime used adhere closely to Edward's (1982) recommendations that the surface area of the container with soda lime covers *ca.* 5% of the soil surface area measured, and that 0.06 g of soda is used per cm^2 of forest floor. A bag of sand was placed on top of the inverted bucket to form a good seal and prevent disruption from wind. All aboveground vegetation was clipped from each sample area immediately prior to beginning respiration measurements. After 24 hours of incubation, the lids were placed back on the tins and returned to the laboratory in the airtight tupperware. The soda lime was again dried at 105°C for 48 hours. At five randomly selected stands at each sample date, one tin of soda lime was placed in closed chamber of similar volume to determine background CO_2 uptake in the absence of soil CO_2 efflux. Respired CO_2 was measured as the difference between oven dry (105°C for 24 hours) weight before and after the soda lime was placed in the field. The increase in weight is directly proportional to the amount of CO_2 adsorbed during the incubation period.

To estimate soil respiration for the growing season I extrapolated rates for *ca.* 2 weeks before and after each sampling date based on the measured rate of CO_2 flux (Toland and Zak 1994, Vogt et al. 1980; Ewel et al. 1987a; 1987b). Cumulative respiration was calculated by summing the respiration flux over the five time periods.

Physical and Chemical Properties

Soil bulk density samples were collected in August using a soil bulk density sampler (Soilmoisture Equipment Corp., CA) by inserted it into the A horizon and sampling a volume of 615 cm^3. Soil bulk density was determined as weight of the soil per unit volume (g/ml) on an oven-dry (105° C) basis.

Soil pH and exchangeable bases were determined from air-dried, initial subsamples of composite soils cores collected in May. Soil pH was determined in water using a 2:1 ratio for mineral soil and 4:1 ratio for organic soil of deionized water: air-dry soil. The samples were shaken for one hour and then pH was measured with a glass electrode. Extractable base cations (Ca, Mg, K, Na) were measured on ammonium chloride extracts using a Direct Current Plasma Atomic Emission Spectrometer (SpectraMetrics/Beckaman, MA). Total exchangeable cations ware determined by multiplying concentration by bulk density.

I used a 25.4 cm x 25.4 cm sampling square to measure the amount of forest floor organic matter at each stand. In August, I collected 3-4 frames from stratified random locations along each transect. The samples were oven dried at 65°C and weighed to determine the amount of forest floor at each stand on an areal basis.

Carbon and N content for soil was determined using air-dried, initial subsamples of composite soils cores collected in May. Forest floor C and N was determined using subsamples from forest floor collected in August. Samples were pulverized in a Kleco 4200 ball mill (Kinetic Laboratory Equipment Company, CA) and analyzed for C and N on a Carlo Erba NA1500 Nitrogen Analyzer (Elantech, NJ). Carbon and N content for soil was determined by multiplying soil C and N concentrations by bulk density. Forest floor C and N content was determined by multiplying concentrations by amount of forest floor at each stand.

Soil Microclimate

I measured soil temperature every 1 or 2 hours for the duration of the field study using 1 WatchDog 100 data logger (Spectrum Technologies, Inc., IL) per transect placed 5 cm below the soil surface. To summarize temperature differences among stands, I calculated the number of growing season degree-days by adding daily average number of degree hours above 0°C in the growing season for each stand.

Soil moisture was measured as moisture tension using WatchDog 400 data loggers and Watermark soil moisture sensors (Spectrum Technologies, Inc., IL) at stand ages 2, 12, 22, 36 and 72. Each soil moisture datalogger accommodated three sensors that were placed at a distance of 6.1 m from the logger and at an azimuth of 0°, 120°, and 240° from each point. Soil moisture was also measured gravimetrically from subsamples of soil collected for initial N pool measurements.

Vegetation

Live understory biomass was sampled in August using a 0.25 m^2 sampling square at two random points along each transect. Plants were clipped at the base and placed in one of the following categories: mosses, lichens, ericaceous shrubs (primarily *Vaccinium* spp.), sand cherry (*Prunus pumila*), graminoids and forbs, sweet fern (*Comptonia peregrina*), bracken fern (*Pteridium aquilinum*) and a miscellaneous category. Samples were composited by transect, dried in a forced air convection oven at 55°C, and then weighed. Total understory biomass was calculated as the total sum of all categories for a particular stand age.

To measure overstory biomass, I established one 7x14 m plot parallel to each transect at stand ages 12 and older. I measured diameter at breast height (dbh) of every live tree (over 1 cm dbh). Overstory biomass was estimated using the following equation:

$$\mathbf{Biomass=0.1054\ (D)^{2.381}}$$

(Green and Grigal 1978; Grigal and Ohmann 1992), where *D* is dbh ($p<0.001$; $r^2=0.983$). At stand age 7, none of the tress reached breast height. Therefore, I built the following regression:

$$\mathbf{Biomass= 0.0014*EXP(0.039*Height)}$$

predicting aboveground biomass from height based on 5 harvested trees ($p<0.001$; $r^2 = 0.994$).

Statistical Analysis

I used linear and nonlinear regressions to analyze changes with stand age in N mineralization, C and N content, C:N ratio, exchangeable cations, pH, number of degree-days and overstory biomass. The function that best fit the relationship was based on the combination of minimum sum of squares of error and lowest p-values. A modified gamma function was fit to the annual total N mineralization data using estimated parameters calculated in CurveExpert (Microsoft, Inc.). The gamma function was modified from the original **[$y=a+bx^c\exp(dx^e)$]** to **[$y=a+bx^c\exp(dx^e)-fx$]**, allowing a lower asymptotic value. A linear **[$y=mx+b$]** function was fit to forest floor C:N ratio, total C, total N, total C:N ratio, forest floor pH, as well as number of degree-days. Quadratic **[$y=ax^2+bx+c$]** and power **[$y=ax^b$]** functions were fit to forest floor pH and soil C:N ratio, respectively. I used hyperbolic **[$y=(a*b)/(b+x)$]** and carrying capacity **[$y=a*(1-\exp(bx))^c$]** functions to fit curves to soil N and overstory biomass, respectively. I used the exponential decay function **[$y=a*\exp(-b*x)$]** to fit curves to soil C and total exchangeable base cations. Stand age 7 was excluded from the regression of N mineralization, total C and N content against stand age. All regression analyses were performed on stand average data to yield an n of 1 for each stand.

I used multiple regression analyses to determine the main variables affecting N mineralization and soil respiration. Soil respiration data were analyzed using all stands (11) and sampling dates (5) yielding an n of 55. Backward elimination procedures were used in multiple regression analysis to select the model with the conceptually strongest parameters and highest adjusted and partial r^2. Two-way analysis of variance was used to determine differences in monthly soil moisture, soil respiration and total N mineralization for all stands.

In multiple regression analyses, N mineralization, soil respiration, C and N content, C: N ratio, exchangeable bases, as well as forest floor mass were ln-transformed to normalize the data. Multiple regression analyses were performed using Statistical Analysis System (SAS) for personal computers (SAS Institute 1987). Analysis of variance was performed using SYSTAT software (Systat Software, Inc.).. Linear and nonlinear regressions were performed using SigmaPlot software (SPSS, Inc.). Significance was accepted at minimum alpha of 0.05.

RESULTS

Soil Carbon and Nitrogen Pools

Forest floor C and N content initially declined and then began to increase after *ca.* 10 years following wildfire, finally reaching a steady state after almost 40 years (Figure 3A-B). The exception to this trend is stand age of 7, which exhibited the highest amount of forest floor C and N. Forest floor C: N ratio (Figure 3C) did not change with stand age ($p=0.1853$). Soil C (Figure 4A) also did not change with stand age ($p=0.0990$). Soil N content (Figure 4B) decreased with stand age ($p<0.0189$, adjusted $r^2=0.42$), however, stand age was not a strong predictor of change in soil N content. Soil C: N ratio (Figure 4C) did not change with stand age ($p=0.2043$). Total C (Figure 5A) content increased with succession ($p<0.0138$, adjusted $r^2=0.50$, whereas total N (Figure 5B) did not change ($p=0.0818$). Total C: N ratio (Figure 5C) increased with stand age ($p<0.0391$; adjusted $r^2=0.325$). Stand age 7 was excluded from the linear regression analysis of total C and N because the high contribution of C and N from the forest floor at that stand made it an outlier.

Net Nitrogen Mineralization

The annual amount of total N mineralized decreased rapidly in the first ten years following wildfire to rates less than what was observed in the mature stands and then slowly increased until reaching a steady state after almost 40 years following wildfire, with rates less than half the initial amount ($p<0.001$; adjusted $r^2=0.80$) (Figure 6). Stand age 7 again was an outlier having the highest amount of total N mineralization (6348.5±1893 mg N/m^2). Total N mineralization increased with increasing forest floor mass (FFM) and decreasing C: N ratio ($p=0.004$; adjusted $r^2=0.69$) resulting in the following equation:

$$\ln(Nmin_{total})=22.67 + 0.511 \ln(FFM) - 6.01 \ln(C: N_{total})$$

The percentage of total variance explained by forest floor mass and C: N ratio individually were 39 and 11 percent, respectively.

The amount of N mineralized in the forest floor initially decreased and then increased approximately ten years following wildfire to an amount double the initial value (Figure 7A). Stand age 7 was again an outlier and had the highest amount of N mineralized in the forest floor (1441±518). Forest floor N mineralization was best explained by forest floor mass (FFM) ($p<0.001$; adjusted $r^2=0.86$) resulting in the following equation:

$$\ln (Nmin_{FF}) = -0.85 + 0.92 \ln(FFM)$$

The amount of N mineralized in the soil decreased by an order of magnitude by 15 years after wildfire (Figure 7C). Stand age 7 did not follow this pattern and had the highest amount of N mineralized in the soil (4907.5±1586). Soil N mineralization was explained by soil C: N ratio, total exchangeable bases and forest floor mass (FFM)($p<0.001$; adjusted $r^2=0.85$), resulting in the following equation:

$$\ln (Nmin_{soil}) = 22.61 - 5.38 \ln(C{:}N_{soil}) + 0.53 \ln(bases) + 0.20 \ln(FFM)$$

The percentage of total variance explained by soil C: N ratio, total exchangeable bases and forest floor mass individually was 62, 44 and 11, respectively.

To gain further insight into the controlling factors of N availability and how it varies with stand age, N mineralization was relativized for N content.
The increase in forest floor N mineralization with succession disappeared when relativized to account for changes in N content (Figure 7B). The trend in soil N mineralization did not change (Figure7D) and therefore soil N pool size did not explain the change in soil N mineralization with stand age. Forest floor N pool at stand age 7 accounted for the high N mineralization rates in the forest floor. However, soil N pool size failed to account for high N mineralization rates in the

soil. The percent of total N mineralization coming from the forest floor (Figure 8) increased linearly with stand age (p=0.001; adjusted r^2=0.676).

A two-way analysis of variance with stand and month as factors showed no significant seasonal differences in total N mineralization between stands (p=0.446) (Table 1). However, the significance of stand age as a factor (p<0.001) indicated that N mineralization was different between stands.

Soil Respiration

Annual CO_2 flux decreases in the first decade following wildfire (Figure 9), increased to rates double the initial values in the next decade and finally declined slowly for the next 50 years. A two-way analysis of variance with stand and month as factors showed a significant effect of season on soil respiration (p=0.001) (Table 2) and a significant interaction between stand age and sampling month (p=0.001). Soil respiration was highest in July in the three youngest stands and stand age of twenty-two, whereas it was higher in August in the four oldest stands (Figure 10). Multiple regression analysis revealed that mean temperature (T) for day of measurement (a), gravimetric moisture from forest floor (M_{FF}) and soil (M_{soil}) best predicted the variance in soil respiration (p< 0.001, r^2 = 0.44) , resulting in the following equation:

$$\mathbf{ln\ (Respiration)=2.95 + 0.379\ ln(T) + 0.0074(M_{FF}) - 0.036(M_{soil})}$$

The percentage of total variance in soil respiration explained by temperature, forest floor moisture and soil moisture individually was 34, 5 and 2 percent, respectively.

Other Soil Chemical Characteristics

Total exchangeable bases (Figure11) decreased exponentially with increasing stand age ($p<0.0001$; adjusted $r^2=0.885$). Calcium (Ca) made up most of the bases, whereas sodium (Na) the least. Both soil and forest floor had an acidic pH at all the stands and decreased with stand age (Figure 12). Soil pH was best described by a quadratic function (p-value=0.0043; adjusted $r^2=0.680$) with little change in pH for the first two decades followed by a steady decline. Forest floor pH decreased linearly with increasing stand age (p-value<0.001; adjusted $r^2=0.752$).

Soil Microclimate

The total number of degree-days above 0°C at 5 cm depth in soil (Figure 13) decreased with increasing stand age (p-value=0.0346), however, a large proportion of the variability was not accounted for by stand age (adjusted $r^2=0.342$). Gravimetric moisture in the forest floor (Figure 14A) was lowest in September at all stands. With the exception of stand age of 2, percent forest floor moisture was higher in the older stands than the younger stands. Gravimetric percent moisture in the mineral soil was lowest in the July and September sampling days (Figure 14B) and was much lower compared to forest floor. A two-way analysis of variance of gravimetric moisture in the mineral soil (Table 3) with month of sampling and stand age as factors indicated that soil moisture varied seasonally ($p<0.001$) and differences were significant between stands ($p=0.017$). There was no interaction between stand age and sampling month ($p=0.175$).

Analysis of variance was not performed on forest floor moisture data because the data for youngest stands were composited, yielding an n of 1. Soil moisture measurements using dataloggers (Figure 15) showed that the months of June and August were the driest. Youngest and oldest stands were the driest, whereas stand age of 22 was wettest.

Vegetation

In the first decade following wildfire, live jack pine biomass (Figure 16) increased slowly to 6.96 Mg/ha, followed by a logarithmic increase in biomass for the next 30 years ($p<0.001$; adjusted $r^2=0.983$). By 50 years following wildfire, jack pine biomass increased to 84.73 Mg/ha, followed by a period of slower biomass accretion.

Understory biomass increased rapidly following wildfire and began to decrease rapidly in less than 10 years (Figure 17). By 50 years, understory biomass began to increase. Stand age of 27 was the exception to this trend having the highest understory biomass.

DISCUSSION

Net Nitrogen Mineralization

In the jack pine chronosequence, forest floor accumulation largely regulates N mineralization. Changes in N mineralization can result from changes in N capital, N turnover, or both. The observed pattern in N mineralization with succession in jack pine forests occurs as a consequence of changes in the distribution (Figures

3-5) and turnover of N in the soil (Figure 7D) and forest floor (Figure 7B) as these forests recovered after wildfire.

