NITROGEN AND PHOSPHORUS AVAILABILITY IN EASTERN MANTIOBA BLACK SPRUCE BOG ECOSYSTEMS 10 YEARS AFTER CLEARCUT LOGGING AND WILDFIRE

BY

DEREK EBNER

A Thesis
Submitted to the Faculty of Graduate Studies
in Partial Fulfilment of the Requirements
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ABSTRACT

Ebner, Derek Lyndon. M.Sc., The University of Manitoba, February, 1999. Nitrogen and Phosphorus Availability in Eastern Manitoba Black Spruce Bog Ecosystems 10 Years After Clearcut Logging and Wildfire. Major Professor; Lesley G. Fuller.

Recent interest by the forestry industry in establishing clearcut logging practices which emulate the effect of natural disturbances, such as wildfire on site productivity, has sparked an increase in comparative studies between anthropogenic and natural disturbances. The objectives of this study were to determine nitrogen and phosphorus availability differences after 10 years between black spruce bog ecosystems affected by either clearcut logging or natural wildfires. This was accomplished by focusing on: 1) differences in the spatial heterogeneity of inorganic N and P concentrations; 2) spatial heterogeneity of nitrogen mineralisation; 3) peat substrate quality differences; and 4) relationships between peat substrate quality and net N/P mineralisation.

Three-way analysis of variance, incorporating spatial factors, exhibited significant differences in inorganic N concentrations between disturbance types with mature stands greater than clearcut sites and burn sites. There were no significant differences in P concentrations between disturbance types. N exhibited microrelief differences (hollow > hummock) while P exhibited depth differences (0-15 > 15-30 cm.

A two month *in situ* incubation was performed to measure net nitrogen mineralisation. Overall, net nitrogen mineralisation rates were not significantly different between disturbance types. Similarities between clearcut and burn sites were unexpected due to the generally colder and wetter conditions within burn sites. Nitrogen mineralisation exhibited microrelief (hummock > hollow) and depth differences (0-15 > 15-30 cm). Favourable soil temperature and moisture regimes and/or higher substrate availability (e.g. labile carbon) likely caused the spatial differences.

Carbon fraction analysis indicated that disturbance types differed with respect to various substrate quality parameters. Labile carbon fractions (water-soluble carbohydrates) and to a lesser degree, recalcitrant carbon fractions (lignin), best discriminated between disturbance types due to the presence of *Pleurozium schreberi* within mature stands. Substrate quality differences between clearcuts and burns could be related to site factors, such as soil temperature and moisture, or to the intrinsic litter quality of *Sphagnum* species which affect microbial activity and peat decay.

Nitrogen and phosphorus mineralisation rates, determined by a 28-day aerobic incubation, were not well predicted by substrate quality parameters. N mineralisation (negative indicating net immobilisation) was not significantly different between clearcuts and burns nor was substrate quality. N mineralisation in burns was best predicted by N content, whereas in clearcuts recalcitrant carbon fractions were significant in predicting N mineralisation. Similar N mineralisation rates and contrasting site conditions and peat substrate quality between clearcut and burn sites indicate that these disturbance types affect N availability differently. However, examination of black spruce productivity and nutrient uptake is necessary to determine long-term differences. Overall, conclusions pertaining to forest sustainability are not possible since trends could be explained by

either the high degree of variance between sites due to poor site matching or actual "treatment" effects.

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FOREWARD

The following thesis was prepared using the manuscript format outlined in the Guide to Thesis Preparation for Graduate Students in the Department of Soil Science. Two of the three manuscripts (Chapters 4 and 5) will be submitted for publication in the Canadian Journal of Soil Science.

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1. INTRODUCTION

The forestry industry has become increasingly interested in establishing clearcut logging practices which emulate the effect of natural disturbances, such as wildfire on site productivity. Site productivity refers to the potential of a site (e.g. a specific forest ecosystem as defined by its physical and biological characteristics) to grow a particular tree species (Taylor et al. 1995). Accordingly, site productivity is determined by climate, availability of site resources (e.g. light, soil moisture and nutrients) and also competition for these resources between commercial and non-commercial plants and microorganisms. Therefore, quantification and qualification of soil properties is essential in determining the impact of disturbance on forest ecosystems. Recognition of the importance of soil in forested ecosystems must be included in the development of ecosystem-based management strategies if sustainable forestry is to be achieved.

Within boreal forested peatlands, site productivity is constrained by low soil temperatures, high moisture and low availability of essential nutrients (Bonan and Shugart 1989; Brumelis and Carleton 1989). Within ombrotrophic bogs (poor minerotrophic peatlands), availability of essential nutrients, particularly nitrogen and phosphorus, are severely limited by both low inputs (e.g. in precipitation; Small 1972a) and slow nutrient turnover due to low biological activity and poor substrate quality (Flanagan and Van Cleve 1983). Nutrient availability for vascular plants is further limited by the sequestration of almost all N and P from atmospheric deposition by the moss layer (Damman 1978; Lee et al. 1986; Malmer 1988). As a result, vascular plants rely on slow decay of aboveground vascular plant litter and nutrient mineralisation in peat as their primary supply of N and P (Damman 1988). Consequently, N and P availability is considered to be one of the main limiting factors affecting black spruce productivity in bogs (Watt and Heinselman 1965).

Measurement and quantification of nutrient availability has always been problematic in forest soils. Factors to which this can be attributed are: (1) high spatial and temporal variability within uncultivated soils; (2) variability in stand requirements over time; and (3) assimilation of nutrients with the aid of mycorrhiza (Mahendrappa et al. 1986). Traditional forest nutrient studies have focused on the availability of inorganic nutrients, such as NH_4^+, NO_3^-, and PO_4^{3-}. NH_4^+ and NO_3^- are the major forms of plant available nitrogen (Binkley and Hart 1989). Consequently, quantities of these ions in soil samples have often been used as an index of N availability. However, most research dealing with nutrient availability in forests has focused on nutrient transformations and their controls. As a result, there are many different methods that try to predict nutrient turnover rates (e.g. Binkley and Hart 1989). The use of nutrient mineralisation rates is important in forest disturbance/recovery studies as mineralisation rates are excellent indicators of forest health and potential productivity. Being a dominantly microbially-mediated process, high degrees of both spatial and temporal variability can make interpretations difficult (Parkin 1993).

In northern bog ecosystems, the use of inorganic pools and mineralisation rates to differentiate between disturbance regimes could have particular significance.

Temperature and aeration control microbial activity (Van Cleve and Alexander 1981) and aeration is also important in affecting solubility of inorganic nutrients (Farnham 1974). Therefore, concentrations of inorganic N and P and mineralisation rates will be determined by temperature and moisture regimes (Avnimelech 1971). These regimes are related to the microrelief patterns within bogs, microhighs (hummocks) vs. microlows (hollows), which, in turn, are characterised by differences in proximity to the water table. With the added effect of disturbance on soil temperature and moisture levels, these within site spatial differences will be important indicators of overall changes caused by disturbance. Disturbance can adversely affect substrate factors which play an integral role in N and P turnover, such as stage of decomposition (Williams and Wheatley 1988) and nutrient content of the peat (Farrish and Grigal 1988). Understanding how disturbance regimes alter environmental and substrate factors is vital in estimating the availability of major nutrients within wetlands.

The effects of disturbance on nutrient availability in forest soils has gained much attention over the years. However, most of the research has focused on upland, mineral soils and has been restricted to short time periods immediately following the disturbance. The lack of research comparing the effects of wildfire and clearcut logging on forest soils is the main reason for this study. The objectives of this study were to determine nitrogen and phosphorus availability differences between black spruce bog ecosystems 10 years after they were affected by either clearcut logging or natural wildfires. This information is important in the generation of an ecosystem-based management strategy for the black spruce bog ecosystem.

2. LITERATURE REVIEW

2.1 Peatland Classification

Wetlands makeup a significant area of land in the northern hemisphere. In Canada, wetlands occupy approximately 127.2 million ha, or about 14% of the country (Zoltai 1988). Of this area, 111.3 million ha are defined as peatlands.

Wetlands are classified as areas where wet soils are prevalent, having a water table at or above the soil surface for most of the thawed season, while supporting hydrophilic vegetation (Zoltai and Pollett 1983). Peatlands, or mires, are wetland ecosystems characterised by the accumulation of organic matter, which is produced and deposited at a greater rate than it is decomposed, leading to the formation of peat (Gore 1983). By definition, peat is material that contains 30% or more organic matter (Soil Classification Working Group 1998).

With differences in site characteristics, northern peatlands, forested or not, are subdivided into two major categories, bogs and fens. According to Zoltai (1988), bogs are peatlands with the water table generally at or near the surface. In addition, the bog surface, which may be raised or level with the surrounding terrain, is virtually unaffected by the nutrient-rich groundwater from surrounding mineral soils and is generally acid and low in nutrients. Consequently, precipitation is the only input of nutrients into the site (termed ombrotrophy) (Heinselman 1970). Peat within bogs is generally dominated by *Sphagnum* moss (Mitsch and Gosselink 1993). Fens are peatlands with the water table usually at or just above the surface (Zoltai 1988). The waters are mainly nutrient-rich and minerotrophic from mineral soils. Fens are slightly to strongly more alkaline compared to bogs (pH < 4 for bogs compared to up to 7 in fens).

2.2 Bog Development

2.2.1 Peat Accumulation and Bog Formation

The characteristic feature of bogs is the large accumulation of peat. Most peats accumulate as a result of waterlogging (Clymo 1991). Waterlogging is a consequence of a net positive water balance, precipitation plus water inflow greater than evaporation plus runoff (Mitsch and Gosselink 1993) into the system. This is conditional on having a physiography or climate that is conducive to slow water movement (Verry 1988). Suitable physiography include flat areas such as glacial lake beds or depressional areas with no or limited outflow such as ice block depressions, or bedrock-controlled basins.

The process of waterlogging coincides with the decay and build-up of plant debris. As dead plant material is continually added to the peat surface, mass is lost (Clymo 1984). During the initial stage of plant decomposition, water is able to flow easily between the structural components of the plant material resulting in partial saturation (Clymo 1991). Continued decay causes the main structural elements within plant matter to lose their structural integrity and finally collapse. The macrostructural collapse of the vegetation results in a decrease in the number and size of pores in the peat (Boelter 1969), lowering the hydraulic conductivity (Boelter 1965). As a result, vertical water movement is almost negligible in dense peat, resulting in a heightened water table (compared to surroundings) as long as precipitation exceeds evapotranspiration (Ingram 1982). The water table level will remain in the upper zone of high hydraulic conductivity resulting in additional water to seep away laterally (Clymo 1991), possibly to other water bodies (e.g. lakes). The final result is a system that has a zone of saturated, and consequently slowly decaying, plant material below a zone of high plant production. Overall, the interactions between plant productivity, decay and hydrology are the main factors influencing peat accumulation.

Given the conditions of water surplus and peat accumulation, bogs develop through variations of two processes, terrestrialization or paludification. Terrestrialization is the classical model of mire formation. In terrestrialization, the direction of mire succession is from aquatic (i.e. shallow lake) towards terrestrial systems (Kangas 1990). Through drying energies (sediment build-up, evapotranspiration, drainage), the small lake progresses toward the climax state of a mesic forest. These mires are usually small and surrounded by mineral uplands (Grigal 1991). Inputs from uplands are confined to the periphery of the bog due to the slow hydraulic conductivity through peat (Ingram 1983).

Paludification, also called "swamping" (Heinselman 1963), refers to the conversion of a dry mineral soil site to a mire due to a rise in the groundwater table (Paavilainen and Päivänen 1995). The encroaching *Sphagnum* mosses and peat act as a water holding reservoir. The water stagnates and oxygen content decreases resulting in death or stunting of trees and accumulation of peat (Paavilainen and Päivänen 1995). Eventually, build-up of *Sphagnum* peat will give rise to a domed surface that rises above its surrounding ("raised bog") (Grigal 1991).

In both cases, ombrotrophic (nutrient poor) conditions are prevalent. After peat accumulates above the water table, isolating the *Sphagnum*-dominated bog flora from their nutrient supply, the bog becomes increasingly nutrient deficient (Mitsch and Gosselink 1993). Nutrients received into the site are from dry and wet deposition (precipitation). The amount and availability of these nutrients is in turn controlled by the chemical-physical-biological interactions of bog ecosystems.

2.2.2 Decay and Its Controls in Bogs

2.2.2.1 Peat Layer Differentiation in Bogs The characteristic slow decay and build-up of peat are the defining features of peatlands. To understand the process of decay, it is important to first discuss the two functional layers (as related to availability of oxygen) that make-up peat-forming systems: an upper 10-50 cm deep aerobic zone of high hydraulic conductivity with a relatively high rate of decay, the acrotelm, and a thicker, usually anaerobic, lower layer, the catotelm, of low conductivity and with a much lower rate of decay (Clymo 1984). With increasing decomposition, plant material at the base of the acrotelm will lose structure coinciding with a decrease in hydraulic conductivity. Continued precipitation will cause a rise in the water table to this level of slow conductivity, resulting in the decayed plant material at the base of the acrotelm to be engulfed. The rate of peat accumulation is not dependent on plant production as much as it is dependent on the amount of material added to the catotelm, which in turn is a reflection of the amount of material left after decay in the aerobic acrotelm. Once peat material enters the catotelm, the structure and chemistry of the peat changes little (Damman 1978), because of very slow decay (Clymo 1984) and negligible water movement (Ingram 1983). Thus, conditions during decay in the acrotelm should be reflected in the bulk density and the C/N ratio of the peat in the catotelm (Damman 1978).

Three morphological soil layers representing different stages of decay that are analogous to L, F, and H organic layers of mineral soils have also been recognised in bogs (Malmer and Holm 1984). The first, the "living moss layer" (Malmer and Holm 1984), consists of the living mosses and their newly formed litter. Carbon fixation and nutrient uptake are characteristic of this uppermost 3-5 cm (Malmer 1988). The second layer, the "litter peat layer" (Malmer and Holm 1984), is only weakly humified and has a loose structure and increasing bulk density with depth (Johnson et al. 1990). Depth of this layer in hummocks can be over 30 cm, while less than 10 cm in hollows. The third and deepest layer, the "peat layer" (Malmer and Holm 1984), is much more compact and has a higher bulk density as it is more humified and decomposed. With reference to the acrotelm and catotelm, the acrotelm contains the "living moss" and "litter peat" layers and may include some of the "peat layer" (Johnson and Damman 1993).

2.2.2.2 *Sphagnum* Decay Incomplete decay of plant litter in ombrotrophic bogs has been described as the main reason for the formation of peat (Malmer et al. 1997). In ombrotrophic bogs most of the plant litter is formed by *Sphagnum* mosses and the belowground parts of vascular vegetation which are deposited a few cm below the surface at the litter deposition level (the LDL; Malmer and Wallén 1993) which forms the limit between the moss layer and the litter layer below (Malmer 1988). Below this level the decay rate in the peat is relatively high although decreasing with depth (Hogg 1993; Johnson and Damman 1993). The distinct decrease in the decay rate where the aerobic acrotelm meets the permanently anaerobic catotelm (Ingram 1978) corresponds to the decay decrease level (the DDL; Malmer and Wallén 1993).

The nature of *Sphagnum* decay has been recently cited as an important regulator of peat growth and subsequent formation of the unique peatland microtopography (Johnson and Damman 1991; Johnson and Damman 1993). This is shown by comparing the decay of various hummock and hollow *Sphagnum* species. Several studies have shown that the decay of *Sphagnum* species occupying dry bog hummocks is slower that those that grow in wet hollows (Bartsch and Moore, 1985; Rochefort et al. 1990; Johnson and Damman 1991; Belyea 1996). Hollow species such as *Sphagnum cuspidatum and S. angustifolium* lose mass at about twice the rate of the hummock species *S. fuscum*, even though conditions for decay are less favourable in hollows (Johnson and Damman 1993). This difference in inherent decay properties of *Sphagnum* species may control the microtopography of the bog surface (Johnson and Damman 1993). The slower decaying hummock species allow for a more rapid build-up of peat above the water table, thus, giving rise to hummocks (Johnson and Damman 1991). Conversely, species in hollows decay faster not allowing for any significant peat build-up above the water table.

There is one important factor that could explain the differences in *Sphagnum* decay, intrinsic litter quality. In fact, the differences in intrinsic litter quality between different *Sphagnum* species are believed to overrule habitat factors in peatlands in regulating decay rates (Johnson and Damman 1993). The intrinsic properties of *Sphagnum* that result in slow decay include: (1) an unusually low concentration of inorganic nutrients in *Sphagnum* litter, which can limit activity in nutrient-deficient bog ecosystems; (2) the abundance of compounds in *Sphagnum* peat, such as phenolic compounds, which inhibit microbial activity; and (3) the abundance of compounds, such as waxes and lignin-like substances, which resist microbial breakdown (Waksman and Stevens 1929; Johnson and Damman 1993).

Sphagnum plants generally contain low concentrations of inorganic nutrients in their tissues (Damman 1978; Malmer 1988). In nutrient-deficient ecosystems, such as ombrotrophic bogs, the low concentration of nutrients within plant materials may limit microbial activity (Martin and Holding 1978). However, the exact role of inorganic nutrients, such as nitrogen and phosphorus, in regulating decay remains to be shown. Studies using amendments of inorganic nutrients, usually in the form of fertilisers, have been inconclusive (Clymo 1965; Coulsen and Butterfield 1978; Rochefort et al. 1990).

Decay of *Sphagnum* peat may be reduced by the presence of compounds which inhibit microbial degradation (Kalviäinen and Karunen 1984). Inhibitory effects have been associated with the occurrence of phenolic compounds. In peatlands, p-hydroxybenzoic acid, a phenolic acid, was believed to have bacteriostatic and fungiostatic properties (Painter 1991). Painter (1991) showed that phenols extracted from fresh moss and peat were not significantly toxic to microorganisms. Tannin, another important phenolic compound important in controlling decay rates in vascular plant litter (Benoit and Starkey 1968; Meentemeyer 1978; Zucker 1983), is not found in *Sphagnum* (Johnson and Damman 1993). In addition, *Sphagnum* does not contain proanthocyanidin (Bendz et al.

1966), the components of condensed tannins which inhibit microbial activity (Zucker 1983). However, it has been shown that sphagnan, a polyuronic acid found in *Sphagnum*, may act as a tanning agent (Painter 1991). Sphagnan may act to inhibit microbial activity by interfering with microbial exoenzymes and by sequestering essential nutrients. Recently, Johnson and Damman (1993) determined that there is a significant negative correlation between polyuronic acid content and mass loss, even though the cause-effect relationship still needs to determined. This is important since polyuronic acids act as the cation-exchanger in the cell wall of *Sphagnum* (Theander 1954; Clymo 1963; Painter and Sørenson 1978) and comprises up to 30% dry weight of the plant (Clymo 1963; Spearing 1972).

Sphagnum contains a high proportion of decay-resistant compounds, such hemicelluloses and lignin-like compounds, that also contribute to its slow decay (Johnson and Damman 1993). Lignin content is an important regulator of plant litter decomposition (Meentemeyer 1978), although *Sphagnum* does not contain true lignin (Erickson and Miksche 1974). The removal of "lignin" and hemicelluloses from *Sphagnum* have been reported to cause a three times increase in CO_2 release compared to *Sphagnum* containing these compounds (Waksman and Purvis 1932). Other decay-resistant compounds, such as waxes and lipids, are also found in *Sphagnum* (Johnson and Damman 1993). The decrease in decay with depth, while a reflection of anoxic conditions, has also been shown to be the result of an accumulation of recalcitrant compounds with depth and age of the peat (Johnson and Damman 1993). With decomposition, the more readily-decomposable compounds (labile) such as sugars and carbohydrates are the first to disappear (Melillo et al. 1989). This results in an increase in the proportion of decay-resistant compounds. Johnson and Damman (1993) later showed through amendment studies that the lack of a readily available carbon source, not nutrients, limits decay with depth in bogs.

2.3 Nitrogen and Phosphorus Availability in Ombrotrophic Bogs

Availability of nitrogen and phosphorus are considered one of the main limiting factors affecting black spruce productivity in bogs (Watt and Heinselman 1965). Poor productivity of bog vegetation is attributed to low concentrations of N and P in foliage (Small 1972a). Factors that result in low foliar concentrations are: (*i*) low supply from slow mineralisation and low inputs (via precipitation), (*ii*) lower requirement of N and P by bog vegetation or (*iii*) adaptive plant responses to low availability. This review will focus on the concept that nutrient availability within peat controls plant productivity of ombrotrophic bogs. Consequently, this review will deal with N and P distribution and transformations within peat bogs as they relate to plant-availability. Unfortunately, discussion of P trends is severely limited by the lack of research dealing with P transformations and availability within ombrotrophic peat.

2.3.1 Nutrient Composition and Distribution in Ombrotrophic Bogs

Ombrotrophic bogs are among the most nutrient deficient ecosystems in the world (Damman 1986). The inorganic constituents of peat are often an important indicator of its nutritive value for plant growth (Stanek 1975). However, the chemical composition and element distribution within ombrotrophic peat vary spatially and temporally. Consequently, there are many factors that affect the chemistry of peat.

2.3.1.1 Processes Affecting the Chemical Composition of Peat There are several processes which affect the inorganic composition of peat. These include; 1) initial concentration in the plant or in the bog water; 2) decay and loss as gas of peat organic matter; 3) relocation of inorganic constituents by physiochemical processes (diffusion and mass flow); and 4) relocation of inorganic constituents by biological processes (e.g. movement from roots to shoots in plants) (Clymo 1983). Damman (1978) concluded that the elemental composition of peat is not affected by the floristic composition of the peat but, in the case of ombrotrophic bogs, depends on the position of the peat with respect to the water table. Various elements increase in concentration towards the water table (e.g. Fe and Al) while others decrease (e.g. K and Na). At the zone of water table fluctuation, some elements (e.g. N, P, Fe, Al, Zn, and Pb) tend to increase in concentration. Consequently, at the peat surface there will be a relationship between elemental composition of the *Sphagnum* and the floristic composition of the vegetation because both are controlled by hydrology. However, once the material is incorporated into the peat, the translocation and accumulation of elements depends solely on the water level.

On the whole, the element concentration in bog vegetation reflects the total concentration in peat. Low supplies of elements in peats of ombrotrophic bogs have been considered the cause of low concentrations of Na, N , P, Ca, and Mg in plant species (Richardson et al 1978). Additional factors that disrupt ion uptake by plants, as result of anaerobic conditions, include: inhibition of absorption of certain ions (Epstein 1972); restricted organic matter mineralisation (Avnimelech 1971), and retarding of root growth causing decreased root absorptive capacity (Gore and Urquhart 1966). Overall, the retention of an element is determined by the biological demand for the element as well by its chemical properties (Damman 1978).

2.3.1.2 Processes Affecting Nutrient Distribution Storage of nitrogen, phosphorus and other nutrients within peat is considerable due to the depth of peat accumulation (Waksman and Stevens 1929; Damman 1978; Clymo 1983). However, large changes in nutrient concentrations in surface layers (Damman 1978; Clymo 1983) and removal of elements before entering the anaerobic catotelm (Damman 1978) result in substantial variations in nutrient distribution with depth. Damman (1986) defined four processes which cause changes in the vertical distribution of elements in peat: (*i*) uptake by plants and enrichment of the surface by litter and leachates, (*ii*) redox reactions resulting in accumulation in the zone of water table fluctuation, (*iii*) surface enrichment by capillary flow and evaporation at the surface, and (*iv*) removal and relocation by leaching. Decomposition and compaction of peat, along with upward growth of the surface, complicate interpretations of elemental distributions (Damman 1978) but do not readily relocate elements (Damman 1986).

Uptake by plants affects primarily the acrotelm and the upper 10-20 cm of the catotelm of hollows and other sites with a near surface water table (Damman 1986). The effect of water table depth on woody plant species has a large influence on root growth and survival due to oxygen availability (Sanderson and Armstrong 1980). On wet sites, roots of black spruce are confined to hummocks, while on dry sites, roots can penetrate to 60 cm (Lieffers and Rothwell 1987). Bhatti et al. (1998) found that more than 80% of black spruce fine roots were confined to the upper 10 cm of peat. As a result, ombrotrophic bogs dominated by black spruce may show different uptake patterns than those with plant species that are more tolerant of wet conditions.

Leaching of nutrients from decomposing foliage and living tissues of vascular plants can provide a valuable nutrient source for *Sphagnum* (Damman 1978, 1986). This can increase concentrations within actively growing parts of the *Sphagnum* plant, although this is probably not the case for N and P (Damman 1978). Leaching of N and P from plant tissues does not occur as readily as, for example, K (Tukey 1970).

2.3.2 Nitrogen and Phosphorus Distribution and Transformations

2.3.2.1 Nitrogen The nitrogen cycle within bogs has three main features (Rosswall and Granhall 1980; Hemond 1983; Urban and Eisenreich 1988). First, all nitrogen is cycled as ammonium (NH_4^+); nitrification is absent and nitrate inputs are quickly taken up by mosses (Lee et al. 1987). Second, nitrogen recycling is largely restricted to the aerobic zone of peat (the acrotelm), mostly owing to mass transport limitations. Finally, cycling rates and losses of nitrogen from the system are low. In the absence of nitrification, loss of N by denitrification is minimal, and ion exchange and assimilatory uptake maintain low concentrations of ammonium in bog waters. As a result, little inorganic nitrogen is lost in runoff.

The only major input of N into ombrotrophic bogs is through atmospheric deposition, however, the annual supply is insufficient for primary production (Malmer and Nihlgård 1980). Requirements of nitrogen through atmospheric deposition provide a greater fraction of total nitrogen required by bog plants (13 to 80%) (Damman 1978; Rosswall and Granhall 1980; Hemond 1983; Urban and Eisenreich 1988), compared to other ecosystems (1 to 25%) (Bormann et al 1977; Van Cleve and Alexander 1981). As noted earlier, this input is generally immobilised by growing *Sphagnum* plants rather than vascular plants (Malmer 1993). This is one possible reason for the very high N concentrations within actively growing parts of *Sphagnum* plants (Damman 1978). Nitrogen (N_2) fixation within bogs also represents an input of N but is generally highly variable, due to the patchiness of wet and dry microhabitats (Urban and Eisenreich 1988). In boreal peatlands, one of the major sources of N-fixation are through the roots of alders (*Almus rugosa*) whose nodules are inhabited by N-fixing bacteria (Brumelis and Carleton 1989).

The supply of N available for plant uptake within most ombrotrophic bogs is determined by the rate of mineralisation (Urban and Eisenreich 1988; Malmer 1993). Mineralisation refers to the degradation of an element in organic form to mineral form (Paul and Clark 1996). Substrate availability for heterotrophic microorganisms is one of the main factors controlling nutrient mineralisation. In ombrotrophic bogs, low temperatures, poor aeration coupled with plant and microbial physiologies control substrate availability affecting mineralisation (Updegraff et al 1995). These factors also act as feedback mechanisms affecting plant production, litter quality, and plant-mediated gas transport. As a result, substrate quality of the organic pool will be a determining factor affecting nitrogen mineralisation. Substrate quality has been found to account for over 70% of the variability of nitrogen mineralisation under aerobic and anaerobic conditions in bogs (Updegraff et al 1995). This is correlated with differences of the size and kinetics of the relatively small labile pool available to microorganisms (100 kg N/ha in labile pool vs. 3300 kg N/ha in passive organic pool) (Rosswall and Granhall 1980).

In ombrotrophic peat, N mineralisation patterns do not follow normal trends. Normally, a C/N greater than 20 means net immobilisation of nitrogen by the decomposer microorganisms. In bogs, net N mineralisation has been detected at C/N quotients between 60 and 100 (Malmer and Holm 1984; Damman 1988; Verhoeven et al. 1990). Net N mineralisation occurs at high C/N because microbial activity is limited (as indicated by low decomposition rates) and populations are low (Damman 1988; Verhoeven et al. 1990). Microbial activity is reduced by many factors including: 1) the acid environment (Verhoeven et al. 1990), 2) chemical composition of the *Sphagnum* litter (Clymo 1965), 3) chemical inhibitors (Kalviäinen and Karunen 1984), 4) nutrient deficiencies (Damman 1978) and 5) lack of a available energy source (Waksman and Stevens 1928; Waksman and Purvis 1932). As a result of low activity, microbial demands of N are low, therefore causing most mineralised N to be released.

During decomposition of *Sphagnum* litter, the nitrogen-rich protoplasm breaks down and releases nitrogen quickly, whereas the bulk of cell walls are decomposed so slowly that not much nitrogen is immobilised in microbial tissue but is instead released into the environment (Verhoeven et al. 1990). Lack of N immobilisation by microorganisms also occurs because N content is not believed to limit decay despite low concentrations (Damman 1988). It should be noted that mineralisation rates are not high due to factors such as low temperature and poor aeration which additionally limit microbial activity (Van Cleve and Alexander 1981). For example, aerobic nitrogen mineralisation is usually two times greater than anaerobic mineralisation (Updegraff et al 1995). Consequently, 30% of the total net nitrogen mineralisation occurs within the top 10 cm of the peat (Rosswall and Granhall 1980). This is why the acrotelm is considered the zone of recycling and mineralisation (Urban and Eisenreich 1988).

The inhibition of N immobilisation results in distinct trends of N content with depth in ombrotrophic peat. C/N ratios tend to increase slightly with depth as a result of rapid release of nitrogen from labile N-rich compounds and the overall slow decomposition of the peat (Damman 1978). The C/N of the peat then decreases but only to levels around 50 (Damman 1988). Absence of a gradual increase in N concentration with depth indicates that N removal more or less keeps pace with organic matter losses during decay. Slight decreases in C/N with depth could be attributed to the relative increase of N in the zone of water table fluctuation and in the inundated peat (Damman 1978). This is a result of leaching of N from well-drained peat layers. This is also suggested by higher N concentrations in hollows compared to hummocks. In addition, net N mineralisation causes N inputs into ombrotrophic peat to be as high as two times greater than amounts accumulated in the peat (Damman 1988). However, there are still large quantities of N that are sequestered within the peat (Clymo 1978).

2.3.2.2 Phosphorus Phosphorus is probably the most limiting nutrient affecting growth and productivity in ombrotrophic bogs (Bhatti et al. 1998). This is attributed to the very low P concentrations within precipitation (Allen et al. 1968). As a result of its low availability, P, like N, tends to be conserved within living organisms (Tate 1984).

Like N, P concentrations increase in the zone of water table fluctuation, and then continue at a low constant level throughout the anaerobic peat (Damman 1978). In addition, living *Sphagnum* contains distinctly higher concentrations and the amount in the annual growth is probably greater than what is supplied in precipitation. This could be a result of retranslocation within *Sphagnum* mosses or translocation of PO_4^{3-} in capillary water due to evapotranspiration at the surface.

Mineralisation of organic P is an important source of P for vascular plants within ombrotrophic bogs and other terrestrial ecosystems (Gressel and McColl 1997). However, due to the physiochemical aspects of the P cycle, P rates and pathways, especially mineralisation, are poorly understood (Tate 1984).

In aerated peat, P occurs mainly in organic form with some bound to Fe and Al (Damman 1978). Uptake of P by vascular plants can affect P concentrations within bogs (Gore and Olsen 1967) but higher concentrations within hollows suggests that leaching from hummocks occurs (Damman 1978). Phosphorus accumulates within the zone of water table fluctuation and near the water level because of higher Fe and Al concentrations in these zones (Damman 1978). The low P content in anaerobic peat is as the result of reduction of Fe from the tri to divalent state, which increases Fe mobility and decreases its concentrations (Damman 1978). As a result, all but the organic P becomes mobile.

2.4 Tree Harvesting and Wildfire Effects on Forest Soils

2.4.1 Tree Harvesting

2.4.1.1 Definition of Clearcutting Defining clearcutting has become an area of confusion perhaps due to the negative connotations that have become associated with the word (Keenan and Kimmins 1993). A clearcut is an area of forest that has been completely cleared of all trees other than seedlings and occasional saplings (Kimmins 1992). All trees are cut at the same time such that all the young trees growing in the area will be similar in age and height. A more ecological definition of clearcutting focuses on the degree of removal of the "forest influence" (Keenan and Kimmins 1993). Keenan and Kimmins (1993) described the forest influence as the effect of the closed canopy on the environment of the land it occupies. This includes the microclimate, and the effect that tree roots have on soil microorganisms and soil structure. This, in turn, affects many ecological processes, such as organic matter decomposition and nutrient cycling, and erosion and weathering of mineral soil. When a forest is clearcut, the forest influence is removed until such a time as the trees regrow and the influence has re-established. However, the surrounding forest maintains a "shadow" of forest influence some distance into the cutover. Only when the harvested patch is large enough that the majority of its area is beyond this forest influence can that area be called a clearcut (Kimmins 1992). Consequently, the minimum size of the opening that constitutes a clearcut under this definition varies with the height of the surrounding forest (Keenan and Kimmins 1993).

2.4.1.2 Forestry Impacts and Issues The debate over forestry and its impacts has been occurring for many years. Unfortunately, long-term impacts of current forestry practices on forest production, nutrient cycling and ecosystem dynamics are still not well understood today (Teng et al. 1997). Concerns have been expressed over nutrient removals associated with clearcutting alone, or in combination with other processes associated with site disturbance, which may deplete nutrient reserves in forests and reduce the long-term sustainability of forests (Powers and Van Cleve 1991). Sustaining forest productivity, thus, involves maintaining site productivity. Site productivity refers to the potential of a site to grow a particular tree species (Taylor et al. 1995). Accordingly, site productivity is determined by climate, availability of site resources (e.g. light, soil moisture and nutrients), the requirements of a particular tree species and also competition for these resources between commercial and non-commercial plants and microorganisms. In cool temperate and boreal forests the major constraints on potential site and harvestable tree productivity are normally soil temperature, soil drainage, and availability of N (Van Cleve and Alexander 1981). In order to achieve sustainable forestry while maintaining site productivity, factors affecting the availability of nutrients and the mechanisms of uptake in different forest ecosystems must be determined (Mahendrappa et al. 1986).

Harvesting impacts on boreal forest ecosystems, particularly black spruce, have been well documented (Gordon 1983; Timmer et al. 1983; Bonan 1990). However, research dealing with tree harvesting impacts on forested bogs in northern latitudes is very scarce (e.g. Trettin et al. 1996; Teng et al. 1997). As a result, discussion of forestry impacts on soils and nutrient cycling will be drawn from research performed on upland soils, except where noted.

Impacts of logging are related to size of the cut, post-logging treatments, planting, tending, thinning, and protection activities (pest and fire management) (Taylor et al. 1995). Other secondary effects may occur associated with development of logging roads, modification of drainage patterns and landscape level impacts, which modify hydrologic and nutrient cycles. Because the productivity of forest ecosystems varies with species composition, local climate, soil texture, drainage, soil depth, and site history (e.g. disturbance type) the impacts of forest harvesting can vary tremendously.

Removal of the forest influence has a major effect on radiation balance, which leads to changes in the temperature and moisture of the air and soil (Keenan and Kimmins 1993). These factors regulate most of the physical and physiological processes that influence the survival and growth of forest tree species. Main changes with radiation and temperature involve: input of short-wave solar radiation at surface is greater (warmer daytime temperatures) and emission of long-wave radiation is greater (cooler surface temperatures on clear, cool nights) (Keenan and Kimmins 1993). Temperature increases can have detrimental effects on seedling survival, on photosynthetic functioning and on growth. Increases in soil temperature are dependent on the degree to which clearcutting and post-harvest site preparation affect understory vegetation, the degree of mineral soil exposure, the reduction in the depth of the forest floor, and other soil thermal properties (soil moisture, bulk density, and pore space) (Kimmins 1997).

Removal of the tree canopy will usually increase soil temperatures due to the increase in solar radiation reaching the forest floor (Frazer et al. 1990; Aust and Lea 1991; Trettin et al. 1995, 1996). Warmer soil temperatures in clearcut sites have also been attributed to soil disturbance exposing darkened humified layers (Trettin et al. 1995). Trettin et al. (1996) showed that whole-tree harvesting on organic soils resulted in a 2°C increase down to 25 cm directly after harvesting. Increased organic matter decomposition due to higher soil temperatures caused by harvesting can persist for more than 10 years in some cases (Kubin and Kemppaninen 1991).

Soil moisture increases following clear-cutting come about because (a) trees intercept precipitation, that depending on climate and canopy architecture, may eventually reach the soil or may evaporate from the canopy, and (b) tree removal results in lower transpiration rates for a period of time because their leaf indexes are much higher than that of shrubs and herbs (Hornung and Newson 1986). Decreased moisture at the soil surface can also occur due to increases in wind speed near the ground, thus, increasing evaporation (Keenan and Kimmins 1993). Generally, soil moisture levels in summer months increase (McColl 1977), however increases are generally short-lived.

