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Development of key components of a nitrogen budget for a forested watershed on the Canadian boreal plain

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Development of key components of a nitrogen budget for a forested watershed on the Canadian Boreal Plain.

by

David Everett Pelster

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Abstract

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This investigation, which took place as part of the Forest Watershed and Riparian Disturbance (FORWARD) study in west-central Alberta on the Boreal Plain, measured key components of a nitrogen (N) budget in a relatively undisturbed, forested watershed. The first component examined was N inputs from bulk deposition and the effect of different forest soil/canopy types (upland deciduous, upland conifer and wetland conifer stands) on N flux from the bulk deposition to the forest floor. Annual total dissolved N (TDN) inputs in bulk deposition during the period 1 November 2006 to 31 October 2007 (2007 water year) were 410 mg N m^{-2}. The forest canopy of each soil/canopy types retained N, decreasing annual inorganic N (IN = nitrate [NO_3^-] + ammonium [NH_4^+]) flux to the forest floor by approximately 55% and decreasing annual TDN flux to the forest floor by 28 to 41%. There was no detectable difference in N flux of throughfall or stemflow between the different soil/stand types.

Nitrogen turnover (mineralization) within the forest soils of these soil/canopy types were also examined during a 12-week period from mid-June to mid-September. Net mineralization (ammonification and nitrification) rates in the forest soils (FH and Ae horizons in upland soils and the Of layer in the wetland soils) were highest in the upland deciduous stands (1526 and 82 mg N m^{-2} for ammonification and nitrification respectively) and lowest in the wetland conifer stands (482 and 33 mg N m^{-2} for ammonification and nitrification respectively). Seasonally, net mineralization rates were greater during early summer than late summer, possibly because soil and air temperatures were warmer during early summer.

Nitrogen export in the surface water was examined for 3 small sub-watersheds within a larger FORWARD study watershed. Each sub-watershed was selected to maximize coverage by one of the main soil/stand types. For the 2007 ice-free period (1 May to 31 October), TDN exports ranged from 25 to 32 mg N m^{-2}. Although TDN exports were similar between the sub-watersheds, there appears to be differences in the forms of N exported from the sub-watersheds. The sub-watershed with high wetland conifer cover exported mainly (over 90%) dissolved organic N (DON), and almost no NO_3^-. The two sub-watersheds with no wetlands exported proportionally less DON and much more NO_3^-. Of the two sub-watersheds with no wetlands, the one comprised of primarily upland conifer stands exported a greater proportion of NH_4^+ than the sub-watershed with primarily upland deciduous stands. The majority (55 to 79%) of TDN exports were exported from all sub-watersheds during the spring snowmelt. Total N retention within all the sub-watersheds was approximately 93% of bulk deposition inputs.

Key Words: Nitrogen budget, Boreal Plain, bulk deposition, throughfall, mineralization, export

Contents

Acronyms

ABS Acrylonitrile-butadiene-styrene

AC Ammonium coefficient

Annamox Anaerobic ammonium oxidation

ANOVA Analysis of variance

ATP Adenosine triphosphate

C Carbon

DBH Diameter at breast height (1.3 m)

DOC Dissolved organic carbon

DON Dissolved organic nitrogen

ELA Experimental Lakes Area

FH Forest floor

FORWARD Forest Watershed and Riparian Disturbance

FWMC Flow weighted mean concentration

HBEF Hubbard Brook Experimental Forest

IN Inorganic nitrogen

ISC/IERB Incubated soil core/ion exchange resin beads

N Nitrogen

N_2 Molecular nitrogen

NC Nitrate coefficient

NO_3^- Nitrate

NH_4^+ Ammonium

NPP Net primary productivity

NSERC National science and engineering research council

ON Organic nitrogen

PVC Polyvinyl chloride

RC Runoff coefficient

SD Standard deviation

SOM Soil organic material

TDN Total dissolved nitrogen

TN Total nitrogen

Figures

Tables

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Chapter 1
Introduction

1.1 STUDY OVERVIEW

Nitrogen (N) cycling has received much attention from scientists and government regulators recently, as increasing amounts of inorganic N (IN = nitrate [NO_3^-] + ammonium [NH_4^+]) are created and released into the environment by human activity. Many temperate and high-latitude forests are thought to have been N limited (Shaver and Chapin 1980; Aumen et al. 1983; Schlesinger 1991, Vitousek and Howarth 1991). However, increased N deposition from anthropogenic sources is leading to N saturation in many areas within the industrialized world. This can cause acidification of soils and loss of soil productivity due to production of nitrate and decreased magnesium (Mg) to N and calcium (Ca) to aluminum (Al) ratios (Aber et al. 1995); loss of forest floor mass and root biomass (McNulty et al. 1991; Gundersen et al. 1998); changes in vegetation community; and leaching of NO_3^-, which can impair ground and surface water quality (Stoddard 1994). Understanding how N cycles through a relatively pristine forest ecosystem, through construction of a simple N budget, is therefore critical to establish a baseline against which changes such as the effects of anthropogenic N deposition can be judged. Examination of N cycling in relatively pristine watershed also provides a test for the N saturation theory proposed by Aber et al. (1989). This theory predicts that areas in stage 0 of N saturation will have low net mineralization rates, very low net nitrification rates and very low NO_3^- exports (Aber et al. 1989). The use of input/output budgets is also an important tool in determining the fate of atmospheric inputs and the health of the ecosystem.

Studies on the Canadian Boreal Plain (Fig. 1-1) have shown that N inputs from atmospheric deposition were quite low (Shaw et al. 1989; Kochy and Wilson 2001), ranging from 424 to 680 mg N m^{-2} yr^{-1}, compared with N deposition rates from the northeastern USA that can be as high as 1600 mg N m^{-2} yr^{-1} (Friedland et al., 1991; Driscoll et al., 2003) so it is unlikely that N saturation in this ecozone is currently a problem. However industrial development in the area, which is expanding dramatically, may have significant impacts on N cycling on the Alberta Boreal Plain. For example oil production from oil sands increased 4-fold during the last 10 years and is estimated to increase 10-fold again by 2015 (Severson-Baker et al. 2008). This increased oil production from the oil sands was predicted to result in a 5-fold increase in NO_x emissions from the production area (Golder Associates 2002). There was also a 7-fold increase in the number of coalbed methane extraction wells from 2003 to 2006 (Government of Alberta 2009a), which along with other fossil fuel exploration and extraction will further increase NO_x emissions in the province. Nitrogen losses from watersheds and the concomitant export into adjacent surface waters may also occur after forest disturbance such as harvesting and wildfire. Since the amount of forest harvesting in this ecozone has doubled during the last 20 years (Canadian Council of Forest Ministers 2008), the combination of increased N loading from industrial development and increased forest harvesting may have serious effects on soil productivity and water quality in the future.

Given the increasing rate of anthropogenic disturbance on the Boreal Plain, the number of studies examining N mineralization and nitrification in soils and/or N export both before and after forest disturbance has also increased. Currently however, there are no studies that measure N inputs and the effect of the forest canopy on N flux in throughfall, and no comprehensive studies that attempt to construct a simple N budget on the Boreal Plain. Instead, to make inferences regarding N cycling and ecosystem health on the Boreal Plain, it is necessary to use a collection of studies, some measuring inputs, others internal cycling and others exports, or extrapolations must be made from studies in other regions of Canada, the USA or Europe. The purpose of this thesis was to address the knowledge gap in N fluxes on the Boreal Plain by measuring key components of a N budget for a small, relatively undisturbed watershed (the Willow watershed) on the Boreal Plain in the Swan Hills of west-central Alberta (Fig. 1-1) as a component of the Forest Watershed and Riparian Disturbance (FORWARD) project.

The FORWARD project, initiated in 2001, is a long-term study designed to develop hydrological and water quality models for direct application to industrial forest planning in the Swan Hills (Smith et al. 2003; Prepas et al. 2008). This study area is upwind of most of the existing oil sands development, and therefore makes an ideal place for a baseline study. However, potential expansion of oil sands development into the Peace River area (Government of Alberta 2009b, Fig. 1-1) along with much of the coalbed methane extraction is northwest of the study area. Since the prevailing winds at the FORWARD study area are from the northwest, the projected westward expansion of industrial development may result in dramatic increases in the N loading rates to the study site. Therefore, this was an excellent opportunity to examine how industrial developments affect N cycling in the boreal forests of Alberta. Before impacts can be examined, an understanding of N cycling in baseline conditions is required. To create a baseline N budget for the Willow watershed, N inputs from atmospheric deposition, cycling from the forest canopy to the forest soil, net N mineralization rates, N concentrations in soil leachate and N exports in surface water were measured.

The thesis begins with an exploration of the effects of forest harvesting on N export (especially IN) from forested watersheds on the Boreal Plain. The expectation was that forest harvesting will increase N export above reference and pre-disturbance levels (Likens et al. 1970, Pardo et al. 1995, Cairns and Lajtha 2005). However because of the differences in wetland cover, forest cover types (i.e. deciduous dominated, coniferous dominated and mixedwoods) and underlying geology between the watersheds, the amount of within type variation was expected to interfere with detecting the impacts of forest harvesting.

The objective for the rest of the thesis therefore, was to examine potential sources of this variability. To accomplish this, the N inputs, cycling and exports of three broad forest soil/stand types (upland coniferous, upland deciduous and wetland coniferous) in a relatively undisturbed watershed were examined.

The hypotheses to be tested, which were expanded on and developed in greater depth within the successive chapters, are as follows:

1. The soil/stand type does not affect N inputs in bulk deposition. Instead, since climate and proximity to industrial sources are considered to be the major factors in N inputs in bulk deposition, the study site should receive relatively little N inputs in bulk deposition compared with other studies in the literature.
2. Since forest canopies in areas with low N inputs in bulk deposition tend to retain N, the throughfall N flux should be less than the N flux of bulk deposition, with the throughfall N flux differing by the forest cover/soil types. Specifically, the greater leaf area index of the upland conifer forests should lead to increased N retention than either the upland deciduous or wetland conifer soil/stand types.
3. The N cycling within the soils, as estimated by net mineralization (ammonification and nitrification) rates, was also expected to differ by soil/stand types. Since mineralization rates are affected by substrate and environmental factors such as temperature and oxygen status the rates are expected to be higher

in the upland, especially deciduous, versus the wetland stands. Also, net nitrification rates were expected to be very low in all soil/stand types.

4. Exports in stream water were expected to be very low, with the composition of the N exported related to soil/stand type. Wetlands, which have higher water tables and therefore experience more reducing conditions than uplands, were therefore expected to export more NH_4^+ than the uplands, which should export more of the oxidized IN species (NO_3^-). Also, because of the longer flowpath of water through organic soil horizons in wetlands versus uplands, the wetlands were expected to export more dissolved organic N (DON) than uplands.

1.2 THESIS OUTLINE

In the first, and current, chapter a brief introduction to N budgets is provided, as well as a brief description of the study area. In the second chapter more detail is provided on what an N budget is, including much of the current state of knowledge regarding N cycling in boreal and temperate regions. Nitrogen cycling in boreal wetlands is summarized in chapter 2 and is included in the publication "Water and nutrient inputs, outputs, and storage in Canadian boreal forest wetlands: a review" in the Journal of Environmental Engineering and Science (JEES) (see Pelster et al. 2008a, Appendix A). My role in the production of this manuscript was to write the summary sections on nitrogen and carbon, as well as much of the introduction and conclusion.

The exports of N from disturbed watersheds on the Boreal Plain were examined in chapter 3. A version of this chapter was also published in JEES (Pelster et al. 2008b) and concludes that forest disturbance, including wildfire and harvesting, have a significant effect on N export in surface water. My role in the production of this manuscript was to analyze most of the data, write some of the introduction and methods sections, write most of the results and discussion sections and submit the manuscript. From the study it was evident that there was much variability within the reference and disturbed watersheds, which may be related to different soil and forest cover types. In chapters 4, 5 and 6 N inputs, cycling and exports from certain common soil and forest cover (stand) type combinations were examined to determine if and how the broad soil/stand types affect N cycling and export from relatively undisturbed Boreal Plain watersheds.

Chapter 4 consists of an examination of N inputs in bulk deposition and the influence of the forest canopy and soil type on the concentration and flux of total dissolved N (TDN) and other N fractions (i.e. NO_3^-, NH_4^+ and dissolved organic N [DON]) in throughfall and stemflow. The role of the surficial soils (the forest floor and the Ae mineral horizon in uplands and the top 20 cm of peat in wetlands) in retaining or releasing N and the fractionation of that N was evaluated in chapter 5. Net mineralization and nitrification rates were examined through a series of *in situ* soil incubations to determine the amount of IN produced from internal soil cycling. The leachate from the upper soil horizons was also examined to determine how much N leached through each soil horizon on hillslopes in two upland stands and a treed wetland stand. Chapter 6 then consists of an investigation of N exports from 3 sub-watersheds, each comprised primarily of one of the soil/stand type combinations.

A synthesis of the previous chapters is provided in chapter 7 including N export patterns from sub-watersheds within the Willow watershed. Since gaseous exchange (e.g. N_2 fixation rates and denitrification) was not measured, literature estimates were used for the gaseous portion. Using the input, export and cycling data presented throughout the thesis, a coherent, albeit simple, conceptualization of an N budget for a small watershed on the Boreal Plain was developed.

1.3 STUDY SITE DESCRIPTION

The Boreal Plain is a large Canadian ecozone, approximately 650 000 km^2 or more than twice the size of Finland, that stretches from Lake Winnipeg westward to the Boreal Cordillera in northern British Columbia. Human population in the area is very low, averaging just over 1 person km^{-2} (Environment Canada 1996). In 1996, about 45% of inhabitants were urban, and the rest were rural (Environment Canada 1996). The dominant industries in the area are generally associated with resource extraction, mainly lumber, oil and gas. There has also been some conversion of forest to agricultural land, mainly along the southern fringe although there has been additional conversion in northwestern Alberta focused around the city of Grande Prairie. The low human population density has resulted in limited infrastructure, remote study sites and until recently, very little scientific interest. Despite the large size of the ecozone, the FORWARD project is the first and only project on the Boreal Plain building towards compiling a long-term data base examining the effects of watershed disturbances on stream water quality and quantity and this thesis is the first study in the ecozone that measures key components of an annual N budget for a reference watershed.

The study site is located in the Swan Hills, a geologic formation underlain with soft sedimentary bedrock, located in the western Boreal Plain approximately 200 km northwest of the city of Edmonton AB. Subsequent glaciations have altered the bedrock to form the rolling moraines of the uplands and lacustrine deposits of the lowlands (Finklestein 1990). Soil formation reflects the importance of forest vegetation that has resulted in downward clay leaching as the dominant soil forming process, such that Luvisolic soils dominate, although organic, brunisolic, gleysolic and regosolic soils are also present (Ecological Stratification Working Group 1996). The majority of the soils in the Swan Hills are fine-textured and Ca-rich and have formed on alkaline parent material of marine origin. As a result, they retain nutrients like phosphorus (P) as calcium (Ca) and magnesium (Mg) phosphates, instead of the iron (Fe) and aluminum (Al) phosphates characteristic of more acidic soils (Reddy et al. 1999).

The forest vegetation in the Swan Hills is dominated by trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.), white spruce (*Picea glauca* (Moench) Voss), and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. latifolia Engelm.) in well-drained sites and black spruce (*Picea mariana* (Mill.) BSP) and tamarack (*Larix laricina* (Du Roi) K. Koch) in poorly drained sites (Ecological Stratification Working Group 1996). Green alder (*Alnus crispa*) is a dominant understorey shrub in upland sites, while river alder (*A. tenuifolia*) is often found in riparian areas. Feather mosses, especially Schreber's moss (*Pleurozium schreberi*), stair-step moss (*Hylocomium splendens*) and knight's plume moss (*Ptilium crista-castrensis*) are also common in the understorey of uplands. Labrador tea (*Ledum groenlandicum*) and various peat mosses (*Sphagnum* spp.) dominate the understorey in wetlands.

The climate is sub-humid and precipitation is variable on both temporal and spatial scales, with lake evaporation at a study site approximately 200 km east typically exceeding precipitation, often by more than 100 mm yr^{-1} (Prepas et al. 2001). This pattern can result in up to 10-fold changes in runoff between adjacent years with normal variation in precipitation (Prepas et al. 2001). The long-term (1978 to 2009) mean annual precipitation for the Whitecourt A weather station, located approximately 20 km southeast of the study area (elevation 782 m), ranged from 364 to 786 mm, of which an average of 24% was snow (Environment Canada 2006). Spatial variation can also be quite high. Among the four meteorological stations operating in the FORWARD study area, covering elevations from 865 to 1025 m and an area of approximately 230 km^2, total precipitation ranged from 454 to 519 mm in 2004, (Prepas et al. unpublished data) while total precipitation was 573 mm at the Whitecourt A weather station.

Runoff patterns within the Willow watershed reflect this variability, with instantaneous discharge during 2007 ranging by 2 orders of magnitude, while annual runoff varied 3-fold between 2002 and 2007. Streamwater pH was near neutral to slightly basic, ranging from 7.2 to 8.2 in the Willow stream during 2007. For more detailed descriptions of the Willow watershed as well as the other FORWARD watersheds, see Burke et al. (2005) and Prepas et al. (2003, 2006).

The Willow watershed (the study watershed) was approximately 15.6 km^2 in size and is a tributary watershed to the Sakwatamau River watershed with a north northeast aspect. Aerial photograph interpretation from 1994 demonstrated that the forest cover in the Willow watershed was approximately 39% conifer-dominated (70% or more conifer crown closure in the forest canopy), 53% deciduous-dominated (70% or more deciduous crown closure), and 6% mixed-wood (21 – 79% conifer crown closure), with the other 2% non-forested. There has been limited forest harvesting in recent history (35 ha clear cut circa 1980), so the only human disturbance, limited to approximately 1% of the watershed, has been road building along the west and south boundaries of the watershed, and oil and gas exploration (cutting of seismic lines) and extraction (building of access roads and wellsites). The forest stands within the Willow watershed were likely from two different cohorts; approximately 85% of the stands (by area) were roughly 70 years old, while the other 15%, mainly on the eastern side of the watershed were about 120 years old.

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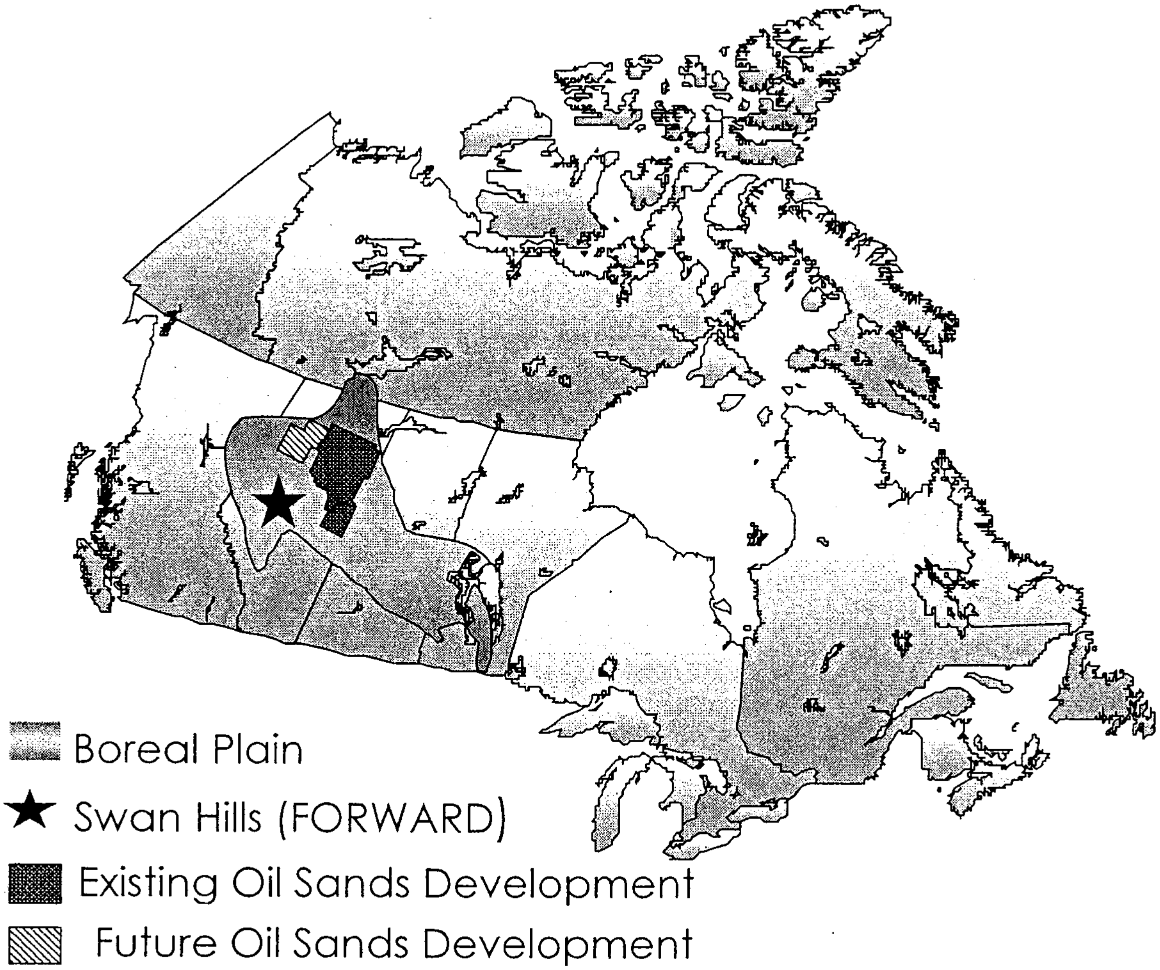
Figure 1-1 Location of the Swan Hills in relation to oil sands development, Alberta, Canada.



Chapter 2

Nitrogen budgets in northern forests: a review[1].

2.1 INTRODUCTION

A nitrogen (N) budget for a forested watershed consists of inputs, storage (or pools), cycling between pools and exports. Inputs include atmospheric deposition, N_2 fixation (conversion of molecular N_2 to NH_4^+) and groundwater flow from adjacent watersheds (Fig. 2-1). Climate, proximity to large industrial sites and urban areas (Kochy and Wilson 2001), and vegetation (Stevenson and Cole 1999) and soil characteristics (Bowden 1987, Sprent and Sprent 1990, Anderson et al. 2004) all influence N input rates.

There are three main N pools in a forested watershed: vegetation, the forest floor and the mineral soil. Internal cycling pathways among these pools consist of throughfall (precipitation dripping through the canopy to the forest floor loses N to or gains N from the canopy), stemflow (precipitation flowing down the trunk of trees to the forest floor loses N to or gains N from the canopy, stems and trunks of trees), litterfall, mineralization (conversion of organically bound N to NH_4^+), nitrification (microbial conversion of NH_4^+ to NO_2^- which is then converted to NO_3^-), immobilization (uptake of N by bacteria, fungi and plant roots), and instream processing (broad term combining immobilization, mineralization, nitrification and adsorption within a stream channel and the associated hyporheic zone) (Fig. 2-1). The size of the N pools and the rates of cycling vary with climate, vegetation type (Likens et al. 1970, Vitousek et al. 1982, Aber et al.

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1991, Parker et al. 2001), elevation (Bernhardt et al. 2003), soil type (DeVito et al. 1999) and type of and time since disturbance (Parker et al. 2001, LeDuc and Rothstein 2007).

Outputs consist of N entrainment in surface and subsurface outflow, volatilization during fire, physical removal of biomass (e.g., forest harvest), denitrification (the bacterial conversion of NO_3^- to gaseous forms of N) and anaerobic ammonium oxidation (anammox - the bacterial conversion of NH_4^+ and NO_2^- to gaseous N_2) (Jetten 2001) (Fig. 2-1). Nitrogen export rates have been correlated with vegetation type (Verry and Timmons 1982, Whigham et al. 1988, Devito et al. 1999, Price et al. 2005, MacCrae et al. 2006), stand age (Vitousek and Reiners 1975), season (Verry & Timmons 1982, DeVito et al. 1989, Mulholland 2004), slope (Dillon et al. 1991), soil properties (MacDonald et al. 2002) and bedrock geology (Williard et al. 2005).

2.1.1 Inputs

There are three ways that N inputs can enter a watershed, the first of which is atmospheric, or bulk deposition. Between 15 and 36% of bulk deposition is composed of dry deposition (Balestrini et al. 2007; Burns et al. 2003; and Zeller et al. 2007), which is usually associated with settling of dust and small N particles. Some descriptions of dry deposited N also include direct uptake by forest vegetation of gaseous ammonia (NH_3) and nitrogen dioxide (NO_2) (Gebler et al. 2002). Dry deposition rates however, tend to be difficult to measure. Wet deposited N comprises the rest of the bulk deposition inputs and enters the watershed as N-containing molecules dissolved or suspended in precipitation.

Atmospheric N deposition rates vary across Canada with differences due to climate and proximity to large sources of industrial and vehicle emissions of nitrogen oxides (NO_X) (Kochy and Wilson 2001). Numerous other studies over the last 20 years have measured bulk N deposition rates across North America and Europe with rates for Canadian boreal forests ranging from 270 to 424 mg N m^{-2} a^{-1} in central Alberta (Shaw et al. 1989) to approximately 1130 mg N m^{-2} yr^{-1} for central Ontario (Molot and Dillon 1993). Outside the boreal region in Canada, Kochy and Wilson (2001) measured N deposition rates ranging from 680 to 2210 mg N m^{-2} yr^{-1} for national parks in western Canada, with the greatest bulk N deposition occurring within an aspen parkland forest surrounded by agricultural land and close to a large urban and industrial center. In comparison, bulk N deposition rates in the eastern U.S. are typically about 2000 mg N m^{-2} yr^{-1} (McNulty et al. 1991, Lawrence et al. 2000), while N deposition rates in Europe can be as high as 3300 mg N m^{-2} yr^{-1} (Table 1-1).

The second N input to the Canadian boreal forest is N_2 fixation. Dinitrogen fixation is an energy intensive process: it requires 16 ATP molecules (or 489 KJ mol^{-1}) and production of the specialized nitrogenase enzyme. There are three classes of N_2 fixing organisms: free-living autotrophic bacteria (primarily cyanobacteria), free-living heterotrophic bacteria and heterotrophic bacteria living as symbionts with vascular and non-vascular plants. The free-living cyanobacteria and heterotrophic bacteria are within the genera *Clostridium*, *Azotobacter*, *Calothrix* and *Mastigocledus*. The cyanobacterial genera *Nostoc* and *Anabaena* can either be free living or they can form a symbiotic relationship, without nodules, with mosses, fungi (i.e., lichens) and certain higher plants (Larcher 1975). Common nodule-forming symbiotic genera include *Rhizobium* and *Frankia*. *Rhizobium* forms nodules on the roots of legumes, while the actinomycete *Frankia* forms nodules on the roots of alder (*Alnus* spp.), sweet gale (*Myrica* spp.), buckthorn (*Hippophae* spp.) and silverberry (*Elaeagnus* spp.) (Larcher 1975).

Dinitrogen fixation rates vary with vegetation type (Larcher 1975), microbial community, soil characteristics (i.e., temperature, pH, and amount of previously fixed N), soil parent materials, moisture conditions and litter quality (Vitousek et al. 2002). Dinitrogen fixation rates were also negatively correlated with atmospheric inputs of inorganic N (IN) (DeLuca et al. 2007). Therefore, N_2 fixation by microorganisms is thought to be an important source of IN for those portions of the boreal forest that receive little IN from atmospheric deposition (e.g. the Boreal Plain in western Canada) (Table 1-1).

Fixation of N_2 in wetlands is the result of both free-living and symbiotic fixation. Estimates of N_2 fixation rates by free-living bacteria in peatlands (wetlands with more than 40 cm peat depth) range from 0.013 mg N kg^{-1} day^{-1} for the top 10 cm of the peat, to 0.061 mg N kg^{-1} day^{-1} (Kravchenko and Doroshenko 2003). Since peat bulk densities range from 82 to 109 kg m^{-3} (Schlotzhauer and Price 1999, Laiho et al. 2004), the N_2 fixation rates for free-living bacteria in the peatlands described by Kravchenko and Doroshenko (2003) would range from 39 to 52 mg N m^{-2} yr^{-1} for the top 10 cm of peat and 183 to 243 mg N m^{-2} yr^{-1} for the 10 to 20 cm depth portion. Symbiotic N_2 fixation in wetlands has been positively associated with the presence, leaf area and biomass of alder saplings, as well as nutrient status (Bowden 1987, Koerselman et al. 1989). However, since both alder and sweet gale are more common in more nutrient-rich wetlands, the correlation between N_2 fixation and nutrient status of the wetland may be because of vegetation differences (Koerselman et al. 1989). Total rates of N_2 fixation in boreal forest wetlands are therefore highly variable and estimates range from 30 to 150 mg N m^{-2} yr^{-1} (Granhall and Selander 1973, Silvester 1977, Schwintzer 1979, Waughman and Bellamy 1980, Koerselman et al. 1989).

Upland forest stands also fix N_2, often with greater fixation rates than wetlands (Bowden 1987, Sprent and Sprent 1990, Anderson et al. 2004). In boreal uplands, non-symbiotic N_2 fixation likely dominates over symbiotic fixation (Cleveland et al. 1999). For example, estimates of N_2 fixation rates in boreal uplands by the cyanobacterium *Nostoc*, which grows on the ubiquitous feather moss *Pleurozium schreberi*, range from 150 to 200 mg N m^{-2} yr^{-1} (DeLuca et al. 2002). However, rates of symbiotic N_2 fixation by *Frankia* associated with alder can be very high. Indeed, estimates of N_2 fixation from alder stands on recessional moraines in Alaska were as high as 6 200 mg N m^{-2} yr^{-1} (Stevenson and Cole 1999). However, early successional forests such as these recessional moraines have much higher N_2 fixation rates than more mature stands (Cleveland et al. 1999), so this rate will decrease with age. In general, total N_2 fixation rates for boreal uplands were estimated to range from 100 to 300 mg N m^{-2} yr^{-1} (Cleveland et al. 1999, Vitousek et al. 2002).

The third N input, groundwater seepage from adjacent watersheds, is quite variable across the boreal region and depends on climate, bedrock and surficial geology, soil type and topography (Winter et al. 2001, Devito et al. 2005). However, groundwater flow between surface water watersheds is very difficult to define. The influence of bedrock and surficial geology means that it is not possible to determine groundwater flow from surface (topographic) surveys (Winter et al. 2003). Also, different groundwater flow systems can be superimposed on one another and divides between groundwater systems are dynamic often moving in response to varying discharge and recharge conditions (Winter et al. 2003). The Boreal Plain is underlain by deep, unsorted glacial tills, which are associated with very complex groundwater flow systems (Winter et al. 2001, Smerdon et al. 2005) that are still poorly understood.

The study site was located in an area that was relatively distant from major industrial and agricultural areas, which should result in low N inputs in atmospheric deposition, similar to other areas in northern Canada (e.g. McEachern et al. 2000 and Morris et al. 2003). The soils in much of the study area were of glacial till or glaciolacustrine origin and contained a large percentage of clay particles. As a result the hydraulic conductivity was very low (Whitson et al. 2003), which likely resulted in limited transfer of N via groundwater flow from adjacent watersheds. However, since the glacial tills were unsorted, there was the possibility of sand or gravel lenses within the watershed that could provide a conduit for water and hence N, transfer from adjacent watersheds. Without a detailed geologic survey however, it was impossible to know. As a result, although this flux was highly uncertain, for this study the transfer of N from adjacent watersheds was assumed to be negligible.

The final input was N_2 fixation. Both alder and feather mosses, which are both positively correlated with N_2 fixation rates, were very common throughout the study area suggesting that rates were quite high. It was expected then, that total N_2 fixation rates for the study site were near the upper end of the range (100 to 300 mg N m^{-2} yr^{-1}) suggested in the literature (e.g. Cleveland et al. 1999, Vitousek et al. 2002).

2.1.2 Internal N pools

There are three major N pools in forested ecosystems: the vegetation, the forest floor and soils. Estimates of the total N contained within each pool have been calculated for mature temperate forests. These range from 10 200 to 57 000 mg N m^{-2} for the vegetation (Nadelhoffer et al. 1999, Watmough et al. 2005), 29 000 to 114 400 mg N m^{-2} for the forest floor and 195 000 to 850 000 mg N m^{-2} for the top 30 cm of the mineral soil for various upland forest communities (Carter et al. 1998, Nadelhoffer et al. 1999, Thomas and Prescott 2000). As a generalization then, the vegetation, forest floor and soils represent about 5%, 12% and 83%, respectively, of the N pool in temperate forests. The size of the N pools have been correlated with stand age, vegetation type (Prescott et al. 1989, Nadelhoffer et al. 1999), soil parent material (Bischoff et al. 2001), soil order (Jurgensen et al. 1997) and disturbance history, type and severity (Weber et al. 1985, Feller 1988, Maynard 1997, Wan et al. 2001, Smithwick et al. 2005, Bradley and Parsons 2007, Leduc and Rothstein 2007, Turner et al. 2007).

The interrelated factors of vegetation and soil type are important in controlling the size of the N pool in forested watersheds. The vegetation in older forest stands typically represents large total N pools because of the greater amount of plant biomass relative to younger stands. Old growth forests have low N uptake rates compared with younger stands on similar sites, which results in larger N pools in the soil and forest floor of old growth stands as well (Entry and Emmingham 1995). However, this N may not be readily available. DeLuca et al. (2007) found less labile N in older stands, attributing the decrease to increased interception and canopy retention in mature stands, which decreased the inputs of bioavailable N to the soils and forest floor.

Vegetation type can also affect total N pool size in two different ways: first, vegetation with higher biomass (i.e., trees) will have greater amounts of N stored in above-ground biomass than herbaceous species; and second, litter quality was correlated with the decomposition rate of the forest floor (Aerts 1997), which results in greater N stores in the forest floor in stands with lower quality litter (Prescott et al. 1989, Nadelhoffer et al. 1999). Soil parent material also affects total N pools, with the most dramatic difference existing between peatlands and uplands. For example, one study in the Adirondacks determined that the N pool of peat was more than five times greater than the N pool of the mineral soils in adjacent uplands (Bischoff et al. 2001).

Forest disturbance, especially fire and harvesting, decrease the N pools in the forested watersheds (Leduc and Rothstein 2007). In severe fires, much of the total N loss is due to combustion of organic material. Volatilization of N begins at 200°C and more than half of the N in organic material is volatilized at temperatures over 500°C. In the case of harvesting, physical removal of biomass also decreases the total N pool on site. As a result, stands that have recently been disturbed tend to have lower ecosystem pools of total N (Entry and Emmingham 1995, Leduc and Rothstein 2007). Also, increased mineralization and nitrification rates were associated with disturbed sites (Wan et al. 2001, Westbrook and Devito 2004), which can result in additional N losses via leaching of NO_3^- (e.g., Likens et al. 1970). Climate models for the western Canadian boreal forest predict that temperatures will increase approximately 3 to 4 °C, resulting in an increase of about 10% for the temperature:precipitation ratio, which is expected to increase the fire frequency and therefore decrease the N pool of forests (Li et al. 2000).

Much of the total N in forests is recalcitrant and not readily available for plants. This recalcitrant N must first be broken down into more labile fractions via decomposition and mineralization (i.e., ammonification and nitrification). The mineralization of organic N (ON) (e.g. litter, deadfall and root exudates) is a critical source of IN for most plants since the supply of labile N from internal cycling is more than 10 times that of atmospheric inputs (Soderlund and Svensson 1976).

Mineralization of ON generally occurs through the actions of enzymes secreted from soil fungi, which actively decompose plant proteins, amino acids and other nitrogenous organic compounds resulting in the release of NH_4^+ (ammonification) (Haynes 1986). The NH_4^+ can then be oxidized to NO_2^-, which can be further oxidized to NO_3^- via nitrification. Nitrification is thought to be carried out largely by autotrophic bacteria, although some heterotrophic pathways have also been identified (Haynes 1986). Both ammonification and nitrification are aerobic processes. Major controls on N mineralization rates include climate (DeLuca et al. 1992, Schimel and Clein 1996), nutrient status, dominant vegetation (Compton et al. 1998), soil compaction (Breland and Hansen 1996, De Neve and Hofman 2000), net primary productivity (NPP)

(Nadelhoffer et al. 1984) and time since and type of disturbance (Maynard 1997, Westbrook and Devito 2004, DeLuca et al. 2006, Turner et al. 2007, Leduc and Rothstein 2007).

Climate affects mineralization rates indirectly by controlling soil moisture and temperature, which often results in distinct seasonal patterns in mineralization rates. For example, mineralization rates were positively correlated with forest floor and soil temperature (Van Cleve et al. 1981, 1990) and moisture (Bridgham et al. 2001, Stottlemyer and Toczydlowski 1999), resulting in increased rates during the spring and fall seasons. However, even though mineralization rates were positively correlated with temperature, microbial processing of N can still be significant in the dormant (winter) season, even under snow cover (Brooks et al 1996, Brooks and Williams 1999, Williams et al 1996). For example, tundra litterbag studies indicated that most mass loss and N loss takes place within the winter and spring thaw periods, suggesting active decomposition of fresh plant litter by cold-tolerant soil microbes beneath snow cover in many high latitude ecosystems (Grogan and Jonasson 2003).

Drying and wetting cycles, along with mild freezing also strongly influence mineralization rates (Groffman et al. 2001, Dhondt et al. 2002). Both the soil drying and rewetting and freeze/thaw cycles can cause cell lysis of soil microbes and fine roots that can be a major source of C, providing energy for the heterotrophic microorganisms involved with mineralization (DeLuca et al. 1992, Schimel and Clein 1996, Ryan et al. 2000, Grogan and Jonasson 2003). These events therefore disrupt the normally tight coupling between mineralization, immobilization and plant uptake (DeLuca et al. 1992, Groffman et al. 2001, Ryan et al. 2000). However, severe drought or severe freezing can drastically diminish (Morley et al. 1983) or alter (Sharma et al. 2006) soil microbial communities, which can decrease mineralization rates until the community re-establishes itself.

Since the mean temperature for the boreal region is expected to increase by 3 to 4 °C (Li et al. 2000), mineralization rates are also expected to increase. Modeled increases in mineralization rates for Canadian boreal forests are as high as 48%, with the change increasing with latitude (Peng and Apps 1998). The increased N mineralization and temperature is also expected to increase net primary productivity (NPP) and hence plant uptake. However, soil temperature limits decomposition up to 10 times more than air temperature limits NPP (Anderson 1991), suggesting that decomposition rates will increase more rapidly than NPP. As a result, the warming of the climate is expected to lead to decreased N pool size in soils and in the forest floor (Anderson 1991, Price et al. 1999).

Dominant vegetation is correlated with mineralization rates in two main ways. Firstly, conifer litter decreases the availability of N (Coté et al. 2000) because the higher C:N ratio and lignin content in the litter promotes N immobilization (Swift et al. 1979). Hence, recalcitrant conifer litter and coarse woody debris, because of the high C:N ratios, are sites of high N immobilization and therefore, low net mineralization (Brady and Weil 1999, Van Miegroet et al. 1990). Secondly, deciduous litter decomposes more rapidly than conifer litter, because manganese, which is essential for the breakdown of lignin, is found in greater concentrations in the deciduous litter (Van Miegroet et al. 1990, Coté et al. 2000). These are corroborated by other studies that found higher gross mineralization rates in deciduous than conifer litter (Flanagan and Van Cleve 1983, Ste-Marie and Paré 1999, Stottlemyer and Toczydlowski 1999).

Litter and woody debris decomposition rates decrease over time because three processes contribute to increase the lignin:N ratio during decay. First, labile compounds decay early in decomposition. Secondly, microorganisms produce lignin-like decay products (Pastor and Post 1986). Finally, as saprotrophic fungi use C as an energy source to break down the litter, the C:N ratio decreases.As the C:N ratio approaches 40, generally in the fibric layer of the forest floor, the fungal community changes to one dominated by mycorrhizal fungi, which then immobilize the N (Lindahl et al. 2007). These may explain why no detectable differences in net N mineralization rates were measured between pine and aspen litter over a 16 month period (Giardina et al. 2001). The dominant vegetation can also exert strong controls on N mineralization rates by altering soil temperature and moisture (Prescott 2002) and mycorrhizal associations.

Soil properties such as pH, nutrient status and texture can also influence mineralization rates (Ste-Marie and Paré 1999). Nutrient status was positively correlated with N mineralization rates; however it may be related to vegetation type since the vegetation on N-rich sites produce litter with higher N-concentrations (Hackl et al. 2004) which have been positively correlated with labile N pools in the forest floor and soil (Pastor et al. 1984, Reich et al. 1997) suggesting higher mineralization rates. Soil texture has also been correlated with N mineralization rates. For example, N mineralization rates in old-growth forests in central Wisconsin increased along a soil texture gradient from sand to silty clay loam soils (Pastor et al 1984, McClaugherty et al 1985). However, this too may be related to the dominant vegetation, since the dominant species changed and the NPP increased along the same soil texture gradient. Change in litter quality also occurred along the soil texture gradient because of species replacement that may be related to the differences in N mineralization rates (Pastor and Post 1986).

Surface soils in the Boreal Plain however, contain higher concentrations of IN than subsurface soils, and wetlands and ephemeral draws contain higher concentrations of IN than upland forest stands (Macrae et al. 2006) suggesting soil texture and type does affect net N mineralization rates. Many of these studies examine net mineralization rates and it has been

postulated that greater microbial immobilization and plant uptake limits the net N mineralization rates (Macrae et al. 2006). However, gross mineralization and immobilization rates in the mineral soil of uplands could also be lower because C limitations in the deeper soil profile limit the available energy for mineralization (Westbrook and Devito 2004).

Soil pH may also affect the dominant vegetation, and therefore the mineralization rates; however pH does have a more direct affect on mineralization rates as well. Since most nitrifying organisms use free ammonia (NH_3), rather than NH_4^+ (Suzuki et al. 1974, Stark and Firestone 1996, Burton and Prosser 2001), increased soil pH shifts the NH_3 / NH_4^+ equilibrium towards NH_3, increasing its availability, and therefore nitrification rates as well.

In general, plants with low productivity usually have low N-uptake demand, although it is unclear whether the low production limits the uptake or whether the low uptake limits the production (Cole 1981). It does seem though, that plants in N deficient systems are more efficient in N use, either by retaining foliage longer or by translocating the N back to living tissue before senescence (Cole 1981, Staaf and Berg 1981).

The boreal forest is typically limited by nitrogen, and the competition for IN can be severe as NO_3^- immobilization rates can be approximately 2 times greater than the gross nitrification rates in all soils (Westbrook and Devito 2004). Nitrate, because of its increased mobility and competition from soil microbes, is therefore very limited during the growing season. As a result, many species of conifers will preferentially take up NH_4^+. Many plants however, both because of the competition for and mobility of NO_3^-, along with adsorption of NH_4^+ to cation sites on soil particles (Dise et al. 1998), can also take up ON from the soil solution (Nasholm et al. 1998).

The N mineralization and nitrification rates are also strongly influenced by disturbances; notably fire and to a lesser extent, harvesting. The most dramatic effects were usually found after stand-replacing events. The removal of the forest canopy typically increases N mineralization rates as competition for ON and NH_4^+ decreases, soil temperatures increase (Vitousek et al. 1992, Van Cleve et al. 1993), and the senescence of fine roots adds N and labile C (Turner et al. 2007). In the case of fire, inputs of charcoal increase dramatically, binding plant-based phenolic compounds that inhibit microbial nitrification (DeLuca et al. 2006). The severity of soil disturbance and the use of herbicides were important factors in determining whether harvesting was correlated with increases in nitrification and mineralization rates. For example, a study in North Carolina found that stands that were mechanically and chemically treated had much higher net mineralization and nitrification rates than untreated sites, or harvested sites with little or no site preparation (Vitousek et al. 1992).

Several studies on the Boreal Plain however, found no detectable difference in net mineralization rates between uncut and harvested soils in either peatland soils or the forest floor of upland stands (Carmosini et al. 2003, Westbrook and Devito 2004), although mineralization rates in the upland mineral soils of one study did increase after harvesting (Carmosini et al. 2003). It was suggested that winter harvesting greatly limited soil and forest floor disturbance in the harvested stands, which limited the effect of harvesting on mineralization rates (Carmosini et al. 2003). Also, these studies measured net N mineralization, so an increase in gross mineralization with a concomitant increase in microbial immobilization would result in no change in net mineralization rates after disturbance.

Harvesting and severe fires can also decrease mineralization rates because these disturbances can deplete forest floor N stocks, diminish soil microbial biomass (Leduc and

Rothstein 2007) and decrease C inputs from litter to where the heterotrophic microorganisms responsible for nitrification and mineralization become C rather than N limited (Kaye and Hart 1997, Turner et al. 2007). This was especially true for nitrification rates after fire, since studies have shown that nitrifiers are more susceptible to fire than other soil microorganisms (Hart et al. 2005). Harvesting often results in compaction of the forest soil, which can also decrease N mineralization rates (Tan et al. 2005). The net result however tends to be an increase in NH_4^+ and NO_3^- pools after disturbance, through increased net mineralization rates (Walley et al. 1996, Wan et al. 2001, Bradley et al. 2007), although these increases tend to be short-lived (Turner et al. 2007).