In mature stands, N turnover was slow (Figure 7B,D) and about 40% of total N capital was tied up in the forest floor. Wildfire had an immediate effect on both the distribution and turnover of N. Wildfire removed most of the forest floor and only about 13% of the total N capital remained there. Even though soil N declined after wildfire, N turnover in the soil increased, leading to a spike in N mineralization. The increase in N turnover can be partially attributed to greater exchangeable cation availability and warmer soil temperatures following wildfire. Soil temperature can increase due to the presence of charcoal and through destruction of forest canopy (Christensen and Muller 1975). Incomplete combustion of organic matter during wildfire results in the formation of charcoal. Because of its low albedo, charcoal can absorb more radiation and heat the soil. Furthermore, the destruction of the forest canopy allows more radiation to reach the soil surface. Because soil temperature can limit microbial metabolic rates (Paul and Clark 1996; Swift et al. 1979), higher soil temperature can lead to higher rates of N mineralization. Even though wildfire causes large losses of total N (see review by Neary et al. 1999; Raison et al. 1985; Grier 1975; Harwood and Jackson 1975), it can also lead to increased availability of less volatile nutrients, such as phosphorus and base cations through the production of ash. Burning of organic matter releases these nutrients and makes them available for plant and microbial uptake. It appears that warmer soil temperatures and the spike in exchangeable cations provide more favorable conditions for increased microbial activity, resulting in higher turnover rate of N remaining after the fire.

However, the stimulating effect of fire was transient. In the first decade following wildfire, a large proportion of exchangeable cations were either taken up by soil microorganisms and recovering vegetation, or lost via leaching. Soil microorganisms have most likely exhausted any sources of labile C and N. Furthermore, forest floor mass was at its lowest levels and contributed to less than 6% of total N capital. Soil N turnover rate rapidly declined in the first decade to levels measured in mature stands. Within 15 years following wildfire, N mineralization was at its lowest levels in the chronosequence.

Nitrogen mineralization rates began to gradually recover *ca.* 15 years following wildfire. As jack pine biomass entered its exponential growth phase, forest floor began to accumulate owing to jack pine needle litter and tree mortality. The increasing forest floor provided fresh substrate for soil microorganisms. The increase in N mineralization can be attributed to a gradual accumulation of the forest floor N pool. The fact that N turnover rate in forest floor (Figure 7B) did not change with stand age further suggests that higher N mineralization rates resulted from more N in the forest floor, not from higher N turnover. As forest floor reached a steady state at *ca*. 40 years, N mineralization rates also stabilized.

Although stand age of 7 was consistently an outlier in terms of N cycling parameters, this stand further illustrated the importance of forest floor as a driving force in the recovery of N mineralization. Stand age of 7 exhibited not only the highest N mineralization rates, but also had the highest forest floor mass and lowest C: N ratio. In the forest floor, N mineralization at this stand was almost an order of magnitude higher than stands of similar age. However, N turnover in the forest floor was similar to the other stands, suggesting that higher N mineralization rates were higher as a result of more forest floor mass, not more rapid N cycling.

The greater accumulation of forest floor at stand age of 7 is most likely a consequence of greater moisture availability. The soil profile (Table 4) revealed the presence of a gravel band, which can slow down percolation of water through the soil profile. In addition, high clay content (Table 4) at this site can also lead to higher moisture content. Greater moisture availability may have reduced the loss of forest floor to volatilization during wildfire. Thus, this stand may have had more forest floor in the beginning of succession than the other stands in the chronosequence. Furthermore, greater water availability may allow for more rapid understory vegetation growth and thus to greater forest floor accumulation.

The results of the multiple regression for soil N mineralization suggest that C: N ratio and mass of forest floor are also important in driving the pattern of N cycling in the mineral soil as stands mature. Forest floor content can influence N mineralization via leaching of organic compounds into the soil and by affecting soil microclimate. Translocation of organic compounds into the mineral soil has been documented (Froberg et al. 2002; Park et al. 2002; Solinger et al. 2001). Dissolved organic matter can include labile compounds such as peptides and amino acids, as well as recalcitrant compounds. Recalcitrant compounds such as fulvic and humic acids may have a negative effect on N mineralization because fulvic acids contain little N and humic acids are not very labile (Paul and Clark 1996). This mechanism is an unlikely scenario in this system because the model produced by the multiple regression predicts a positive effect of forest floor content on N mineralization. However, leaching of labile compounds from forest floor into the soil may have a positive effect on N mineralization. Forest floor can also protect mineral soil from drying out during the hottest months.

The results partially support the hypothesis that N mineralization will increase as stands begin to recover and decrease with subsequent succession. My original hypothesis did not incorporate the transient stimulating effect of fire on N mineralization. I also hypothesized a decrease in N mineralization in mature stands. Even though forest floor mass has reached a steady state at the end of the chronosequence, N mineralization rates may decline as a result of decreasing substrate quality as evidenced by the widening total C: N ratio.

The observed pattern is different from what is found in the boreal forest of Alaska (Van Cleve and Viereck 1981; Van Cleve et al. 1983) where forest floor accumulation is greater, but N mineralization decreases with succession and N immobilization occurs in mature stands (Van Cleve and Nooman 1975; Van Cleve and Viereck 1981). The three major differences between jack pine forests of Michigan and more northern forests are number of days in the growing season, the composition of the understory and succession of the overstory. The lower number of days in the growing season of boreal forests limits the amount of N mineralized annually. Furthermore, the development of a moss layer in mature stands may inhibit N mineralization (Wardle and Lavelle 1997). Lastly, overstory succession from deciduous to conifer species may explain the decrease in N availability. The deciduous litter decomposes more rapidly than litter from conifers due to the acidic nature and low chemical quality of coniferous litter (Flannagan and Van Cleve 1983; Miles 1985). Furthermore, the deciduous litter prevents the formation of a moss layer early in succession (Van Cleve and Viereck 1981). Paré et al. (1993) also did not observe a decrease in N mineralization with succession after wildfire in a southern boreal forest and partially attribute the maintenance of N availability to persistence of some deciduous species in late successional stages.

In the jack pine forests of Michigan, N mineralization began to recover after *ca.* 15 years following wildfire (Figure 6) and reached a steady state by *ca.* 40 years. The rate of N turnover declined to predisturbance levels by 20 years and remained constant. Measurements of N mineralization rates suggest that rotation age of greater than 40 years should sustain yields in Michigan jack pine forests.

Soil Respiration

The pattern of annual soil respiration is most likely controlled by different factors throughout succession. The decline in soil respiration early in succession can be attributed to a decline in heterotrophic respiration. The increase in soil respiration 10 years after wildfire is most likely a factor of accumulation of forest floor and overstory production, whereas the decline as stands mature is a consequence of decreasing substrate quality and decline in jack pine root respiration as productivity declines.

Dead roots can serve as a primary source of C for heterotrophic microbes after wildfire (Klopatek and Klopatek 1987), but the source can be quickly exhausted, causing the decline in soil respiration. In the first decade following wildfire, the decline in soil respiration coincided with a decline in substrate availability (i.e. forest floor mass). Other studies have also shown an initial decrease in soil respiration following wildfire (Amiro et al. 2003; Wang et al. 2002). Amiro et al. (2003) documented recovery of soil respiration to the same rate as that of a mature site in Canadian boreal forests between 10-30 years after fire. In the jack pine forests of Michigan, soil respiration also begins to increase in the same time frame. I attribute the increase in soil respiration to increasing jack pine biomass and forest floor accumulation. This time period coincides with both the highest rate of jack pine growth and a rapid increase in forest floor carbon (Figure 3A). Rapid jack pine growth aboveground likely corresponds with increased belowground production and root respiration (Ryan et al. 1997). Because the forest floor in boreal forests represents the zone of greatest microbial activity (Van Cleve and Moore 1978), increasing forest floor accumulation may lead to greater heterotrophic respiration. Thus, both root and heterotrophic respiration probably contribute to the increase in soil respiration. Soil respiration rates declined after 30 years onward. The decline in soil respiration can result from decreasing substrate quality, decreasing gas diffusivity through the soil profile or less favorable microclimate for microbial respiration. The decrease in substrate quality can lead to a decline in heterotrophic respiration. Even though total C: N ratio widened in matured stands, the relationship between C: N ratio and age was not strong and therefore may not be a contributing factor to declining soil respiration. However, C: N ratio may not have been the best predictor of substrate quality in these stands. Not only may the acidic nature of the coniferous litter contribute to high C:N ratio of the soil, this litter may also have high lignin content, which also may retard soil microbial activity (Oades 1988). Furthermore, the presence of ericaceous shrubs (Figure 18) at some sites may indicate an input of polyphenol compounds into the soil, which has been shown to affect litter quality (Hättenschwiler and Vitousek 2000). Thus, in these soils, a different measure such as % lignin or polyphenols content could be a better indicator of substrate quality. A decline in diffusivity, associated with greater moisture content, can contribute to declining soil respiration (Davidson and Trumbore 1995; Risk et al. 2002). Decreasing diffusivity is an unlikely explanation for declining soil respiration because the data indicates decreasing soil moisture at older stands. Lastly, decreasing soil temperature and moisture at older stands may have caused a decline in heterotrophic respiration.

Soil respiration also varied seasonally (Figure 10) and the variation was most likely a factor of changing soil temperature and moisture through the season. Many studies have illustrated the influence of temperature (Edwards 1975, for reviews see Singh and Gupta 1977; Reich and Schlesinger 1992) and soil moisture (Edwards 1975, Linn and Doran 1984, Raich and Schlesinger

1992) on soil respiration. Temperature appears to regulate a general level of respiratory activity, whereas moisture is a secondary factor dictating the maximum level of CO_2 evolution (Cowling and MacLean 1981). Power, exponential (Q_{10}) and Arrhenius equations have often been used to relate soil respiration to temperature (see Lloyd and Taylor 1994 for review), whereas quadratic (Howard and Howard 1993) and linear relationships (Davidson et al. 1998) have been used to correlate soil respiration to moisture content or matric potential. Linear relationships are especially utilized when data on both temperature and moisture are included in the analysis (e.g. Gupta and Singh 1981).

Mean temperature during the incubation, as well as soil and forest floor moisture were significant predictors of soil respiration but explained only 44 percent of the variation. Poor prediction by these parameters may be due to several reasons. (1) Gravimetric soil moisture was measured one day after the end of the respiration measurement and therefore may not represent the conditions while soil respiration was measured; (2) moisture and temperature were not measured at the same point as the soil respiration;(3) other factors, such as C quantity (Trumbore et al. 1995) and quality, as well as diffusivity (Davidson and Trumbore 1995) affect soil respiration but were not included in the analysis because those factors were not measured for every soil respiration sampling point; (4) gravimetric soil moisture might be a poor predictor in soils that are prone to desiccation, such as the sandy soil in these stands, and matric potential is a more appropriate expression of soil water status (Davidson et al.

1998). Some of the variation in soil respiration could have been due to changes in seasonal root turnover and root respiration, but these parameters were not measured.

In a review of soil respiration rates from a variety of terrestrial habitats, Raich and Schlesinger (1992) found a significant linear trend between soil respiration and annual temperature, but the models explained only 49 and 31 percent of the variation in temperate coniferous and temperate deciduous forests, respectively. Depending on the season, volumetric water content explained between 22 and 48 percent of variation in soil respiration in a mixed hardwood forest (Davidson et al. 1998). Thus, temperature or soil moisture alone do not always correlate well with soil respiration. Studies of soil respiration rates in jack pine stands of eastern Ontario (Weber 1985) found similar CO_2 flux rates ranging from 45-56 mg C $hr^{-1}m^{-2}$. The stands ranged from 6-63 years of age and regenerated from either wildfire or experimental burns. Some differences between stands were documented and attributed mostly to differences in N pools.

My prediction that soil respiration continues to increase after wildfire is not supported. These data suggest a different trend in recovery controlled by substrate quantity for heterotrophic respiration in early succession, substrate quantity and biomass accumulation at middle stages and substrate quality and root respiration in mature stands. Interestingly, the recovery of soil respiration is similar to N mineralization, suggesting that labile substrate is being exhausted for both C and N mineralization.

Vegetation

Changes in live understory biomass appear to be driven by an increase in resource availability immediately after fire, and then by decreased solar radiation as jack pine stands develop. The immediate response to wildfire is an increase in live understory vegetation biomass (Figure 17). This recovery period is likely enhanced by post-fire nutrient and light availability. The decrease in N mineralization and nutrients in the first decade most likely limits further understory biomass accumulation. Furthermore, jack pine biomass begins to increase (Figure 16) and therefore limits light penetration to the forest floor. The increase in the understory biomass in mature stands may be caused by increased light penetration to the forest floor as jack pine mortality increases and stands start to break up. Even though I did not measure light penetration directly, I did observe that stand age of 27 is much more open than the other older stands allowing higher understory vegetation growth. This is illustrated by the abundance of reindeer moss (*Cladonia spp.*), which requires high light and thrives in open canopy and tundra habitats (Ahmadjian and Hale 1973; Cringan 1957).

Jack pine biomass accumulation conforms to a classic pattern of slow increase, then rapid increase, and followed again by a period of slow increase (Figure 16) (Ryan et al. 1997). Understory biomass serves as a source of forest floor in the first decade following wildfire. As jack pine growth entered a period of exponential growth, forest floor accumulation was at its highest rate. Jack pine needle litter and tree mortality became the main source of forest floor inputs at this time allowing for increased N availability. It appears that understory vegetation litter may serve as source of available N for initial jack pine exponential growth, but the cycling of the needle litter sustains further jack pine growth.

Jack pine productivity at maturity may be partially limited by N availability. Single applications of N fertilizer in jack pine have resulted in greater total volume growth (Morrison and Foster 1990; Weetman et al. 1987). Vogel and Gower (1998) also demonstrated greater overstory C in boreal jack pine forest growing with green alder compared to stands growing without alder. They partially attributed higher growth in the former to greater N availability, associated with N-fixing ability of green alder. However, Foster and Morrison (2002) showed that C accumulation in a productive semi-mature stand in Ontario was weakly constrained by N. Therefore, jack pine productivity is site dependant and may depend on inherent soil fertility and N turnover.