Water table depth in peatlands greatly affects soil aeration, hence changes in the water table following harvesting also would impact organic matter decomposition (Trettin et al. 1995). In undrained wetlands where the water table normally remains within 30 cm of the soil surface, the amplitude of water table fluctuations after harvesting increase, but the average depth will usually remain the same (Verry 1986). This effect is not consistent, as tree harvesting has caused a significant rise in the groundwater level in some peatlands (Berry and Jeglum 1991). One way to improve tree growth following harvesting is to drain the peatland (Paavilainen and Päivänen 1995). This will lower the water table, thus, adjusting the water content of the soil to a level which ensure sufficient aeration (Päivänen 1973). In the case of black spruce, improved aeration may increase growth (Jeglum 1974) and increase wood production to a more optimum rate on peatlands (Haavisto and Jeglum 1991). However, drainage is still not used in Manitoba and is currently being experimented with in other provinces (Haavisto and Jeglum 1991).

Another hydrologic change resulting from clearcutting is increased stream flow due to increased surface runoff, water movement through the soil profile and reduced evapotranspiration (Hornbeck et al. 1986). This effect will not be as important within ombrotrophic bogs where runoff and water movement is negligible or not apparent. In addition, there is increased snow depth and changes in the amount and timing of runoff after snowmelt (Berndt 1965).

In northern wetlands, numerous site preparation systems are used, with most involve some sort of mounding (Sutton 1993). Mounds are created by either disking or excavation (Trettin et al. 1995). Mounds provide an elevated planting surface and mitigate against increased water table levels following harvesting. This technique along with the previous section on soil disturbance is not of concern with the present study as stands were winter-logged (peat was frozen) and naturally regenerated with no site preparation. Therefore, there was very little soil disturbance and/or compaction.

With tree harvesting, site conditions favour increased microbial activity and decomposition (Covington 1981) and, consequently, nutrient availability (Van Cleve and Yarie 1986). Along with favourable temperature and moisture levels, litter deposited on the forest floor by pioneer species following harvesting tends to be of higher quality (less phenolic compounds, lower C/N) (Edmonds 1980). This helps maintain the high decomposition and nutrient mineralisation rates following clearcutting and is a source of short-term fertility (Kimmins 1997). High decomposition rates following logging have also lead to a decrease in the forest floor depth, and a reduction of the total amount of nutrients in that layer (Keenan and Kimmins 1993). However, inputs of slash, decaying roots and stumps can offset decomposition losses (Hendrickson et al. 1989). Deposition of slash material may contain more recalcitrant materials which initially inhibits decomposition and nutrient mineralisation (Covington 1981). By immobilising nutrients immediately after harvesting, slash can prevent nutrient losses due to leaching (Gordon 1983). Removal of slash is usually not recommended as it does provide a long-term nutrient source when it starts to decay.

In peatlands, research into harvesting effects has focused on C loss via decomposition (Lieffers 1988; Trettin et al. 1995, 1996). In most cases, organic matter decomposition increased following harvesting which usually resulted in a net loss of soil C from the wetland (Trettin et al. 1995), with temperature as the main determining factor (Trettin et al. 1996).

Changes in the nutrient capital of the forest are important as they relate to the long-term sustainability of the site. With harvesting, nutrients contained within the boles (in the case of stem-only harvesting) are removed from the site, resulting in a net loss of nutrients (Teng et al. 1997). Teng et al. (1997) found that for a black spruce peatland removal of N, P, K, Ca and Mg from stem-only harvesting would be 43, 8, 48, 205 and 15 kg ha^{-1}, respectively. Leaving the foliage in the site is important as it contains up to 46% of total N and 36% of total P while representing only 13% of the total biomass (Teng et al. 1997). Removal of such large quantities of bases, particularly Ca, from the ecosystem may cause severe nutrient depletion and acidification (Timmer et al. 1983). In the cases where the crown biomass is very high, a more severe nutrient loss would occur from full-tree harvesting (Teng et al. 1997). Keeping slash on the site would be a significant nutrient source for the succeeding rotation and represent a substantial contribution to the sustainability of stand production (Timmer et al. 1983). This is especially important on peatlands due to the low nutrient availability of many peat deposits (Damman 1988) and the slow mineralisation of nutrients from peat (Clymo 1965). Unfortunately, research dealing with harvesting impacts on nutrient pools in peat is very scarce.

In addition to losses from tree removal, nutrients released from decomposition of fresh litter are especially susceptible to removal via leaching and runoff during the first few years after harvesting (Hornbeck and Kropelin 1982). Losses via leaching are mainly the result of reduced vegetation coverage and the associated reduction in nutrient absorption (Teng et al. 1997). While it is known that decreased plant uptake can last from two to several years following disturbance (Marks 1974), questions still remain unanswered about the duration of heightened nitrogen mineralisation rates (Frazer et al. 1990). The return of decomposition, nutrient cycling, and nutrient availability to pre-harvest levels depends on rate of revegetation of trees and understory plants (Keenan and Kimmins 1993). This also determines rate at which forest microclimate returns. Nitrogen losses can also occur by nitrification and denitrification, however, they are both insignificant in acidic, ombrotrophic bogs (Urban and Eisenreich 1988).

2.4.2 Wildfire

2.4.2.1 Fire Terminology Lightning-induced wildfires are a common occurrence in northern forest ecosystems (Wein and MacLean 1983). The type of fire history that characterises an ecosystem is called its fire regime (Heinselman 1981). The elements which define the fire regime are 1) fire type or intensity (e.g. crown fires, severe surface fires and light surface fires); 2) size of typical significant fires; and 3) frequency or return intervals for specific land units. The fire rotation (Heinselman 1973) or fire cycle (Van Wagner 1978) is the average time required for a fire regime to burn over an area equivalent to the total area of an ecosystem.

In the boreal forest the dominant regime is high-intensity crown fires or severe surface fires of very large size – often more than 10,000 ha, and sometimes more than 400,000 ha (Heinselman 1981). Fire rotations are shorter in drier regions of Canada, where they average 50-100 years, than in high precipitation areas, where they may average 200 years or more (Heinselman 1981). Long rotations are common for peatlands, where crown fire regimes in black spruce dominated sites occur at cycles of 150-200 years (Heinselman 1973) and surface fires can occur at cycles up to 1000 years (Kuhry 1994). Organic terrain (i.e. peatland) fires can burn deep into the peat and may exhibit glowing combustion (low energy-release rates) (Wein 1983). These types of fires only occur in extremely droughty years or after drainage.

2.4.2.2 Fire Impacts on Soil Fire is an important agent in the release of nutrients stored up in slowly decaying organic matter in boreal forests (Rowe and Scotter 1973). Nutrient release following fire helps increase nutrient cycling, while rejuvenating the ecosystem.

The effect that fire has on an ecosystem will depend on the successional stage of the forest and the time since disturbance (MacLean et al. 1983). Both successional stage and time since disturbance have a major impact on the nutrient dynamics and pools (young forest vs. old-growth forest) which could be affected by fire. The impact of fire on ecosystem functioning can be viewed by looking at the effects during fire and post-fire changes.

During fire, nutrients can be lost from the system as a result of three processes: 1) loss through volatilisation, 2) loss of particulate matter and 3) convection action removing particulate matter and mineral matter from the site (Woodmansee and Wallach 1981; MacLean et al. 1983). Volatilisation removes large quantities of nutrients from the site, with N losses much greater than P losses (500-800 kg ha^{-1} and <40 kg ha^{-1}, respectively) (MacLean et al. 1983). Volatilisation losses can increase with high intensity burns, up to 60% higher (Knight 1966).

Another change occurring during fire is a large transfer of mineral nutrients to ash layer. which is deposited on the soil surface (Ahlgren and Ahlgren 1960). Ash mostly consists of oxides and metallic cations which are released from the oxidation of organic matter. The final major effect during fire is the heating of biomass and upper soil layers (MacLean et al. 1983). A consequence of this is the loss of plant biomass from the site. However, a sizeable portion of this biomass may be returned to the soil as uncombusted and freshly killed litter. This plus the dead roots of killed vegetation, can provide a valuable nutrient and carbon source for microorganisms in the soil (Woodmansee and Wallach 1981).

Post-fire changes are those which affect the soil environment (i.e. temperature and moisture) and nutrient cycling. Following the combustion of vegetation and litter and blackening of the soil surface by charcoal and ash, soil temperature generally increases (Viro 1974; MacLean et al. 1983). Blackening of the soil surface acts to lower the albedo, thus absorbing more solar radiation. Decreasing the thickness of the forest floor also results in increased soil temperature (Ahlgren and Ahlgren 1960). Higher soil temperature will occur for some time afterwards, until the shading effect of the vegetation canopy is restored. This effect is more complicated in peatlands as any decrease in thickness will cause the water table to be closer to the surface and thus, result in lower soil temperatures.

Soil moisture content can be affected by two processes: 1) increased soil temperature and 2) low water-holding capacity of charred humus (Viro 1974). Higher soil temperature may increase evaporation near the soil surface, thus, drying out the soil. In sites where the water table is close to the surface, destruction of the forest by fire will cause a rise in water table (Lutz 1956 cited in Ahlgren and Ahlgren 1960), which can affect vegetation recolonisation due to wetter conditions. The final environmental change is an increase in soil pH (MacLean et al. 1983). This a consequence of the large concentrations of alkaline cations in the ash, especially Ca^{2+}. This effect is normally short-lived as leaching of cations will return the pH to pre-fire levels (Ahlgren and Ahlgren 1960; Viro 1974).

Following fire there is generally a large increase in readily available nutrients in the ash which provide a nutrient 'pulse' (Viro 1974; MacLean et al. 1983). These nutrients can be taken up by pioneer vegetation and microorganisms, leached into the soil or lost in runoff (water and wind erosion) (Woodmansee an Wallach 1981). Nutrients, such as P, K, Ca and Na, increase in solubility in the ash which contributes to their vulnerability to leaching (Smith 1970). This along with plant uptake is why nutrient concentrations return to pre-fire concentrations, or lower in some cases, relatively quickly (< 1 year). In sites where there is still organic matter in the soil, nutrients may be absorbed on exchange sites to reduce leaching losses (Viro 1974).

Increased microbial activity following fire also causes an increase in nutrient availability due to high decomposition and nutrient mineralisation rates (Woodmansee and Wallach 1981; MacLean et al. 1983). After fire, microbial numbers in the soil surface can increase multifold (Ahlgren and Ahlgren 1965). In addition, these microorganisms have a new and large source of carbon from deep root systems and residual aboveground litter, and more favourable growing conditions because of increased soil temperatures (Lloyd 1971), more favourable pH (Fowells and Stephenson 1933), greater amounts of nutrients in ionic form from ash (Ahlgren and Ahlgren 1965) and usually more available soil water (Jorgenson and Wells 1971). The net result is usually an increase in mineralisation which can increase NH_4^- concentrations (Viro 1974). Microbial immobilisation also will increase until labile carbon sources have been depleted but net mineralisation will usually predominate (Woodmansee and Wallach 1981). Nutrients mineralised are also vulnerable to leaching or to being stored on exchange sites (Viro 1974). Overall, nutrient availability may be enhanced in spite of a net loss of nutrients from the system caused by initial or subsequent effect of fire (Woodmansee and Wallach 1981). This increase in nutrient availability is very important as it aids vegetation re-establishment. In boreal peatlands, any increase in production resulting from the release of nutrients following fire does not, however, compensate for the loss of peat due to burning (Kuhry 1994). This is only important when ground fires burn peat, but is not the case when just aboveground vegetation is lost.

In general, *Sphagnum*-dominated boreal peatlands are well adapted to fire disturbance as nutrients released by burning are leached into peat (Kuhry 1994), where they are probably absorbed to prevent loss. When peat is burned, pre-fire conditions generally return within decades (a short time relative to fire rotation length) and long-term vegetation development is not affected (Kuhry 1994).

2.5 Conclusion

Most research dealing with nutrient cycling processes in peatland ecosystems has not dealt with the impacts of disturbance. While the controls on nutrient availability and transformations have only recently become more clear, not much speculation has been made concerning what impact canopy removal, via clearcut logging or wildfire, would have on these controls. Utilisation of forested bog ecosystems for sustainability forestry requires that we understand the changes in site conditions (e.g. soil temperature and water table levels) and nutrient transformations that will directly affect forest re-growth and recovery.

3. SPATIAL VARIABILITY OF MINERAL NITROGEN AND PHOSPHORUS IN DISTURBED BLACK SPRUCE BOG ECOSYSTEMS

3.1 Abstract

Inorganic nitrogen (N) and phosphorus (P) concentrations were studied for two months within 12 black spruce (*Picea mariana* (Mill.) B.S.P.) bog ecosystems in eastern Manitoba. Stands were classified based on disturbance type: undisturbed mature forests (>110 years old), winter-logged clearcut stands (stem-only; 10-14 years old), and wildfire burn stands (11 years old). The objective of this study was to determine differences in the spatial heterogeneity of inorganic N (NH_4^+ and NO_3^-) and P (PO_4^{3-}) concentrations within disturbed ombrotrophic bogs, affected by wildfire or clearcut logging. Within disturbance types, inorganic N and P concentrations were determined according to spatial gradients: (1) microrelief and (2) depth. Nutrient concentrations were expected to exhibit patterns based on differences in site conditions (water table level, soil temperature and plant uptake) and as influenced by disturbance type. Inorganic N concentrations showed significant differences between disturbance types most notably with mature stands greater than clearcut and burn sites. There were no significant differences in P concentrations between disturbance types. N exhibited microrelief differences (hollow > hummock) while P exhibited depth differences (0-15 > 15-30 cm). These results indicate that spatial and temporal variation in nutrient availability must be taken in to account before

conclusions can be made on disturbance effects and sustainability. Further work is needed to evaluate plant uptake rates and nutrient storage in re-colonising vegetation.

3.2 Introduction

Within boreal forested peatlands, site productivity is constrained by low soil temperatures, high moisture and low availability of essential nutrients (Bonan and Shugart 1989; Brumelis and Carleton 1989). Within ombrotrophic bogs (poor minerotrophic peatlands), low availability of essential nutrients, particularly nitrogen and phosphorus, are limited by both low inputs (e.g. in precipitation) (Small 1972a) and slow nutrient turnover due to low biological activity and poor substrate quality (Flanagan and Van Cleve 1983). Nutrient availability for vascular plants is further limited by the accumulation of almost all N and P found within atmospheric deposition by the moss layer (Damman 1978; Lee et al. 1986; Malmer 1988). As a result, vascular plants rely on slow decay of aboveground vascular plant litter and other microbial processes as their primary supply of N and P. Consequently, N and P availability is considered to be the main limiting factor affecting black spruce productivity in bogs (Watt and Heinselman 1965).

One of the main goals of sustainable forestry requires that we maintain site productivity, defined as the potential of a site to grow a particular tree species (Taylor et al. 1995), while maintaining the ecosystem's function and biodiversity. Accordingly, site productivity is determined by climate, availability of site resources (e.g. light, soil moisture and nutrients) and competition for these resources between commercial and non-commercial plants and microorganisms as well as the inherent requirements of the species of interest. Recently, there has been increased interest by those involved with forestry to emulate the effect of clearcut logging on site productivity to that of wildfire.

Traditional forest nutrient studies have focused on the availability of inorganic nutrients, such as NH_4^-, NO_3^-, and PO_4^{3-}. NH_4^- and NO_3^- are the major forms of plant available nitrogen (Binkley and Hart 1989). Consequently, quantities of these ions in soil samples have often been used as an index of N availability. While the constraints of measuring inorganic pools at a particular point in time are well known (Binkley and Hart 1989; Aber and Melillo 1991), they are still used in disturbance studies, particularly fire (e.g. Rashid 1987).

In northern bog ecosystems, the use of inorganic pools to differentiate between disturbance regimes could have particular significance. Temperature and aeration control microbial activity (Van Cleve and Alexander 1981) and aeration is also important in affecting solubility of inorganic nutrients (i.e. through redox reactions) (Farnham 1974). Therefore, concentrations of inorganic N and P will be determined by temperature and moisture regimes (Avnimelech 1971). These regimes are related to the microrelief patterns within bogs, microhighs (hummocks) vs. microlows (hollows), which, in turn, are characterised by differences in proximity to the water table. With the added effect of disturbance on soil temperature and moisture levels, these within site spatial differences will be important indicators of overall changes caused by disturbance through their effect on nutrient concentrations.

The objective of this study was to determine differences in the spatial and temporal heterogeneity of inorganic N (NH_4^+ and NO_3^-) and P (PO_4^{3-}) concentrations within disturbed ombrotrophic bogs, affected by wildfire or clearcut logging. This was accomplished by focusing on concentration differences based on: (1) microrelief; (2) depth; and (3) time (seasonal changes).

3.3 Materials and Methods

3.3.1 Site description

Sites were chosen within the Manitoba Model Forest, a 900 000 ha area located on the east side of Lake Winnipeg, Manitoba (96° 15' W) extending eastwards to the Ontario border (95° 07' W). Its north-south borders reach from the Winnipeg River (50° 20' N) to just north of the Wanipigow River and includes an area on the north side of Wallace Lake (51° 05' N). The area is characteristic of the Canadian Shield, predominantly granite bedrock with the remaining area split between organic soils and deep lacustrine, glaciofluvial and till deposits. Mean precipitation is 564.9 mm and average January temperature is −19.5°C with July temperature of 18.6°C (Environment Canada 1996). For this study, 12 *Picea mariana* (Mill.) B.S.P. (black spruce) stands with organic deposits greater than 1 m in thickness were chosen. The shrub layer within these sites was dominated by *Ledum groenlandicum*, *Chamaedaphne calyculata* and *Vaccinium vitis-idaea*. The moss community consisted of *Pleurozium schreberi*, *Sphagnum magellanicum*, *S. fuscum*, *S. girgensohnii*, *S. nemoreum*, *Dicranum undulatum*, *Polytrichum commune*, *P. juniperinum* and *P. strictum*. Within the burn sites only, *Pinus banksiana* was also present. All sites (except B2 - minerotrophic fen) are classified as ombrotrophic bogs (poor minerotrophic and acidic, pH < 4) with *Sphagnum* moss dominating the entire thickness of the peat. Sites were separated on the basis of disturbance with four sites from each disturbance type; undisturbed mature (**M**) forests (trees > 110 years old and >10 cm diameter at chest height; closed canopy), winter-logged clearcut (**C**) stands (stem-only; approximately 10-14 years old), and wildfire burned (**B**) stands (approximately 10 years old). Table 3.1 shows soil classifications, total N and pH values for sites within this study.

Table 3.1 Soil classification, total nitrogen and pH values from various sites selected for this study.

Site[a]	**Soil classification**[b]	**Total N**[c] mg g dry peat^{-1}				**pH**[d]
		Hummock 0-15 cm	Hummock 15-30 cm	Hollow 0-15 cm	Hollow 15-30 cm	
B1	Typic Fibrisol	6.77	7.37	9.32	8.33	3.11
B2	Humic Mesisol	14.22	15.16	15.40	14.27	4.68
B3	Fibric Mesisol	6.66	11.85	12.17	13.25	3.17
B4	***	7.75	6.16	10.08	10.78	***
C1	Terric Humic Fibrisol	7.14	9.52	10.17	10.63	3.17
C2	Fibric Mesisol	8.28	11.37	11.15	14.57	3.25
C3	Fibric Mesisol	7.45	7.63	10.62	9.68	3.19
C4	***	6.56	9.20	10.33	6.96	***
M1	Mesic Fibrisol	8.40	7.55	9.40	8.32	3.10
M2	Typic Mesisol	8.18	7.97	9.14	11.98	3.13
M3	Humic Fibrisol	5.40	6.72	11.74	9.10	3.15
M4	***	6.95	8.17	9.48	9.72	***

Note: *** - measurements not taken.

[a] Site classification = disturbance type + replicate number.

[b] Soil Classification Working Group (1998)

[c] Total nitrogen averaged from six samples taken from July and August 1996.

[d] pH determined using a 1:4 ratio in 0.01M $CaCl_2$

3.3.2 Inorganic N and P

Sampling for inorganic nitrogen (NO_3^--N and NH_4^+-N) and phosphorus (PO_4^--P) involved selecting three hummocks and three hollows within each site. The living moss was removed and peat was sampled from 0-15 cm and 15-30 cm depths using handsaws. Sampling occurred on 2 July 1996 and 14 August 1996. Samples were doubled bagged in polyethylene bags and stored on ice until returning to the lab. On return, samples were placed in freezers until they were extracted. Nitrogen and phosphorus extractions were performed using 5 g oven dry equivalent field moist soil. Samples for nitrogen determination were extracted with 100 ml of 2M KCl solution, shaken for 1 hour and then filtered through Whatman #2 filter paper. Samples for phosphorus extraction were extracted with 100 ml of deionized water and 1 g of washed charcoal, shaken for 1 hour and then filtered through Whatman #42 filter paper. All filtrates were frozen following extraction. Colourimetric analysis of nitrogen filtrates was performed on a Technicon Autoanalyzer II. Nitrate was analysed with the cadmium reduction procedure and ammonium by the indophenol blue procedure (Technicon® Instrument Corp. 1971, 1973). Phosphorus was analysed following the ammonium molybdate-ascorbic acid procedure for water-soluble P after Olsen and Sommers (1982). All values were expressed as μg NH_4^+-N, NO_3^--N, and PO_4^--P g dry peat^{-1}. Inorganic nitrogen values were summed to give a total inorganic N (μg N dry peat^{-1}) since nitrate concentrations comprised a minor component of total inorganic N.

3.3.3 Water Table and Soil Temperature Monitoring

For the summer of 1996 water table depth and soil temperature were monitored at two week intervals. Water table depth was determined using piezometers constructed from

PVC pipes which were inserted in two hummocks within each site. Soil temperature changes were monitored using thermocouples which were placed within one hummock and one hollow at each site. Temperatures were taken from the surface of the living moss (0 cm), 10, 20, 30, 60 and 90 cm into the peat.

3.3.4 Total Nitrogen

Samples were oven dried (70 °C) and ground with a ball mill prior to analysis for carbon and nitrogen content. Total N (% dry weight) was determined by sample combustion on a Leco CHN analyser (Leco Corporation, St. Joseph, Michigan). Concentrations were expressed as mg N/g dry peat.

3.3.5 Statistical Analyses

Differences in inorganic nitrogen and phosphorus concentrations were evaluated between the three disturbance types. 3 factor ANOVAs were performed with either disturbance type or site type, microrelief classification and depth as factors. 3 factor ANOVAs were also performed for each disturbance type separately with its individual sites, microrelief classification and depth as factors. An $\alpha = 0.10$ was chosen due to high inherent variability characteristic of natural soil ecosystems. All statistical analyses were done using SYSTAT 7.0 (SPSS Inc., Chicago, IL).

3.4 Results and Discussion

3.4.1 Soil Temperature

Hummocks were generally warmer than hollows for most sites and disturbance types and soil temperatures decreased with depth from 20 to 30 cm (Figures 3.1 to 3.4). Soil temperatures for both hummocks and hollows at 20 cm and 30 cm within undisturbed mature stands and clearcut stands were not noticeably different. However, burn sites appear to take longer to warm up in the spring and remained colder than the mature and cut stands for most of the summer and into the fall.

Removal of the tree canopy, whether from fire (Viro 1974; MacLean et al. 1983) or tree harvesting (Frazer et al. 1990; Aust and Lea 1991; Trettin et al. 1995, 1996), typically increase soil temperatures due to an increase in solar radiation reaching the forest floor. Additionally, deposited ash and charcoal readily absorb solar radiation (due to their dark colour) and contribute to warmer soil temperatures (Viro 1974). Similarly warmer soil temperatures in clearcut sites have been attributed to soil disturbance exposing darkened humified layers (Trettin et al. 1995). This is not an issue, however, for these sites used in this study as they were winter-logged and disturbance was minimal. Trettin et al. (1996) showed that whole-tree harvesting on organic soils resulted in a 2°C increase down to 25 cm directly after harvesting. These increases as indicated in the literature are not noticeable in our sites likely as a consequence of the time frame (> 10 years after disturbance) and re-establishment of shrub cover.

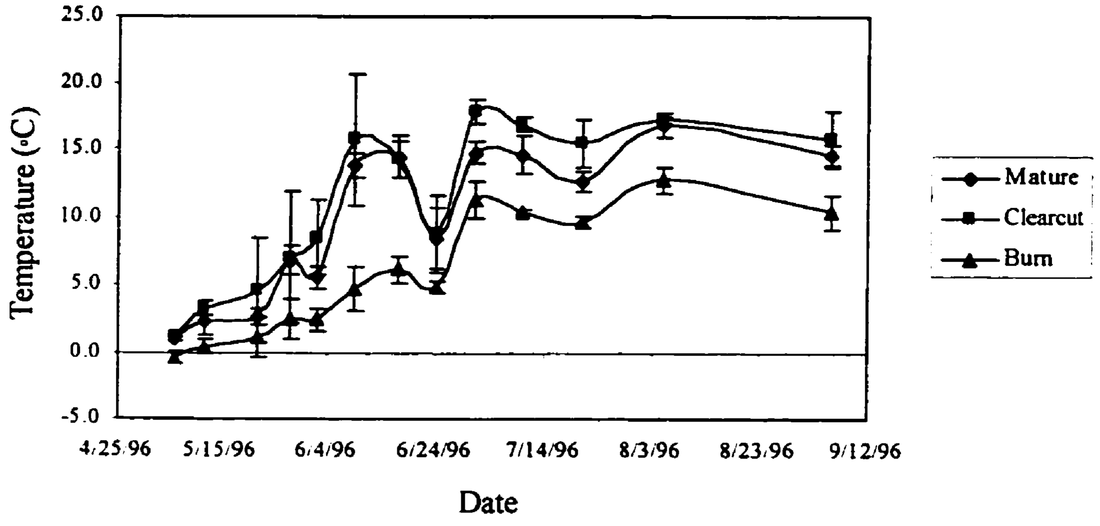


Figure 3.1 Soil temperature variation in hummocks 20 cm below moss surface.

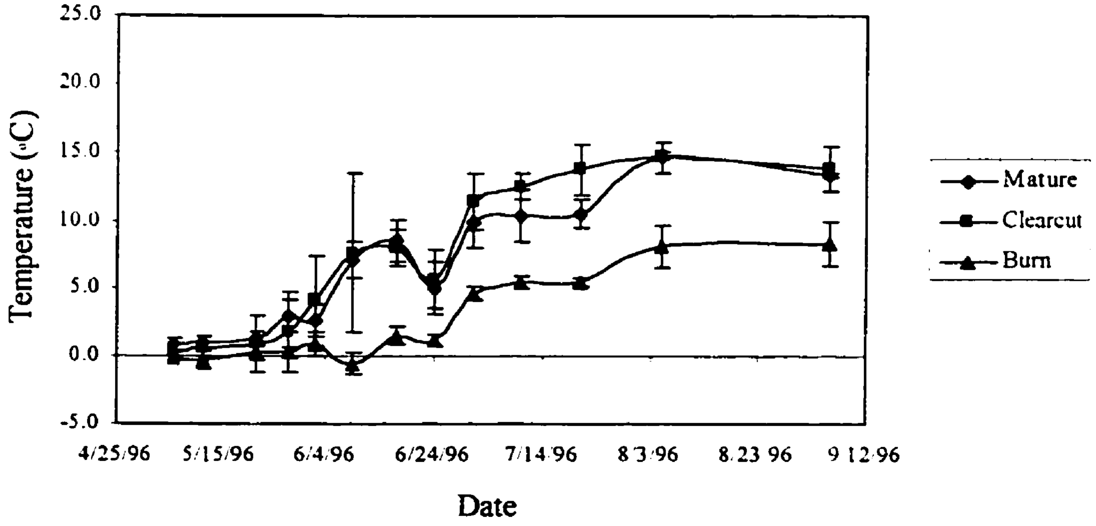


Figure 3.2 Soil temperature variation in hummocks 30 cm below moss surface.

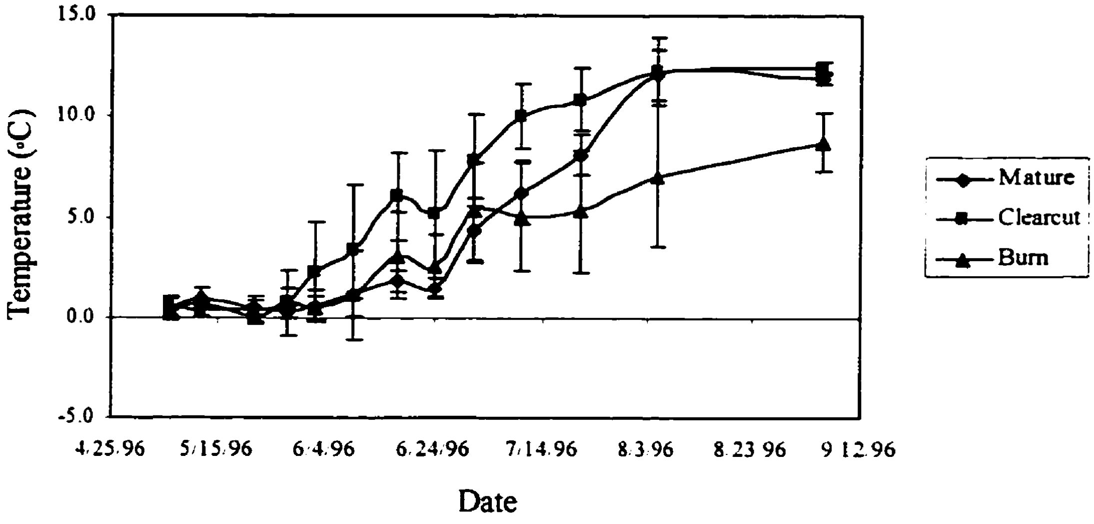


Figure 3.3 Soil temperature variation in hollows 20 cm below moss surface.

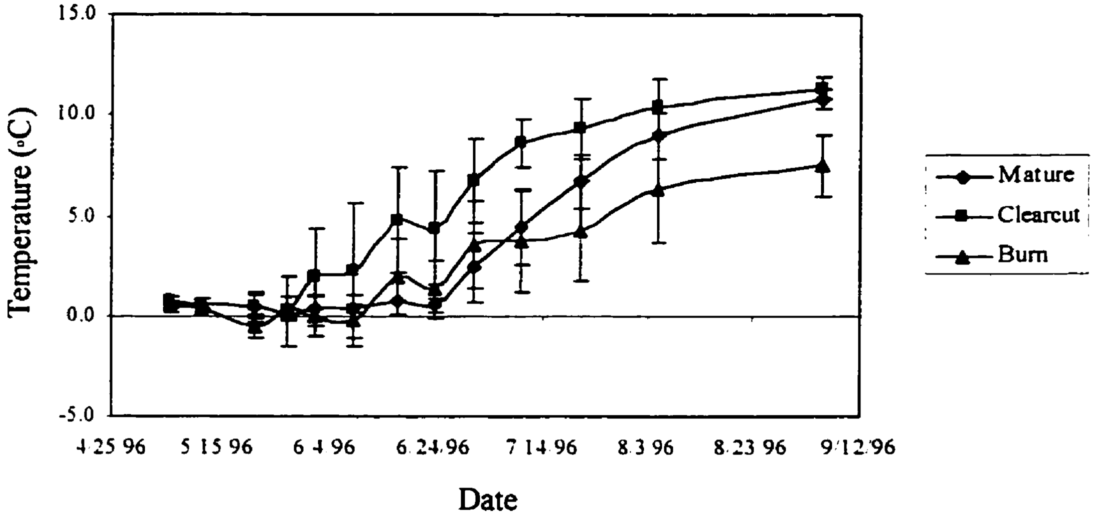


Figure 3.4 Soil temperature variation in hollows 30 cm below moss surface.

Cooler soil temperatures in the burn sites could be attributed to dense shrub cover or higher water tables (Figures 3.5; see next section). With re-establishment of the moss carpet and shrubs, any effect of lowered albedo on soil temperature within these burn sites would not be evident anymore. It should be noted that any conclusions concerning increases or decreases in soil temperature (or water table level or nutrient levels) are purely speculative since pre-disturbance conditions are unknown.

3.4.2 Water Table

For each disturbance types, water table levels were high in the spring due to snowmelt and then fell gradually during the summer months (Figures 3.5). Tree removal in peatlands generally results in both an increase in the water table and in its fluctuations (Trettin et al. 1995). However, data presented in Figures 3.5 is slightly misleading due to variability in height differences between hummocks and hollows between sites. Within each site hummock heights and hollows depths varied considerably (data not shown). This affected the proximity to the water table for samples taken at similar depths. For example, M3 and M2 water table levels are only different by approximately 10 cm on average. However, because of hummock-hollow height discrepancy, the water table was almost at the surface of the hollows in M3 while in M2 hollows were noticeably drier. In addition, the hollows present in B2 were almost always inundated with water. The near surface water table in M3 and B2 is important in light of the effect that water saturation has on soil aeration (Lahde 1969), microbial activity (Lahde 1969; Williams and Crawford 1983) and elemental dynamics (Damman 1978).

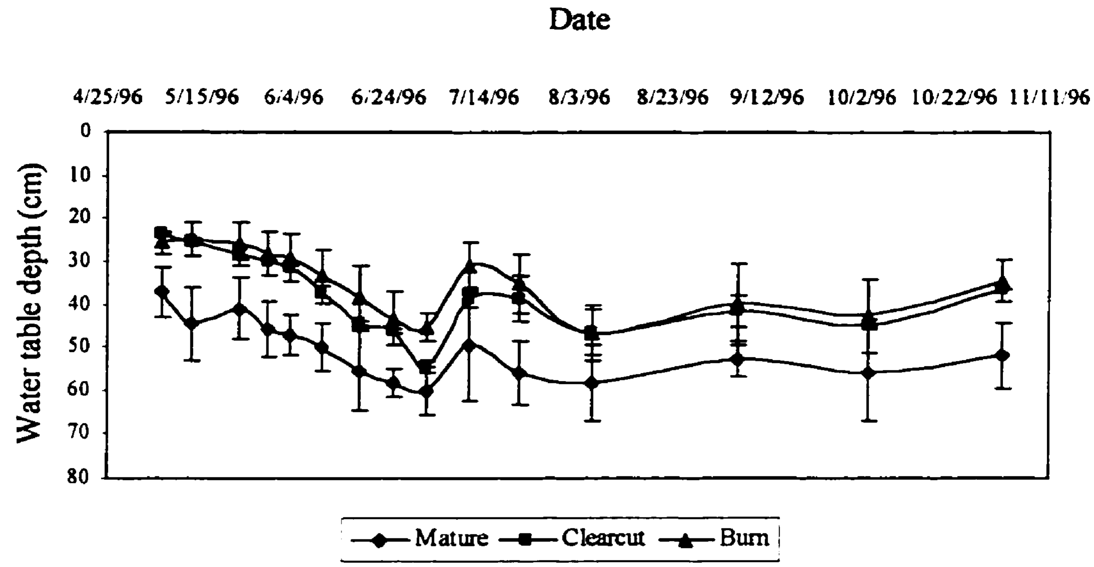


Figure 3.5 Water table fluctuations during the spring and summer of 1996 within each disturbance type (as measured in hummocks only).

Taking into account the hummock-hollow height differences, most of the disturbed sites are noticeably wetter than the mature sites, excluding M3 which is significantly wetter than the other matures. These differences between the replicate sites within each disturbance type are the result of high natural variability or possibly due to problems with site matching (i.e. sites may not be the same type of bog).

The higher water tables in disturbed sites can be attributed to tree removal which eliminates water uptake by the trees (Trettin et al. 1995). The higher water table in M3 compared to M2 and M1 is likely due to the greater proportion of *Sphagnum* making up the forest floor in M3 (interestingly, this is also found in all of the disturbed sites). The high water-holding capacity of *Sphagnum* (Paavilainen and Paivanen 1995) could explain moisture differences found in the mature stands. Regarding mature sites and disturbed site differences, it is possible that all of the cuts were similar to M3 since there was no evidence of the drier moss, *Pleurozium schreberi*, within the soil profile. There was also no evidence of *P. schreberi* in any of the burns, however, if *Pleurozium* formed the moss community at the time of the fire there is a good chance it could have been combusted because of its low water content. Evidently, it is more difficult to ascertain which mature community-type dominated the burn sites prior to disturbance.