The N cycling from the forest vegetation to the forest floor and soils is composed of throughfall, stemflow and litterfall. In natural forests across Wisconsin and Minnesota USA, litterfall N rates ranged from 3400 to 4100 mg N m^{-2} yr^{-1} depending on the dominant tree species (Reich et al. 1997). Measurements of annual N flux in throughfall and stemflow for the boreal forest meanwhile range from 207 to 1600 mg N m^{-2} yr^{-1} (Table 2-1).

The N flux in throughfall and stemflow, which unlike litterfall is immediately bioavailable, may be more important than litterfall to plant nutrition (Mahendrappa and Ogden 1973) and is variable, depending on nutrient status (Mahendrappa and Ogden 1973), forest type (Henderson et al. 1977, Verry and Timmons 1977, Michalzik et al. 2001), season (Henderson et al. 1977, Verry and Timmons 1977, Morris et al. 2003) and the source, timing and amount of incoming precipitation (Hill et al. 1999, Neal et al. 2003).

Nitrogen flux in throughfall of black spruce (*Picea mariana*) stands in New Brunswick that were fertilized was greater than the throughfall N flux of control stands (Mahendrappa and Ogden 1973), suggesting a positive correlation between throughfall N flux and nutrient status.

This pattern was consistent with Dise et al. (1998) who, in a summary of European data, found that the N flux in throughfall was highest in areas that have experienced N saturation (i.e., changes to forest soil N dynamics that occur when the supply of N is so large that bioavailable N was in excess of biotic demand). A study in high elevation conifer forests in Vermont however did not see any correlation between throughfall N concentrations and the nutrient status (McNulty and Aber 1993).

Canopy type may also be significant in determining the annual N flux in throughfall since the N flux under a deciduous canopy tended to be greater than the N flux under a coniferous canopy (Henderson et al. 1977, Verry and Timmons 1977). Seasonal effects on throughfall flux however, are less clear. Verry and Timmons (1977) measured increased flux rates during the growing season, while Henderson et al. (1977) measured increased flux rates during the dormant season. Some of the differences in seasonal effects however may be related to other factors such as climate.

The source of precipitation can also alter the chemistry of throughfall. For example, since cloud water has much higher N concentrations than either rainwater or throughfall, forests where fog interception may be a large contributor of precipitation tend to have higher N concentrations in throughfall (Neal et al. 2003). Short-term differences in throughfall flux were also related to the timing of the precipitation with the highest N concentrations typically occurring at the start of a storm event and concentrations quickly decreasing as the storm proceeds (Hill et al. 1999, Pryor and Barthelmie 2005). The mechanism for this may be related to dry deposition, which can be an important source of N (Lovett and Lindberg 1984, Kelly and Meagher 1986, Swank and Waide 1987, Sievering et al. 2000). The decreasing N concentration in throughfall during a storm therefore may be caused by the storm event washing off the N that had accumulated in the canopy as dry deposition.

While it would be expected that forest disturbance would affect throughfall N flux, a study in Finland found that harvesting the canopy had no detectable effect on total N flux to the soil, although it did change the composition. After harvesting the N flux was dominated by IN whereas before harvesting, the N flux was dominated by DON (Piirainen et al 2003). In general, although most studies show an increase in N concentration as precipitation passes through a forest canopy because of interception water losses, the total N flux usually remains unchanged or decreases relative to bulk deposition (Henderson et al. 1977, Friedland et al. 1991, Potter et al. 1991, Piirainen et al. 1998). However, there are some studies where an increase of N flux in throughfall was measured (Verry and Timmons 1977, Brinson et al. 1980, Blew et al. 1993). The influence of all these factors results in large variation in throughfall and stemflow flux in forests across North America (Table 2-1).

Within the study site, the relatively low N flux in atmospheric deposition suggests that N will be retained by the canopy of all forest types. As a result, throughfall N flux should be less than the N flux in bulk deposition. The cooler climate means that soil temperatures should be relatively low throughout the year, limiting decomposition and mineralization rates compared with more temperate climes. However, the soils in the area freeze during most years. As a result, the freeze/thaw period during the spring may produce high N mineralization rates within the forest soils due to lysis of soil microorganisms and fine roots. Also, the high temporal variation in precipitation may lead to drastic changes in soil moisture, which affects soil microorganism populations and communities altering both the decomposition and mineralization rates. Therefore it was expected that although the rates of N cycling were limited by N availability and cooler temperatures, the rates would also be highly variable based on temporal variation in precipitation, temperature and soil moisture (i.e. drainage class).

2.1.3 N export

Export of N from watersheds is considered to be related to the biomass increment hypothesis, which states that nutrient loss from watersheds is controlled largely by net biomass increment or net accumulation of nutrients in living or dead biomass (Vitousek and Reiners 1975). Most undisturbed temperate forests are N limited (i.e., in the process of accumulating N in biomass) and therefore experience very little N export in surface water. Lysimeter studies in temperate forests support this hypothesis in that the N contained in throughfall and stemflow was rapidly mineralized and immobilized when it reaches the forest floor (Hornbeck et al. 1997). The majority of the N is taken up by soil microorganisms and plants, although NO_3^- can also be converted to N_2O or N_2 gas through denitrification or reduced to nitrite (dissimilatory reduction of NO_3^-), which can react with organic matter to produce the less mobile DON. As a result, the median N export in surface water from 17 studies in Canada, the USA and Europe was only 6% of bulk deposition inputs (Watmough et al. 2005). Nitrogen losses from temperate forests occur through the processes of denitrification, anammox, physical removal of biomass, volatilization or as entrainment in surface and subsurface outflow (Fig. 2-1). Increased N export in surface water was often noted after forest disturbances, such as fire and harvesting.

Denitrification and anammox result in gaseous losses of N, with rates positively correlated with IN concentrations (Davidson and Swank 1986, Koerselman et al. 1989, Davidsson and Stahl 2000, Jetten 2001), soil moisture (Rolston et al. 1984), soil texture (Groffman and Tiejde 1989) and soil C content (Robertson and Tiedje 1984, Myrold and Tiedje 1985, Devito et al. 2000). Both processes require IN, anaerobic conditions and an energy source (typically C) resulting in "hotspots" of denitrification and anammox activity where saturated soils occur in close proximity to IN and C sources. For example, denitrification rates in the Catskill Mountains of New York were highest in soils that received water inputs from groundwater springs (Ashby et al. 1998). Denitrification and anammox may be key pathways for N removal in certain watersheds, especially wetlands impacted by excessive N inputs (e.g. the northeast USA and central Europe) (Jansson et al. 1994, Whitmire and Hamilton 2005, Penton et al. 2006).

The dynamic environments (i.e., variable water table and adjacent aerobic and anaerobic zones) found in wetlands provides the substrates and anaerobic conditions necessary to allow for greater rates of denitrification and anammox. Measured losses of N from wetlands due to denitrification and anammox range from 6 to 2000 mg m^{-2} yr^{-1} (Bowden 1987, Regina et al. 1996, Silvan et al. 2002) and were positively correlated with minerotrophic status and the height of the water table (Regina et al. 1996, 1999). However, since N is a limiting nutrient in most temperate forests (Vitousek and Howarth 1991), low IN concentrations generally limit denitrification and anammox losses (Koerselman et al. 1989, Davidsson and Stahl 2000). As a result, average denitrification rates for the boreal region were estimated to be 135 mg m^{-2} yr^{-1} (Söderlund and Svensson 1975).

The entrainment of N in water is another means of N export from watersheds that varies by the type (surface vs subsurface) and path of the flow. Interflow, or shallow sub-surface flow, and groundwater seepage can export substantial amounts of N from watersheds. In Minnesota for example, uplands exported roughly 60% of TN as interflow and deep seepage, compared with 40% exported as surface flow (Verry and Timmons 1982). Topography alters groundwater flowpaths through soils, which then alter surface water chemistry and N export. For example ephemeral draws and wetlands on the Boreal Plain were found to have higher N concentrations than adjacent uplands (Macrae et al. 2006). Since the concentration of surface water reflects concentrations in soil water (Macrae et al. 2006), these higher concentrations should result in higher exports. Also, total nitrogen (TN) concentrations in seepages within the Hubbard Brook Experimental Forest (HBEF) were relatively high compared with other areas within the watersheds (Likens et al. 2006). Other physical factors that control NO_3^- concentrations in groundwater, such as slope, stratigraphy and hydraulic conductivity, can also play a significant role in controlling annual NO_3^- export (Schiff et al. 2002).

Surface runoff may export substantial amounts of N from watersheds. Estimates of N export in surface flow were typically below 700 mg m^{-2} yr^{-1} (Verry and Timmons 1982, Watmough et al. 2005), although values as high as 5000 mg m^{-2} yr^{-1} have been measured (Dise et al. 1998). The mass of particulate and dissolved N exported from the watershed as surface runoff depends on the quantity of N inputs to the system (Watmough et al. 2005), season (Likens et al. 1970, Cameron and Haynes 1986, Goodale et al. 2000, Hong et al. 2005), mineralization rates, soil type (DeVito et al. 1999), topography, dominant vegetation (Likens et al. 1970, Vitousek et al. 1982, Aber et al. 1991), elevation (Bernhardt et al. 2003), successional status (Goodale et al. 2000), hydrologic flowpath (Dittman et al. 2007) and the history of and time since disturbance (Vitousek and Reiners 1975, Vitousek et al. 1997, Titus et al. 1998, Minshall et al. 2001, Aber et al. 2002).

Leaching losses of N were positively correlated with the N inputs in throughfall for North American and European forests (Dise et al. 1998, MacDonald et al. 2002, Watmough et al. 2005, Howarth et al. 2006). While the relationship can be attributed in part to N saturation in the system, it has also been suggested that increased precipitation results in shorter water residence time in riparian wetlands and low-order streams. Shorter residence time leads to less biological uptake and lower denitrification losses and hence more leaching (Howarth et al. 2006). As a result, the frequency, intensity, amount and TN concentration of rainfall are all important factors determining the pattern and extent of N leaching (Cameron and Haynes 1986).

Seasonal patterns of N export rates were noted in northern and temperate forests with higher export rates occurring during plant dormant periods (late fall, winter and early spring) and lower rates during the summers (Likens et al. 1970, Cameron and Haynes 1986, Goodale et al. 2000, Hong et al. 2005). These patterns were likely due to increased nutrient demand by vegetation and heterotrophic activity as soils warm (Likens et al 1970). Also, in northern forests the spring peak in N flux tends to be higher than the autumn peak (Likens and Buso 2006). This spring peak was likely due to microbial and fine root mortality and lysis from freeze thaw patterns that release previously immobilized N into (Cooper et al. 2007) and/or stimulate nitrification within the soils (DeLuca et al. 1992). For example, after an anomalous cold period for four sites in the northeast U.S., NO_3^- losses increased dramatically (Mitchell et al. 1996). Indeed, cell lysis caused a 10-fold increase in DON concentration in forest floor leachate of a lodgepole pine in Wyoming (Yavitt and Fahey 1984). Thus, soil freezing may markedly affect NO_3^- loss, especially when followed by hydrological conditions that facilitate transfer of solutes to surface waters (Mitchell et al. 1996).

In warmer climes such as Tennessee however, the pattern can be reversed with peak N exports occurring during summer instead (Mulholland 2004). The input of litter in the fall increases the C:N ratio in the forest floor and soil which increases the N demand within the watershed; because these soils do not freeze, continual microbial immobilization during the fall and winter decreases the amount of N exported (Mulholland 2004). In some studies however, N export showed no seasonality at all (Goodale et al. 2000).

Depth and duration of the snowpack during plant dormant periods also have dramatic influence on these export patterns (Brooks et al. 1999). Given similar winter temperatures, a shallow snow pack may increase soil freezing, limiting heterotrophic immobilization of N, while a continuous, deep snowpack limits primary production, which in turn limits C availability and hence N immobilization (Brooks et al. 1999). In both cases, N leaching will be high. However, a deep snowpack that develops in early winter provides sufficient labile C and warmer soil temperatures to allow heterotrophic N immobilization to continue throughout the winter, dramatically lessening the N export during the spring snowmelt (Brooks et al. 1999).

Many studies also suggest that N export is strongly related to changes in N mineralization rates. For example, many older forests have higher rates of N loss (Goodale et al. 2000), which were found to be related to higher N mineralization and lower plant N uptake (Vitousek et al. 1989, Aber et al., 1989). Also, the variation in mineralization rates from different soil temperature and moisture regimes was more than 10 times the variance in atmospheric inputs based on typical annual variations (Hong et al. 2005), suggesting that soil conditions that govern mineralization rates were likely one of the most important factors influencing N export. Isotopic tracer studies support this hypothesis in that stream NO_3^- was enriched in ^{15}N, indicating that N is cycled through plants and microorganisms before being exported (Nadelhoffer et al 1999). This was further supported by a storm hydrograph study in the Adirondacks, which found NO_3^- concentrations peaked early on the rising limb of a hydrograph. Combined with soil and groundwater data this early peak suggests that the expression of NO_3^- was due to the displacement of groundwater by infiltrating precipitation (translatory flow) rather than runoff of the recently deposited precipitation (Inamdar et al. 2004).

Leaching losses of N were also related to soil texture, horizon and parent material. In general, N exports were greater from sandy than clay soils (Cameron and Haynes 1986). High immobilization rates in the upper soil horizons were thought to make these horizons major N sinks (Mead and Pritchett 1975, Miller et al. 1976, Melin et al. 1983, Raison et al 1990) perhaps because the high C:N ratio promotes immobilization of N (Mulholland 1992). However, a more recent study found that N mineralization rates in the forest floor can exceed plant and microbial immobilization and as a result, the forest floor can act as a large N source with most N retention occuring in the upper mineral horizons (Dittman et al. 2007).

Soil type also strongly influences the dominant N fraction exported. In wetlands, water retention times are high and N availability is limited, so rapid uptake of bioavailable IN allows plants and soil microorganisms to immobilize most of the incoming N as biomass. Once these organisms die, low decomposition rates in boreal wetlands cause retention of N as biomass followed by conversion to and export as DON. For example, on the Boreal Shield, even though N inputs were split evenly between inorganic and organic fractions, N export was predominantly DON (1330 to 2550 mg N m^{-2} yr^{-1} DON compared with 175 to 1730 mg N m^{-2} yr^{-1} DIN) (DeVito et al. 1989). Other studies from northern wetlands found that DON export from northern wetlands composed between 67 and 89% of the TN export (Bowden 1987, Devito et al. 1989, Prepas et al. 2001), and a study in New York found that DON concentrations in lakes were positively correlated with wetland cover (Ito et al. 2007).

Wetland cover was also correlated with the form of IN exported since the water-logged soils favour export of reduced N fractions. For example, positive correlation was noted between

NH_4^+ export and wetland cover within Boreal Plain watersheds (Prepas et al. 2006). Also, the proportion of IN as NH_4^+ was much higher in Boreal Plain than Boreal Shield lakes (D'Arcy and Carignan 1997, Prepas et al. 2001), which was probably due to greater wetland cover on the Boreal Plain. Other studies in the Canadian boreal forest found that increased NO_3^- export occurs from upland areas while NH_4^+ export was higher from wetland areas (Bayley et al. 1992, Prepas et al. 2006). However, the presence of permafrost may alter these correlations. A study in Alaska found that subsurface flowpaths in watersheds with high permafrost cover were sources of NO_3^-, while subsurface flowpaths in watersheds with low-permafrost cover deplete NO_3^-, regardless of peatland cover (Petrone 2005). Another study in Minnesota however, found that proportions of the three main N fractions were similar between upland and wetland soils; with about 85% exported as ON, 10% as NH_4^+ and 5% as NO_3^- (Verry and Timmons 1982).

The N uptake rates and cycling patterns were specific to a given ecosystem and ecosystem condition. In particular, wetlands typically have much different rates of N cycling than adjacent uplands. It is thought that sorption of IN to soil particles within wetlands could also add to retention and immobilization of IN in wetlands, however sorption seems to be limited to cation and anion exchange sites and, because other cations and anions quickly displace the IN, would not contribute to long-term storage of N. However, rapid immobilization of NH_4^+ and NO_3^- by abiotic factors is important for some forested ecosystems and may be under-estimated in many studies (Bernston and Aber 2000). Also, a UK study found that the combination of time since the soil was last flushed and rewetting of the H horizon strongly influenced NO_3^- export and that the mechanism is likely related to moisture dependent biological activity (i.e., mineralization) in the soil (Cooper et al. 2007). These results suggest that long-term trends like drought may limit N export by not only decreasing runoff, but also decreasing mineralization rates that limit the supply of mobile N upon re-wetting (Starke and Firestone 1995, Cooper et al. 2007).

The dominant N fraction is another factor determining total N export. Ammonium is unlikely to be leached from soils not only because of the immobilization by the microbial biomass, but also because of cation exchange, fixation within clay lattices, and abiotic fixation by soil organic matter (Cameron and Haynes 1986). The adsorption of NH_4^+ to soil particles helps explain why in small headwater streams in central Ontario, NH_4^+ export and total phosphorus export were positively correlated (Dillon et al. 1991). Both nutrients adsorb to soil particles and therefore are exported via erosion of soil particles.

Forest disturbance appears to dramatically increase N losses from temperate forests. In fires, N is easily volatilized while forest harvesting removes much of the aboveground biomass. In most ecosystems however, including the boreal forest, wildfires are infrequent (e.g. the return interval in Alberta is between 40 and 100 years [Larsen 1997]) resulting in relatively low annual losses. However, the fire frequency may increase due to a predicted increase in mean annual temperature of 3 to 4 °C, which would result in increased N losses from fire (Li et al. 2000). Most harvesting systems meanwhile, leave the leaves and small twigs, which contain the highest concentrations of N, on site limiting N losses from the biomass removal during harvesting.

However, forest disturbance such as wildfire and harvesting can also increase N, especially NO_3^-, losses by leaching (Likens et al. 1970, Borman and Likens 1979, Pardo et al. 1995, Carignan et al. 2000, Bradley et al. 2000, Prescott et al. 2003). An intense fire in the experimental lakes area of northwestern Ontario increased NO_3^-, NH_4^+ and total dissolved nitrogen (TDN) exports (Schindler et al. 1980, Bayley et al. 1992), which was consistent with a study in northern Alberta where lakes in burned catchments had higher concentrations of TDN,

NO_3^- and NH_4^+ (1.2, 3, and 1.4 times respectively) (McEachern et al. 2000). These results differ from a prescribed fire study in S. Carolina that showed no effect on streamwater volume-weighted concentrations of either NO_3^- or NH_4^+ (Richter et al. 1982). This was probably related to the severity of the burn since less than 1/3 of the forest floor at the S. Carolina site was consumed. A study from Alaska found that stream NO_3^- concentrations increased for only a short time after a less severe fire (i.e. the majority of the organic layer left intact), suggesting that less severe fires that leave an intact riparian zone may have only a minor, short-term effect on stream chemistry (Petrone 2005).

Clearcut harvest operations were also positively correlated with N (especially NO_3^-) exports in surface water in the northeast USA (Likens et al. 1970, Pardo et al. 1995, Burns and Murdoch 2005), the southeast USA (Swank and Waide 1980), Finland (Ahtiainen 1992, Lepisto et al. 1995), Quebec (Carignan et al. 2000, Lamontagne et al. 2000) and the west coast of North America (Feller and Kimmins 1984, Bradley et al. 2000, Prescott et al. 2003, Cairns and Lajtha 2005). In addition to the IN, harvesting can also increase leaching of DON from the forest floor to mineral soil horizons (Piirainen et al. 2003). However, most of the DON was immobilized and retained in the mineral soil horizons on site (Piirainen et al. 2003). The high C:N ratio of logging residue leads to increased immobilization and retention of N as well (Piirainen et al. 2003)As a result, the increased N exports tend to be dominated by NO_3^- although NH_4^+ exports can also be important. For example, a study in Finland found that much of the N exported after harvest was NH_4^+ with export rates positively correlated with stream drainage density (Lepisto et al. 1995) suggesting that increased bank erosion after harvesting is washing soil particles, along with adsorbed NH_4^+, into the streams for export. In contrast to all the increased export measured in temperate forests, there are some studies from the Boreal Plain in western Canada that did not detect an increase in N export after harvest (Prepas et al. 2001, Macrae et al. 2006). However, this may be related to rapid responses by the understory vegetation and soil microbial community to harvesting, which result in small, short-lived increases in N export (Zak et al. 1990, Groffman et al. 2001, Piirainen et al. 2003).

There are differences in N export response to harvesting by region, which are thought to be the result of several factors. In the northeast USA and much of Europe, increased atmospheric deposition of N from industrial and urban sources has led to N saturation and high N exports in many of the forested ecosystems. Rapid growth of N fixing alder after harvesting on the west coast likely has a similar affect, causing the system to become temporarily saturated with N which may also lead to large N exports (Cairns and Lajtha 2005), and may explain why the increases in N export last longer (up to 10 years after harvesting) than elsewhere. In both cases, it is thought that the cessation of litter inputs from the canopy and the resulting decrease in labile C sources causes the microbial communities in the forest floor and soils to become C- rather than N-limited, leading to decreased assimilation of NO_3^- and the flush of available NO_3^- that is characteristic of clearcuts (Prescott 1997, Bradley et al. 2000). In New York's Catskill Mountains for example, even though there was no increase in mineralization rates, there were still increases in stream water NO_3^- concentrations after harvesting (Burns and Murdoch 2005). However in northern Michigan, which does not experience the same atmospheric loadings as New York (Table 1-1), nitrification rates did increase after harvesting (LeDuc and Rothstein 2007). As a result, areas that have not seen large increases in N input, such as the Boreal Plain, experience high rates of N immobilization by soil microorganisms and understory vegetation after harvest that remain tightly coupled with inputs even after disturbance. Also, even though fire and harvesting are the two major disturbances in temperate (especially boreal) forests, other disturbances to the forest canopy, such as ice and wind storms, also cause increase N export (Schindler et al. 1980, Bernhardt et al. 2003).

Rather than being passive conduits exporting water and solutes from the watershed, streams play an active role in N retention and transformation within a watershed. Small headwater streams are very effective at N processing, retaining between 20 and 50% of inputs, with most uptake and removal occurring in the stream sediments and on biofilms (Triska et al. 1984, Peterson et al. 2001, Mulholland 2004). Uptake rates range from 29 to 191 mg N m^{-2} day^{-1}, mg N m^{-2} day^{-1} (Hall et al. 1998, Mulholland et al. 2000). Uptake rates however can significantly diminish exports, especially after disturbance. For example, after an ice storm at the HBEF, N export would have been up to 140% higher if not for concurrent in-stream N processing and uptake rate increases (Bernhardt et al. 2003, Hall 2003).

The concentration of IN within streams is in a dynamic balance, controlled by input, nitrification, biological uptake, N fraction, sorption and regeneration (Peterson et al. 2001). Most NH_4^+ uptake is by sediment sorption and immobilization by autotrophic microorganisms (e.g., periphyton) and heterotrophic organisms. This is especially true during spring when high light availability stimulates high rates of in-stream primary productivity, which can substantially decrease exports (Hill et al. 2001). The NH_4^+ uptake length is often correlated with discharge, suggesting little biotic interaction (Tank et al. 2000, Peterson et al. 2001), although another study found that uptake length was negatively correlated with water temperature indicating at least some biotic control (Tank et al. 2000). Riparian sediments act as temporary storage sites for NH_4^+ (Triska et al. 1994) and can be a source of NH_4^+ to the stream when DOC concentrations are low (Mulholland 1992), likely altering the timing and form of IN transport (Triska et al. 1994). Nitrate is far more mobile than NH_4^+, traveling up to 10 times farther in streams before uptake or removal (Peterson et al. 2001). The removal of NO_3^- is mainly by biological assimilation and denitrification, which results in declines in concentrations with distance downstream of NO_3^- inputs (seepages or springs) (Mulholland 1992).

In general the study area, located on the western Boreal Plain in west-central Alberta, was N limited so N export within surface water was expected to be low (especially IN). Also, the fine textured soils impede percolation into deeper groundwater forcing much of the water through the organic-rich upper soil horizons and forest floor. The flow through these organic-rich horizons should result in a large proportion of the N to be exported as ON rather than IN. Also, since surface water runoff is very uncommon in the boreal forest, storm flow in streams was expected to be composed primarily of "old" water that is pushed into the streams and replaced in the soils by the "new" water. Therefore, the N that enters the stream should be derived more from N that has been cycled within the watershed already instead of the freshly deposited N from the bulk deposition.

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2.3 Tables:

Table 2-1 Annual nitrogen inputs (mg m^{-2} $year^{-1}$) in bulk deposition for regions across North America and Europe.

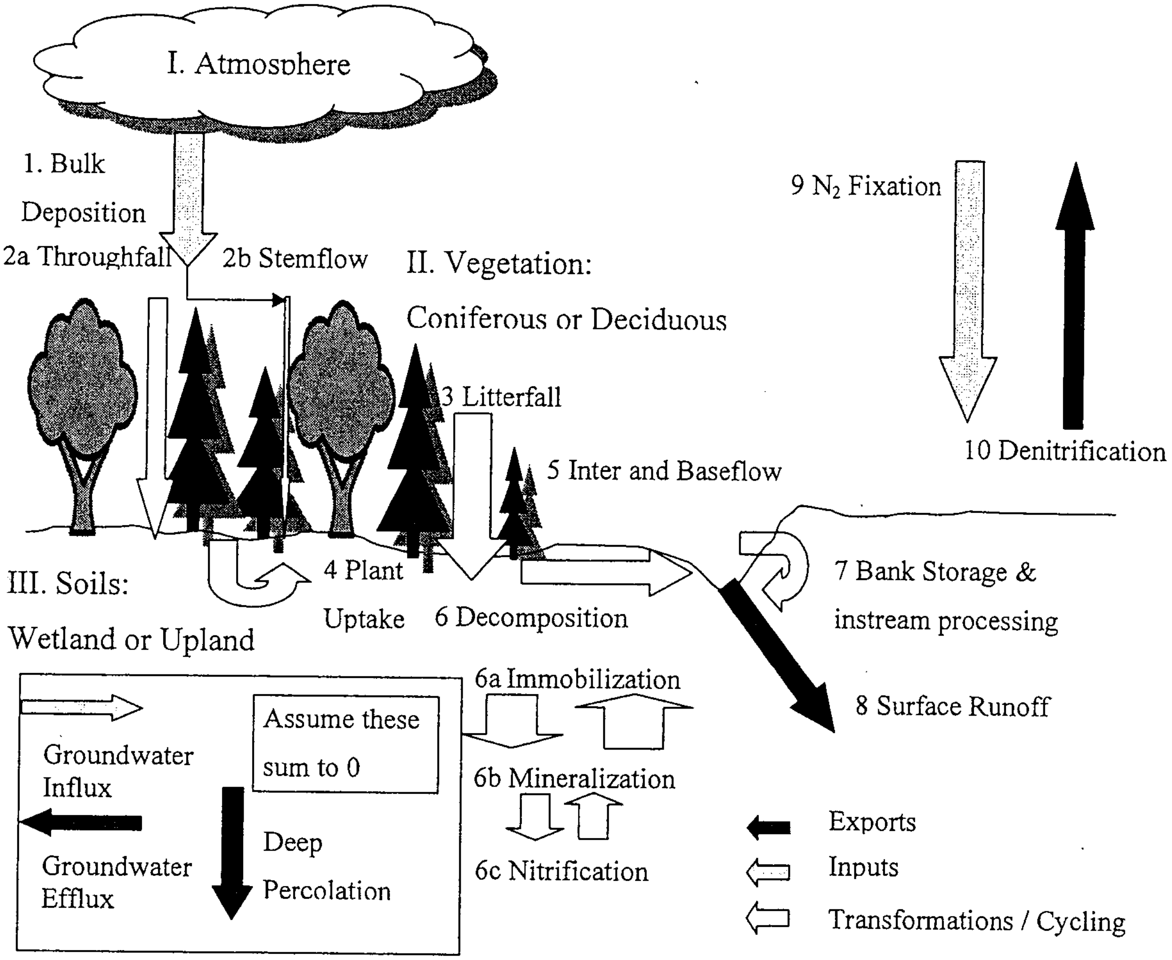
Location	Annual input	Source
Sweden	900	Gundersen et al. 1998
Wales	1000	Gundersen et al. 1998
New York (Whiteface Mountains)	1600	Friedland et al. 1991
New York (Catskill Mountains)	1360	Lawrence et al. 2000
Eastern Tennessee (Walker Branch)	1240	Kelly and Meagher 1986
North Carolina (Coweeta)	920	Swank and Waide 1987
North Carolina (Coastal Plain)	580	Brinson et al. 1980
South Carolina (Coastal Plain)	510	Richter et al. 1983
Indiana	1600	Pryor and Barthelmie 2005
Michigan	910-1180	DeForest et al. 2004
Michigan (Upper Peninsula)	680	DeForest et al. 2004
Northern Quebec	310	Duchesne and Houle 2006
Eastern Ontario	990	Devito et al. 1989
Central Ontario	1130	Molot and Dillon 2003
Northwestern Ontario	217-254	Morris et al. 2003
Central Saskatchewan	270	Huang and Schoenau 1997
Central Alberta	424	Shaw et al. 1989
Oregon (Western Cascades)	220	Stednick 2008

Table 2-2 Annual nitrogen flux (mg m^{-2} $year^{-1}$) in throughfall for the boreal forest.

Region	**Annual N flux**	**Source**
Sweden	1300	Gundersen et al. 1998
E. Finland	293	Piirainen et al. 1998
New Brunswick	363	Mahendrappa and Ogden 1973
Minnesota	698	Verry and Timmons 1977
NW. Ontario	207 – 247	Morris et al. 2003
SW Alberta	680	Blew et al. 1993

2.4 Figures:

Figure 2-1 Nitrogen cycle in forested watersheds.



Note: amount of N cycled for each arrow are as follows:

1. Bulk Deposition: 217 to 424 mg N m^{-2} (McEachern et al. 2000, Morris et al. 2003)
2. Throughfall and stemflow: 207 to 247 mg N m^{-2} (Morris et al. 2003)
3. Litterfall: 615 to 4100 mg N m^{-2} (Mahendrappa and Ogden 1973, Reich et al. 1997)
4. Plant uptake: 6 500 mg N m^{-2} (Söderlund and Svensson 1976)
5. Inter and baseflow: 450 to 525 mg N m^{-2} *
6. Mineralization / Immobilization: 1300 to 4500 mg N m^{-2} (Flanagan and Van Cleve 1983)
7. Bank storage and in-stream processing: 240 to 435 mg N m^{-2} (Clilverd et al. 2008)**
8. Stream export: 90 to 210 mg N m^{-2} (Watmough and Dillon 2003)
9. N_2 fixation: 100 to 300 mg N m^{-2} (Cleveland et al. 1999, Vitousek et al. 2002)
10. Denitrification: < 100 mg N m^{-2} (Barton et al. 1999).

* Clilverd et al. (2008) calculated that 60 to 80% of river exports were removed in the hyporheic zone. The values given here assume that the stream export values represent 20 to 40% of the total amount of N that enters the stream from interflow and baseflow. ** This amount is calculated by subtracting the stream exports from the amount entering the stream from interflow and baseflow.

Chapter 3

Runoff and inorganic nitrogen export from Boreal Plain watersheds six years after wildfire and one year after harvest[2]

3.1 ABSTRACT

In this investigation in the Swan Hills, Alberta, located on the Canadian Boreal Plain, May through October runoff before, during and six years after wildfire in a 4th order watershed, compared to a 3rd order reference watershed was examined. Runoff and inorganic nitrogen flow-weighted mean concentration and areal export for one year after winter harvest in four 1st order watersheds compared to five reference 1st and 2nd order watersheds were also examined. Runoff and areal exports were normalized to precipitation at each site. Runoff impact ratios (year 1 post-disturbance value divided by the pre-disturbance value) for burned and harvested watersheds were 60 and 70% higher, respectively, than reference watersheds ($P = 0.06$). Runoff from the burned watershed remained elevated 6 years after fire. A tendency for higher nitrate and ammonium concentrations, combined with higher runoff yielded impact ratios for areal ammonium and nitrate exports that were 130 and 170% higher, respectively, in harvested than reference watersheds ($P = 0.08$ for both). The proportion of the watershed harvested was positively related to runoff ($r^2 = 0.94$, $P = 0.03$) and ammonium impact ratios ($r^2 = 0.96$, $P = 0.02$), but not nitrate impact ratios ($P = 0.30$). Areal nitrate export in snowmelt was low in harvested watersheds compared to their pre-harvest condition and to reference watersheds.

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Key words – nitrate, ammonium, inorganic nitrogen, runoff, boreal forest, forest harvest, wildfire.

3.2 INTRODUCTION

Since many temperate-zone forests are nitrogen limited (Shaver and Chapin 1980; Vitousek and Howarth 1991), increased rates of nitrogen loss from watersheds can decrease forest productivity, as well as enrich downstream surface waters. Consequently, nitrogen export to surface waters has been used as a primary response variable in studies of forest disturbance (e.g., Likens et al. 1970; McEachern et al. 2000; Bernhardt et al. 2003). Enhanced nitrogen loss in surface waters from forested watersheds has been attributed to climatic factors (Mitchell et al. 1996), atmospheric deposition leading to nitrogen saturation (Vitousek et al. 1997; Fenn et al. 1998), wildfire (Richard and Spencer 1998; Minshall et al. 2001; Parker et al. 2001), forest harvest (Mann et al. 1988; Titus et al. 1998), and other landscape disturbances (Aber et al. 2002; Houlton et al. 2003).

Bioavailable (inorganic) forms of nitrogen (nitrate-nitrite and ammonium) typically constitute a small portion of forest soil nitrogen pools (Fenn et al. 1998). In northern temperate (i.e. boreal) forests, wildfire and forest harvest are dominant disturbances that affect nitrate and ammonium availability in soils in two main ways. Within the context of local (e.g., substrate quality) and regional (e.g., soil type) factors, vegetation removal in boreal forests is often associated with alterations to nitrogen transformations in soils, specifically increased mineralization, nitrification, and denitrification rates (Walley et al. 1996; Bradley et al. 2002; Carmosini et al. 2003). These changes are usually attributed to higher soil temperatures (less shade) and soil moisture (less evapotranspiration) (Bhatti et al. 2000).

Vegetation removal in boreal forests is also associated with increased runoff, particularly during peak flow periods, such as spring melt and summer storms (Verry et al. 1983; DeBano 2000, Prepas et al 2003). In a review of 93 forest catchment studies in the U.S., Bosch and

Hewlett (1982) estimated that annual runoff increased by 40 and 25 mm yr^{-1} for every 10% reduction in conifer and deciduous cover, respectively. Higher mineralization rates, runoff, and entrainment of nitrate and ammonium in overland and subsurface flow (Viney et al. 2000) has led to higher inorganic nitrogen export (especially nitrate) in streams draining harvested (Feller and Kimmins 1984) and burned (Bayley et al. 1992) forested watersheds.

Inputs of inorganic nitrogen from watersheds to surface waters have implications for water quality. Most research on nitrogen loading has focused on receiving waters downstream of agricultural watersheds, where nitrate can reach concentrations that are toxic to aquatic organisms (3 mg L^{-1} nitrate-N) and humans (10 mg L^{-1} nitrate-N) (Environment Canada 2003; Health Canada 2006). However, freshwater communities have responded to increased bioavailable nitrogen at much lower concentrations (Goldman et al. 1990), especially when nitrogen treatments were co-amended with phosphorus. For example, field and laboratory experiments have demonstrated that phytoplankton and zooplankton biomass and cyanobacterial growth and toxin production increase after nitrogen and phosphorus amendments (Sivonen 1990; Olsson et al. 1992; Scrimgeour and Chambers 2000; Lafrancois et al. 2003).

This study is a component of the Forest Watershed and Riparian Disturbance (FORWARD) project. The FORWARD project, initiated in 2001, is a long-term study designed to develop hydrological and water quality models for direct application to industrial forest planning in Boreal Plain watersheds in the Swan Hills, Alberta (Smith et al. 2003) and Boreal Shield watersheds in the Legacy Forest, Ontario. Based on data from four large (>100 km^2) 3rd and 4th order (Strahler 1952) FORWARD watersheds on the Boreal Plain, we previously demonstrated that runoff and phosphorus exports were higher in burned than reference watersheds during four open-water seasons (May 1 through October 31) after a wildfire in 1998

(Prepas et al. 2003; Burke et al. 2005). The FORWARD design also includes nine small (2 to 16 km^2) 1st and 2nd order watersheds monitored for two years before experimental harvest in four of the watersheds in winter 2003-2004 (Table 3-1). The goals of this paper are to: 1) examine runoff recovery in a large burned watershed relative to a large reference watershed through Year 6 post-fire, 2) compare runoff and ammonium and nitrate flow-weighted mean concentrations (FWMC) and exports in small harvested watersheds to reference and pre-harvest data in Year 1 post-harvest and 3) describe seasonal ammonium and nitrate export patterns in these streams draining Boreal Plain watersheds.

3.3 METHODS

3.3.1 Site description

The two large and nine small watersheds are located in the Swan Hills, 230 km northwest of Edmonton, Alberta (Table 3-1; Fig. 3-1). Dominant soils are Luvisols, Organics and Brunisols, but Gleysols and Regosols also occur (Ecological Stratification Working Group 1996). The boreal forest vegetation is dominated by trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.), white spruce (*Picea glauca* (Moench) Voss), and lodgepole pine (*Pinus contorta* Dougl. ex Loud.var. latifolia Engelm) in well-drained sites and black spruce (*Picea mariana* (Mill.) BSP) and tamarack (*Larix laricina* (Du Roi) K. Koch) in poorly drained sites (Ecological Stratification Working Group 1996). Aerial photograph interpretation from 1994 shows that the two large watersheds are approximately 82% conifer-dominated (80% or more conifer crown closure in the forest canopy). Conifer-dominated areas comprised 44 ± 6% (Mean ± Standard Error) and deciduous-dominated areas (80% or more deciduous crown closure in the forest canopy) comprised 50 ± 8% of the small watersheds before experimental harvest. Harvesting of 52 to 84% of the area of four small watersheds occurred in

February and March 2004 (Table 3-1). Tree-length harvesting was conducted in most blocks, which involved cutting with a feller-buncher, and skidding the trees to roadside. Two blocks were cut-to-length harvested, which involves delimbing and bucking the tree near the stump and bringing the logs to roadside with a forwarder.

The climate is sub-humid (Zoltai et al. 1998) and precipitation is variable on an annual scale. At the Whitecourt A weather station, approximately 20 km southeast of the study area (elevation 782 m), the long-term (1980 to 2004) mean annual precipitation ranged from 364 to 786 mm, of which an average of 24% was snow (Environment Canada 2005a). Precipitation is also variable on a spatial scale. For example, among the four meteorological stations operating in the FORWARD study area, covering elevations from 865 to 1025 m and an area of approximately 230 km^2, total precipitation ranged from 454 to 519 mm in 2004, while total precipitation was 573 mm at the Whitecourt A weather station. Regional runoff patterns reflect this variability. Total annual runoff from the Sakwatamau River near Whitecourt varied by a factor of more than 6 from 1980 to 2004 (Fig. 3-2) (Environment Canada 2005b). Streamwater pH is circumneutral, ranging from 6.4 to 7.3 among the small streams and from 8.1 to 8.2 in large streams during the study period. For more detailed descriptions of the FORWARD watersheds, see Burke et al. (2005) and Prepas et al. (2003, 2006).

3.3.2 Stream sampling

Pre-fire year. Stream gauging in the two large watersheds in the pre-fire year (1983) is fully described in Munn and Prepas (1986). Briefly, except for sixteen 2-d periods, the stream outlets of the two large watersheds (Fig. 3-3) were sampled at least twice daily from May 1 to October 31. Staff gauge level was recorded and instantaneous discharge determined by measuring stream velocity (60% of depth at 0.5- or 1-m intervals across the stream channel) with a Price current meter. Water level was recorded with continuous recorders. For dates when gauging was not conducted, mean daily discharge was calculated from the relationship between water level and instantaneous discharge. Nitrogen data were not collected in the pre-fire year.

All other years. Stream outlets for all 11 watersheds (Fig. 3-3) were instrumented with rain gauges and Global water level dataloggers, which collected data at 10-min. intervals from May 1 through October 31. Streams were visited weekly to empty rain gauges, download dataloggers, and measure stage height and current velocity (60% of depth at locations spaced 0.05 to 0.9 m apart in small stream channels and 0.5 to 2 m apart in large stream channels). Mean daily discharge was calculated as described above. In the event of problems with water level recorders, discharge was estimated from a relationship between discharge for that stream and a nearby stream with continuous water level recorder data. "Grab" water samples were collected weekly. Ammonium (unfiltered) and nitrate (passed through Millipore 0.45-μm pore size filters) water samples were stored at -20°C for up to 3 weeks before analysis on a Technicon Autoanalyzer II (Methods 154-71 and 158-71, respectively). Since the nitrate analysis involved cadmium reduction to nitrite, the nitrate values reported here include nitrite.

3.3.3 Data analysis

For all 11 watersheds, the following variables were calculated each year for the 184-d period comprising May 1 through October 31. Recall that inorganic nitrogen data were not collected from the large watersheds during the pre-fire year. Inorganic nitrogen concentrations were assumed to not vary with discharge and therefore, the concentrations for days when sampling did not occur were estimated by linear interpolation between sampling dates. Daily exports (kg N) were the products of total daily discharge and mean daily nitrate or ammonium concentration. Flow-weighted mean concentrations ($\mu g\ N\ L^{-1}$) were calculated by dividing the total mass of nitrate or ammonium exported by the total volume of water exported in the stream channel during the sampling period. Runoff (mm) for each watershed was calculated by dividing the total water volume (dam^3) exported by the watershed area (km^2). Areal inorganic nitrogen exports were calculated by dividing the total mass of ammonium or nitrate exported during the sampling period by the watershed area (kg N km^{-2}), as in Prepas et al. (2006).

To normalize for the high interannual and spatial variability in precipitation in the study area, runoff and areal inorganic nitrogen exports for each watershed were divided by the total precipitation that fell on that watershed over the 184-d period. These normalized values are referred to as runoff, ammonium, and nitrate coefficients (RC, AC, and NC, respectively). For each watershed, an "impact ratio" was derived for RC, AC, and NC, as well as for nitrate and ammonium FWMC, by dividing the post-disturbance (1999 for fire, 2004 for harvest) value by the pre-disturbance (1983 for fire, 2003 for harvest) value. Impact ratios could not be calculated for inorganic nitrogen variables in the large watersheds, because inorganic nitrogen data were not collected in the pre-fire year.

Mean RC, AC, and NC impact ratios for small reference ($n = 5$) and harvested ($n = 4$) watersheds were compared with one-tailed *t*-tests after checking variance (Zar 1996). Due to the relatively small sample size ($df = 3$), differences were considered significant at $P \leq 0.10$. The RC, AC, and NC values calculated as above were only qualitatively compared between the large burned and reference watersheds, due to a lack of replication. Simple linear regression analysis was conducted between the following dependent and independent variables, respectively: 1) RC, AC, and NC impact ratios versus percent area harvested in the harvested watersheds ($n = 4$); 2) total daily runoff from the large burned watershed versus total daily runoff from the large reference watershed in the pre-fire year ($n = 101$), fire year ($n = 12$), and each of the 6 years after fire (n = 19 to 35); and 3) total daily areal ammonium and nitrate exports versus total daily runoff for reference (means of the five watersheds calculated for each day) and harvested watersheds (means of the four watersheds calculated for each day) in the post-harvest year (n = 184). Slopes of regression lines describing relationships from (2) above were compared between the pre-fire year and Year 6 post-fire with a two-tailed t-test (Zar 1996).

3.4 RESULTS

On a regional scale, the first year after wildfire was drier than the pre-fire year (Fig. 3-4), therefore runoff from the single large reference and large burned watershed in the first post-fire year were only 53 and 84% of pre-fire values, respectively (Table 3-2). Conversely, the first year after harvest was wetter than the pre-harvest year (Table 3-2; Fig. 3-2). Therefore in the post-harvest year, runoff was 10 to 84% higher in small reference watersheds and 70 to 210% higher in small harvested watersheds (Table 3-2). Among all of the small watersheds, ammonium FWMC varied by a factor of 2 within each of the two study years, while nitrate FWMC varied by a factor of 10 and 14 in the pre-harvest and post-harvest year, respectively (Table 3-2). Among these watersheds, runoff and areal ammonium and nitrate exports varied by factors of 5, 6 and 51, respectively, in the pre-harvest year and by factors of 4, 4 and 21, respectively, in the post-harvest year (Table 3-2). Our analysis considered this variability by normalizing runoff and nitrogen data to precipitation and by using impact ratios derived from data collected within the same watershed before and after disturbance.