CONCLUSIONS

In the jack pine forests of Michigan, rapid loss followed by gradual accumulation of forest floor after wildfire drives N mineralization and soil respiration dynamics. The forest floor contains a large pool of nutrients and a source of N and C for soil microorganisms, which make inorganic N available for plant uptake. This pool is rapidly volatilized by wildfire and takes approximately 40 years to recover. If Michigan jack pine productivity is limited by N availability, a disturbance frequency of more than 40 years is required to sustain maximum yield without fertilization. If the time interval between disturbance events is less than 40 years, loss of nutrients during a wildfire or removal of nutrients in a clear-cut may lead to a remaining nutrient supply that is insufficient to sustain growth or biomass accumulation levels previously observed.

CHAPTER 3

SUMMARY & CONCLUSIONS

- In Michigan jack pine forests, the recovery of nitrogen mineralization and soil respiration is largely driven by accumulation of forest floor and occurs approximately 40 years following wildfire.
- Understanding changes in soil microbial community composition may provide further insights into the mechanisms that drive the observed recovery patterns.
- Even though understory vegetation was measured in this study, a more intense survey of understory species composition may also prove helpful in understanding the role of certain plants, such as mosses and ericaceous shrubs, in N and C cycling.
- Jack pine in Michigan grows on sandy outwash plains. Because these soils are inherently infertile, jack pine productivity may largely be dependant on the accumulation of forest floor for a continuous supply of nutrients. However, whether or not jack pine productivity in Michigan is actually limited by N availability is uncertain. Fertilization trials at different stand ages should provide useful information regarding if and when N limitation to productivity is greatest.
- In order to make better forest management decisions, comparisons need to be made between forest recovery patterns after wildfire and after harvesting.

APPENDIX A:

Tables

Table 1. ANOVA results for monthly total N mineralization rates.

Adjusted R^2= 0.465

Source	Sum-of-Squares	df	Mean-Square	F-ratio	p-value
AGE	17071.606	10	1707.161	5.139	0.000
MONTH	1242.849	4	310.712	0.935	0.446
AGE*MONTH	13457.850	40	336.446	1.013	0.464
Error	36542.196	110	332.202		

Table 2. ANOVA results for monthly soil respiration rates.

Adjusted R^2=0.888

Source	Sum-of-Squares	df	Mean-Square	F-ratio	p-value
AGE	4909365.939	10	490936.594	16.021	0.000
MONTH	1.46211E+07	4	3655286.721	119.282	0.000
AGE*MONTH	7225093.773	40	180627.344	5.894	0.000
Error	3370851.926	110	30644.108		

Table 3. ANOVA results for monthly soil moisture.

Adjusted R^2=0.549

Source	Sum-of-Squares	df	Mean-Square	F-ratio	p-value
AGE	137.533	10	13.753	2.300	0.017
MONTH	361.808	4	90.452	15.128	0.000
AGE*MONTH	301.134	40	7.528	1.259	0.175
Error	657.703	110	5.979		

Table 4. Age, location, vegetation and soil properties of chronosequence sites.

Age (y)	Lat. (N)	Long (W)	% Jack Pine[1]	Stem Density[2]	A horizon pH[3]	Gravel Band[4]	Silt + Clay[5] (%)
1	44°31'	84°16'	ND	ND	4.23	No	11
2	44°36'	84°00'	ND	ND	4.19	No	10
4	44°28'	84°20'	ND	ND	4.33	No	7
7	44°30'	84°18'	97	10741	4.24	Yes	18
12	44°43'	84°29'	89	2755	4.05	Yes	7
14	44°27'	84°16'	100	2585	4.26	Yes	10
22	44°36'	84°03'	100	7040	4.34	No	9
27	44°43'	84°25'	100	1564	4.27	No	8
36	44°26'	84°14'	100	4149	4.11	Yes	8
52	44°33'	84°21'	98	1326	3.86	No	8
72	44°34'	84°24'	99	1530	3.77	No	9

[1]Jack Pine Basal Area/Total stand basal area * 100.
[2]Live, overstory trees (#/ha).
[3]In 1:2, soil:water paste.
[4]Yes indicates the presence of at least one subsurface horizon with > 10 % coarse fragments by mass.
[5]In upper B horizon, determined by Bouyoucos hydrometer method (Bouyoucos 1962).

Table 5. ANOVA results for potential nitrogen mineralization.
(T=temperature Ψ=matric potential)

R^2= 0.812

Source	Sum-of-Squares	df	Mean-Square	F-ratio	p-value
STAND	14.526	3	4.842	19.773	0.000
T	150.080	3	50.027	204.302	0.000
Ψ	18.982	3	6.327	25.840	0.000
STAND*T	2.229	9	0.248	1.011	0.432
STAND* Ψ	7.360	9	0.818	3.340	0.001
T* Ψ	6.514	9	0.724	2.956	0.003
STAND*T* Ψ	3.058	27	0.113	0.462	0.990
Error	47.014	192	0.245		

Table 6. ANOVA results for potential carbon mineralization.
(T=temperature Ψ=matric potential)

R^2= 0.821

Source	Sum-of-Squares	df	Mean-Square	F-ratio	p-value
STAND	52.636	3	17.545	35.468	0.000
T	232.184	3	77.395	156.456	0.000
Ψ	112.262	3	37.421	75.647	0.000
STAND*T	3.886	9	0.432	0.873	0.551
STAND* Ψ	9.102	9	1.011	2.044	0.037
T* Ψ	13.701	9	1.522	3.077	0.002
STAND*T* Ψ	11.981	27	0.444	0.897	0.616
Error	94.977	192	0.495		

Table 7. ANOVA results for relative nitrogen mineralization.
(T=temperature Ψ=matric potential)

R^2= 0.801

Source	Sum-of-Squares	df	Mean-Square	F-ratio	p-value
STAND	16.569	3	5.523	20.902	0.000
T	150.080	3	50.027	189.332	0.000
Ψ	18.982	3	6.327	23.947	0.000
STAND*T	2.229	9	0.248	0.937	0.494
STAND* Ψ	7.360	9	0.818	3.095	0.002
T* Ψ	6.514	9	0.724	2.739	0.005
STAND*T* Ψ	3.058	27	0.113	0.429	0.994
Error	50.732	192	0.264		

Table 8. ANOVA results for relative carbon mineralization.
(T=temperature Ψ=matric potential)

R^2= 0.811

Source	Sum-of-Squares	df	Mean-Square	F-ratio	p-value
STAND	1.272	3	0.424	23.937	0.000
T	8.082	3	2.694	152.141	0.000
Ψ	3.915	3	1.305	73.701	0.000
STAND*T	0.109	9	0.012	0.685	0.722
STAND* Ψ	0.335	9	0.037	2.100	0.031
T* Ψ	0.480	9	0.053	3.015	0.002
STAND*T* Ψ	0.413	27	0.015	0.864	0.662
Error	3.400	192	0.018		

Table 9. ANOVA results for potential nitrogen immobilization. (T=temperature Ψ=matric potential)

R^2= 0.482

Source	Sum-of-Squares	df	Mean-Square	F-ratio	p-value
STAND	25762.202	3	8587.401	4.444	0.005
T	144856.465	3	48285.488	24.988	0.000
Ψ	63286.043	3	21095.348	10.917	0.000
STAND*T	18728.059	9	2080.895	1.077	0.382
STAND* Ψ	3280.379	9	364.487	0.189	0.995
T* Ψ	60640.643	9	6737.849	3.487	0.001
STAND*T* Ψ	28005.662	27	1037.247	0.537	0.971
Error	371010.549	192	1932.3		

APPENDIX B:

Figures

Figure 1. Accumulation of forest floor as a function of stand age after a clear-cut (Covington 1981).

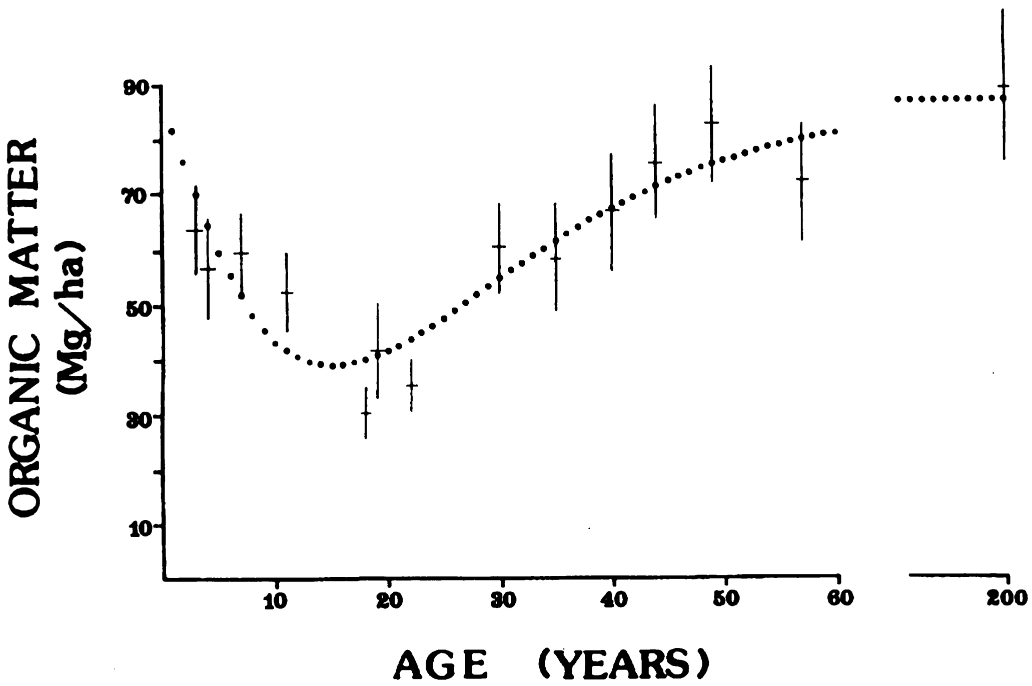


Figure 2. Site locations and dates of stand origin of *Pinus banksiana* chronosequence.

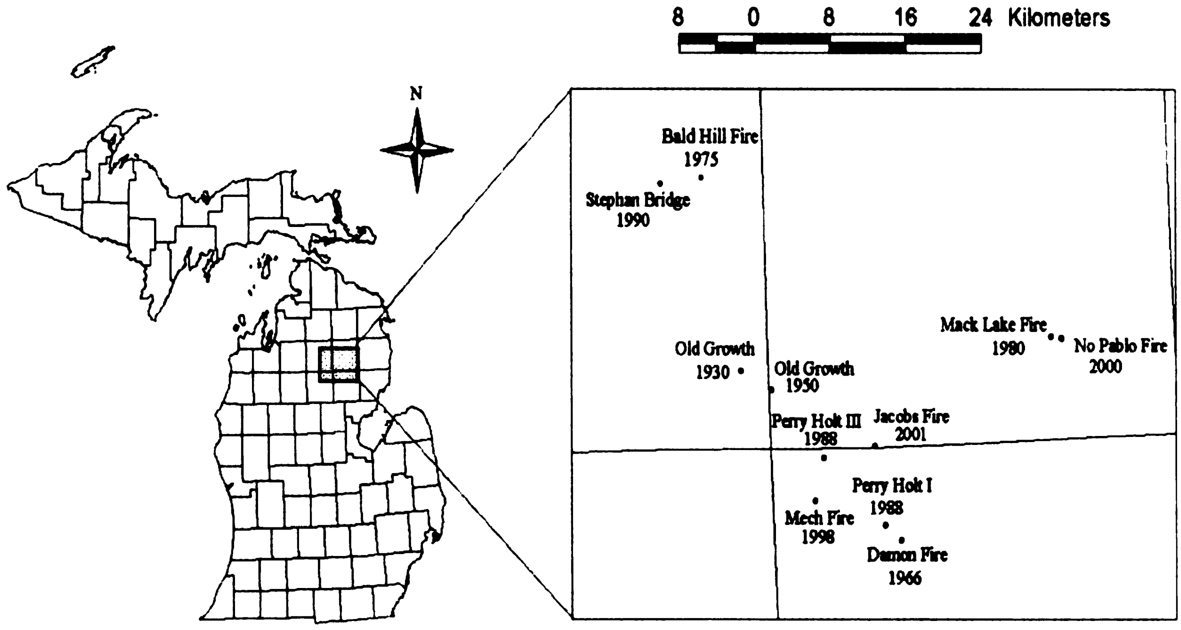


Figure 3. Forest floor (FF) C content (A), N content (B) and C:N ratio as a function of stand age. Note differences in scale between panels.

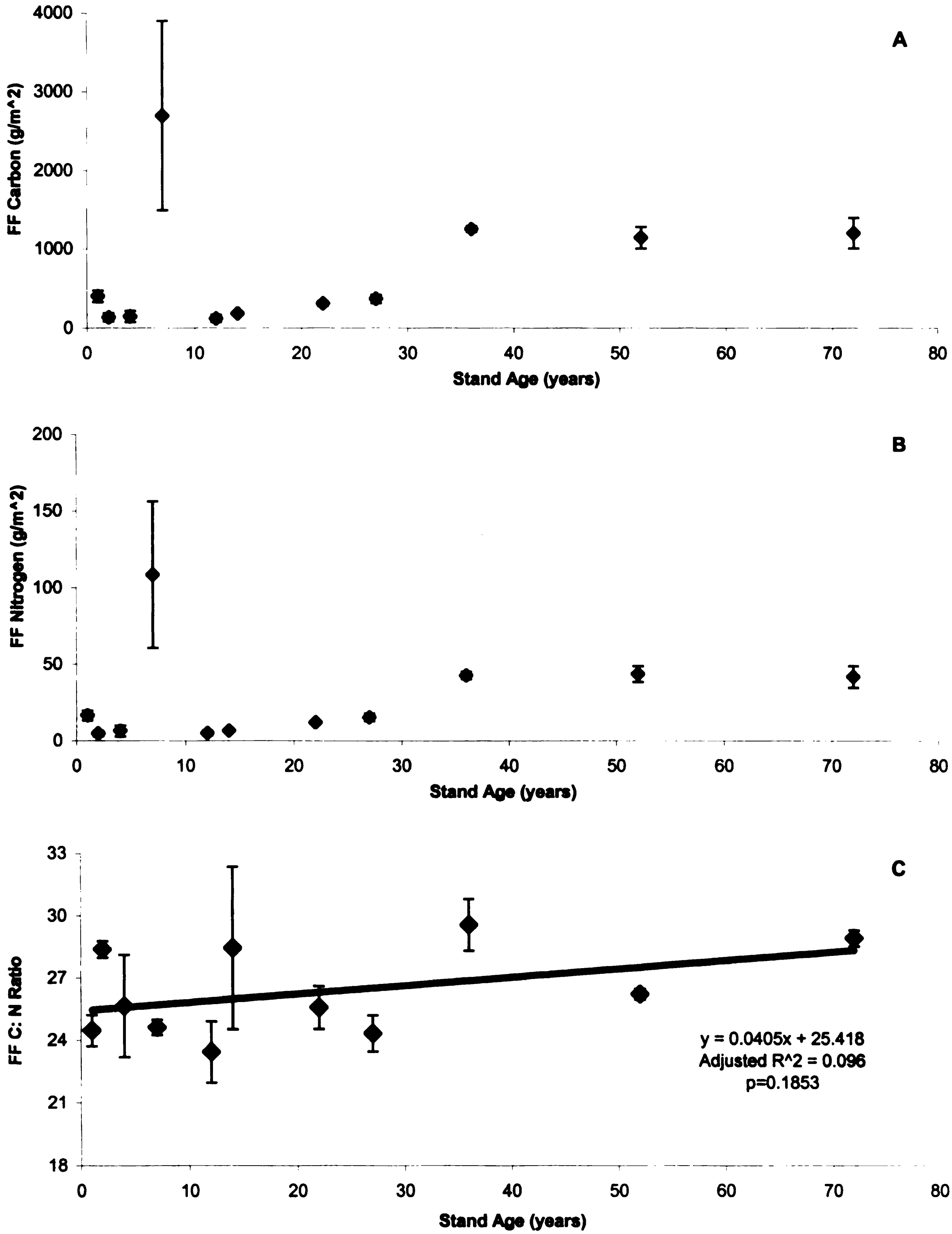


Figure 4. Soil C content (A), N content (B) and C:N ratio (C) as a function of stand age. Note differences in scale between panels.