3.4.3 Nitrogen

3.4.3.1 Disturbance Effects. Incorporating inorganic nitrogen values for all microrelief classes and depths showed that the disturbance types were significantly different with undisturbed mature stands generally having greater inorganic N than clearcut sites and burn sites (Table 3.2 and Figures 3.6 and 3.7). Although inorganic nitrogen differences due to disturbance type are evident, individual sites show considerable variation due to inherent variability of natural systems (Figures 3.8 and 3.9). This is a consequence of problems with site matching for each disturbance type.

Following disturbance, such as fire or forest harvesting, there is generally an increase in nitrogen mineralisation in forest soils (Woodmansee and Wallach 1981; Gordon and Van Cleve 1983; Matson and Boone 1984; Frazer et al. 1990). This results in a flush of nutrients within the forest floor that are readily available for microbial and plant uptake (Ahlgren and Ahlgren 1965; Mroz et al. 1980). However, physical and chemical factors within less fertile sites such as ombrotrophic bogs can restrain nitrogen mineralisation (Vitousek 1981).

Table 3.2 Analysis of variance results for inorganic nitrogen and phosphorus concentrations based on disturbance type.

Inorganic Nitrogen	df	MS	*F*	*P*
Source[a]				
Disturbance	2	1.634	6.601	0.002
Microrelief	1	3.038	12.274	0.001
Depth	1	0.033	0.133	0.715

Extractable Phosphorus	df	MS	*F*	*P*
Source[a]				
Disturbance	2	0.117	0.83	0.437
Microrelief	1	0.067	0.476	0.491
Depth	1	0.958	6.022	0.010
Disturbance x Depth	2	0.537	3.825	0.023

[a] Only significant interactions from ANOVA are shown ($P < 0.10$).

For example, the high C/N of woody slash and peat can result in increases in gross nitrogen immobilisation, causing decreases in nitrogen availability until organic matter quality facilitates net mineralisation. Conversely, "small slash" (twigs and branches) (Covington 1981) from stem-only harvesting and ash from wildfires can provide a very rich N source which is mineralised readily (Viro 1974; Covington 1981; MacLean et al. 1983). Clearcut logging and wildfire differ with respect to their effect on nitrogen levels in that wildfires remove much more nitrogen from the forest - through volatilisation - than does logging (500-800 kg ha^{-1} and 43 kg ha^{-1} respectively) (MacLean et al. 1983; Teng et al. 1997). Higher extractable N values in cut sites may be a consequence of this, but total N in peat was not noticeably higher in cut sites. N content of the peat would probably portray the differences in losses better than extractable N.

While disturbance effects on N seem to be not reflected in peat N content, extractable N concentrations are probably related to differences in other controlling factors, such as temperature, moisture or plant uptake. Burn sites generally were wetter and colder than the cut sites and mature sites (Figures 3.1 to 3.5; refer to discussion on water table fluctuation). This could have had a detrimental effect on microbial activity, reducing organic matter decomposition. Warm and drier conditions within the undisturbed mature stands instead would provide conditions that are beneficial to microbial activity. This could be one reason why the mature stands had the highest available N concentrations.

From our measurements of inorganic and total N (Table 3.1), it seems that if there was any initial increase in nitrogen following disturbance it was not apparent after 10 years. The higher total nitrogen values of B2 and also B3 can be attributed to the presence of *Alnus rugosa* (alder) which, due to the presence of root associated N-fixing bacteria has been shown to increase nitrogen content of peat (Bhatti et al. 1998). However, higher total N did not result in higher extractable nitrogen within these sites (Figures 3.8 and 3.9). Based on soil temperature data it is possible that low N availability and high total N could be attributed to colder soil temperatures within burn sites (Figures 3.1 to 3.4), and may result in lower microbial activity. It should be noted that any increase in available and total N could be distorted due to nitrogen uptake by the re-colonising vegetation within the disturbed sites. The regenerating black spruce seedlings and shrubs could severely deplete available pools weakening availability indices unless annual plant uptake rates (trees, shrubs, herbs and mosses) are known. These analyses were not performed for this study.

3.4.3.2 Spatial Variability of N. Extractable N showed significant differences for microrelief (hollows > hummocks) (Table 3.2, Figures 3.6 and 3.7) despite considerable variation within individual sites (Figures 3.8 and 3.9). Examining each combination of microrelief and depth also showed differences between mature, clearcut and burn stands as expressed previously (Figures 3.6 and 3.7). For instance, clearcut and burn sites were not noticeably different from mature stands in the month of August except in hollows at 15-30 cm. Higher water table levels (reducing aerobic microbial activity) in hollows in disturbed sites could account for differences between disturbed sites with mature stands for the 15-30 cm depth in hollows in August. From the July sampling period burn sites were generally lower at the 15-30 cm depth for both hummocks and hollows. This could be due to colder soil temperatures (Figures 3.1 to 3.4) or to plant uptake differences. Also, there was no significant difference between disturbance types in the 0-15 cm depth for both hummocks and hollows for July and August sampling times. These similarities are probably related to differences in plant uptake and microbial processes occurring in this biologically active zone.

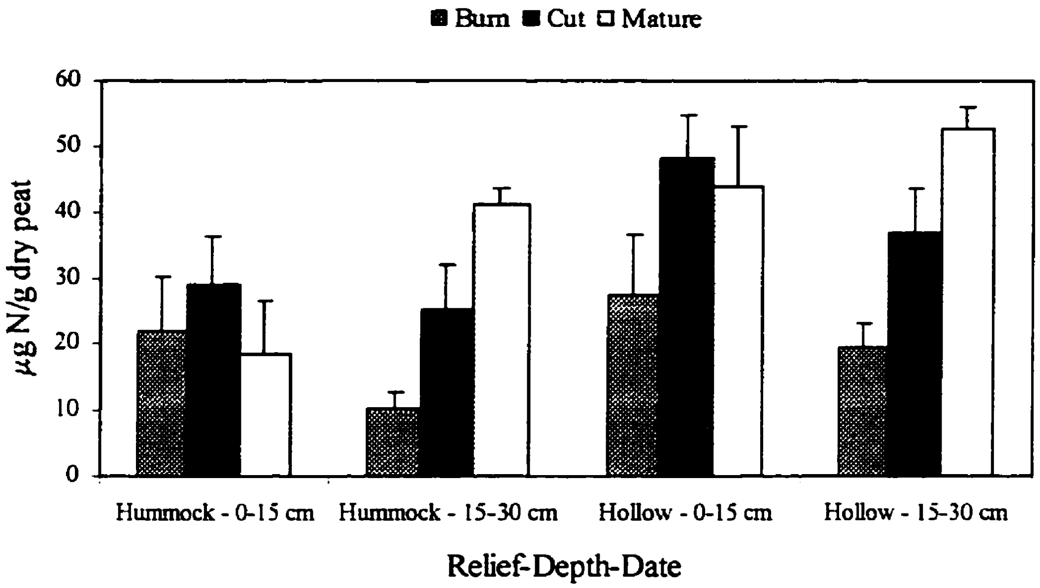


Figure 3.6 Inorganic nitrogen concentrations for July 1996 for each disturbance type. Mean ± standard error.

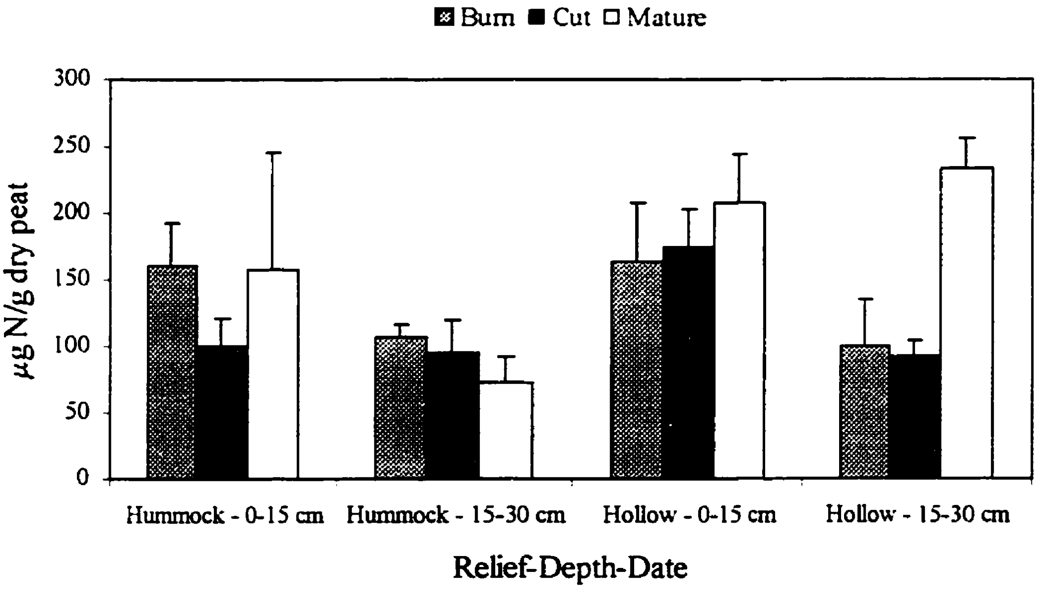


Figure 3.7 Inorganic nitrogen concentrations for August 1996 for each disturbance type. Mean ± standard error.

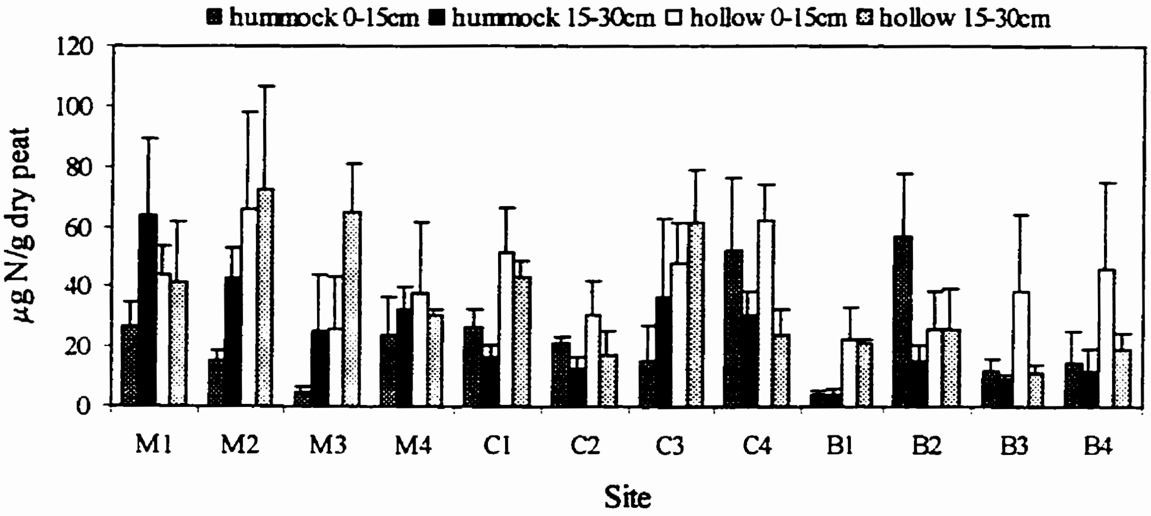


Figure 3.8 Inorganic nitrogen concentrations for July 1996 for each site. Mean ± standard error.

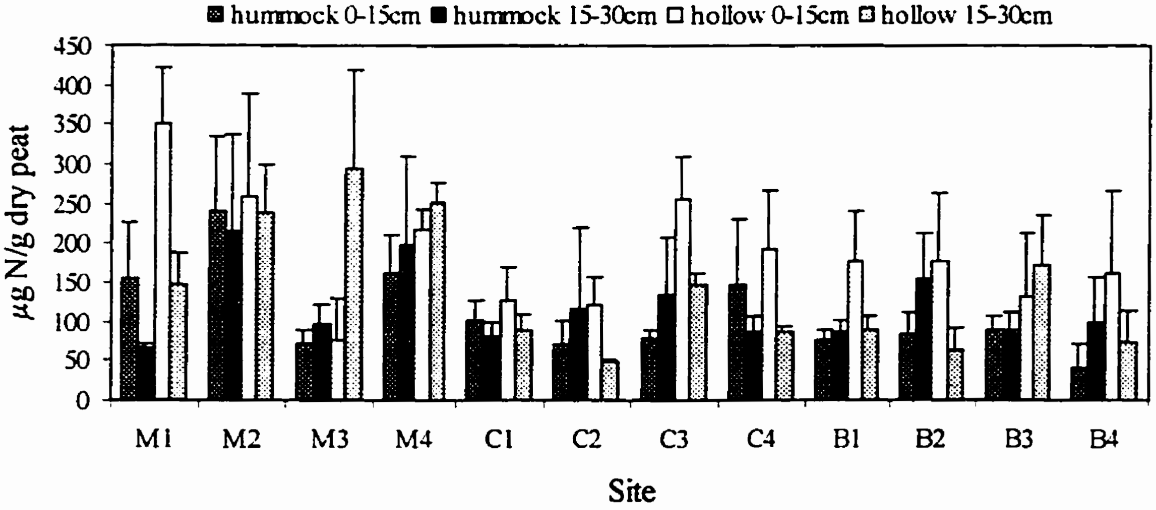


Figure 3.9 Inorganic nitrogen concentrations for August 1996 for each site. Mean ± standard error.

Examining each disturbance type separately showed similar trends for microrelief (hollow > hummock) (Tables 3.3 to 3.5 and Figures 3.6 and 3.7).

Lower concentrations of nitrogen (both extractable and total (Table 3.1)) in hummocks compared to hollows could be the result of three different processes: (1) leaching from hummocks to hollows (Damman 1978); (2) greater concentration of root biomass in hummocks causing nitrogen depletion (increased plant uptake); or (3) higher decomposability of *Sphagnum* species found within hollows (Johnson and Damman 1991). While it is generally assumed that most nitrogen mineralisation occurs within hummocks due to improved aeration (Richardson et al. 1978), leaching of nitrogen and other elements from hummocks occurs readily in bogs with similar microrelief variation (Damman 1978).

Table 3.3 Analysis of variance results for inorganic nitrogen and phosphorus concentrations for mature stands.

Inorganic Nitrogen	df	MS	*F*	*P*
Source[a]				
Site	3	0.566	1.973	0.125
Microrelief	1	1.189	4.221	0.043
Depth	1	0.340	1.208	0.275

Extractable Phosphorus	df	MS	*F*	*P*
Source[a]				
Site	3	0.274	2.875	0.042
Microrelief	1	0.008	0.088	0.767
Depth	1	0.049	0.511	0.477
Site x Microrelief	3	0.361	3.787	0.014

[a] Only significant interactions from ANOVA are shown ($P < 0.10$).

Table 3.4 Analysis of variance results for inorganic nitrogen and phosphorus concentrations for clearcut stands.

Inorganic Nitrogen	df	MS	*F*	*P*
Source[a]				
Site	3	0.339	2.110	0.106
Microrelief	1	0.993	6.181	0.015
Depth	1	0.385	2.396	0.126

Extractable Phosphorus	df	MS	*F*	*P*
Source[a]				
Site	3	0.229	1.306	0.279
Microrelief	1	0.287	1.633	0.205
Depth	1	0.673	3.873	0.054

[a] Only significant interactions from ANOVA are shown ($P < 0.10$).

Table 3.5 Analysis of variance results for inorganic nitrogen and phosphorus concentrations for burned stands.

Inorganic Nitrogen	df	MS	*F*	*P*
Source[a]				
Site	3	0.229	0.701	0.555
Microrelief	1	0.937	2.872	0.094
Depth	1	0.082	0.250	0.618

Extractable Phosphorus	df	MS	*F*	*P*
Source[a]				
Site	3	0.735	6.391	0.001
Microrelief	1	0.001	0.009	0.927
Depth	1	1.385	12.035	0.001

[a] Only significant interactions from ANOVA are shown ($P < 0.10$).

Seasonal variations in biological processes and periodic changes in water table level are reflected in elemental fluxes (Damman and French 1987). Between the two sampling dates there was an increase in the water table (up to 25 cm in M3; data not shown) and subsequent drop in almost all of the sites (Figures 3.5). This wetting-drying event could have stimulated microbial activity (increased nitrogen mineralisation) causing the flush of nitrogen. There could have also been a change in plant uptake, but N (and P) do not normally show such a dramatic fall peak because concentrations are controlled by microbial decay and not leaching from dead and senescent plants (Damman and French 1987). In addition, warmer soil temperatures later in the summer coinciding with lower plant uptake rates could explain higher N concentrations in August compared to July (Figures 3.6 and 3.7).

Differences in nitrogen availability with depth were not evident ($P > 0.7$) likely due to plant uptake. Bhatti et al. (1998) found that 80% of black spruce fine root biomass was within the top 10 cm of peat where nutrients and aeration are most favourable. While greater mineralisation in aerated layers produces higher concentrations of NH_4^+ (Avnimelech 1971), the high fine root biomass would accordingly deplete these pools. No depth differences in hollows could also be attributed to leaching of inorganic N from hummocks and anaerobic conditions in hollows thereby decreasing mineralisation rates. The high water table in the hollows of almost every disturbed site would reduce aerobic microbial activity responsible for N mineralisation and hindering N accumulation within the profile. Consistent nitrogen concentrations with depth in hollows were also evident with total N determinations (Table 3.1).

3.4.4 Phosphorus

3.4.4.1 Disturbance Effects. Phosphate levels were not significantly different between disturbance types (Table 3.2), although, site differences were apparent (Figures 3.12 and 3.13). Site differences in available P, however, showed no obvious trends due to high variability.

Disturbance effects on phosphorus should be similar to nitrogen since phosphorus is also found in much higher concentrations in organic form compared to inorganic in ombrotrophic bog systems (Damman 1978). After fire, P concentrations can be as much as 488% higher in the ash compared to unburned organic matter within forest floors (Smith 1970). However, like nitrogen, any initial increases diminish with time, potentially decreasing to pre-burn levels in three months (Smith 1970). Phosphorus losses in fire are also larger than clearcut logging (<40 kg ha^{-1} compared to 8 kg ha^{-1}) though not as significant as nitrogen differences (MacLean et al. 1983; Teng et al. 1997). Highly decomposable slash (not boles) left on clearcut sites should provide a good supply of available P for pioneer vegetation following disturbance, since the foliage within black spruce peatlands can contain up to 36% of the total P within the site (Teng et al. 1997). Unfortunately, research of P dynamics following logging is very limited compared to N. Comparisons of total P were not conducted in this experiment and literature values of total P in disturbed ombrotrophic bogs were not available.

3.4.4.2 Spatial Variability of P. Available phosphorus showed significant differences for depth (0-15 > 15-30 cm) (Table 3.2 and Figures 3.10 and 3.11). Finding no significant differences in microrelief was unexpected since P tends to concentrate in hollows due to leaching (Damman 1978). Increases in available P in August are probably the result of increased biological activity or changes in plant uptake as described for nitrogen. Also, as with nitrogen, there was variation in the results from individual sites, though not as extreme (Figures 3.12 and 3.13). Means determined for all possible combinations of factors did not show many differences between disturbance types (Figures 3.10 and 3.11). The only notable exception was the 15-30 cm depth for hollows in July and August in which disturbed sites had lower P concentrations relative to mature stands. This depth was consistently inundated in the disturbed sites. In aerated peat, P is almost always in organic form, with some complexed with Fe and Al (Damman 1978). In the zone of water fluctuation there is usually a large concentration of Fe and Al. Consequently, once within anaerobic peat, low concentrations of P are connected to the reduction of Fe from tri- to divalent state, thus Fe is mobile and present in very low concentrations. This causes almost all P to become mobile excluding the organic P pool.

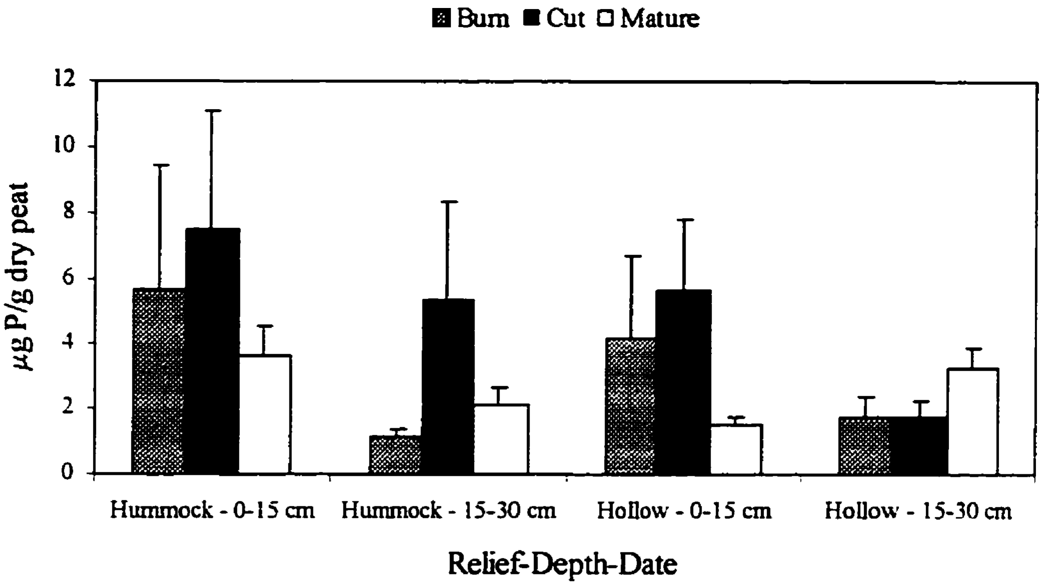


Figure 3.10 Extractable phosphorus concentrations for July 1996 for each disturbance type. Mean ± standard error.

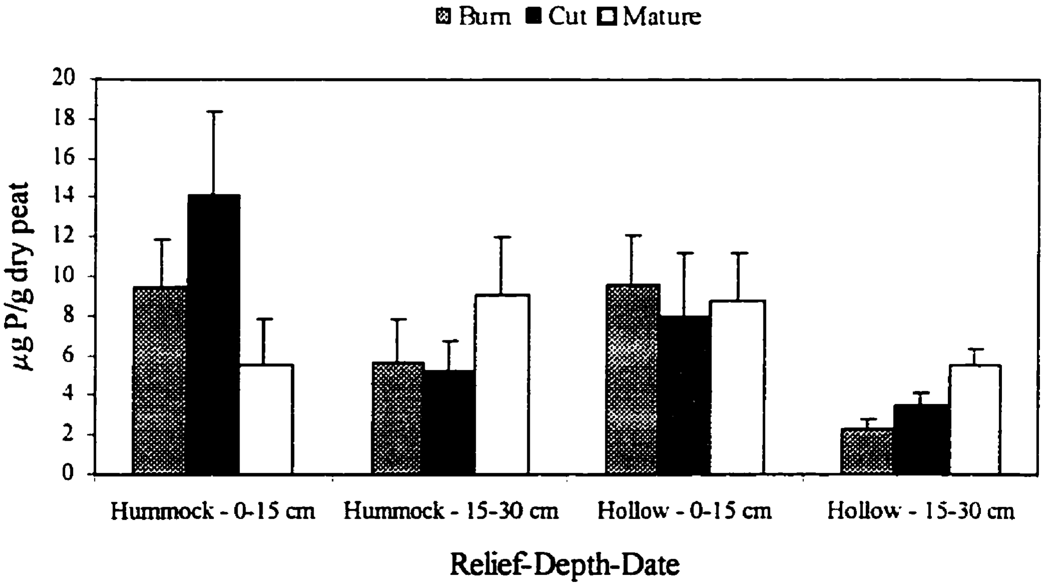


Figure 3.11 Extractable phosphorus concentrations for August 1996 for each disturbance type. Mean ± standard error.

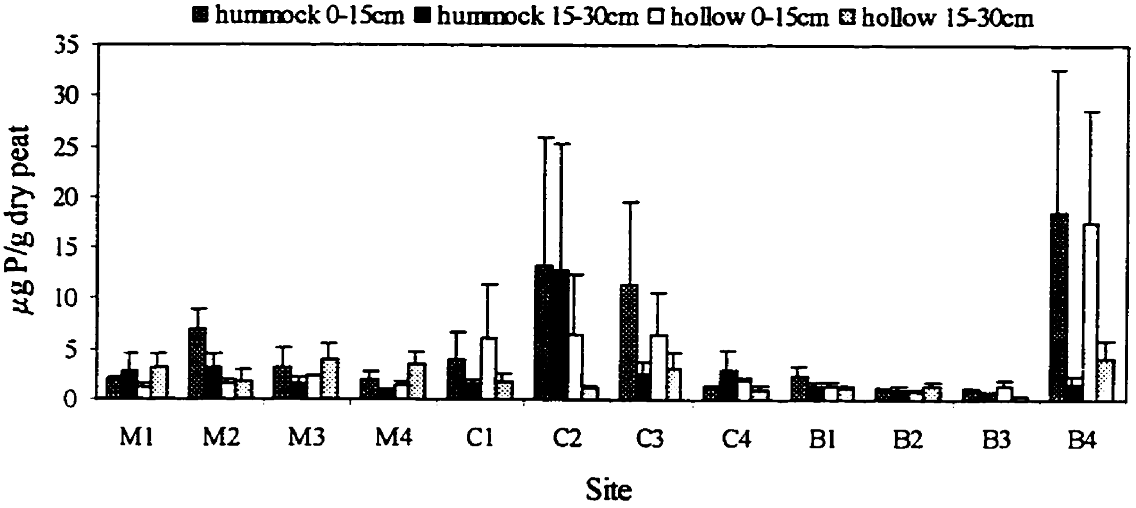


Figure 3.12 Extractable phosphorus concentrations for July 1996 for each site. Mean ± standard error.

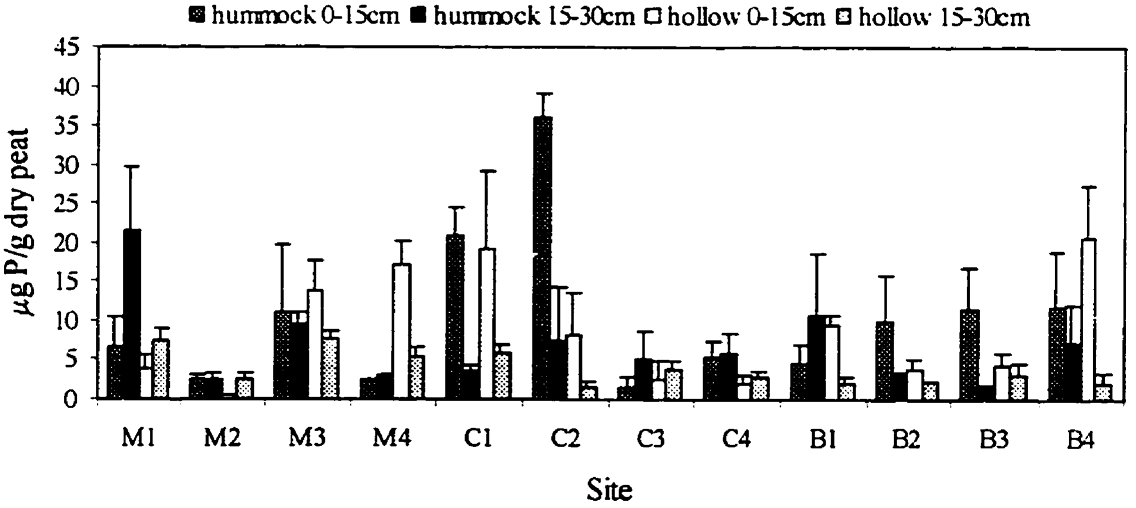


Figure 3.13 Extractable phosphorus concentrations for August 1996 for each site. Mean ± standard error.

Within each disturbance type, differences were also apparent (Tables 3.3 to 3.5). Depth trends were exhibited within every disturbance type except mature stands which had no depth differences (Table 3.3). This could be the result of greater leaching of high P levels in surface horizons within the mature sites or because of more consistent moisture conditions to 30 cm due to the lower water table. Drier conditions with depth may allow for higher P mineralisation and lower P complexation, thus increasing available P.

Higher concentrations of available P within 0-15 cm as compared to 15-30 cm is probably the result of Fe and Al complexation as mentioned previously. Normally Fe and Al concentrations increase as one approaches the zone of water table fluctuation, resulting in P in the soil solution to decrease as a result of complexation. In addition, P concentrations tend to increase towards the surface of peat due to P conservation in the actively growing parts of *Sphagnum* and slow release of P from organic matter during decomposition (Damman 1978). Even though P turnover is slow, this should result in higher concentrations of available P in surface horizons. It should be noted, however, that the P measured with these extractions determined labile P which can result from both mineralisation and the physico-chemical release of P from adsorbed and bound P (Verhoeven et al. 1990). Since different chemicals can extract different P pools, variations in extraction techniques used by researchers usually make comparisons between studies of P dynamics extremely difficult if not impossible.

3.5 Summary and Conclusions

Inorganic N and P concentrations showed different patterns based on disturbance type, microrelief and depth. Nitrogen showed differences based on disturbance type (matures > clearcuts and burns) and microrelief (hollow > hummock). Phosphorus exhibited differences for depth (0-15 > 15-30 cm). Differences between the effect of microrelief and depth on available N in particular were also apparent between disturbance types. Burns appeared to have caused a rise in water tables and decreases in soil temperature. Also concentrations of available nutrients for re-colonising vegetation were quite different from older mature stands. For the most part, however, concentrations of N and P were not significantly different between clearcuts and burns. Differences in re-colonisation and subsequent nutrient sequestration within the vascular plant biomass may exhibit significant differences between burns and clearcuts. This type of data is necessary for studies that focus on nutrient pools because of the high variability that nutrient pools show both temporally and spatially (Binkley and Hart 1989). In addition, while high levels probably indicate high availability, lower levels may not indicate infertile soils (Aber and Melillo 1991). With large amount of re-colonising trees, shrubs and herbs on disturbed sites it could be assumed that lower concentrations are the result of higher plant uptake due to higher fine root biomass.

From our results it is apparent that there is high spatial variability within each site and between individual sites within each disturbance type. The large standard errors for the nutrient data make analyses difficult and interpretation problematic. High spatial variability of nutrient concentrations and dynamics coincide with the high spatial variability exhibited by microbial processes. In many cases this variability precludes precise quantification (Parkin 1993). In addition to within site variability, the high between site variability of each disturbance type stresses the need of multiple sites when focusing on natural ecosystems. Making statements on clearcut and burn effects on site productivity based on the results of two sites could provide very different interpretations. If the goal of sustainable forestry is to maintain site productivity, we must focus on our inability to predict and quantify nutrient availability patterns. This means that research into nutrient availability and mechanisms of uptake needs to focus on increasing the number and type of forest ecosystems studied. Only then could the goal of sustainable forestry and maintenance of site productivity be achieved (Mahendrappa et al. 1986).

4. SPATIAL VARIABILITY OF NITROGEN MINERALISATION IN DISTURBED BLACK SPRUCE BOG ECOSYSTEMS

4.1 Abstract

A two month *in situ* incubation was performed to measure net nitrogen mineralisation within 9 black spruce (*Picea mariana* (Mill.) B.S.P.) bog ecosystems in eastern Manitoba. Sites were classified based on disturbance type; undisturbed mature forests (>110 years old), winter-logged clearcut stands (stem-only; 10-14 years old), and wildfire burn stands (11 years old). The objective of this study was to explore the spatial heterogeneity of nitrogen mineralisation within disturbed ombrotrophic bogs, affected by either natural wildfires or clearcut logging. Within sites, net nitrogen mineralisation was determined according to spatial gradients: (1) microrelief and (2) depth. Mineralisation rates were expected to exhibit patterns based on differences in site conditions (water table level, soil temperature and plant uptake) and substrate quality (total N) as influenced by disturbance type. Overall, net nitrogen mineralisation rates were not significantly different between disturbance types. Similarities between clearcut and burn sites were unexpected due to the generally colder and wetter conditions within burn sites. Nitrogen mineralisation exhibited microrelief (hummock > hollow) and depth differences (0-15 > 15-30 cm). These differences were not related to N content (total or extractable) within the peat. Favourable soil temperature and moisture regimes and/or higher substrate availability (e.g. labile carbon) likely caused the spatial differences. These results point

to a need for incorporation of spatial components into measurements of microbial transformations to allow for proper assessment of disturbance effects in forest management. Further work is required to evaluate the influence of plant uptake rates and nutrient storage in re-colonising vegetation on nitrogen mineralisation rates.

4.2 Introduction

Release of nitrogen from decaying organic matter is the major source of biologically available nitrogen within both forest and peatland ecosystems (Damman 1978; Van Cleve et al. 1983; Vitousek and Matson 1985). Within ombrotrophic bogs, nutrient mineralisation is the primary source of nitrogen for vascular plants and microorganisms as atmospheric nutrient inputs are sequestered by the living moss layer (Damman 1978; Lee et al. 1986; Malmer 1988). As a consequence of high nitrogen demands by vascular plants and microbial populations, the nitrogen pool is small and turnover is rapid (Vitousek and Matson 1984, Urban and Eisenreich 1988). Therefore, low nitrogen levels could be interpreted as being caused by high uptake rather than infertile soils (Aber and Melillo 1991; also refer to Chapter 3).

Soil nitrogen transformations are controlled by environmental factors (e.g. moisture and temperature) and substrate availability (Vitousek 1981). Disturbances, such as forest harvesting and wildfire, impact nitrogen turnover by affecting organic matter decomposition through changes in soil temperature, moisture, fertility and organic matter quality (Armenteno and Menges 1986; Trettin et al. 1995). The net result is increased nitrogen mineralisation (Gordon and Van Cleve 1983; MacLean et al. 1983; Matson and

Boone 1984) coinciding with decreased plant uptake. While it is known that decreased plant uptake can last from two to several years following disturbance (Marks 1974), unanswered questions still remain about the duration of heightened nitrogen mineralisation rates (Frazer et al. 1990).

The objectives of this study were to determine *in situ* nitrogen mineralisation rates within disturbed black spruce ombrotrophic bogs, affected by either clearcut logging or natural wildfires 10 years after disturbance. N mineralisation differences between microrelief and depth were chosen to evaluate the effect of changes in soil temperature and moisture regimes on microbial activity following disturbance. The relationship between substrate quality of peat (total N) and nitrogen mineralisation was also studied to determine if mineralisation/immobilisation rates differed with respect to disturbance history.

4.3 Materials and Methods

4.3.1 Site Description

Sites were chosen within the Manitoba Model Forest, a 900 000 ha area located on the east side of Lake Winnipeg, Manitoba (96° 15' W) extending eastwards to the Ontario border (95° 07' W). Its north-south borders reach from the Winnipeg River (50° 20' N) to just north of the Wanipigow River and includes an area on the north side of Wallace Lake (51° 05' N). The area is characteristic of the Canadian Shield, predominantly bedrock with the remaining area split between organic soils and deep lacustrine, glaciofluvial and till deposits. Mean precipitation is 564.9 mm and average January temperature is –19.5°C with July temperature of 18.6°C (Environment Canada 1996).

For this study, 9 *Picea mariana* (Mill.) B.S.P. (black spruce) stands with organic deposits greater than 1 m in thickness were chosen. The shrub layer within these sites was dominated by *Ledum groenlandicum*, *Chamaedaphne calyculata* and *Vaccinium vitis-idaea*. The moss community consisted of *Pleurozium schreberi*, *Sphagnum magellanicum*, *S. fuscum*, *S. girgensohnii*, *S. nemoreum*, *Dicranum undulatum*, *Polytrichum commune*, *P. juniperinum* and *P. strictum*. Within the burn sites only, *Pinus banksiana* was also present. All sites (except B2 - minerotrophic fen) are classified as ombrotrophic bogs (poor minerotrophic and acidic, pH < 4) with *Sphagnum* moss dominating the entire thickness of the peat. Sites were separated on the basis of disturbance with four sites from each disturbance type; undisturbed mature forests (**M**) (trees > 110 years old and >10 cm diameter at chest height; closed canopy), winter-logged clearcut stands (**C**) (stem-only; approximately 10-14 years old), and wildfire burned stands (**B**) (approximately 10 years old). Table 4.1 shows soil classifications and pH values for most of the sites within this study.

Table 4.1 Soil classification and pH values from sites selected for this study.

Site[a]	**Soil classification**[b]	**pH**[c]
B1	Typic Fibrisol	3.11
B2	Humic Mesisol	4.68
B3	Fibric Mesisol	3.17
C1	Terric Humic Fibrisol	3.17
C2	Fibric Mesisol	3.25
C3	Fibric Mesisol	3.19
M1	Terric Mesic Fibrisol	3.10
M2	Typic Mesisol	3.13
M3	Humic Fibrisol	3.15

[a] Site classification = disturbance type + replicate number.