Harvesting and wildfire had a similar immediate influence on runoff. The RC impact ratio was 60% higher in the large burned watershed than the large reference watershed and the mean RC impact ratio was 70% higher in the small harvested watersheds than the small reference watersheds (P = 0.06) (Fig. 3-3). Reference watershed 1A had high runoff and areal inorganic nitrogen exports compared to other reference systems (Table 3-2), possibly because of the presence of a large aquifer and a relatively large proportion of toe seepage areas in this watershed (Prepas et al. 2006). Among the four harvested watersheds, there was a positive relationship between the RC impact ratio and the proportion of the watershed harvested (see Table 3-1) ($r^2 = 0.94$, $P = 0.03$) (dashed line in Fig. 3-4). This relationship (Equation 1) however is based on a limited dataset ($n = 4$).

[1] RC impact ratio = $0.04 \times$ percent area harvested $- 1.08$

A positive relationship existed between total daily runoff from the large burned watershed and total daily runoff from the large reference watershed in 1983 (pre-fire year), 1998 (fire year) and 1999 through 2004 (Years 1 to 6 post-fire) ($r^2 = 0.54$ to 0.99, $P < 0.001$ for all regression lines) (Fig. 3-5). The slope of the regression line describing these relationships was smallest in the pre-fire year (0.36), and then increased dramatically in the fire year (2.86). The low slope in the pre-disturbance year indicates that when fully vegetated, the burned watershed would export much less water than the reference watershed, and is likely related to certain watershed characteristics such as wetland coverage. Recovery of the perturbed runoff regime in the large burned watershed after fire is demonstrated by the declining slope of this line, beginning with the fire year and moving through to Year 6 post-fire (Fig. 3-5). However, the slope for Year 6 (0.46) was still steeper than the pre-fire year ($P < 0.001$), suggesting that the recovery is not complete.

Although there was a tendency for higher ammonium and nitrate FWMC impact ratios in harvested compared to reference watersheds (dashed bars in Fig. 3-6), treatment means were not detectably different ($P = 0.21$ and 0.15, respectively). However, combined with higher runoff, these concentrations yielded AC and NC impact ratios that were 130 and 170% higher, respectively, in harvested than reference watersheds ($P = 0.08$ for both) (solid bars in Fig. 3-6). These values exceeded the RC impact ratio, which suggests that the inorganic nitrogen export response is additive to the runoff response. Among the four harvested watersheds, the AC impact ratio was positively related to the proportion of the watershed harvested (see Table 3-1) ($r^2 = 0.96$, $P = 0.02$) (solid line in Fig. 3-4). This relationship (equation 2) is based on a limited dataset ($n = 4$). No such relationship existed for the NC impact ratio ($P = 0.30$).

$$[2]\ \text{AC impact ratio} = 0.07 \times \text{percent area harvested} - 2.76$$

As expected, positive relationships existed between total daily areal ammonium and nitrate exports and total daily runoff in reference and harvested watersheds in the post-harvest year ($P < 0.001$ in all four cases). For the areal ammonium export relationship, the residual error was similar for the reference and harvested datasets ($r^2 = 0.82$ and 0.81, respectively). Areal nitrate exports and runoff were more tightly coupled in harvested than reference watersheds ($r^2 = 0.97$ and 0.23, respectively) (Fig. 3-7). There also was a slight, but detectable decrease for the harvested watersheds in the slope of the regression between areal nitrate exports and runoff ($P < 0.001$). In addition, high areal nitrate exports were evident in reference watersheds in May (circled points in Fig. 3-7a). This pattern was also observed in the pre-harvest year (2003), when all nine small watersheds exported more nitrate relative to runoff in early May than during the rest of the May through October period (data not shown).

3.5 DISCUSSION

3.5.1 Wildfire

Wildfire in the Swan Hills, Alberta, was followed by an increase in runoff from the burned watershed relative to the reference watershed (Prepas et al. 2003; Burke et al. 2005), which was still apparent at Year 6 following disturbance. A similar analysis in the Experimental Lakes Area (ELA) on the Boreal Shield in northwestern Ontario demonstrated an increase in the slope of the line describing the relationship between weekly streamflow volume from a completely burned sub-basin (Y axis) relative to an unburned sub-basin (X axis) in the first year after the fire, followed by a decline to pre-fire levels (Schindler et al. 1980). However, this recovery in the burned Boreal Shield watershed was complete by Year 4. The difference in the recovery time between the Boreal Plain and Boreal Shield does not appear to be due to variations in fire conditions, because both fires were severe events consuming much of the organic material. However, drier conditions in the Swan Hills area after fire could have slowed recovery of the vegetation and hydrologic response. The total precipitation during the 4 years after wildfire in the FORWARD study area was 1895 mm, whereas it was 2662 mm during the 4 years after wildfire in the ELA study area (Environment Canada 2005a).

The areal nitrate export from the burned watershed was approximately 60% higher than the reference watershed in Year 1 post-fire and 20% higher in Year 6 post-fire (data not shown). This downward trend suggests that the nitrate levels immediately following the fire were elevated and are recovering to pre-fire levels, however, a lack of pre-fire nitrogen data prevents further examination of nitrogen recovery after fire in these watersheds.

3.5.2 Forest harvest

Similar to wildfire, harvesting was associated with an increase in the RC in the first year after harvest, relative to reference systems. Runoff increases after both types of disturbance have been attributed to lower uptake and evapotranspiration of water by vegetation (Schindler et al. 1980) and crusting of soils exposed to raindrop impact (Farres 1978; Arshad and Mermut 1988). Soil hydrophobicity after wildfire and soil compaction and ancillary activities related to forest harvest (e.g., roads) have been associated with increased incidence of overland flow (Gresswell 1999; McNabb et al. 2001; Whitson et al. 2003), which is rare in undisturbed boreal forests. As with fire, the recovery trajectory for runoff from the harvested watersheds will depend upon the precipitation regime, with recovery hindered in dry years. However, post-harvest silvicultural activities will likely shorten the time to hydrological recovery after harvest relative to fire. The study watersheds are managed by Millar Western Forest Products Ltd. and were subject to both mechanical (donaran mounder, shear blade and excavator brush rake) and chemical (aerial spraying of glyphosate) site preparation. For more information on post-harvest treatments, see Godin et al. (2008).

The export of both inorganic nitrogen fractions was higher after harvest relative to reference systems, but the impact ratio was higher for nitrate. Feller and Kimmins (1984) did not detect an increase in ammonium export after forest harvest. Increased nitrate export after harvest has also been observed in forests in New Hampshire (Likens et al. 1970), Oregon (Harr and Fredriksen 1988), and Finland (Ahtiainen 1992). The greater impact ratio for nitrate may be related to increased stream flows, even during periods of baseflow, which would tend to produce more turbulent conditions. Increased aeration from the additional turbulence could have affected the reduction-oxidation potential in a way that favoured in-stream biochemical conversion of ammonium to nitrate.

The seasonal nitrate export patterns observed for the reference watersheds concur with previous studies in New Hampshire (Likens et al. 1970), the Adirondack Mountains (Shepard et al. 1990) and northwestern Ontario (Bayley et al. 1992). That is, inorganic nitrogen exports in stream water, dominated by nitrate, peak in the spring and decrease during the summer months when there is an increase in nutrient demand from the growing vegetation. Thus, in relatively undisturbed watersheds in winter, microbial mineralization continues and/or sublimation and evaporation of the snowpack concentrates the nutrients. As snow melts, nitrate concentration within the snowpack may decrease more rapidly than water content, resulting in very high nitrate concentrations in the early snowmelt (Jeffries and Semkin 1983). Also, microbial lysis during freeze-thaw events, mainly in the spring, can release large amounts of nutrients into the soil solution (Grogan and Jonasson 2003). During the spring melt then, much of this nitrate is flushed out of the watershed before the plants become active. Our results reflect this pattern: nearly half of the open-water nitrate export occurred in May in the reference watersheds. However, harvested watersheds did not display a nitrate peak in spring melt, suggesting that harvesting either diminished microbial mineralization during the winter or altered the freeze-thaw cycle in the spring. Also, snowmelt-derived peak flows may have occurred earlier in harvested areas, because they are more exposed to the sun (Verry et al. 1983; Matheussen et al. 2000). Nitrate-rich peak flows may have occurred prior to the sampling period in harvested watersheds.

The high variability in runoff and inorganic nitrogen export among the small watersheds, even before disturbance, is the result of the interplay between localized precipitation patterns (seasonal and annual), slope, aspect, watershed geology, soil type, peatland cover, forest composition, stream geomorphology, and in-stream nitrogen sorption or transformations (Bernhardt et al. 2002; Prepas et al. 2006). Net nitrogen mineralization rates have been related to vegetation and soils on the Boreal Shield, with higher rates ascribed to deciduous stands and till soils than coniferous stands and clay soils (Côté et al. 2000). Giardina et al. (2001) found no correlation between net nitrogen mineralization rates and soils or vegetation in pine and aspen forests of Colorado, although there tended to be increased mineralization rates in aspen stands over the first 150 days. It has been suggested that aspen litter is more labile and broken down more quickly than pine litter (Coté et al. 2000), resulting in more rapid turnover of nutrients in aspen stands. In the FORWARD watersheds, runoff and areal ammonium exports appear to be positively related to conifer cover in undisturbed watersheds (Prepas, unpubl. data), however there is an autocorrelation between conifer cover and peatland cover, since most peatlands are small treed fens (Couling et al. 2007). Runoff and areal ammonium exports were positively related to peatland cover in undisturbed FORWARD watersheds over two open-water seasons ($r^2 = 0.50$ to 0.90; $P < 0.05$ to $<<0.01$) (Prepas et al. 2006). Mineralization rates in areas dominated by different vegetation types are the subject of ongoing research.

The stream is far from being a passive conduit, moving water and associated dissolved and particulate constituents from the watershed to receiving waters. Rather, in-stream processes change the form and amount of nitrogen in stream water (Davis and Minshall 1999; Bernhardt et al. 2002; Hall 2003). In headwater streams, nitrogen processing occurs mainly on biofilms on submerged surfaces and in sediments (Peterson et al. 2001) and at the hyporheic zone (Dahm et al. 1998). Ammonium transformations include assimilation by autotrophic and heterotrophic organisms, sorption to sediments, nitrification and possibly anaerobic ammonium oxidation, whereas nitrate transformations include assimilation and denitrification (Peterson et al. 2001; Burgin and Hamilton 2007). The type of stream sediment therefore can affect the concentration of inorganic nitrogen within the stream, creating additional variation among streams.

Superimposed upon this inherent high variation was the positive association between the proportion of the watersheds harvested and the runoff and ammonium export response. In addition, harvesting altered nitrate export patterns relative to peatland cover. In the two years that all of the small watersheds were monitored prior to harvest, peatland cover was not detectably related to areal nitrate export for the May through October period ($P > 0.45$). After harvest, peatland cover was still not related to areal nitrate export in the five reference watersheds ($P = 0.34$), but it was related to areal nitrate export from the four harvested watersheds ($r^2 = 0.84$, $P = 0.09$). Water and inorganic nitrogen budgets in Boreal Plain peatlands are the focus of ongoing studies.

3.6 CONCLUSIONS

In this study on the western Canadian Boreal Plain, wildfire was associated with higher runoff from a burned watershed relative to a reference system. The recovery trajectory was protracted, with runoff still elevated six years after fire, possibly because vegetation regrowth rates are slow in this sub-humid region. Forest harvesting on the Boreal Plain was also associated with increased runoff from four small watersheds relative to five reference watersheds, a finding that is consistent with many studies across North America (e.g., Likens et al. 1970; Carignan et al. 2000). Recovery trajectories after harvest may be shortened relative to post-fire by post-harvest treatments that promote vegetation regrowth. Although there tends to be greater ammonium and nitrate FWMC in streams draining harvested watersheds, these variables were not detectably different from reference stream values. Our results differ from studies in the northeastern (Likens et al. 1970) and northwestern U.S. (Harr and Fredriksen 1988), which detected higher nitrate concentrations immediately after harvest. However combined with higher runoff, these FWMC values yielded 130 and 170% higher areal ammonium and nitrate exports, respectively, from harvested watersheds compared to reference watersheds, which is consistent with studies on the Boreal Shield (e.g., Lamontagne et al. 2000). Finally, areal inorganic nitrogen export peaks during the snowmelt and decreases through the summer. However, the nitrate export in snowmelt from harvested watersheds was low compared with reference watersheds, which we suggest is due to decreased microbial mineralization during the winter, an altered freeze-thaw cycle in the spring, or earlier melt (i.e. prior to our sampling period) in harvested watersheds.

3.7 ACKNOWLEDGEMENTS

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3.9 Tables:

Table 3-1. Characteristics of study watersheds in the Swan Hills. Numbers refer to watershed outlet sites indicated in Figure 3-1.

Watershed		Area (ha)	Area experimentally disturbed (%)
Number	Name		
	Large Reference		
1	Two Creek	12,930	0
	Large Burned		
2	Sakwatamau A	24,700	89
	Small Reference		
3	Mosquito	311	0
4	1A	510	0
5	Cassidy	593	0
6	Thistle	848	0
7	Willow	1,561	0
	Small Harvested		
8	Pierre	257	84
9	Toby	263	60
10	Millions	335	52
11	Kashka	398	58

Table 3-2. Total precipitation, runoff, and areal ammonium-N (NH_4^+) and nitrate-N (NO_3^-) exports and flow-weighted mean concentrations (FWMC) for the May 1 through October 31 period in the study watersheds in the pre-disturbance year (Pre) and first year post-disturbance (Post).

Watershed	Year	Precip. (mm)	Runoff (mm)	Areal export (kg N km^{-2})		FWMC (µg N L^{-1})	
				NH_4^+	NO_3^-	NH_4^+	NO_3^-
Large Reference[a]							
Two Creek	Pre	460	220	---	---	---	---
	Post	322	117	1.6	1.0	14.0	8.3
Large Burned[a]							
Sakwatamau A	Pre	460	147	---	---	---	---
	Post	322	124	1.7	1.6	13.5	12.9
Small Reference							
Mosquito	Pre	246	40	0.9	1.8	23.4	45.5
	Post	466	44	1.5	0.6	33.4	14.1
1A	Pre	326	96	1.9	10.2	19.8	106
	Post	470	177	2.9	8.5	16.6	47.7
Cassidy	Pre	240	50	1.5	7.0	29.4	142
	Post	462	78	1.4	4.0	18.1	51.9
Thistle	Pre	240	51	1.1	0.5	21.9	10.2
	Post	462	92	1.4	0.5	15.4	5.2
Willow	Pre	240	42	1.1	0.8	27.4	19.9
	Post	462	70	1.3	0.4	18.2	5.9
Small Harvested							
Pierre	Pre	297	20	0.4	0.2	20.6	14.6
	Post	404	62	1.7	0.5	28.0	7.9
Toby	Pre	297	83	1.7	1.2	21.3	12.0
	Post	404	174	3.7	2.5	21.4	14.3
Millions	Pre	246	57	1.3	1.6	23.3	27.5
	Post	466	97	1.5	1.0	15.8	10.4
Kashka	Pre	246	23	0.3	1.0	14.9	45.0
	Post	466	55	0.9	1.0	16.3	17.8

[a] Pre-fire data from Munn (1984).

3.10 Figures:

Figure 3-1 The two large and nine small FORWARD watersheds in the Swan Hills, Alberta, Canada. See Table 3-1 for names of numbered watershed outlet sites.

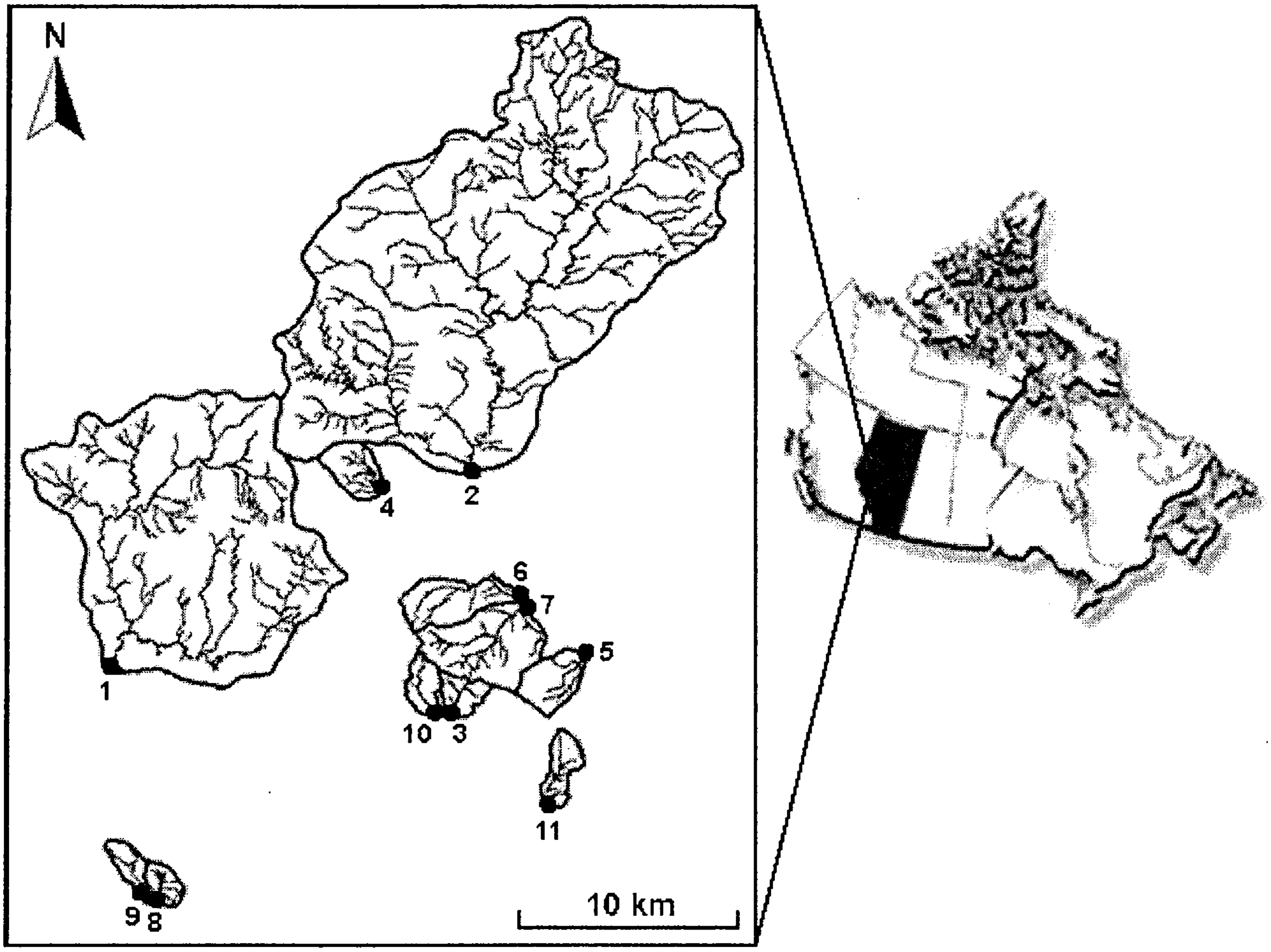


Figure 3-2 Total annual runoff from the Sakwatamau River for 1980 to 2004. Horizontal arrow indicates long-term (1980 to 2004) average runoff (132 mm). Data courtesy of Environment Canada (2005b).

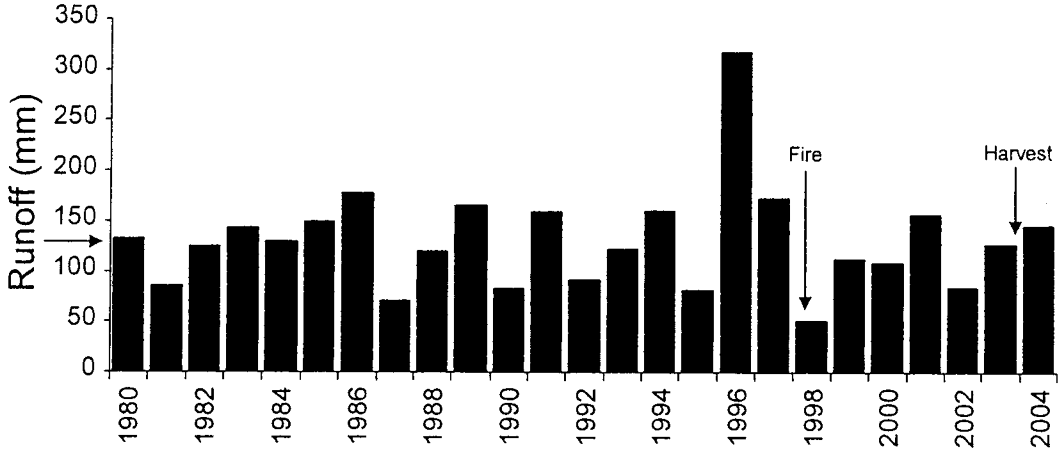


Figure 3-3 Normalized runoff coefficient (RC) impact ratios for large reference (*n* = 1), large burned (*n* = 1), small reference (*n* = 5), and small harvested (*n* = 4) watersheds. The dashed line at 1 represents no change between the pre- and post-disturbance year. Error bars represent Standard Error.

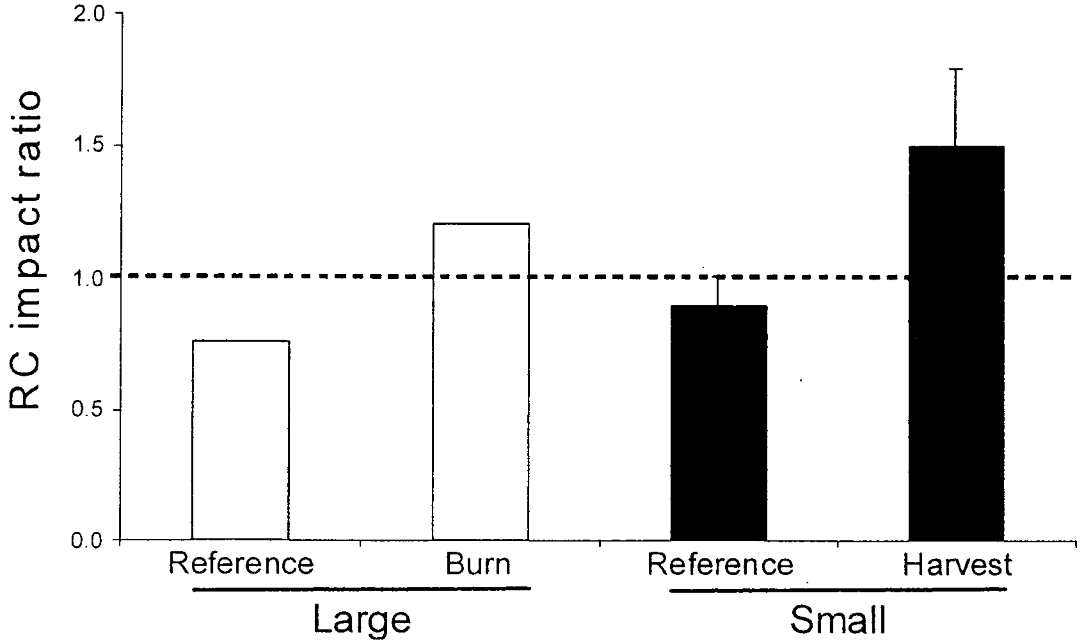


Figure 3-4 Relationships between impact ratios for normalized runoff (dashed line) and ammonium coefficients (solid line) and the proportion of the watershed harvested for the four small harvested watersheds.

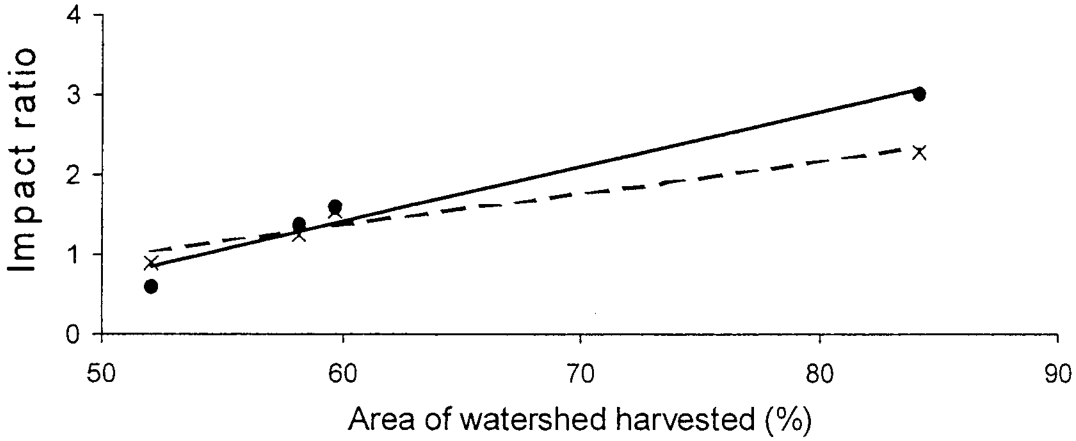


Figure 3-5 Regression lines between total daily runoff from the large burned and large reference watersheds for the pre-fire year, fire year and Years 1 through 6 post-fire. Relationships are based on 12 to 101 data points per year. A 1:1 ratio between the burned and reference watersheds indicated by dashed line.

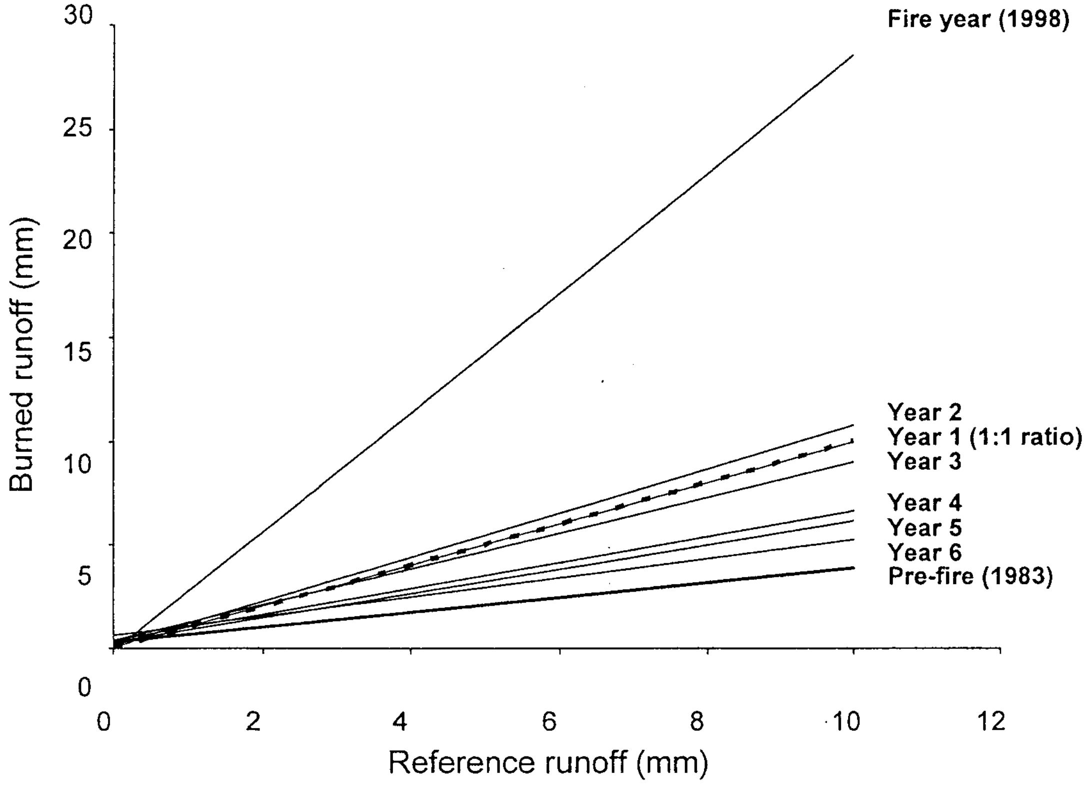


Figure 3-6 **Impact ratios for normalized areal nitrate and ammonium fluxes (solid bars) and flow-weighted mean concentrations (dashed bars) in the reference (*n* = 5) and harvested (*n* = 4) watersheds. Error bars represent Standard Error.**

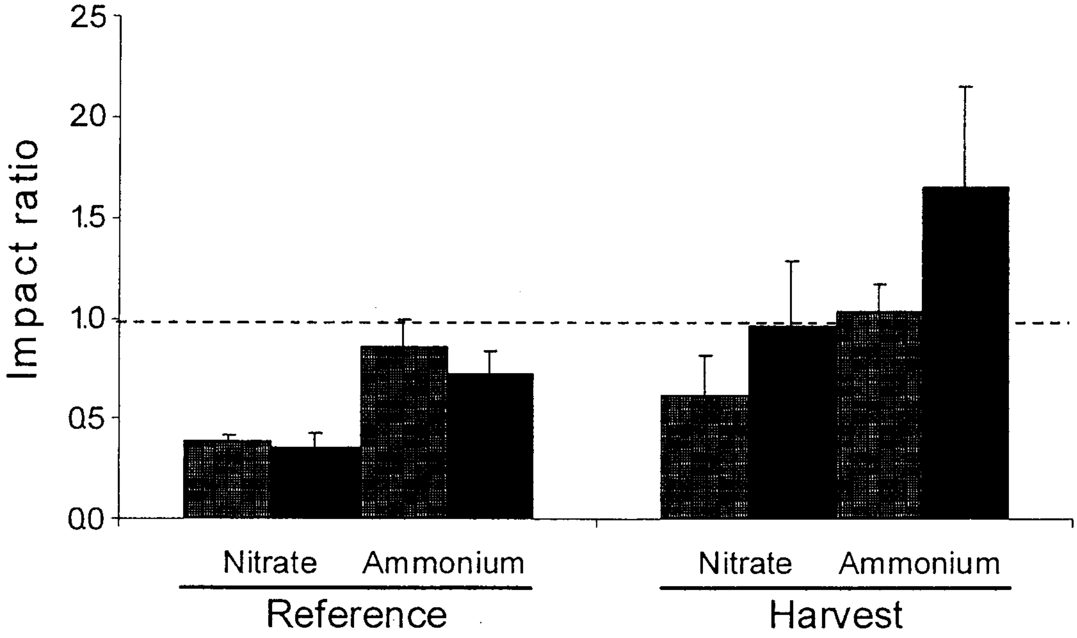
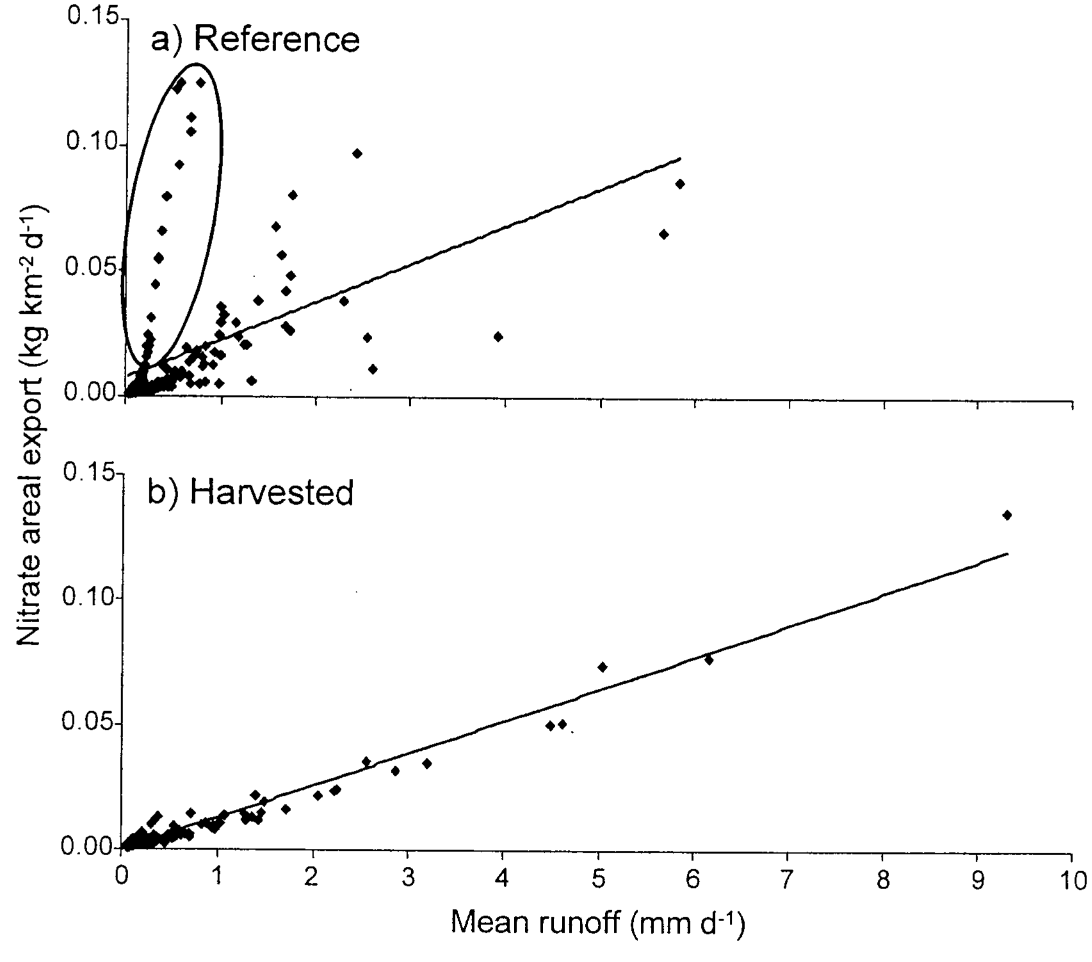


Figure 3-7 Relationships between total daily areal nitrate export and total daily runoff from a) reference and b) harvested watersheds in the post-harvest year. The 184 datapoints are reference (*n* = 5) and harvested (*n* = 4) daily means. Circled data points are from the snowmelt period in early May.



Chapter 4

Influence of overstory vegetation on the flux of nitrogen and dissolved organic carbon from the atmosphere to the forest floor: Boreal Plain, Canada

4.1 ABSTRACT

Nitrate, ammonium, total dissolved nitrogen (TDN), dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) concentrations and flux were measured for one year in bulk deposition and throughfall from three stand types (upland deciduous, upland conifer and wetland conifer) on the Boreal Plain, Canada. Annual (November 2006 to October 2007 water year) flux rates in bulk deposition were 80, 216, 114 and 410 mg N m^{-2} for nitrate, ammonium, DON and TDN respectively and 3.5 g C m^{-2} for DOC. The nitrate and ammonium flux in throughfall were approximately 50% of the flux in bulk deposition, while TDN flux in throughfall was 60 to 74% of the flux in bulk deposition. The DOC flux in throughfall was approximately 2 times greater than DOC flux in bulk deposition, while there was no detectable difference in DON flux. The forest canopy generally had the most impact on throughfall chemistry during the active growing season as compared with the dormant season, although DOC flux in throughfall of deciduous stands was highest during autumn. Total dissolved N flow weighted mean concentrations (FWMC) in the snowpack were not detectably different from the FWMC in throughfall and bulk deposition throughout the rest of the year. However, ammonium FWMC were lower and DON FWMC were higher in the snowpack than in either throughfall or bulk deposition for the other seasons, suggesting some transformation of ammonium to DON within the snowpack.

Key words – inorganic nitrogen, dissolved organic carbon, runoff, boreal forest, throughfall, atmospheric deposition.

4.2 INTRODUCTION

Although many temperate forests are naturally nitrogen (N) limited (Shaver and Chapin 1980; Vitousek and Howarth 1991), much of the research on N deposition, cycling and export in forested ecosystems (see Gundersen et al. 1998; Michalzik et al. 2001 for summaries) has been conducted in areas of potential N saturation (e.g., northeastern United States and central Europe). Nitrogen saturation describes changes to forest soil N dynamics that occur when the supply of N is so large that bioavailable N is in excess of biotic demand (Aber et al. 1989). It implies that other factors, such as light or other nutrients have become more limiting than N. Knowledge is lacking in terms of baseline N deposition in regions with low N deposition, such as the Boreal Plain. This ecozone in western Canada, covers about 650 000 km^2, an area greater than Finland and Norway combined (Fig. 4-1). Although there are some estimates of N flux in bulk deposition within this vast region (Alberta Environment 2008; Kochy and Wilson 2001; Shaw et al. 1989), none of these previous studies measured the effect of the forest canopy on N flux to the forest soils. As a result knowledge of how forest canopy types affect N flux in throughfall for this region is lacking.

Much of the Boreal Plain is quite remote and, historically, has not received high inputs of N from industrial or agricultural sources. However, oil production from oil sands in the province of Alberta increased more than 4-fold during the last 10 years, and is expected to increase another 10-fold by 2015 (Severson-Baker et al. 2008). Increased production, combined with changes in mining procedures, has led to a modeled 5-fold increase in nitrogen oxides (NO_x) emissions from approximately 60 Mg day^{-1} in 1990 to a projected rate of 300 Mg day^{-1} by 2012 (Golder Associates 2002). There was also a 7-fold increase in coalbed methane extraction from 2003 to 2006 within the province of Alberta (Government of Alberta 2009). The effects of the cumulative industrial development will likely impact the inorganic N (IN) and total N deposition on the Boreal Plain, making it essential to examine current rates of N deposition.

Throughfall (precipitation passing through the forest canopy) and stemflow (precipitation dripping down plant branches and stems) chemistry and flux tend to be related to the flux in incoming bulk deposition. In areas with greater annual N deposition rates, throughfall and stemflow may be enriched with N (Dise et al. 1998). In areas of relatively low N deposition however, forest canopies generally retained N (Duchesne and Houle 2006; Friedland et al. 1991; Piirainen et al. 1998; Potter et al. 1991). In fact, negligible throughfall N fluxes generally occur when annual IN deposition rates are less than 400 mg N m^{-2} (Dise et al. 1998). Throughfall flux was also correlated with the dominant vegetation type. Morphological differences between conifer and deciduous species (e.g. crown form, leaf shape and cuticle thickness) often result in differences in throughfall and stemflow chemistry and flux by stand type (DeSchrijver et al. 2007; Henderson et al. 1977; Michalzik et al. 2001; Verry and Timmons 1977).

Dissolved organic carbon (DOC) is often correlated to N fluxes in boreal forest soils. For example, nitrate (NO_3^-) removal rates in riparian soils in southern Ontario (Devito et al. 2000; Hill et al. 2000) and boreal wetland soils in southern Sweden (Davidsson and Stahl 2000) were positively related with DOC content. Also, C:N ratios in boreal forest floor and soils were positively correlated with N immobilization rates (Cameron and Haynes 1986; McNulty et al. 1991). As a result, the C:N ratio has been used as an indicator of potential mineralization and nitrification rates, and to predict N losses through inorganic N (IN = NO_3^- + ammonium [NH_4^+]) leaching (McNulty et al. 1991). Therefore, understanding how various soil and stand types affect DOC flux to the soil is important for understanding how different soil and stand types affect N cycling and exports.

This study is a component of the Forest Watershed and Riparian Disturbance (FORWARD) Project, a long-term, multidisciplinary study designed to develop hydrological and water quality models for direct application to industrial forest planning in Boreal Plain watersheds (Prepas et al. 2008*a*). Studies measuring annual N flux in bulk deposition and throughfall often assist with predicting N export in streams draining watersheds (Dise et al. 1998). In addition, accurate measurements of the differences in N flux above and below the forest canopy in common soil/stand types indicate the forest canopy's role in retaining, transforming or enriching the nutrient flux to the forest soils. The forest canopy can then be entered into these export models as a specific compartment that will assist the FORWARD project with the development of predictive water quality models both in reference and disturbed watersheds. Therefore, the purpose of this study was to: 1) measure the effect of different forest soil and overstory vegetation types (upland conifer, upland deciduous and wetland conifer stands) on aqueous N and DOC flux to soils in a small (15.6 km^2) relatively undisturbed watershed on the Boreal Plain; 2) examine the relative amounts of IN and dissolved organic N (DON) comprising the total dissolved N (TDN) flux; and 3) relate the flux rates to patterns of N deposition across North America.

4.3 METHODS

4.3.1 Site description

The Willow watershed (15.6 km^2; Fig. 4-2) was within the FORWARD project study area in the Swan Hills, located 230 km northwest of Edmonton, Alberta (Fig. 4-1). Dominant soil orders in the Swan Hills are Luvisolic, Organic and Brunisolic, but Gleysolic and Regosolic soil types also occur (Ecological Stratification Working Group 1996). The forest vegetation was dominated by trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.), paper birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench) Voss), lodgepole pine (*Pinus contorta* Dougl. ex Loud.var. latifolia Engelm) and balsam fir (*Abies balsamea* (L.) Mill) in well-drained sites and black spruce (*Picea mariana* (Mill.) BSP) and tamarack (*Larix laricina* (Du Roi) K. Koch) in poorly drained sites (Ecological Stratification Working Group 1996).

Aerial photograph interpretation from 1994 demonstrated that the land cover in the Willow watershed was approximately 53% deciduous-dominated (30% or less conifer crown closure), 39% conifer-dominated forest (70% or more conifer crown closure in the forest canopy), 5% mixed-wood forest (21 to 69% conifer crown closure), and 3% non-forested. The watershed was relatively undisturbed with limited harvesting (35 ha clear cut in 1980), some road building along the west and south boundaries of the watershed and minor amounts (approximately 1% of the watershed area) of oil and gas exploration (cutting of seismic lines) and extraction (building of access roads and well sites).

The climate is sub-humid (Zoltai et al. 1998) and precipitation is temporally and spatially variable (Pelster et al. 2008). Annual precipitation from 1978 to 2008 ranged from 394 to 777 mm, with a mean of 577 mm (Environment Canada 2008a). Runoff patterns reflect this variability, with instantaneous discharge in the Willow watershed during 2007 ranging by a factor of more than 100-fold, and annual runoff varying 3-fold between 2002 and 2007. Streamwater pH was near neutral to slightly basic, ranging from 7.2 to 8.2 in the Willow stream during 2007. For more detailed descriptions of the Willow watershed, see Burke et al. (2005) and Prepas et al. (2006, 2008*b*).

4.3.2 Sampling

Four stands from each of three stand types (upland conifer, upland deciduous and wetland conifer – see Table 4-1) were randomly selected within the Willow watershed (Fig. 4-2). Crown closure was measured at 25 points along two 60-m transects set up in a cross formation within each stand (Fig. 4-2). The points were assigned to four (0 to 25%, 26 to 50%, 51 to 75%, and 76 to 100%) crown closure classes. Three sampling locations were selected from each stand using stratified random sampling to ensure proportional representation of the crown closure classes.

Throughfall samplers were elevated 0.6 m above the ground and consisted of two 15.2 cm inner diameter polyethylene funnels connected by polyvinyl tubing to a 2 L brown, opaque, high-density polyethylene Nalgene bottle. Sample bottles were partially buried (approximately 80% of bottle below-ground) to keep samples relatively cool and out of the sun. Four bulk deposition collectors were also installed in the open within the watershed (Fig. 4-2): these consisted of a single 25.4 cm inner diameter polyethylene funnel elevated approximately 3 m above the ground and attached to a 2 L brown sample bottle as above. Bulk deposition collectors were situated to ensure minimal effect of forest vegetation (i.e., the slope from the samplers to the top of the adjacent treeline did not exceed 30° from the horizontal). Locations were selected to provide good coverage of bulk open deposition patterns across the watershed area. A Campbell Scientific weather station was installed within the Willow watershed, less then 2 km from the bulk deposition and throughfall sample locations, and provided continuous (every 10 minutes) monitoring of precipitation volume and air temperature (Fig. 4-2). Precipitation data from the weather station, along with an Environment Canada weather station located approximately 40 km southeast were used to verify bulk deposition volume measurements and provide additional estimates of precipitation within the watershed.

Throughfall and stemflow collection began in mid-May 2007 and continued throughout the snow-free season (1 May to 31 October). Samples were generally collected every two weeks, although during periods with heavy rains, the sample period was shortened. During the autumn period very little precipitation fell (25.4 mm between 17 August and 31 October), and as a result, only one set of samples could be collected during this time. The volume of throughfall and bulk deposition was measured and chemistry samples from stemflow, throughfall and bulk deposition were collected approximately every two weeks from May through August. Throughfall and bulk deposition collectors were rinsed with distilled water after each sample was collected. Although stemflow chemistry was measured, the volumes could not be accurately determined because of consistent bear damage.

Samples were stored on ice until they could be processed and preserved. Since biocide was not added to the sample bottles and samples were collected every two weeks, bioconversion and immobilization of N could have been a problem, particularly during the warm summer months. However in August, samples were collected on an event basis to test this hypothesis and regression analysis found no relationship (n=80, P=0.88) between the number of days the sample was stored in the sample bottle and percent DON. This suggests that immobilization of IN by microbes in the samples was limited.