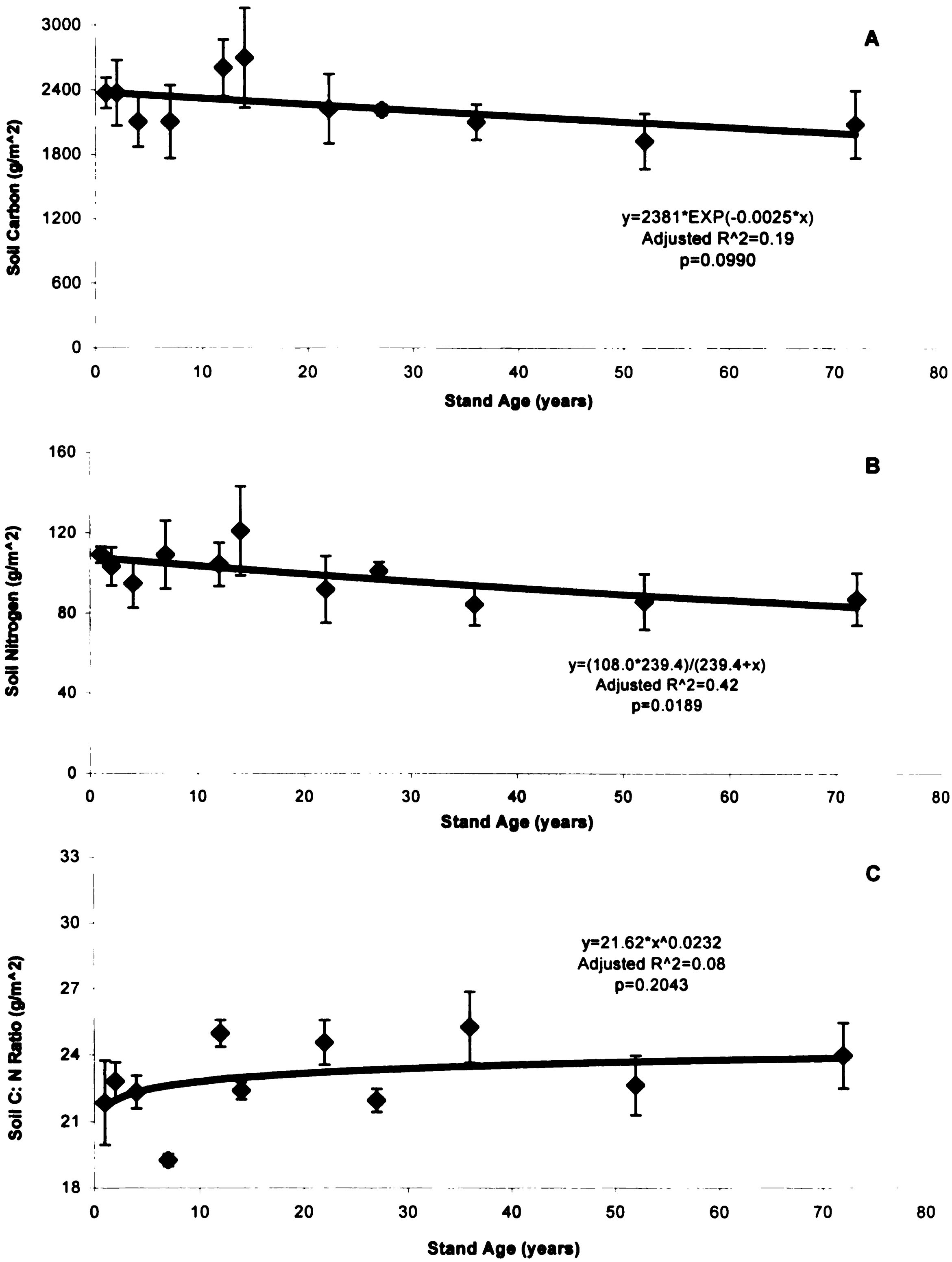


Figure 5. Total C content (A), N content (B) and C:N ratio (C) as a function of stand age. Note differences in scale between panels. Unfilled data points were excluded from the analysis.

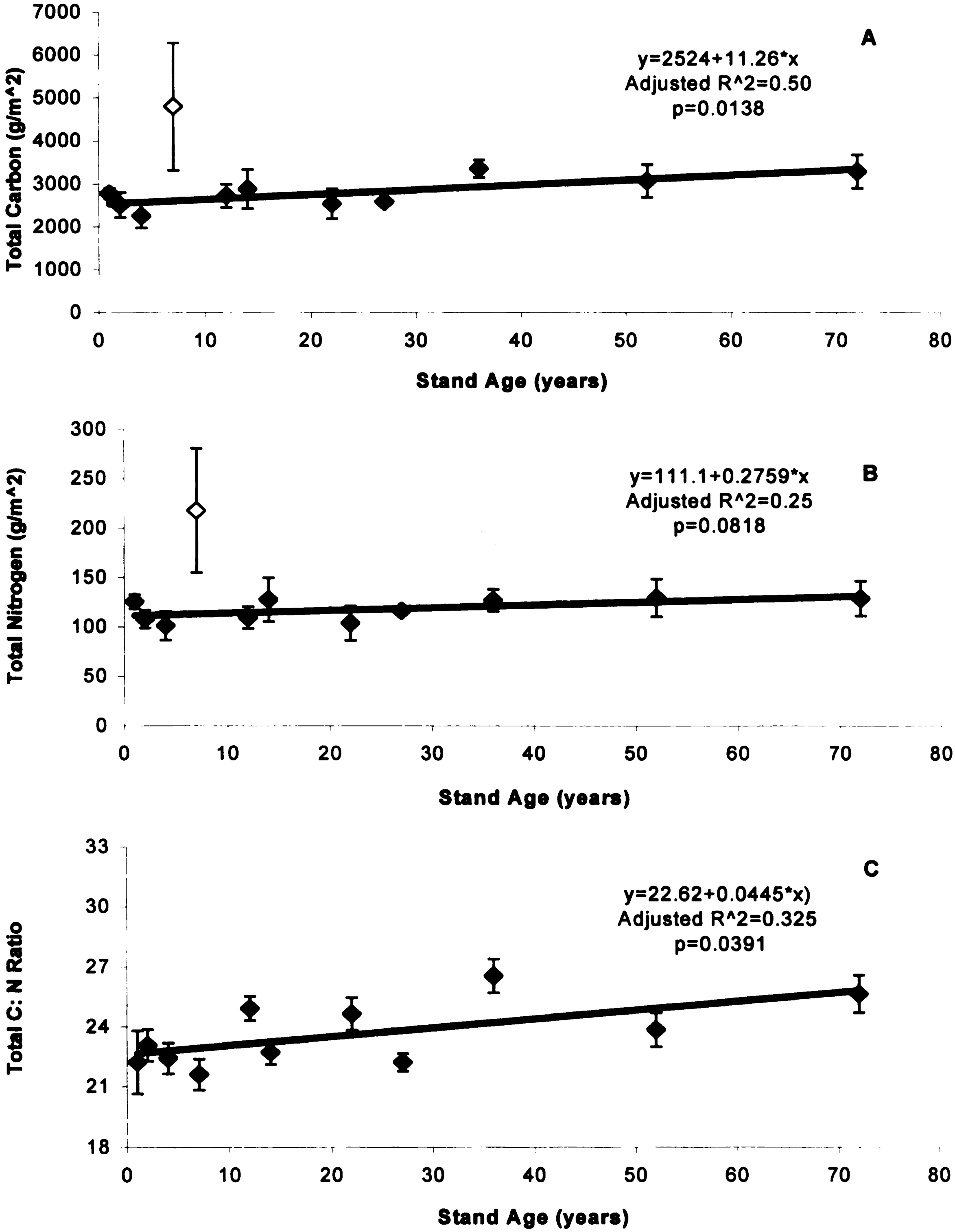


Figure 6. Total annual N mineralization as a function of stand age. Value for stand age 7 is off the scale (6348.5 ±1893).

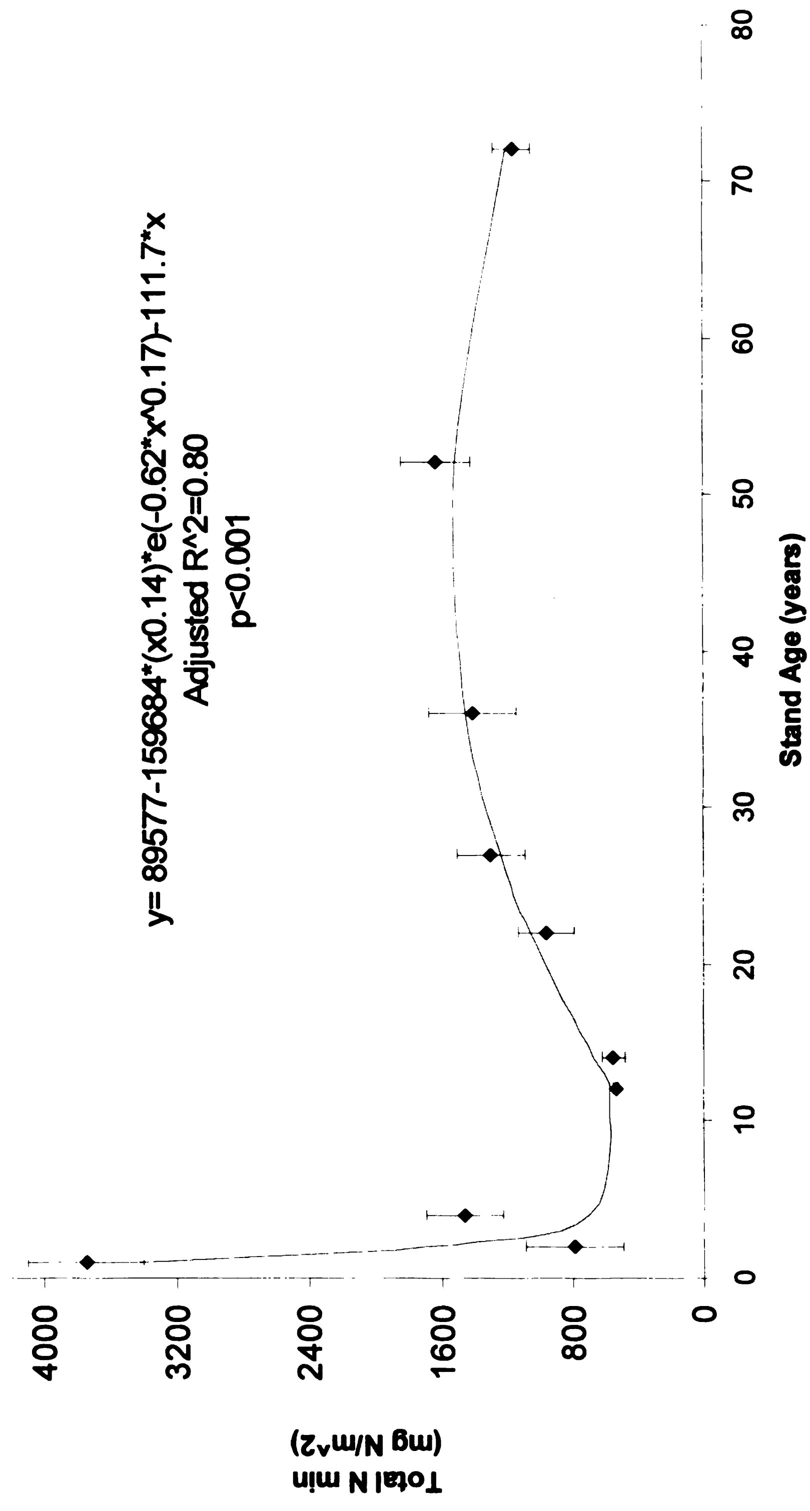


Figure 7. Annual and relativized N mineralization in forest floor (A, B) and soil (C, D) as a function of stand age. Note that scales are different between panels. Values for forest floor N mineralization, soil N mineralization and soil relative N mineralization for stand age 7 are off scale and are 1441.0 (±518), 4907.5 (±1586) and 0.046 (±0.0132), respectively.