[b] Soil Classification Working Group (1998)

[c] pH determined using a 1:4 ratio in 0.01M $CaCl_2$

4.3.2 *In Situ* Nitrogen Mineralisation

Nitrogen mineralisation was determined by measuring inorganic N concentrations in peat samples incubated in polyethylene bags buried *in situ* for two months (Hart et al. 1994). Sampling for the incubation experiment involved selecting three hummocks and three hollows within each site. The living moss was removed and peat was sampled from 0-15 cm and 15-30 cm depths using handsaws. Sampling occurred on 2 July 1996. Samples were divided into two in the field with one half placed into a 1-mm thick polyethylene bag and then reburied in its original hole for 2 months. The other half, to be used for determination of initial inorganic N (NH_4^+ and NO_3^-) concentrations, was doubled bagged in polyethylene bags and stored on ice until returning to the lab. All samples were placed in freezers until they were extracted. Nitrogen extractions were performed using 5 g oven dry equivalent field moist soil. Samples for nitrogen determination were extracted with 100 ml of 2M KCl solution, shaken for 1 hour and then filtered through Whatman #2 filter paper. All filtrates were frozen following extraction. Colourimetric analyses of nitrogen filtrates were performed on a Technicon Autoanalyzer II. Nitrate was analysed by the cadmium reduction procedure and ammonium by the indophenol blue procedure ((Technicon® Instrument Corp. 1971, 1973 respectively)). All values were expressed as µg NH_4^+-N and NO_3^--N (g dry peat)$^{-1}$. Inorganic nitrogen values were summed to give a total inorganic N (µg N g dry peat^{-1}). Net N mineralisation rates were then calculated by subtracting initial inorganic-N concentrations from final inorganic-N concentrations. Net nitrification was not determined due to very low nitrate concentrations.

4.3.3 Water Table and Soil Temperature Monitoring

For the summer of 1996 water table depth and soil temperature was monitored every two weeks. Water table depth was determined using piezometers constructed from slotted PVC pipes which were inserted in two hummocks within each site. Soil temperature changes were monitored using thermocouples which were placed in one hummock and one hollow within each site. Temperatures were taken from the surface of the living moss (0 cm), 10, 20, 30, 60 and 90 cm into the peat.

4.3.4 Total Nitrogen

Samples were oven dried (70 °C) and ground with a ball mill prior to analysis for carbon and nitrogen content. Total N (% dry weight) was determined by sample combustion on a Leco CHN analyser (Leco Corporation, St. Joseph, Michigan). Concentrations were expressed as mg N/g oven dry soil.

4.3.5 Statistical Analyses

Differences in (1) nitrogen mineralisation, (2) initial inorganic nitrogen concentrations and (3) total nitrogen were evaluated by analysis of variance between the three disturbance types. 3-factor ANOVAs were performed with disturbance type, microrelief classification (e.g. hummock vs. hollow) and depth as factors. 3-factor ANOVAs were also performed for each disturbance type separately with site replicates, microrelief classification and depth as factors. An $\alpha = 0.10$ was chosen due to high inherent variability of natural soil ecosystems. All statistical analyses were done using SYSTAT 7.0 (SPSS Inc., Chicago, IL).

4.4 Results and Discussion

4.4.1 Soil Temperature

Refer to section 3.4.1 for the discussion of soil temperature differences between disturbance types, microrelief and depth. Figures 4.1 to 4.4 show soil temperature fluctuations for the period of the *in situ* incubation. Soil temperature, as well as aeration status (as affected by water table height; see below), are important factors influencing microbial activity and thus, mineralisation rates.

4.4.2 Water Table

Refer to section 3.4.2 for the discussion of water table height differences between disturbance types. Figure 4.5 shows water table fluctuations for the period of the *in situ* incubation.

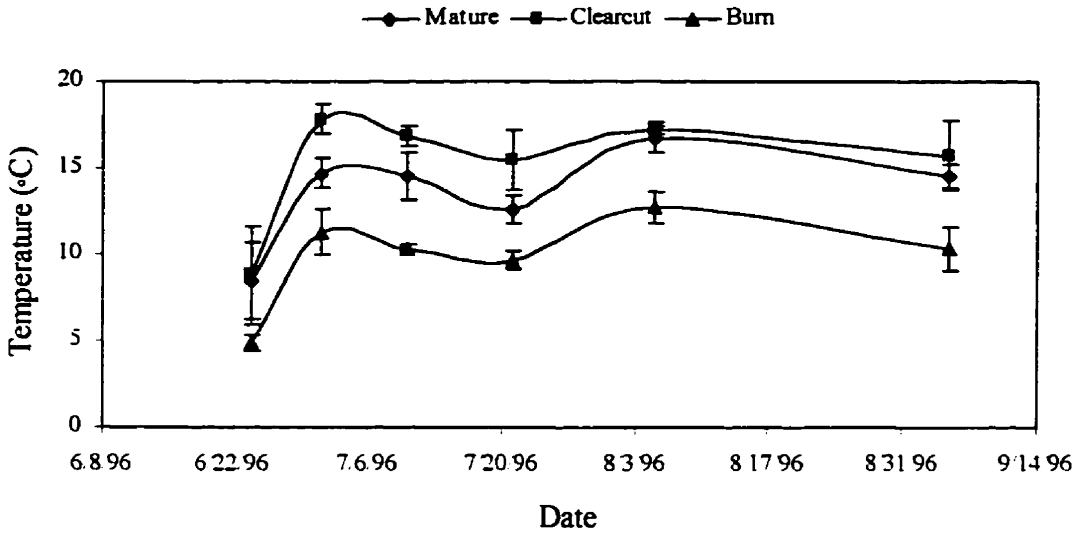


Figure 4.1 Soil temperature variation in hummocks 20 cm below moss surface.

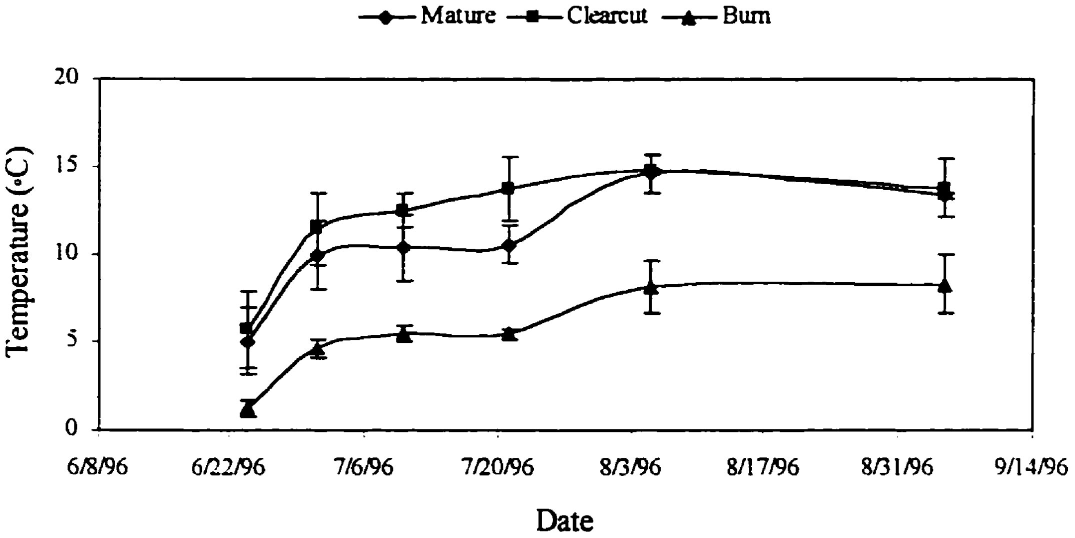


Figure 4.2 Soil temperature variation in hummocks 30 cm below moss surface.

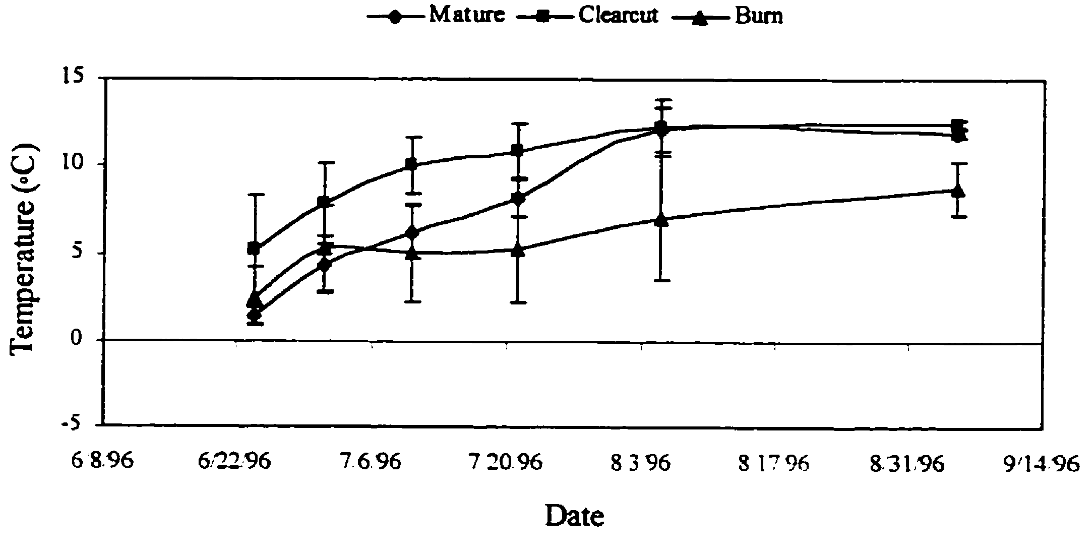


Figure 4.3 Soil temperature variation in hollows 20 cm below moss surface.

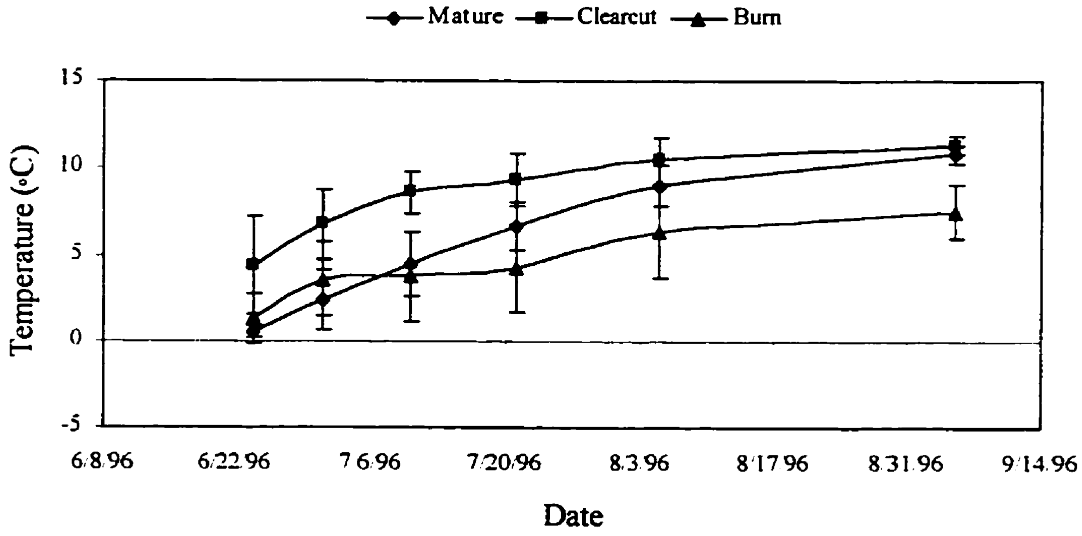


Figure 4.3 Soil temperature variation in hollows 30 cm below moss surface.

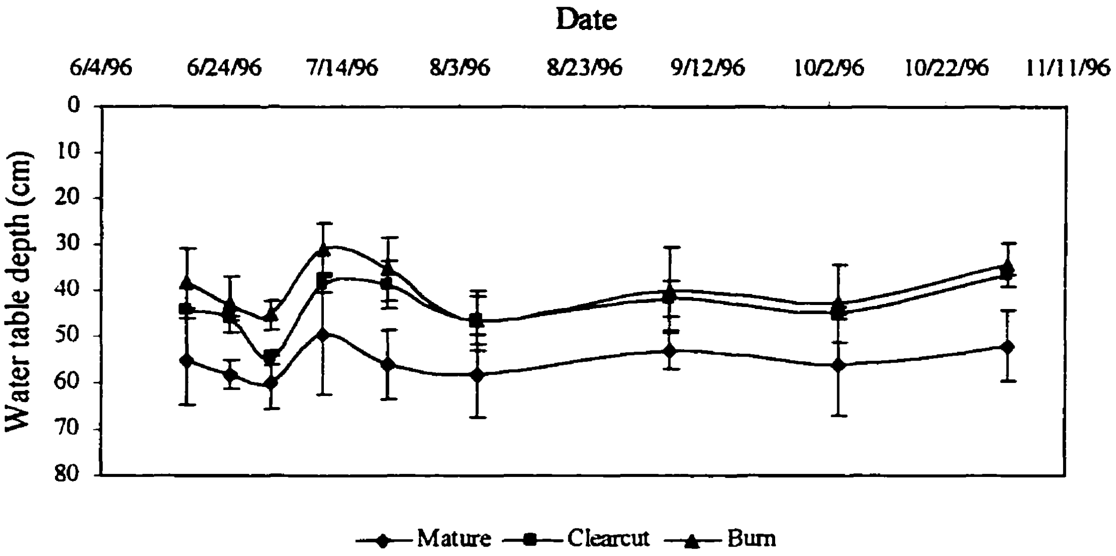


Figure 4.5 Water table fluctuation for each disturbance type for the duration of the incubation (as measured in hummocks only).

4.4.3 Nitrogen Mineralisation

Results from the 2 month incubation period indicated that there were no significant differences between disturbance types (Table 4.2; refer to Figure 4.6). Lack of statistically different nitrogen mineralisation rates is in accordance to the considerable variation (Figure 4.9), within and between sites. This was further demonstrated by the large standard errors associated with mineralisation measurements.

In less fertile sites such as ombrotrophic bogs, increases in nitrogen mineralisation due to disturbance may not follow typical patterns exhibited in upland forest soils (Vitousek 1981). With both fire and logging death of trees and understory vegetation results in an increase in substrate availability in the form of slash and dead roots. Additionally, microbial activity and subsequent mineralisation rates increase as a result of decreased

Table 4.2 Analysis of variance results for net nitrogen mineralisation, initial extractable nitrogen and total nitrogen for all disturbance types and spatial parameters.

Net Nitrogen Mineralisation	df	MS	*F*	*P*
Source[a]				
Disturbance	2	0.001	1.585	0.210
Microrelief	1	0.002	4.757	0.032
Depth	1	0.003	9.961	0.002

Initial Inorganic Nitrogen	df	MS	*F*	*P*
Source[a]				
Disturbance	2	0.096	3.921	0.023
Microrelief	1	0.281	11.484	0.001
Depth	1	0.033	1.336	0.251

Total Nitrogen	df	MS	*F*	*P*
Source[a]				
Disturbance	2	0.865	5.608	0.005
Microrelief	1	2.334	15.164	<0.001
Depth	1	0.042	0.272	0.603
Disturbance x Depth	2	0.376	2.436	0.093

[a] Only significant interactions from ANOVA are shown ($P < 0.10$).

nutrient competition microbial communities and vascular plants. However, vegetation on less fertile soils tend to have higher C/N ratios, which favour nutrient immobilisation. Therefore any increases in nitrogen mineralisation rates may be delayed, for up to 15 years (Covington 1981), until C/N ratios decline enough to favour net mineralisation (Vitousek 1981). Mineralisation/immobilisation trends in ombrotrophic bogs will depend on the extent of changes in site conditions and whether there are significant inputs of easily decomposable and nutrient-rich organic material following disturbance. Both nitrogen immobilisation and microbial activity in ombrotrophic bogs are limited not by low N concentrations, but by other nutrient deficiencies (Damman 1988) and the chemical composition of *Sphagnum* litter (Clymo 1965). Consequently, nitrogen mineralisation in bogs can occur at C/N ratios > 40 (Malmer and Holm 1984; Damman 1988; Verhoeven et al. 1990). Any changes in microbial activity (i.e. in the form of increased decomposition) following disturbance will coincide with increased nitrogen mineralisation depending on the substrate quality and as long as microbial nitrogen demand remains low. If microbial activities increase due to favourable site conditions and improved substrate quality, gross immobilisation rates could also increase as microbial N demands rise. Higher total N concentrations in the disturbed sites (Figure 4.7) could be indicative of inputs of nutrient-rich organic inputs. Similarities in N mineralisation between the disturbed sites and mature stands indicated a lack of correlation between N mineralisation and total N. N mineralisation at low N contents further establishes the fact that nitrogen content does not influence mineralisation rates within ombrotrophic bogs (Damman 1988; Verhoeven et al. 1990). Similar mineralisation rates in clearcut and burn sites cannot be explained by environmental conditions alone. Burn sites are generally cooler and wetter (Figures 4.1 to 4.5; refer to discussion in sections 3.4.1 and 3.4.2) which may limit microbial activity significantly. Therefore, other factors besides aeration and temperature, such as nutrient deficiencies, seem to be affecting N mineralisation rates.

Both microrelief and depth had significant effects on nitrogen mineralisation (Table 4.2). Net nitrogen mineralisation was higher in hummocks than hollows and higher at 0-15 cm than 15-30 cm (Figure 4.6). These differences could be attributed to the effect of temperature and/or redox conditions on microbial activity (Verhoeven et al. 1990).

Hummocks are generally warmer and drier than hollows, and moisture contents increased with depth. Higher mineralisation in the 0-15 cm depth could also be the result of decreasing C availability (labile carbon compounds) with depth rather than nutrient availability (Johnson and Damman 1993). This subsequently decreases microbial activity and decomposition rates. There was also a change in total nitrogen content with relief (hummock < hollow) but not with depth (Table 4.2 and Figure 4.7). However, higher nitrogen content within hollows did not coincide with higher mineralisation rates. In addition, higher N mineralisation at 0-15 cm compared to 15-30 cm were not related to N content. The absence of any relationship between total N and net mineralisation was also evident when examining individual sites for each microrelief type and depth (Figures 4.8 and 4.9). Initial inorganic nitrogen values followed the same trends (hummocks < hollows), and again higher inorganic nitrogen did not lead to higher mineralisation rates (Table 4.2 and Figures 4.6 and 4.10). Comparisons of initial inorganic nitrogen/net nitrogen mineralisation (%) showed that hollows and the 15-30 cm had either low microbial activity or not as high a demand for nitrogen as indicated by high % (data not shown). However, higher % in mature stands compared to the disturbed sites is probably indicative of poorer substrate quality (low total N). Therefore, not as much nitrogen is released compared to peat in clearcuts and burns. As shown previously (Chapter 3), higher nitrogen concentrations in hollows are probably the result of leaching from hummocks (Damman 1978). Higher N mineralisation rates and high concentrations of fine roots (i.e. high plant N uptake) in surface horizons could explain similarities for extractable N with depth.

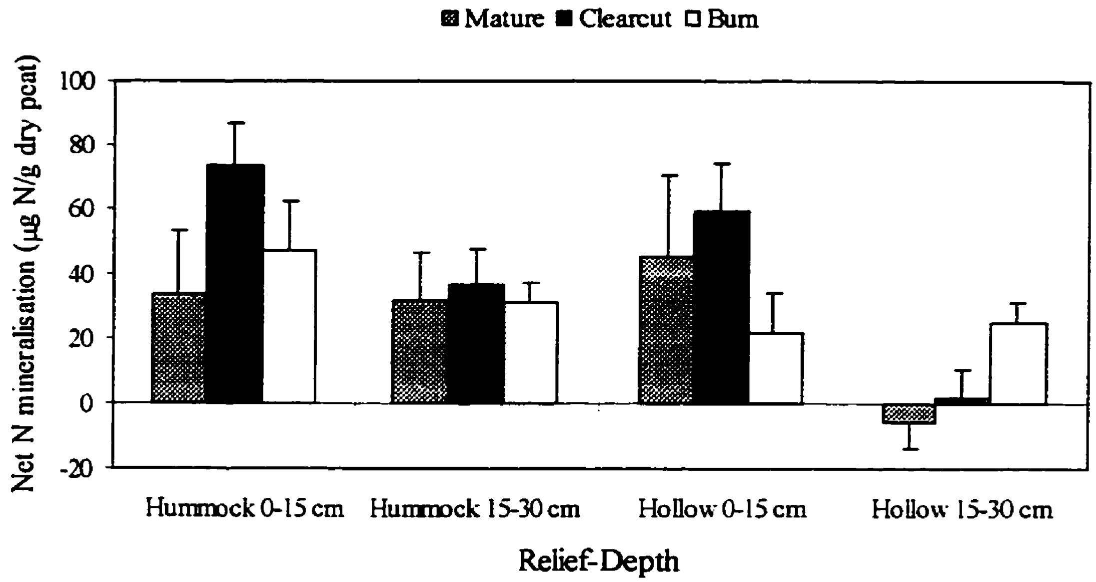


Figure 4.6 Net nitrogen mineralisation rates at each spatial combination for all disturbance types. Mean ± standard error.

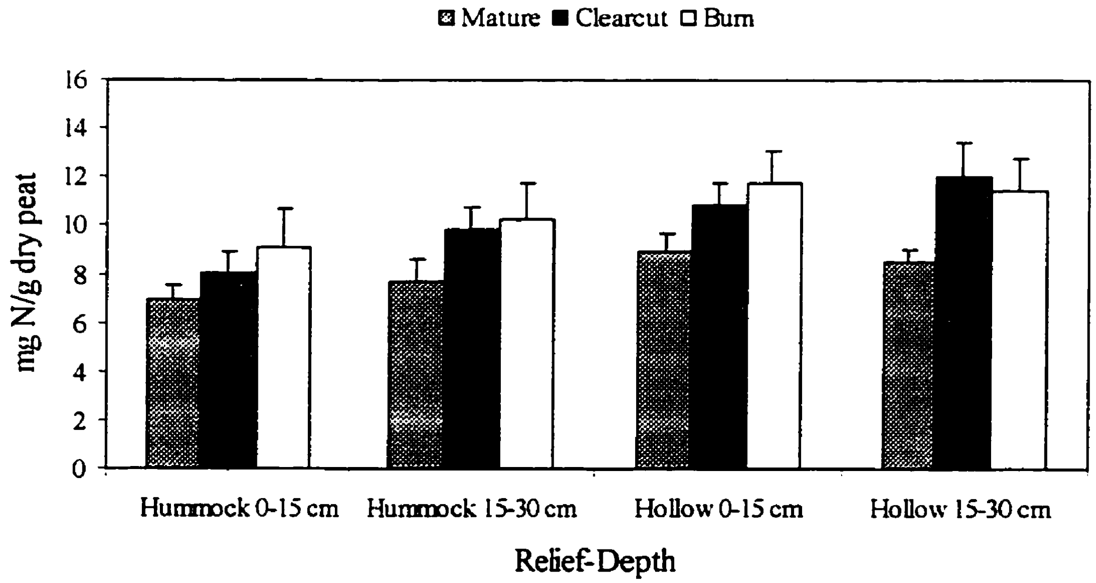


Figure 4.7 Total nitrogen concentrations at each spatial combination for all disturbance types. Mean ± standard error.

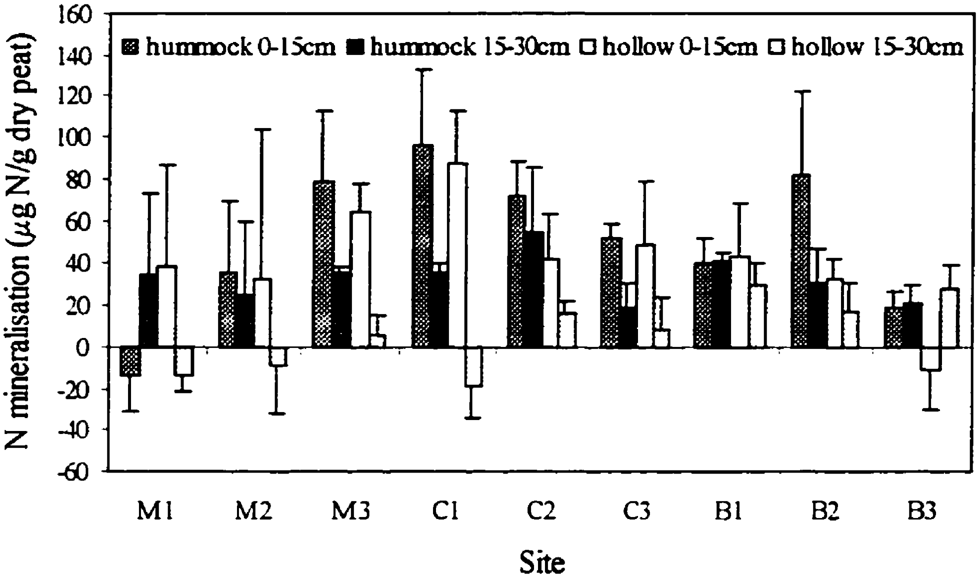


Figure 4.8 Net nitrogen mineralisation rates at each spatial combination for all sites. Mean ± standard error.

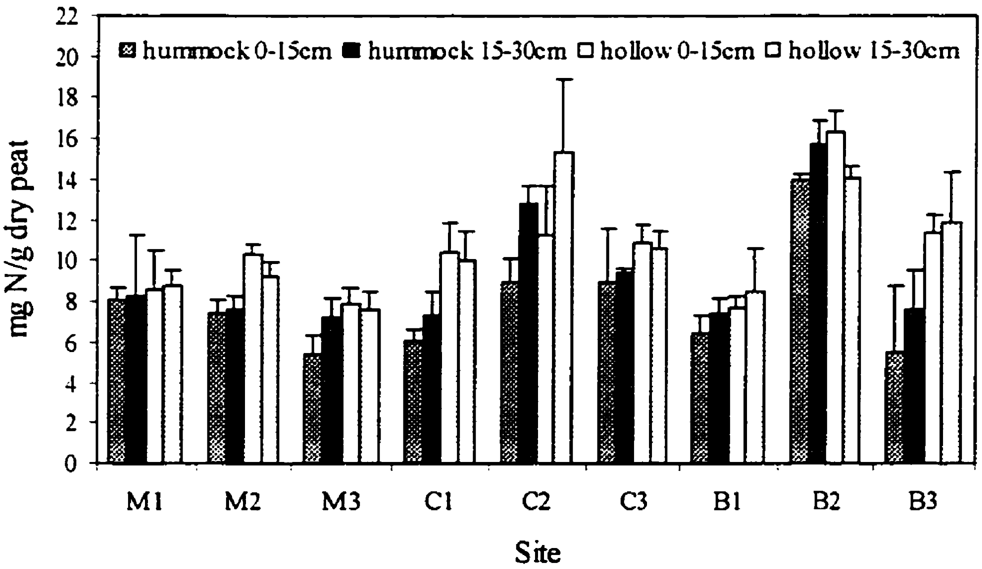


Figure 4.9 Total nitrogen concentrations at each spatial combination for all sites. Mean ± standard error.

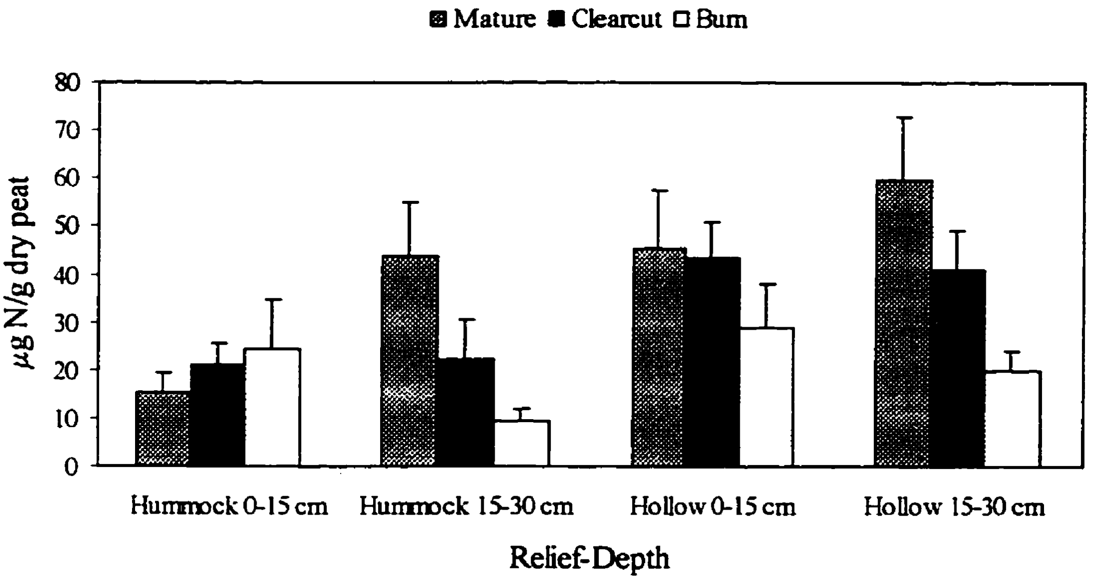


Figure 4.10 Initial inorganic nitrogen concentrations at each spatial combination for all disturbance types. Mean ± standard error.

In the surface horizon of hummocks, N mineralisation rates were not noticeably different between disturbance types (Figure 4.6). Equal N mineralisation rates are relevant considering black spruce seedlings tend to establish on drier hummocks and requirements of re-generating black spruce may be higher. Burn sites showed net N mineralisation in hollows at 15-30 cm which is unexpected considering the complete saturation of this horizon. Non-significant differences between disturbance types can be explained by the large standard errors, a consequence of high variability within the sites (Figure 4.9).

Examination of each disturbance type independently provided further insight into N mineralisation trends. Only clearcut sites exhibited microrelief and depth trends significantly (Tables 4.3 to 4.5). Compared to clearcuts and burns, mature stands had noticeably higher variation in N mineralisation rates (Figure 4.9). It should be noted that similar mineralisation rates for each relief type and depth within mature and burn sites did not lead to similar extractable N levels (Tables 4.3 and 4.5; Figures 4.6 and 4.10), possibly due to plant uptake or leaching. The effect of plant uptake on nutrient concentrations was best exemplified in clearcuts as higher mineralisation rates in hummocks and surface horizons did not lead to higher extractable N (Table 4.4 and Figures 4.6 and 4.10).

Table 4.3 Analysis of variance results for net nitrogen mineralisation, initial extractable nitrogen and total nitrogen for mature stands.

Net Nitrogen Mineralisation	df	MS	*F*	*P*
Source[a]				
Disturbance	2	0.001	1.165	0.329
Microrelief	1	0.000	0.455	0.506
Depth	1	0.001	1.599	0.218

Initial Inorganic Nitrogen	df	MS	*F*	*P*
Source[a]				
Disturbance	2	0.504	2.947	0.072
Microrelief	1	0.849	4.960	0.036
Depth	1	0.658	3.845	0.062

Total Nitrogen	df	MS	*F*	*P*
Source[a]				
Disturbance	2	0.025	1.913	0.173
Microrelief	1	0.063	4.737	0.041
Depth	1	0.001	0.050	0.826

[a] Only significant interactions from ANOVA are shown ($P < 0.10$).

Table 4.4 Analysis of variance results for net nitrogen mineralisation, initial extractable nitrogen and total nitrogen for clearcut stands.

Net Nitrogen Mineralisation	df	MS	*F*	*P*
Source[a]				
Disturbance	2	0.000	0.828	0.449
Microrelief	1	0.001	4.435	0.046
Depth	1	0.003	16.175	<0.001

Initial Inorganic Nitrogen	df	MS	*F*	*P*
Source[a]				
Disturbance	2	0.150	1.653	0.213
Microrelief	1	0.978	10.799	0.003
Depth	1	0.010	0.115	0.737

Total Nitrogen	df	MS	*F*	*P*
Source[a]				
Disturbance	2	0.070	4.046	0.031
Microrelief	1	0.121	6.982	0.014
Depth	1	0.041	2.382	0.136

[a] Only significant interactions from ANOVA are shown ($P < 0.10$).

Table 4.5 Analysis of variance results for net nitrogen mineralisation, initial extractable nitrogen and total nitrogen for burned stands.

Net Nitrogen Mineralisation	df	MS	*F*	*P*
Source[a]				
Disturbance	2	0.000	2.830	0.079
Microrelief	1	0.000	2.457	0.130
Depth	1	0.000	0.321	0.576

Initial Inorganic Nitrogen	df	MS	*F*	*P*
Source[a]				
Disturbance	2	0.608	4.907	0.016
Microrelief	1	0.546	4.409	0.046
Depth	1	0.125	1.010	0.325
Site x Microrelief	2	0.348	2.813	0.080

Total Nitrogen	df	MS	*F*	*P*
Source[a]				
Disturbance	2	0.343	17.003	<0.001
Microrelief	1	0.132	6.535	0.018
Depth	1	0.017	0.841	0.369
Site x Microrelief	2	0.069	3.427	0.050

[a] Only significant interactions from ANOVA are shown ($P < 0.10$).

4.5 Summary and Conclusions

Nitrogen mineralisation showed significant differences for microrelief and depth, but none between disturbance types. This is due to high spatial variability both within and between sites and disturbance types. These results stress the need for multiple sites when examining the effects of disturbance on nutrient cycling in natural ecosystems. Using only one site per disturbance type could have produced much different results. In terms of ecosystem recovery, similar mineralisation rates between disturbance types after 10 years appear to have been achieved. However, whether similar N mineralisation for an older mature stand compared to a young growing stand is adequate on these disturbed bogs remains to be seen. This is of more concern considering that the low mineralisation rates present in these sites may lead to severely N-limited black spruce (Foster et al. 1997). To supply adequate nitrogen (via mineralisation) for satisfactory tree growth it is generally assumed that peat N levels have to be greater than 1.5% (Foster et al. 1997). Consequently, almost every site used in this study had peat N levels below this standard.

Higher N mineralisation in hummocks and at the 0-15 cm depth did not lead to higher extractable N pools and was not correlated to total N concentrations. These results support the current belief that N concentrations do not control nitrogen mineralisation, rather other limiting factors such as overall nutrient deficiencies, environmental variables, C limitation and plant uptake affect microbial activity and thus nitrogen mineralisation (Damman 1988, Verhoeven et al. 1990). In addition, severe limitations on microbial activity act to reduce the microbial populations ability to immobilise N (Damman 1988). Consequently, nitrogen mineralisation was greater than immobilisation even though total N levels of the peat suggest that immobilisation should precede mineralisation. However, mineralisation rates in ombrotrophic bogs, and subsequent N released, would still produce insufficient N for plant requirements (Foster et al. 1997). This results in widespread N deficiencies in all vegetation within ombrotrophic bogs and stresses the need to conserve nutrients (Small 1972a). One way to do this is by forestry practices which leave advanced growth of tree seedlings (careful logging) to ensure nutrients released by increased activity following disturbance are not lost (Foster et al. 1997).

Microbial-mediated N mineralisation plays an integral role in forest re-colonisation and sustainability of stand production. If mineralisation produces insufficient N for both vegetation and microbial communities this could have severe limitations on re-establishing plant populations. Thus, an increased understanding of this process is a necessary component in any attempt to maintain site productivity in bog ecosystems. Questions remain to be answered about the effect of increased disturbance frequency (e.g. shortening of rotation lengths or increases in fire frequency due to global warming) and subsequent impacts on forest sustainability.

5. SUBSTRATE QUALITY INFLUENCE ON NITROGEN AND PHOSPHORUS MINERALISATION IN DISTURBED BLACK SPRUCE BOG ECOSYSTEMS

5.1 Abstract

A 28-day aerobic incubation was performed to measure net nitrogen and phosphorus mineralisation within 9 black spruce (*Picea mariana* (Mill.) B.S.P.) bog ecosystems in eastern Manitoba. Sites, classified according to disturbance type included; undisturbed mature forests (>110 years old), winter-logged clearcut stands (stem-only; 10-14 years old), and wildfire burn stands (11 years old). The objectives of this study were two-fold: (1) to assess peat substrate quality differences within black spruce bogs affected by either clearcut logging or natural wildfires and (2) to determine whether there are any significant relationships between peat substrate quality and net N/P mineralisation. Peat samples were taken from the 0-15 cm horizon of hummocks (microhighs) only. N and P mineralisation was expected to exhibit patterns based on substrate quality and disturbance type. Multiple discriminant analysis showed that disturbance types differed with respect to substrate quality. Labile carbon fractions (water-soluble carbohydrates) and to a lesser degree, recalcitrant carbon fractions (lignin), best discriminated between the groups. The latter may be attributed to high percentage lignin within mature stand samples due to the invasion of *Pleurozium schreberi*. Principal component analysis indicated that samples were described by three different components related to carbon, phosphorus and nitrogen compounds respectively. Using principal component scores, N mineralisation was best predicted by N content ($P < 0.01$) and recalcitrant carbon fractions ($P < 0.10$), while P mineralisation was only significantly explained by N content ($P < 0.10$). However, proportion of variance explained by substrate quality parameters was very low ($r^2 < 0.17$). Both N and P mineralisation rates within burn sites were predicted significantly by N content ($r^2 = 0.562$ and 0.302, respectively), while N mineralisation within clearcuts depended on recalcitrant carbon content ($r^2 = 0.26$). Results indicate substrate quality parameters influence N and P mineralisation differently in clearcuts and burns. Substrate quality parameters, however, explain < 17% of the variance in the data indicating that there are other factors controlling N and P mineralisation. Net negative N and P mineralisation (immobilisation) for all disturbance types may point to a problem with methodologies (e.g. incubation period) since microbial immobilisation of nutrients, especially N, is inhibited within ombrotrophic bogs due to factors such as nutrient and available energy deficiencies. In light of this, predicting N and P mineralisation from substrate quality in bogs should be incorporated with comparisons with site conditions to allow for a better understanding of disturbance effects on microbial transformations.