The remoteness of the sites and depth of the snowpack made it unfeasible to collect multiple samples during the winter. As a result, a snowpack survey was completed in early March 2007 as a proxy for throughfall and stemflow to estimate dissolved N flux during the winter season (1 November 2006 to 30 April 2007). Three snow cores were collected using a copper coring tube (ID = 5.08 cm) at each of nine throughfall/stemflow sample locations (three samples from each stand type) and at three bulk deposition sample locations. Samples from each location were assumed to represent throughfall or bulk deposition with no redistribution from other areas. Snow water equivalent (SWE) was measured and used as a surrogate for precipitation and samples were collected for nutrient analysis. The SWE was compared with continuous measurements for snowfall from a Campbell Scientific weather station fitted with a snowfall conversion adapter and located within the Willow watershed. This method, while not optimal, was still expected to provide suitable estimates of N flux during winter, since another study found no detectable difference in NO_3^- and NH_4^+ concentrations between snowpack surveys and bulk deposition samplers from the National Atmospheric Deposition Program (Hidy 2003).

The samples were analyzed for NH_4^+, NO_3^-, total dissolved N (TDN) and DOC concentrations. Dissolved organic N concentration was calculated by subtracting IN from TDN concentrations. When the IN concentration exceeded TDN (approximately 18% of the samples), DON was assumed to be zero. Ammonium, NO_3^- and DOC samples were filtered through a 0.45 μm pore size Millipore filter within 48 h of collection and the NH_4^+ and NO_3^- samples were preserved with sulfuric acid. TDN samples were filtered using a Whatman GF/F filter (mean pore size 0.7 μm). All samples were refrigerated at 4°C until they could be analyzed (maximum storage time was 3 weeks). TDN samples were digested with potassium persulfate and reduced to nitrite in the presence of cadmium. Ammonium, NO_3^- and digested TDN samples were analyzed colorimetrically using a Lachat QuikChem 8500 FIA automated ion analyzer, whereas DOC samples were analyzed using a Shimadzu 5000A TOC Analyzer.

4.3.3 Data analysis

Daily nutrient fluxes ($\mu g\ m^{-2}\ day^{-1}$) in bulk deposition and throughfall for the growing season and autumn were calculated by multiplying the amount of net precipitation (in mm) by the nutrient concentration (in μg L^{-1}) of the sample and then dividing by the number of days since the sampler had last been emptied and cleaned. During the winter however, daily nutrient flux in bulk deposition and throughfall was calculated by multiplying the SWE by the nutrient concentration in each snow core and dividing by the age (in days) of the snowpack. This assumes no nutrient losses during the winter. Since stemflow volumes could not be accurately established, it was instead assumed that 6%, 1% and 0.4% of incoming precipitation was converted to stemflow by upland deciduous, upland conifer and wetland conifer stands, respectively, for the growing season and autumn (1 May to 31 October 2007). These values are within the range for the trees in these stand types reported in previous studies in other boreal and north temperate regions (Mahendrappa, 1990; Piirainen et al., 1998; Verry and Timmons, 1977). Stemflow was assumed to be negligible during the winter season. Therefore, daily nutrient flux in stemflow during the growing season and autumn was estimated by multiplying the sample concentration by the estimate of stemflow volume and dividing by the number of days since the previous sample date.

For most dates with missing flux rates, linear interpolation was used to fill in gaps, although the daily flux rate for the last sampling date (11 October 2007) was assumed to remain constant until 31 October 2007. Annual flux rates were then calculated by summing the daily flux rates for the entire water year (1 November 2006 to 31 October 2007), while nutrient flow-weighted mean concentration (FWMC) was calculated by dividing the total nutrient flux by the total precipitation for three time periods: winter (1 November 2006 to 30 April 2007, estimated from the snowpack survey), growing season (1 May to 31 August 2007) and autumn (1 September to 31 October 2007).

Daily nutrient flux rates and seasonal nutrient concentrations in bulk deposition and throughfall under the three canopy types (upland deciduous, upland conifer, wetland conifer and bulk deposition) were compared using a repeated measures analysis of variance (ANOVA). Annual flux rates and mean FWMC for bulk deposition and the three stand types were compared using a single factor ANOVA. Multiple comparisons for significant ANOVA results were tested using the least squares difference and Scheffe's test. All statistical analyses were conducted using SPSS 16.0.

4.4 RESULTS

The sampling year represented a typical year for the study area in terms of precipitation inputs as rain and snow. Total precipitation for the 1 November 2006 to 31 October 2007 water year was 547 mm at the Willow weather station. For comparison, total precipitation for the same time period was 582 mm at the Whitecourt weather station, approximately 50 km southeast of the study site, of which 25% fell as snow and 75% as rain (Environment Canada, 2008a). This is within 1% of the long-term (1971-2000) average annual precipitation for Whitecourt of 577 mm, with 24% falling as snow and 76% as rain (Environment Canada 2008b).

Snow began to accumulate on 20 October 2006 and was completely melted by 15 April 2007 (Environment Canada 2008a). Since the snowpack survey occurred 8 March 2007, approximately 13% of the snowfall was not included in the survey. Snowfall measurements at the Willow weather station indicate that approximately 5% of incoming snow in bulk deposition and upland stands was lost to sublimation or melting before the snowpack survey. Losses in the wetland conifer stands were higher, approximately 45% of incoming snow. Consequently the snowpack survey provided a good first approximation of winter throughfall.

The NO_3^- FWMC was consistently higher in bulk deposition than in throughfall from all stand types during the growing season ($P<0.001$ for three stand types, Fig. 4-3a). The NO_3^- FWMC in throughfall from all stand types was lowest during the growing season and highest in the winter snowpack, whereas the NO_3^- FWMC in bulk deposition did not differ among seasons (Fig. 4-3a). During the growing season, NH_4^+ FWMC was also higher in bulk deposition than in throughfall from the three stand types ($P=0.01$, 0.03 and 0.01 for upland deciduous, upland conifer and wetland conifer respectively, Fig. 4-3b). The NH_4^+ FWMC in the two upland stand types and the bulk deposition were lowest in the winter snowpack, while in the wetland stands the NH_4^+ FWMC were not detectably different by season (Fig. 4-3b). During the growing season, neither the NO_3^- nor the NH_4^+ FWMC differed among stand types.

There was no detectable difference in the annual DON or TDN FWMC between throughfall of the various stand types and bulk deposition ($P=0.26$ and 0.34, respectively). However during the growing season both upland stand types had throughfall DON FWMCs that were greater than the FWMCs in throughfall of the wetland stands and in bulk deposition (Figs. 3c & d). The TDN FWMC in the wetland stands were higher in the winter snowpack than in throughfall during the other seasons ($P<0.001$, Fig. 4-3c), while TDN FWMC in throughfall of the other stand types was not detectably different by season. In fact, during the winter, the DON and TDN FWMCs for the snowpack in the wetland conifer stand types were approximately double the FWMCs in the upland stand types and in bulk deposition (Fig. 4-3).

The DOC FWMC in throughfall for all three stand types was higher than bulk deposition ($P<0.001$, Fig. 4-4). Through most of the year, the DOC FWMCs in throughfall were similar in the two conifer stand types (Fig. 4-4). For the winter period however, the DOC FWMC was higher in the wetland than the upland conifer type (Fig. 4-4). Seasonal trends were also apparent in the two upland stand types: the deciduous stands had the highest DOC FWMC during the autumn, while the conifer stands had the lowest DOC FWMC during the winter (Fig. 4-4). Both upland stand types had lower DOC concentrations during the winter compared to the other two seasons.

Daily flux rates for NO_3^-, NH_4^+ and TDN in throughfall were less than flux rates in bulk deposition ($P<0.01$ for each, Fig. 4-5). Conversely, DOC daily flux rates were greater in throughfall of the upland deciduous and conifer stands than in bulk deposition ($P=0.02$ and 0.04 respectively), although there was no detectable difference between the throughfall of the wetland conifer stand and bulk deposition ($P=0.18$, Fig. 4-5). There were however, no detectable differences between DON daily flux rates between any of the stand types and bulk deposition ($P=0.16$).

Annual NO_3^-, NH_4^+ and TDN flux rates to the forest floor of the three stand types were not detectably different, however the annual flux of all three N fractions below the canopy in all three stand types was consistently lower than the annual flux in bulk deposition ($P<0.001$ for each, Table 4-2). Annual DON flux rates in stemflow and throughfall of the three canopy types were similar to bulk deposition rates, although the DON flux was higher under deciduous stands than either the upland or wetland conifer stands ($P=0.04$).

In total, the annual IN flux below the canopy was approximately 50% of the IN flux in bulk deposition ($P<0.001$ for both NO_3^- and NH_4^+, Table 4-2). Annual TDN flux below the canopy was between 60 and 70% of the flux in bulk deposition whereas there was no detectable difference in annual DON flux between the throughfall of any stand type and bulk deposition (Table 4-2). Annual DOC flux though, was 2 to 3 times greater under all three forest canopies than in bulk deposition (*P*=0.01, Table 4-3). Finally, the mean C:N mass ratio was 3 to 4 times higher in throughfall of all stand types than in bulk deposition (Fig. 4-6).

4.5 DISCUSSION

The NO_3^- and NH_4^+ FWMCs in throughfall were approximately two-thirds of the FWMCs in bulk deposition (Fig. 4-3), which suggests retention of IN by the forest canopy. The height of the trees and the multiple layers of foliage allow the forest to be much more efficient at intercepting dry deposition N than plastic funnels (Balestrini et al. 2007). As a result, the bulk deposition collectors likely underestimate the areal N deposition that occurs in the forest canopy. Thus, the amount of IN retained by the forest canopy may be greater than the data originally suggests.

Total dissolved N FWMCs were similar in bulk deposition and in throughfall, and if the bulk deposition value was an underestimate, some of the TDN fraction may have been retained by the forest canopy as well. In other words, the additional material retained in the forest canopy would be flushed through the canopy into the throughfall collectors during rain events, which would result in higher FWMCs in throughfall compared with bulk deposition for a given dry deposition rate. Since the bulk deposition and throughfall TDN FWMCs were similar, it is likely that some N retention occured within the forest canopy.

The forest canopy retains N either through foliar uptake, absorption onto the leaf surface or assimilation by epiphytes and microorganisms within the canopy (Krupa 2003; Lovett 1994; Wilson 1992). Wilson (1992) proposed that the mechanism for uptake is diffusion, however other research has noticed that N uptake is often correlated with a release of K^+, Mg^{2+} and Ca^{2+}, as well as some weak organic acids (Draaijers et al. 1996; Lovett et al. 1985), suggesting active exchange of N for base cations. If N uptake in the forest canopy were strictly a function of diffusion of nutrients through the stomata, DON and IN FWMCs would be consistent. Instead, during the active growing season, the DON FWMC below the canopy was higher than DON FWMC in bulk deposition; opposite to the pattern observed for IN FWMC (Fig. 4-3). The increased DON FWMC in throughfall may be due to washing off of some dry deposited DON or leaching of weak organic acids (Draaijers et al. 1996). The inconsistent effect of the forest canopy on the different N fractions suggests that N uptake by the canopy is actively controlled, with preferential uptake of IN.

The increase in the DOC FWMC in throughfall (Fig. 4-4) suggests either leaching from the canopy or flushing of excess DOC that was deposited on the stems and foliage. Washing dry deposition off the foliage should not alter the C:N ratio, however the C:N ratio of throughfall was much greater than the C:N ratio of the bulk deposition (Fig. 4-6). In remote areas, most of the atmospheric ON composition is organic nitrates, predominantly peroxyacetyl nitrate (PAN) (Neff et al. 2002). The C:N ratio of PAN is very low, leading to a low C:N ratio in bulk deposition. The increased C:N ratio in throughfall indicates a different source of ON than just atmospheric deposition, consistent with previous studies that measured leaching of organic acids from the foliage (Draaijers et al. 1996).

Similar to other studies in north temperate ecosystems the NH_4^+ and NO_3^- FWMC in throughfall was lower than the FWMC in bulk deposition ($P<0.001$ for both N fractions, Table 4-2) (Duchesne and Houle 2006; Friedland et al. 1991; Piirainen et al. 1998; Potter et al. 1991; Pryor and Barthelmie 2005). Throughfall studies are not all consistent though, as some studies show enrichment of N in throughfall (e.g., Henderson et al. 1977; Mahendrappa and Ogden 1973; Terauda and Nikodemus 2007). The contrary results in throughfall N flux between various studies seem to be related to N deposition rates. Assimilation of IN by the canopy tends to occur in areas with low N deposition rates (less than 400 mg N m^{-2} yr^{-1}), while N enrichment in throughfall occurs in areas with high N deposition (Dise et al. 1998). The lower IN concentrations under the canopy therefore suggest that IN is still limiting in this region.

The concentrations of all N fractions and DOC were highly variable among sample dates (data not shown). Some of the variability in concentrations was due to the length of the sample period (increased dry deposition over time) and the volume and intensity of precipitation (dilution of the dry N deposition) (e.g., Chapin and Kedrowski 1983; Morris et al. 2003; Shaw et al. 1989). Since dry deposition of N can be fairly high, ranging from 20% to 50% of bulk N inputs (Kelly and Meagher 1986; Lovett and Lindberg 1984; Sievering et al. 2000; Swank and Waide 1987), much of the dry N deposition intercepted by the canopy may remain on the leaf surface until precipitation washes it through the canopy. As a result, the concentration of N in throughfall is typically highest at the beginning of storm events, with concentrations quickly decreasing as the event proceeds (Hill et al. 1999; Pryor and Barthelmie 2005).

There were interesting seasonal patterns in the N FWMC in the throughfall. The NO_3^- FWMCs were higher in the winter snowpack than in throughfall during other seasons, while the NH_4^+ FWMCs were lower in the snowpack. There were no detectable seasonal changes in DON or TDN FWMC. These findings were contrary to Morris et al. (2003), who found that DON concentrations of throughfall in northwestern Ontario black spruce stands approached zero during the winter. This difference from Morris et al. (2003) in winter DON concentrations was likely related to different sampling methods. To estimate N loading to the soils and surface water during the spring snowmelt, this study measured N flux for the winter period by sampling snow cores near the end of the season, whereas Morris et al. (2003) sampled the snow numerous times throughout the winter. Unfortunately, the remoteness of the site and the depth and lack of consolidation within the snowpack made this method unfeasible. However, since the TDN FWMCs in bulk deposition and throughfall under the upland canopies do not differ by season (Fig. 4-3), any additional sources of DON to the snowpack (e.g. decomposition of forest litter within the snowpack) were likely minimal.

In the wetland snowpack however the TDN FWMC was higher than the FWMC during other seasons, even more than would be expected given sublimation losses, and may indicate an additional source of N in these wetlands. Greater sublimation losses suggest longer retention of snow within the canopy leading to greater snow loads on the branches and longer contact time between the snow and foliage. Longer contact time may lead to additional N transfer from the foliage to the snow, while the increased snow loads may lead to increased loss of foliage and small shoots, which then end up in the snowpack. In addition, since DON concentration was estimated by calculating the difference between TDN and IN, the measurement error was potentially compounded.

The decreased NH_4^+ and concurrent increased DON FWMC suggests conversion of NH_4^+ to DON within the snowpack. This conversion was unexpected since immobilization rates and temperature tend to be positively correlated. However, there are some microorganisms that are adapted to snow-covered conditions and can immobilize IN throughout the winter period (Schmidt and Lipson, 2004) that may be responsible for the production of DON in the snowpack.

The TDN, NH_4^+ and DON FWMCs of the snowpack in wetland conifer stands were much higher (approximately double) than the TDN, NH_4^+ and DON FWMC of the upland stands and bulk deposition. Examination of the snowpack in the various stand types demonstrated that for the March snow survey, the SWE in the wetland stands was about 55% of the SWE in the other two stand types and open areas. The lower SWE and increased nutrient concentrations were probably related to higher interception and sublimation rates during winter for black spruce stands compared with either aspen or lodgepole pine stands (Pomeroy et al. 1998). Similar nutrient flux rates between stand types, combined with increased sublimation were likely responsible for the higher FWMC.

The seasonal patterns for DOC FWMC in throughfall were expected since other studies in boreal forests have detected similar patterns (Morris et al., 2003; Verry and Timmons 1977). Decreased concentrations during winter, even for the conifer stands, suggest that an active canopy allows more DOC through than a dormant one. This indicates additional sources of DOC in throughfall besides dry deposition; likely the leaching of weak organic acids, which is known to occur in the forest canopy (Draaijers et al. 1996). These seasonal patterns were consistent with other studies that also determined that the effect of the canopy on nutrient concentration was greatest during the active growing season (Henderson et al. 1977; Potter et al. 1991).

Similar to the one year of data collected previously by Shaw et al. (1989), most of the annual NO_3^-, NH_4^+ and TDN flux occurred during the growing season (Fig. 4-5). Since N flux in bulk deposition within the region was positively correlated with the amount of precipitation (Shaw et al. 1989), the large summer storms typical of the Boreal Plain result in greater N fluxes than during the rest of the year when precipitation is more limited.

Annual NO_3^-, NH_4^+ and TDN flux rates to the soil under the three stand types (i.e., the sum of N in stemflow and throughfall) were not detectably different, however the total annual flux below any canopy type was consistently lower than the total annual flux in bulk deposition ($P<0.001$ for NO_3^-, NH_4^+ and TDN flux, Table 4-2). The lack of a difference by stand type is uncommon, since many other studies in temperate forests typically find differences by stand type (Henderson et al. 1977; Michalzik et al. 2001; Verry and Timmons 1977). There was a fairly high degree of variation within each treatment type that may prevent detection of differences between the soil/stand types. Also, a meta-analysis of throughfall studies indicates that differences in throughfall IN flux between conifer and deciduous stands were much smaller where the annual N flux in bulk deposition is less than 1000 mg N m^{-2} (De Schrijver et al. 2007). Since the annual IN flux in bulk deposition for 2007 was only 296 mg N m^{-2}, the throughfall N flux in the different stands were likely to be much more similar than many of the previous studies that were conducted in areas of greater N deposition.

Current estimates of annual bulk N deposition for the study area from another study range from 470 to 540 mg N m^{-2} (Table 4-4, Alberta Environment 2008), slightly higher than the flux measured in this study. However, this other estimate was based on kriging between seven air quality monitoring stations across the province and therefore has a large degree of uncertainty (modeled coefficient of variation was greater than 30%) associated with it. Also, kriging does not take into account prevailing winds, which come from the less polluted northwest; this suggests that these estimates for the area may be too high. Therefore, the measured annual N flux in this study was probably more typical of N deposition in this area for an average precipitation year.

Annual bulk N deposition rates measured in Canadian boreal forests range from a low of 230 mg N m^{-2} year^{-1} in northwestern Ontario to approximately 1130 mg N m^{-2} year^{-1} in a study in central Ontario (Table 4-4). There appears to be a gradient from west to east, as higher flux rates were generally recorded in eastern Canada, although certain, more remote areas, such as northwestern Ontario still have low N loading rates (e.g., Morris et al. 2003). This gradient in atmospheric N deposition rates across Canada may be due to differences in climate and proximity to agricultural sources of ammonia and large sources of industrial and vehicle emissions of NO_X. For example, Kochy and Wilson (2001) found that total N deposition rates ranged from 680 to 2210 mg N m^{-2} $year^{-1}$ for various national parks in western Canada, with the greatest N deposition occurring within an aspen parkland forest surrounded by agricultural land and immediately downwind of a large urban and industrial center. In comparison, N deposition rates in the eastern U.S. are approximately 1200 to 1600 mg N m^{-2} $year^{-1}$ (Table 4-4), while rates in parts of Europe can be as high as 6400 mg N m^{-2} $year^{-1}$ (Gundersen 1995).

The N in bulk deposition was dominated by IN fractions, which comprised approximately 72%, while only 28% of the N in bulk deposition was DON. This composition was similar to the 30% suggested in a meta-analysis of North American and European studies (Neff et al. 2002). Organic N meanwhile was a major component of throughfall, comprising between 41% and 54% of N flux in all three stand, similar to what was found in North Carolina, where approximately 50% of N in throughfall consisted of DON (Qualls et al. 1991).

The higher annual DOC flux in throughfall and stemflow were similar to a study in Minnesota where DOC flux was 6 to 12 times greater under a canopy than in the open (Kolka et al. 1999). Unlike the Minnesota study however, the DOC flux in this study increased by only a factor of 2 to 3 (Table 4-3). Summer storms at the study site tend to be short and intense, so the contact time between the rainfall and the foliage was likely short. This would result in lower leaching rates from the canopy than areas that tend to have more prolonged and less intense summer precipitation events. The annual DOC flux rates in bulk deposition (Table 4-3) were at the low end of the range (4 to 16 g m^{-2} $year^{-1}$) for 42 temperate sites across North America and Northern Europe (Kolka et al. 1999; Michalzik et al. 2001). The low annual DOC flux rates were likely related to the sub-humid climate since annual DOC flux rates in bulk deposition were positively correlated with annual precipitation (Michalzik et al. 2001).

4.6 CONCLUSIONS

Bulk deposition, throughfall and stemflow are important sources of labile N for forest vegetation; however no previous research has been conducted on the Boreal Plain to examine how a forest canopy alters the chemistry and flux of N to the soils. For an average precipitation year, the IN FWMC in throughfall was lower than the FWMC in bulk deposition. However there were no detectable differences between the annual IN, TDN or DON flux rates of throughfall and stemflow in different soil/stand types. Instead, all canopies were equally able to remove N from bulk deposition, resulting in less N flux in throughfall and stemflow compared with bulk deposition. The inability to detect differences between the different stand types may be related to low N deposition rates in the region. The flux of DOC however, increased under the three forest canopy types, due to either leaching of organic compounds from the canopy or flushing of dry deposited DOC from the canopy.

The N inputs in bulk deposition were primarily IN, although DON comprised approximately 28% of the TDN. Dissolved ON however, composed a larger proportion (48%) of the throughfall flux. Seasonally, the canopy was much more active in taking up IN during the growing season and these effects were dramatically lower during the winter. In general, the annual N and DOC flux rates were low relative to other studies across North America and Europe but similar to previous studies in the region (Shaw et al. 1989), suggesting that the impact of industrial and agricultural development, both known sources of atmospheric N, remains limited in this portion of the Canadian Boreal Plain.

Since annual N deposition in bulk deposition varies with precipitation (Shaw et al. 1989), this estimate of 410 mg N m^{-2} yr^{-1} is likely valid for years that also have precipitation rates similar to the annual average. Since more than 60% of the years on record have annual precipitation more than 10% away from the mean, it is likely that the bulk deposition and throughfall estimates are appropriate for approximately 40% of years. Therefore, although this study provides an estimate of bulk deposition and throughfall flux for an average year, many more years of data collection are required to understand the range of variation for N flux in bulk deposition and throughfall within this region.

4.7 ACKNOWLEDGEMENTS

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4.9 Tables:

Table 4-1 Site characteristics for dominant stand types in the Willow watershed.

	Stand type		
	Upland deciduous (≤ 20% conifer cover)	**Upland conifer (≥ 80% conifer cover)**	**Wetland conifer (≥ 80% conifer**
Dominant forest vegetation	trembling aspen balsam poplar paper birch	lodgepole pine white spruce balsam fir	black spruce lodgepole pine
Mean % crown closure ± 1 SD	85 ± 10	89 ± 8	74 ± 22
Mean age (yrs)	65	78	65
Mean DBH ± 1 SD (cm)	18.9 ± 8.4	24.7 ± 7.4	11.0 ± 3.8
Dominant soil orders	Luvisolic; Brunisolic	Luvisolic; Brunisolic	Organic

Table 4-2 Mean ± 1 SE annual (November 2006 to October 2007) nitrogen flux above (bulk deposition) and below the forest canopy for three stand types in Willow watershed.

	Mean annual nitrogen flux (mg N m^{-2} yr^{-1})			
	Above canopy	**Upland deciduous**	**Upland conifer**	**Wetland conifer**
	Nitrate			
Bulk deposition	80.3 ± 6.9			
Throughfall		32.8 ± 3.7	45.2 ± 1.7	40.6 ± 3.6
Stemflow		0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0
Total below canopy		32.9 ± 3.7	45.3 ± 1.7	40.7 ± 3.6
	Ammonium			
Bulk deposition	216.0 ± 10.1			
Throughfall		97.4 ± 6.0	94.9 ± 6.2	97.8 ± 9.0
Stemflow		6.0 ± 0.1	1.8 ± 0.2	0.6 ± 0.0
Total below canopy		103.4 ± 6.0	96.7 ± 6.4	98.4 ± 9.0
	Dissolved organic nitrogen			
Bulk deposition	113.5 ± 10.7			
Throughfall		144.5 ± 11.7	96.9 ± 6.4	132.4 ± 13.8
Stemflow		14.2 ± 0.5	2.0 ± 0.3	0.4 ± 0.0
Total below canopy		158.7 ± 11.3	98.9 ± 6.3	132.8 ± 13.8
	Total dissolved nitrogen			
Bulk deposition	409.8 ± 19.9			
Throughfall		274.7 ± 14.0	237.0 ± 7.7	270.8 ± 9.1
Stemflow		20.3 ± 0.5	4.0 ± 0.6	1.1 ± 0.0
Total below canopy		295.0 ± 13.8	240.9 ± 8.1	271.9 ± 9.0

Table 4-3 Mean ± 1 SE annual dissolved organic carbon flux above (bulk deposition) and below the forest canopy for three stand types in Willow watershed.

	Mean annual flux (g C m^{-2} $year^{-1}$)			
	Above canopy	Upland deciduous	Upland conifer	Wetland conifer
Bulk deposition	3.49 ± 0.64			
Throughfall		9.64 ± 1.58	7.80 ± 1.21	7.23 ± 1.38
Stemflow		0.78 ± 0.03	0.37 ± 0.05	0.14 ± 0.01
Total below canopy		10.42 ± 1.58	8.17 ± 1.18	7.38 ± 1.38

Table 4-4 Annual nitrogen inputs (mg N m^{-2} $year^{-1}$) in bulk deposition for regions across North America.

Location	Annual input	Source
New York (Whiteface Mountains)	1600	Friedland et al., 1991
New York (Catskill Mountains)	1360	Lawrence et al., 2000
Eastern Tennessee (Walker Branch)	1240	Kelly and Meagher, 1986
North Carolina (Coweeta)	920	Swank and Waide, 1987
North Carolina (Coastal Plain)	580	Brinson et al., 1980
South Carolina (Coastal Plain)	510	Richter et al., 1983
Indiana	1600	Pryor and Barthelmie, 2005
Northern Quebec	310	Duchesne and Houle, 2006
Eastern Ontario	990	Devito et al., 1989
Central Ontario	1130	Molot and Dillon, 2003
Northwestern Ontario	230	Morris et al., 2003
Central Saskatchewan	270	Huang and Schoenau, 1997
Central Alberta	424	Shaw et al., 1989
Central Alberta	470 to 540	Alberta Environment, 2008
Alberta (Boreal Plain)	410	This study
Oregon (Western Cascades)	220	Stednick, 2008

4.10 Figures:

Figure 4-1 Location of the Swan Hills, Alberta, Canada.

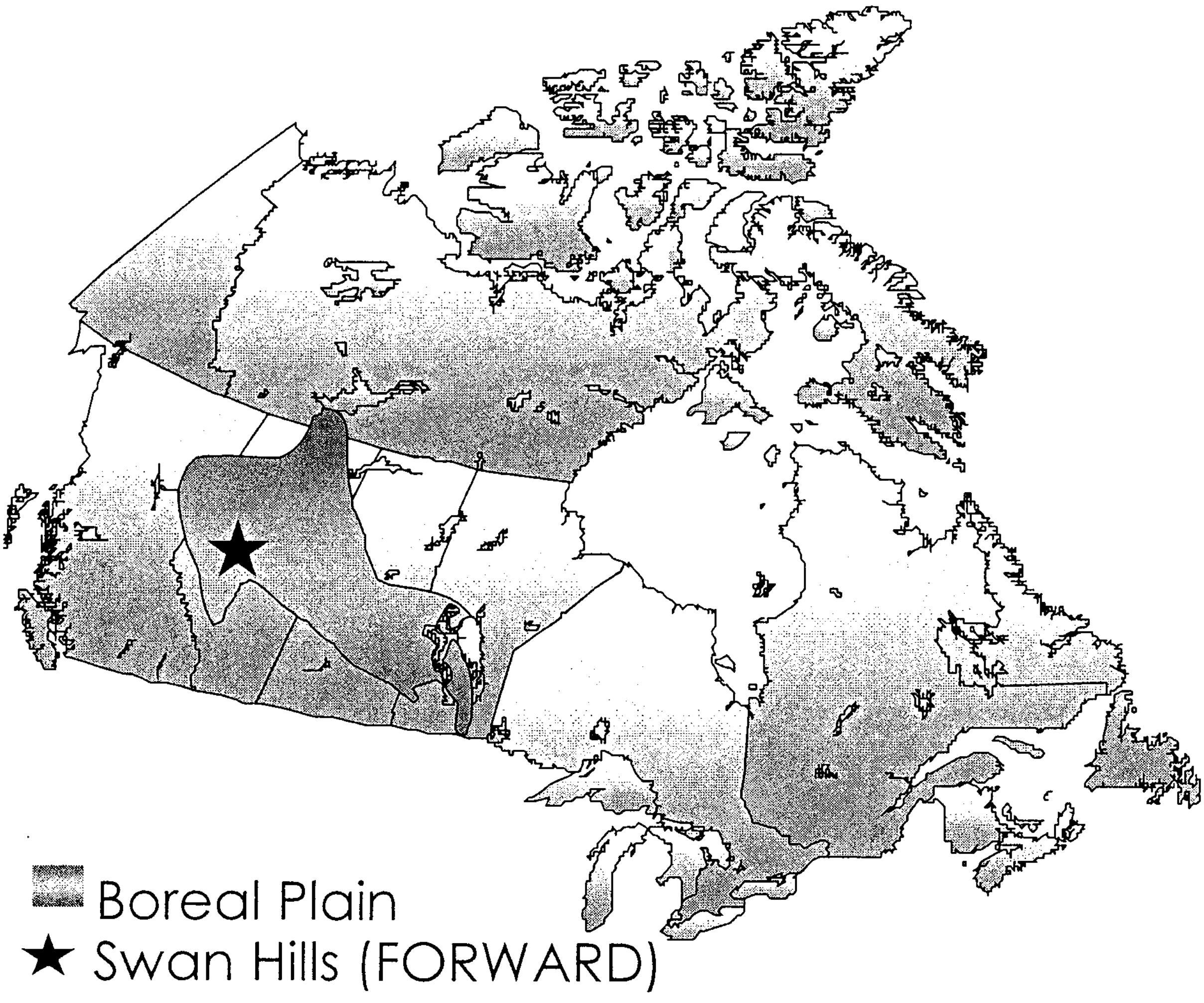


Figure 4-2 Forest cover map for the Willow watershed, with throughfall and stemflow sample plot layout.

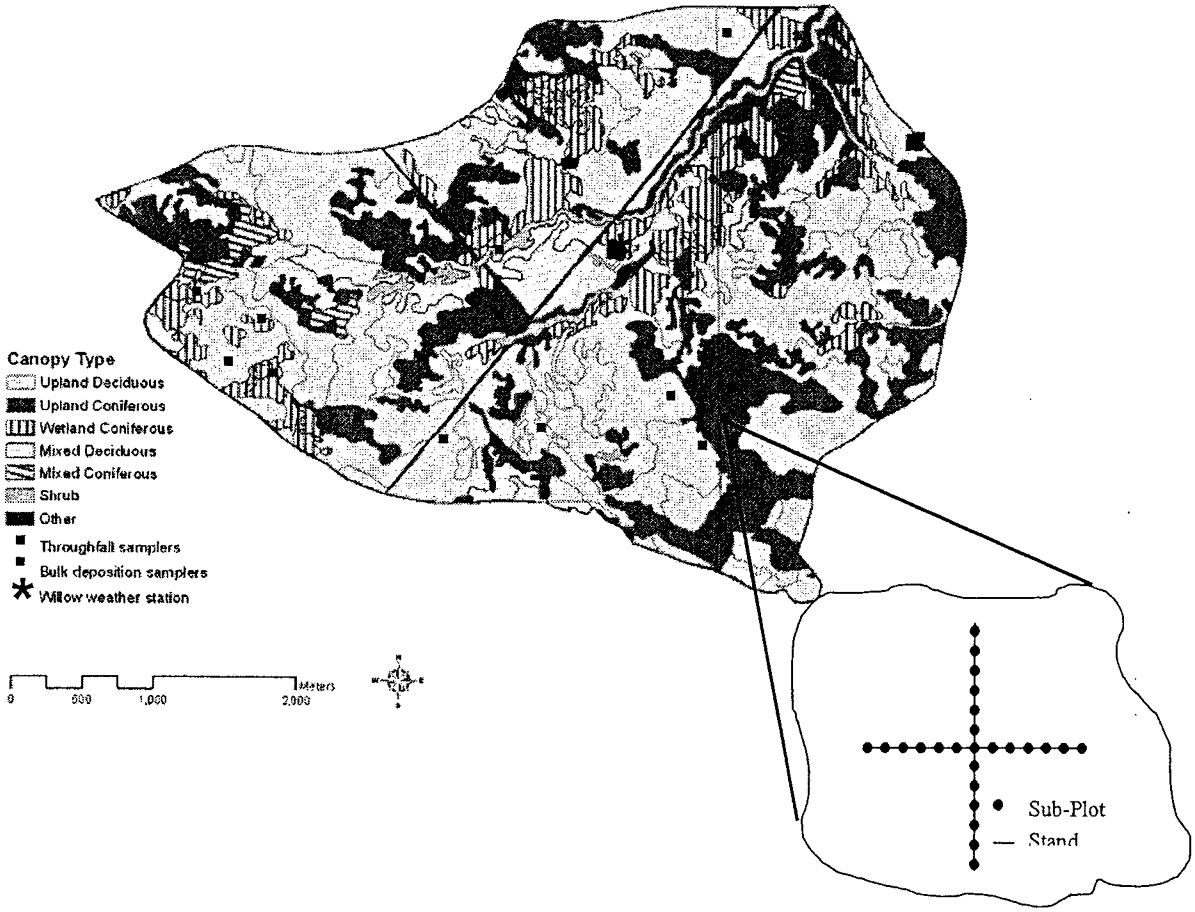


Figure 4-3 Seasonal flow weighted mean nutrient concentrations in bulk deposition and throughfall from three stand types for the Willow watershed. Scale for panels on the right are the same as panels on the left. Different letters above bars refer to differences (P<0.05) between stand types.

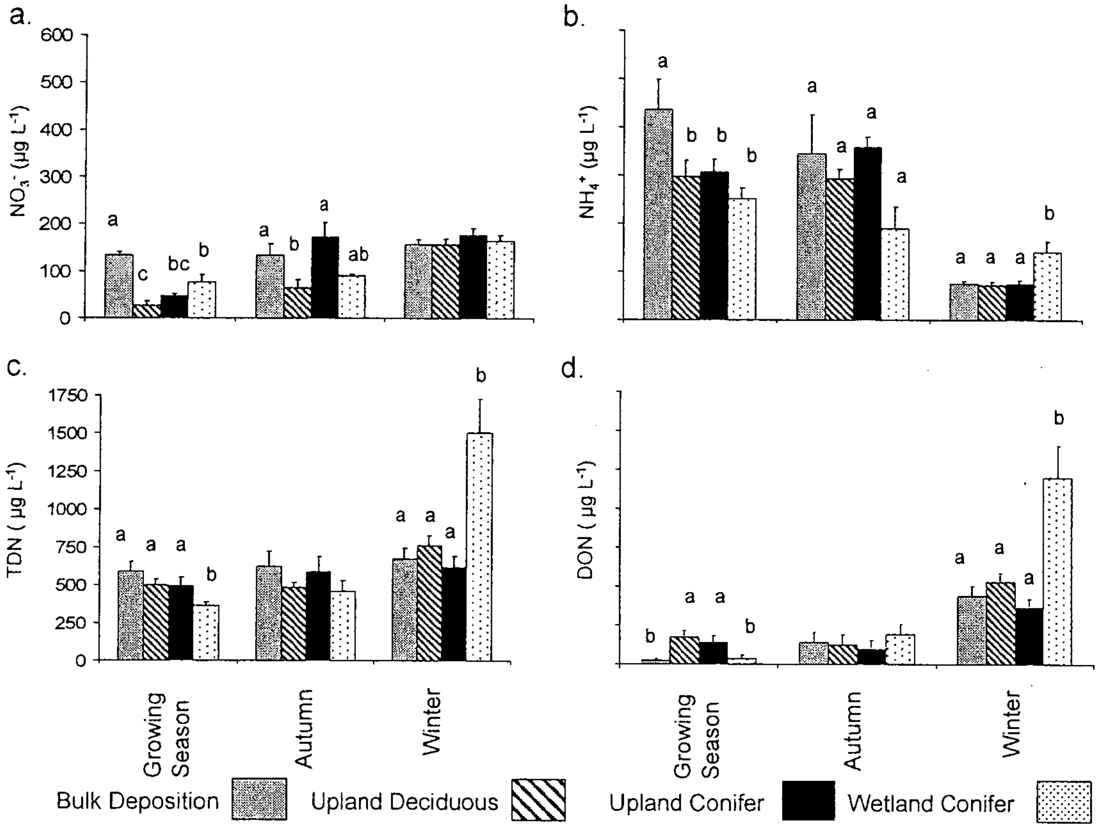


Figure 4-4 Seasonal flow weighted dissolved organic carbon mean concentration in bulk deposition and throughfall from three stand types for the Willow watershed. Different letters above bars refer to differences ($P<0.05$) between stand types.

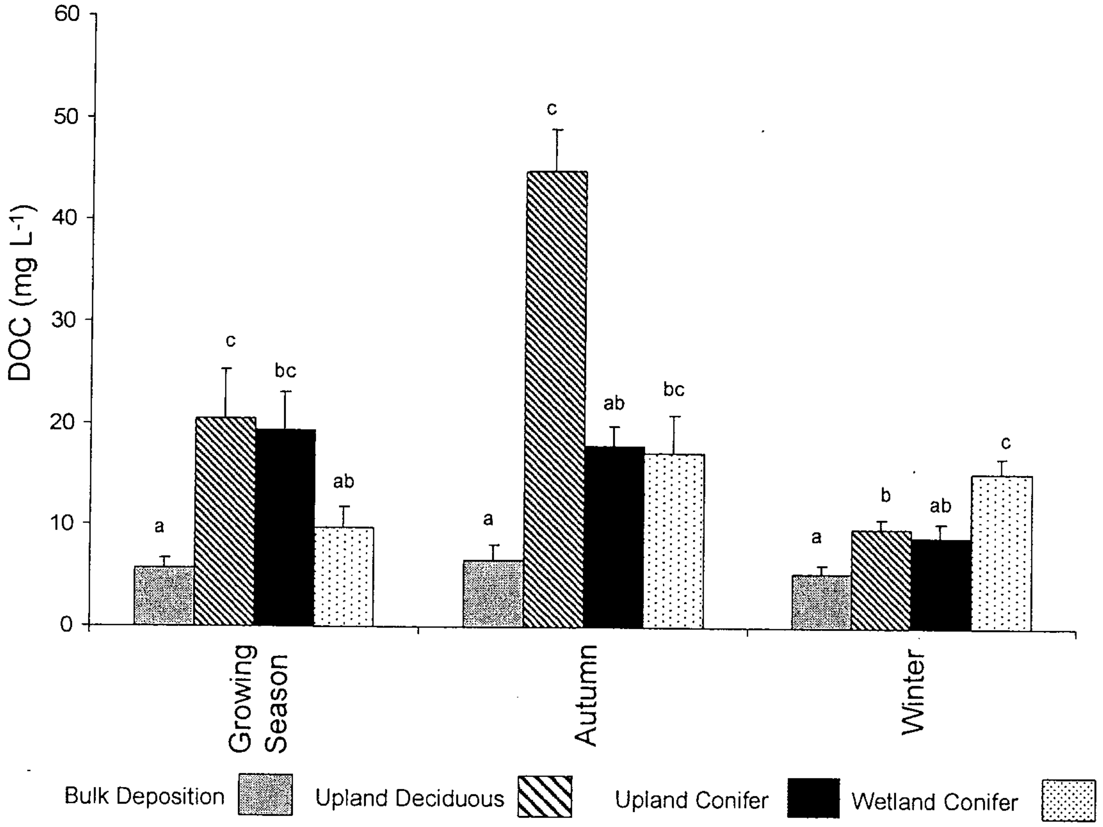


Figure 4-5 Daily nutrient flux rates in bulk deposition and throughfall of three stand types for the Willow watershed. Note change in scale.

Bulk Deposition —— Upland Deciduous —· Upland Conifer ······ Wetland Conifer – –

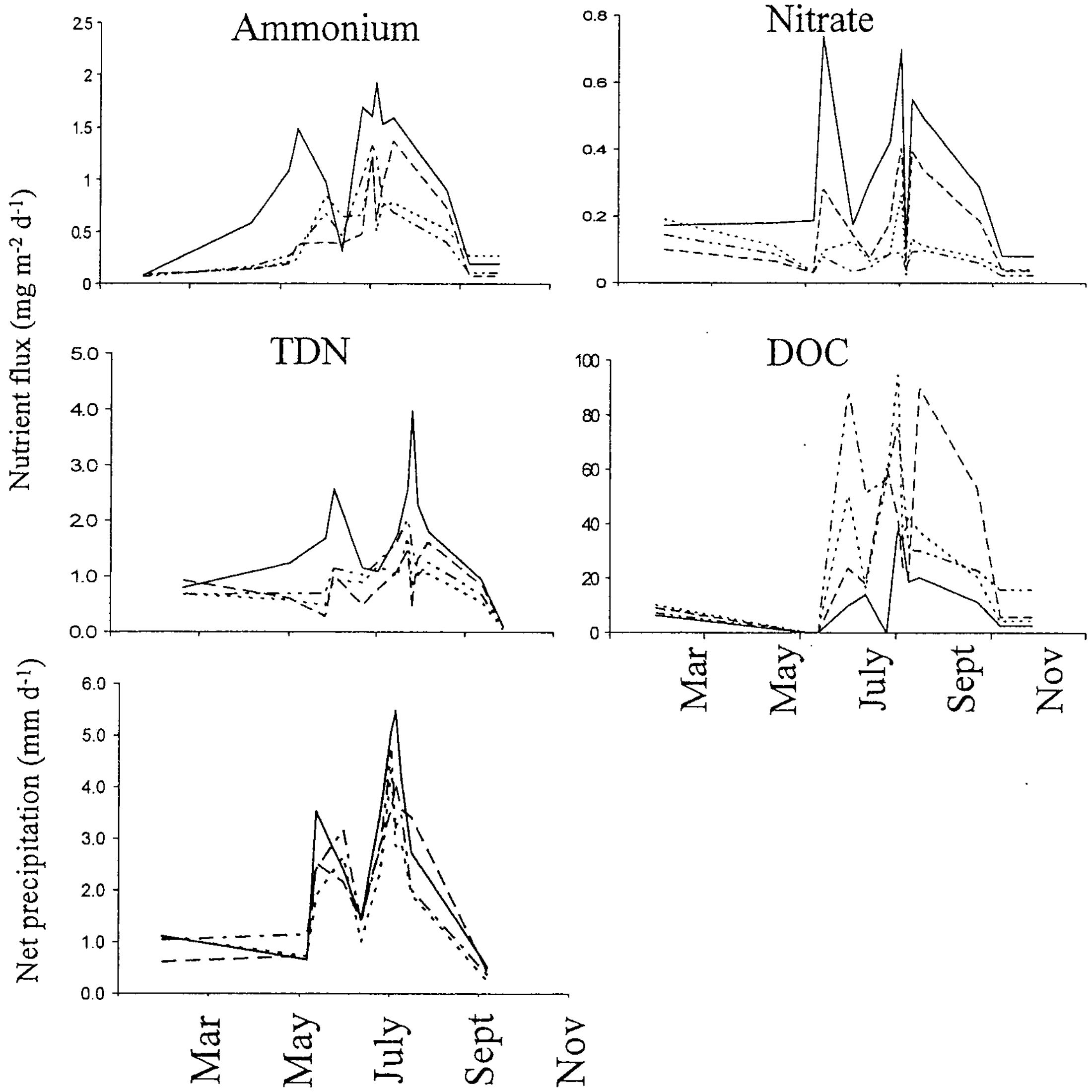
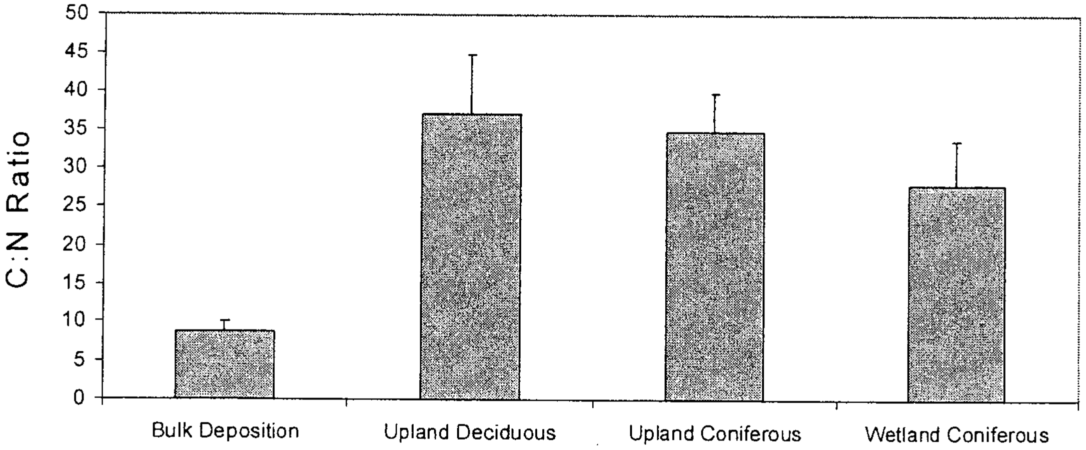


Figure 4-6 C:N mass ratios for bulk deposition and the throughfall of three stand types for the Willow watershed.