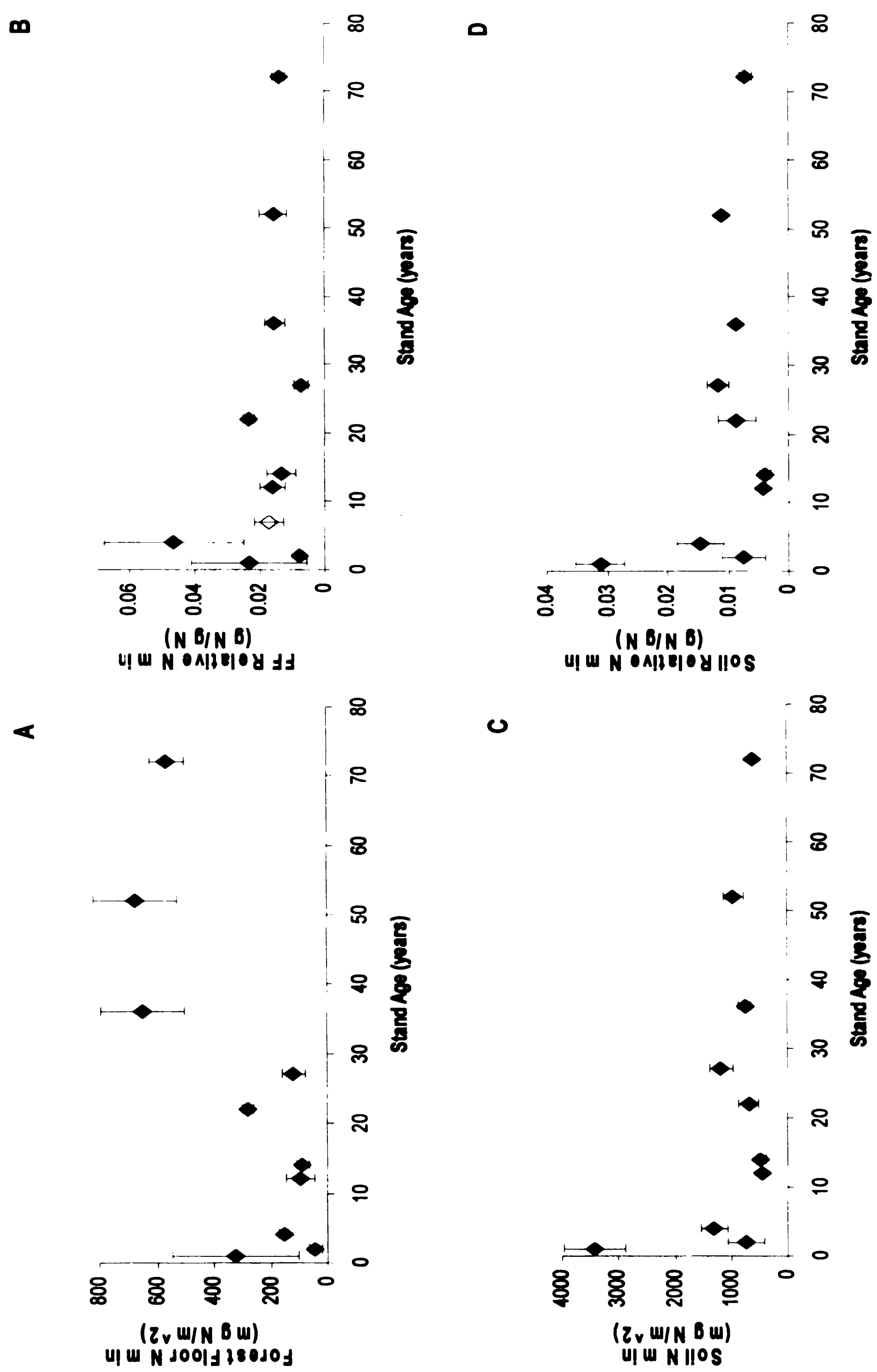


Figure 8. Percent of total nitrogen mineralized from forest floor as a function of stand age.

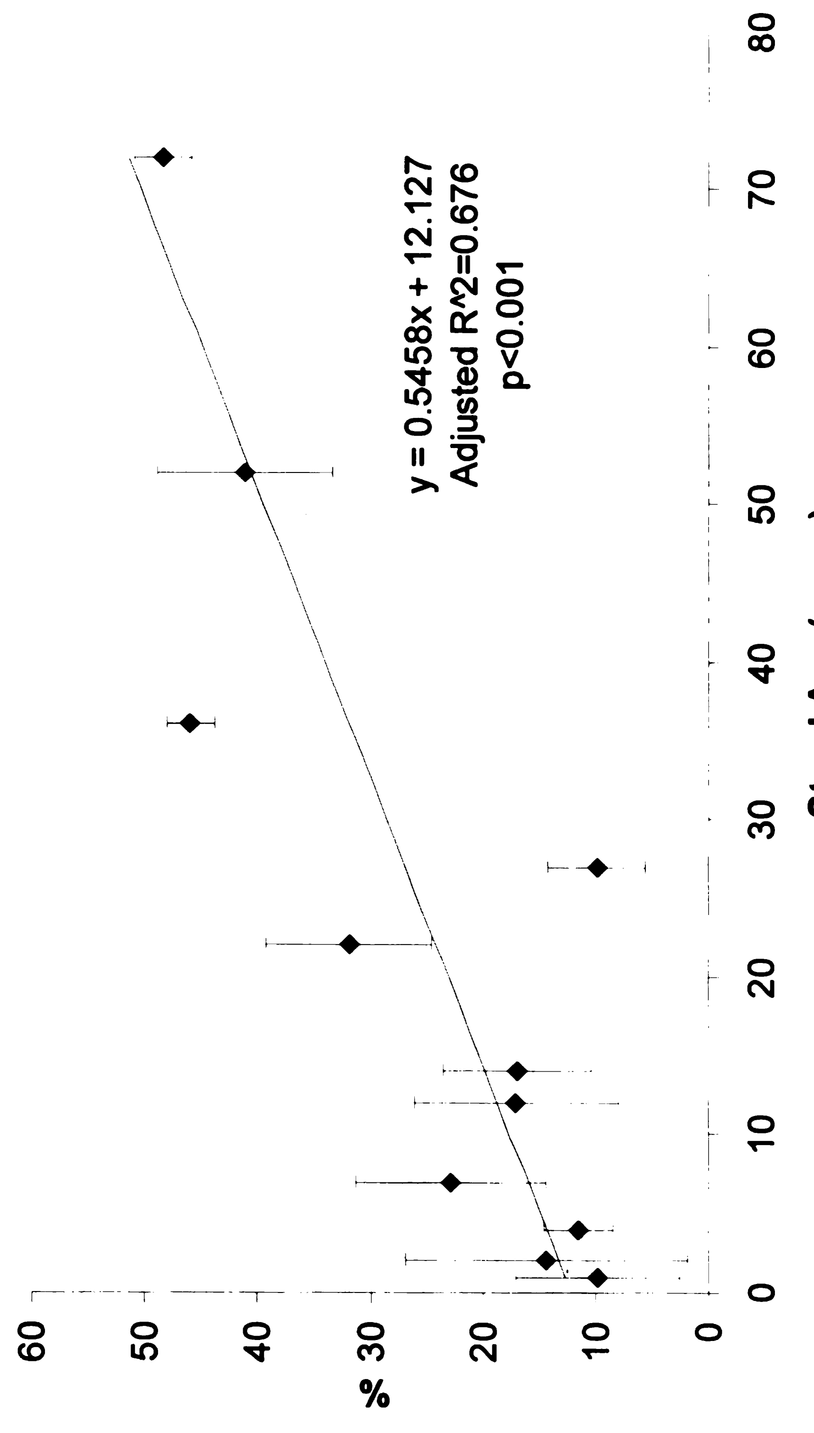


Figure 9. Soil respiration for the growing season as a function of stand age.

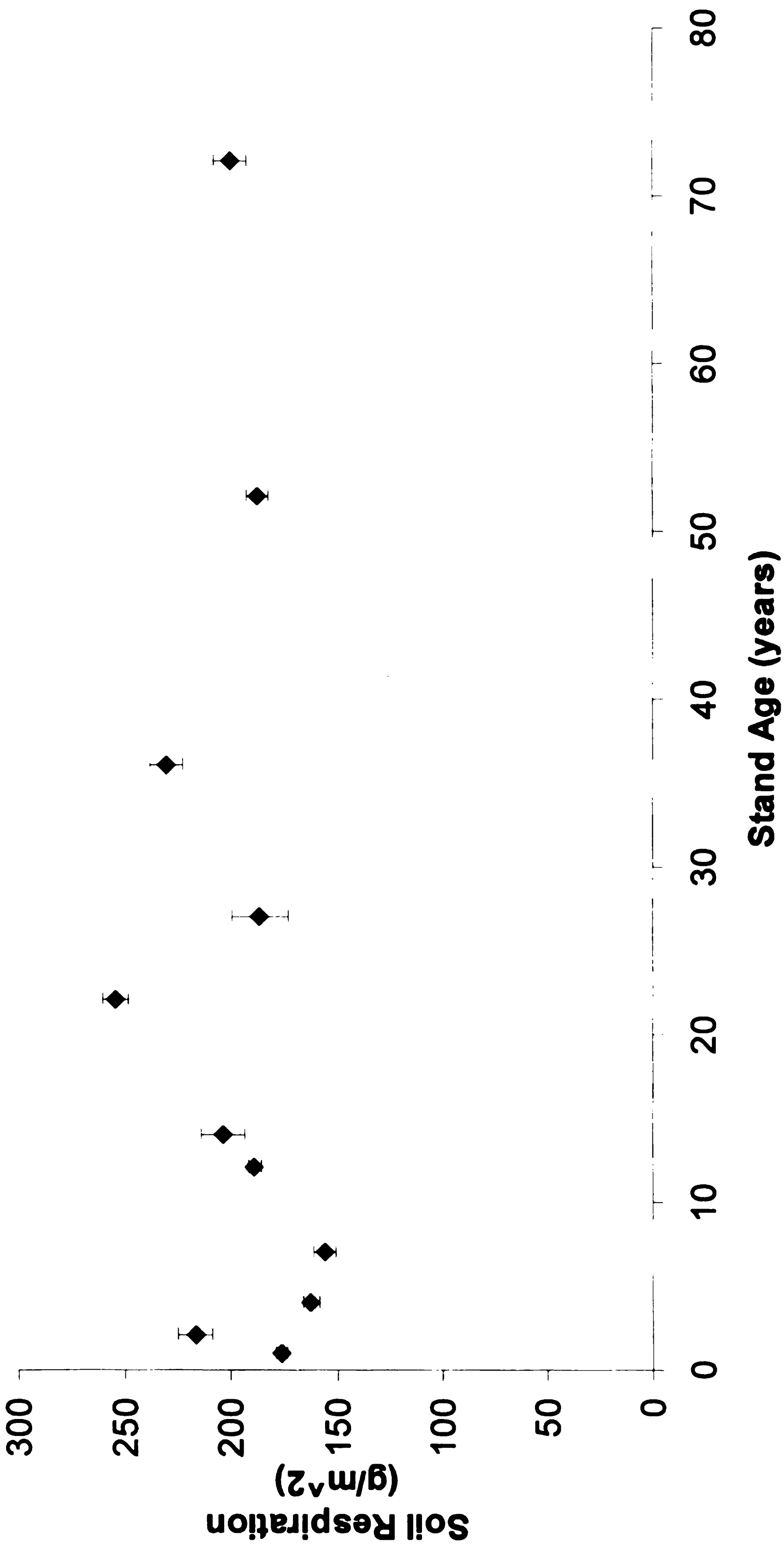


Figure 10. Monthly soil respiration rates as a function of stand age.

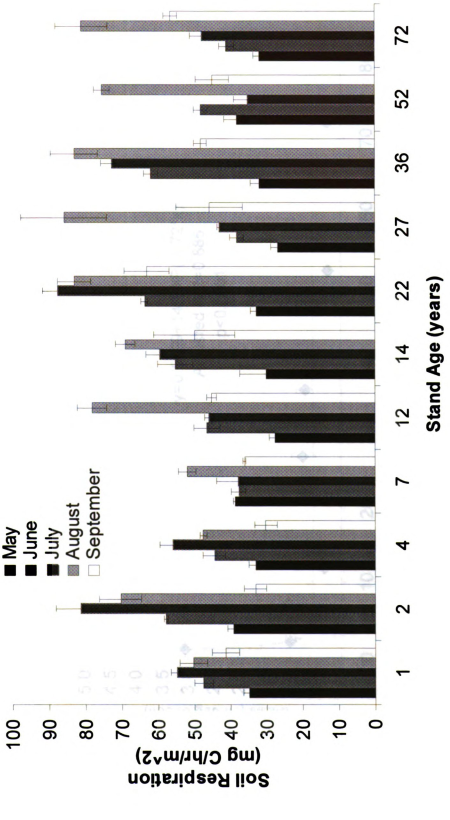


Figure 11. Total exchangeable bases as a function of stand age.