5.2 Introduction

Decomposition and subsequent nutrient release is influenced by the interaction of three main factors: resource quality, environmental conditions and the decomposer community (Swift et al. 1979). Resource, or substrate quality, is defined by the chemical composition of plant litter (e.g. types of carbon compounds, nutrient concentrations). Its effects on decomposition and nutrient mineralisation have been exhibited in both upland (e.g.

Melillo et al. 1982; Melillo et al. 1989) and wetland ecosystems (e.g. Johnson and Damman 1991; Updegraff et al. 1995).

In ombrotrophic bogs, nutrient inputs are solely from precipitation which are subsequently sequestered within the living *Sphagnum* carpet (Damman 1978). This results in an enrichment of nitrogen and phosphorus in peat (Clymo 1978). Consequently, nutrient availability for both vascular plant and microbial communities is controlled by nutrient mineralisation in peat (Damman 1988). Within ombrotrophic bogs, intrinsic litter quality is the dominant factor regulating *Sphagnum* decay (Johnson and Damman 1993). Characteristically, *Sphagnum* decay is slow, a result of deficiencies of essential inorganic nutrients, lack of an easily metabolised energy source, presence of decay inhibitors and/or decay resistant compounds. Controversy surrounds the importance of these variables in controlling peat decomposition and subsequent nutrient mineralisation. Nonetheless, substrate quality of peat plays an integral role in nutrient cycling especially when considering the large organic nutrient pools in bog ecosystems (Verhoeven et al. 1988).

Disturbance of wetland soils and vegetation results in an increase in the rate of organic matter decomposition either by alteration of soil moisture and temperature regimes, or by increasing substrate availability to soil microorganisms (Armentano and Menges 1986; Trettin et al. 1995). Substrate factors which play an integral role in N and P turnover, including stage of decomposition (Williams and Wheatley 1988) and nutrient content of the peat (Farrish and Grigal 1988), can be adversely affected by disturbance.

Understanding how disturbance regimes alter environmental and substrate factors is vital in estimating the availability of major nutrients within wetlands.

The objectives of this study were two-fold: (1) to assess peat substrate quality differences within black spruce (*Picea mariana* (Mill.) B.S.P.) bogs affected by either clearcut logging or natural wildfires and (2) to determine whether there are any significant relationships between peat substrate quality and net N and P mineralisation.

5.3 Materials and Methods

5.3.1 Site Description

Sites were chosen within the Manitoba Model Forest, a 900 000 ha area located on the east side of Lake Winnipeg, Manitoba (96° 15' W) extending eastwards to the Ontario border (95° 07' W). Its north-south borders reach from the Winnipeg River (50° 20' N) to just north of the Wanipigow River and includes an area on the north side of Wallace Lake (51° 05' N). The area is characteristic of the Canadian Shield, predominantly bedrock with the remaining area split between organic soils and deep lacustrine, glaciofluvial and till deposits. Mean precipitation is 564.9 mm and average January temperature is −19.5°C with July temperature of 18.6°C (Environment Canada 1996). For this study, 9 *Picea mariana* (Mill.) B.S.P. (black spruce) stands with organic deposits greater than 1 m in thickness were chosen. The shrub layer within these sites was dominated by *Ledum groenlandicum*, *Chamaedaphne calyculata* and *Vaccinium vitis-idaea*. The moss community consisted of *Pleurozium schreberi*, *Sphagnum magellanicum*, *S. fuscum*, *S. girgensohnii*, *S. nemoreum*, *Dicranum undulatum*, *Polytrichum commune*, *P. juniperinum* and *P. strictum*. Within the burn sites only, *Pinus banksiana* was also present. All sites (except B2 - minerotrophic fen) are classified as ombrotrophic bogs (poor minerotrophic and acidic, pH < 4) with *Sphagnum* moss dominating the entire thickness of the peat. Sites were separated on the basis of disturbance with four sites from each disturbance type; undisturbed mature forests (**M**) (trees > 110 years old and >10 cm diameter at chest height; closed canopy), winter-logged clearcut stands (**C**) (stem-only; approximately 10-14 years old), and wildfire burned stands (**B**) (approximately 10 years old). Table 5.1 shows soil classifications and pH values for most of the sites within this study.

Table 5.1 Soil classification and pH values from sites selected for this study.

Site[a]	**Soil classification**[b]	**pH**[c]
B1	Typic Fibrisol	3.11
B2	Humic Mesisol	4.68
B3	Fibric Mesisol	3.17
C1	Terric Humic Fibrisol	3.17
C2	Fibric Mesisol	3.25
C3	Fibric Mesisol	3.19
M1	Mesic Fibrisol	3.10
M2	Typic Mesisol	3.13
M3	Humic Fibrisol	3.15

[a] Site classification = disturbance type + replicate number
[b] Soil Classification Working Group (1998)
[c] pH determined using a 1:4 ratio in 0.01M $CaCl_2$

5.3.2 N and P Mineralisation

Sampling for the nitrogen and phosphorus mineralisation incubation experiment involved selecting eight hummocks within each site and removing peat from the 15 cm depth using handsaws. Sampling occurred in mid August 1997. Samples were doubled bagged in polyethylene bags and stored on ice until returning to the lab. On return, samples were placed in freezers until the incubation was to begin. An aerobic incubation was performed to determine mineralisation rates of N and P within each site (refer to Binkley and Hart 1989). Field moist soil was divided into two separate fractions; one for immediate extraction and the other for incubation. Incubation samples were placed into separate Mason jars and sealed. The soil was then incubated for 28 days in the dark at 10°C (temperature determined from temperature data loggers used during a 10 week decomposition trial). A dish of water was placed within each jar to minimise water loss. Jars were opened once a week for 45 minutes to maintain aerobic conditions. Following the incubation period, samples were extracted. Net N and P mineralisation rates were then calculated by subtracting initial inorganic-N and P concentrations from final inorganic-N and P concentrations. Using samples with original moisture contents and using an incubation temperature that simulated natural conditions was necessary to allow us to estimate the inherent N and P mineralisation within each site.

Nitrogen and phosphorus extractions were performed using 3 g oven dry equivalent field moist soil. Samples for nitrogen determination were extracted with 180 ml of 2M KCl solution, shaken for 1 hour and then filtered through Whatman #2 filter paper. Samples for phosphorus extraction were extracted with 180 ml of deionized water and 1 g of washed charcoal, shaken for 1 hour and then filtered through Whatman #42 filter paper. All filtrates were frozen following extraction. Colourimetric analysis of nitrogen filtrates was performed on a Technicon Autoanalyzer II. Nitrate was analysed with the cadmium reduction procedure and ammonium by the indophenol blue procedure (Technicon® Instrument Corp. 1971, 1973 respectively). Phosphorus was analysed following the ammonium molybdate-ascorbic acid procedure for water-soluble P after Olsen and Sommers (1982). All values were expressed as µg NH_4^+-N, NO_3^--N, and PO_4^--P (g dry peat)$^{-1}$. Inorganic nitrogen values were summed to give a total inorganic N (µg N g dry peat^{-1}) as nitrate concentrations comprised a minor component of total inorganic nitrogen.

5.3.3 CO_2 Production

Concurrent measurement of CO_2 evolution (as an index of microbial activity) was performed to aid in interpretation of net N and P mineralisation rates obtained during the aerobic incubation. A 7 ml scintillation vial with 5 ml of 0.1 *M* NaOH was placed into each Mason jar. These vials were replaced every week for the entirety of the incubation. CO_2-C concentration was determined using a total organic C method modified for use with the Technicon AutoAnalyzer II (Technicon® Instrument Corp. 1978).

5.3.4 Substrate Quality Determination

Total C and N were determined by sample combustion on a Leco CHN analyser (Leco Corporation, St. Joseph, Michigan). Total P was determined by digesting samples with H_2SO_4-H_2O_2 and analysing extracts on ICP. Cellulose and "lignin" content were determined by the Acid Detergent Fibre-H_2SO_4 procedure (Rowland and Roberts 1994). Here lignin refers to the recalcitrant organic fraction found within peat as *Sphagnum* peat does not contain true lignin (Erickson and Miksche 1974). Water-soluble carbohydrates were determined by a hot-water extraction (TAPPI 1993) followed by colourimetric analyses of the extracts (Dubois et al. 1956).

5.3.5 Statistical Analyses

Differences in nitrogen and phosphorus mineralisation were evaluated by mean comparisons between the three disturbance types and the nine individual sites independently. All values were log-transformed prior to analyses to correct for non-normality. Identical analyses were performed on substrate quality parameters to show differences of substrate quality between disturbance types. All substrate quality variables were also log-transformed to correct for non-normality except for lignin/N ratios and %water-soluble carbohydrates. Mean separation was accomplished using Fisher's Least Significant Difference (LSD) test. An $\alpha = 0.10$ was chosen due to high inherent variability of natural soil ecosystems. All statistical analyses mentioned above were performed using SYSTAT 7.0 (SPSS Inc., Chicago, IL). Two additional multivariate analyses were done to evaluate substrate quality differences between disturbance types. Multiple discriminant analysis (MDA) was used to maximally distinguish between disturbance types based on substrate quality variables. This is accomplished by obtaining linear composites (axes) which maximise the between groups variance relative to the variance within groups. From this we were able to determine which substrate quality variables were most useful in discriminating between disturbance types. In addition to MDA, principal component analysis (PCA) was performed to evaluate substrate quality variable trends amongst samples. The PCA began with ten measured and calculated substrate quality variables. The principal components model was then reduced to a three-dimensional variable space. Reduction to three component axes describing substrate quality was accomplished as a result of the strong correlation between the various substrate quality parameters. Component axes were calculated by eigenanalysis of a $p \times p$

correlation matrix. Component scores were then calculated for each individual sample based on eigenvector elements of a given ordination axis. The resulting ordination biplots (also constructed for MDA) show how substrate quality parameters and samples relate in variable space. Similarities between samples and substrate quality variables are indicated by high positive or negative 'weights' (eigenvector elements) along the ordination axes. Simple regression was used to assess the relationship between substrate quality and mineralisation rates by using the PCA component scores. All multivariate analysis was performed with SYN-TAX ver. 5.02 (Podani 1994).

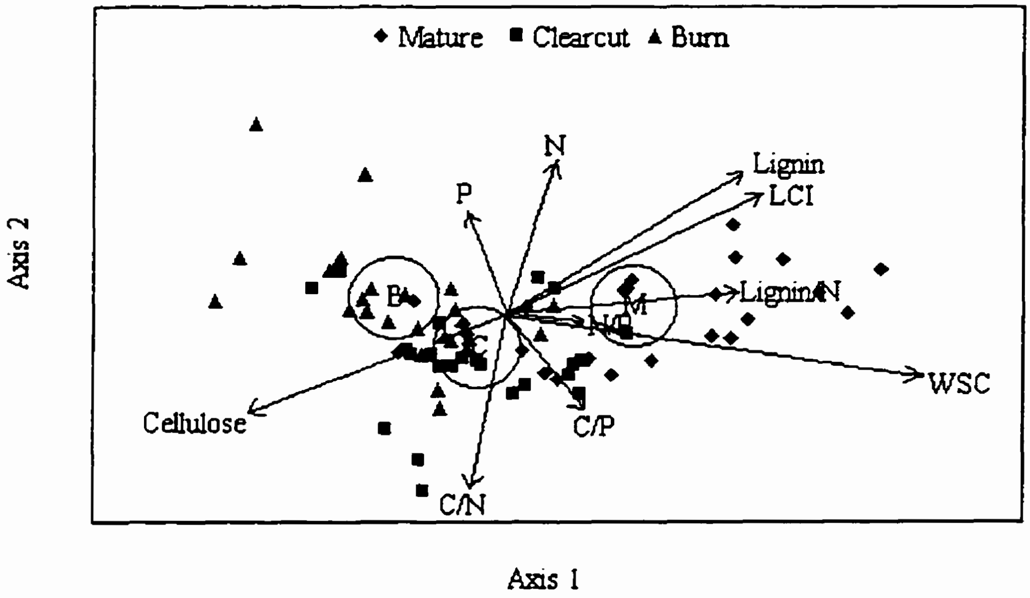


Figure 5.1 Multiple discriminant analysis results for substrate quality differentiation between disturbance types.

5.4 Results and Discussion

5.4.1 Substrate Quality

Peat from mature black spruce stands had noticeably higher lignin/N ratios, lignocellulose indices (LCI = %lignin/(%lignin + %cellulose) and higher percentage lignin and water-soluble carbohydrates (labile carbon) than disturbed sites (Table 5.2). Multiple discriminant analysis (MDA) results also exhibited substrate quality differences between the three disturbance types (Figure 5.1). MDA indicated that all three disturbance types were significantly different (95% confidence ellipses) from one another based on substrate quality parameters. However, only parameters related to C quality (specifically water-soluble carbohydrates and lignin) discriminated among disturbance types ($P < 0.001$). According to the vectors in Figure 5.1, mature stands were strongly weighted with parameters such as lignin (including lignin/N and LCI) and water-soluble carbohydrates while burns and clearcuts were strongly weighted with cellulose. Clearcuts

Table 5.2 Peat substrate quality characteristics for each disturbance type.

		Disturbance type		
Soil properties	Mature	Clearcut	Burn	*P*
%C	46.26 (0.22)	45.75 (0.20)	45.21 (0.26)	0.079
%N	0.83 (0.05)	0.67 (0.03)	0.83 (0.07)	0.041
%P	0.06 (0.01)	0.05 (0.00)	0.06 (0.01)	
C/N ratio	60.33 (3.25)	72.16 (3.42)	62.19 (4.55)	0.048
C/P ratio	1318.61 (443.41)	1123.71 (178.68)	820.98 (72.62)	
N/P ratio	24.48 (9.09)	16.68 (3.30)	14.35 (1.79)	
%Lignin	30.93 (2.21)	20.87 (1.35)	23.41 (1.92)	0.001
%Cellulose	32.26 (2.36)	41.45 (1.92)	40.93 (2.04)	0.003
%Water-soluble carbohydrates	5.66 (0.21)	4.74 (0.15)	3.88 (0.24)	0.000
Lignin/N ratio	39.30 (2.58)	32.16 (2.16)	29.97 (1.93)	0.012
LCI[a]	0.49 (0.04)	0.34 (0.02)	0.36 (0.03)	0.001

[a] LCI = %lignin/(%lignin + %cellulose)

were also positively correlated with C/N and C/P. All of these trends were similar to the results in Table 5.2. Principal component analysis indicated that substrate quality differences were best explained by three component axes (eigenvalues) which accounted for 89% of sample variation (Figures 5.2-5.4). Component 1, corresponding to recalcitrant carbon fractions, had percentage lignin, cellulose and LCI strongly weighted. Component 2, corresponding to phosphorus, had total P and C/P ratios strongly weighted, while component 3 had total N, lignin/N, C/N and N/P ratios heavily weighted. Variable weightings from component 1 seem to separate mature stands from clearcuts and burns best, while both components 2 and 3 showed no obvious disturbance differences. Thus, both MDA and PCA indicated that there are differences in carbon chemistry between the disturbance types. Differences due to carbon chemistry in both the MDA and PCA are partly the result of *Pleurozium schreberi* within mature stands which had significantly higher lignin contents than *Sphagnum* (lignin: *Pleurozium schreberi* = 38-48%, *Sphagnum* generally < 25%; $P < 0.001$).

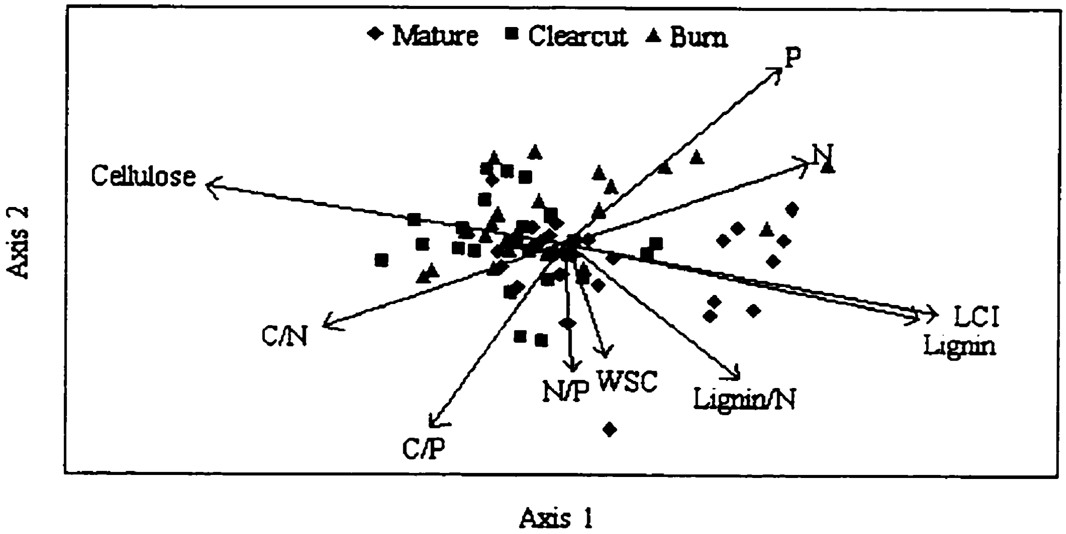


Figure 5.2 Ordination biplot for component axes 1 & 2.

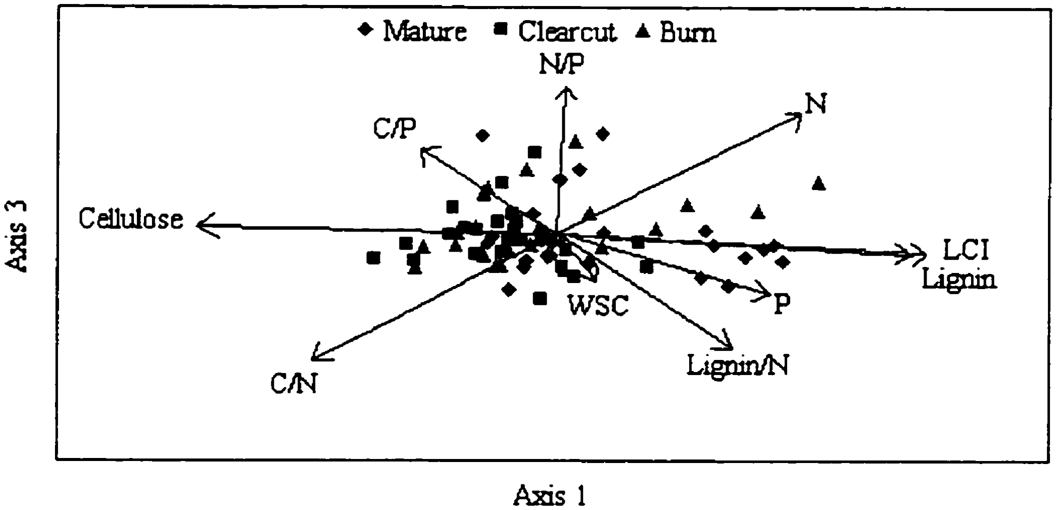


Figure 5.3 Ordination biplot for component axes 1 & 3.

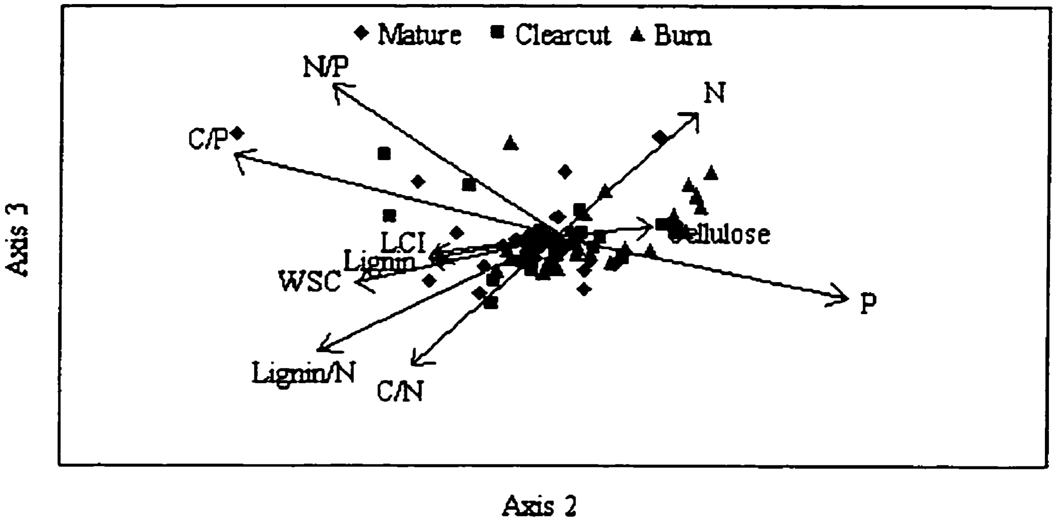


Figure 5.4 Ordination biplot for component axes 2 & 3.

Higher percentage N within the mature and burn sites compared to the clearcut sites (Table 5.2) is a function of two different scenarios. Carbon fraction analysis showed that *Pleurozium schreberi* litter found within mature stands contained higher percentage lignin and N than most *Sphagnum* samples (Figure 5.5). The higher percentage N within *Pleurozium schreberi* litter could be due to decomposition dynamics similar to vascular plant litter or higher N uptake rates as compared to *Sphagnum*. It is generally believed that N release (i.e. net mineralisation) from plant foliage litter in nutrient-poor sites will not occur until lignin degradation begins (Berg and McClaugherty 1987). However within ombrotrophic bogs, site conditions, particularly available carbon and nutrient deficiencies, do not favour microbially mediated N immobilisation by the microbial

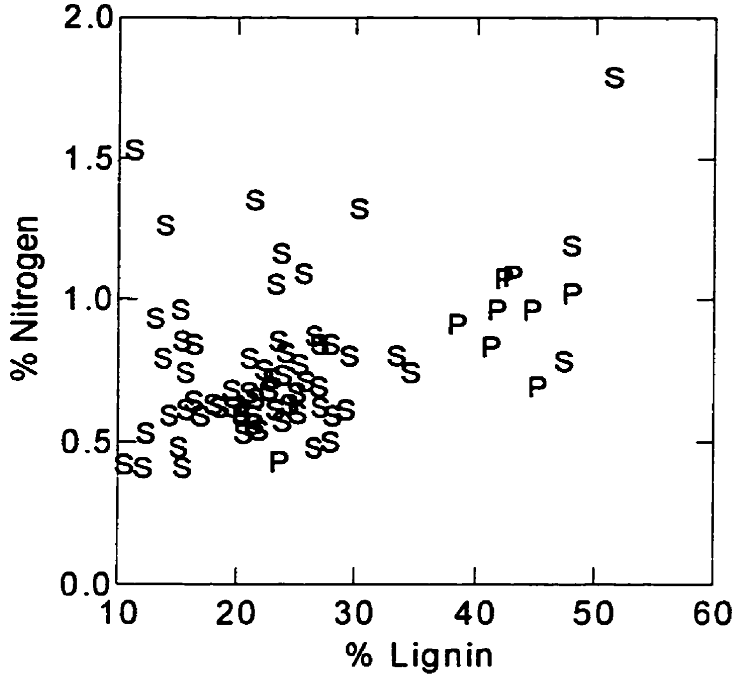


Figure 5.5 Relationship between nitrogen and lignin as determined by peat origin. S = *Sphagnum*, P = *Pleurozium*.

community thus N loss occurs at high C/N ratios and lower "lignin" contents (Damman 1988). This is mainly the result of very slow decomposition rates due to low microbial activity (Verhoeven et al. 1990). The invasion of *Pleurozium schreberi* into the bogs is probably the result of favourable growth conditions, i.e. canopy closure and tree water uptake which cause the peat surface to dry out. This successional change could have important implications on ecosystem functioning within these bogs. For example, as succession alters species composition , any changes in substrate quality that result will have a significant impact on nutrient turnover and thus, stand nutrition. This could affect the way these forests respond to disturbance and therefore, should be considered in management strategies.

The high percentage N within the burn sites is a result of one site, B2, which had a large population of *Alder rugosa* (alder). Peatlands with alder have been shown to have a large fine root biomass within the top 10 cm (Bhatti et al. 1998), accompanied by lower C/N ratios caused by the N-fixing ability of alder (Brumelis and Carleton 1989). Therefore, peat within B2 could support a large, flourishing microbial population. And this could explain the presence of highly degraded peat (lignin > 45%) within the top 15 cm within B2. It is important to note that the high N concentration within fine roots of alder-dominated stands (Bhatti et al. 1998) could have been responsible for the high N content in the peat as separation of roots from this highly degraded material was extremely difficult. Overall, these site differences within the various disturbance types are due to problems with site matching and may actually be more important than "treatment" effects (refer to Chapters 3 and 4 for further examples).

5.4.2 Nitrogen and Phosphorus Mineralisation

Nitrogen mineralisation was significantly different between the three disturbance types with rates decreasing in the following order: matures, clearcuts then burns (Table 5.3). In each disturbance type, net N mineralisation was negative relating to net immobilisation. High net immobilisation in burn sites was a consequence of the high rate of immobilisation within B2 (Figure 5.6). Net P mineralisation, also negative for each disturbance type, showed burns > matures > clearcuts. High rates of immobilisation within clearcuts was attributed to C1 and C2 (Figure 5.7). These two sites along with M3 had significantly higher P immobilisation rates than the rest of the sites ($P < 0.05$). Carbon mineralised (i.e. respiration, measured as mg CO_2/g C during the incubation) was higher within clearcut sites (Table 5.3). However, high rates of respiration were not strongly related to N or P mineralisation ($r^2 = 0.076$ and 0.043, respectively), with the exception of burn sites (see below).

Table 5.3 Mean (standard error) initial extractable ($_{ext}$) and net mineralisation ($_{min}$) totals (mineralisation concentrations = change after 28 days). C mineralised (mg CO_2/g C) during incubation also given as indication of microbial activity.

	N_{ext}	P_{ext}	N_{min}	P_{min}	CO_2
	(µg/g dry peat)				(mg CO_2/g C)
Mature	22.65 (2.66)	17.85 (5.43)	-2.49 (3.21)	-13.27 (4.85)	17.51 (0.78)
Clearcut	35.81 (6.75)	43.90 (7.48)	-14.97 (6.79)	-25.70 (5.25)	19.84 (0.81)
Burn	48.53 (13.29)	7.19 (0.83)	-24.25 (9.02)	-3.13 (1.16)	16.84 (1.05)
P		0.000	0.079	0.001	0.049

Net immobilisation rates for both N and P were unexpected. Immobilisation of N within ombrotrophic bogs is limited due to reduced microbial activity and because N does not limit decay even at low N concentrations (Damman 1988; Verhoeven et al. 1990). N mineralisation has been shown to occur in bogs with high C/N (> 40) (Malmer and Holm 1984; Damman 1988; Verhoeven et al. 1990). Verhoeven et al. (1990) also speculated that while easily degradable N-rich compounds are decomposed by a sparse microbial community, the bulk of carbon compounds were hardly degraded at all. This resulted in the release of mineralised inorganic N into the environment and not incorporated into the microbial biomass. Inhibition of microbial activity and decomposition is believed to be caused by either the recalcitrant nature of *Sphagnum* litter (Clymo 1965), or due to chemical inhibitors produced by *Sphagnum* (Kalviäinen and Karunen 1984) such as

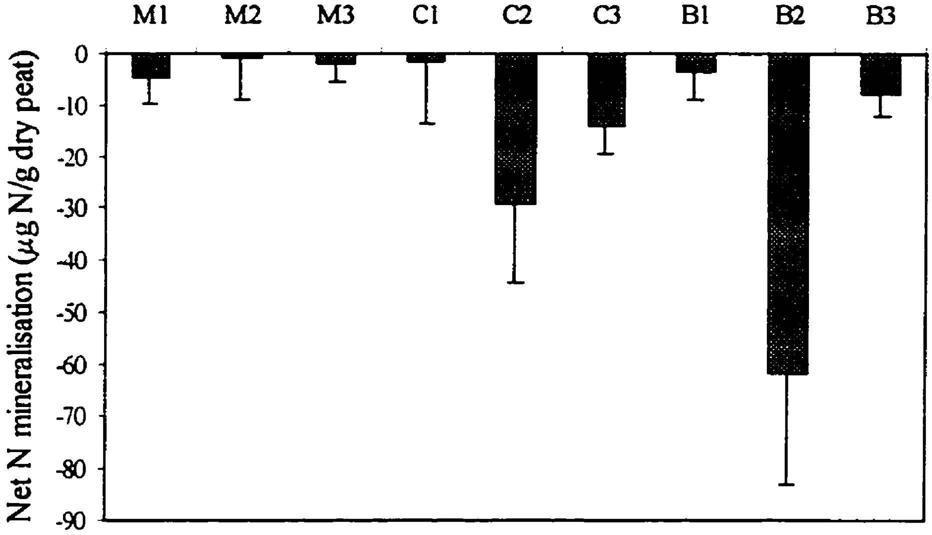


Figure 5.6 Net N mineralisation across all sites. Means (± standard error).

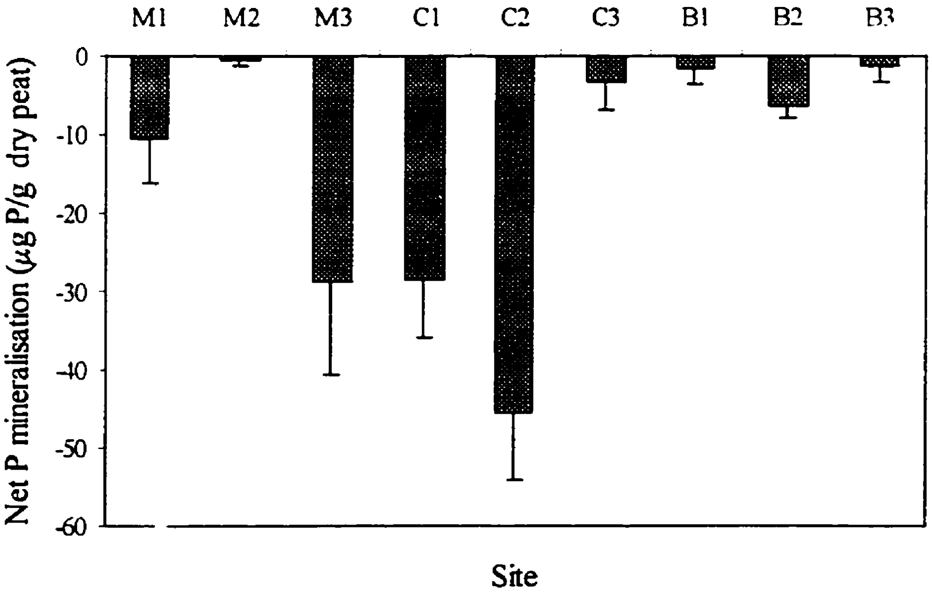


Figure 5.7 Net P mineralisation across all sites. Means (± standard error).

sphagnan (Painter 1991). Low microbial activity has also been attributed to nutrient deficiencies (Damman 1978) and lack of labile C (Waksman and Stevens 1928).

Phosphorus transformations are slightly more complicated. Forests and other natural ecosystems depend heavily on mineralisation of organic-P (Gressel and McColl 1997), which typically comprises 30-80 % of total P in litter and soil (Stevenson 1986). However, once in the soil solution, P can be bound as Fe or Al phosphates (Damman 1978). This is largely related to proximity to the water table and subsequent reducing conditions. Transfers from inorganic 'labile' phosphate to inorganic 'bound' phosphate (chemically adsorbed and precipitated P) (Nichols 1983) make mineralisation measurements extremely difficult. Additionally, phosphorus mineralised may not accumulate in ionic form, thus, causing underestimates of P mineralisation (Aber and Melillo 1991). Overall, net immobilisation for both N and P could be attributed to increased microbial activity (but only if the C:N or C:P ratio of the peat being metabolised is high). Thus, aerobic conditions of the incubation may have stimulated microbial activity and promoted immobilisation of mineral N and P (Williams 1984).

5.4.3 Peat Substrate Quality vs. N and P Mineralisation

Component scores from the PCA were regressed against net mineralisation rates for each sample in order to determine if N and P mineralisation rates could be predicted from substrate quality. The principal component scores describing substrate quality explained only 17% of the variance in N mineralisation and only 6% of the variance in P mineralisation (Table 5.4). Component axis 3 (corresponding to N) was more important in predicting both N and P mineralisation, although, the proportion of variance explained

Table 5.4 Regression results of net N and P mineralisation vs. PCA component scores.

	F	r^2
Net Nitrogen Mineralisation		
Axis 1	3.151*	0.043
Axis 2	1.547	0.022
Axis 3	8.149**	0.104
All axes	4.609**	0.169
Net Phosphorus Mineralisation		
Axis 1	0.044	0.001
Axis 2	0.104	0.001
Axis 3	4.289*	0.058
All axes	1.443	0.060

$*P < 0.10$; $**P < 0.01$.

was very low ($r^2 = 0.104$ and 0.058 respectively). Factors other than those measured (i.e. proportion of inhibitory compounds) appear to play a significant role in controlling N and P mineralisation rates. Weak relationships between P and substrate quality are likely attributed to additional chemical transformations occurring within the peat.

Substrate quality influence on N and P mineralisation in mature stands was not apparent (Table 5.5). None of the component axes were significantly correlated to either N or P mineralisation rates. This was best illustrated by the comparison of percentage lignin vs. N mineralisation as affected by peat origin. *Pleurozium* samples, with higher lignin percentages, did not have significantly different mineralisation rates than *Sphagnum* (Figure 5.8). Regression data shown in Table 5.5 indicated that component axis 1 (describing recalcitrant carbon fractions) was important in explaining N mineralisation within clearcuts ($r^2 = 0.262$). Component axis 3 (describing nitrogen) was significant in predicting both N ($r^2 = 0.562$) and P mineralisation ($r^2 = 0.302$) in burn sites. In addition,

Table 5.5 Regression results of net N and P mineralisation vs. PCA component scores for each disturbance type.

	Mature		Clearcut		Burn	
Source	*F*	r^2	*F*	r^2	*F*	r^2
N_{min}						
Axis 1	1.461	0.062	7.820*	0.262	2.543	0.104
Axis 2	0.146	0.007	0.703	0.031	1.190	0.051
Axis 3	1.679	0.071	0.405	0.018	28.200**	0.562
All axes	0.800	0.107	2.903*	0.303	9.282**	0.582
P_{min}						
Axis 1	0.050	0.002	0.412	0.018	0.023	0.001
Axis 2	1.195	0.051	0.317	0.014	0.179	0.008
Axis 3	2.464	0.101	2.736	0.111	9.506**	0.302
All axes	0.949	0.125	0.948	0.125	4.054*	0.378

*$P < 0.10$; **$P < 0.01$.

N mineralisation within burn sites were related to the percentage of water-soluble carbohydrates ($r^2 = 0.289$; $P < 0.01$). In both cases, N immobilisation within burns increased with increasing % water-soluble carbohydrates and nitrogen. Although percentage of water-soluble carbohydrates were not strongly weighted with PCA but were very important in discriminating between disturbance types as demonstrated with MDA.