Chapter 5

Influence of overstory vegetation and soil type on nitrogen mineralization rates and inorganic nitrogen soil concentrations: Boreal Plain, Canada

5.1 ABSTRACT

Net ammonification and net nitrification rates were measured using two 6-week *in situ* incubations throughout the summer 2008, in three soil/stand types (upland deciduous, upland conifer and wetland conifer) on the Canadian Boreal Plain. The incubations were conducted at two depths: the forest floor (FH) and Ae mineral horizon in the upland, orthic gray luvisol soils; and in the Of and Oh horizons of the wetlands. A preliminary survey of soil porewater chemistry within the same three stand types and soil horizons was also undertaken. Areal net ammonification rates were similar in the two upland stands ($P = 0.24$) and greater in the Ae horizon than the FH layer ($P = 0.042$). However rates were higher in the upland deciduous stands than in the wetland conifer stands ($P = 0.010$). Net nitrification rates were higher in the upland deciduous stands than the upland conifer and wetland conifer stands ($P = 0.050$) with no difference between soil horizons in either uplands or wetlands ($P = 0.9$). Net ammonification rates were higher in early summer than late summer for all stand types ($P = 0.01$), whereas net nitrification rates were not detectably different ($P = 0.6$). The soil porewater survey suggests that NH_4^+ and NO_3^- concentrations were higher in the spring than in the summer for all stand types. Also, NH_4^+ concentrations did not appear to differ by stand type, whereas the NO_3^- concentrations appeared to be lower in the wetlands than either of the upland stands.

Key words –nitrogen mineralization, in situ incubations, boreal forest, upland, wetland, conifer, deciduous

5.2 INTRODUCTION

Primary productivity in the boreal forest is often limited by nitrogen (N) availability (Vitousek and Howarth 1991, McFarland et al. 2002). While inputs from atmospheric deposition and fixation of N_2 are important sources of N to these forests, it is the recycling of N within the watershed via decomposition and mineralization (conversion of organic N (ON) to inorganic N (IN = ammonium [NH_4^+] + nitrate [NO_3^-])) that provides most of the bioavailable N available for plant nutrition. For example, a study from the boreal forests on Isle Royale MI, found that annual gross mineralization rates were at least 11 000 mg m^{-2} compared with annual N deposition rates of only 300 mg m^{-2} for the same time period (Stottlemyer et al. 1999). Simlarly, N_2 fixation rates for boreal forests ranged from 50 to 300 mg N m^{-2} yr^{-1} (Cleveland et al. 1999, Zackrisson et al. 2004). Therefore, the turnover of N in forest soils is critical to forest health and productivity and must be included in the construction of an ecosystem N budget.

Soil N mineralization occurs in three stages. First, exoenzymes secreted by fungi break down insoluble ON to soluble ON. Second, ammonification occurs when the soluble ON is broken down within microbial (fungal and bacterial) cells and NH_4^+ is excreted as a waste product. Note, ammonification only occurs under conditions when carbon is limiting; if carbon is not limiting, then the N is immobilized within microbial cells instead of being excreted as NH_4^+. Third, some of the excreted NH_4^+ is oxidized to NO_3^- through biological (i.e. mediated by nitrifying bacteria) or chemical nitrification.

Nitrogen mineralization can be expressed as either a gross or net rate. Gross N mineralization refers to the sum of NH_4^+ and NO_3^- that is either released into the soil or immobilized by either microbial cells as described above, plant uptake or sorption to soil organic matter (SOM). Biotic immobilization tends to be dominated by soil microorganisms. In one study, microorganisms immobilized more than 10 times the amount of labeled $^{15}NH_4^+$ compared with plant uptake (McFarland et al. 2002). Net N mineralization ignores the immobilized N (equals the gross N mineralization minus immobilized N).

Many different factors, including soil moisture and temperature, pH and litter quality, influence N mineralization rates. Generally, gross N mineralization rates increase with temperature (Updegraff et al. 1995, Rustad et al. 2001, Gilliam et al. 2005), leading to increased N mineralization rates during the summer for boreal forests (Van Cleve et al. 1993), as well as higher N mineralization rates in tropical than boreal or temperate forests (Aerts 1997). The moisture content of soils was also positively correlated with gross mineralization rates (Stottlemyer and Toczydlowski 1999), although saturated conditions can lead to anaerobic conditions which can decrease N mineralization rates (Bridgham et al. 1998). Although soil pH was not found to influence ammonification rates, pH was determined to strongly affect nitrification rates (Dancer et al. 1973). An experiment in Quebec found that increasing soil pH stimulated net nitrification while decreasing the pH depresses net nitrification, with no net nitrification below pH 4.5 (Ste-Marie and Paré 1999).

The impact of substrate quality (i.e. high quality litter generally defined as having higher concentrations of base cations, less lignin and a lower C:N ratio) on N mineralization rates is still much debated. Some studies suggest that decomposition and N leaching are positively related to initial litter quality (Fogel and Cromack 1977, Berg 1986), while other studies suggest litter quality influences litter decomposition only during the early stages of decomposition (Melillo et al. 1989, Giardina et al. 2001). Still other studies suggest that litter with high N content (low C:N ratio) may be mineralized rapidly at first, however as mineralization proceeds, the C:N ratio increases because the N left tends to be tied up in more recalcitrant forms (e.g., lignin), which can retard decomposition rates (Fog 1988, Berg and Matzner 1997). Another aspect of litter quality is the concentration of base cations and manganese (Mn), which are essential for lignin degradation. Both base cation and Mn concentrations were positively correlated with litter decomposition rates (Berg et al. 2006), and both were greater in deciduous than conifer litter (Van Miegroet et al. 1990, Coté et al. 2000). This pattern suggests that deciduous litter, because of the lower C:N ratio and higher base cation and Mn concentrations, decomposes quicker than conifer litter.

Many plant species (e.g. ericaceous shrubs) produce litter with high polyphenol concentrations (Wardle et al. 1998; DeLuca et al. 2002). The formation of protein-tannin complexes in litter with high polyphenol concentrations tends to suppress N mineralization and may be a strategy by which the vegetation shifts the dominant N cycling pathway away from production of IN toward production of DON (Yu et al. 2003). Compared with IN, DON is less mobile and less available to soil microorganisms and therefore is less likely to be lost by leaching or denitrification (Northup et al. 1995). This allelopathic inhibition of mineralization can provide a competitive advantage for plants with mycorrhizal symbionts, which are able to take up simple organic N from the soil and forest floor (Northup et al. 1995).

Since net N mineralization rates are the result of gross mineralization minus immobilization, factors that affect N immobilization can dramatically influence net mineralization rates. Soils with a high C:N ratio (e.g. woody debris, forest floor), tend to have high N immobilization rates because, as noted above, microorganisms will not excrete NH_4^+ if C is not limiting. This results in low net mineralization rates (Gilliam et al. 2005). Also, the presence of reduced metals in the soil can reduce NO_3^- to NO_2^-, which can then be adsorbed by SOM (Fitzhugh et al. 2003). This immobilization is positively correlated with concentrations of NO_3^-, reduced metals and SOM, and negatively correlated with pH (Fitzhugh et al. 2003). Immobilization by adsorption to SOM can remove up to 50% of NO_3^- added to soils (Dail et al. 2001). As a result of biotic and abiotic competition for IN, the IN produced by net mineralization is generally insufficient to meet the needs of plants in many temperate and boreal ecosystems (McFarland et al. 2002).

The Boreal Plain comprises much of the boreal forest in western Canada, covering approximately 60% of the province of Alberta. Unlike many other regions in the world, the Boreal Plain has not received high inputs of N from industrial or agricultural sources and likely represents near pristine conditions. However, oil production from oil sands in Alberta is expected to increase 10-fold by 2015 (Severson-Baker et al., 2008), which has led to a modeled 5-fold increase in NO_x emissions, from approximately 60 tonnes day^{-1} in 1990 to a projected rate of 300 tonnes day^{-1} by 2012 (Golder Associates, 2002). Also there has been a 7-fold increase in coalbed methane extraction within the province of Alberta from 2003 to 2006 (Government of Alberta, 2009).

The cumulative effects of this industrial development will likely affect the supply of N to forests on the Boreal Plain, making it essential to establish a baseline survey of N cycling. There is substantial literature examining N mineralization in northern forests (e.g. van Cleve et al. 1993, Persson et al. 1995, Rustad et al. 2001, Hackl et al. 2004, Westbrook et al. 2004), however, very few of these studies examine N mineralization on the Boreal Plain. Further, the limited number of N mineralization studies on the Boreal Plain (e.g., Carmosini et al. 2003, Tan and Chang 2008) do not examine the effects of soil and stand type on N mineralization in undisturbed forest stands as a component of a more comprehensive understanding of N dynamics.

The objective was to examine N cycling within soils of a Boreal Plain forest. Since atmospheric inputs (i.e. bulk deposition, throughfall and stemflow) have already been measured, the annual N flux to the watershed was already known. However knowledge of the amount of N cycled within forest soils was also needed to construct a watershed N budget. In this chapter net mineralization rates were examined within three forest soil/stand types (upland conifer, upland deciduous and wetland conifer) and shallow and deep soil horizons. In the upland stands, net mineralization rates were determined for both the forest floor (FH layer) and the top-most mineral horizon (Ae horizon), while in the wetlands, the Of (litter/fibric layer corresponding to top 10 cm of peat) and the Oh (humified peat at 11 to 20 cm depth) horizons were sampled. It was expected that upland sites, particularly the FH layer, will have higher net N mineralization rates than wetlands because upland soils are typically warmer than wetland soils. Further, because of the higher quality litter, upland deciduous stands were expected to have greater net N mineralization rates than upland conifer stands (Aerts 1997, Coté et al. 2000). Seasonal patterns in net N mineralization rates were also expected, with greater net N mineralization rates apparent early in the summer. Finally, higher net N mineralization rates in the upland deciduous stands should lead to greater IN concentrations in the soil porewater than either the upland conifer or wetland conifer stands.

5.3 MATERIALS AND METHODS

5.3.1 Study site

The study site was a small (15.6 km^2) watershed in the FORWARD study area within the Virginia Hills, located in west-central Alberta. Tree cover was composed of primarily aspen

(*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.), lodgepole pine (*Pinus contorta* Dougl. Ex Loud. var *latifolia*) and white spruce (*Picea glauca* (Moench) Voss) in upland sites and black spruce (*P. mariana* (Mill.) BSP) in lowland sites. The dominant stand types in the study watershed were upland deciduous, upland conifer and wetland conifer stands (Table 5-1).

Upland soils have developed from glacial till parent material, and are mainly orthic grey luvisols, although other luvisols, brunisols and gleysols were also common. Wetlands are common in low-lying areas, with the majority of lowlands classified as poor, treed fens (Couling et al. 2007). Peat depths in these wetlands range from 20 cm to more than 200 cm. The upland soils used in the study were all orthic gray luvisols of the Hubalta series. These soils were moderately calcareous at depth, weakly saline, moderately to slowly permeable and were derived from medium-textured Edson till (Agriculture and Agri-Food Canada 2006), which is 2 to 5 m thick and overlies weathered bedrock of the Wapiti group (Knapik and Lindsey 1983). Soils tend to be moderately acidic in upper horizons, with high amounts of silt (Table 5-2).

5.3.2 Net N mineralization rates.

The net N mineralization rates for the three dominant stand types (Table 5-1) were measured using two 6-week *in situ* soil incubations (20 June to 1 August 2008 and 8 August to 22 September 2008). Three replicates of each stand type were selected randomly from the study watershed. Soils typically are fairly heterogeneous in terms of N concentration. To minimize variation within treatment types, soil pits were dug at each upland sample location to ensure that all upland samples were orthic gray luvisols. In another study, Prepas et al. (unpublished data) found that a sample size of 10 provided a standard error that was between 20 and 40% of the mean for NO_3^- analysis and around 30% of the mean for NH_4^+. To try to maintain a similar standard error during both incubation periods, three incubation tubes were installed in two different soil horizons (FH and Ae horizon in upland stands and the Of and Oh horizon in the wetlands) for each of three sample points within each randomly selected stand for a total of 27 subsamples per stand. The three subsamples from each sample point within each stand were then combined to create one composite sample for each soil horizon.

A variation of the incubated soil core and ion exchange resin bag (ISC/IERB) method proposed by DiStefano and Gholz (1986) was employed. Briefly, 5.1 cm ID PVC pipes were used to isolate the soil cores, with the cutting edges bevelled on the outside to limit compaction (Fig. 5-1). Soil cores were removed, and the soil horizon of interest was isolated. To capture IN that might leach out of the PVC pipe, a resin bag containing 7.5 g of anion and 7.5 g of cation exchange resin beads (JT Baker cat. number 4601-01 and 1927-01 respectively) was placed below the horizon. To prevent the capillary transfer of IN from lower soil horizons, a layer of sand was placed below the resin bag (Brye et al. 2002).

The incubation tubes were capped with a nylon mesh to exclude particulates, but still allow throughfall to enter the tubes, which allowed for the soil moisture within the cores to fluctuate parallel to external soils. There was some concern regarding additional N inputs from the throughfall, however the amount of N contained in throughfall (see chapter 4) was less than 0.001% of estimated internal N cycling rates (Carmosini et al. 2003) and was considered negligible. Although the buried bag technique, which involves incubating soil cores within a polyethylene bag (Eno 1960), and ISC/IERB method have been found to give similar results (Zou et al. 1992, Burns and Murdoch 2005) the ISC/IERB method is generally considered to be an improvement over the buried bag technique, because disturbance to the soil profile, inherent in the buried bag technique, tends to increase mineralization and nitrification rates (Raison et al.

1987, Bélanger et al. 2008). Also, the ISC/IERB method is better at maintaining site-specific soil temperature and moisture fluctuations (Knoepp and Swank 1995).

Reference soil cores immediately adjacent to the incubation sites were removed and processed immediately, whereas the *in situ* incubations were replaced and left for 6 weeks. Soil cores were air dried, crushed, ground and sent to the University of Saskatchewan for analysis. The IN was extracted using 2M KCl (Brye et al. 2002) and NO_3^- and NH_4^+ concentrations were measured on a Technicon Autoanalyzer (Methods 158-71 and 154-71, respectively). Lower analytical detection limits for both NO_3^- and NH_4^+ are 1 $\mu g\ L^{-1}$. Total N and total C were determined by dry combustion at 1150 °C, using a CNS-2000 analyzer. Inorganic N from the resin beads was also extracted as above, filtered through 0.45 μm pore size Millipore filter, preserved with sulfuric acid and analyzed for NO_3^- and NH_4^+ concentrations on a Technicon Autoanalyzer as above. Soil pH was measured using a Fisher Scientific Accumet 1001 pH meter on a slurry solution made by adding distilled deionized water to air dried soil samples.

Automated soil temperature and moisture stations were established in three wetland conifer, three upland conifer and three upland deciduous stands. These stations measured soil temperature at 10 and 30 cm depth and moisture content at 10 and 50 cm depth every hour throughout the incubation periods. However, within the wetland conifer stands, the automated samplers were installed on top of hummocks, whereas the incubations took place on the sides of the hummocks. As a result, the measured soil temperature at 30 cm was likely more representative of the temperature of the *in situ* incubations within the wetland conifer stands. The soil moisture and temperature for incubations within the upland deciduous and upland conifer stands however were more closely estimated using the 10 cm depth. The soil moisture conditions for the incubations in the wetland conifer stands were between the conditions at 50 cm and 10 cm depth, however there was likely a step-wise progression between the two depths, making it very difficult to estimate the true moisture conditions of the wetland *in situ* incubations.

5.3.3 Soil porewater.

As with soils, porewater samples were collected from the FH and Ae horizons within the upland stands, and from the Of and Oh layers in the wetlands. Soil porewater samples were collected using zero-tension lysimeters installed the previous summer and allowed to acclimate to the soils for at least 12 months. The lysimeters were installed along a single hillslope transect adjacent to a stream within each of the stand types. Transects were established perpendicular to the streams and lysimeters were installed directly adjacent to the stream (riparian samples), mid-way up the slope (mid-slope) and at the top of the slope (upper slope). Within the wetlands, no slope was discernable, therefore samples were collected adjacent to the stream (riparian), and at distances of 10 and 20 m from the stream channel (considered mid- and upper slope respectively). Since the water table was generally too high for lysimeter installation within wetlands and along stream banks, groundwater wells were used to sample the soil porewater. Lysimeters and wells were checked for samples biweekly from May 2008 through September 2008.

The lysimeters were composed of 20.1 cm ID polyethylene funnels filled with 0.5 mm acid-washed sand and buried just beneath the soil horizon of interest. The funnels drained through polyvinyl tubing into a 5.1 cm ID ABS (Acrylonitrile-Butadiene-Styrene) tube installed vertically, with the top meter sticking out of the ground (MacDonald et al. 2007). Wells were composed of PVC pipes with holes drilled at particular depths that were fitted with geotextile material. Samples were collected by emptying the lysimeters and wells using a hand vacuum pump and a clean filter flask. Inorganic N from the groundwater samples was filtered through

0.45 μm pore size Millipore filter, preserved with sulfuric acid and analyzed for NO_3^- and NH_4^+ concentrations on a Technicon Autoanalyzer as above. The minimum detection limits were 1 and 2 μg N L^{-1} for NO_3^- and NH_4^+ respectively.

5.3.4 Statistical analysis.

Individual incubations were tested using repeated measures analysis of variance (ANOVA) to test for differences in mineralization rates between stand types (upland deciduous, upland conifer and wetland conifer), soil horizons (FH and Ae for upland stands; Of and Oh for wetland stands), and incubation period (early versus late summer). Mineralization rates from both incubation periods were summed for each site to compare total mineralization for the entire growing season among the stand types using one-way ANOVA. To compare areal mineralization rates between upland and wetland stands, the FH and Ae horizons (combined depth was approximately 10 cm) from the upland stands were summed together and compared with the Of horizon (depth was approximately 10 cm) from wetland stands using a one-way ANOVA. Weekly mean soil temperature and moisture conditions for each stand type were compared using repeated measures ANOVA. Because of the limited sample size and spatial heterogeneity inherent in forest soils, $\alpha = 0.10$ was used to determine significance.

The NO_3^- and NH_4^+ concentrations within the soil porewater were also compared between stand types, soil horizons and slope location. Since many lysimeters and wells were dry when sampled, resulting in missing samples and a limited data set, no ANOVA tests could be used. Also, since the distributions were skewed towards higher concentrations, medians rather than means were used to compare the IN porewater concentrations between stand types.

5.4 RESULTS

The soils in the upland stands were all orthic grey luvisols and had similar properties in terms of texture and bulk density (Table 5-2). Not surprisingly, large differences in the bulk density and C:N ratios existed for the two upland soil horizons, with the Ae horizon having greater bulk density ($P < 0.001$) and a lower C:N mass ratio ($P < 0.001$) than the overlying FH horizon (Table 5-2). The wetland conifer soils had much higher C:N mass ratios than upland stands for both horizons ($P < 0.001$), and similar to the upland stands, the C:N mass ratio was lower in the deeper horizon ($P = 0.082$). The pH was not detectably different by stand type ($P = 0.11$) or soil horizon ($P = 0.70$), however the interaction of stand type and soil horizon was significant ($P < 0.001$). In the upland stands, the soil pH was greater in the top (FH layer) horizon than in the deeper (Ae) horizon, while in the wetland stands, the soil pH was greater at depth (Table 5-2).

The soil temperature increased through the early summer incubation, and then decreased during the second incubation (Fig. 5-2), however there was no detectable difference between the stand types ($P = 0.21$ and 0.23 for the early and late summer incubations respectively) for either of the incubation periods. Differences in soil moisture between the stand types were marginal at both 10 and 50 cm depth (Figs. 18 and 19, $P = 0.12$ and 0.11 respectively). The moisture content at 10 cm depth however, suggests that wetland conifer stands were drier than the upland deciduous and upland conifer stands (Fig. 5-3), although this may be due to the installment of the sampling locations on top of hummocks. At 50 cm depth however, the wetland conifer stands had the highest soil moisture content, while the upland deciduous had the lowest soil moisture content (Fig. 5-4).

The bulk density of the Ae horizon was much greater than the organic horizons.As a result, the areal net ammonification and nitrification rates (mg N m^{-2} day^{-1}) showed different patterns than those based on soil dry mass alone. For both incubation periods, although areal net ammonification rates were similar in the two upland stands (*P* = 0.24), rates were greater in the Ae horizon than in the FH horizon (Fig. 5-5a,b, *P* = 0.042). Conversely, mean areal net nitrification rates for both incubations were greater in the upland deciduous than in the upland conifer stands (*P* = 0.050), although there was no difference between the soil horizons (Fig. 5-5c,d). Mean areal net ammonification rates for the top 10 cm of soil (combination of FH and Ae horizon for the upland stands and just the Of horizon in the wetlands) were highest in the upland deciduous stands and lowest in the wetland conifer stand (*P* = 0.010) (Fig. 5-6). There were no detectable differences in mean areal net nitrification rates by stand type (*P* = 0.14), however similar to net ammonification, the highest net nitrification rates were found in the upland deciduous stands (Fig. 5-7).

The net areal ammonification rates were higher during the early summer than late summer incubations (*P* = 0.006, Fig. 5-6). However, there was no detectable difference in net areal nitrification by season for any of the three stand types (*P* = 0.47, Fig. 5-7). Throughout the entire summer (i.e., the sum of both incubation periods), the net ammonification rates tended to be highest in the upland deciduous stands and lowest in the wetland conifer stands (*P* = 0.10, Table 5-3), with the upland conifer stand not detectably different from either. There was however, no detectable difference in net nitrification for the entire summer (*P* = 0.12), although there was a tendency for greater nitrification rates in the upland deciduous stands (Table 5-3).

The soil porewater study showed some interesting patterns for both NH_4^+ and NO_3^- concentrations. In general soil porewater in upland deciduous stands had similar median NO_3^- concentrations to the upland conifer stands, and both had higher concentrations than the wetland conifer stands. Median NH_4^+ concentrations were similar amongst all three stand types. The median NH_4^+ and NO_3^- concentrations in soil porewater samples collected in May (early spring) were higher than samples collected throughout the rest of the summer (1 June to 31 August) in all stand types (Fig. 5-8). In fact, NO_3^- concentrations in the wetlands throughout the summer were consistently below the minimum detection limit. There did not appear to be any discernable pattern in IN concentrations from the top of the hillslope to the stream bank (data not shown).

5.5 DISCUSSION

The relatively high net areal ammonification and nitrification rates (per unit soil mass) in the wetland conifer stands (Figs. 20 and 21) were quite surprising since the stands were all peatlands and other studies have found that mineralization rates tend to be lower in peatlands than uplands (Devito et al. 1999, Grant 2004). The low aeration status, pH and cooler temperatures common in peatlands tend to decrease mineralization rates (Van Cleve et al. 1981, 1990, Reich et al. 1997, Bridgham et al. 1998, Devito et al. 1999). However the peatland soils in this study were warm and dry (Figs. 17, 18) for most of the summer. Since warm, dry conditions in peat have been positively correlated with increased N mineralization rates (Updegraff et al. 1995, Rustad et al. 2001, Venterink et al. 2002), mineralization rates within the peatlands were likely stimulated during the two incubation periods.

Areal net ammonification rates were 3 to 6 times higher during the early summer incubation than during the late summer incubation for the upland deciduous and wetland conifer stands (Fig. 5-6). The lower ammonification rates during late summer may be linked to decreasing air temperatures, which was 2 °C cooler during the second incubation period. However, mean soil temperature at 10 cm for the upland stands did not change between the two periods. The minimum soil temperature however, decreased by 0.5 °C to 4 °C on average, which may be more important to net mineralization rates than mean temperatures. Also, the soil temperature was highest at the end of the first incubation and lowest at the end of the second incubation (Fig. 5-2), and net mineralization rates may be related to soil conditions immediately prior to removal of the soil cores for analysis. Interestingly, net areal nitrification rates were not detectably lower during the late summer incubation (Fig. 5-7).

Areal estimates of net mineralization rates were comparable to other studies in boreal and temperate forests, ranging from 14 to 38 mg N m^{-2} day^{-1} (Reich et al. 1997, Devito et al. 1999, Carmosini et al. 2003). The mineralization patterns within uplands were also consistent with other studies that found higher net mineralization rates in deciduous than in conifer stands in northwestern Quebec (Coté et al. 2000) and the B.C. interior (Thomas and Prescott 2000). Finally, since current N saturation theory predicts low net nitrification rates in baseline (stage 0) forested ecosystems (Aber et al. 1989), the low net areal nitrification rates suggest that the study area was still N limited and not heavily impacted by anthropogenic N.

Increased base cation concentrations in deciduous litter (Ste-Marie and Paré 1999) tend to increase nutrient cycling rates in the forest floor of deciduous stands relative to conifer stands. Also, the Mn concentration, which is a necessary component of the lignin-degrading enzyme Mn-peroxidase, is positively correlated with net mineralization rates (Berg et al. 2006) and tends to be highest in certain deciduous litter (Coté et al. 2000). Finally, relative to deciduous stands, higher C:N ratios in the soils and forest floor of the conifer stands may lead to increased immobilization, resulting in lower net areal mineralization rates within the conifer stands (Thomas and Prescott 2000).

Unlike other studies, the mean net areal ammonification rates in the upland stands tended to be higher in the Ae horizon than in the FH horizon, while net areal nitrification rates tended to be similar between the different soil horizons (Fig. 5-5). Since the C:N ratio was higher in the

FH than Ae horizon, it is likely that NH_4^+ was rapidly immobilized by heterotrophic microorganisms within the FH horizon. It is surprising however that net nitrification rates do not follow a similar pattern. If substrate (NH_4^+) availability was the limiting factor for nitrification, then net nitrification rates should also be higher in the Ae horizon. Since these rates are similar between the two horizons, there is likely another factor controlling net nitrification rates in these upland soils. For example, nitrifying bacteria tend to be weak competitors for NH_4^+, while ericaceous shrubs and conifer trees both release chemical compounds that inhibit nitrification (Robertson 1982, White 1994). The allelopathic properties of the shrubs and trees may limit populations of nitrifying bacteria in the FH and Ae horizons, which along with the inability to compete effectively for NH_4^+ may explain the limited, but consistent, production of NO_3^- in both soil horizons.

Contrary to net areal ammonification rates, which did not vary by stand type, net areal nitrification rates were approximately 500% greater in upland deciduous stands than in upland conifer stands (Figs. 23 and 24). The lower net nitrification rates in conifer stands may be related to different communities of microorganisms. For example, nitrification in a jack pine stand in northern Quebec could only be stimulated by inoculation of the site with forest floor material from an aspen stand, suggesting that nitrifying microorganisms were absent from the pine stand (Ste-Marie and Paré 1999). Also, many conifer species prefer NH_4^+ rather than NO_3^- as the N source (Bigg and Daniel 1978) and take up NH_4^+ very rapidly. As a result, there is rapid immobilization of NH_4^+, which limits the supply of a substrate for nitrification. Also, mature conifer forests in many boreal forests have an increased presence of ericaceous shrubs, which has been positively correlated with polyphenol concentrations. Since polyphenols are known to impede mineralization and especially nitrification (Yu et al. 2003), the presence of these shrubs could lead to decreased nitrification rates within the conifer stands. Finally, conifer litter tends to be high in monoterpenes, which promote growth of heterotrophic microorganisms and the rapid immobilization of N (White 1994), which would also decrease net nitrification rates.

The soil porewater study also suggests a seasonal pattern, with much higher IN concentrations in the spring than the summer. This was likely related to several factors. Firstly, the warmer soils during the summer promote immobilization of IN in microbial and plant biomass. Secondly, freeze-thaw events in the spring can cause lysis of fine roots and microorganisms (Morley et al. 1983) releasing large amounts simple ON molecules, which may be rapidly mineralized, causing a flush of IN to the soils (DeLuca et al. 1992, Schimel and Clein 1996). Thirdly, N mineralization may occur in the snowpack throughout the winter (Brooks and Williams 1999) while immobilization of NO_3^- from the melting snowpack is generally insignificant (Campbell et al. 2007). Finally, all the IN input over the winter (see chapter 4) will be released during the snowmelt which, because the plants are not yet active, may result in leaching of IN through the soil profile.

The soil porewater appear to be inconsistent with the net mineralization results. During the summer months, even though the net areal ammonification rates were higher in the upland deciduous stands, the median NH_4^+ concentrations in the soil porewater tended to be higher in the wetland conifer stands than in either of the upland stand types. Since the incubations excluded plant uptake, the greater nutrient demand by the upland vegetation necessary to maintain the increased net primary productivity likely depleted NH_4^+ more in the upland than in the wetland stands. Another inconsistency with the soil incubations was that the median NO_3^- concentration in the soil porewater of the upland conifer stands did not appear to be different from concentrations in the upland deciduous stands. It has been found that many conifer species have a low capacity for absorbing NO_3^-, and can actually show decreased growth due to an N-metabolism disorder when NO_3^- is the dominant N source (Xiaoyang and Jinfeng 2007). Therefore it is possible that much of the NO_3^- produced in the conifer stands was lost due to leaching, whereas much of the NO_3^- produced from nitrification in deciduous stands was taken up by vegetation.

The limited amount of NO_3^- in the wetland conifer stands was consistent with the incubation study which also found low nitrification rates in the wetland soils. However, even low nitrification rates should produce NO_3^- concentrations above the minimum detection limits. The complete lack of NO_3^- in the summer could be related to the timing of the porewater sampling. Unlike the upland stands, the only time during the summer that samples could be collected in the wetland conifer stands was when the water table was within 20 cm of the peat surface. The high water table results in anaerobic conditions, which would reduce NO_3^- to NH_4^+. Therefore the lack of NO_3^- in the wetland porewater may be due to reducing conditions that precede the movement of IN through the wetland soil profile rather than a lack of NO_3^- production within the peat.

5.6 CONCLUSION

As expected, the soil and stand type had a detectable effect on net ammonification rates in this Boreal Plain watershed with the greatest net ammonification rates in the upland deciduous stands and the lowest rates in the wetland conifer stands. A similar tendency was noted in net areal nitrification rates, however this was not significant. The high net mineralization rates in wetlands were probably related to a warm, dry summer that enhanced N mineralization in the wetland soils. Net areal N mineralization rates were higher during the early summer than late summer because of cooler mean and minimum temperatures in late summer. Similar NH_4^+ concentrations in soil porewater were consistent with the similar net ammonification rates between the three stand types, while increased net nitrification rates in upland deciduous stands did not appear to lead to increased NO_3^- concentrations in the porewater of those stands. Both the NH_4^+ and NO_3^- concentrations appeared to be elevated during spring and lower in summer.

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5.8 Tables:

Table 5-1 Site characteristics for dominant stand types in the Willow watershed.

	Stand type		
	Upland deciduous (≤ 20% conifer cover)	Upland conifer (≥ 80% conifer cover)	Wetland conifer (≥ 80% conifer cover)
Dominant forest vegetation	trembling aspen balsam poplar paper birch	lodgepole pine white spruce balsam fir	black spruce lodgepole pine
Mean % crown closure ± 1 SD	85 ± 10	89 ± 8	74 ± 22
Mean age (yrs)	65	78	65
Mean DBH ± 1 SD (cm)	18.9 ± 8.4	24.7 ± 7.4	11.0 ± 3.8
Dominant soil orders	Luvisolic; Brunisolic	Luvisolic; Brunisolic	Organic

Table 5-2 Selected soil properties for *in situ* incubation sites in upland deciduous, upland conifer and wetland conifer stands.

	Upland Deciduous		Upland Conifer		Wetland Conifer	
	FH	Ae	FH	Ae	Of	Oh
C:N ratio	23.8	15.3	28.1	15.6	41.7	34.5
Bulk Density (g cm^{-3})	0.21	1.35	0.21	1.35	0.13	0.25
pH	5.0	4.5	4.8	4.6	4.6	5.1
Texture		Silt Loam		Silt Loam		

Table 5-3 Mean (± 1 Standard Error) net ammonification and nitrification (mg N m^{-2}) for 20 June to 22 September 2008.

	Upland Deciduous	Upland Conifer	Wetland Conifer
Net ammonification	$1526^{a} \pm 417$	$914^{ab} \pm 420$	$482^{b} \pm 155$
Net nitrification	$81.7^{a} \pm 29.0$	$11.6^{b} \pm 21.3$	$33.0^{b} \pm 12.4$

Note: the letters (a, b and ab) signify differences in ammonification or nitrification rates between stands ($P < 0.10$)

5.9 Figures:

Figure 5-1 Schematic of *in situ* soil incubation tube (Modified from Brye et al. 2002).

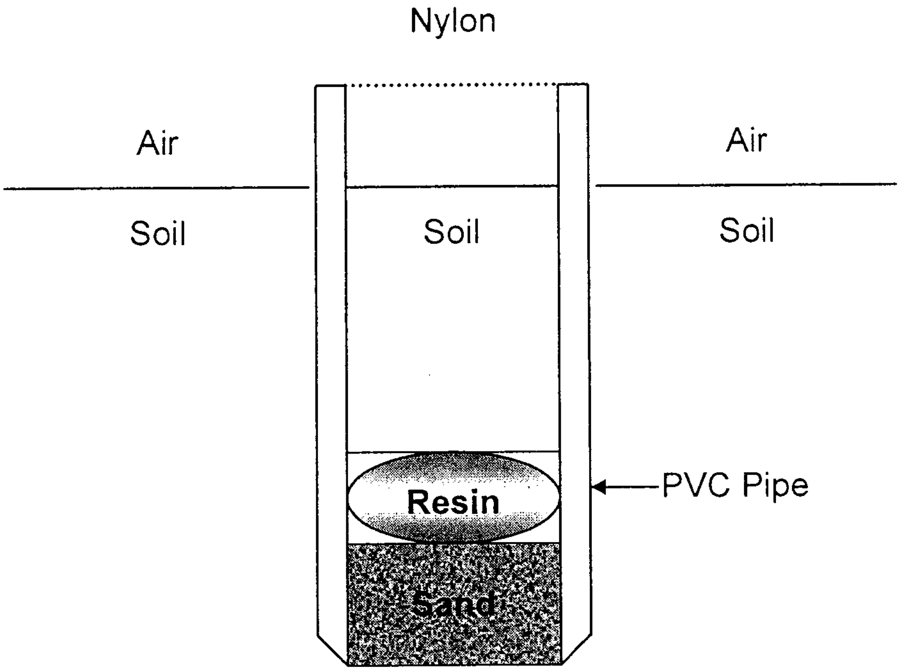
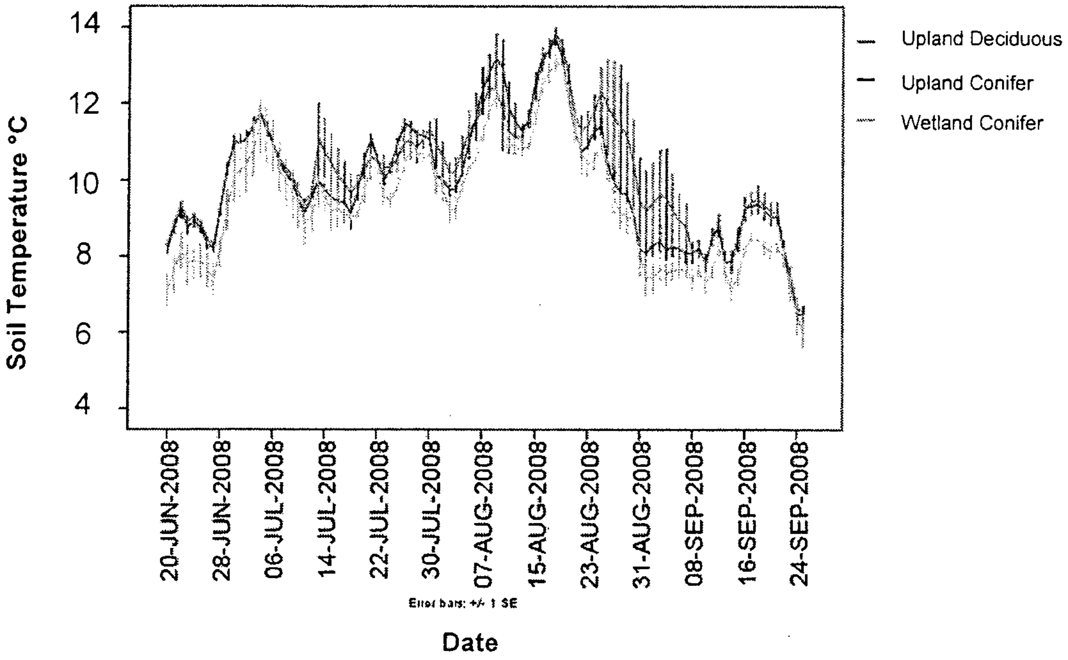


Figure 5-2 Mean daily soil temperature during two 6-week *in situ* incubations during early summer (June 20 to August 1) and late summer (August 8 to September 22) 2008.



Note: Because soil thermometers in the wetland conifer stands were installed on top of hummocks, the figure uses temperatures from 30 cm depth in the wetland conifer stands and 10 cm depth in the upland conifer and upland deciduous stands. These depths will better correspond with depths of the actual *in situ* incubation tubes.

Figure 5-3 Mean daily soil moisture content (%) at 10 cm depth during two 6-week *in situ* incubations during early summer (June 20 to August 1) and late summer (August 8 to September 22) 2008.

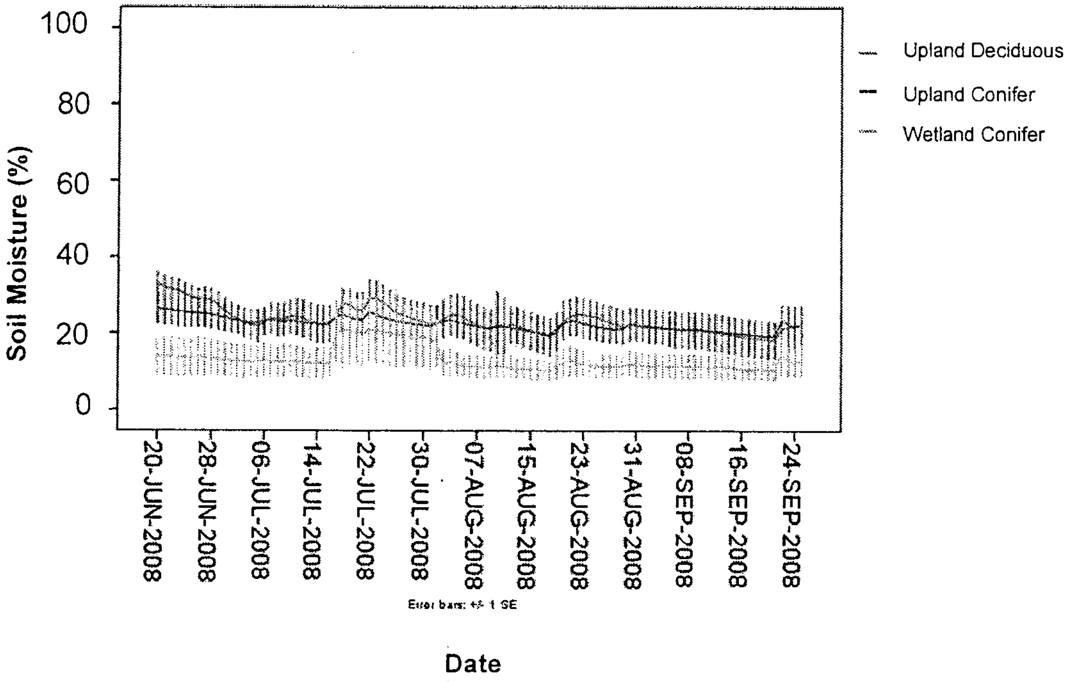


Figure 5-4 Mean daily soil moisture content (%) at 50 cm depth during two 6-week *in situ* incubations during early summer (June 20 to August 1) and late summer (August 8 to September 22) 2008.

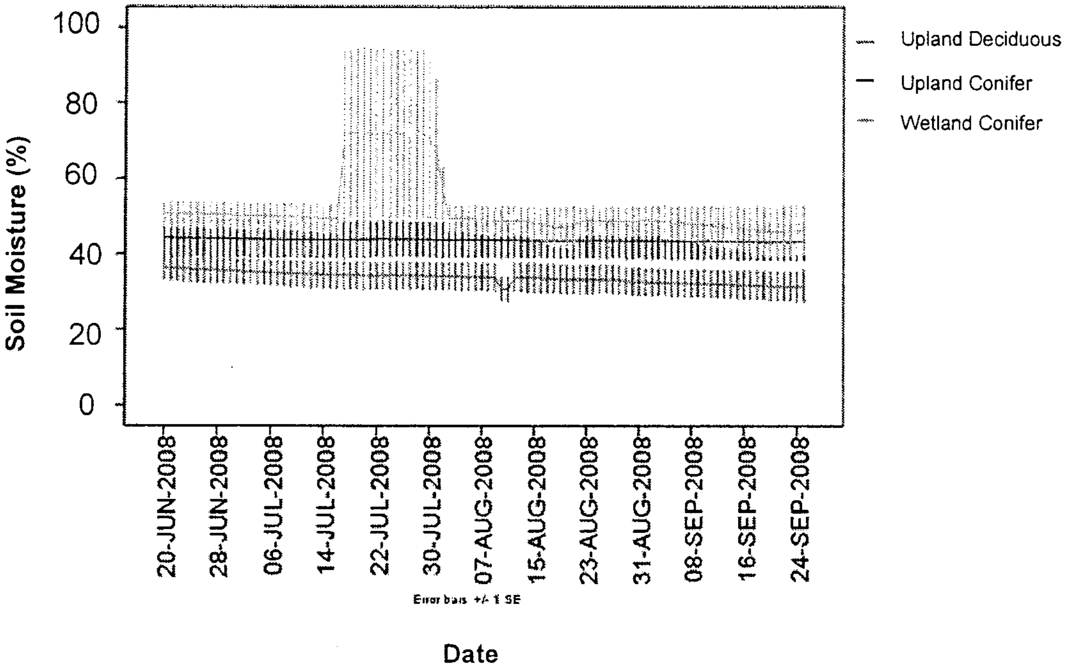


Figure 5-5 Areal net ammonification and nitrification rates for upland stands on the Boreal Plain by soil horizon for two 6-week incubations: a) net ammonification rates 20 June to 1 August; b) net ammonification rates 8 August to 22 September 2008; c) net nitrification rates 20 June to 1 August; b) net nitrification rates 8 August to 22 September 2008.

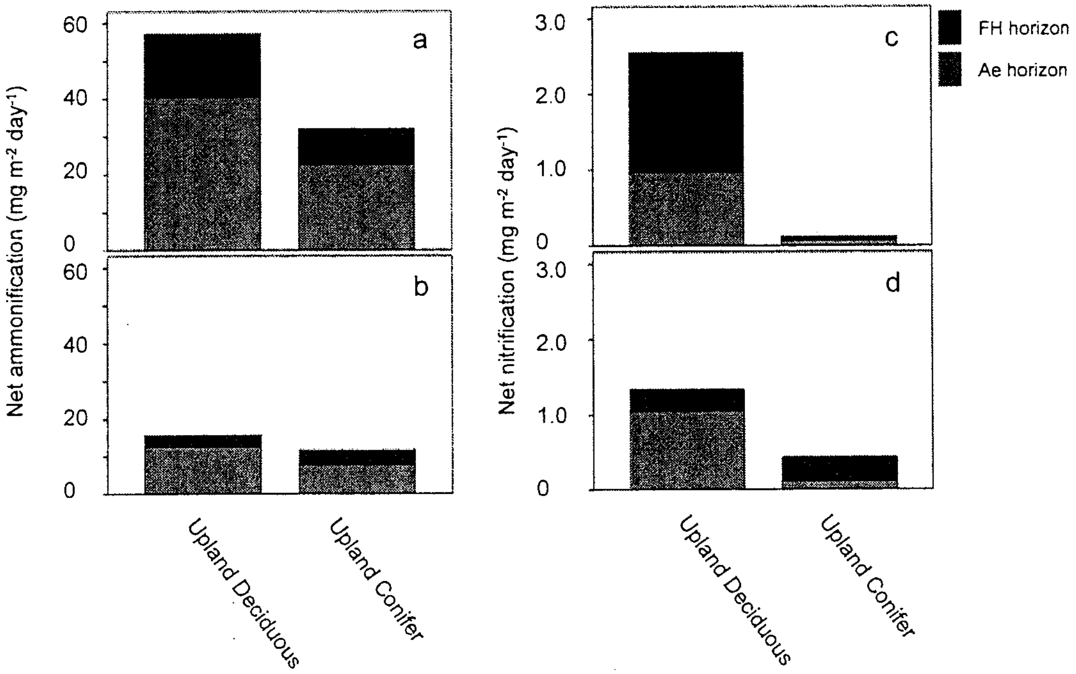


Figure 5-6 Areal net ammonification rates for the top 10 cm of soil within 3 stand types on the Boreal Plain for two 6-week incubations (20 June to 1 August and 8 August to 22 September 2008).