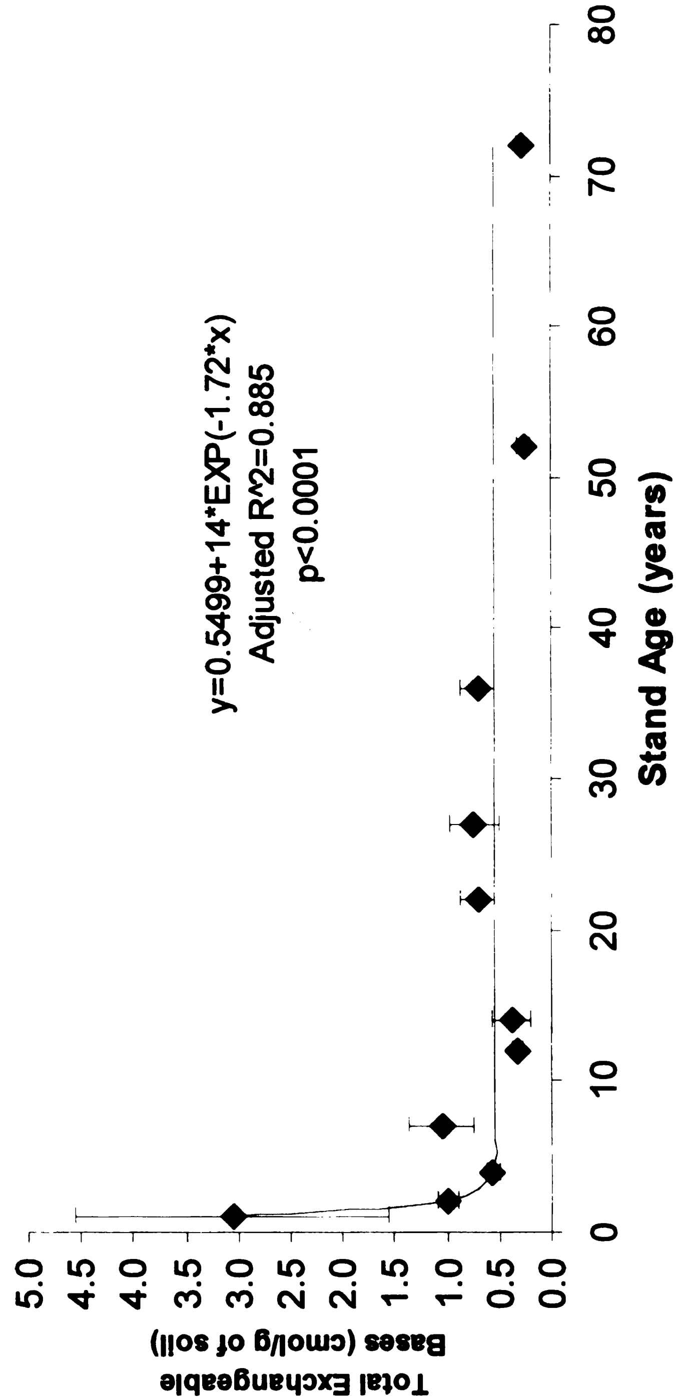
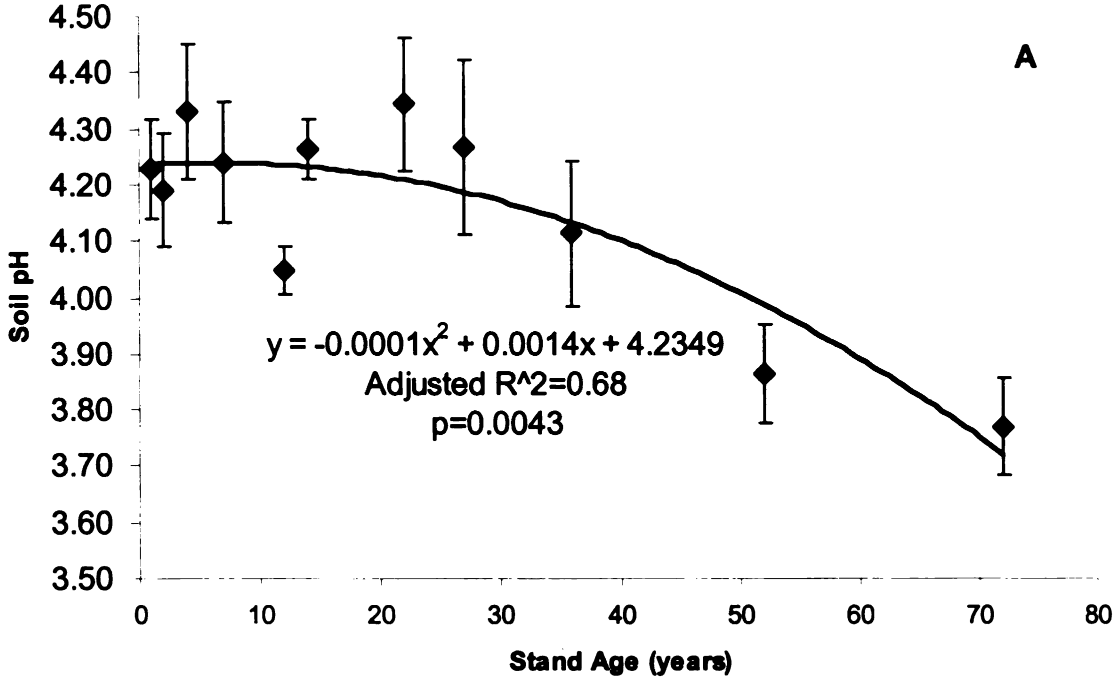


Figure 12. Soil (A) and forest floor (B) pH as a function of stand age. Errors bars are missing where samples were composited to yield n of 1.



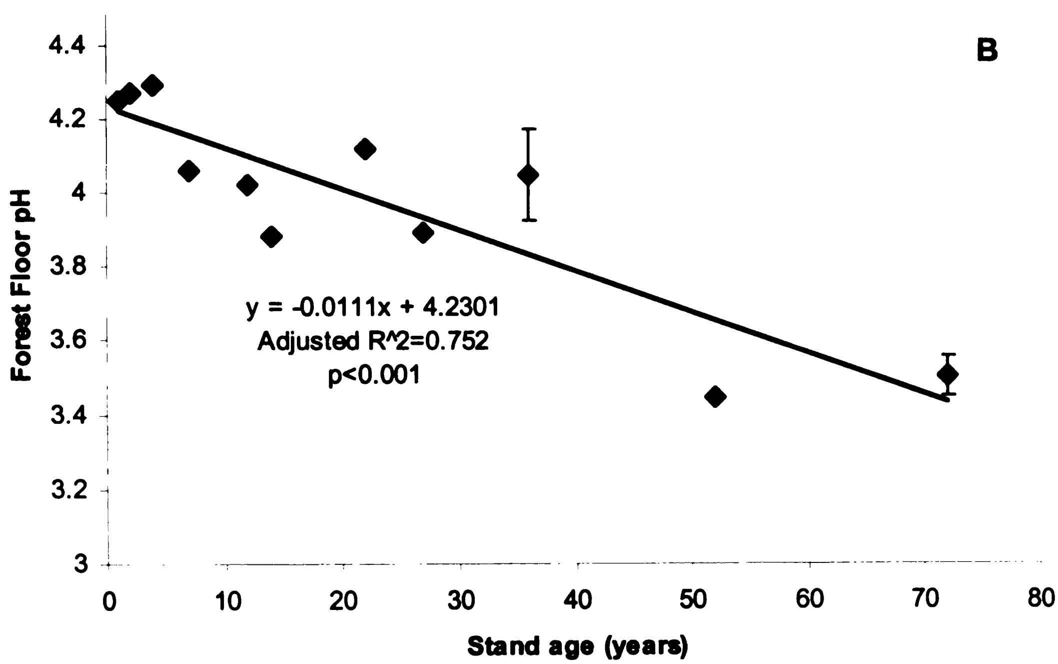


Figure 13. Total number of degree-days in the growing season as a function of stand age.

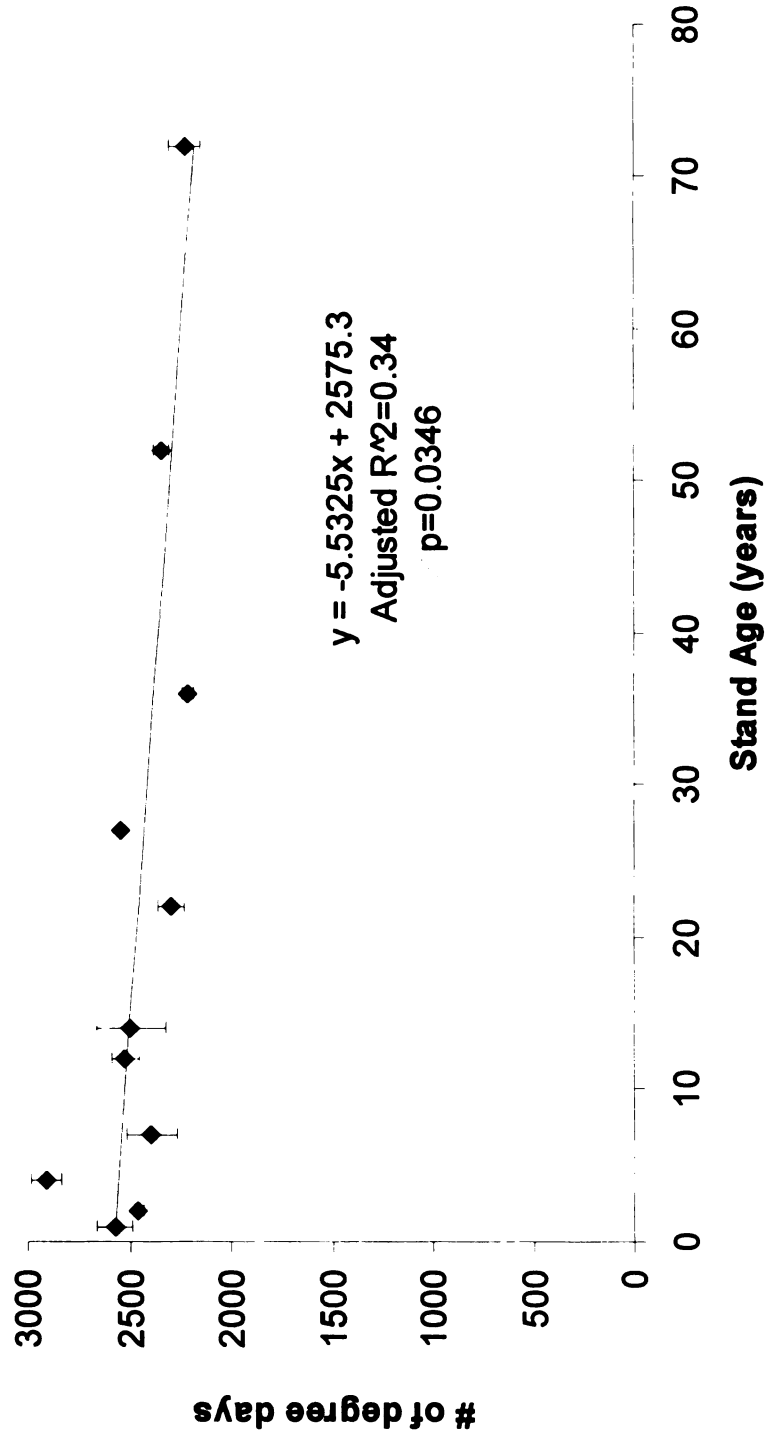


Figure 14. Seasonal gravimetric percent moisture in forest floor (A) and soil (B) as a function of stand age. Errors bars are missing where samples were composited to yield n of 1.

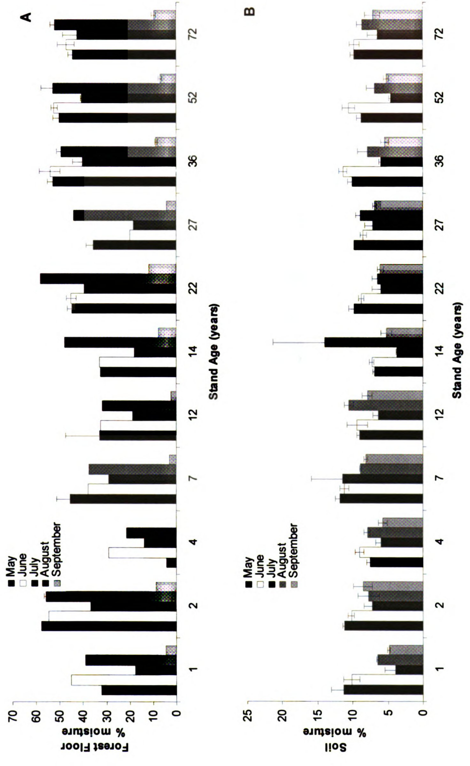


Figure 15. Average moisture tension data at selected stands at 5 different sampling periods. May data were not available for stand age 22. The higher the value, the lower the moisture content.

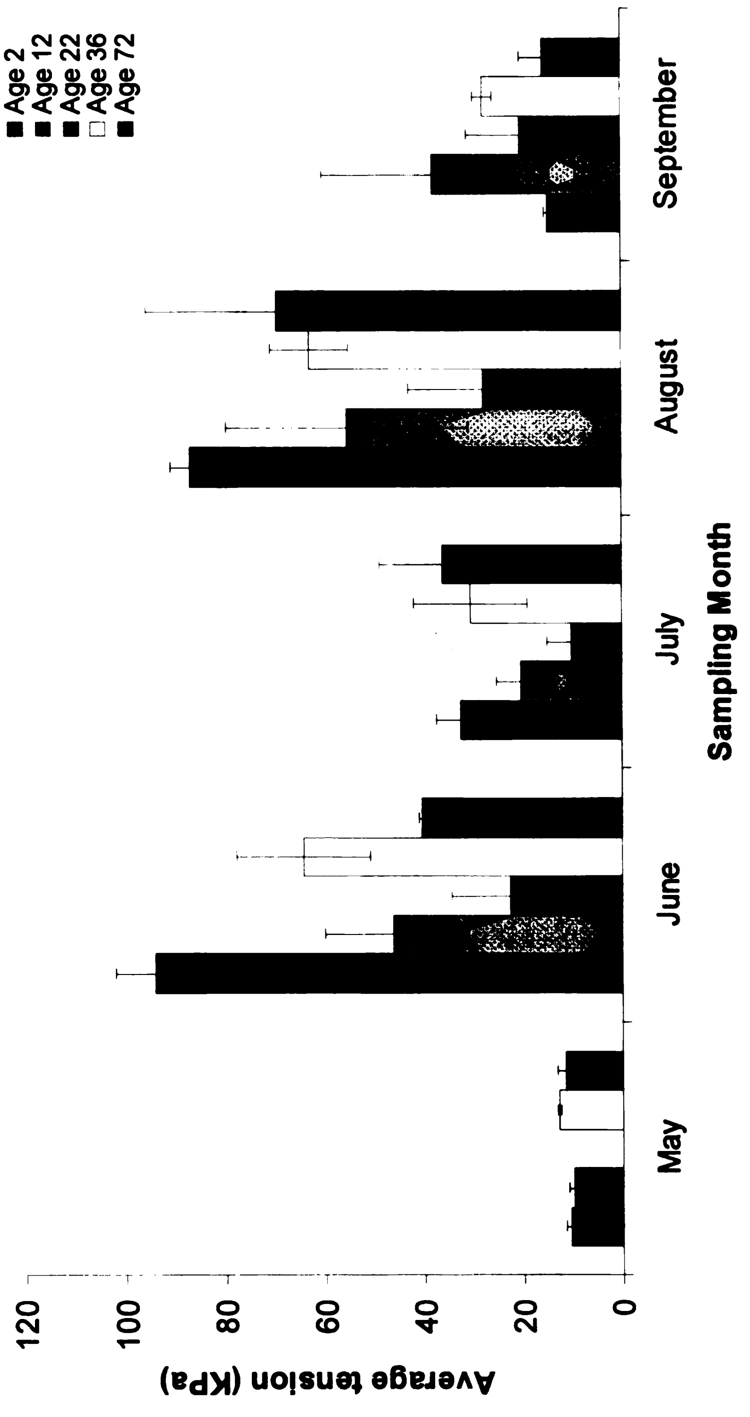


Figure 16. Jack pine biomass as a function of stand age.