N immobilisation appears to increase with increasing N content due to high immobilisation within B2 ($r = -0.603$). Plant species present in B2 are characteristic of minerotrophic fens, which by definition are less acidic and more nutrient-rich compared to ombrotrophic bogs. N immobilisation in fens is not uncommon since nutrient deficiencies affecting microbial activity are lessened. Thus, nutrient pools may depleted by an active microbial community. This was demonstrated by B2 samples which had large initial extractable N levels and also experienced the greatest N immobilisation (with

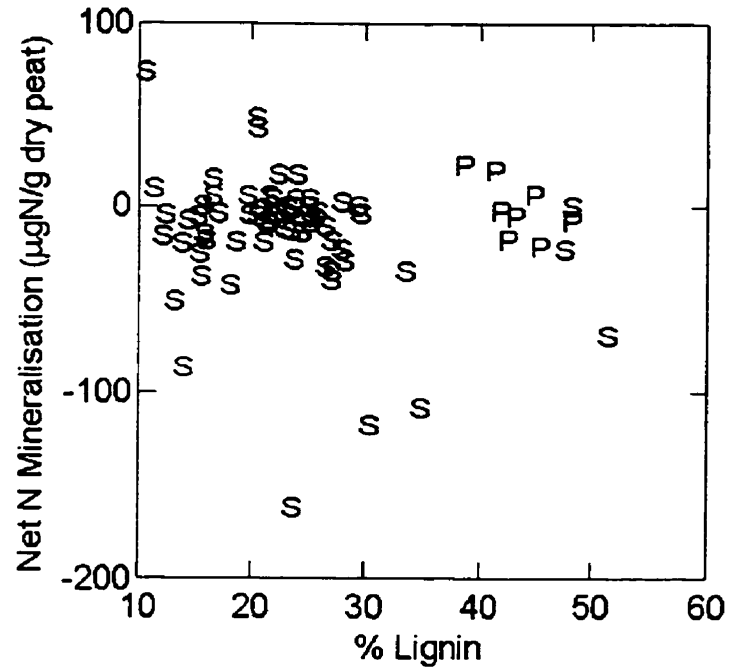


Figure 5.8 Relationship between net N mineralisation and lignin content as affected by peat origin. S = *Sphagnum*, P = *Pleurozium*. ($r^2 = 0.016$)

and without three B2 samples with high net immobilisation; $r = -0.884$ and $r = -0.522$, respectively; Figure 5.9). In addition, C mineralised during the incubation within B2 and all burn samples increased with net immobilisation ($r^2 = 0.664$ and 0.365, respectively) indicative of higher microbial activity. High rates of microbial activity, possibly due to high substrate quality, are likely the cause of net immobilisation. This trend was only noticeable for N immobilisation and not with P.

After 10 years, similar N immobilisation rates within clearcuts and burns indicate that disturbance type does not significantly alter microbial processes within these sites.

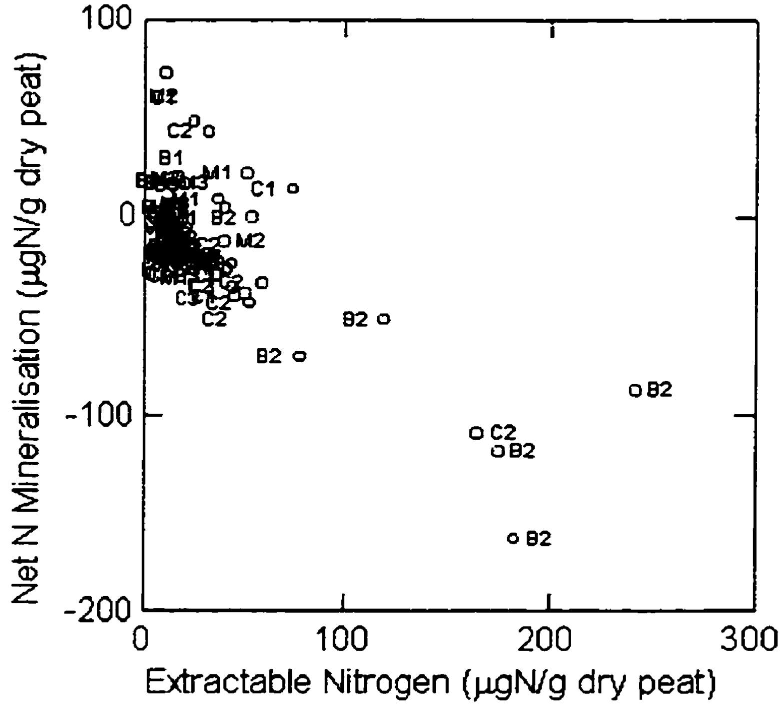


Figure 5.9 Relationship between net N mineralisation and initial extractable N across all sites. ($r^2 = 0.622$)

However, the two disturbances differ with respect to the factors controlling N and P mineralisation. For example, N mineralisation was most influenced by carbon fractions in clearcuts while nitrogen best predicted N mineralisation in burns. This could be a consequence of site factors, such as soil temperature and moisture regimes, or intrinsic differences in *Sphagnum* litter quality (i.e. concentrations of chemical inhibitors) which influence microbial activity and decomposition. Changes in microbial-mediated decomposition rates could affect substrate quality and, in turn, impact nutrient mineralisation.

5.5 Summary and Conclusions

Peat substrate quality was different between disturbance types. Labile carbon fractions (i.e. water-soluble carbohydrates), and to a lesser degree recalcitrant carbon fractions (i.e. lignin), proved to be the best parameters for use in distinguishing disturbance types. Increasing recalcitrant carbon fractions with succession from disturbed sites to mature stands was attributed to increasing proportions of *Pleurozium schreberi* comprising the forest floor. Substrate quality differences between clearcuts and burns after 10 years following disturbance could be related to site factors, such as soil temperature and moisture, or to the intrinsic litter quality of *Sphagnum* species which affect microbial activity and peat decay. N mineralisation was not noticeably different between clearcuts and burns. N mineralisation within burns was most affected by N content, whereas in clearcuts recalcitrant carbon fractions were significant in predicting N mineralisation. Thus, while we are seeing similar magnitudes of N mineralisation after 10 years in clearcuts and burns, different controlling factors indicate that the recovery of these sites may be significantly different. Further research into microbial inhibitors within *Sphagnum* peat are necessary if we are to fully understand N transformations.

Unlike nitrogen, phosphorus mineralisation was not predicted very well except within burns. The use of current techniques to describe P mineralisation are inadequate owing to problems with chemical transformations (Aber and Melillo 1991). This could explain poor prediction of P mineralisation by substrate quality parameters despite having similar accumulation patterns with respect to N in bogs (Damman and French 1987).

Trends associating N and P mineralisation with substrate quality might have been stronger if alternative methodologies were used. The overall net immobilisation for both N and P was largely unexpected due to inhibitions on microbial activity common within ombrotrophic bogs (Damman 1988). Updegraff et al. (1995) found net N mineralisation to be well predicted by labile carbon fractions and greater than 70% of the variation in N mineralisation was predicted by peat substrate quality. Their methodology differed in that they focused on long-term mineralisation potential of the peat while this study tried to measure mineralisation rates over the short-term. Therefore, it is possible that short-term mineralisation determinations are not adequate for predicting relationships with substrate quality. Our results are still significant in that they identify discrepancies between clearcuts and burns with respect to substrate quality controls of N and P mineralisation. However, there are large amounts of variance with both N and P mineralisation rates that still require explanation.

6. GENERAL DISCUSSION

Harvesting and fire impacts on boreal forest ecosystems, particularly black spruce, have been well documented (Gordon 1983; Timmer et al. 1983; Bonan 1990). However, research dealing with tree harvesting and wildfire impacts on forested bogs in northern latitudes is very scarce (e.g. Trettin et al. 1996; Teng et al. 1997). Because of the lack of knowledge with respect to long-term effects of fire and logging on soil temperature and moisture levels and nutrient cycling within forested bog ecosystems, this study's aim was to determine nitrogen and phosphorus availability differences after 10 years between black spruce bog ecosystems affected by either clearcut logging or natural wildfires. Site and spatial variability between disturbed stands resulted in similarities and differences with respect to different aspects of N and P availability.

Soil temperature and moisture regimes in disturbed sites were different than mature, undisturbed stands. Burn and clearcut sites exhibited higher water tables than the mature stands while only the burn sites had lower soil temperatures. Removal of the tree canopy will usually increase soil temperatures due to increased exposure to solar radiation (Frazer et al. 1990; Aust and Lea 1991; Trettin et al. 1995, 1996) and may or may not result in higher water tables (Verry 1986; Berry and Jeglum 1991). Warmer soil temperatures in clearcut sites have also been attributed to soil disturbance exposing darkened humified layers (Trettin et al. 1995). This is not an issue, however, for these sites used in this study as they were winter-logged and disturbance was minimal. Trettin et al. (1996) showed that whole-tree harvesting on organic soils resulted in a 2°C increase down to 25 cm directly after harvesting. These increases as indicated in the literature are not noticeable in our sites likely as a consequence of the time frame (> 10 years after disturbance) and re-establishment of shrub cover. In undrained wetlands where the water table normally remains within 30 cm of the soil surface, the amplitude of water table fluctuations after harvesting increase (Verry 1986). This effect was not as evident with our results possibly due to the time frame.

Disturbed sites had lower extractable N than mature stands, but clearcuts were not noticeably different from burns. Extractable P was not significantly different between all three disturbance types. Immediately following disturbance, either by logging or fire, improved site conditions and increased substrate availability lead to a nutrient flush (MacLean et al. 1983; Kimmins 1992). Low temperatures and high water tables in burn sites probably caused the overall lower extractable N values by inhibiting microbial activity. The ash deposited during and after fire also provides a large source of various elements (Ahlgren and Ahlgren 1960). It is apparent that higher nutrient availability does not exist any longer within these disturbed sites relative to the mature stands.

Both N and P concentrations were expected to show patterns based on spatial gradients. This was in relation to changes in soil temperature, water table level and fluctuations and plant uptake that occur spatially within each site. Spatial differences were evident for N (hummocks < hollows) and P (0-15 > 15-30 cm). While both N and P are influenced by plant uptake and microbial mineralisation, other processes may be at work. Higher extractable N in hollows is likely the result of leaching from the well-drained hummocks (Damman 1978). Greater concentrations of P at lower depths is probably the result of complexation with Fe and/or Al ions, which are found at high levels towards the zone of water table fluctuation (Damman 1978). At the 0-15 cm horizon in hummocks, both N and P levels were not noticeably different between all disturbance types. This is very important as this is the zone of high concentration of fine roots from vascular plants (Bhatti et al. 1998). Consequently, levels of essential nutrients may be important indicators of plant availability but low levels may not indicate infertile soils (Binkley and Vitousek 1989). Because of this, measurements of nutrient fluxes are important to understand supply rates.

In situ nitrogen mineralisation, an important indicator of field nutrient supply rates, was not significantly different between all disturbance types. Soil nitrogen transformations are controlled by environmental factors (e.g. moisture and temperature) and substrate availability (Vitousek 1981). Disturbances, such as forest harvesting and wildfire, impact nitrogen turnover by affecting organic matter decomposition through changes in soil temperature, moisture, fertility and organic matter quality (Armenteno and Menges 1986; Trettin et al. 1995). The net result is increased nitrogen mineralisation (Gordon and Van Cleve 1983; MacLean et al. 1983; Matson and Boone 1984) coinciding with decreased plant uptake. After 10 years it is apparent that increased nitrogen mineralisation is not occurring. This is in contrast to other studies examining mineral forest soils that have found heightened mineralisation rates for greater than 10 years (Frazer et al. 1990).

Performing *in situ* incubations allows soils to be exposed to actual site conditions (Binkley and Hart 1989). Similar N mineralisation rates between clearcuts and burns were initially unexpected as burns were generally colder and wetter. Thus site conditions were not the only factor influencing mineralisation rates. This was also shown through examination of spatial differences within disturbance types. Only clearcut sites showed significant differences between relief (hummocks > hollows) and depth (0-15 > 15-30 cm) which followed the expected pattern of higher mineralisation rates in warmer and better aerated horizons (Verhoeven et al. 1990). Even though N content of the peat in disturbed sites was higher than mature stands, N mineralisation was not related to this as was expected (Damman 1988). Therefore, other intrinsic qualities of the peat may be influencing mineralisation rates.

Peat substrate quality was significantly different between the disturbance types. Labile carbon fractions (water-soluble carbohydrates) and to a lesser degree, recalcitrant carbon fractions (lignin) were the best discriminators between disturbance types. Differences in the impacts of disturbance on site conditions and substrate availability could affect substrate quality parameters. Because disturbance types were best differentiated by carbon fractions, this may relate more to the degree of decomposition of the peat except that trends associated with lignin are mainly the result of the presence of *Pleurozium schreberi* in mature stands (high % lignin). This successional change in peat origin could have important implications on decomposition, nutrient turnover and thus, stand nutrition. This would significantly affect the way forests respond to disturbance.

Net N and P mineralisation rates (actually net immobilisation) were not well predicted by substrate quality parameters. Relationships were, however, slightly stronger with the individual disturbance types. Carbon fractions predicted N mineralisation significantly within clearcuts, while both N and P mineralisation within burns was predicted significantly by N content. N immobilisation rates were similar between the disturbed sites, while the factors controlling the rates were different. This indicates that there may be other factors controlling mineralisation rates, such as chemical inhibitors. This correlates with previous work where *in situ* N mineralisation was similar for clearcuts and burns while site conditions were not.

Net immobilisation was not expected as microbial immobilisation of nutrients, particularly N, is inhibited within ombrotrophic bogs due to nutrient deficiencies (Damman 1978), available energy sources (Waksman and Stevens 1928) or to chemical inhibitors produced by *Sphagnum* (Kalviäinen and Karunen 1984). Increased N immobilisation, due to increased microbial activity, has been attributed to the aerobic conditions of incubation techniques, such as those used in this study (Williams 1984). Phosphorus transformations are complicated by transfers from inorganic 'labile' phosphate to 'bound' phosphate (chemically adsorbed and precipitated P) (Nichols 1983) thus, making relationships to substrate quality extremely difficult to quantify.

The results of this study indicate that there are still differences in site conditions and the availability of nitrogen and phosphorus between clearcut logged, burned and mature stands. However, it is unknown whether differences that were detected were a result of the high amount of variance that occurred between the replicate sites for each disturbance, and thus due to poor site matching, or due to "treatment" (disturbance) effects. Thus, whether differences in these factors affect the long-term sustainability of black spruce bog ecosystems, affected by either clearcut logging or wildfire, remains to be seen. Incorporation of site productivity and vegetation diversity measurements with our results may provide useful in determination of site sustainability. By focusing on the impact of clearcut logging and wildfire 10 years after disturbance, this study provides information about disturbance effects on site conditions and nutrient availability that has not been performed to any great extent in the past. One of the objectives of this study was to try to develop a system for the management of lowland black spruce forests. With the relatively large amount of data dealing with effects immediately following disturbance, our results may provide an important step in long-term predictions of site sustainability for black spruce bog ecosystems.

7. SUMMARY AND CONCLUSIONS

The findings of this study are summarized below:

1. Soil temperature and moisture regimes in disturbed sites were still different than mature stands after 10 years. Clearcut sites were not noticeably different from mature stands with respect to soil temperature levels, whereas burns were colder. Water table levels in disturbed sites were slightly higher than mature stands possibly due to the slow re-establishment of the tree canopy.

2. Disturbance, microrelief and depth affected inorganic N and P concentrations in peat. Nitrogen showed differences based on disturbance type (matures > disturbed sites) and microrelief (hollows > hummocks). Phosphorus exhibited concentrations differences for depth (0-15 > 15-30 cm). High N concentrations in hollows is likely caused by leaching and preferential plant uptake of nutrients in hummocks. Lower concentrations of P with depth could be attributed to higher complexation with Fe and Al as the water table is approached.

3. *In situ* N mineralisation displayed significant differences for microrelief and depth, but none between disturbance types. The absence of disturbance effects were attributed to the high spatial variability both within and between sites and disturbance types. N mineralisation was higher in hummocks and at 0-15 cm but these did not correlate with extractable N pools or total N content. High N mineralisation in

hummocks and at 0-15 cm was attributed to warmer soil temperatures and better aeration. Similar N mineralisation rates between clearcuts and burns were unexpected as burns were generally colder and wetter. This pointed to other factors which influence microbially mediated N mineralisation other than environmental parameters.

4. Disturbance types differed with respect to various substrate quality parameters. Labile carbon fractions (water-soluble carbohydrates) and to a lesser degree, recalcitrant carbon fractions (lignin), best discriminated between disturbance types. Increasing lignin content with succession from disturbed sites to mature stands was attributed to increasing proportions of *Pleurozium schreberi* comprising the forest floor. Substrate quality differences between clearcuts and burns could be related to site factors, such as soil temperature and moisture, or to the intrinsic litter quality of *Sphagnum* species which affect microbial activity and peat decay.

5. Nitrogen and phosphorus mineralisation were not well predicted by substrate quality parameters. Only 17% and 6% of the variance in N and P mineralisation was accounted for, respectively. N mineralisation (actually negative indicating net immobilisation) was not significantly different between clearcuts and burns nor was substrate quality. N mineralisation in burns was best predicted by N content, whereas in clearcuts recalcitrant carbon fractions were significant in predicting N mineralisation. P mineralisation was not predicted very well except within burns. This is attributable to the inadequacies of current techniques to describe P transformations due to interference of other chemical reactions.

Nitrogen and phosphorus availabilities were, for the most part, not different after 10 years between clearcut and burned black spruce bog ecosystems. Spatial variability was cited as the main reason for most similarities between disturbance types as variability was high within and between sites. Thus, distinguishing between actual "treatment" effects and variance due to poor site matching is probably not possible. These results stress the need for multiple sites and good site matching when focusing on natural ecosystems. High degrees of spatial variability of N and P within the peat was attributable to differences in soil temperature and moisture regimes, and possibly plant uptake. Differences in re-colonisation and subsequent nutrient sequestration by vascular plants between disturbance types stress the need for these measurements in future studies.

Nitrogen transformations in the peat, in particular, pointed to differences between clearcuts and burns. While N mineralisation rates were not significantly different, the controls of this microbially mediated transformation were. Clearcuts and burns differed with respect to site conditions and substrate quality. However, differences in regeneration between the disturbed sites and low nutrient supplies may mean that similar N mineralisation rates are inadequate for site recovery. Measurements of stand densities and biomass may be important indicators of long-term impacts of burns and clearcuts and should be explored. This will give insight into how site productivity is affected by these two different disturbances.

8. CONTRIBUTION TO KNOWLEDGE

There has been a substantial amount of research into the effects of fire and logging on forest soils, particularly on nutrient cycling and availability. However, most of the work has focused on the effects of disturbance on upland, mineral soils immediately following disturbance. This study provided insight into the impacts of clearcut logging and wildfire on nutrient availability within black spruce bog ecosystems after 10 years. It was determined that, for the most part, indices of nutrient availability within mature stands were not significantly different from 10 year-old disturbed sites. Similarities in nutrient availability after 10 years between these disturbed and mature stands may prove indicative of successful ecosystem recovery. Further work is necessary to back up this statement such as measurements of plant productivity and nutrient uptake.

Recent interest by the forestry industry in establishing clearcut logging practices which emulate the effects of wildfire on site productivity has sparked an increase in comparative studies between anthropogenic and natural disturbances. This study's main purpose was to compare the effects on clearcut logging vs. natural wildfire on N and P availability. Our results have shown important differences between clearcuts and burns with respect to the controls of nutrient availability, such as site conditions and peat substrate quality, even though N and P availability was not significantly different. However, as noted above, measurements of plant uptake and nutrient levels in the plant biomass may show important differences within these ecosystems not indicated by soil processes.

9. REFERENCES

Aber, J. D. and Melillo, J. M. 1991. Terrestrial ecosystems. Saunders College Publishing, Philadelphia, PA.

Ahlgren, I. F. and Ahlgren, C. E.. 1960. Ecological effects of forest fires. Bot. Rev. **26**: 483-533.

Ahlgren, I. F. and Ahlgren, C. E. 1965. Effects of prescribed burning on soil microorganisms in a Minnesota jack pine forest. Ecology **46**: 304-310.

Allen, S. E., Carlisle, A., White, E. J. and Evans, C. C. 1968. The plant nutrient content of rain water. J. Ecol. **56**: 497-504.

Armentano, T. V. and Menges, E. S. 1986. Patterns of change in the carbon balance of organic soil wetlands of the temperate zone. J. Ecol. **74**: 755-774.

Aust, W. M. and Lea, R. 1991. Soil temperature and organic matter in a disturbed forest wetland. Soil Sci. Soc. Am. J. **55**: 1741-1746.

Avnimelech, Y. 1971. Nitrate transformations in peat. Soil Sci. **111**: 113-118.

Bartsch, I. and Moore, T. R. 1985. A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Quebec. Can. J. Bot. **63**: 1241-1248.

Belyea, L. R. 1996. Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. Oikos. 77: 529-539.

Bendt, W. W. 1965. Snow accumulation and disappearance in lodgepole pine clearcut blocks in Wyoming. J. For. **63**: 88-91.

Benoit, R. E. and Starkey, R. L. 1968. Inhibition of decomposition of cellulose and some other carbohydrates by tannin. Soil Sci. **105**: 291-296.

Berg, B. and McClaugherty, C. 1987. Nitrogen release from litter in relation to the disappearance of lignin. Biogeochem. **4**: 219-224.

Berry, G. J. and Jeglum, J. K. 1991. Hydrology of drained and undrained black spruce peatlands: Groundwater table profiles and fluctuations. Can-Ontario For. Resour. Dev. Agree. CONFRDA Rep. 3307. 38 p.

Bhatti, J. S., Foster, N. W. and Hazlett, P. W. 1998. Fine root biomass and nutrient content in a black spruce peat soil with and without alder. Can. J. Soil. Sci. **78**: 163-169.

Binkley, D. and Hart, S. C. 1989. The components of nitrogen availability assessments in forest soils. Adv. Soil Sci. **10**: 57-112.

Binkley, D. and Vitousek, P. M. 1989. Soil nutrient availability. Pages 75-96 *in* R. Pearcy, H. Mooney, J. Ehleringer, and P. Rundel (eds.). Physiological plant ecology: Field methods and instrumentation. Chapman & Hall, London, England.

Boelter, D. H. 1965. Hydraulic conductivity of peats. Soil Sci. **100**: 227-231.

Boelter, D. H. 1969. Physical properties of peats related to degree of decomposition. Soil Sci. Soc. Am. Proc. **33**: 606-609.

Bonan, G. B. 1990. Carbon and nitrogen cycling North American boreal forests. II. Biogeographic patterns. Can. J. For. Res. **20**: 1077-1088

Bonan, G. B. and Shugart, H. H. 1989. Environmental factors and ecological processes in boreal forests. Ann. Rev. Ecol. Syst. **20**: 1-28.

Bormann, F. H., Likens, G. E., and Melillo, J. M. 1977. Nitrogen budget for an aggrading northern hardwood forest ecosystem. Science. **196**: 981-983.

Bowden, W. B. 1987. The biogeochemistry of nitrogen in freshwater wetlands. Biogeochem. **4**: 313-348.

Brumelis, G. and Carleton, T. J. 1989. The vegetation of post-logged black spruce lowlands in central Canada. II. Understory vegetation. J. App. Ecol. **26**: 321-339.

Clymo, R. S. 1965. Experiments on breakdown of *Sphagnum* in two bogs. J. Ecol. **53**: 747-757.

Clymo, R. S. 1978. A model of peat growth. Pages 187-223 *in* O. W. Heal and D. F. Perkins, eds. Production ecology of British moors and montane grasslands. Springer-Verlag, New York, NY.

Clymo, R. S. 1983. Peat. Pages 159-224 *in* A. J. P. Gore, ed. Mires: swamp, bog, fen and moor. Ecosystems of the world. vol. 4A. Elsevier, Amsterdam, The Netherlands.

Clymo, R. S. 1984. The limits to peat bog growth. Phil. Trans. Roy. Soc. Lon. Ser. B. **303**: 605-654.

Clymo, R. S. 1991. Peat growth. Pages 76-112 *in* L. C. K. Shane and E. J. Cushing, eds. Quaternary landscapes. Belhaven, London, UK.

Coulson, J. C. and Butterfield, J. E. 1978. An investigation of the biotic factors determining rates of plant decomposition on blanket bog. J. Ecol. **66**: 631-650.

Covington, W. W. 1981. Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods. Ecology **62**: 41-48.

Damman, A. W. H. 1978. Distribution and movement of elements in ombrotrophic peat bogs. Oikos. **30**: 480-495.

Damman, A. W. H. 1986. Hydrology, development, and biogeochemistry of ombrogenous peat bogs with special reference to nutrient relocation in a western Newfoundland bog. Can. J. Bot. **64**: 384-394.

Damman, A. W. H. 1988. Regulation of nitrogen removal and retention in *Sphagnum* bogs and other peatlands. Oikos. **51**: 291-305.

Damman, A. W. H. and French, T. W. 1987. The ecology of peat bogs of the glaciated northeastern United States: A community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85(7.16). 100 p.

Dickinson, C. H. 1983. Pages 225-245 *in* A. J. P. Gore, ed. Mires: swamp, bog, fen and moor. Ecosystems of the world. vol. 4A. Elsevier, Amsterdam, The Netherlands.

Dickinson, C. H., Wallace, B., and Given, P. H. 1974. Microbial activity in Florida Everglades peat. New Phytol. **73**: 107-113.

Dubois, M., Gilles, K. A., Hamilton, J. K., Rebers, P. A. and Smith, F. 1956. Colourimetric method for determination of sugars and related substances. Anal. Chem. **28**: 350-356.

Edmonds, R. L. 1980. Litter decomposition and nutrient release in Douglas-fir, red alder, western hemlock, and Pacific silver fir ecosystems in western Washington. Can. J. For. Res. **10**: 327-337.

Environment Canada. 1996. Canadian climate normals (1961-1990) – Bissett, Manitoba. http://www.cmc.ec.gc.ca/climate/normals/MANB006.HTM

Epstein, E. 1972. Mineral nutrition of plants: Principles and perspectives. Wiley and Sons, New York.

Erickson, M. and Miksche, G. E. 1974. On the occurrence of lignin or polyphenols in some mosses and liverworts. Phytochemistry. **13**: 2295-2299.

Farnham, R. S. 1974. Use of organic soils for wastewater filtration. Pages 111-118 *in* A. R. Aandahl, ed. Histosols: Theirs characteristics, classification and use. SSSA, Madison, WI.

Farrish, K. W. and Grigal, D. F. 1988. Decomposition in an ombrotrophic bog and minerotrophic fen in Minnesota. Soil Sci. **145**: 353-358.

Flanagan, P and Van Cleve, K. 1983. Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. Can. J. For. Res. **13**: 795-817.

Fowells, H. A. and Stephenson, R. E. 1933. Effects of burning on forest soils. Soil Sci. **38**: 175-181.

Frazer, D. W., McColl, J. G. and Powers, R. F. 1990. Soil nitrogen mineralisation in a clearcutting chronosequence in a northern California conifer forest. Soil Sci. Soc. Am. J. **54**: 1145-1152.

Gordon, A. G. 1983. Nutrient cycling dynamics in differing spruce and mixedwood ecosystems in Ontario and the effects of nutrient removals through harvesting. Pages 97-118 *in* R. W. Wein, R. R. Wein, and I. R. Methven, eds. Resources and dynamics of the boreal zone: Proceedings of a conference held at Thunder Bay, ON, August, 1982. Association of Canadian Universities for Northern Studies, Ottawa, ON.

Gordon, A. M. and Van Cleve, K. 1983. Seasonal patterns of nitrogen mineralisation following harvesting in the white spruce forests of interior Alaska. Pages 119-130 118 *in* R. W. Wein, R. R. Wein, and I. R. Methven, eds. Resources and dynamics of the boreal zone: Proceedings of a conference held at Thunder Bay, ON, August, 1982. Association of Canadian Universities for Northern Studies, Ottawa, ON.

Gore, A. J. P. 1983. Introduction. Pages 1-34 *in* A. J. P. Gore, ed. Mires: swamp, bog, fen and moor. Ecosystems of the world. vol. 4A. Elsevier, Amsterdam, The Netherlands.

Gore, A. J. P. and Allen, S. E. 1965. Measurement of exchangeable and total cation content for H^+, Na^+, K^+, Mg^{++}, Ca^{++}, and iron in high level blanket peat. Oikos 7: 48-55.

Gore, A. J. P., and Urquhart, C. 1966. The effects of waterlogging on the growth of *Molinia caerulea* and *Eriophorum vaginatum*. J. Ecol. **54**: 617-633.

Gore, A. J. P. and Olsen, J. 1967. Preliminary models for the accumulation of organic matter in an *Eriophorum-Calluna* ecosystems. Aquilo Ser. Bot. **6**: 297-313.

Granhall, U., and Selander, H. 1973. Nitrogen fixation in a subarctic mire. Oikos. **24**: 8-14.

Gressel, N. and McColl, J. G. 1997. Phosphorus mineralisation and organic matter decomposition: A critical review. Pages 297-309 *in* G. Cadisch and K. E. Giller (eds.). Driven by nature: Plant litter quality and decomposition. CAB International Wallingford, UK.

Grigal, D. F. 1991. Elemental dynamics of forested wetlands bogs in northern Minnesota. Can. J. Bot. **69**: 539-546.

Haavisto, V. F. and Jeglum, J. K. 1991. Peatland potentially available for forestry in Canada. Pages 30-37 *in* J. K. Jeglum and R. P. Overland, eds. Symposium '89: Peat and peatlands: Diversification and innovation. Peatland Forestry: Proceedings. Vol. I. 7-11 August 1989, Quebec City, PQ. Can. Soc. for Peat and Peatlands, Dartmouth, NS.

Hart, S. C., Stark, J. M., Davidson, E. A. and Firestone, M. K. 1994. Nitrogen mineralisation, immobilisation, and nitrification. Pages 985-1018 *in* Methods of soil analysis: Microbiological and biochemical properties. SSSA Book Series no. 5, Part 2. SSSA, Madison, WI.

Heinselman, M. L. 1963. Forest sites, bog processes, and peatland types in Glacial Lake Agassiz region, Minnesota. Ecol. Monogr. **33**: 327-374.

Heinselman, M. L. 1970. Landscape evolution, peatland types, and the environment in the Lake Agassiz Peatlands Natural Area, Minnesota. Ecol. Monogr. **40**: 235-261.

Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe area, Minnesota. Quat. Res. **3**: 329-382.

Heinselman, M. L. 1981. Fire and succession in the conifer forests of northern North America. Pages 374-405 *in* D. C. West, H. H. Shugart, and D. B. Botkin, eds. Forest succession: Concepts and applications. Springer-Verlag, New York, NY.

Hemond, H. F. 1983. The nitrogen budget of Thoreau's bog. Ecology. **64**: 99-109.

Hendrickson, O. Q., Chatarpaul, L. and Burgess, D. 1989. Nutrient cycling following whole-tree and conventional harvest in northern mixed forest. Can. J. For. Res. **19**: 725-735.

Hornbeck, J. W. and Kropelin, W. 1982. Nutrient removal and leaching from a whole-tree harvest of northern hardwoods. J. Environ. Qual. **11**: 309-316.

Hornbeck, J. W., Martin, C. W., Pierce, R. S., Bormann, F. H., Likens, G. E. and Eaton, J. S. 1986.. Clearcutting northern hardwoods: Effects on hydrologic and nutrient ion budgets. For. Sci. **32**: 667-686.

Hornung, M and Newson, M. 1986. Upland afforestation: Influences on stream hydrology and chemistry. Soil Use Manage. **2**: 61-65.

Ingram, H. A. P. 1982. Size and shape in raised mire ecosystems: A geophysical model. Nature. **297**: 300-303.

Ingram, H. A. P. 1983. Hydrology. Pages 67-158 *in* A. J. P. Gore, ed. Mires: swamp, bog, fen and moor. Ecosystems of the world. vol. 4A. Elsevier, Amsterdam.

Johnson, L. C. and Damman, A. W. H. 1991. Species-controlled *Sphagnum* decay on a south Swedish raised bog. Oikos. **61**: 234-242.

Johnson, L. C. and Damman, A. W. H. 1993. Decay and its regulation in *Sphagnum* peatlands. Adv. Bryol. **5**: 249-296.

Johnson, L. C., Damman, A. W. H. and Malmer, N. 1990. *Sphagnum* macrostructure as an indicator of decay and compaction in peat cores from an ombrotrophic south Swedish peat bog. J. Ecol. **78**: 633-647.

Jorgensen, J. R. and Wells, C. G. 1971. Apparent nitrogen fixation in soil influenced by prescribed burning. Soil Sci. Soc. Am. Proc. **35**: 806-810.

Kalviäinen, E. an Karunen, P. 1984. On the growth, senescence and decay-resistance of *Sphagnum* mosses. Proceedings 7th International Peat Congress, Dublin, Ireland. Vol. IV: 263-275.

Kangas, P. C. 1990. Long-term development of forested wetlands. Pages 25-51 *in* A. J. P. Gore, M. Brinson, and S. Brown, eds. Forested wetlands. Ecosystems of the world. vol. 15. Elsevier, Amsterdam, The Netherlands.

Keenan, R. J. and Kimmins, J. P. 1993. The ecological effects of clear-cutting. Environ. Rev. **1**: 121-144.

Kimmins, J. P. 1992. Balancing act: Environmental issues in forestry. UBC Press, Vancouver, BC.

Kimmins, J. P. 1997. Forest ecology: A foundation for sustainable management. 2nd edition. Prentice Hall, Upper Saddle River, NJ.

Knight, H. 1966. Loss of nitrogen from the forest floor by burning. For. Chron. **42**: 149-152.

Kubin, E. and Kemppainen, L. 1991. Effect of clearcutting of boreal spruce forest on air and soil temperature conditions. Acta For. Fenn. **225**: 1-42.

Kuhry, P. 1994. The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada. J. Ecol. **82**: 889-910.

Lahde, E. 1969. Biological activity in some natural and drained peat soils with special reference to oxidation-reduction conditions. Acta For. Fenn. **94**: 1-64.

Latter, P. M., Cragg, J. B. and Heal, O. W. 1967. Comparative studies on the microbiology of four moorland soils in the North Pennines. J. Ecol. **55**: 445-463.

Lee, J. A., Press, M. C., Woodin, S. and Ferguson, P. 1987. Responses to acidic deposition in ombrotrophic mires. Pages 549-560 *in* T. C. Hutchinson and K. M. Meema, eds. The effects of acidic deposition on forest, wetland, and agricultural ecosystems. Springer-Verlag, New York, NY.

Lee, J. A. and Woodin, S. J. 1988. Vegetation structure and the interception of acidic deposition by ombrotrophic mires. Pages 137-147 *in* J. T. A. Verhoeven, G. W. Heil, and M. J. A. Werger, eds. Vegetation structure in relation to carbon and nutrient economy. SPB Academic Publishing, The Hague, The Netherlands.

Lieffers, V. J. 1988. *Sphagnum* and cellulose decomposition in drained and natural areas of an Alberta peatland. Can. J. Soil Sci. **68**: 755-761.

Lieffers, V. J. and Rothwell, R. L. 1987. Rooting of peatland black spruce and tamarack in relation to depth of water table. Can. J. Bot. **65**: 817-821.

Lloyd, P. S. 1971. Effects of fire on the chemical status of herbaceous communities of Derbyshire Dales. J. Ecol. **59**: 261-273.

Lutz, H. J. 1956. The ecological effects of forest fires in the interior of Alaska. U. S. Dept. Agr., Tech. Bull. 1133.

MacLean, D. A., Woodley, S. J., Weber, M. G. and Wein, R. W. 1983. Fire and nutrient cycling. Pages 111-132 *in* R. W. Wein and D. A. MacLean, eds. The role of fire in northern circumpolar ecosystems. John Wiley & Sons, New York, NY.

Mahendrappa, M. K., Foster, N. W., Weetman, G. F. and Krause, H. H. 1986. Nutrient cycling and availability in forest soils. Can. J. Soil Sci. **66**: 547-572.

Malmer, N. 1988. Patterns in the growth and the accumulation of inorganic constituents in the *Sphagnum* cover on ombrotrophic bogs in Scandinavia. Oikos. **53**: 105-120.

Malmer, N. 1992. Processes of acquisition, transport and deposition of inorganic constituents in surface peat layers. Pages 165-174 *in* O. M. Bragg, P. D. Hulme, H. A. P. Ingram, and R. A. Robertson, eds. Peatland ecosystems and man: An impact assessment. International Peat Society, Jyväskylä, Finland.

Malmer, N. 1993. Mineral nutrients in vegetation and surface layers of *Sphagnum*-dominated peat-forming systems. Adv. Bryol. **5**: 223-248.

Malmer, N. and Nihlgård, B. 1980. Supply and transport of mineral nutrients in a subarctic mire. Pages 63-95 *in* M. Sonesson, ed. Ecology of a subarctic mire. Swedish Natural Sci. Res. Council, Stockholm, Sweden.