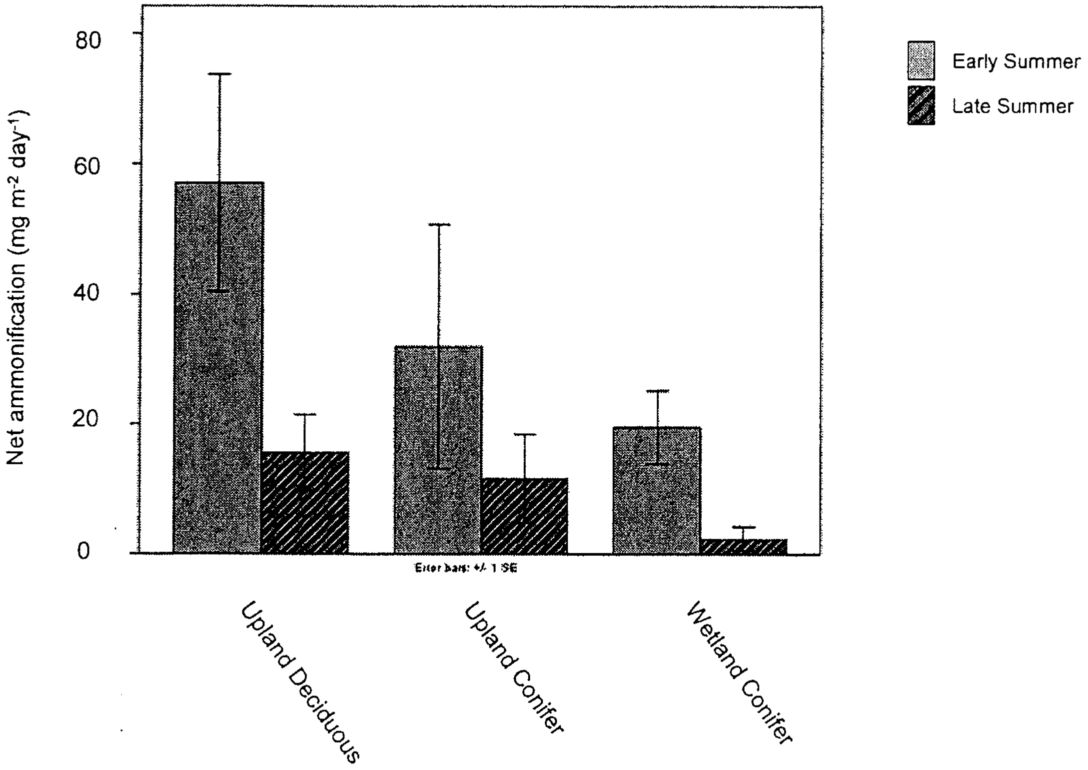


Figure 5-7 Areal net nitrification rates for the top 10 cm of soil within 3 stand types on the Boreal Plain for two 6-week incubations (20 June to 1 August and 8 August to 22 September 2008).

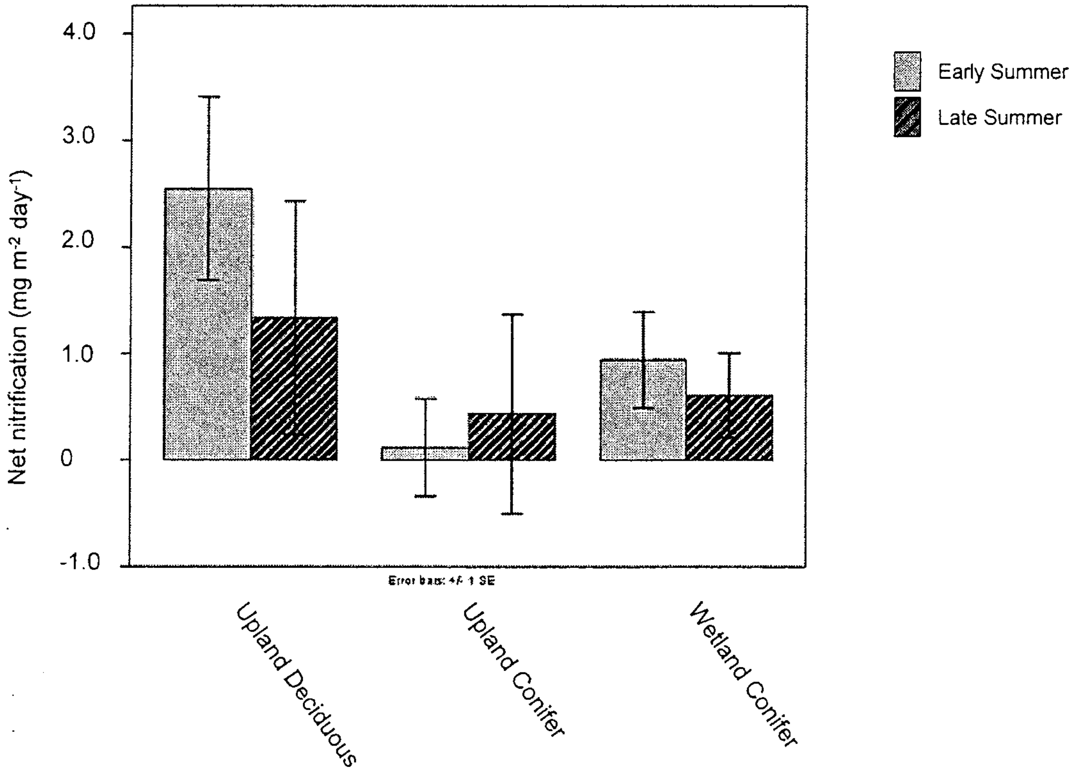
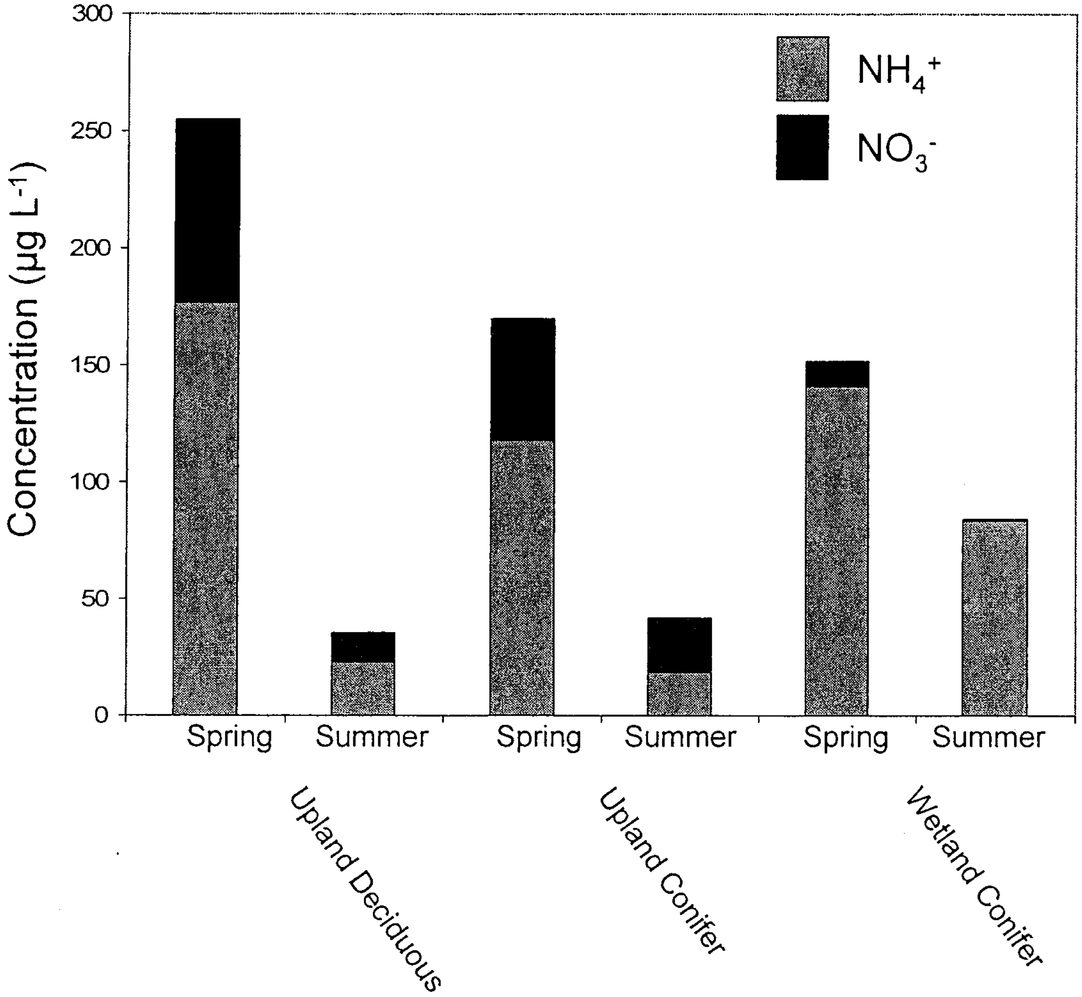


Figure 5-8 Inorganic nitrogen concentrations (μg L^{-1}) for soil porewater in three different stand types on the Boreal Plain for early spring (May) and summer (June to August) 2008.



Chapter 6

An examination of the role of soil and stand type in water and nitrogen exports in reference sub-watersheds on the Boreal Plain of western Canada

6.1 INTRODUCTION:

Since many temperate-zone forests are nitrogen (N) limited (Shaver and Chapin 1980; Vitousek and Howarth 1991), increased rates of nitrogen loss from watersheds as a result of forest disturbance (Likens et al. 1970) can decrease forest productivity and enrich downstream surface waters. Consequently, N export to surface waters has been used as a primary response variable in studies of forest disturbance (e.g., Likens et al. 1970; McEachern et al. 2000; Bernhardt et al. 2003). The limited amount of information on N export from watersheds on the Boreal Plain makes it very important to examine N export in undisturbed forested watersheds to understand some of the landscape patterns and processes that affect annual and spatial variation on the large ecozone.

Nitrogen export is a function of total runoff and streamwater N concentration, so factors that influence both runoff and N concentration need to be examined. On a regional scale, proximity to large industrial or agricultural emissions of inorganic N (IN = nitrate [NO_3^-] + ammonium [NH_4^+]) and climate are both related to leaching losses of N (Dise et al. 1998, Watmough et al. 2005). The proximity to large emissions of IN increases N inputs to the watershed, which can lead to N saturation and excess N exports. Climate effects are a little more complex. Increased precipitation rates result in shorter water residence time and hence less biological uptake and denitrification losses, and therefore greater N export (Howarth et al. 2006).

Also, warmer temperatures increase mineralization rates, which have been positively correlated with N export rates.

Nitrogen mineralization rates are also important in determining N exports. For example, many older forests have higher rates of N loss (Goodale et al. 2000), which were found to be related to higher N mineralization rates and lower plant N uptake (Vitousek et al. 1989, Aber et al., 1989). Isotopic tracer studies support this hypothesis in that stream NO_3^- is enriched in ^{15}N, suggesting that N is cycled through plants and microorganisms before being exported (Nadelhoffer et al 1999). However, since high immobilization rates in the upper soil horizons make these horizons major N sinks (Mead and Pritchett 1975, Miller et al. 1976, Melin et al. 1983, Raison et al. 1990), perhaps because the high C:N ratio promotes immobilization of N by the soil microorganisms (Mulholland 1992), gross mineralization rates may overestimate N export. Rather, net mineralization rates may predict N export more accurately. Since net mineralization rates differed by soil/stand types (upland deciduous, upland conifer and wetland conifer – see Chapter 5), these same soil/stand types should also affect N export rates.

On a more localized scale, spatial variation in runoff and N export is affected by the soil texture. In general, N exports are greater from sandy soils than clay soils (Cameron and Haynes 1986), because the decreased hydraulic conductivity of clay increases water residence time, enhancing biological uptake. Also, clay particles have a greater cation exchange capacity, which slows movement of the positively charged N species. Differences between upland and wetland (organic) soils also impact forms of N exported from watersheds.

Soil type influences the dominant N fraction exported from a watershed. In wetlands, water retention times are high and N availability is limited, so rapid uptake of bioavailable IN allows plants and soil microorganisms to immobilize most of the incoming N as biomass. Once these organisms die, low decomposition rates in boreal wetlands cause retention of N as biomass followed by conversion to and export as dissolved organic N (DON). As a result, dissolved N exports from wetlands are predominantly DON (Bowden 1987, Devito et al. 1989, Prepas et al. 2001), and DON concentrations in surface waters are positively correlated with wetland cover (Ito et al. 2007). Wetland cover is also positively correlated with NH_4^+ export since the water-logged soils favour export of reduced N fractions (Prepas et al. 2006), while uplands tend to export a larger proportion of NO_3^- (Bayley et al. 1992). One study in Minnesota however, found that proportions of the three main N fractions were similar between upland and wetland soils; about 85% exported as DON, 10% as NH_4^+ and 5% as NO_3^- (Verry and Timmons 1982).

The dominant forest type also affects N export. Several reviews found that the increase in runoff after removal of the forest canopy was greater if the watershed was covered by conifers than if the watershed was covered by deciduous tree species (Bosch and Hewlett 1982, Sahin and Hall 1996, Brown et al. 2005). This was because conifers actively transpire for a greater portion of the year and because conifer stands tend to have greater interception and sublimation losses. If N concentrations remain the same, higher runoff from deciduous stands should also produce greater N exports. However, annual pan evaporation in the area exceeds precipitation by more than 50 mm yr^{-1} (Prepas et al. 2001), often leading to water deficits in the forest soils particularly during the autumn when precipitation typically is very limited. In fact, approximately 62% of the annual precipitation in the study area falls during the summer (May through August) (Environment Canada 2008). As a result, the greater ET rates of deciduous species during the active growing season (Kozlowski and Pallardy 1997, LaMalfa and Ryel 2007) may cause less annual runoff from deciduous stands contrary to previous studies in other ecozones (e.g. Bosch and Hewlett 1982, Sahin and Hall 1996, Brown et al. 2005).

Seasonally, N export rates in northern and temperate forests were higher during plant dormant periods (late fall, winter and early spring) than during the summer (Likens et al. 1970, Cameron and Haynes 1986, Goodale et al. 2000, Hong et al. 2005), likely because biological uptake increases as soils warm (Likens et al 1970). In northern forests the spring peak in N flux tends to be higher than the autumn peak (Likens and Buso 2006). The high peak during spring was caused by higher N concentrations, likely caused by freeze-thaw cycles in the soils, occurring concurrently with the spring freshet (Mitchell et al. 1996). The freeze-thaw cycles cause mortality and lysis of soil microorganisms and fine roots, releasing previously immobilized N into the soils (Cooper et al. 2007) and (or) stimulating nitrification within the soils (DeLuca et al. 1992). The increased dissolved N in the soils would then be flushed from the watershed as the snow melts.

In this chapter the effects of soil/stand type on water and N export from undisturbed watersheds on the Boreal Plain were examined for two years. The Boreal Plain is a large ecozone in western Canada with deep, fine glacial till soils and a cool, sub-humid climate with the majority of precipitation occurring during the summer. These features make the Boreal Plain unique compared with other, better studied ecozones across North America and Europe, and may alter the response in runoff and N export to dominant soil/stand types. In spite of the Boreal Plain's large size and unique properties; the remote access and northern climate has greatly restricted scientific inquiry into N exports in surface water from undisturbed forested watersheds.

Similar to previous studies in other ecozones, the dominant soil/stand type was expected to affect the patterns and processes governing N export in surface water. The objectives therefore were as follows: 1) examine the role of soil/stand type on the annual and seasonal N export rates during one year with an extremely deep, early snowpack and one year with an average snowpack; and 2) examine the effect of soil/stand type on the form of N exported during one year with a deep, early snowpack and one year with an average snowpack. More specifically, the hypotheses tested were: 1) greater snow-water equivalent for the year with a deep, early snowpack caused greater flows during the spring snowmelt that resulted in greater N exports from all 3 soil/stand types; 2) total dissolved N (TDN) exports were greater from uplands with a larger percentage of IN than the N export from wetlands; and 3) the IN export from wetlands consisted primarily of the reduced N fraction (NH_4^+) while the more mobile, oxidized form of IN (NO_3^-) comprised most of the IN export from uplands.

6.2 MATERIALS AND METHODS:

6.2.1 Study Site:

The study site is a small (15.6 km^2), third-order watershed (named the Willow watershed) in the FORWARD study area within the Virginia Hills, located on the Boreal Plain in west-central Alberta. Tree cover is composed primarily of aspen (*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.), lodgepole pine (*Pinus contorta* Dougl. Ex Loud. var *latifolia*) and white spruce (*Picea glauca* (Moench) Voss) in upland sites and black spruce (*P. mariana* (Mill.) BSP) in lowland sites. The dominant soil/stand types in the study watershed were upland deciduous, upland conifer and wetland conifer stands (Table 6-1).

Upland soils have developed from glacial till parent material, and were mainly Hubalta series orthic grey luvisols, although other luvisols, brunisols and gleysols were also common. These soils were moderately calcareous at depth, weakly saline, moderately to slowly permeable and are derived from medium-textured Edson till (Agriculture and Agri-Food Canada 2006), which is 2 to 5 m thick and overlies weathered bedrock of the Wapiti group (Knapik and Lindsey 1983). Wetlands frequently occur in low-lying areas, with the majority of lowlands classified as poor, treed fens (Couling et al. 2007). Peat depths in these wetlands ranged from 20 cm to more than 200 cm.

The three sub-watersheds examined were all within the Willow watershed. The sub-watersheds were selected specifically to maximize the percent coverage by one specific soil/stand type (either upland deciduous, upland conifer or wetland conifer stands) (Table 6-1). The sub-watersheds were named depending on whether the stand types were predominantly upland deciduous, upland conifer or wetland conifer types and were designated the Aspen, Pine and Black Spruce sub-watershed respectively (Table 6-1; Fig. 6-1). Although the Black Spruce sub-watershed was not covered by a majority of wetland conifer stands, the wetland comprises a large percentage of the sub-watershed area and is located at the base of the sub-watershed. Therefore the wetland was expected to have a large effect on N and water exports.

The sub-watersheds were all first order and range in size from 9.2 ha for the Black Spruce sub-watershed, to 29.4 ha for the Aspen sub-watershed to 63.9 ha for the Pine watershed. All stands within the Aspen and Black Spruce sub-watersheds were from a single 70-year old cohort. Most stands within the Pine sub-watershed were from a 120-year old cohort, although 15% of the area was harvested in 1980. All three sub-watersheds were on north-facing slopes in the upper portion of the Willow watershed (Fig. 6-1), however the mean slope of the Black Spruce sub-watershed was considerably less than the mean slope of the two upland sub-watersheds.

6.2.2 Sample Collection:

At the base of each sub-watershed, a V-notch weir was installed in the summer 2006. For the 2007 and 2008 sample period, Global water level recorders were installed and recorded stage height in the pool directly above the weir every 10 minutes. Actual discharge over the weirs was measured using the bucket method (i.e. timing how long it takes for the water flowing over the weir to fill a bucket of known volume). Stage height was calibrated to actual discharge to provide accurate estimates of discharge throughout the entire ice-free period (May through October). For both years, there was too much snow and ice within the stream channels to install water level recorders or accurately measure discharge until mid-May. As a result, discharge during these periods was calculated using a linear regression between the outlet of the Willow watershed and each of the sub-watersheds ($R^2 = 0.63$, 0.88 and 0.58 for the Pine, Aspen and Black Spruce sub-watersheds respectively).

Weekly grab samples were collected upstream of the pool created by the V-notch weir and refrigerated for up to 48 hours before processing. Ammonium and NO_3^- samples were passed through Millipore 0.45-μm pore size filters and preserved with sulfuric acid. Total dissolved N samples were passed through a Whatman GF/F filter (mean pore size 0.7 μm). Since the GF/F filter has a larger pore size than the Millipore filter, the TDN sample should contain all the IN as well as the organic nitrogen (ON), including the larger ON in the 0.45 to 0.7 μm size range. Dissolved organic N therefore was calculated as the difference between the TDN and IN concentration. All samples were refrigerated at 4°C until they could be analyzed (maximum storage time was 4 weeks for IN samples and 8 weeks for TDN samples). TDN samples were digested with potassium persulfate and reduced to NO_2^- in the presence of cadmium. Since the NO_3^- analysis also involved cadmium reduction to NO_2^-, the NO_3^- values reported here include NO_2^-. Ammonium, NO_3^- and digested TDN samples were analyzed colorimetrically using a Lachat QuikChem 8500 flow injected analysis (FIA) automated ion analyzer. Minimum detection limits were 1 and 2 μg N L^{-1} for NO_3^- and NH_4^+ respectively.

6.2.3 Data Analysis:

For all three sub-watersheds, the following variables were calculated each year for the 184-d period comprising May 1 through October 31. For days that were not sampled IN concentrations were estimated by linear interpolation between sampling dates. Daily exports (mg N) were the products of total daily discharge and mean daily TDN, NO_3^- or NH_4^+ concentration. Since the streams generally do not flow during the winter, the annual exports (mg N) were calculated by summing all daily exports for the 184-d period (1 May to 31 October), which generally coincides with the ice-free season. Runoff (mm) from each sub-watershed was calculated by dividing the total water volume (dam^3) exported by the watershed area (km^2). Areal N exports were calculated by dividing the total mass of TDN, DON, NH_4^+ or NO_3^- exported during the sampling period by the watershed area (mg N m^{-2}), as in Prepas et al. (2006). Two years of runoff and IN exports (2007 and 2008) and one year (2007) of TDN and DON exports from these sub-watersheds were available. Correlations between runoff and nutrient concentrations were estimated using Pearson's correlation coefficient, while annual runoff, NO_3^- export and NH_4^+ export were compared between the two years using a paired t-test.

6.3 RESULTS AND DISCUSSION:

The weather during the two sample years was very different. During the 2007 water year (1 November 2006 to 31 October 2007), the snowpack was very early and deep. By November 1, 2006 the snow pack was already 25 cm deep, much deeper than the long term median value of 0 cm and almost 2-times deeper than the next deepest snowpack on record (Environment Canada 2008). Total precipitation meanwhile, was 582 mm, which was very close to the 30-year average of 577 mm (Environment Canada 2008). The second year of the study was very different. Although only 424 mm of total precipitation fell during the 2008 water year, approximately 73%

of the 30-year average, the winter was much more typical; mean daily temperatures during November and December 2007 were well below 0°C (-4 and -13 respectively), and the snowpack did not develop until early January 2008 (Environment Canada 2008).

Runoff from three first order sub-watersheds were not detectably different between 2007 (extreme snowpack) and 2008 (average snowpack) ($P = 0.13$, Fig. 6-2). The inability to detect a difference however may be related to the high variation between the sub-watersheds, since runoff patterns appear to be quite different. For example, in 2008 there is a second large peak in runoff at the end of May for all three sub-watersheds, and an additional peak in June for the Pine sub-watershed. Both of these additional peaks were lacking in 2007 (Fig. 6-2).

Peak daily runoff occurred during the spring snowmelt for both years reaching a maximum at approximately 4 mm day^{-1} (Fig. 6-2). This was surprising since the snow water equivalent during the 2007 snow survey was about 50% greater than the 2008 survey, while precipitation during late autumn (September through October) 2006 was about 172 mm, much more than the 26 mm of precipitation that fell during late autumn 2007 (Environment Canada 2008). The precipitation data therefore suggest that runoff should have been much higher during spring 2007 than spring 2008.

So why are spring flows similar between years with very different antecedent conditions? This apparent paradox was likely related to soil temperature patterns during the winter. The heavy snowfall during mid-October 2006 provided the soils with a large amount of insulation during the extreme snowpack year. As a result, the soil temperature decreased to a low of only -0.4°C in the uplands and -1.5°C in the wetlands (Appendix B). During the spring, the unfrozen soils allowed the water from the spring snowmelt to infiltrate the soils and recharge the soil groundwater. During the average snowpack year (winter 2007/2008) the soils froze, decreasing to -6°C in the wetlands and -2°C in the uplands (Appendix B). During the snowmelt after the winter with an average snowpack, the majority of the meltwater likely ran over the frozen soils and directly into the stream channels. Therefore different flowpaths, caused by different frost regimes, during the spring runoff resulted in similar spring flows even though the antecedent moisture and snowpack conditions were very different between the two years.

Monthly variation in runoff was very high for all 3 sub-watersheds, peaking during the snowmelt period in May and then rapidly decreasing to less than 1 mm day^{-1} for July through October (Fig. 6-2). During both summers, the Black Spruce and Aspen sub-watersheds ran dry, while continuous flow from the larger Pine sub-watershed made it more responsive to precipitation events. The stream channel within the Pine sub-watershed was more incised than the other streams surveyed, which may allow for a larger proportion of the water exported as surface, as opposed to the sub-surface flows. In the broader less incised channels draining the Aspen and Black Spruce sub-watersheds, sub-surface flows probably dominate water exports during low flow periods.

Unlike other studies from the eastern U.S. where watersheds covered with conifer stands export less water than watersheds with deciduous stands (Swank and Douglass 1974, Peel et al. 2001), it appears that the deciduous dominated watershed exported less water than the conifer dominated watershed, particularly during 2008 (Table 6-2, Fig. 6-2). The general pattern on the Boreal Plain of cold spring and dry autumn conditions limits the amount of water lost through ET by the active conifer canopy during the period when deciduous trees are mostly dormant. The greater runoff from the Pine and Black Spruce sub-watersheds in response to precipitation in late May and June 2008 (Fig. 6-2) indicates that the higher daily ET rates for deciduous species (Kozlowski and Pallardy 1997) during the growing season, when most of the precipitation occurs, has a greater influence on annual flows in this region than the spring and autumn ET rates in the conifer stands (Table 6-2).

During the spring of 2007, after an extremely deep snowpack, the IN export from all sub-watersheds was primarily composed of NH_4^+, which was unexpected since NO_3^- is more mobile. The higher NH_4^+ exports in the spring 2007 may be related to high soil water content, leading to reducing conditions and transformation of NO_y^- to NH_4^+ within the soil, before export from the watershed. There was no correlation between NH_4^+ concentrations and stream discharge (P = 0.322), rather, concentrations stay relatively constant throughout the season. Since NH_4^+ often binds with soil particles, high NH_4^+ concentrations during the spring snowmelt may also be related to increased bank erosion, as well as high soil moisture, while during the summer period low flows and warm water temperatures lead to decreased dissolved oxygen, and therefore create reducing conditions within the stream that convert NO_3^- to NH_4^+. The larger NH_4^+ exports from the Black Spruce sub-watershed during May 2008 compared with May 2007 are probably related to the increased NO_3^- exports from the upland sub-watersheds during May 2008. Unlike the upland watersheds however, the additional NO_3^- in the Black Spruce sub-watershed would first be reduced to NH_4^+ before being exported.

Unlike the NH_4^+ concentrations, NO_3^- concentrations were positively correlated with discharge ($P = 0.004$). During both years though, high flows occurred only during the spring when soil temperatures and plant uptake rates were low. Therefore, the correlation between discharge and NO_3^- concentrations may be related to low immobilization rates during the spring snowmelt rather than discharge itself. During 2004 for example, even though flows peaked in July, flow weighted mean concentrations were still highest during the spring (Appendix C), indicating that plant uptake is more important in regulating NO_3^- concentrations in streams than discharge.

Similar to runoff, the snowmelt exports of NH_4^+ were similar between the two years (P = 0.13, Fig. 6-3). The NO_3^- exports from the three sub-watersheds appear to be different between the two years (Fig. 6-4), although any difference was not detectable ($P = 0.20$). The lack of a detectable difference however was likely related to the high degree of variance in NO_3^- exports from the different watersheds. Under the frozen soil conditions in 2008 described above, the maximum daily NO_3^- export was 4 and 8 times higher, for the Pine and Aspen sub-watersheds respectively, than the maximum daily export during 2007 (Fig. 6-4). These much larger peaks resulted in similar increases in NO_3^- exports for both the snowmelt and the entire ice-free periods (Table 6-2). Since the majority of the 2007 annual TDN export occured during May (62 to 83% of TDN exports) the dramatic increases in NO_3^- exports during May 2008 may indicate greater TDN exports as well.

There are two potential mechanisms that may explain the higher NO_3^- exports during 2008. Firstly, the frozen soils impeded percolation of the meltwater, so the majority of the NO_3^- input in winter bulk deposition would flow over the frozen soils, directly into the stream channels. Secondly, the frozen soils may have experienced a number of freeze/thaw events which are known to lyse microbial and fine root cells (Morley et al. 1983). The release of labile C from the lysing cells enhanced net mineralization, which along with the IN released during lysis, increased the IN concentrations in the soil porewater (DeLuca et al. 1992, Schimel and Clein 1996, Grogan and Jonasson 2003). This N enriched water then flows through the upper soil horizons into the stream channels.

During the extreme snowpack year, 2007, annual TDN areal exports from the three sub-watersheds were similar, with values of 24.6, 29.4 and 32.0 mg N m^{-2} for the Aspen, Pine and Black Spruce sub-watersheds respectively. However, the patterns of N export and composition of the different N fractions varied between the sub-watersheds. Total dissolved N exports for both the Pine and Aspen sub-watersheds peaked during the snowmelt period, accounting for over 60% of the annual exports (Fig. 6-5, Table 6-2). The TDN exports for the Black Spruce sub-watershed also peaked during the snowmelt period, however unlike the two upland sub-watersheds, there was an additional peak starting in late June during which similar amounts of TDN were exported as during the snowmelt period (Fig. 6-5).

The large TDN export in late June from the Black Spruce sub-watershed was comprised primarily of NH_4^+ and DON (Figs. 6-3, 6-6) and coincided with a large storm event in late June (94 mm of precipitation in 3 weeks) that followed a month-long dry period (7.8 mm of precipitation during the previous 31 days) (Environment Canada 2008). The large areal export of DON and NH_4^+ from the Black Spruce sub-watershed was probably due to high decomposition and mineralization rates that occurred in the peat during the dry period (Chapter 5), followed by flushing of the dissolved N from the watershed when the water table increased and the water discharged to the sub-watershed outlet. The rise in groundwater stage would also have resulted in anaerobic conditions in the peat, reducing NO_3^- to NH_4^+, as observed in the soil porewater (Chapter 5), leading to predominantly DON and NH_4^+ exports (Fig. 6-3). It seems that this dry period preceding the high flows is necessary for the high NH_4^+ and DON exports since similar high flows from the Black Spruce sub-watershed during late June 2008 resulted in much less NH_4^+ export (Fig. 6-3).

Areal TDN exports from all sub-watersheds during 2007 ranged from 6.1 to 7.8% of N inputs in bulk deposition (see Chapter 4 for inputs), which was consistent with other studies that estimated median TN exports from 7 watersheds in Ontario to be 6% (Watmough and Dillon 2003). However, during the 2008 season, although TDN exports are still unknown, IN export from the sub-watersheds were 1.7 to 3.2 times greater than during the 2007 season, suggesting that TDN exports may also be substantially higher.

As described above, the meltwater during the spring snowmelt likely exhibited differences in hydrologic flow paths each year; subsurface flow during the melting of the deeper snowpack in 2007 versus surface flow over frozen ground in 2008, which may have resulted in different proportions of IN versus ON exports. Since the residence time of water in the organic rich forest floor is limited when soils are frozen, IN fractions may dominate exports under these more typical conditions. When soils are not frozen however, residence times of the water in the forest floor are likely longer. Also, soil microorganisms are able to immobilize IN as it percolates through the soils, which result in higher ON and lower IN exports during snowmelt. Therefore, although the relative proportions of TDN exports may vary from year to year, the actual annual TDN exports may not vary as much as the IN data initially suggested.

Although annual and spatial variation in TDN exports may be limited, there appears to be spatial variation in the forms of N exported from the different sub-watersheds (Fig. 6-7. While all three sub-watersheds exported predominantly DON, the upland watersheds tended to export more IN than the Black Spruce watershed. In the two upland watersheds, the proportion of IN ranged from 21 to 24% (for the Aspen and Pine sub-watersheds respectively), compared with the Black Spruce sub-watershed where IN comprised only 9% of TDN exports (Table 6-2). During both years, the amount of NO_3^- exported from the Black Spruce sub-watershed was very low;

only 0.37 mg m^{-2} in 2007 (about 1% of TDN exports) and 0.58 mg m^{-2} in 2008. The areal NO_3^- exports from the two upland sub-watersheds were much higher than exports from the Black Spruce sub-watershed; 4 to 5 times greater during 2007 and 14 to 24 times greater during the more typical year (2008) (Table 6-2). The anaerobic conditions present in the soils of the Black Spruce sub-watershed, particularly during the spring when the water table was high, either reduced NO_3^- to NH_4^+ or enabled the NO_3^- to be converted to NO_2 or N_2 via denitrification resulting in very low NO_3^- exports in stream water from the watershed.

6.4 CONCLUSION:

On the sub-humid and N-limited Boreal Plain, three forested sub-watersheds retained much of the precipitation and N inputs. Runoff during the 2007 ice-free period ranged from 39 to 53 mm, approximately 9% of precipitation, while runoff during 2008 ranged from 45 to 105 mm or 11 to 25% of precipitation. Differences in runoff between the two years were attributed to different soil freezing patterns through the winter and early spring. As expected, areal N exports from the three sub-watersheds were quite low. During 2007, annual areal TDN exports ranged from 24.6 and 32.0 mg N m^{-2} for the sub-watersheds, approximately 7% of N inputs in bulk deposition, and consisted of predominantly DON. Data are not yet available for TDN exports during 2008. The high retention of N, particularly NO_3^- was consistent with a system still limited by N (i.e. in stage 0 of N saturation, Aber et al. 1989), suggesting that this study area can be used to approximate N exports in baseline conditions.

Annual variation in IN exports were also apparent; spring snowmelt over frozen soils appears to enhance IN export over years where the soils were not frozen. Also, watersheds with high conifer coverage (both upland and wetland) appear to export greater amounts of NH_4^+ than watersheds with more deciduous cover, while watersheds with high areal wetland conifer coverage export very little NO_3^-.

One interesting question raised by this study is how the patterns in the headwater sub-watersheds relate to patterns in N export from the larger 3rd order Willow watershed. The issue of scaling is quite difficult however, since it fails to take into account the role of in-stream processing as well as the retention potential of downstream beaver ponds, which are quite prevalent in Willow. Another confounding factor is the weather. Also, the two years examined by the study were very different in terms of snowpack and precipitation patterns, which may have dramatic effects on N export. However, the scaling up of N exports from the sub-watershed to the watershed level is currently under examination.

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6.6 Tables:

Table 6-1: Forest composition (%) of three sub-watersheds within the Willow watershed on the Boreal Plain.

Stand Type	Sub-watersheds		
	Pine	Aspen	Black Spruce
Upland Deciduous	47	72	65
Upland Conifer	53	28	
Wetland Conifer			35

Note: The upland deciduous stands consist of 70% or more deciduous crown closure, upland conifer stands consist of 30% or less deciduous crown closure with peat depths less than 20 cm, while wetland conifer stands consist of 30% or less deciduous crown closure with peat depths greater than 20 cm.

Table 6-2: Runoff and NO_3^- and NH_4^+ exports from three sub-watersheds for the ice-free (1 May to 31 October) and the snowmelt (1 May to 31 May) periods for 2007 and 2008.

		Sub-watersheds					
		Pine		Aspen		Black Spruce	
Year		2007	2008	2007	2008	2007	2008
Runoff (mm)	Ice-free	62.2	88.1	47.2	44.0	51.3	52.8
	Snow melt	42.0	55.6	41.3	40.5	41.7	48.3
NO_3^- export (mg N m^{-2})	Ice-free	1.46	14.17	2.09	8.07	0.37	0.58
	Snow melt	1.21	12.01	1.98	7.91	0.25	0.53
NH_4^+ export (mg N m^{-2})	Ice-free	5.54	8.06	2.98	2.77	2.30	3.92
	Snow melt	3.04	7.08	2.07	2.62	0.58	3.85
DON export (mg N m^{-2})	Ice-free	22.38		19.50		29.34	
	Snow melt	14.00		16.20		18.23	
TDN export (mg N m^{-2})	Ice-free	29.39		24.57		32.01	
	Snow melt	18.25		20.25		19.06	

6.7 Figures

Figure 6-1: Stand cover map of three sub-watersheds (Pine, Aspen and Black Spruce,) within the Willow watershed on the Canadian Boreal Plain.

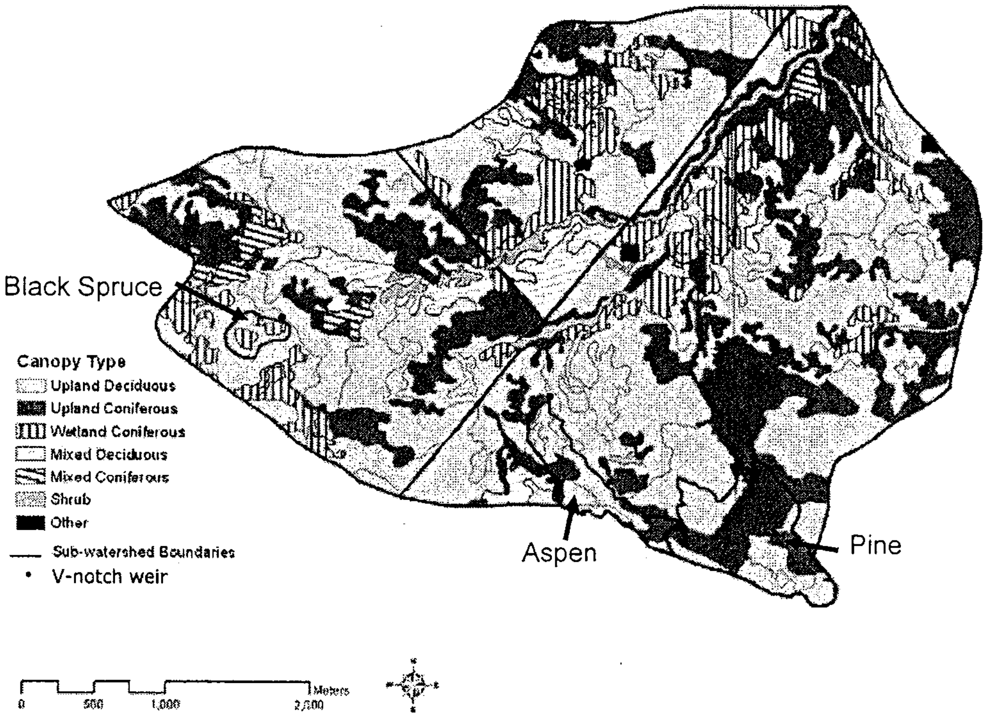


Figure 6-2: Runoff (mm) for ice-free period (1 May to 31 October) from 2007 and 2008 for three small sub-watersheds on the Canadian Boreal Plain.

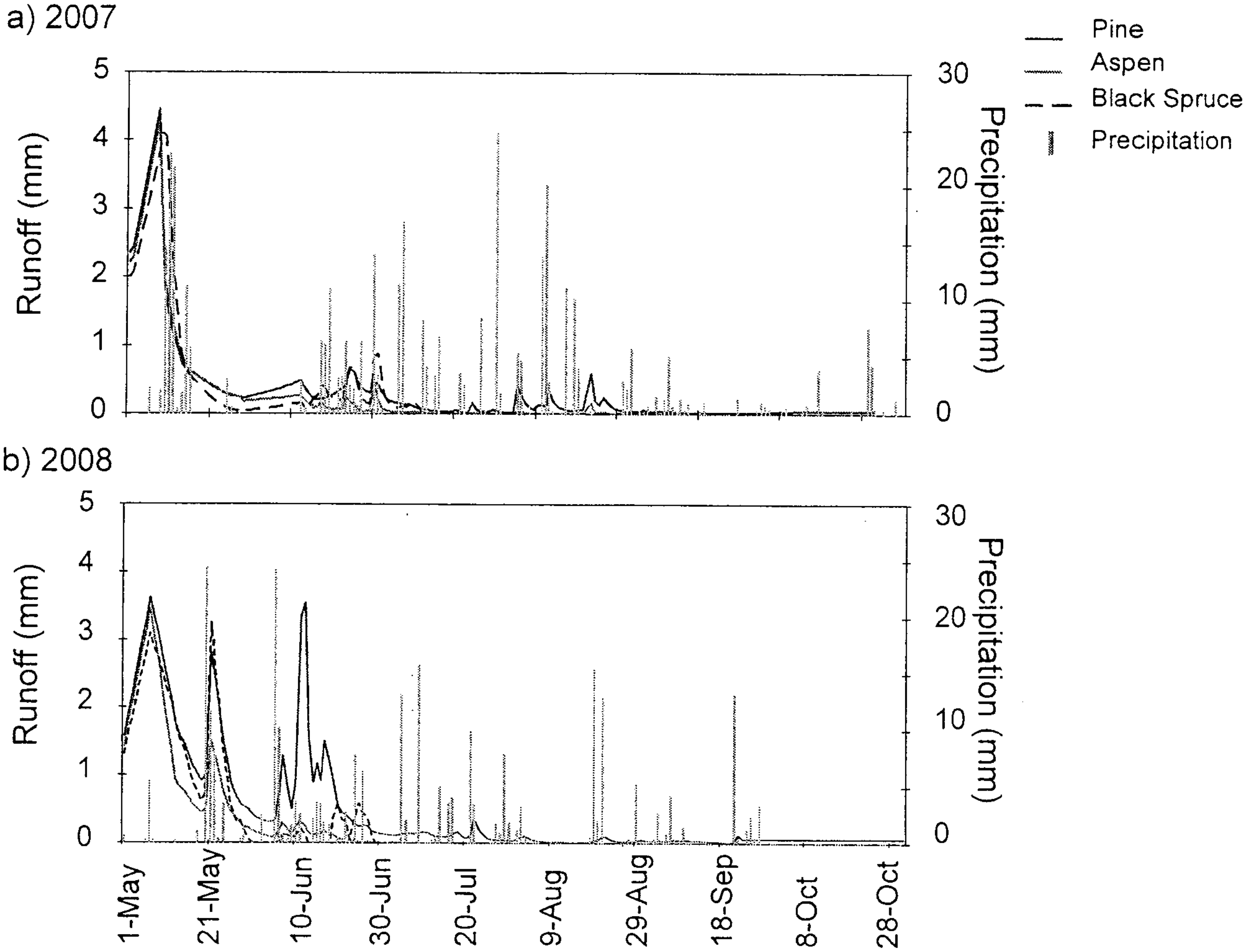


Figure 6-3: NH_4^+ exports (mg N m^{-2}) for ice-free period (1 May to 31 October) from 2007 and 2008 for three small sub-watersheds on the Canadian Boreal Plain.