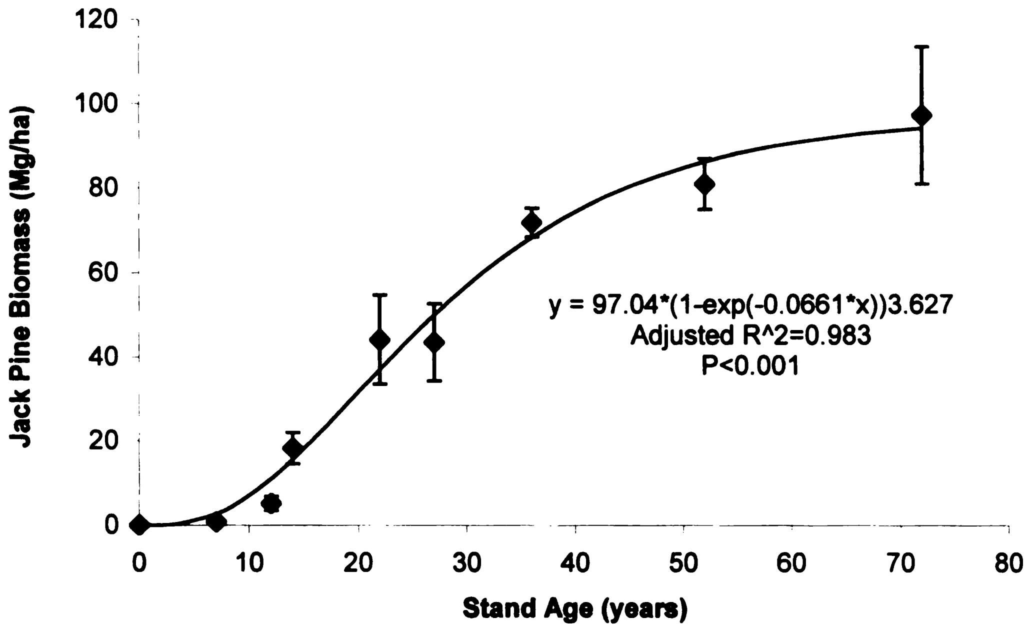


Figure 17. Live understory biomass as a function of stand age.

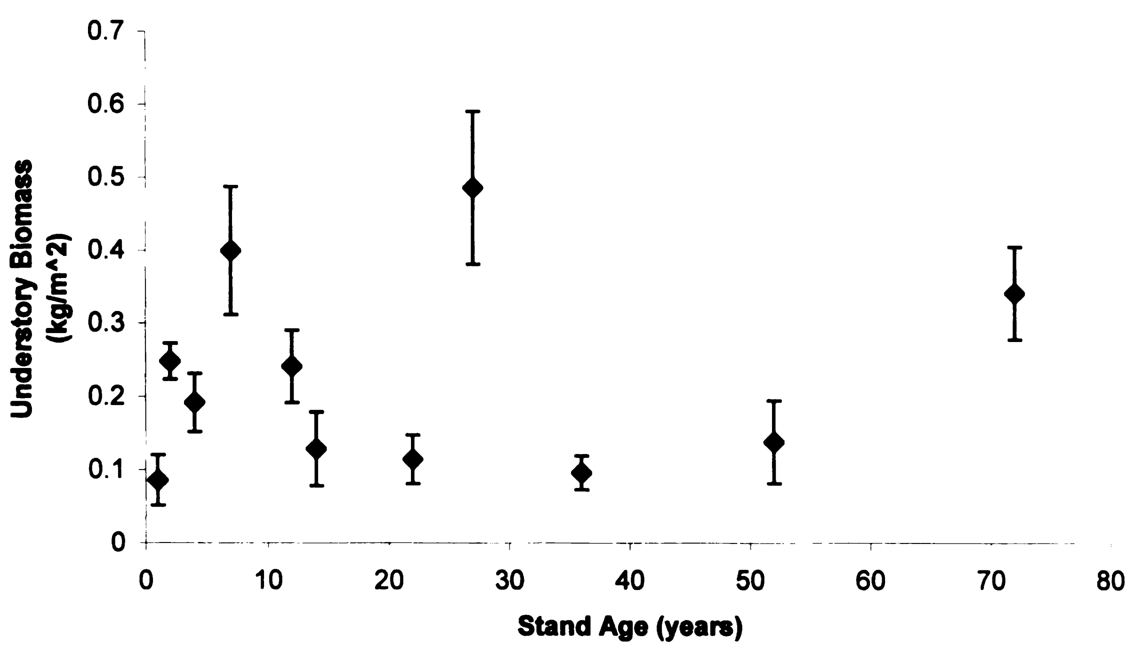


Figure 18. Biomass of selected understory vegetation categories as a function of stand age.

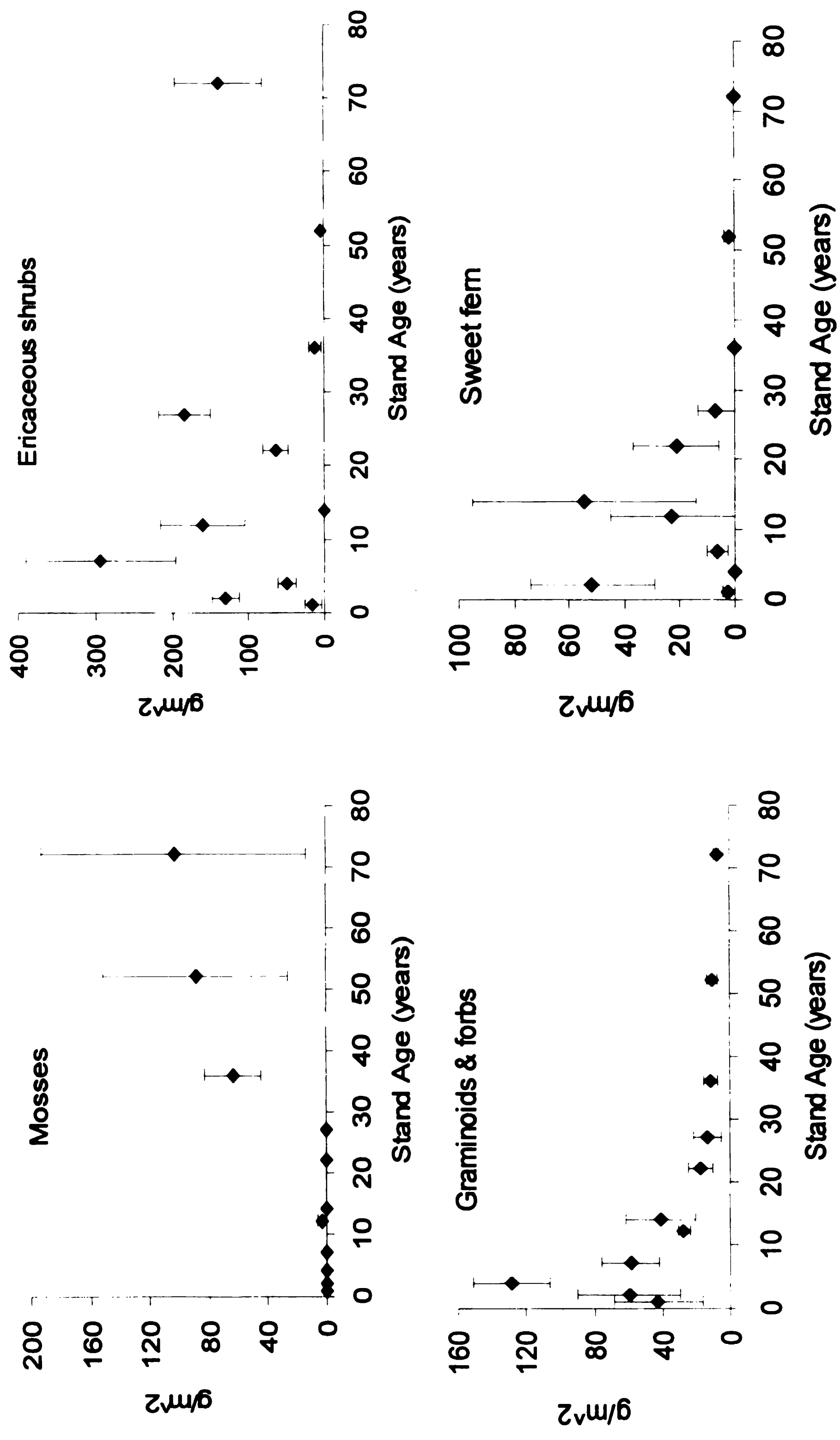


Figure 19. Monthly microbial biomass in the soil as a function of stand age.

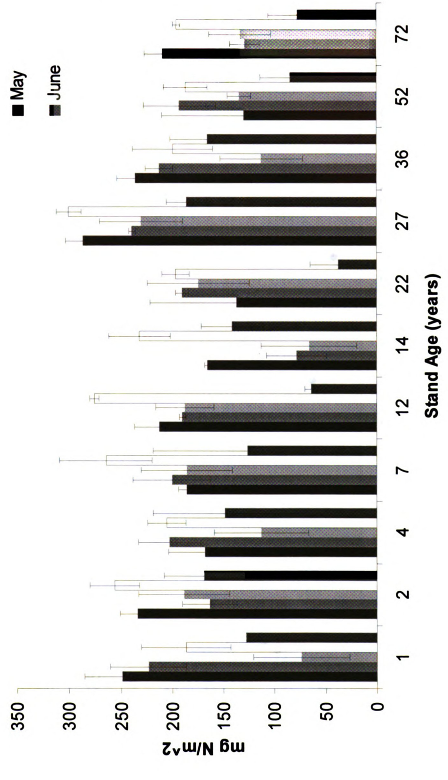


Figure 20. Available phosphorus as a function of stand age.

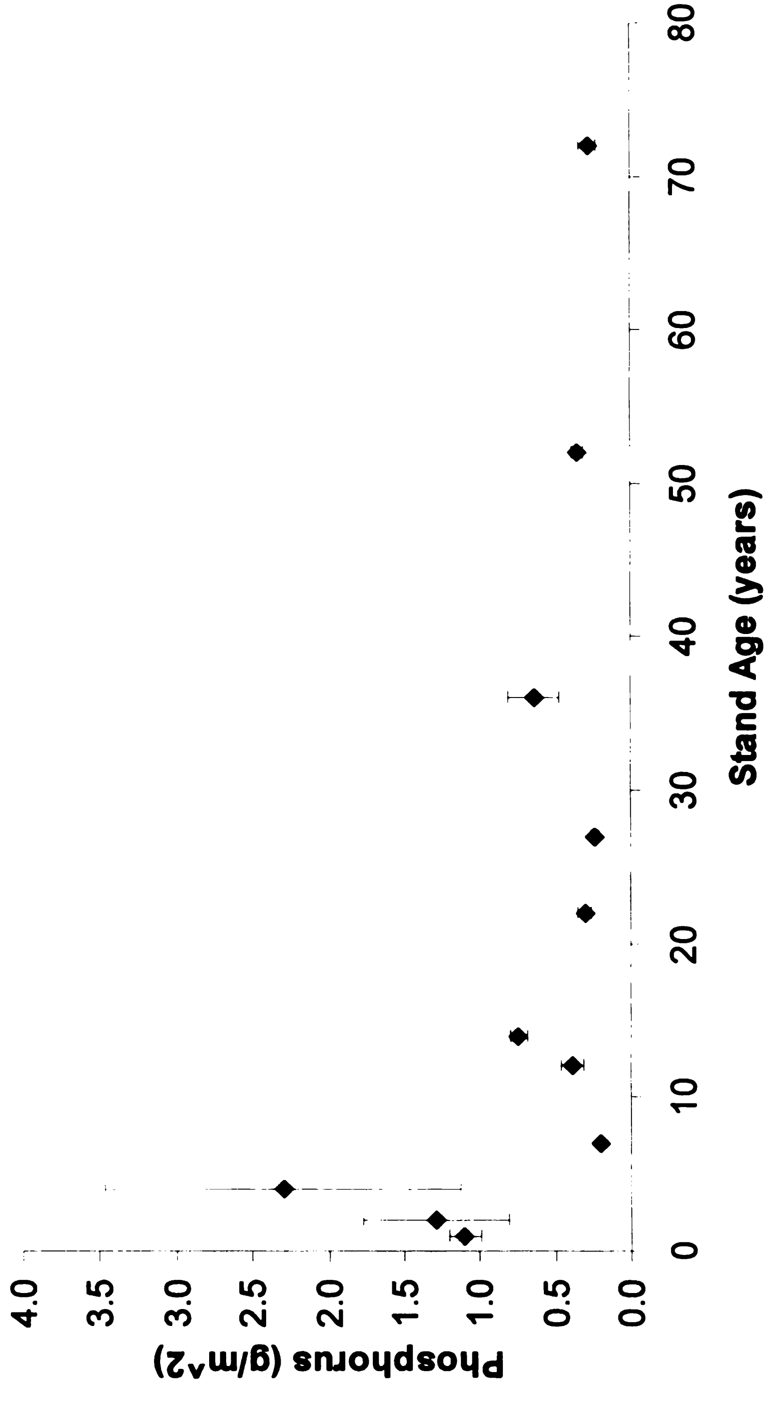


Figure 21. Potential carbon mineralization as a function of temperature for four moisture treatments and four stands.