Malmer, N. and Holm, E. 1984. Variation in the C/N quotient of peat in relation to decomposition rate and age determination with ^{210}Pb. Oikos. **43**: 171-182.

Malmer, N., Svensson, G. and Wallén, B. 1997. Mass balance and nitrogen accumulation in hummocks on a south Swedish bog during the late Holocene. Ecography. **20**: 535-549.

Marks, P. L. 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwoods ecosystems. Ecol. Mono. **44**:73-88.

Martin, N. J., and Holding, A. J. 1978. Nutrient availability and other factors limiting microbial activity in the blanket peat. Pages 113-135 *in* O. W. Heal and D. F. Perkins, eds. Production ecology of British moors and montane grasslands. Springer-Verlag, New York, NY.

Matson, P. A. and Boone, R. D. 1984. Natural disturbance and nitrogen mineralisation: Wave-form dieback of mountain hemlock in the Oregon Cascades. Ecology **65**: 1511-1516.

McColl, J. G. 1977. Retention of soil water following forest cutting. Soil Sci. Soc. Am. J. **41**: 984-988.

Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. Ecology **59**: 465-472.

Melillo, J. M., Aber, J. D. and Muratore, J. F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology **63**: 621-626.

Melillo, J. M., Aber, J. D., Linkins, A. E., Ricca, A., Fry, B. and Nadelhoffer, K. J. 1989. Carbon and nitrogen dynamics along the decay continuum: Plant litter to soil organic matter. Plant Soil. **115**: 189-198.

Mitsch, W. J. and Gosselink, J. G. 1993. Wetlands. 2nd edition. Van Nostrand Reinhold, New York, NY.

Mroz, G. D., Jurgensen, M. F., Harvey, A. E. and Larsen, M. J. 1980. Effects of fire on nitrogen in forest floor horizons. Soil Sci. Soc. Am. J. **44**: 395-400.

Nicholson, D. S. 1983. Capacity of natural wetlands to remove nutrients from wastewater. J. Water. Poll. Cont. Fed. **55**: 495-505.

Olsen, S. R. and Sommers, L. E. 1982. Phosphorus. Pages 403-430 *in* A. L. Page et al. (eds.). Methods of soil analysis, Agronomy Monograph 9, Part 2. 2nd edition. ASA, Madison, WI.

Paavilainen, E., and Päivänen, J. 1995. Peatland forestry: Ecology and principles. Springer-Verlag, New York, NY.

Painter, T. J. 1991. Lindow Man, Tollund Man and other peat-bog bodies: The preservative and antimicrobial action of sphagnan, a reactive glycuronoglycan with tanning and sequestering properties. Carbohydrate Polymers **15**: 123-142.

Painter, T. J. and Sørenson, N. A. 1978. The cation exchanges of *Sphagnum* mosses: An unusual form of holocellulose. Carbohydrate Research **66**: C1-C3.

Päivänen, J. 1973. Hydraulic conductivity and water retention in peat soils. Acta For. Fenn. **129**: 1-70.

Parkin, T. B. 1993. Spatial variability of microbial processes in soil – A review. J. Environ. Qual. **22**: 409-417.

Podani, J. 1994. Multivariate data analysis in ecology and systematics. A methodological guide to the SYN-TAX 5.0 package. SPB Academic Publ., The Hague, The Netherlands.

Powers, R. F. and Van Cleve, K. 1991. Long-term ecological research in temperate and boreal forest ecosystems. Agron. J. **83**: 11-24.

Rashid, G. 1987. Effects of fire on soil carbon and nitrogen in a Mediterranean oak forest of Algeria. Plant Soil **103**: 89-93.

Richardson, C. J., Tilton, D. L., Kadlec, J. A., Chamie, J. P. M., and Wentz, W. A. 1978. Nutrient dynamics of northern wetland ecosystems. Pages 217-241 *in* R. E. Good, D. F. Whigham, and R. L. Simpson, eds. Freshwater wetlands: Ecological processes and management potential. Academic Press, New York, NY.

Rochefort, L., Vitt, D. H. and Bayley, S. E. 1990. Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. Ecology **71**: 1986-2000.

Rosswall, T., and Granhall, U. 1980. Nitrogen cycling in a subarctic ombrotrophic mire. Pages 209-234 *in* M. Sonesson, ed. Ecology of a subarctic mire. Swedish Natural Sci. Res. Council, Stockholm, Sweden.

Rowe, J. S. and Scotter, G. W. 1973. Fire in the boreal forest. Quat. Res. **3**: 444-464.

Rowland, A. P. and Roberts, J. D. 1994. Lignin and cellulose fraction in decomposition studies using acid-detergent fibre methods. Comm. Soil Sci. Plant. Anal. **25**: 269-277.

Ryden, B. E. and Kostov, L. 1980. Thawing and freezing in tundra soils. Pages 251-281 *in* M. Sonesson, ed. Ecology of a subarctic mire. Swedish Natural Sci. Res. Council, Stockholm, Sweden.

Sanderson, P. L. and Armstrong, W. 1980. The response of conifers to some of the adverse factors associated with waterlogging soils. New Phytol. **85**: 351-362.

Small, E. 1972a. Ecological significance of four critical elements in plants of raised *Sphagnum* peat bogs. Ecology **53**: 498-503.

Small, E. 1972b. Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. Can. J. Bot. **50**: 2227-2233.

Smith, D. W. 1970. Concentrations of soil nutrients before and after fire. Can. J. Soil Sci. **50**: 17-29.

Soil Classification Working Group. 1998. The Canadian system for soil classification. Agriculture and Agri-food Canada. Publ. 1646 (revised). Ottawa, Ontario.

Spearing, A. M. 1972. Cation-exchange capacity and galacturonic acid content of several species of *Sphagnum* in Sandy Ridge Bog, central New York State. Bryol. **75**: 134-148.

Stanek, W. 1975. Annotated bibliography of peatland forestry. Environment Canada Libraries. Bibliography Series 76, 1.

Stevenson, F. J. 1986. Cycles of soil. C, N, P, S, micronutrients. Wiley, New York, NY.

Sutton, R. F. 1993. Mounding site preparation: A review of European and North American experience. New For. 7: 151-192.

Swift, M. J., Heal, O. W. and Anderson, J. M. 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkeley, CA.

TAPPI. 1993. Water solubility of wood and pulp. ?. Technical Association of the Pulp and Paper Industry, Atlanta, GA. 2 pp.

Tate, K. R. 1984. The biological transformation of P in soil. Plant Soil **76**: 245-256.

Taylor, M. E., Kershaw, H. M., Jeglum, J. K. and Morris, D. M. 1995. Long-term productivity of boreal forest ecosystems. I. Annotated bibliography. Nat. Resour. Can., Canadian Forest Service-Sault Ste. Marie, Sault Ste. Marie, ON. NODA Note No. 8. 144 p.

Technicon Instrument Corporation. 1971. Nitrate and nitrite in water. Industrial method no. 32-69W. Technicon Instrument Corporation, Tarrytown, NY.

Technicon Instrument Corporation. 1971. Ammonia in water and seawater. . Industrial method no. 154-71W. Technicon Instrument Corporation, Tarrytown, NY.

Technicon Instrument Corporation. 1978. Total carbon/dissolved organic carbon in water and wastewater. Industrial method no. 455-76W/A. Technicon Instrument Corporation, Tarrytown, NY.

Teng, Y., Foster, N. W., Hazlett, P. and Morrison, I. K. 1997. Nutrient removals associated with harvesting peatland black spruce forest. Pages 341-352 *in* C. C. Trettin, D. F. Grigal, M. F. Jurgensen, M. R. Gale, and J. K. Jeglum, eds. Northern forest wetlands ecology and management. Proc. of International Symposium on the Ecology and Management of Northern Forested Wetlands, Traverse City, MI. 29-31 Aug. 1994. CRC Lewis Publishers, Boca Raton, FL.

Theander, O. 1954. Studies of *Sphagnum* peat. III. A quantitative study on the carbohydrate constituents of *Sphagnum* mosses and *Sphagnum* peat. Acta Chemica Scandinavica **8**: 989-1000.

Timmer, V. R., Savinsky, H. M. and Marek, G. T. 1983. Impact of intensive harvesting on nutrient budgets of boreal forests. Pages 131-147 *in* R. W. Wein, R. R. Wein, and I. R. Methven, eds. Resources and dynamics of the boreal zone: Proceedings of a conference held at Thunder Bay, ON, August, 1982. Association of Canadian Universities for Northern Studies, Ottawa, ON.

Timmons, D. R., Verry, E. S., Burwell, R. E. and Holt, R. F. 1977. J. Environ. Qual. **6**: 188-192.

Trettin, C. C., Jurgensen, M. F., Gale, M. R. and McLaughlin, J. W. 1995. Soil carbon in northern forested wetlands: Impacts of silvicultural practices. Pages 437-461 *in* W. W. McFee and J. M. Kelley, eds. Carbon forms and functions in forest soils. SSSA, Madison, WI.

Trettin, C. C., Davidian, M., Jurgensen, M. F. and Lea, R. 1996. Organic matter decomposition following harvesting and site preparation of a forested wetland. Soil Sci. Soc. Am. J. **60**: 1994-2003.

Tukey, H. B. 1970. The leaching of substances from plants. Ann. Rev. Plant Physiol. **21**: 305-324.

Updegraff, K., Pastor, J., Bridgham, S. D. and Johnston, C. A. 1995. Environmental and substrate controls over carbon and nitrogen mineralisation in northern wetlands. Ecol. Appl. **5**: 151-163.

Urban, N. R. and Eisenreich, S. J. 1988. Nitrogen cycling in a forested Minnesota bog. Can. J. Bot. **66**: 435-449.

Van Cleve, K. and Alexander, V. 1981. Nitrogen cycling in tundra and boreal ecosystems. Pages 375-404 *in* F. E. Clark and T. Rosswall, eds. Terrestrial nitrogen cycles. Swedish Natural Sci. Res. Council, Stockholm, Sweden.

Van Cleve, K., Dyrness, C. T., Viereck, L. A., Fox, J., Chapin, F. S. and Oechel, W. C. 1983. Taiga ecosystems in interior Alaska. Biosci. **33**: 39-44.

Van Cleve, K. and Yarie, J. 1986. Interaction of temperature, moisture, and soil chemistry in controlling nutrient cycling and ecosystem development in the Alaskan Taiga. Pages 160-189 *in* K. Van Cleve, F. S. Chapin, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness, eds. Forest ecosystems of the Alaskan taiga: A synthesis of structure and function. Springer-Verlag, New York, NY.

Van Wagner, C. E. 1978. Age-class distribution and the forest fire cycle. Can. J. For. Res. **8**: 220-227.

Verhoeven, J. T. A., Koerselman, W. and Beltman, B. 1988. The vegetation of fens in relation to their hydrology and nutrient dynamics: A case study. Pages 249-282 *in* J. J. Symoens (ed.). Handbook of vegetation science, Vol. 15. The vegetation of inland waters. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Verhoeven, J. T. A., Maltby, E. and Schmitz, M. B. 1990. Nitrogen and phosphorus mineralisation in fens and bogs. J. Ecol. **78**: 713-726.

Verry, E. S. 1986. Forest harvesting and water: The Lake States experience. Water Res. Bull. **22**: 1039-1047.

Verry, E. S. 1988. The hydrology of wetlands and man's influence on it. Publ. Acad. Finl. 5: 41-61.

Verry, E. S. and Timmons, D. R. 1982. Water-borne nutrient flow through an upland-peatland watershed in Minnesota. Ecology **63**: 1456-1467.

Viro, P. J. 1974. Effects of forest fire on soil. Pages 7-45 *in* T. T. Kozlowski and C. E. Ahlgren, eds. Fire and ecosystems. Acad. Press, New York, NY.

Vitousek, P. M. 1981. Clear-cutting and the nitrogen cycle. Pages 631-642 *in* F. E. Clark and T. Rosswall, eds. Terrestrial nitrogen cycles. Swedish Natural Sci. Res. Council, Stockholm, Sweden.

Vitousek, P. M. and Matson, P. M. 1984. Mechanisms of nitrogen retention in forested ecosystems: A field experiment. Science **225**: 51-52.

Vitousek, P. M. and Matson, P. M. 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. Ecology **66**: 1360-1376.

Waksman, S. A., and Stevens, K. R. 1929. Contributions to the chemical composition of peat. V. The role of micro-organisms in peat formation and decomposition. Soil Sci. **28**: 321-340.

Waksman, S. A. and Purvis, E. R. 1932. The microbiological population of peat. Soil Sci. **34**: 95-114.

Watt, R. F. and Heinselman, M. L. 1965. Foliar nitrogen and phosphorus level related to site quality in a northern Minnesota spruce bog. Ecology **46**: 357-361.

Waughman, G. J., and Bellamy, D. J. 1980. Nitrogen fixation and the nitrogen balance in peatland ecosystems. Ecology **61**: 1185-1198.

Wein, R. W. 1983. Fire behaviour and ecological effects in organic terrain. Pages 81-95 *in* R. W. Wein and D. A. MacLean, eds. The role of fire in northern circumpolar ecosystems. John Wiley & Sons, New York, NY.

Wein, R. W. and MacLean, D. A. 1983. The role of fire in northern circumpolar ecosystems. John Wiley & Sons, New York, NY.

Williams, B. L. 1984. The influence of peatland type and the chemical characteristics of peat on the content of readily mineralised nitrogen. Proceedings 7th International Peat Congress, Dublin, Ireland. Vol. IV: 410-418.

Williams, B. L. and Wheatley, R. E. 1988. Nitrogen mineralisation and water-table height in oligotrophic deep peat. Biol. Fert. Soils **6**: 141-147.

William, R. T. and Crawford, R. L. 1983. Effects of various physio-chemical factors on microbial activity in peatlands: Aerobic biodegradation processes. Can. J. Microbiol. **29**: 1430-1437.

Woodmansee, R. G. and Wallach, L. S. 1981. Effects of fire regimes on biogeochemical cycles. Pages 649-669 *in* F. E. Clark and T. Rosswall, eds. Terrestrial nitrogen cycles. Swedish Natural Sci. Res. Council, Stockholm, Sweden.

Zoltai, S. C. 1988. Wetland environments and classification. Pages 1-26 *in* C. D. A. Rubec, ed. Wetlands of Canada. Ecological Land Classification Series no. 24. Environment Canada, Ottawa, ON.

Zoltai, S. C., and Pollet, F. C. 1983. Wetlands in Canada: Their classification, distribution, and use. Pages 245-268 *in* A. J. P. Gore, ed. Ecosystems of the world. vol. 4B. Mires: Swamp, bog, fen and moor. Elsevier, Amsterdam, The Netherlands.

Zucker, W. V. 1983. Tannins: Does structure determine function? An ecological perspective. Am. Nat. **121**: 335-365.

APPENDICES

Ia. Burns. Inorganic nitrogen and phosphorus, total N and C:N from summer 1996.

Site	Microrelief	Depth	Time	Nitrate ug/g peat	Ammonium ug/g peat	Tot. Ext. N ug/g peat	Phosphate ug/g peat	Tot. N mg/g peat	C:N
B1	Hummock	0-15	July	3.53	3.26	6.79	1.02	6.00	73.27
B1	Hummock	0-15	July	3.22	0.00	3.22	1.27	8.20	50.91
B1	Hummock	0-15	July	1.43	0.00	1.43	4.55	5.30	83.13
B2	Hummock	0-15	July	2.50	68.62	71.11	1.30	13.80	30.13
B2	Hummock	0-15	July	0.00	16.35	16.35	0.69	14.50	29.68
B2	Hummock	0-15	July	1.14	83.03	84.17	0.90	13.80	29.93
B3	Hummock	0-15	July	0.00	9.19	9.19	1.56		
B3	Hummock	0-15	July	0.00	20.31	20.31	0.70	8.80	46.11
B3	Hummock	0-15	July	0.00	6.30	6.30	0.47	2.20	202.00
B4	Hummock	0-15	July	1.16	0.00	1.16	46.61	4.70	95.02
B4	Hummock	0-15	July	7.70	27.73	35.44	7.95	13.90	32.75
B4	Hummock	0-15	July	8.43	0.00	8.43	0.99	5.40	81.11
B1	Hummock	15-30	July	1.26	0.00	1.26	0.89	8.20	54.76
B1	Hummock	15-30	July	2.00	5.74	7.74	2.11	8.20	55.83
B1	Hummock	15-30	July	2.78	0.00	2.78	1.43	5.80	78.38
B2	Hummock	15-30	July	9.81	9.98	19.79	0.43	17.50	23.17
B2	Hummock	15-30	July	2.52	19.57	22.09	0.63	13.80	30.64
B2	Hummock	15-30	July	5.36	0.00	5.36	1.67	16.00	26.22
B3	Hummock	15-30	July	0.00	7.68	7.68	0.32	7.50	57.75
B3	Hummock	15-30	July	0.00	11.79	11.79	0.84	11.10	40.68
B3	Hummock	15-30	July	0.00	7.77	7.77	0.50	4.30	103.58
B4	Hummock	15-30	July	3.61	1.08	4.69	2.93	6.90	65.36
B4	Hummock	15-30	July	5.69	21.45	27.14	0.87		
B4	Hummock	15-30	July	1.09	4.18	5.27	1.15	4.90	83.14
B1	Hollow	0-15	July	5.01	25.85	30.86	0.66	6.60	66.89
B1	Hollow	0-15	July	3.81	32.14	35.95	2.20	8.60	52.65
B1	Hollow	0-15	July	0.89	0.00	0.89	1.38	8.00	56.00
B2	Hollow	0-15	July	0.00	8.98	8.98	0.65	17.40	25.66
B2	Hollow	0-15	July	3.64	16.13	19.78	0.45	14.10	30.41

Ia (cont.). Burns. Inorganic nitrogen and phosphorus, total N and C:N from summer 1996.

Site	Microrelief	Depth	Time	Nitrate ug/g peat	Ammonium ug/g peat	Tot. Ext. N ug/g peat	Phosphate ug/g peat	Tot. N mg/g peat	C:N
B2	Hollow	0-15	July	14.80	35.40	50.20	1.12	17.30	24.47
B3	Hollow	0-15	July	5.27	10.17	15.45	0.70	10.70	40.56
B3	Hollow	0-15	July	0.00	89.62	89.62	2.34	13.10	30.72
B3	Hollow	0-15	July	0.00	10.97	10.97	1.32	10.30	40.54
B4	Hollow	0-15	July	4.15	28.19	32.34	6.54	10.80	39.45
B4	Hollow	0-15	July	3.86	2.41	6.28			
B4	Hollow	0-15	July	0.00	101.03	101.03	28.74	10.80	37.02
B1	Hollow	15-30	July	1.69	16.95	18.64	1.01	12.80	36.73
B1	Hollow	15-30	July	2.83	20.00	22.83	1.14	6.50	68.55
B1	Hollow	15-30	July	2.62	19.82	22.45	1.57	6.20	73.05
B2	Hollow	15-30	July	0.00	9.82	9.82	0.75	14.30	31.88
B2	Hollow	15-30	July	0.00	17.33	17.33	0.83	13.00	34.23
B2	Hollow	15-30	July	3.68	48.39	52.07	2.38	14.90	28.24
B3	Hollow	15-30	July	0.00	16.43	16.43	0.33	14.90	30.40
B3	Hollow	15-30	July	0.00	9.88	9.88	0.39	13.90	33.47
B3	Hollow	15-30	July	0.00	7.83	7.83	0.42	6.70	67.34
B4	Hollow	15-30	July	0.00	18.79	18.79	4.43	13.20	32.69
B4	Hollow	15-30	July	1.29	9.32	10.61	0.97	13.40	31.24
B4	Hollow	15-30	July	3.54	25.38	28.92	7.24	9.50	44.28
B1	Hummock	0-15	August	0.00	93.20	93.20	4.49	7.00	61.59
B1	Hummock	0-15	August	21.53	31.25	52.78	0.60	8.30	53.37
B1	Hummock	0-15	August	18.81	63.37	82.18	8.57	5.80	76.52
B2	Hummock	0-15	August	11.76	99.55	111.31	9.66	14.90	27.13
B2	Hummock	0-15	August	19.01	1007.04	1026.06	20.12	15.30	26.95
B2	Hummock	0-15	August	11.04	45.45	56.49	0.32	13.00	31.47
B3	Hummock	0-15	August	0.00	65.32	65.32	14.33	5.70	76.54
B3	Hummock	0-15	August	9.38	114.84	124.22	18.87	9.90	42.41
B3	Hummock	0-15	August	37.80	40.24	78.05	1.07	6.70	65.72
B4	Hummock	0-15	August	0.00	0.00	0.00	1.83	5.70	72.47

Ia (cont.). Burns. Inorganic nitrogen and phosphorus, total N and C:N from summer 1996.

Site	Microrelief	Depth	Time	Nitrate ug/g peat	Ammonium ug/g peat	Tot. Ext. N ug/g peat	Phosphate ug/g peat	Tot. N mg/g peat	C:N
B4	Hummock	0-15	August	12.35			25.92	6.50	65.14
B4	Hummock	0-15	August	28.04	42.99	71.03	7.60	10.30	42.72
B1	Hummock	15-30	August	0.00	111.43	111.43	3.48	6.90	65.14
B1	Hummock	15-30	August	0.00	54.76	54.76	1.71	6.10	69.39
B1	Hummock	15-30	August	0.00	89.38	89.38	26.65	9.00	47.81
B2	Hummock	15-30	August	9.34	109.34	118.68	3.18		
B2	Hummock	15-30	August	6.31	67.96	74.27	3.51	16.50	25.53
B2	Hummock	15-30	August	0.00	269.71	269.71	2.95	12.00	34.28
B3	Hummock	15-30	August	25.58	74.42	100.00	1.50	13.20	32.58
B3	Hummock	15-30	August	11.18	111.76	122.94	2.10	15.80	28.01
B3	Hummock	15-30	August	23.30	21.36	44.66	0.69	19.20	21.75
B4	Hummock	15-30	August	26.80	186.60	213.40	16.55	7.80	53.67
B4	Hummock	15-30	August	0.00	71.05	71.05	4.40	5.00	87.70
B4	Hummock	15-30	August	0.00	14.53	14.53	0.81	6.20	66.05
B1	Hollow	0-15	August	0.00	297.10	297.10	11.09	9.40	47.44
B1	Hollow	0-15	August	25.49	136.27	161.76	10.53	9.00	45.49
B1	Hollow	0-15	August	0.00	77.86	77.86	6.97	14.30	32.01
B2	Hollow	0-15	August	0.00	351.19	351.19	6.03	14.90	28.41
B2	Hollow	0-15	August	19.91	76.55	96.46	1.50	17.30	24.29
B2	Hollow	0-15	August	12.50	75.00	87.50	3.86	11.40	37.78
B3	Hollow	0-15	August	4.07	285.19	289.26	3.19	17.00	25.45
B3	Hollow	0-15	August	9.90	77.60	87.50	2.58	13.20	32.32
B3	Hollow	0-15	August	0.00	22.82	22.82	7.21	8.70	48.72
B4	Hollow	0-15	August	0.00	76.92	76.92	30.85	9.00	44.43
B4	Hollow	0-15	August	16.11	355.70	371.81	8.60	11.30	36.56
B4	Hollow	0-15	August	0.00	35.88	35.88	23.00	8.50	47.69
B1	Hollow	15-30	August	0.00	65.38	65.38	0.51	4.90	87.63
B1	Hollow	15-30	August	9.93	113.48	123.40	1.60	9.50	47.32
B1	Hollow	15-30	August	0.00	80.51	80.51	3.74	10.10	46.37

Ia (cont.). Burns. Inorganic nitrogen and phosphorus, total N and C:N from summer 1996.

Site	Microrelief	Depth	Time	Nitrate ug/g peat	Ammonium ug/g peat	Tot. Ext. N ug/g peat	Phosphate ug/g peat	Tot. N mg/g peat	C:N
B2	Hollow	15-30	August	16.28	86.05	102.33	2.09	14.60	30.21
B2	Hollow	15-30	August	0.00	10.38	10.38	2.31	14.80	30.36
B2	Hollow	15-30	August	0.00	77.17	77.17	2.16	14.00	30.45
B3	Hollow	15-30	August	9.22	52.43	61.65	1.28	15.40	31.82
B3	Hollow	15-30	August	0.00	179.01	179.01	6.29	15.20	29.11
B3	Hollow	15-30	August	0.00	279.07	279.07	1.70	13.40	34.14
B4	Hollow	15-30	August	5.97	24.53	30.50	0.90	9.60	43.59
B4	Hollow	15-30	August	0.00	34.12	34.12		7.90	51.19
B4	Hollow	15-30	August	6.59	150.18	156.78	3.23	11.10	36.56

Ib. Clearcuts. Inorganic nitrogen and phosphorus, total N and C:N from summer 1996.

Site	Microrelief	Depth	Time	Nitrate ug/g peat	Ammonium ug/g peat	Tot. Ext. N ug/g peat	Phosphate ug/g peat	Tot. N mg/g peat	C:N
C1	Hummock	0-15	July	0.00	39.25	39.25	0.71	4.80	88.54
C1	Hummock	0-15	July	0.00	19.05	19.05	9.57	6.70	64.84
C1	Hummock	0-15	July	0.00	21.56	21.56	1.80	6.70	66.46
C2	Hummock	0-15	July	0.00	18.08	18.08	0.65	9.80	44.94
C2	Hummock	0-15	July	0.00	21.09	21.09	0.77	10.50	42.30
C2	Hummock	0-15	July	0.00	25.61	25.61	38.60	6.70	67.39
C3	Hummock	0-15	July	0.00	39.91	39.91	27.07	10.20	43.94
C3	Hummock	0-15	July	0.93	1.64	2.57	0.47	4.00	108.98
C3	Hummock	0-15	July	1.19	2.38	3.56	6.96	12.70	35.47
C4	Hummock	0-15	July	13.69	15.37	29.06	1.30	8.00	52.15
C4	Hummock	0-15	July	8.29	92.61	100.90	0.88		
C4	Hummock	0-15	July	11.56	15.05	26.60	1.41	6.50	67.88
C1	Hummock	15-30	July	0.00	17.18	17.18	2.33	5.00	88.96
C1	Hummock	15-30	July	0.00	23.98	23.98	0.62	8.70	51.17
C1	Hummock	15-30	July	5.28	4.66	9.94	1.54	8.20	52.20
C2	Hummock	15-30	July	6.86	12.31	19.16	0.48	13.50	32.60
C2	Hummock	15-30	July	0.00	12.72	12.72	0.53	13.90	30.04
C2	Hummock	15-30	July	6.42	0.00	6.42	37.65	11.00	40.09
C3	Hummock	15-30	July	0.00	88.91	88.91	1.34	9.30	47.44
C3	Hummock	15-30	July	0.00	15.26	15.26	1.63	9.20	48.53
C3	Hummock	15-30	July	3.96	2.64	6.61	4.89	9.80	44.11
C4	Hummock	15-30	July	2.73	39.18	41.91	6.83	7.40	60.08
C4	Hummock	15-30	July	0.00	36.14	36.14	1.04	10.10	44.52
C4	Hummock	15-30	July	0.00	14.41	14.41	0.93	6.70	66.51
C1	Hollow	0-15	July	0.00	68.10	68.10	1.34	11.10	38.22
C1	Hollow	0-15	July	0.00	65.10	65.10	16.80	12.50	36.27
C1	Hollow	0-15	July	0.00	20.76	20.76	0.53	7.70	58.60
C2	Hollow	0-15	July	0.00	22.76	22.76	0.46	14.70	29.36
C2	Hollow	0-15	July	0.00	15.46	15.46	0.92	12.60	36.75

Ib (cont.). Clearcuts. Inorganic nitrogen and phosphorus, total N and C:N from summer 1996.

Site	Microrelief	Depth	Time	Nitrate ug/g peat	Ammonium ug/g peat	Tot. Ext. N ug/g peat	Phosphate ug/g peat	Tot. N mg/g peat	C:N
C2	Hollow	0-15	July	5.32	48.46	53.77	18.26	6.60	68.67
C3	Hollow	0-15	July	5.36	68.77	74.13	14.55	12.20	36.38
C3	Hollow	0-15	July	0.00	32.55	32.55	1.35	11.30	38.50
C3	Hollow	0-15	July	1.33	37.36	38.69	3.72	9.30	47.82
C4	Hollow	0-15	July	1.93	0.47	48.38	1.69	50.31	1.71
C4	Hollow	0-15	July	0.00	49.91	49.91		8.30	46.06
C4	Hollow	0-15	July	9.56	77.02	86.57	2.25	13.60	32.69
C1	Hollow	15-30	July	8.23	24.08	32.30	0.68	9.70	46.42
C1	Hollow	15-30	July	0.00	50.28	50.28	0.88	12.70	33.97
C1	Hollow	15-30	July	6.72	40.78	47.50	3.54	7.80	56.88
C2	Hollow	15-30	July	0.00	10.97	10.97	0.79	21.60	20.17
C2	Hollow	15-30	July	0.00	8.36	8.36	1.00	15.00	28.97
C2	Hollow	15-30	July	6.54	26.81	33.36	1.67	9.50	45.77
C3	Hollow	15-30	July	6.19	27.95	34.14	1.23	11.70	39.04
C3	Hollow	15-30	July	4.74	88.22	92.95	2.31	11.30	40.43
C3	Hollow	15-30	July	5.26	52.86	58.12	6.10	8.80	51.68
C4	Hollow	15-30	July	0.00	9.35	9.35	0.31	7.00	63.83
C4	Hollow	15-30	July	11.66	26.61	38.26	1.78	4.00	113.95
C4	Hollow	15-30	July	4.41	21.13	25.54	0.82	10.00	45.60
C1	Hummock	0-15	August	0.00	69.66	69.66	24.91		
C1	Hummock	0-15	August	0.00	154.44	154.44	24.16	5.70	74.96
C1	Hummock	0-15	August	0.00	79.79	79.79	13.68	11.80	36.15
C2	Hummock	0-15	August	0.00	43.70	43.70		9.10	50.34
C2	Hummock	0-15	August	0.00	131.43	131.43	39.18	7.00	61.31
C2	Hummock	0-15	August	0.00	40.00	40.00	32.94	6.60	64.86
C3	Hummock	0-15	August	34.94	51.81	86.75	0.92	6.70	67.15
C3	Hummock	0-15	August	29.67	63.74	93.41	3.73	4.70	92.36
C3	Hummock	0-15	August	26.92	26.15	53.08	0.23	6.40	69.47
C4	Hummock	0-15	August	0.00	88.17	88.17	7.26	4.50	92.40

Ib (cont.). Clearcuts. Inorganic nitrogen and phosphorus, total N and C:N from summer 1996.

Site	Microrelief	Depth	Time	Nitrate ug/g peat	Ammonium ug/g peat	Tot. Ext. N ug/g peat	Phosphate ug/g peat	Tot. N mg/g peat	C:N
C4	Hummock	0-15	August	0.00	39.64	39.64	7.55	6.40	70.05
C4	Hummock	0-15	August	0.00	311.48	311.48	1.19	7.40	58.89
C1	Hummock	15-30	August	0.00	118.63	118.63	3.38	12.70	35.63
C1	Hummock	15-30	August	0.00	69.81	69.81	4.93	5.50	78.27
C1	Hummock	15-30	August	0.00	55.26	55.26	2.12	17.00	25.61
C2	Hummock	15-30	August	0.00	12.43	12.43		8.40	52.00
C2	Hummock	15-30	August	0.00	221.48	221.48	14.41	11.60	37.59
C2	Hummock	15-30	August	0.00	0.00	0.00	0.51	9.80	45.31
C3	Hummock	15-30	August	0.00	52.17	52.17	2.74	6.50	67.88
C3	Hummock	15-30	August	0.00	282.18	282.18	12.35	6.70	61.42
C3	Hummock	15-30	August	15.33	54.00	69.33	0.21	4.30	102.51
C4	Hummock	15-30	August	16.39	45.08	61.48	6.30	9.90	38.30
C4	Hummock	15-30	August	22.50	103.33	125.83	1.05	11.60	36.97
C4	Hummock	15-30	August	12.80	60.98	73.78	10.15	9.50	45.37
C1	Hollow	0-15	August	0.00	73.33	73.33	36.29	9.10	47.92
C1	Hollow	0-15	August	0.00	212.26	212.26	1.95	8.60	48.95
C1	Hollow	0-15	August	0.00	91.95	91.95	19.12	12.00	35.16
C2	Hollow	0-15	August	0.00	169.12	169.12	4.41	11.40	38.84
C2	Hollow	0-15	August	4.69	140.85	145.54	18.99	10.50	40.16
C2	Hollow	0-15	August	0.00	48.15	48.15	0.96	11.10	40.12
C3	Hollow	0-15	August	18.85	335.08	353.93	0.45	15.10	27.22
C3	Hollow	0-15	August	11.34	159.79	171.13	0.48	6.90	61.64
C3	Hollow	0-15	August	21.38	226.42	247.80	7.03	8.90	50.39
C4	Hollow	0-15	August	0.00	321.64	321.64	1.08	7.60	53.04
C4	Hollow	0-15	August	0.00	191.84	191.84	1.23	12.60	33.52
C4	Hollow	0-15	August	0.00	62.80	62.80	4.09	7.30	57.14
C1	Hollow	15-30	August	0.00	120.39	120.39	5.47	12.20	34.51
C1	Hollow	15-30	August	0.00	96.97	96.97	7.78	9.40	46.50
C1	Hollow	15-30	August	0.00	48.42	48.42	4.67	12.00	37.40

Ib (cont.). Clearcuts. Inorganic nitrogen and phosphorus, total N and C:N from summer 1996.

Site	Microrelief	Depth	Time	Nitrate ug/g peat	Ammonium ug/g peat	Tot. Ext. N ug/g peat	Phosphate ug/g peat	Tot. N mg/g peat	C:N
C2	Hollow	15-30	August	0.00	55.56	55.56	0.25	13.90	33.74
C2	Hollow	15-30	August	0.00	47.01	47.01	2.07	15.60	28.60
C2	Hollow	15-30	August	0.00	40.32	40.32	2.28	11.80	38.52
C3	Hollow	15-30	August	0.00	176.95	176.95	5.77	9.20	50.58
C3	Hollow	15-30	August	18.75	111.88	130.63	3.55	7.40	58.27
C3	Hollow	15-30	August	19.62	112.66	132.28	2.34	9.70	46.53
C4	Hollow	15-30	August	38.46	63.25	101.71	1.16	6.80	67.22
C4	Hollow	15-30	August	0.00	80.54	80.54	2.77	8.60	50.64
C4	Hollow	15-30	August	10.67	66.00	76.67	4.19	5.50	79.04

Ic. Matures. Inorganic nitrogen and phosphorus, total N and C:N from summer 1996.

Site	Microrelief	Depth	Time	Nitrate ug/g peat	Ammonium ug/g peat	Tot. Ext. N ug/g peat	Phosphate ug/g peat	Tot. N mg/g peat	C:N
M1	Hummock	0-15	July	0.00	17.55	17.55	2.43	9.00	50.08
M1	Hummock	0-15	July	0.00	19.39	19.39	1.29	6.80	65.37
M1	Hummock	0-15	July	0.00	43.11	43.11	1.92	8.40	53.02
M2	Hummock	0-15	July	0.91	20.21	21.12	4.20	7.80	58.37
M2	Hummock	0-15	July	2.26	6.09	8.35	5.98	8.40	56.08
M2	Hummock	0-15	July	0.00	16.25	16.25	10.65	6.10	73.87
M3	Hummock	0-15	July	5.52	2.45	7.97	1.22	5.40	84.93
M3	Hummock	0-15	July	4.48	0.00	4.48	7.26	7.10	65.70
M3	Hummock	0-15	July	1.65	0.00	1.65	1.14	3.80	118.92
M4	Hummock	0-15	July	8.88	40.56	49.44	0.92	8.70	47.72
M4	Hummock	0-15	July	0.00	13.43	13.43	3.47	6.60	65.86
M4	Hummock	0-15	July	1.24	8.96	10.19	1.34	6.30	71.29
M1	Hummock	15-30	July	0.00	20.80	20.80	1.51	4.30	98.95
M1	Hummock	15-30	July	0.00	61.41	61.41	0.64	6.30	63.98
M1	Hummock	15-30	July	0.00	109.43	109.43	6.13	14.20	31.02
M2	Hummock	15-30	July	6.27	23.89	30.16	5.55	8.80	66.67
M2	Hummock	15-30	July	1.15	34.78	35.93	3.39	7.70	54.21
M2	Hummock	15-30	July	5.05	57.74	62.79	0.62	6.40	71.81
M3	Hummock	15-30	July	0.00	12.63	12.63	1.06	5.50	80.11
M3	Hummock	15-30	July	0.58	0.00	0.58	2.70	8.50	51.13
M3	Hummock	15-30	July	0.00	62.33	62.33	1.23	7.80	59.50
M4	Hummock	15-30	July	0.00	32.38	32.38	0.96	7.40	58.32
M4	Hummock	15-30	July	12.64	33.33	45.97	0.92	5.70	79.37
M4	Hummock	15-30	July	3.77	16.29	20.07	1.08	7.30	60.14
M1	Hollow	0-15	July	0.00	59.69	59.69	0.87	10.50	40.59
M1	Hollow	0-15	July	0.00	27.15	27.15	1.99		
M1	Hollow	0-15	July	3.35	43.27	46.62	0.44	6.60	66.17
M2	Hollow	0-15	July	2.90	3.87	6.77	1.93		
M2	Hollow	0-15	July	0.00	75.08	75.08	1.07	9.90	45.64

Ic (cont.). Matures. Inorganic nitrogen and phosphorus, total N and C:N from summer 1996.