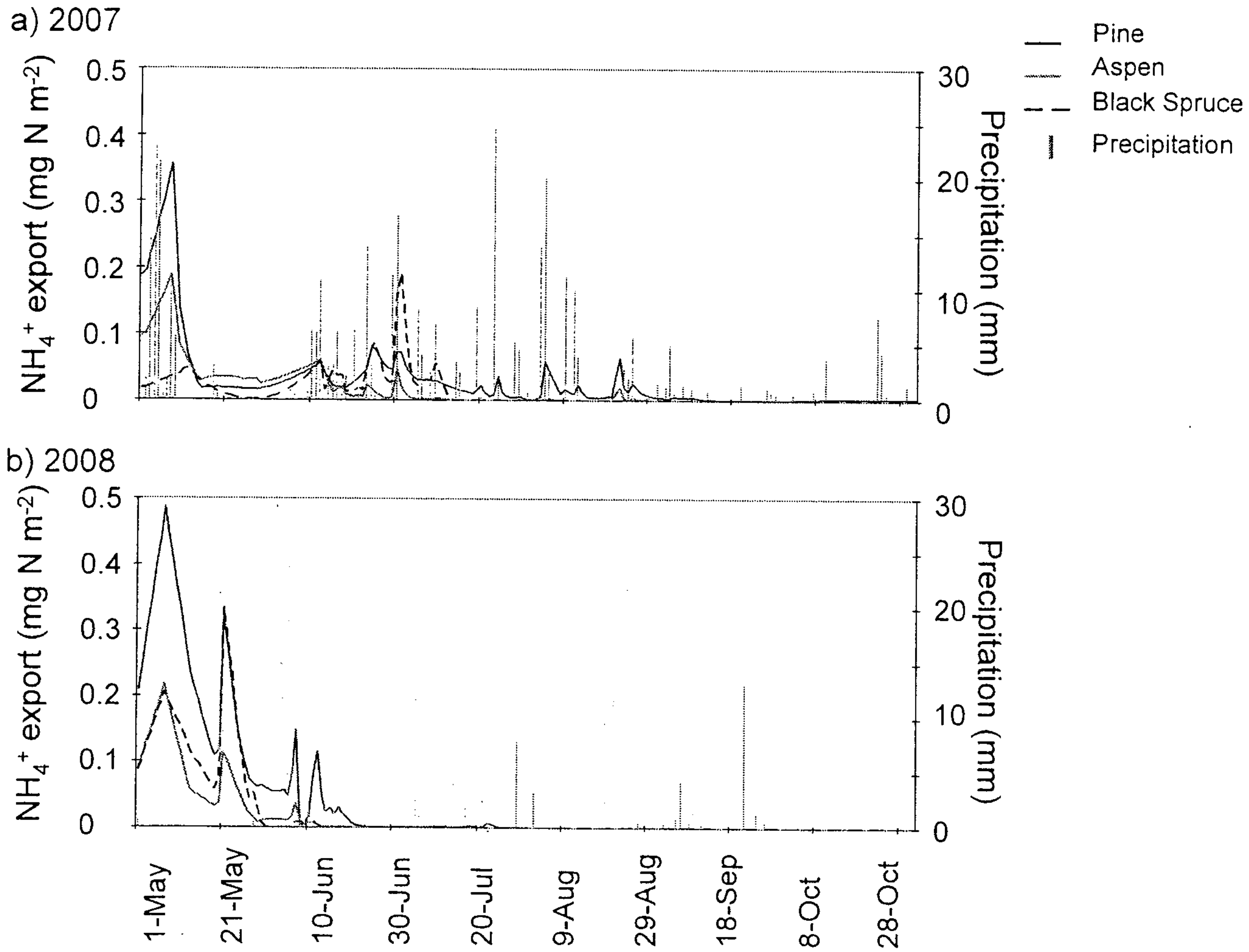


Figure 6-4: NO_3^- **exports (mg N** m^{-2}**) for ice-free period (1 May to 31 October) from 2007 and 2008 for three small sub-watersheds on the Canadian Boreal Plain.**

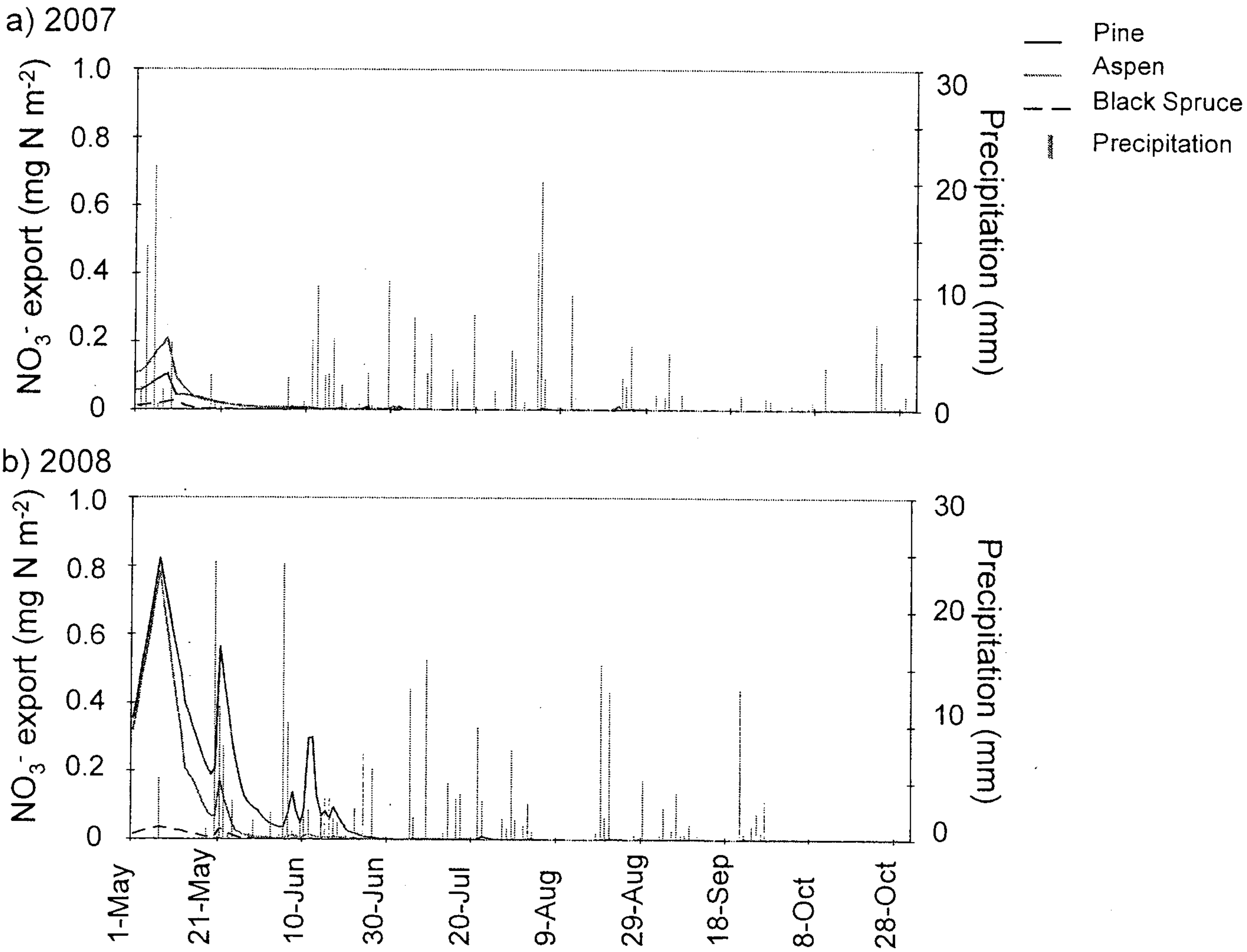


Figure 6-5: TDN exports (mg N m^{-2}) for the 2007 ice-free period (1 May to 31 October) for three small sub-watersheds on the Canadian Boreal Plain.

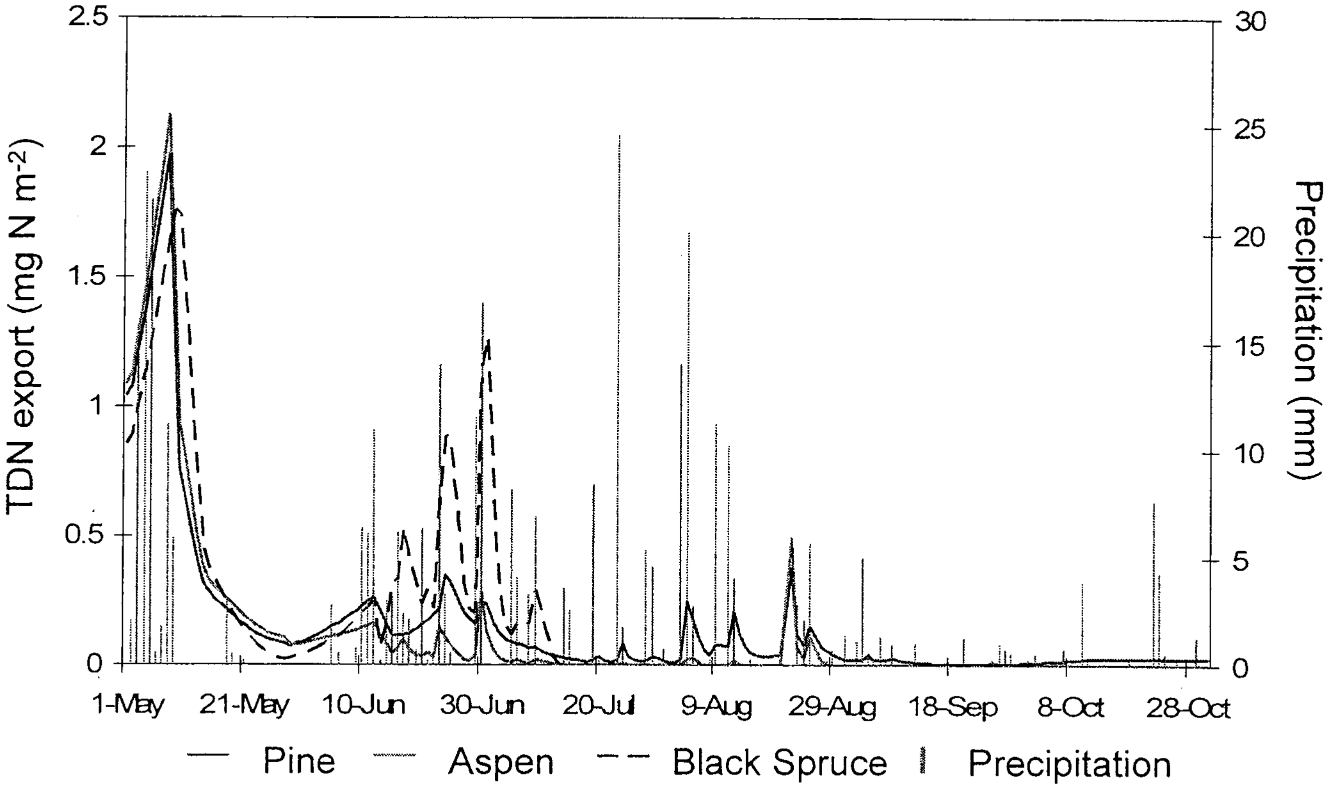


Figure 6-6: DON exports (mg N m^{-2}) for the 2007 ice-free period (1 May to 31 October) for three small sub-watersheds on the Canadian Boreal Plain.

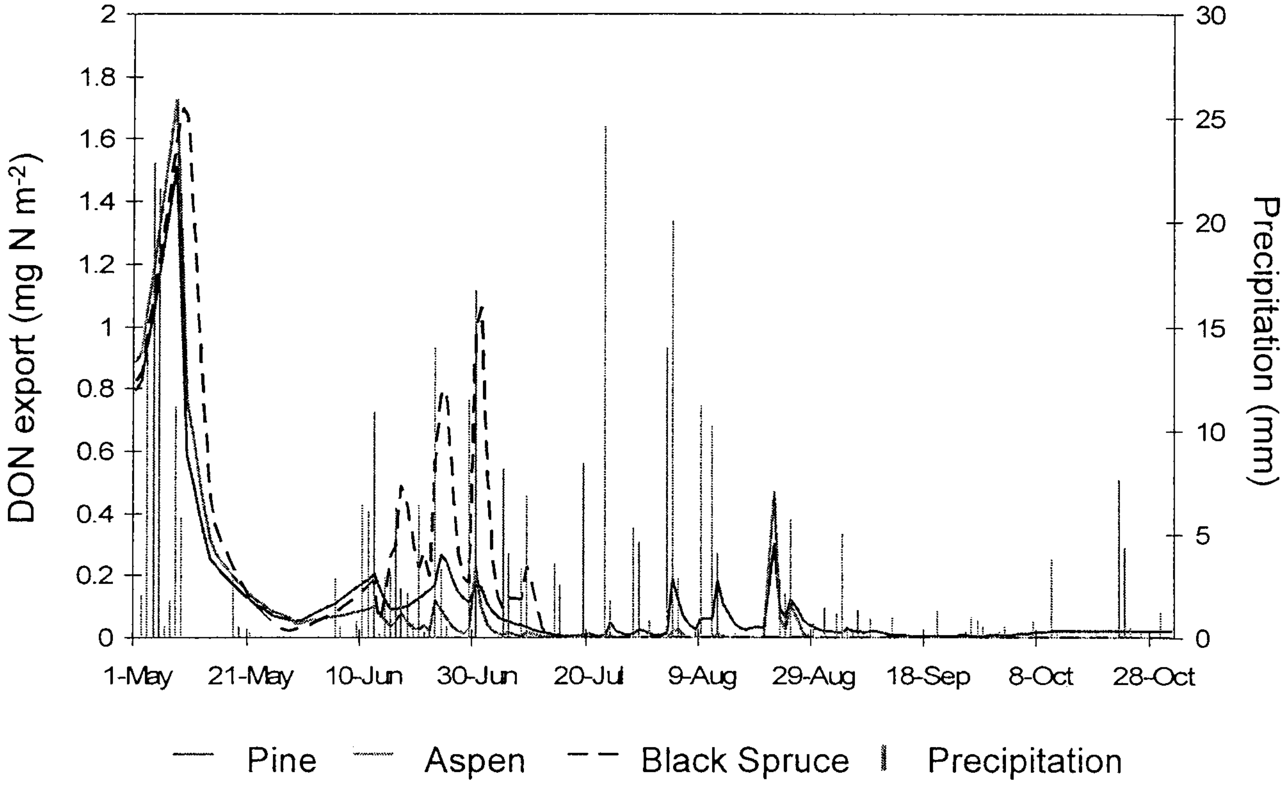
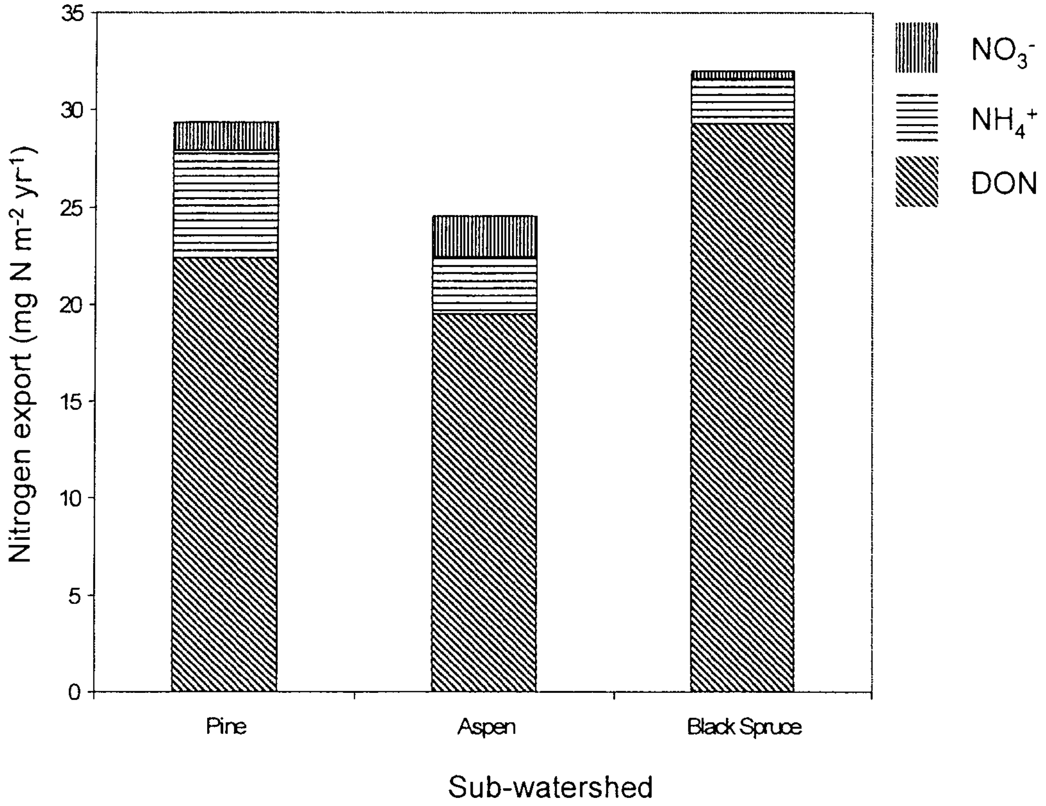


Figure 6-7: Composition of total dissolved nitrogen exports for the 2007 ice-free period (1 May to 31 October) for three small sub-watersheds on the Canadian Boreal Plain.



Chapter 7

Summary, Implications and Future Directions

7.1 SUMMARY OF NITROGEN BUDGET COMPONENTS

7.1.1 Introduction

This thesis constitutes an examination of key components of a nitrogen (N) budget for a watershed on the Boreal Plain in western Canada. The Boreal Plain is approximately 650 000 km^2 and stretches from Lake Winnipeg westward to the Boreal Cordillera in northern British Columbia. Human population in the area is very low, averaging just over 1 person km^{-2} (Environment Canada 1996). The low human population density has resulted in limited infrastructure, remote study sites and until recently, very little scientific interest. Therefore, although a significant body of research on N cycling within and export from forested watersheds exists, there are few examples of N budgets in undisturbed forested watersheds (Bormann et al. 1977, Hemond 1983, Watmough et al. 2005), and none on the Boreal Plain.

Most studies examining N in forested watersheds focus on only one or two components of the budget, for example comparing internal N cycling within or exports from disturbed and reference watersheds (e.g. Likens et al. 1970, Bayley et al. 1992, Devito et al. 1999, Piirainen et al. 2002, Carmonsini et al. 2003). As a result, the knowledge that is available lacks coherency, limiting our understanding of how various components of an N budget affect each other and how these interactions affect N transfer between various ecological compartments. Also, it is common to find a high degree of variation among watersheds, even between reference watersheds in identical ecozones (Pelster et al. 2008), making it difficult to relate studies of inputs to other studies examining cycling and/or exports. The lack of baseline knowledge in N budgets for watersheds on the remote Boreal Plain therefore, restricts our ability to properly manage the forested lands in this vast region.

Therefore, the purpose of this thesis is to fill this knowledge gap by providing a better understanding of how and to what magnitude N is transported through the various compartments of three dominant soil/stand types (upland deciduous dominated, upland conifer dominated and wetland conifer dominated stands) on the Boreal Plain. Ultimately, this description of key components of an N budget on the Boreal Plain will allow better understanding of variation in N exports spatially and temporally across the Boreal Plain, and will facilitate more accurate predictions of N export in the face of increasing industrial development and landscape disturbances. The key components of the N budget that were measured are as follows: the inputs of N in bulk deposition and their interactions with the forest canopy to affect N deposition to the forest floor (i.e. throughfall); the cycling of N within the forest floor and upper soil horizons (i.e. net mineralization); the leaching of N through the soil horizons; and the export of N in surface waters.

The specific hypotheses tested are as follows:

1. The soil/stand type does not affect N inputs in bulk deposition. Instead, since climate and proximity to industrial sources are considered to be the major factors in N inputs in bulk deposition, the study site should receive relatively little N inputs in bulk deposition.
2. Since forest canopies in areas with low bulk deposition N tend to retain N, the throughfall N flux should be less than the N flux of bulk deposition, with the throughfall N flux differing by the different soil/stand types.

3. The N cycling within the soils, as estimated by net mineralization rates, is also expected to differ by soil/stand types. Since mineralization rates are affected by substrate and environmental factors such as temperature and oxygen status the rates are expected to be higher in the upland, especially deciduous, versus the wetland conifer stands.
4. Export patterns are also expected to be related to soil/stand type. Wetlands, which have higher water tables and therefore experience more reducing conditions than uplands, are expected to export more NH_4^+ than the uplands, which should export more of the oxidized IN species (NO_3^-). Also, because of the longer flowpath of water through organic soil horizons in wetlands versus uplands, the wetlands are expected to export more dissolved organic N (DON) than uplands.

7.1.2 Discussion

The first compartment examined is the forest canopy and the role different canopy types play in intercepting atmospheric bulk N deposition and the cycling via throughfall and stemflow. As expected, the N inputs in bulk deposition were relatively low (410 mg N m^{-2}), confirming the first hypothesis that N deposition to this area is not yet heavily affected by industrial and agricultural activities. The throughfall study (Chapter 4) confirmed part of the second hypothesis, namely that in areas with low N deposition, the forest canopy retains much (over 50%) of the inorganic N (IN = nitrate [NO_3^-] + ammonium [NH_4^+]) inputs and about 35% of total dissolved N (TDN) inputs in bulk deposition. Contrary to expectations however, the N flux in throughfall and stemflow of the different soil and stand types were not detectably different.

The forest canopy also cycles N in the form of litterfall. Using dry weights of annual litterfall (Appendix D) from the different soil/stand types and a mean N concentration of 0.0094 g N g^{-1} litter for temperate forests (Aerts et al. 1997), the estimated transfer of N in the form of litterfall is approximately 1940 mg N m^{-2} yr^{-1} (Fig. 7-1). This estimate is consistent with other studies in northern forests where measurements ranged from 615 mg N m^{-2} for a black spruce forest in New Brunswick (Mahendrappa and Ogden 1973) to 4100 mg N m^{-2} for deciduous forests in Minnesota and Wisconsin (Reich et al. 1997).

The next budget component examined was the cycling of N in the forest soils. This compartment tends to experience rapid N turnover and was expected to be the major source of labile N in the watershed (Bormann et al. 1977). *In situ* soil incubations were used to determine net mineralization rates within the forest soils for each dominant stand type Chapter 5). Unlike bulk deposition and throughfall rates, which did not differ by stand and soil type, areal net mineralization rates were highest in the upland deciduous stands (Fig. 7-1), thus confirming the third hypothesis. Although net mineralization was measured for 12 weeks out of the year, the amount of IN produced greatly exceeded the annual TN input from bulk deposition. Therefore in undisturbed forest systems, differences in N mineralization and immobilization rates are likely more important in determining N exports than differences in throughfall and stemflow.

The IN concentrations in the soil pore water, which tended to be higher in the upland than in the wetland stands, decreased dramatically from spring to mid-summer. Since the spring snowmelt is responsible for much of the IN export from Boreal Plain watersheds (Pelster et al. 2008, Chapter 6), the high IN concentrations in upland soil porewater during spring may result in greater IN exports from upland than wetland stands. Within the porewater of the wetland conifer stands, NO_3^- concentrations were very low, while NH_4^+ concentrations were quite high. Since porewater samples from the upper peat layers could only be collected during periods when the peat was saturated, the NO_3^- was likely reduced to NH_4^+ before sample collection. Since the wetland stream flowed only when the peat was saturated, the IN export from the wetland should also be predominantly NH_4^+.

The final component of the N budget was N exports. The IN exports from three sub-watersheds within the study watershed were measured for two ice-free seasons (2007 and 2008), while TDN and DON exports are currently only available for 2007. As described earlier (Chapter 6), 582 mm of precipitation fell during 2007, very close to the 30-year average of 577 mm while precipitation during 2008 was only 73% of the 30-year average. However, the winter period for the 2007 water year (1 November to 31 October) was extreme, while the winter period for the 2008 water year was much more typical of the 30-year averages.

The three sub-watersheds were selected specifically to examine differences in surface water export of N from the three soil/stand types. The percentage of the sub-watersheds covered by the various stand types ranged from 0 to 35% wetland conifer stands, 0 to 53% upland conifer stands and 47 to 72% upland deciduous stands (Table 6-1). The conifer stands are composed of at least 70% conifer crown closure, while the deciduous stands consist of a minimum of 70% deciduous crown closure. Upland soils have developed from glacial till parent material, and are mainly orthic grey luvisols, although other luvisols, brunisols and gleysols are also common. Wetlands are common in low-lying areas, with the majority of lowlands classified as poor, treed fens (Couling et al. 2007). Peat depths in these wetlands range from 20 cm to more than 200 cm. Tree cover is composed of primarily aspen (*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.), lodgepole pine (*Pinus contorta* Dougl. Ex Loud. var *latifolia*) and white spruce (*Picea glauca* (Moench) Voss) in upland sites and black spruce (*P. mariana* (Mill.) BSP) in lowland sites.

Since net areal mineralization rates differed by soil/stand type, the exports, particularly the various N fractions, were hypothesized to also differ between the different sub-watersheds based on the different soil/stand composition. Given the N input rates in bulk deposition and the net mineralization rates, the N exports from the three subwatersheds for 1 May to 31 October 2007 period are very low, averaging just 29 mg N m^{-2} (Fig. 7-1) (approximately 7% of inputs in bulk deposition - Chapter 6).

Although the last hypothesis concerning differences in N export from the different soil/stand types was not confirmed, there are some interesting patterns in N exports, in particular the N fractions exported, from the different different sub-watersheds. During 2007, the year with the extreme snowpack, the IN exports accounted for approximately 22% of TDN exports from the upland sub-watersheds while accounting for only 9% of exports from the Black Spruce sub-watershed (Fig. 32). However, consistent with the last hypothesis, the Black Spruce sub-watershed, which is covered by much more of the wetland conifer stand type than the other sub-watersheds, appears to export a greater percentage of DON and much less NO_3^- than the two upland sub-watersheds. The majority of N exported from all sub-watersheds occurred during the month of May (Chapter 6) indicating that the spring snowmelt period is critical to N export patterns on the Boreal Plain.

To complete the N budget, inputs through N_2 fixation and exports as denitrification are also needed. While the N_2 fixation and denitrification rates were not directly measured, estimates from other, similar regions are available in the literature. Estimates of N_2 fixation for example range from 100 to 300 mg N m^{-2} for boreal forests (Cleveland et al. 1999, Vitousek et al. 2002). Mean denitrification rates across the boreal forest are estimated to range from 100 to 250 mg N m^{-2} (Seitzinger et al. 2006).

The final compartment required in this budget is uptake and retention by the vegetation and forest floor. Vegetation and forest floor accretion rates were not measured directly, however a mass balance approach, using N_2 fixation and denitrification rates from the literature, indicates that annual accretion rates range from 228 to 685 mg N m^{-2} (Table 7-1). This is substantially lower than other studies that measured accretion rates of approximately 1 600 mg N m^{-2} for forests in Alaska (Rhoades et al. 2008) and the northeastern U.S. (Bormann et al. 1977). However, the N_2 fixation rates in these other study sites were much greater than the estimates for the Boreal Plain. Also, the site in Alaska was on a floodplain and much of the N accretion within the forest was hypothesized to be from periodic flooding.

The estimates of N accretion however, do correspond well with estimates of N demand using biomass production within the Virginia Hills area. Timber production, expressed as annual incremental growth, ranges from 1.7 m^3 ha^{-1} yr^{-1} for black spruce to 3. 4 m^3 ha^{-1} yr^{-1} for aspen (Millar Western Forest Products 2007). This incremental growth was converted to annual N demand using Equation 3.

[3] Annual vegetation N demand = AI x BEF x %N x 1000

The annual vegetation N demand is calculated as the amount of N (in mg m^{-2}) required by the forest vegetation. AI is the annual incremental increase in total wood volume for the current 10 year age class (Table 7-2, Millar Western Forest Products Ltd. 2007). The biomass expansion factors (BEF) are parameters used to calculate total biomass from the total wood volume (Table 15, Lehtonen et al. 2004). The %N is the mean concentration of N within a tree, estimated to be approximately 0.34% (Kozlowski and Pallardy 1997). The final term (1000) is used to convert the units to mg N m^{-2}. The N accretion rates calculated using Equation 3 are 630, 712 and 453 mg N m^{-2} for the upland deciduous, upland conifer and wetland conifer stands respectively. These accretion values are near the upper range of values estimated using the mass balance approach (Table 7-1).

The accretion values estimated using the mass balance approach, are low compared with other sites (Bormann et al. 1977, Rhoades et al. 2008), or with other methods (e.g. Equation 3). These low estimates are probably related to the literature values of N_2 fixation and denitrification used in the mass balance. The upland stands in the Willow watershed contain a significant amount of alder, which is known to form symbiotic relationships with N-fixing bacteria. As a result, the estimate of N_2 fixation rates from the literature, which is a very broad estimate for across the boreal region, may be lower than the actual N_2 fixation rates within the watershed. Also, soil nitrification rates and NO_3^- concentrations in the soil porewater were low. Since NO_3^- is required for denitrification, the limited amounts of available NO_3^-, particularly during the summer when soils are warm and biological activity is high, should lead to low denitrification rates. Therefore, the literature values of denitrification may be too high. Increasing N inputs and decreasing N outputs would increase accretion rates and bring them more in line with estimates from other ecozones and other methods. However a study on the N_2 fixation and denitrification rates within the study watershed is required to confirm these hypotheses.

According to the N saturation theory, northern forested ecosystems with baseline atmospheric N inputs (i.e. stage 0 of N saturation) are N limited (Aber et al. 1989). These forests typically retain N bulk deposition inputs within the forest canopy (Dise et al. 1998); are supplied with labile N primarily through mineralization (Vitousek et al. 1984); have very low net nitrification rates (Aber et al. 1989); and export low amounts of N in surface water (Aber et al.

1989). The results from the previous chapters of this thesis were consistent with an N limited forest suggesting that the boreal forests in west-central Alberta were still in stage 0 of N saturation and were a good reference location for studying N cycling.

However, if bulk N deposition rates increase as a function of the proposed industrial developments, it is possible that the location may move into stage 1 of N saturation. As a result, N mineralization rates may increase. If the soil pH is high enough, nitrification rates may also increase. This may cause increased N content of the foliage and increased leaf area index, which may lead to enrichment of N in throughfall compared with bulk deposition. Given the remoteness of the sites however, it is unlikely that the region will experience actual N saturation and a decline in productivity in the near future.

7.2 FUTURE DIRECTIONS

There are many more aspects of an N budget that should be investigated further. First and foremost, additional years for N exports from the small sub-watersheds should be collected and examined. The one year of TDN data currently available was extreme in terms of the snowpack, which would affect the TDN exports, particularly in the spring freshet. As a result, the second year of TDN data, which should be available shortly, will provide information on TDN exports in more typical years. Further years of export data would allow a more thorough examination of how the soil and stand types affect N exports during more typical years. Also, since the spring and early summer flows tend to be responsible for the majority of the annual N flux, it would be worthwhile to more closely examine this period to see if there are differences in N concentrations between the rising and falling limbs of the spring freshet.

The N exports during spring appear to be closely related to soil freeze/thaw patterns, which are known to lyse microbial and fine root cells, resulting in higher concentrations of IN in soil leachate (DeLuca et al. 1992). However export patterns may also be related to the amount of snowmelt water that is able to percolate into the soils. If infiltration is impeded by either high antecedent moisture conditions or frozen soils, N exports should be much higher than if infiltration occurs. As a result, the role of soil type and stand composition on the depth and timing of soil freeze and thaw events may also help explain temporal variation in N exports.

As mentioned earlier, another study that should be completed is to use the acetylene reduction and acetylene block techniques to measure N_2 fixation and denitrification rates rather than using literature estimates. Finally, since soil porewater concentrations vary dramatically between seasons, a few more years of data would provide sufficient information to determine if there are differences in porewater concentrations between soil and stand types and whether porewater concentrations are consistent with N concentrations and exports in the streamwater.

7.3 IMPLICATIONS

This thesis is the first study that examines baseline N transport and retention patterns in three of the dominant stand types on the Boreal Plain as one single study, essentially tracking N flux through an entire watershed. By measuring N flux between various components of different soil and stand types, this examination hoped to explain spatial and temporal variation in N export in relatively undisturbed reference watersheds. The main difference in the budgets of the three soil/stand types was detected in the net mineralization study. Therefore, spatial variation in N export due to differences in soil/stand composition was likely because of different mineralization rates within the various soil/stand types.

This thesis has several other implications as well. Firstly, the biomass increment hypothesis states that N export is largely controlled by net biomass increment or net accumulation of nutrients in living or dead biomass (Vitousek and Reiners 1975). Since the majority of labile N inputs (either from atmospheric deposition or net mineralization) is retained via immobilization, the exports are indeed controlled by increases in biomass. Secondly, the estimates of N input compared with estimates of N export indicate that this ecosystem is accreting N at a rate ranging from 228 to 685 mg N m^{-2}, resulting in retention of about 93% of N inputs which is consistent with other forests with low N bulk deposition inputs (Watmough et al. 2005). Harvesting the trees at the year with maximum mean annual increment in this area removes between 3 260 and 7 260 mg N m^{-2} (Millar Western Forest Products Ltd. 2007), therefore even using the lower estimate for N accretion (228 mg N m^{-2} yr^{-1}), the N removed from harvesting could be replenished in under 35 years. This is much less time than the average rotation age for harvesting, suggesting that the current harvest practices should not lead to long-term N depletion. Wildfires, particularly those that consume much of the forest floor however can remove much more N than harvesting, and at current accretion rates will require much longer periods to replenish N pools in the system.

Thirdly, since forest vegetation immobilizes between 900 and 2000 mg N m^{-2}, the moderate increases of no more than 3.3 mg N m^{-2} exported after forest harvesting (Chapter 3) suggest a massive shift in N use to other ecosystem components, such as soil microorganisms and lower vegetation such as shrubs, herbs and forbs, that help retain much of the N within the watershed. Thus, to minimize N loss from the watersheds after disturbance, minimal damage to the soil and regrowth of vegetation should be encouraged.

Finally, since an average of approximately 75% of total 2007 TDN exports from these subwatersheds occurred during the month of May, care should be taken during harvesting to minimize N losses during the spring. Winter harvesting on frozen ground should limit soil disturbance and rutting, which should decrease N losses. Also, harvesting operations should be designed to extend the melting period (i.e. retain some live trees within the harvest areas, orient the long axis of winter harvest blocks east-west rather than north-south, etc). Therefore, although current harvest practices on the Boreal Plain already avoid operations during the spring thaw period because of concerns for rutting, soil compaction and increased wear on road networks, harvesting during the spring thaw should also be avoided in order to maintain ecosystem N pools.

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7.5 Tables:

Table 7-1: Mass balance for three sub-watersheds on the Canadian Boreal Plain.

Inputs (mg N m^{-2} $year^{-1}$)	
Bulk Deposition	410
N_2 Fixation	100 to 300[1]
Total	510 to 710
Outputs (mg N m^{-2} $year^{-1}$)	
Stream Export	25 to 32
Denitrification	0 to 250[2]
Total	25 to 282
Change in Storage (Accretion) (mg N m^{-2} $year^{-1}$)	228 to 685

Note: [1] Estimates of N_2 fixation rates from Cleveland et al. 1999 and Vitousek et al. 2002. [2] Estimates of denitrification rates are from Seitzinger et al. 2006.

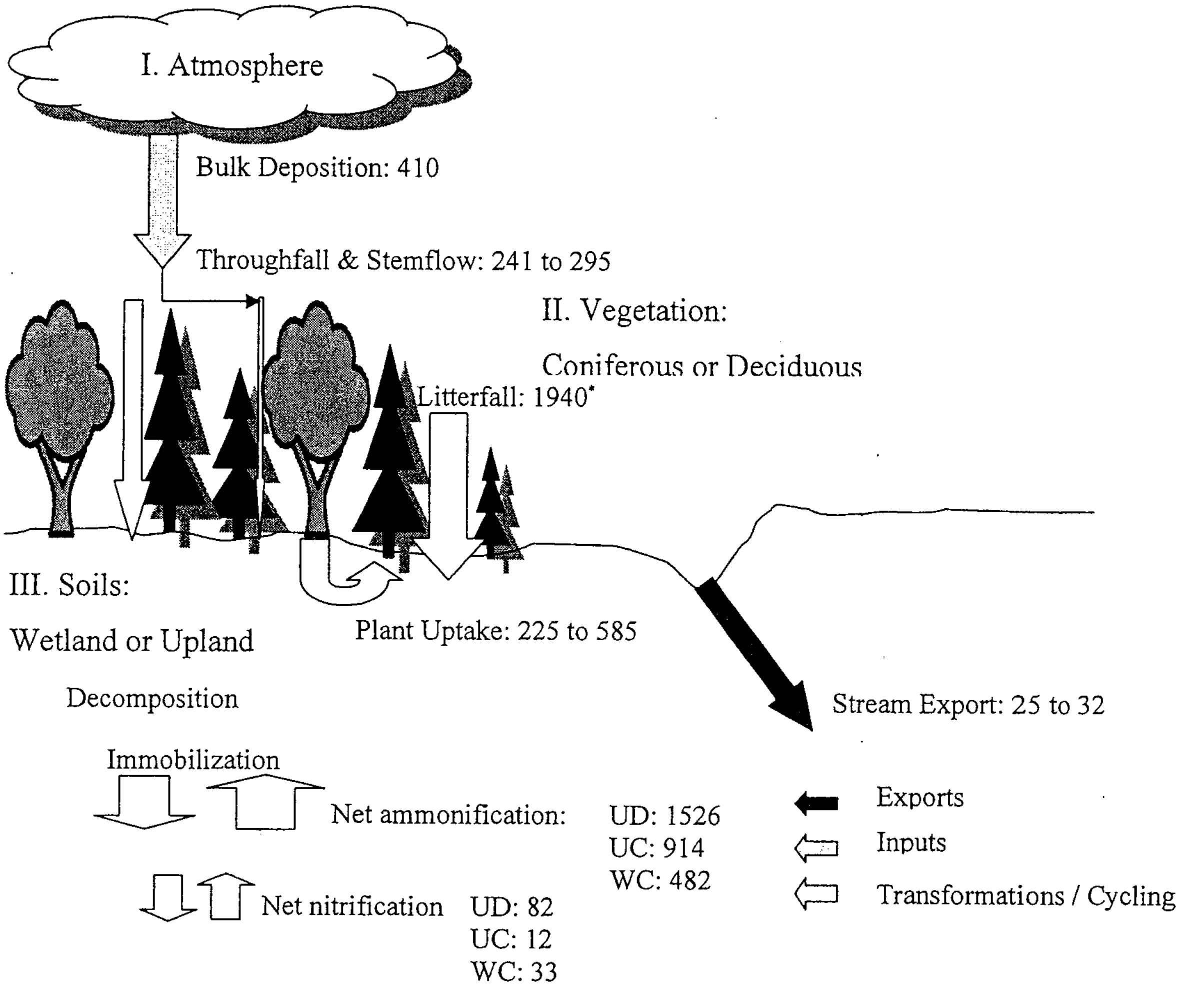
Table 7-2: Parameters used to estimate N accretion (Equation 3).

Soil/Stand Type	Dominant Species	Stand Age (yrs)	Annual Increment[1] (m^3 ha^{-1})	Biomass Expansion Factor[2]
Upland deciduous	Trembling aspen	80	3.4	0.545[3]
Upland conifer	Lodgepole pine	120	3.0	0.698
Wetland conifer	Black spruce	80	1.7	0.784

Note: [1] Estimates for annual increment taken from Millar Western Forest Products Ltd. 2007. [2] Biomass expansion factors (used to convert from timber volume [m^3 ha^{-1}] to biomass [Mg ha^{-1}] taken from Lehtonen et al. 2004. [3] BEF for aboveground biomass only.

7.6 Figures

Figure 7-1: Input, cycling and export rates for key components of a nitrogen budget for a watershed on the Canadian Boreal Plain.



Note: numeric values refer to respective rates. All rates are in mg N m^{-2} yr except for net ammonification and nitrification rates, where rates are for the period 20 June to 20 September. Values are for total dissolved nitrogen except for litterfall (total nitrogen), net ammonification (NH_4^+) and net nitrification (NO_3^-). For net ammonification and nitrification, the rates are split by stand type: Upland deciduous stands (UD), Upland conifer stands (UC) and Wetland conifer stands (WC). * Estimate of litterfall is based on average N content in litterfall of temperate forests (from Aerts et al 1997) multiplied by mean dry weights of litterfall (Appendix B).

Appendix A

Water and nutrient inputs, outputs and storage in Canadian boreal forest wetlands: a review

Water and nutrient inputs, outputs and storage in Canadian boreal forest wetlands: a review

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ABSTRACT:

Boreal wetlands, primarily peatlands, are important global carbon (C) reservoirs and integral components of regional hydrological networks. This paper summarizes our current state of knowledge regarding components of water and nutrient budgets in northern wetlands, with a focus on Canada. Boreal wetland water budgets are strongly influenced by the following: seasonal weather patterns as they relate to the timing of precipitation and meltwater inputs and evapotranspiration (ET) losses; vegetation cover in the wetland and surrounding uplands as it relates to rain and snow interception and evapotranspiration; and connectivity of the wetland to the regional hydrological network. Key factors that influence boreal wetland phosphorus (P) budgets are: spatial and temporal variability in the water table as they relate to reduction-oxidation conditions and rewetting of highly decomposed peat; concentrations of metals and ions involved in P complexation and release; vegetation age and type (herbaceous versus woody); and seasonal weather patterns as they relate to water retention time. As with other components of the boreal forest, wetlands are often limited in bioavailable nitrogen (N), therefore bulk deposition and symbiotic fixation are key N sources. Within many wetlands, N is rapidly cycled through vegetation and microbial communities, and converted to gaseous N or exported as organic N in outflows. In terms of C budgets, boreal wetlands are important reservoirs, converting inorganic and organic C inputs to peat. Climate change and anthropogenic N loading threaten the water and C balance in boreal wetlands.

Key words: boreal forest, wetlands, peatlands, hydrology, phosphorus, nitrogen, carbon.

INTRODUCTION

Wetlands are dominant landscape features in the Canadian boreal forest (Figure 1), a vast region located between 50 and 60 degrees north latitude, containing the Boreal Shield ecozone in central and eastern Canada and the Boreal Plain and Cordillera ecozones in the west. Wetlands, ranging in size from < 1 km^2 to several thousand km^2, are estimated to account for > 1 million km^2 or 20% of the Canadian boreal forest region (National Wetlands Working Group 1988), though this value may be an underestimate (Smith et al. 2007). They form important transition zones between terrestrial and aquatic habitats, often exhibit considerable biodiversity and endemism and are major carbon (C) reservoirs. In addition, they are integral components of regional hydrological networks, where they are associated with the amount and quality of water moving through boreal forest watersheds (Dillon and Molot 1997*a*; Schiff et al. 1998; Prepas et al. 2001, 2006). Peat harvesting, mining, agriculture and other landscape disturbances have led to degradation or loss of > 65% of the wetland area in Canada, relative to pre-settlement estimates (Wilson et al. 2001; Conference on Canadian Wetlands Stewardship 2003). Changes in climate regimes in recent decades also have the potential to alter wetland temperature patterns, moisture regimes, vegetation communities and microbial activity, particularly in northern latitudes where wetlands are underlain by permafrost (Zoltai et al. 1998; Rouse 2000; Beilman et al. 2001). As a result, the ecological significance of wetlands has been placed in the scientific spotlight during the past decade (e.g., Conference on Canadian Wetlands Stewardship 2003; Smith et al. 2007).

Wetland development depends on topographic, geologic and hydraulic constraints, as well as climate factors that relate to water balance (Price et al. 2005). They develop in low-lying areas or depressions where an impermeable layer impedes water infiltration or where the regional or local groundwater table is shallow (National Wetlands Working Group 1988). Also, areas with low topographic relief, poorly-defined or nonexistent channel drainage systems, and soils with low hydraulic conductivity tend to slow surface and subsurface flow, encouraging wetland development (Brooks et al. 2003). Regional geology and climate influence the extent of surface and groundwater interactions (Rouse 2000). Poor percolation of precipitation to deep aquifers caused by shallow, impermeable bedrock on the central

Canadian Boreal Shield and low hydraulic conductivity glacial till on the western Boreal Plain (Pawlowicz and Fenton 1995; Ecological Stratification Working Group 1996) result in mainly near-surface lateral flow paths (Reeve et al. 2000) and restrict regional groundwater contributions to the water balance of a given wetland (Ferone and Devito 2004). Further, evapotranspiration (ET: sum of evaporation and transpiration) typically exceeds rainfall during the growing season (Whitson et al. 2004; Devito et al. 2005); therefore discharge from wetlands usually originates from near-surface flows, instead of deeper ground water and tends to be coupled to seasonal weather patterns (Devito et al. 1996, 1999). The presence of permafrost under a wetland will also act as a barrier between surface and ground waters, restricting their interactions to the active layer that develops after thaws (Rouse 2000).

As water moves through wetlands during its journey from uplands to streams, water quality is modified by the uptake and transformation of nutrients by vascular plants, algae, bacteria and fungi and by abiotic processes like sorption, particulate sedimentation and burial (Reddy et al. 1999). Wetlands modify water chemistry to a greater extent than river or lake water surfaces of equivalent area (Saunders and Kalff 2001). Nutrient uptake and transformations depend upon the location and connectivity of the wetland relative to the watershed drainage network, the quality of inflow water, wetland soils, water table conditions and water retention time (Johnston et al. 1990; Jansson et al. 1994; Saunders and Kalff 2001). Among wetland types, peatlands (see Wetland Classification below) in particular exhibit anisotropic flow, with the direction of groundwater flow changing over a range of spatial and temporal scales (Drexler et al. 1999). Peatlands produce piston or translatory flow, whereby water entering the peatland displaces water that was in equilibrium with organic soil water (Hewlett and Hibbert 1967; McEachern et al. 2006). Given that peatlands are also the dominant wetland type by area in the Canadian boreal forest (Conference on Canadian Wetlands Stewardship 2003; Smith et al. 2007), they have the greatest potential to influence on hydrology and surface water quality in boreal forest watersheds.