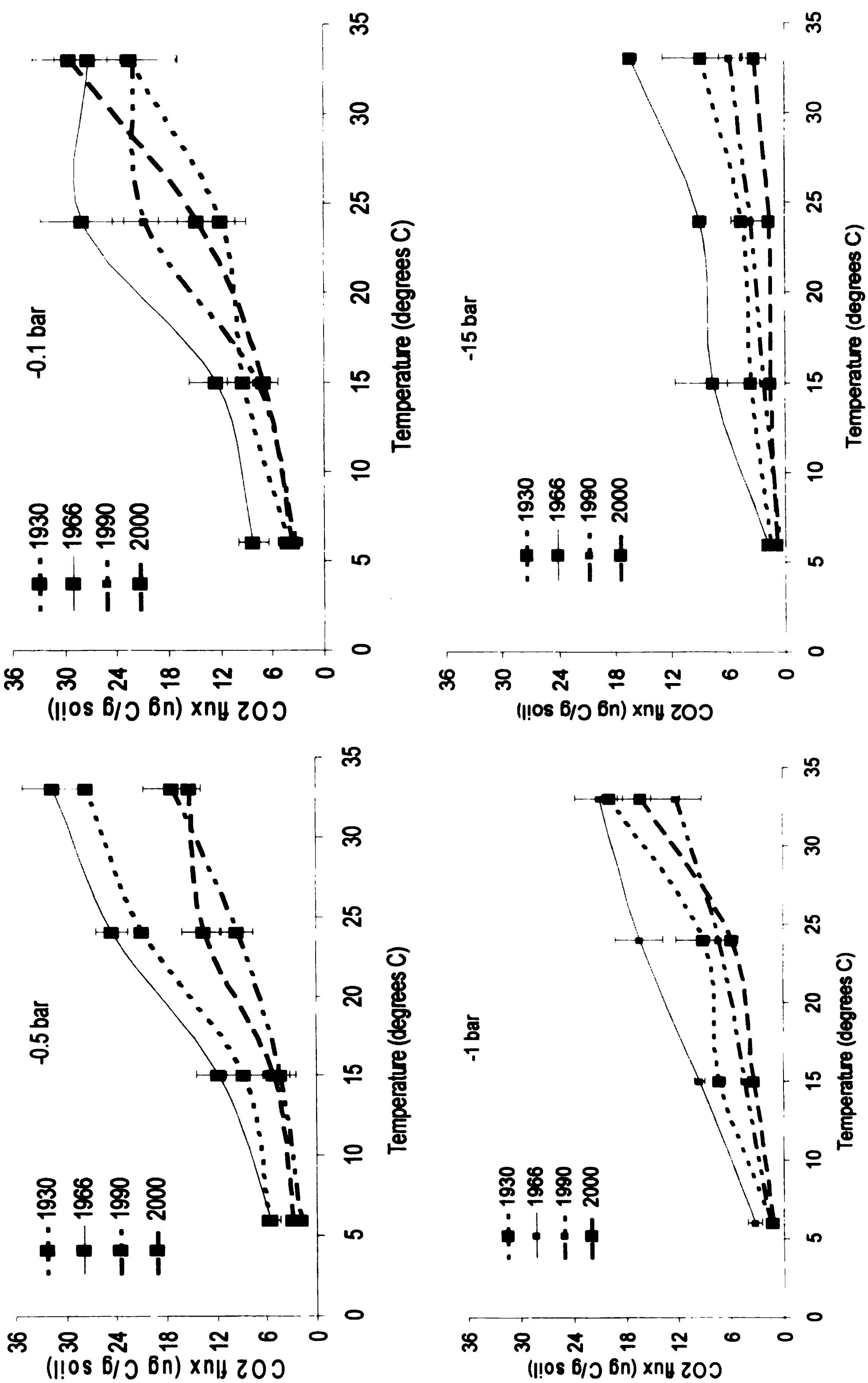


Figure 22. Potential nitrogen mineralization as a function of temperature for four moisture treatments and four stands.

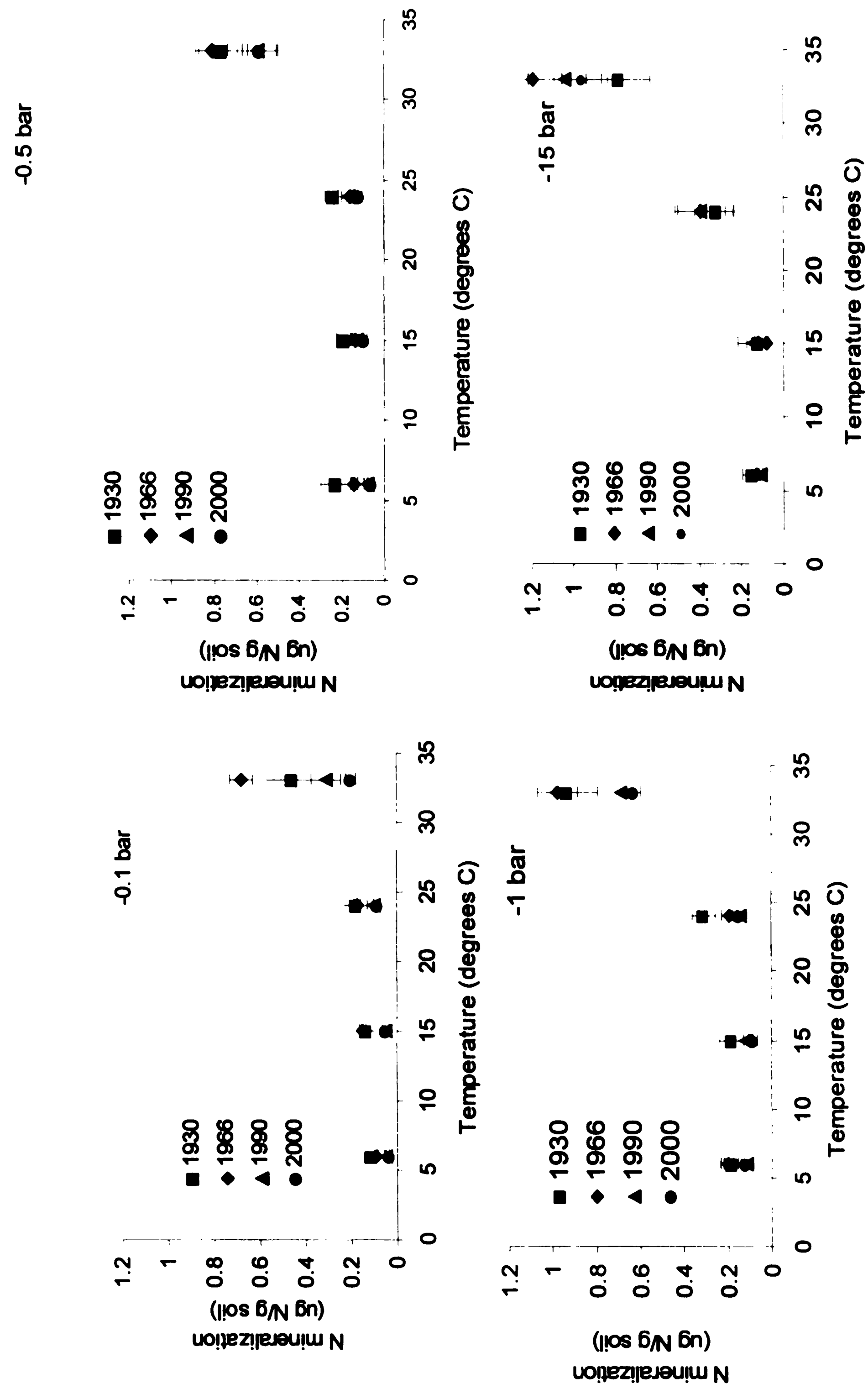
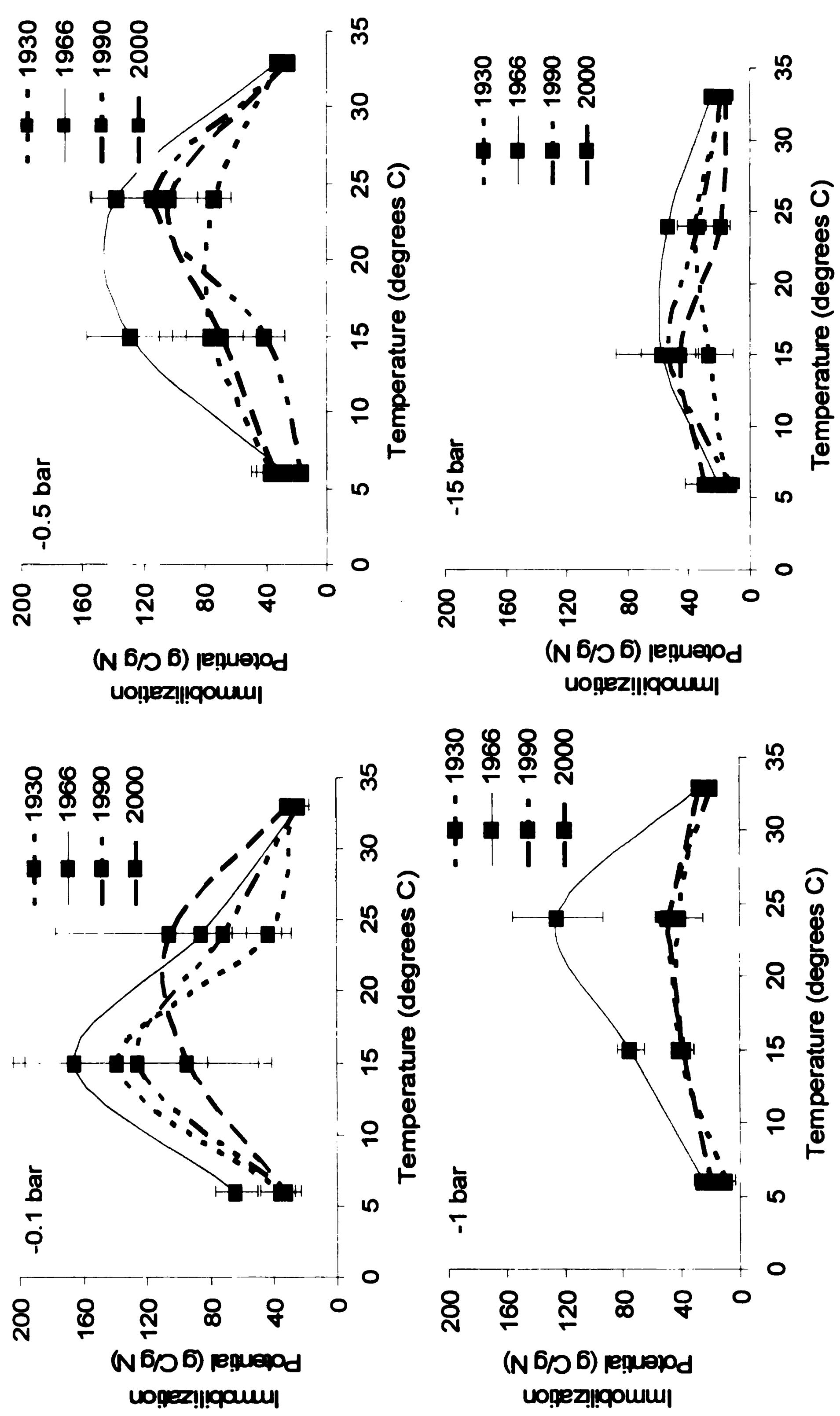


Figure 23. Potential nitrogen immobilization as a function of temperature for four moisture treatments and four stands.



APPENDIX C:

Additional Methods

Microbial Biomass

Soil microbial biomass N was measured five times on mineral and organic soil separately. Soil microbial biomass N was determined using the chloroform fumigation-extraction technique (Beck et al. 1997; Brookes et al. 1985). Two subsamples of the soil cores collected for determination of initial extractable NH_4^+- and NO_3^-- N (see above) were used to measure microbial biomass N. One subsample of 20 g mineral and 5 g organic fresh weight soil was shaken for 1 hour with 50 ml 0.5 M potassium sulfate and then extracted using Whatman #1 filter paper. The second subsample of 20 g mineral and 5 g organic soil was fumigated with chloroform in a desiccator for 5 days followed by extraction with 0.5 M K_2SO_4 (Cabrera and Beare 1993). The extracts were analyzed for total N by persulfate digestion, followed by colorimetric analysis for NO_3^- on the Alpkem Flow Solution IV Auto-Analyzer. Results are presented on an oven dry (105°C for 48 hours) basis.

Understory Composition

Live biomass was sampled and separated into eight different categories: mosses, lichens, ericaceous shrubs (primarily *Vaccinium* spp.), sand cherry (*Prunus pumila*), graminoids and forbs, sweet fern (*Comptonia peregrina*), bracken fern (*Pteridium aquilinum*) and a miscellaneous category. Samples were composited by transect, dried in a forced air convection oven at 55°C, and then weighed.

Phosphorus

Available phosphorus was determined using the Mehlich 3 method (Mehlich 1984). Two grams of air-dry soil was extracted with Mehlich 3 solution (acetic acid, ammonium nitrate nitric acid, ammonium fluoride, ethylenediaminetetraacetic acid). A working solution (ammonium molybdate, antimony, potassium tartrate, sulfuric acid) was added to the filtrate for color development, which was analyzed at a wavelength of 882 nm on a ThermoSpectronic spectrophotometer.

Incubation Experiment

To determine the relative importance of microclimate in driving N and C dynamics of a forest recovering from a wildfire disturbance, I collected soil from 4 jack pine forests of the following ages: 2, 12, 36, 72. Soil was collected in September 2002. I used stratified random design to sample 3 points along each transect. Soil along each transect was composited. I collected soil to a 10-cm depth using a 5.08-cm diameter core. Additional three samples were collected and composited at each stand for an additional replicate. The soils were kept in a cooler for transport and thereafter stored in the refrigerator until processed through a 4 mm sieve within 48 hours. The roots were removed, the soil homogenized by hand and air-dried at room temperature.

I incubated 10-g soil subsamples from each transect in plastic sample cups at 16 different temperature (6°C, 15°C, 24°C and 33°C) and matric potential (-0.1, -0.5, -1 and –15 bars) combinations that encompass field conditions. Prior to the start of the incubation, I used a ceramic-membrane pressure extractor (Soil Moisture Corp., Santa Barbara, CA) to determine the volumetric moisture content of the soils samples that correspond to the matric potentials used in the study. I adjusted each sample gravimetrically to the desired matric potential by misting the soil with deionized water and then mixing the soil to evenly distribute moisture.

The soil samples were then placed into 924-mL glass Mason jars sealed with lids containing rubber septa for gas sampling. The jars were then placed in incubators and maintained at the different temperature treatments. Carbon dioxide evolution was measured 9, 19 and 26 days after the start of the incubation using a Tracor 540 gas chromatograph (Tracor Instrument, Austin, TX). Soil moisture was adjusted gravimetrically after each gas sampling. Carbon flux was determined as the cumulative CO_2 divided by days of incubation per gram of soil.

To measure potential N mineralization, I extracted a 10-g fresh weight subsample of each soil at the start of the incubation and each incubated soil sample at the end of the incubation. The samples were shaken with 50 mL of 2 M potassium chloride (KCL) for 1 hour to extract NH_4^+- and NO_3^-- N. The extracts were poured through Whatman #2 filter paper and stored frozen until analysis for inorganic nitrogen using the Alpkem Flow Solution IV Auto-Analyzer. An additional soil subsample was used to determine gravimetric soil moisture. Potential N mineralization rates were calculated on an oven-dry (105°C for 48 hours) mass basis as soil increase in inorganic NH_4^+- and NO_3^-- N over the incubation period. Carbon and nitrogen content was determined on an additional subsample of the soil. Carbon and nitrogen content was determined on air-dry ground samples and analyzed on the Carlo Erba CN analyzer. Percent C and % N results are expressed on a 105°C oven-dry soil mass basis.

The effect of stand age, soil moisture and soil temperature on potential and relative N and C mineralization, as well as N immobilization was analyzed using three-way analysis of variance. Potential and relative nitrogen mineralization, and N immobilization data were ln-transformed, whereas potential and relative C mineralization data were transformed using square root to normalize the data. Significance was accepted at minimum alpha of 0.05. All analyses were analyzed with statistical package SYSTAT (SPSS, Inc.)

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