Site	Microrelief	Depth	Time	Nitrate ug/g peat	Ammonium ug/g peat	Tot. Ext. N ug/g peat	Phosphate ug/g peat	Tot. N mg/g peat	C:N
M2	Hollow	0-15	July	0.00	116.01	116.01	1.88	10.80	40.56
M3	Hollow	0-15	July	1.81	7.90	9.71	2.42	8.70	53.28
M3	Hollow	0-15	July	0.00	61.08	61.08	2.38	7.20	62.42
M3	Hollow	0-15	July	1.28	6.31	7.59			
M4	Hollow	0-15	July	3.30	14.52	17.82	1.02	6.50	68.37
M4	Hollow	0-15	July	0.00	84.34	84.34	0.95	11.40	38.01
M4	Hollow	0-15	July	2.03	10.97	13.00	2.12	9.10	47.96
M1	Hollow	15-30	July	0.00	6.87	6.87	5.65	10.00	41.88
M1	Hollow	15-30	July	3.15	71.75	74.90	2.03	8.90	48.11
M1	Hollow	15-30	July	4.90	38.88	43.78	2.08	7.50	60.48
M2	Hollow	15-30	July	0.00	138.72	138.72	0.59	9.30	45.99
M2	Hollow	15-30	July	5.02	50.61	55.63	2.91	8.20	53.24
M2	Hollow	15-30	July	4.18	19.06	23.24		10.40	44.10
M3	Hollow	15-30	July	0.00	63.12	63.12	3.17	8.70	52.75
M3	Hollow	15-30	July	5.42	88.79	94.20	6.98	8.20	53.57
M3	Hollow	15-30	July	4.54	33.37	37.91	1.90	6.00	73.67
M4	Hollow	15-30	July	0.00	34.48	34.48	3.35	6.00	74.58
M4	Hollow	15-30	July	9.13	19.60	28.73	1.40	8.20	54.73
M4	Hollow	15-30	July	2.96	26.84	29.80	5.84	9.90	43.59
M1	Hummock	0-15	August	0.00	126.98	126.98	3.04	7.90	52.27
M1	Hummock	0-15	August	0.00	50.63	50.63	2.73	8.00	54.65
M1	Hummock	0-15	August	0.00	290.91	290.91	14.13	10.30	41.01
M2	Hummock	0-15	August	12.75	112.75	125.50	1.86	8.80	47.49
M2	Hummock	0-15	August	0.00	428.57	428.57	2.02	10.20	44.43
M2	Hummock	0-15	August	0.00	170.40	170.40	3.54	7.80	55.55
M3	Hummock	0-15	August	15.79	36.84	52.63	0.68	5.10	89.20
M3	Hummock	0-15	August	16.10	90.68	106.78	3.69	4.50	99.91
M3	Hummock	0-15	August	0.00	57.42	57.42	28.49	6.50	69.58
M4	Hummock	0-15	August	0.00	145.56	145.56	2.37	6.10	70.00

Ic (cont.). Matures. Inorganic nitrogen and phosphorus, total N and C:N from summer 1996.

Site	Microrelief	Depth	Time	Nitrate ug/g peat	Ammonium ug/g peat	Tot. Ext. N ug/g peat	Phosphate ug/g peat	Tot. N mg/g peat	C:N
M4	Hummock	0-15	August	0.00	88.71	88.71	2.84	5.50	77.58
M4	Hummock	0-15	August	0.00	252.43	252.43	1.73	8.50	52.00
M1	Hummock	15-30	August	0.00	65.32	65.32	6.35	6.40	66.63
M1	Hummock	15-30	August	0.00	77.12	77.12	24.49	6.10	67.75
M1	Hummock	15-30	August	0.00	54.80	54.80	33.75	8.00	52.61
M2	Hummock	15-30	August				3.10	6.50	68.77
M2	Hummock	15-30	August	9.63	83.03	92.66	0.68	8.60	50.88
M2	Hummock	15-30	August	12.05	325.30	337.35	3.58	9.80	45.98
M3	Hummock	15-30	August	21.57	120.26	141.83	12.40	7.60	57.42
M3	Hummock	15-30	August	9.91	50.45	60.36	9.19	4.40	102.57
M3	Hummock	15-30	August	0.00	88.89	88.89	6.99	6.50	65.98
M4	Hummock	15-30	August	0.00	419.69	419.69	2.12	11.30	37.87
M4	Hummock	15-30	August	0.00	96.15	96.15	3.01	7.40	55.11
M4	Hummock	15-30	August	0.00	82.46	82.46	2.97	9.90	41.81
M1	Hollow	0-15	August	0.00	263.44	263.44	2.05	10.50	40.42
M1	Hollow	0-15	August	7.88	290.64	298.52	7.60	9.00	48.74
M1	Hollow	0-15	August	0.00	492.31	492.31	1.91	10.40	38.58
M2	Hollow	0-15	August	9.57			0.46	9.30	46.34
M2	Hollow	0-15	August	0.00	456.14	456.14	0.45	7.70	55.25
M2	Hollow	0-15	August	0.00	310.16	310.16	0.32	8.00	54.05
M3	Hollow	0-15	August	19.75	162.96	182.72	6.29	24.70	17.36
M3	Hollow	0-15	August	0.00	37.31	37.31	18.66	9.50	46.64
M3	Hollow	0-15	August	0.00	9.36	9.36	16.77	8.60	46.85
M4	Hollow	0-15	August	0.00	269.77	269.77	14.48	9.30	43.46
M4	Hollow	0-15	August	0.00	198.02	198.02	13.54	9.30	47.68
M4	Hollow	0-15	August	0.00	189.19	189.19	23.38	11.30	37.43
M1	Hollow	15-30	August	0.00	70.94	70.94	10.35	9.20	47.97
M1	Hollow	15-30	August	0.00	167.68	167.68	5.25	7.20	61.03
M1	Hollow	15-30	August	0.00	207.55	207.55	6.31	7.10	60.30

Ic (cont.). Matures. Inorganic nitrogen and phosphorus, total N and C:N from summer 1996.

Site	Microrelief	Depth	Time	Nitrate ug/g peat	Ammonium ug/g peat	Tot. Ext. N ug/g peat	Phosphate ug/g peat	Tot. N mg/g peat	C:N
M2	Hollow	15-30	August	0.00	240.57	240.57	3.41	12.30	35.46
M2	Hollow	15-30	August	15.15	121.97	137.12	2.97	23.30	18.38
M2	Hollow	15-30	August	0.00	342.11	342.11	1.53	8.40	52.32
M3	Hollow	15-30	August	0.00	104.29	104.29	6.79	7.30	59.14
M3	Hollow	15-30	August	8.77	517.54	526.32		9.10	47.74
M3	Hollow	15-30	August	10.69	244.27	254.96	8.68	8.70	51.62
M4	Hollow	15-30	August	0.00	295.20	295.20	3.23	12.70	34.05
M4	Hollow	15-30	August	0.00	251.21	251.21	5.90	11.80	36.44
M4	Hollow	15-30	August	0.00	208.33	208.33	7.24		

II. Initial N, net N mineralisation, total N and C:N ratios from *in situ* N mineralisation experiment.

Site	Microrelief	Depth	initialN ug/g peat	NetN min. ug/g peat	Total N mg/g peat	C:N
B1	hummock	0-15	6.79	45.75	6.00	73.27
B1	hummock	15-30	1.26	43.46	8.20	54.76
B1	hummock	0-15	3.22	57.46	8.20	50.91
B1	hummock	15-30	7.74	35.48	8.20	55.83
B1	hummock	0-15	1.43	17.47	5.30	83.13
B1	hummock	15-30	2.78	45.93	5.80	78.38
B1	hollow	0-15	30.86	33.61	6.60	66.89
B1	hollow	15-30	18.64	20.68	12.80	36.73
B1	hollow	0-15	35.95	5.42	8.60	52.65
B1	hollow	15-30	22.83	17.49	6.50	68.55
B1	hollow	0-15	0.89	91.18	8.00	56.00
B1	hollow	15-30	22.45	50.77	6.20	73.05
B2	hummock	0-15	71.11	92.08	13.80	30.13
B2	hummock	15-30	19.79	59.85	17.50	23.17
B2	hummock	0-15	16.35	145.74	14.50	29.68
B2	hummock	15-30	22.09	3.03	13.80	30.64
B2	hummock	0-15	84.17	7.49	13.80	29.93
B2	hummock	15-30	5.36	28.32	16.00	26.22
B2	hollow	0-15	8.98	14.21	17.40	25.66
B2	hollow	15-30	9.82	42.89	14.30	31.88
B2	hollow	0-15	19.78	50.30	14.10	30.41
B2	hollow	15-30	17.33	8.43	13.00	34.23
B2	hollow	0-15	50.20	32.39	17.30	24.47
B2	hollow	15-30	52.07	0.59	14.90	28.24
B3	hummock	0-15	9.19	34.84		
B3	hummock	15-30	7.68	37.87	7.50	57.75
B3	hummock	0-15	20.31	8.71	8.80	46.11
B3	hummock	15-30	11.79	16.71	11.10	40.68
B3	hummock	0-15	6.30	14.42	2.20	202.00
B3	hummock	15-30	7.77	8.27	4.30	103.58
B3	hollow	0-15	15.45	-15.45	10.70	40.56
B3	hollow	15-30	16.43	29.36	14.90	30.40
B3	hollow	0-15	89.62	-41.44	13.10	30.72
B3	hollow	15-30	9.88	47.12	13.90	33.47
B3	hollow	0-15	10.97	23.61	10.30	40.54
B3	hollow	15-30	7.83	7.71	6.70	67.34

Note: Successive measurements from 0-15 to 15-30 cm depths are from same pit.

II (cont.). Initial N, net N mineralisation, total N and C:N ratios from *in situ* N mineralisation experiment.

Site	Microrelief	Depth	initialN ug/g peat	NetN min. ug/g peat	Total N mg/g peat	C:N
C1	hummock	0-15	39.25	64.55	4.80	88.54
C1	hummock	15-30	17.18	28.98	5.00	88.96
C1	hummock	0-15	19.05	168.68	6.70	64.84
C1	hummock	15-30	23.98	43.61	8.70	51.17
C1	hummock	0-15	21.56	56.88	6.70	66.46
C1	hummock	15-30	9.94	35.20	8.20	52.20
C1	hollow	0-15	68.10	121.77	11.10	38.22
C1	hollow	15-30	32.30	3.15	9.70	46.42
C1	hollow	0-15	65.10	101.78	12.50	36.27
C1	hollow	15-30	50.28	-48.55	12.70	33.97
C1	hollow	0-15	20.76	38.98	7.70	58.60
C1	hollow	15-30	47.50	-10.85	7.80	56.88
C2	hummock	0-15	18.08	71.18	9.80	44.94
C2	hummock	15-30	19.16	32.18	13.50	32.60
C2	hummock	0-15	21.09	100.59	10.50	42.30
C2	hummock	15-30	12.72	18.26	13.90	30.04
C2	hummock	0-15	25.61	45.93	6.70	67.39
C2	hummock	15-30	6.42	114.87	11.00	40.09
C2	hollow	0-15	22.76	1.08	14.70	29.36
C2	hollow	15-30	10.97	8.33	21.60	20.17
C2	hollow	0-15	15.46	60.24	12.60	36.75
C2	hollow	15-30	8.36	13.19	15.00	28.97
C2	hollow	0-15	53.77	65.80	6.60	68.67
C2	hollow	15-30	33.36	27.50	9.50	45.77
C3	hummock	0-15	39.91	66.58	10.20	43.94
C3	hummock	15-30	88.91	1.61	9.30	47.44
C3	hummock	0-15	2.57	45.65	4.00	108.98
C3	hummock	15-30	15.26	16.87	9.20	48.53
C3	hummock	0-15	3.56	42.61	12.70	35.47
C3	hummock	15-30	6.61	39.87	9.80	44.11
C3	hollow	0-15	74.13	91.86	12.20	36.38
C3	hollow	15-30	34.14	13.21	11.70	39.04
C3	hollow	0-15	32.55	-8.44	11.30	38.50
C3	hollow	15-30	92.95	-20.28	11.30	40.43
C3	hollow	0-15	38.69	64.49	9.30	47.82
C3	hollow	15-30	58.12	32.12	8.80	51.68

Note: Successive measurements from 0-15 to 15-30 cm depths are from same pit.

II (cont.). Initial N, net N mineralisation, total N and C:N ratios from *in situ* N mineralisation experiment.

Site	Microrelief	Depth	initialN ug/g peat	NetN min. ug/g peat	Total N mg/g peat	C:N
M1	hummock	0-15	17.55	-15.27	9.00	50.08
M1	hummock	15-30	20.80	100.52	4.30	98.95
M1	hummock	0-15	19.39	15.35	6.80	65.37
M1	hummock	15-30	61.41	-33.66	6.30	63.98
M1	hummock	0-15	43.11	-42.24	8.40	53.02
M1	hummock	15-30	109.43	37.54	14.20	31.02
M1	hollow	0-15	59.69	-56.90	10.50	40.59
M1	hollow	15-30	6.87	0.56	10.00	41.88
M1	hollow	0-15	27.15	100.80		
M1	hollow	15-30	74.90	-24.25	8.90	48.11
M1	hollow	0-15	46.62	70.90	6.60	66.17
M1	hollow	15-30	43.78	-17.68	7.50	60.48
M2	hummock	0-15	21.12	-19.77	7.80	58.37
M2	hummock	15-30	30.16	15.19	8.80	66.67
M2	hummock	0-15	8.35	97.93	8.40	56.08
M2	hummock	15-30	35.93	89.25	7.70	54.21
M2	hummock	0-15	16.25	27.75	6.10	73.87
M2	hummock	15-30	62.79	-31.00	6.40	71.81
M2	hollow	0-15	6.77	132.23		
M2	hollow	15-30	138.72	20.14	9.30	45.99
M2	hollow	0-15	75.08	71.93	9.90	45.64
M2	hollow	15-30	55.63	-55.63	8.20	53.24
M2	hollow	0-15	116.01	-106.58	10.80	40.56
M2	hollow	15-30	23.24	10.16	10.40	44.10
M3	hummock	0-15	7.97	62.58	5.40	84.93
M3	hummock	15-30	12.63	39.24	5.50	80.11
M3	hummock	0-15	4.48	143.95	7.10	65.70
M3	hummock	15-30	0.58	36.88	8.50	51.13
M3	hummock	0-15	1.65	30.25	3.80	118.92
M3	hummock	15-30	62.33	29.76	7.80	59.50
M3	hollow	0-15	9.71	85.80	8.70	53.28
M3	hollow	15-30	63.12	-13.51	8.70	52.75
M3	hollow	0-15	61.08	38.21	7.20	62.42
M3	hollow	15-30	94.20	18.39	8.20	53.57
M3	hollow	0-15	7.59	68.76		
M3	hollow	15-30	37.91	12.67	6.00	73.67

Note: Successive measurements from 0-15 to 15-30 cm depths are from same pit.

III. Peat substrate quality parameters from mineralisation study in 1997.

Site	Lignin %	Cellulose %	Lignin/N	LCI[a]	WSC[b]	N mg/g peat	P mg/g peat	C:N	N:P	C:P	Moss Species[c]
B1	22.26	48.72	29.68	0.31	4.43	7.50	0.76	62.40	9.91	618.25	S
B1	26.94	34.72	39.05	0.44	3.25	6.90	0.79	65.35	8.79	574.30	S
B1	25.21	44.44	32.74	0.36	5.56	7.70	0.49	60.45	15.65	945.90	S
B1	15.25	46.56	15.88	0.25	4.90	9.60	0.49	48.28	19.60	946.31	S
B1	20.54	42.61	38.76	0.33	4.82	5.30	0.42	86.04	12.52	1077.03	S
B1	15.12	47.26	31.51	0.24	5.11	4.80	0.34	93.15	14.12	1315.00	S
B1	16.42	50.59	25.65	0.24	4.61	6.40	0.50	72.03	12.90	929.38	S
B1	24.05	33.45	29.69	0.42	4.00	8.10	0.90	54.49	8.96	488.36	S
B2	23.19	40.11	22.09	0.37	3.37	10.50	0.85	44.40	12.40	550.77	S
B2	25.06	49.88	41.77	0.33	2.53	6.00	0.55	74.53	10.93	814.90	S
B2	23.65	29.64	20.39	0.44	2.84	11.60	0.22	38.01	52.94	2012.11	S
B2	13.88	43.46	11.02	0.24	2.35	12.60	0.71	34.84	17.85	621.92	S
B2	30.32	28.55	22.97	0.52	2.67	13.20	1.02	33.92	12.90	437.47	S
B2	51.45	17.92	28.74	0.74	1.64	17.90	1.04	24.06	17.22	414.45	S
B2	48.10	18.45	40.42	0.72	2.45	11.90	0.71	35.71	16.86	602.08	S
B2	13.07	45.94	14.05	0.22	1.75	9.30	0.66	46.53	14.06	654.14	S
B3	21.81	43.44	40.39	0.33	4.50	5.40	0.55	85.65	9.84	842.41	S
B3	19.55	51.83	28.74	0.27	3.98	6.80	0.46	67.31	14.84	998.98	S
B3	18.54	49.79	29.91	0.27	5.00	6.20	0.63	75.31	9.88	744.03	S
B3	25.55	30.29	23.44	0.46	4.73	10.90	1.08	40.92	10.12	414.02	S
B3	21.42	46.80	38.24	0.31	4.82	5.60	0.59	84.36	9.54	804.60	S
B3	16.96	52.45	28.74	0.24	4.77	5.90	0.52	75.64	11.35	858.27	S
B3	15.49	47.42	37.77	0.25	4.91	4.10	0.36	111.59	11.53	1286.08	S
B3	28.10	37.87	47.62	0.43	4.01	5.90	0.61	77.49	9.72	752.86	S

III (cont.). Peat substrate quality parameters from mineralisation study in 1997.

Site	Lignin %	Cellulose %	Lignin/N	LCI[a]	WSC[b]	N mg/g peat	P mg/g peat	C:N	N:P	C:P	Moss Species[c]
C1	14.29	42.47	24.21	0.25	5.71	5.90	0.42	75.97	13.89	1055.31	S
C1	26.97	33.39	32.11	0.45	4.29	8.40	0.10	53.61	84.00	4503.00	S
C1	22.65	31.49	33.31	0.42	5.56	6.80	0.62	66.81	11.01	735.67	S
C1	10.49	33.04	24.98	0.24	4.64	4.20	0.43	104.29	9.66	1007.40	S
C1	15.75	47.64	25.82	0.25	4.99	6.10	0.72	73.87	8.44	623.53	S
C1	16.42	51.71	19.55	0.24	3.75	8.40	0.77	53.10	10.94	580.94	S
C1	23.53	29.41	54.72	0.44	4.82	4.30	0.54	105.67	7.90	834.75	Po
C1	27.94	28.13	55.88	0.50	3.18	5.00	0.49	89.00	10.28	914.92	S
C2	26.45	54.71	30.41	0.33	5.44	8.70	0.24	54.16	36.83	1994.75	S
C2	20.44	41.68	34.07	0.33	4.85	6.00	0.55	77.93	10.84	845.02	S
C2	34.73	29.25	46.94	0.54	5.27	7.40	0.77	63.23	9.56	604.67	S
C2	18.00	45.99	28.58	0.28	4.39	6.30	0.40	73.98	15.66	1158.59	S
C2	27.02	38.27	43.58	0.41	5.62	6.20	0.61	74.77	10.12	756.71	S
C2	23.45	49.56	27.58	0.32	6.09	8.50	0.71	55.24	11.90	657.30	S
C2	15.41	39.88	18.13	0.28	4.08	8.50	0.77	54.35	11.07	601.78	S
C2	21.03	38.35	31.39	0.35	5.71	6.70	0.51	69.39	13.19	915.50	S
C3	21.51	43.19	33.10	0.33	4.64	6.50	0.51	69.80	12.65	882.97	S
C3	23.75	30.54	41.67	0.44	4.81	5.70	0.16	77.54	36.62	2839.85	S
C3	12.05	52.12	29.40	0.19	4.95	4.10	0.35	110.27	11.62	1280.95	S
C3	23.81	50.37	32.62	0.32	3.72	7.30	0.54	62.10	13.40	832.13	S
C3	15.69	51.61	21.20	0.23	4.13	7.40	0.42	62.31	17.48	1089.07	S
C3	12.31	53.79	23.23	0.19	4.28	5.30	0.50	86.15	10.52	906.18	S
C3	13.73	51.58	17.38	0.21	4.66	7.90	0.82	59.47	9.59	570.32	S
C3	33.52	26.67	41.90	0.56	4.30	8.00	0.61	58.86	13.21	777.74	S

III (cont.). Peat substrate quality parameters from mineralisation study in 1997.

Site	Lignin %	Cellulose %	Lignin/N	LCI[a]	WSC[b]	N mg/g peat	P mg/g peat	C:N	N:P	C:P	Moss Species[c]
M1	48.18	17.40	47.24	0.73	6.30	10.20	0.80	46.25	12.69	586.75	P
M1	29.28	29.79	48.00	0.50	5.54	6.10	0.49	75.34	12.44	937.58	S
M1	42.37	15.25	39.60	0.74	6.64	10.70	0.91	41.79	11.77	491.92	P
M1	19.64	40.28	31.68	0.33	5.49	6.20	0.41	75.52	15.06	1137.06	S
M1	24.39	37.72	38.71	0.39	5.71	6.30	0.56	69.73	11.30	787.60	S
M1	11.26	54.60	7.36	0.17	4.08	15.30	0.46	29.24	32.99	964.83	S
M1	38.52	26.04	42.33	0.60	7.02	9.10	0.04	49.40	229.32	11327.40	P
M1	45.28	20.23	65.62	0.69	6.57	6.90	0.53	66.58	12.93	860.95	P
M2	27.94	31.59	33.26	0.47	5.19	8.40	0.18	55.14	47.23	2604.21	S
M2	41.79	23.13	43.53	0.64	5.14	9.60	0.79	47.69	12.08	576.16	P
M2	44.78	20.71	46.64	0.68	6.57	9.60	0.48	49.60	20.00	992.08	P
M2	20.39	42.72	34.56	0.32	3.94	5.90	0.45	77.93	13.25	1032.46	S
M2	22.94	39.61	31.86	0.37	5.01	7.20	0.60	65.60	12.05	790.32	S
M2	29.54	30.89	36.92	0.49	4.94	8.00	0.53	58.28	15.23	887.51	S
M2	47.49	13.22	60.88	0.78	4.73	7.80	0.50	58.74	15.60	916.40	S
M2	21.01	37.16	26.60	0.36	4.50	7.90	0.46	57.00	17.31	986.91	S
M3	43.11	17.32	39.92	0.71	6.39	10.80	1.21	44.32	8.95	396.64	P
M3	41.28	22.67	49.73	0.65	6.48	8.30	1.12	58.17	7.40	430.28	P
M3	21.30	37.22	36.10	0.36	5.48	5.90	0.60	78.81	9.90	780.00	S
M3	25.74	39.27	36.26	0.40	7.23	7.10	0.49	65.49	14.43	944.88	S
M3	23.21	45.85	38.05	0.34	4.77	6.10	0.71	77.75	8.61	669.15	S
M3	26.51	49.12	55.23	0.35	6.23	4.80	0.50	96.46	9.53	918.88	S
M3	25.00	42.64	37.31	0.37	4.31	6.70	0.70	68.40	9.56	654.01	S
M3	21.43	39.85	15.87	0.35	7.52	13.50	0.48	34.77	27.97	972.60	S

IV. Nitrogen and phosphorus mineralisation, initial inorganic N and P concentrations, and total respiration (CO_2 production) from 1997.

Disturbance Type	Site	NetN ug/g peat	NetP ug/g peat	InitialPO$_4$ ug/g peat	InitialNO$_3$ ug/g peat	InitialNH$_4$ ug/g peat	InitialN ug/g peat	CO$_2$ mg/g C
M	M1	-8.27	-10.01	10.60	6.54	14.67	21.21	16.56
M	M1	-0.47	-48.97	49.85	0.00	6.23	6.23	16.92
M	M1	-18.53	-0.98	2.33	5.45	26.15	31.60	18.49
M	M1	-4.88	-1.19	2.42	0.00	10.77	10.77	13.22
M	M1	-14.07	-13.80	14.48	4.76	16.27	21.03	13.15
M	M1	8.72	-3.51	5.15	0.00	36.94	36.94	19.75
M	M1	21.99	-5.22	12.12	8.44	43.30	51.74	17.88
M	M1	-21.77	0.52	2.55	0.00	34.23	34.23	24.68
M	M2	1.95	-3.85	4.24	0.00	6.36	6.36	14.69
M	M2	-2.52	-1.24	1.61	0.00	13.83	13.83	12.01
M	M2	5.73	-0.46	0.92	7.05	4.79	11.84	15.02
M	M2	47.77	1.04	0.62	0.00	25.18	25.18	17.85
M	M2	-12.66	-1.76	9.29	0.00	40.00	40.00	19.08
M	M2	-4.33	-1.59	2.30	6.56	7.43	13.99	15.24
M	M2	-23.43	-0.36	1.00	0.00	43.99	43.99	20.91
M	M2	-19.79	3.61	0.73	0.00	28.60	28.60	19.21
M	M3	-5.86	-63.84	84.90	6.29	15.57	21.86	17.71
M	M3	19.33	-28.52	50.69	0.00	17.10	17.10	25.06
M	M3	-9.25	-77.06	84.07	0.00	15.24	15.24	20.03
M	M3	-3.23	-3.42	3.68	0.00	8.34	8.34	7.65
M	M3	-0.70	-59.52	60.75	0.00	13.93	13.93	18.83
M	M3	-11.12	-2.42	5.20	0.00	19.66	19.66	18.24
M	M3	3.81	6.83	15.13	0.00	40.93	40.93	20.96
M	M3	-8.09	-2.82	3.75	0.00	9.01	9.01	17.17
C	C1	-7.90	-6.92	7.51	0.00	11.22	11.22	18.76
C	C1	-39.87	-7.56	41.22	0.00	45.74	45.74	17.31
C	C1	-3.19	-47.27	47.53	0.00	3.19	3.19	10.53
C	C1	72.44	-48.97	50.67	0.00	11.21	11.21	19.91
C	C1	-19.31	-35.08	37.70	0.00	28.36	28.36	26.92
C	C1	14.06	-37.38	75.48	0.00	74.19	74.19	25.99
C	C1	-5.97	-47.24	80.55	0.00	9.24	9.24	19.37
C	C1	-23.82	3.24	9.85	0.00	35.59	35.59	19.18
C	C2	-33.15	-14.14	59.60	0.00	59.19	59.19	25.45
C	C2	42.59	-25.30	61.23	0.00	32.61	32.61	23.06
C	C2	-109.27	-38.85	97.57	0.00	165.10	165.10	17.97
C	C2	-43.21	-52.22	55.53	0.00	53.00	53.00	19.92
C	C2	-35.34	-88.37	129.62	0.00	43.95	43.95	19.51
C	C2	-13.34	-30.04	43.03	0.00	23.59	23.59	22.49
C	C2	-38.75	-46.79	56.81	0.00	51.00	51.00	25.81
C	C2	-2.03	-68.15	117.61	0.00	19.72	19.72	21.69
C	C3	5.49	-11.91	13.87	0.00	17.19	17.19	18.30
C	C3	-28.95	-2.54	3.24	0.00	36.71	36.71	14.37
C	C3	-16.63	-4.06	6.11	0.00	24.03	24.03	16.83
C	C3	3.61	-3.95	6.58	0.00	4.33	4.33	18.53

IV (cont.). Nitrogen and phosphorus mineralisation, initial inorganic N and P concentrations, and total respiration (CO_2 production) from 1997.

Disturbance Type	Site	NetN ug/g peat	NetP ug/g peat	InitialPO$_4$ ug/g peat	InitialNO$_3$ ug/g peat	InitialNH$_4$ ug/g peat	InitialN ug/g peat	CO$_2$ mg/g C
C	C3	-16.07	-0.81	1.91	10.31	10.84	21.14	18.36
C	C3	-4.79	-20.07	24.20	0.00	12.96	12.96	13.68
C	C3	-20.36	15.19	9.57	0.00	31.82	31.82	20.53
C	C3	-35.42	2.45	16.55	11.19	33.05	44.24	21.79
B	B1	16.56	-0.43	5.66	0.00	14.21	14.21	15.16
B	B1	-19.08	-3.43	5.41	0.00	25.47	25.47	14.64
B	B1	-8.62	-1.89	4.00	12.99	7.31	20.29	9.82
B	B1	-25.92	-5.63	6.42	6.31	35.49	41.81	17.07
B	B1	-6.10	-8.98	13.36	5.38	8.38	13.76	11.53
B	B1	-5.92	-1.66	2.29	0.00	10.52	10.52	14.31
B	B1	5.49	-1.38	10.06	0.00	15.86	15.86	18.44
B	B1	16.86	11.16	7.42	15.50	5.19	20.68	24.63
B	B2	-2.28	-7.91	8.38	0.00	9.02	9.02	17.41
B	B2	-0.31	-0.78	0.94	0.00	13.44	13.44	15.23
B	B2	-162.70	-10.50	11.87	7.58	175.83	183.41	29.78
B	B2	-87.29	-7.56	15.14	0.00	242.69	242.69	25.35
B	B2	-118.58	-1.97	2.88	0.00	175.27	175.27	18.30
B	B2	-70.29	-6.55	6.92	0.00	77.64	77.64	20.10
B	B2	-0.38	-2.90	3.38	2.99	51.04	54.03	8.18
B	B2	-51.44	-13.42	14.53	7.51	112.14	119.64	16.84
B	B3	3.24	7.15	8.68	0.00	12.67	12.67	16.43
B	B3	5.39	-10.66	11.35	0.00	2.84	2.84	9.10
B	B3	-20.06	-1.02	2.17	5.36	29.43	34.79	19.76
B	B3	-6.60	2.65	9.08	0.00	13.40	13.40	19.42
B	B3	-9.53	-0.19	5.37	0.00	14.60	14.60	18.86
B	B3	-4.30	-7.37	8.26	0.00	7.95	7.95	14.89
B	B3	-0.49	2.53	1.87	0.00	4.36	4.36	10.54
B	B3	-29.55	-4.28	6.98	7.80	28.67	36.47	18.34

V. Soil profile descriptions and peatland classification for sites used in *in situ* incubation and substrate quality experiments.

Site	Horizon designation	Horizon depth	Peatland classification
M1	Of	0-90 cm	Basin Bog
	Om	90-120 cm	
	Cg	120+ cm	
M2	Of	0-65 cm	Shore Bog
	Om	65-140 cm	
	Of	140-160 cm	
M3	Of	0-85 cm	Basin Bog
	Om	85-110 cm	
	Oh	110-160 cm	
C1	Of	0-71 cm	Flat Bog
	Om	71-80 cm	
	Oh	80-110 cm	
	Cg	110+ cm	
C2	Of	0-10 cm	Flat Bog
	Om	10-15 cm	
	Oh	15-52 cm	
	Om	52-120 cm	
	Of	120-160 cm	
C3	Of	0-70 cm	Basin Bog
	Om	70-100 cm	
	Oh	100-120 cm	
	Om	120-160 cm	
B1	Of	0-160 cm	Shore Bog
B2	Of	0-20 cm	Horizontal or Basin Fen
	Oh	20-80 cm	
	Om	80-160 cm	
B3	Of	0-55 cm	Basin Bog
	Om	55-120 cm	
	Of	120-160 cm	

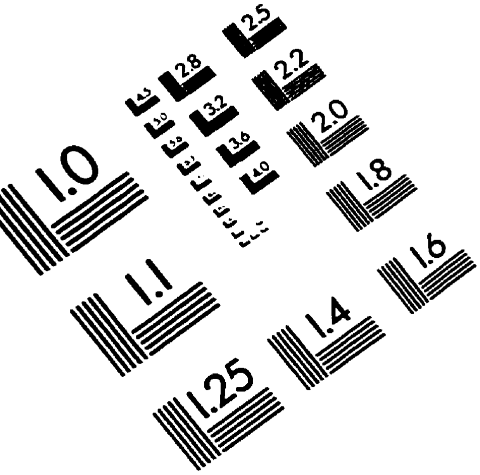
VI. Physical properties of peat depending on degree of humification.

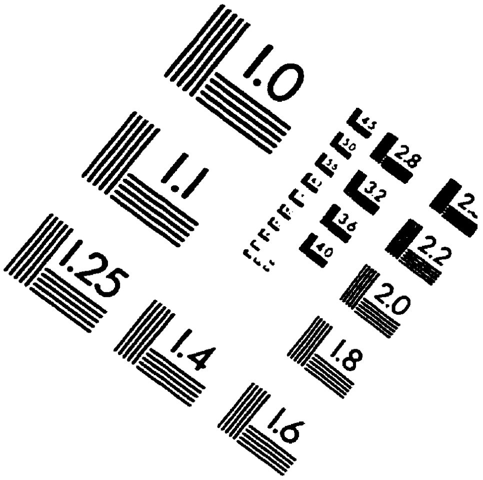
	Degree of humification		
	Fibric	Mesic	Humic
Bulk density (g cm^{-3})	<0.075	0.075-0.195	>0.195
Total porosity (% vol)	>90	90-85	<85
0.01 MPa water content (% vol)	<48	48-70	>70
Hydraulic conductivity (cm hr^{-1})	>6	6-0.1	<0.1

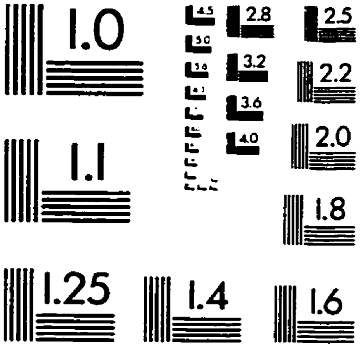
(Soil Classification Working Group 1998; page 19)

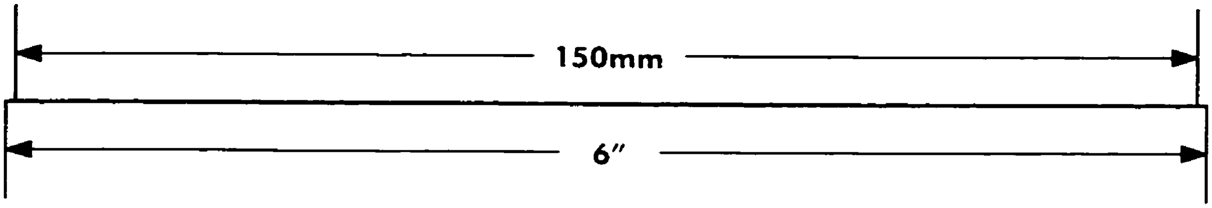
Note: Most peat samples used in Chapters 4 and 5 were of fibric origin.

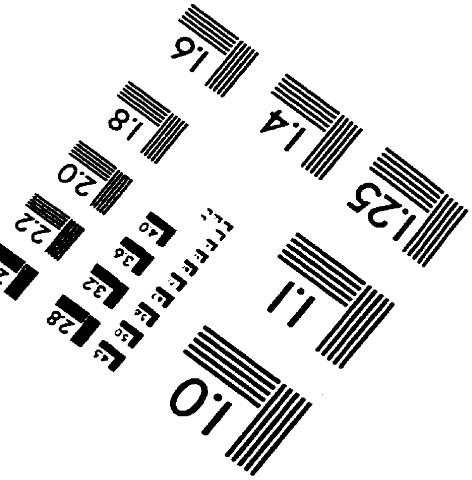
IMAGE EVALUATION
TEST TARGET (QA-3)











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