Indeed, peatlands are a very significant watershed feature influencing the amount and quality of water moving through forested watersheds that constitute part of the Forest Watershed and Riparian Disturbance (FORWARD) project area in the Swan Hills, Alberta (Boreal Plain). During the ice-free season (01 May to 31 October), the total volume of water and mass of nutrients exported at the stream outlet from the watershed were positively correlated with peatland cover (Prepas et al. 2006; Prepas et al. unpubl. data), likely because wetlands in boreal watersheds with deep soils retain fewer nutrients than adjacent uplands (Verry and Timmons 1982). Data from the FORWARD study area in the Legacy Forest, Ontario (Boreal Shield) also suggest that wetlands are important components of the hydrological network in watersheds during the ice-free season (Prepas et al. unpubl. data). This contribution examines water, phosphorus (P), nitrogen (N) and C inputs, retention and outputs by Canadian boreal wetlands (primarily peatlands), drawing upon examples from other locations (i.e., northern U.S.A. and Europe) when necessary.

WETLAND CLASSIFICATION

Wetlands are broadly characterized by predominantly hydrophytic plant communities, which are distinct from adjacent upland areas (Bowden 1987). The National Wetlands Working Group (1997) classifies Canadian boreal wetlands as bogs, fens, swamps, marshes and shallow open water (Figure 2). Peatlands (bogs, fens and some swamps) have accumulations of at least 400 mm of peat. Since peat accumulation is positively associated with cooler temperatures (Clymo et al. 1998), peatlands are prevalent in the boreal forest, comprising approximately 90% (approximately 60% bog and 30% fen) of the total wetland area in Canada (Conference on Canadian Wetlands Stewardship 2003; Smith et al. 2007). As well, permafrost depth and continuity increase moving from southern to northern boreal locations (warmer to cooler mean annual temperature) (Zoltai et al. 1998; Beilman et al. 2001). Peatlands protect and promote permafrost by a combination of mechanisms that act to insulate the permafrost in summer and enhance freezing in the winter (Beilman et al. 2001).

Bogs are ombrotrophic ("cloud fed") peatlands; they are essentially hydrologically isolated from surface and groundwater inputs, and thus receive most water and nutrients from the atmosphere (Zoltai and Pollett 1983). As a result, water tables in bogs, which typically are 400 to 600 mm below the surface, fluctuate in response to precipitation events (Smith et al. 2007) (Figure 2). Bogs are usually host to plant communities endemic to poorly buffered, acidic and nutrient-poor conditions (Gorham and Janssens

1992). These acidophilic flora, particularly *Sphagnum* spp., release hydrogen ions and sustain the acidic nature of bogs (Clymo 1987) (Figure 2). Black spruce (*Picea mariana* (Mill.) BSP) may also be present in bogs that receive little precipitation (Zoltai et al. 1998). Bogs are common in the more humid boreal regions east of the Great Lakes (Zoltai et al. 1998) (Figure 1).

In contrast, fens are peatlands that are connected to surface water and groundwater tables and consequently provide buffered and fertile habitats with less variable water tables and outflow rates than bogs (Figure 2). Also, the water table is much more shallow in fens than in bogs. Vegetation cover is dominated by sedges (*Carex* spp.) and bryophytes, particularly brown mosses like *Drepanocladus* spp. and *Scorpidium* spp. (National Wetlands Working Group 1997; Zoltai et al. 1998). The relative importance of fens is higher in the sub-humid boreal region bounded by the Rocky Mountains and Great Lakes (Zoltai et al. 1998) (Figure 1). In these western Canadian boreal forests, treed (primarily black spruce) fens appear to be the dominant wetland (Locky et al. 2005; Couling et al. 2007).

Swamps and marshes are characterized by low peat accumulation rates compared to bogs and fens. Some northern boreal conifer swamps can be peatlands (Zoltai et al. 1998), though the peat material tends to be more highly decomposed than in bogs and fens (Smith et al. 2007). Swamps are wooded wetlands, with predominantly deciduous cover (e.g., alder (*Alnus* spp.) and black ash (*Fraxinus nigra* Marsh.)) in southern boreal forests and conifer cover (e.g., black spruce and tamarack (*Larix laricina* (Du Roi) K. Koch)) in the north. They are often positioned between peatlands and upland forests (Zoltai and Vitt 1995; Zoltai et al. 1998). High primary production and decomposition and low peat accumulation rates in swamps imply that they are nutrient rich compared to fens and bogs (Figure 2). Marshes are also nutrient-rich and well buffered (Verry 1997) and have high rates of decomposition and primary productivity (Thormann et al. 1999; Bayley and Mewhort 2004) (Figure 2). Lastly, shallow open waters (< 2 m deep) are free of emergent vegetation, but often feature high macrophyte biomass. They are generally found in low-lying areas throughout bogs, fens, swamps and marshes (Zoltai and Pollett 1983). For a more detailed description of wetland types in the Canadian boreal forest, see Smith et al. (2007).

WETLAND WATER BUDGETS

Simply stated, wetland water levels are determined by the difference between water inputs and outputs. Input sources are precipitation (after interception losses from vegetation), surface and subsurface flow (interflow) from upland areas, groundwater recharge (if applicable) and in the case of riparian wetlands, stream overbank flooding (Figure 3). Outputs consist of surface outflow (where present), subsurface flow (including deep seepage) and ET. Because precipitation and ET are both strongly influenced by climate, boreal wetland water balances are at risk of modification due to changing climates. Further, given that half the land area of Canada is permanently frozen (Environment Canada 2004), and that an estimated 506 billion m^3 of water is stored within perennially frozen peatlands (Tarnocai 2006), the warming trend at northern latitudes is a growing concern. Warming will lead to degradation of the permafrost, resulting in subsidence of peat that previously was uplifted by ice. This subsidence creates depressions and can lead to conversion from treed bogs to fens with internal lawns (Vitt et al. 1994), altering active layer development and ET (Beilman et al. 2001; Price et al. 2005).

Precipitation inputs into wetlands, either directly onto the wetland surface or as runoff from the surrounding uplands, vary with climate. On the sub-humid Boreal Plain, precipitation ranges from approximately 400 to 600 mm annually, whereas on the Boreal Shield, precipitation can be as high as 1600 mm annually (Natural Resources Canada 2007*a*). Across the boreal forest region, approximately 20 to 35% of the annual precipitation falls as snow. Wetland vegetation intercepts some precipitation, which evaporates (and sublimates in the case of snow) and therefore does not reach wetland soils. Canopy interception of rain increases with canopy density and leaf area, but the situation is more complex for snow. Where the forest canopy is less dense (e.g., willow), disrupted airflow above the canopy and low canopy interception combine to increase snow deposition relative to conifer forest stands (where interception is high) or open wetlands (where snow can be redistributed to margins by wind) (Metcalfe and Buttle 1998). These factors may account for snow deposition onto Boreal Plain pond-peatland complexes that was not sufficient to recharge peat storage or supply snowmelt runoff (Ferone and Devito 2004). Published canopy interception estimates range from 12% of annual precipitation in a black spruce dominated peatland in northwestern Ontario (Table 1) to 41% of precipitation that fell during the growing season on a black spruce bog in the St. Lawrence lowlands of southern Quebec (Dubé et al. 1995). Regardless of these losses, precipitation is still the dominant source of water to some wetlands, particularly ombrotrophic bogs.

Water table levels fluctuate seasonally and annually in wetlands as a result of precipitation patterns, wetland size and connectivity to surface, subsurface and groundwater sources. For example, peak stream flows in snowmelt-dominated systems, such as the eastern Boreal Shield, generally occur during the spring freshet, resulting in high water tables during the spring. However, if the snowmelt runoff is generated before upland and wetland soils thaw, it can be flow over the wetland or through only shallow peat layers, essentially bypassing the wetland (Metcalfe and Buttle 2001). On the Boreal Plain, peak stream flows usually occur as a consequence of summer storms during late June or July; therefore wetlands are usually recharged during the summer months. The exception is dry years, when transpiration by upland vegetation can be sufficient to prevent runoff from reaching wetlands (Ferone and Devito 2004). The extent of seasonal variation in water level also depends on the size and connectivity of the wetland to the regional hydrological network. Due to a greater storage capacity, large wetlands tend to have less variation in the height of the water table than smaller wetlands. Wetlands that are connected to groundwater sources continue to be recharged long after precipitation has ceased, and therefore the height of the water table fluctuates less than in isolated, ombrotrophic bogs (Petrone et al. 2007).

In general, the dominant water output from most wetlands is ET, because water availability does not limit transpiration and even non-vegetated areas tend to be moist, causing high evaporation rates (Table 1). Wetland ET losses have been estimated to constitute 50% of annual precipitation for peatlands in the Hudson Bay Lowlands (Prowse 1990), 49 to 60% of annual precipitation for a bog in southern Ontario and 114% of annual precipitation for a pond-peatland complex in northern Alberta (Table 1). During the growing season, ET rates can equal or exceed precipitation inputs and potential ET (PET: evaporation rate of open water that would occur at a given air temperature and humidity level), particularly during the day (see Crundwell 1986 and Table 1). In a northern Manitoba peatland, ET exceeded precipitation by as much as 98 mm, resulting in a soil moisture deficit of between 31 and 116 mm for the June to September period (Rouse et al. 2002). The mean daily ET value for the growing season was 2.3 mm d^{-1} for a bog in southern Ontario (Lafleur et al. 2005). Mean daily ET was similar in *Sphagnum* fens in Canada and Minnesota, with values during the growing season ranging from 2.5 to 4.8 mm d^{-1} (Lafleur and Roulet 1992; Moore et al. 1994; Kim and Verma 1996). Seasonal fluctuations in ET are positively related to air and soil temperature and photosynthetic activity (i.e., incoming solar radiation and vapour pressure deficit) , resulting in much greater ET losses during the summer (Rouse et al. 2002; Arain et al. 2003). Cold and frozen soils, typical of spring and autumn, lower the viscosity of water and decrease root permeability, restricting root uptake of soil moisture and hence decreasing ET rates (Halldin et al. 1980; Teskey et al. 1984). However, losses to ET during the non-growing season can still be substantial. For example, at the Mer Bleue bog in southern Ontario, non-growing season ET still accounted for about 25% of annual ET losses (Lafleur et al. 2005).

In addition to this seasonal variation, losses to ET vary spatially, with the height of the water table, type and depth of surface litter, and type and density of vegetation as contributing factors (Lafleur et al. 2005). Most studies agree that vegetated wetlands have ET rates that exceed pan evaporation rates (Koerselman and Beltman 1988), although there are a few that suggest the opposite (see Crundwell 1986 for a comprehensive summary). The state of growth for the hydrophytic vegetation is related with the ET losses from wetlands (Crundwell 1986). This is likely because of greater transpiration rates, since vegetation height is positively correlated with canopy resistance to evaporation (Campbell and Williamson 1997). The canopy alters the micrometeorological conditions (e.g., air turbulence, solar radiation) just above the water, changing the evaporation rate (Petrone et al. 2007). The type of plants present in the wetland will alter ET patterns as well. The presence of vascular plants, which are able to conduct water from deeper in the soil profile, allows ET to continue in wetlands until the water table drops below the rooting zone (Lafleur et al. 2005). *Sphagnum*-dominated systems however, undergo substantial decreases in ET once the water table drops more than 30 mm below the surface (Lafleur and Roulet 1992). Overall, ET seems to be related strongly with PET, with the height of the water table positively correlated with the slope of the relationship between PET and actual ET (Lafleur et al. 2005).

Soils in some wetlands, especially ombrotrophic bogs, have low conductivity and hence do not permit much groundwater flow. It is likely though that some groundwater losses occur in all types of wetlands. For example, in two pond-peatland complexes in Alberta, groundwater exports ranged from 4 to 5% of inputs, almost 5 times greater than exports in stream discharge (Ferone and Devito 2004). In the more humid climate of northern Minnesota, groundwater export from a bog was approximately 9% of inputs, while stream discharge was approximately 45% of inputs (Verry and Timmons 1982), suggesting that groundwater exports are much less variable than surface discharge. For other wetlands that are connected to the regional groundwater, deep seepage may result in substantial losses to groundwater.

WETLAND PHOSPHORUS BUDGETS

Phosphorus enters wetlands associated with dissolved and particulate organic and inorganic matter in wet and dry atmospheric deposition, or in surface and subsurface runoff from upland areas. Outputs consist of entrainment of dissolved and particulate P in surface (where present) and subsurface flow into adjacent downstream areas. Atmospheric P deposition in Canada ranges from 20 mg m^{-2} a^{-1} in central Alberta to 27 mg m^{-2} a^{-1} in central Ontario (Table 2). These values are low compared to those measured in Europe and the northern USA, particularly near industrial developments (Table 2). Inputs of P to wetlands from subsurface and groundwater sources range from 14 to 275 mg m^{-2} a^{-1} (Table 2). Annual P exports from wetlands in Canada range from 4.9 mg m^{-2} for a treed fen in west-central Alberta (Couling 2006) to 247 mg m^{-2} for a sedge fen in central Ontario (Table 2). Periphyton, bacteria, fungi and aquatic plants assimilate, store and release P (Richardson 1985; Reddy et al. 1999), processes that occur rapidly in the aerobic surface portions of wetlands. Verhoeven et al. (1990) found that P mineralization rates are much higher at 100 mm than 250 mm below the surface of the peat. This is consistent with Bridgham et al. (1998), who determined that P mineralization rates are positively correlated with aeration status, suggesting that reduction-oxidation (redox) potential and temperature affect P mineralization. Interestingly, P mineralization is greater in ombrotrophic peatlands than in minerotrophic fens (Verhoeven et al. 1990; Bridgham et al. 1998). It has been postulated that greater concentrations of ash and extractable aluminum (Al) and iron (Fe) in minerotrophic fens leads to greater immobilization and burial of P in wetland sediment, decreasing the amount of labile P.

Adsorption and release of P are dynamic processes that are also affected by the presence of metals, especially Al and Fe, and other ions (e.g., calcium (Ca)), sediment organic content, pH and redox conditions. In saturated soils at neutral to basic pH, P binds to Ca to form insoluble compounds like hydroxyapatite, whereas under acidic conditions (particularly pH < 5.5), P binds to Fe or Al to form insoluble Al and Fe phosphates (Stumm and Morgan 1996). Also, organic, P-bearing compounds may be chelated with Al and Ca ions and bound to wetland sediment (Novak and Watts 2006). Release of P from wetland sediment can occur under reducing conditions, as observed in sediment cores from a Boreal Plain lake, where the P had been complexed with Ca and magnesium (Burley et al. 2001). Also, short-chained organic acids released from plant roots and microbes stressed by water table changes (Sylvia et al. 1999; Joslin et al. 2000) can participate in direct ligand exchange or complexation of ions that are bound to P, stimulating P release (Hinsinger 2001).

Hydrologic regime is also correlated with P release, with undisturbed wetland soils releasing P when reflooding follows a dry period (Aldous et al. 2005). However, the amount of P released into the pore water seems to be related to the degree of peat decomposition; highly decomposed peat releases much higher concentrations of P after rewetting than either moderately or poorly decomposed peat (Zak and Gelbrecht 2007). The proximity of aerobic and anaerobic zones in wetlands, which shift vertically in response to water table fluctuations, surface oxygen transfer and aerobic degradation rates, means that P release and adsorption could potentially occur at several depths in the wetland profile at different times.

Plant uptake of P is most effective when vegetation communities are first developing; therefore emergent and submergent plants are used in constructed wetlands to remove P and other nutrients from highly enriched water. Herbaceous plants like wetland mosses have a greater ability to assimilate P (Chapin et al. 1987), but trees (i.e., black spruce) in forested wetlands provide longer-term P storage (Reddy and DeBrusk 1987), because the period of standing biomass development is longer and wood degrades more slowly than herbaceous material. Evidence from lake sediment indicates that the net effect of microbial activity is to convert bioavailable P to cell-bound or refractory organic P, which is then subject to burial (Gächter and Meyer 1993). Physical sedimentation and burial of P-bearing organic and inorganic matter is still considered the most important mechanism of P storage in wetlands (Richardson and Marshall 1986; Walbridge and Struthers 1993; Mitsch et al. 1995), with total P concentrations often correlated with sediment organic content and oxalate-extractable Al and Fe concentrations (Novak and Watts 2006). Wetland soils therefore provide a more stable, long-term P storage location compared to plants, because the P in the deep saturated layers essentially becomes unavailable (Brooks et al. 2003).

On an annual basis, wetlands retain P through the physical and biological mechanisms above. For example, peatlands in northern Minnesota retained an average of 61% of P inputs per annum (Table 2), whereas riparian marshes in Illinois retained from 53 to 92% of P inputs (Mitsch et al. 1995). Seasonal patterns for P retention are not universal among wetland types. Peak P retention occurred during the summer months when biotic demand was greatest for three different types of wetlands in central Ontario (Devito et al. 1989), whereas peak retention occurred during the spring in a bog in northern Minnesota (Verry and Timmons 1982). The latter observation was attributed to both the plant community (black spruce, ericaceous shrubs and *Sphagnum* moss), which still actively transpires and takes up nutrients in spring, and the lack of overland flow during the spring freshet (Verry and Timmons 1982).

WETLAND NITROGEN BUDGETS

Wetlands have been reported to act as sources (Prepas et al. 2006), sinks (Verry and Timmons 1982; Kadlec 1986) and transformation sites (Jonasson and Shaver 1999) for inorganic and organic N, depending on climate and physical and chemical characteristics of the wetland and surrounding environment. Inputs consist of atmospheric deposition, biological N fixation, and surface and subsurface runoff from upland areas. Outputs consist of N entrainment in wetland surface and subsurface outflow and microbially-mediated conversion of nitrate (NO_3^-) and ammonium (NH_4^+) to gaseous N (Table 3).

Reported N deposition rates for Canada's boreal region range from 270 mg m^{-2} a^{-1} in New Brunswick (Table 3) to approximately 1130 mg m^{-2} a^{-1} in central Ontario (Molot and Dillon 1993). This variation is likely due to regional differences in climate and proximity to urban development and associated industrial and vehicle NO_X emissions. Total N deposition rates ranged from 680 to 2210 mg m^{-2} a^{-1} for various national parks in western Canada, with the highest rate recorded at a site south of the boreal forest and close to large urban and industrial centers (Kochy and Wilson 2001). As a result of industrial development and agricultural activities, there is a general trend for N deposition rates to decrease from east to west across North America. Evidence from Europe demonstrates a link between N deposition rates, ranging from 200 to 2000 mg m^{-2} a^{-1} and C retention in peat bogs; supplementary N promotes decomposition and C loss via CO_2 flux and dissolved organic C (DOC) release (Bragazza et al. 2006).

Microbial N fixation by free-living and symbiotic bacteria living in association with certain vascular plant species can form a large portion of N inputs in some wetlands, particularly minerotrophic fens (Table 3). Woody plants such as alder (*Alnus* spp.), sweet gale (*Myrica gale*) and buckthorn (*Hippophae rhamnoides*) support symbiotic N-fixing bacteria within their root systems, greatly enhancing N fixation. Koerselman et al. (1989) found that N fixation rates in two fens in the Netherlands were positively related with *Alnus* spp. leaf area and biomass. N fixation rates for wetlands supporting N-fixing plants range from 210 to 3440 mg m^{-2} a^{-1} (Table 3). Fixation rates for free-living bacteria in Russia range from 39 to 52 mg m^{-2} a^{-1} for the top 100 mm of peat and from 183 to 243 mg m^{-2} a^{-1} for the 100 to 200 mm depth portion (Kravchenko and Doroshenko 2003) (summarized in Table 3).

The proportion of particulate and dissolved nitrogen in water entering wetlands in runoff depends on the size of the contributing area, the dominant vegetation type (Likens et al. 1970; Vitousek et al. 1982; Aber et al. 1991), elevation (Bernhardt et al. 2003), soil type (Devito et al. 1999) and the timing and magnitude of watershed disturbance (Vitousek et al. 1997; Titus et al. 1998; Aber et al. 2002). Measured N inputs to Canadian boreal forest wetlands from surface and subsurface runoff range from 535 to 9510 mg m^{-2} a^{-1} (Table 3). The subsurface flow path influences the form of dissolved N in the runoff water from upland areas, because concentrations of NO_3^- are generally low in the shallow soils of the boreal forest, especially during the growing season (Hill et al. 1999). However, subsurface flow through ephemeral draws can have higher NO_3^- and NH_4^+ concentrations than deep upland soils (Macrae et al. 2006) and may be a substantial N source to wetlands.

Wetland soils are commonly limited in labile N, with prolonged water retention periods. As a result, incoming bioavailable inorganic N (NH_4^+ and NO_3^-) is rapidly taken up by plants and microbes. In marshes and fens in Alberta, the vegetation was considered more N limited than P limited, since TN:TP ratios were < 14 in plant tissues (Bayley and Mewhort 2004). Due to low decomposition rates, the organic N in plant detritus tends to accumulate in boreal peatlands, although it is eventually leached from peat layers and exported as dissolved organic N. Devito et al. (1989) for example, reported that inorganic and organic fractions of N entering a Boreal Shield wetland were roughly equivalent, while organic N comprised 60 to 90% of total N exports. Sorption of inorganic N to soil particles within wetlands is limited to cation and anion exchange sites; hence abiotic N storage in soils is of short duration, since N is readily displaced from exchange sites by other ions. Though few data exist on N sorption rates by boreal wetland sediment, it appears to be quite low. For instance, the sorption rate for inorganic N within a tidal marsh in North Carolina was only 220 mg m^{-2} a^{-1} (Craft 1997).

Nitrogen can be transformed in wetlands via several pathways: 1) mineralization of organic N to NH_4^+; 2) nitrification of NH_4^+ to NO_3^-; 3) dissimilatory NO_3^- reduction to NH_4^+; 4) denitrification of NO_3^- into gaseous forms; and 5) anaerobic oxidation of NH_4^+ by NO_2^- to N_2 gas (anammox). Mineralization and nitrification are both aerobic processes, and nitrification rates are also highly temperature-dependent (Bridgham et al. 2001), indicating that this process is most important during the summer months. Denitrification and anammox are anaerobic processes that are limited by NO_3^- concentrations and in the case of anammox, NH_4^+ and NO_2^- concentrations as well (Koerselman et al. 1989; Jetten 2001). In agricultural or municipal watersheds impacted by excessive N, denitrification and anammox within wetlands are key pathways for N removal (Jansson et al. 1994; Whitmire and Hamilton 2005; Penton et al. 2006). The dynamic environments found in wetlands (i.e., variable water table and adjacent aerobic and anaerobic zones) may provide the electron acceptors and substrates to allow nitrification, denitrification and anammox to occur. However, given that N is a limiting nutrient in most forests

(Vitousek and Howarth 1991), these processes may be limited in undisturbed forested watersheds by low NH_4^+, NO_3^- and NO_2^- concentrations. Loss of N from wetlands via denitrification or anammox depends on minerotrophic status and height of the water table (Regina et al. 1996; Whitmire and Hamilton 2005). Measured losses of gaseous N from wetlands, traditionally attributed solely to denitrification, range from 6 to 2000 mg m^{-2} a^{-1} (Table 3).

Potential N retention in wetlands is high, in part because retention estimates usually include atmospheric losses. Following a survey of the North American and European literature, Saunders and Kalff (2001) estimated that total N retention was 64% of inputs for wetlands, compared to 2 and 34% retention for rivers and lakes, respectively. Moore et al. (2004) found that ombrotrophic bogs in eastern Canada accumulate N at rates between 500 and 4800 mg m^{-2} a^{-1}. They also noted that local topography is correlated with N accumulation rates, with hummocks accumulating N more readily than depressions. Wetland N retention rates are also dependent on water retention period, which determines the relative efficiency of biotic uptake and sorption to sediment. Temporal variations in the water table, which often show seasonal patterns, and the presence of adjacent oxidizing and reducing zones in the soil and water profile, enhance N transformation rates and thus retention (or removal) rates as well. As well, soil temperature and biotic activity and uptake peak during the summer months, often leading to increased N retention during summer, and less retention (or even net loss) occurring during the fall and winter (Verry and Timmons 1982; Devito et al. 1989).

WETLAND CARBON BUDGETS

Northern wetlands, which are mainly peatlands, comprise a massive pool of between 270 and 455 Pg (10^{15} g) of C, which constitutes between 20 and 30% of the global pool of soil C, and from one-half to two-thirds of total atmospheric C (Gorham 1991; Turunen et al. 2002). Approximately 95% of wetland C is stored as peat; typically only 1.5% is living plant biomass (Gorham 1991). In peatlands, net primary productivity (NPP) rates (gross primary productivity inputs minus respiration) exceed decomposition rates, resulting in net C accumulation (peat formation) over time (Rivers et al. 1998). Carbon sequestration in peatlands depends upon water table conditions (aerobic and anaerobic zones, water balance), vegetation transitions and microbial activity (assimilation and mineralization). Therefore, changes in wetland moisture and temperature due to climate change can affect C storage (Griffis et al. 2000; Pastor et al. 2003; Belyea and Malmer 2004). Draining of peatlands can result in increased flux of CO_2 to the atmosphere. In addition and as noted above, increased atmospheric N deposition (and other supplementary N loading) has the potential to promote decomposition of peat and reduce C storage in peatlands (Bragazza et al. 2006).

Carbon enters wetlands via biotic C fixation (primarily photosynthesis, but also other autotrophic pathways), and as particulate C, DOC and dissolved inorganic C (DIC) in surface and subsurface flow and precipitation. In general, DOC and DIC inputs in precipitation and ground water are low relative to biotic C fixation. DIC and DOC atmospheric inputs to central Ontario lakes were 140 mg m^{-2} a^{-1} and 850 mg m^{-2} a^{-1} respectively (Dillon and Molot 1997*b*) (Table 4). Values for Minnesota were higher; mean DIC and DOC loading rates from precipitation were approximately 310 mg m^{-2} a^{-1} (Peters and Bonelli 1982) and 1210 mg m^{-2} a^{-1} (Kolka et al. 1999), respectively (Table 4). DIC concentrations in groundwater recharge through peatlands tend to be low relative to ground water from upland sources (< 30 and > 150 mg L^{-1}, respectively) (Hunt et al. 1997; Rivers et al. 1998), resulting in low DIC inputs to wetlands. Among peatland types however, fens tend to have higher DIC concentrations than bogs, because fens are hydrologically connected with the surrounding landscape. The primary route for C entry into peatlands therefore is NPP, which for boreal wetlands has been estimated at between 1.1×10^5 and 4.3×10^5 mg m^{-2} a^{-1} (Table 4). Rates of NPP vary depending upon trophic status of the peatland (Frolking et al. 1998), mean annual temperature (Moore 1989*a*; Thormann et al. 1998), solar radiation, water table conditions (Szumigalski and Bayley 1997) and local topography (i.e., presence of hummocks and hollows) (Griffis et al. 2000).

Wetland C is exported as particulate C, DIC and DOC in surface and sub-surface water. Peatlands in Minnesota exported approximately 3.1×10^4 mg m^{-2} a^{-1} DOC in surface water (Kolka et al. 2001) (Table 4). However, fluctuating water tables can increase C mineralization rates by up to 300% (Aerts and Ludwig 1997) and as a result, total C exports in surface waters can range from 1.0×10^3 to 1.7×10^5 mg

m^{-2} a^{-1} (Table 4). Surface water DOC export from watersheds on the Canadian Boreal Plain, Boreal Shield and in northern Sweden were positively correlated to wetland cover (Schiff et al. 1998; Laudon et al. 2004; Prepas et al. 2006), possibly because of increased contact with organic-rich soil layers as water was routed through shallow flow paths. However, because saturated conditions in peatlands limit organic production, DOC concentrations in outflow tend to decrease after prolonged wet periods (Hinton et al. 1997; Schiff et al. 1998). Therefore, peatlands appear to be major DOC sources to surface waters after prolonged dry periods, although this influence is greatly reduced after flushing events. Wetland C budgets are challenging though, because as noted by Pastor et al. (2003), fluctuations in the water table affect both decomposition and discharge from the wetland, two variables that are difficult to separate *in situ*.

Export of C from wetlands can also occur as volatilization of CO_2 produced from plant respiration and decomposition of organic matter (microbial respiration and fermentation), and methane (CH_4) produced from methanogenesis of organic acids and CO_2. Peatlands are considered CO_2 sinks and CH_4 sources, though a given peatland area can alternate between these two states depending on water table conditions. As the water table falls, CO_2 efflux increases and CH_4 efflux decreases; the reverse is true when the water table rises (Moore and Knowles 1989). Efflux of CO_2 directly measured from wetland soils and pools is thought to derive in large part from root respiration, with rates ranging from 2.6×10^4 to 2.9×10^5 mg m^{-2} a^{-1} (Moore 1989*b*). Estimates of boreal peatland net ecosystem exchange (NEE; equal to NPP minus soil respiration), which is also used as a measure of CO_2 flux, vary widely in the literature, from a net C export of 5.0×10^4 mg m^{-2} a^{-1} (Sellers et al. 1997) to a net C input of 1.3×10^5 mg m^{-2} a^{-1} (Vitt et al. 2000). Multiple-year studies have also shown high year-to-year variation in NEE within a wetland. The NEE is strongly influenced by precipitation (Bubier et al. 1999), with warm dry years associated with C losses of up to 5.5×10^4 mg m^{-2} a^{-1} (Rouse et al. 2002). Flux of CH_4 from peatlands has been estimated to account for 5 to 10% of the global annual atmospheric load (Blodau 2002). Methane flux has been positively correlated with the minerotrophic status of the wetland (Moore and Knowles 1989), soil temperature (Crill et al. 1988; Werner et al. 2003), height of the water table (Roulet et al. 1992; Moore and Dalva 1993) and local topography (Griffis et al. 2000; Moore 1989*b*). Specific flux measurements range from 256 to 3.2×10^5 mg m^{-2} a^{-1} (Crill et al. 1988; Moore 1989*b*; Moore and Knowles 1989). Flux rates may also vary throughout the day, although reported patterns are inconsistent. For example, Hargreaves and Fowler (1998) measured higher CH_4 flux during daylight hours, Mikkela et al. (1995) found greater flux at night and Werner et al. (2003) detected no diurnal patterns at all. The higher CH_4 flux from northern wetlands noted since 1970 (Christensen et al. 2004) is likely due to the conversion of treed bogs to fens with internal lawns from loss of permafrost (Vitt et al. 1994), since both CO_2 and CH_4 flux rates are greater in the internal lawns. Over the long term however, peatlands accumulate C at rates ranging from 1.9×10^4 to 3.5×10^4 mg m^{-2} a^{-1} (Gorham 1991; Vitt et al. 2000; Turunen et al. 2002).

NUTRIENT RATIOS

Wetlands appear to differentially retain N and P: the N:P ratio of the dissolved inputs (bulk deposition and surface and groundwater flow) is different from the N:P ratio of the dissolved (excluding gaseous exchange) exports (Table 5). Where the N:P ratio increased in water after passage through the wetland, the implication is that the wetland was P limited (the P was preferentially assimilated into living biomass) or the abiotic retention of P (sorption to sediment) was sufficient to alter the ratio, or both. Where the N:P ratio decreased between inflow and outflow water, the implications (not mutually exclusive) are that the wetland was not P limited, the sorption capacity of the soils was saturated with regards to P or wetland soil conditions (redox, rewetting) facilitated P release from the sediment to the soil water. Alternately (or additively), a lower N:P ratio could indicate that N was lost to the atmosphere. Ratios for C:N and C:P tend to be higher in exports than inputs, suggesting that N and P are retained (or in the case of N, lost to the atmosphere) across a range of wetland types (Table 5). However, the amount of retention and the accompanying change to the C:N and C:P ratios vary widely among wetland types. In a central Ontario study, both the C:N and C:P ratios in conifer swamps, beaver ponds and a fen showed increases between inputs and outputs of a magnitude of no more than 3 times (Table 5). By comparison, the C:N ratio for a Minnesota bog was 16 times higher for the export than the inputs, and the C:P ratio for the export was over 200 times greater than the input (Table 5).These results can be attributed to C enrichment of precipitation water contacting organic soils.

CONCLUSIONS

Data from boreal and north temperate forests support the idea that wetlands play a key role in moderating surface water quantity and quality. Boreal wetlands historically have been viewed as sinks for C, N and P, where a high water table, anaerobic conditions and low temperatures lead to low decomposition rates and an accompanying accumulation of organic matter (i.e., peat). Labile N and P pools are generally a small percentage of the total pool in wetlands, therefore uptake of bioavailable N and P is rapid. Within wetlands, particularly peat bogs, labile N and P are converted to recalcitrant forms, much of which is retained within the peat (or lost to the atmosphere in the case of N). The retention of labile, inorganic forms of N and P is typical of boreal wetlands. The export of proportionally more organic N and P than is imported can be seen in the elevated C:N and C:P ratios in dissolved exports from wetlands. Although wetlands typically retain more nutrients than lakes, ponds or other surface waters, they are not as efficient as uplands in retaining N or P (Verry and Timmons 1982). Therefore, what is sometimes perceived as a paradox (i.e., nutrients are retained in wetlands, yet a positive correlation is often observed between watershed nutrient exports and wetland area) can be explained by their poor nutrient retention ability relative to upland areas in the watershed.

Differences in the areal estimation methodologies and classification systems contribute to high variation in wetland cover estimates across the Canadian boreal forest. Ground truthing is the most accurate method of wetland assessment, but is often impractical for remote locations or extensive wetland complexes. Application of satellite remote sensing techniques is limited by the ability of optical sensors to penetrate dense cover in vegetated wetlands (Sader et al. 1995). Radar imaging has had more success, and permits distinction between treed and non-treed wetlands (Moghaddam et al. 2000), but this technique cannot distinguish between bogs and fens. Given the importance of ET in the water balance of wetlands, linking the hydrological function of wetlands to their classification would be facilitated by an ability to accurately quantify vegetation, particularly non-vascular plants (i.e. *Sphagnum*), over large landscape areas.

Landscape-scale disturbances in the form of anthropogenic N deposition and climate change, which may include periodic droughts, will have significant influences on the water balance and C, N and P sequestration in and removal by boreal peatlands. Whereas some field studies demonstrate the linkage between weather patterns and hydrological patterns in peatlands, very few (e.g., Verry and Timmons 1982 in northern Minnesota) extend the linkage to nutrient dynamics. Some aspects of nutrient budgets, such as mineralization, NPP, methanogenesis and denitrification, have been studied in laboratory and mesocosm studies, adding to our understanding some of the mechanisms of how a changing climate could alter nutrient cycling in wetlands. However, there are only a small number of field studies that collect consistent, long-term data with which to test the hypotheses these laboratory and mesocosm studies generate. In addition, controls of some seasonal patterns in wetland water budgets are only detectable within long-term datasets (> 10 year) (e.g., Eaton and Rouse 2001). Further, an understanding of interannual variation in hydrological conditions is required to detect possible effects of climate change on biogeochemical processes in wetlands in the Canadian boreal forest.

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Table 1. Annual (unless noted) water inputs and outputs for boreal and north temperate wetlands.

Region	Water inputs (mm a^{-1})		Water outputs (mm a^{-1})			Source	Wetland type
	Precipitation	Surface / ground water	Outflow	Evapotrans.	Interception		
Central Alberta	455	43	201	342		Prepas et al. unpubl. data	Fen
Northern Alberta	347	20	18*	396		Ferone and Devito 2004	Pond-peatland
Northwestern Ontario	700				88 (bog) to 162 (swamp)	Morris et al. 2003	Bog, swamp
Central Ontario	914 to 1032		431 to 695	532 to 576		Devito et al. 1996	Swamp
Southern Ontario	750 to 1015			422 to 520		Lafleur et al. 2005	Bog
Southern Quebec†	212		0	281		Van Seters and Price 2001	Bog
Southern Quebec‡	524				183 (fen); 215 (bog)	Dubé et al. 1995	Fen, bog
Newfoundland§	120		12	126		Price and Maloney 1994	Fen
Northern Minnesota	800	339	524	505 to 525		Verry and Timmons 1982	Bog
Sweden‖	200		43	256		Kellner and Halldin 2002	Bog

* Sum of shallow and deep groundwater outflow / seepage.
† Seasonal budget (May 9 to August 13, 1998).
‡ Seasonal budget (June to September, 1991).
§ Seasonal budget (July 5 to August 14, 1990).
‖ Seasonal budget (May 24 to October 4 1996).

Table 2. Phosphorus inputs and outputs for boreal and north temperate wetlands.

Region	Phosphorus inputs (mg m^{-2} a^{-1})		Phosphorus outputs (mg m^{-2} a^{-1})	Estimated loss (-) or retention (%)	Source	Wetland type
	Bulk deposition	Surface / ground water	Outflow			
Central Alberta	20				Shaw et al. 1989	Not defined
Central Ontario	27	14 to 84	42 to 94	< 1 to 15	Devito et al. 1989	Swamp
Central Ontario	23	275	247	17	Devito et al. 1989	Fen
Central Ontario	23 to 27	43 to 118	95 to 135	-44 to 7	Devito et al. 1989	Beaver pond
Northern Minnesota	60	57	46	61	Verry and Timmons 1982	Bog
Wisconsin	132*			14	Johnston 1993	Swamp
The Netherlands	54 to 69	52 to 58	68 to 104	0 to 47	Koerselman et al. 1990	Fen

* Study wetland was near industrial/agricultural developments, which likely increased particulate deposition into the wetland.

Table 3. Nitrogen inputs and outputs for boreal and north temperate wetlands.

Region	Nitrogen inputs (mg m^{-2} a^{-1})			Nitrogen outputs (mg m^{-2} a^{-1})		Source	Wetland type
	Bulk deposition	Fixation	Surface / ground water	Outflow	Denitrification[*]		
Central Alberta	424					Shaw et al. 1989	Not defined
Central Ontario	979		535 to 2 649	1 500 to 3 640		Devito et al. 1989	Swamp
Central Ontario	994		9 510	9 940		Devito et al. 1989	Fen
Central Ontario	979 to 994		2 420	3 260 to 3 940		Devito et al. 1989	Beaver pond
Eastern Canada	270 to 810					Moore et al. 2004	Bog
Northern Minnesota	729		540	640		Verry and Timmons 1982	Bog
Massachusetts		3 440[†]				Schwintzer 1979	Fen
Russia		222 to 295[‡]				Kravchenko and Doroshenko 2003	Bog
Central Finland					6 to 2 000	Regina et al. 1996; Silvan et al. 2002	Bog, fen
The Netherlands	4 200 to 4 370	210 to 1 270[†]	730 to 2 090	1 030 to 2 120	110 to 140	Koerselman et al. 1989, 1990	Fen

[*] In some cases, gaseous N loss was attributed to entirely to denitrification before anammox pathways were understood.

[†] Nitrogen fixation by symbiotic bacteria living in root nodules.

[‡] Nitrogen fixation by free-living bacteria.

Table 4. Carbon inputs and outputs for boreal and north temperate wetlands.

Region	Carbon inputs ($mg\ m^{-2}\ a^{-1}$)			Carbon outputs ($mg\ m^{-2}\ a^{-1}$)		Source	Wetland type
	Bulk deposition	Net primary productivity[*]	Surface / ground water	Outflow	Respiration[†]		
Central Alberta		2.6×10^5 to 3.0×10^5				Szumigalski and Bayley 1997	Bog
Central Alberta		2.1×10^5 to 3.6×10^5				Szumigalski and Bayley 1997	Fen
Northern Manitoba		1.6×10^5			1.6×10^5	Trumbore et al. 1999	Bog
Northern Manitoba		2.8×10^5 to 4.3×10^5			1.9×10^5 to 2.7×10^5	Trumbore et al. 1999	Fen
Central Ontario	822		11 340 to 15 950	3.6×10^4 to 5.3×10^4		Devito et al. 1989	Swamp
Central Ontario	750		1.6×10^5	1.7×10^5		Devito et al. 1989	Fen
Central Ontario	750 to 822		3.8×10^4 to 5.3×10^4	4.6×10^4 to 5.1×10^4		Devito et al. 1989	Beaver pond
Central Ontario	990			1×10^3 to 4×10^4		Dillon and Molot 1997*b*; Schiff et al. 1998	Peatland
Northern Quebec		1.1×10^5 to 3.4×10^5				Bartsch and Moore 1985	Peatland
Northern Minnesota	1 520[‡]		2 270	3.1×10^4		Peters and Bonelli 1982; Kolka et al. 1999, 2001	Peatland

[*] Net primary productivity includes only macrophytes.

[†] Respiration includes only respiration by soil microbes.

[‡] DIC input from Peters and Bonelli (1982) and DOC input from Kolka et al. (1999).

Table 5. Summary of mean nutrient ratios for northern and boreal wetlands.

Location	N:P ratio		C:N ratio		C:P ratio		Source	Wetland type
	Input*	Output†	Input*	Output†	Input*	Output†		
Central Ontario	34.3	37.2	10.6	26.6	366	979	Devito et al. 1989	Swamp
Central Ontario	35.4	40.2	15.1	16.9	535	680	Devito et al. 1989	Fen
Central Ontario	38.3	32.8	13.4	13.7	477	430	Devito et al. 1989	Beaver pond
Northern Minnesota	10.9	13.9	3.0	48.8	32	677	Verry and Timmons 1982	Bog
The Netherlands	48.8	20.5					Koerselman et al. 1990	Fen

[*] Inputs exclude gaseous exchanges (e.g. nitrogen and carbon fixation).

[†] Outputs exclude gaseous exchange (e.g. denitrification, anammox, methane flux and respiration).

Figure 1. Map of Canada indicating areas where wetlands cover from < 5% of the area to 63% of the area. The northern and southern edges of the boreal forest region are indicated by heavy dashed lines. Modified from Natural Resources Canada (2007b).

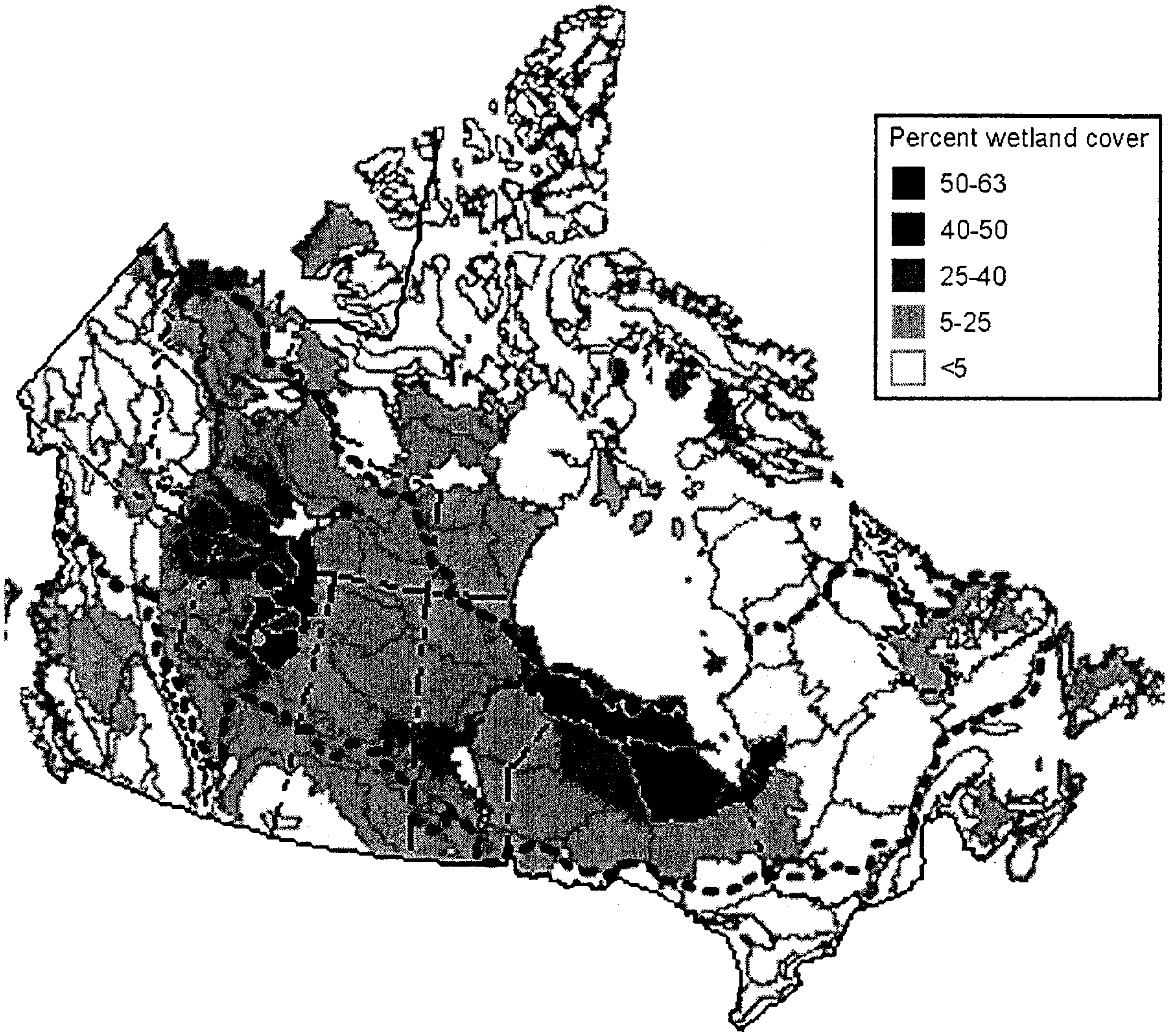


Figure 2. The five classes of the Canadian Wetland Classification System (indicated by capital letters) relative to important gradients. Water level fluctuation and acidity should be interpreted as distance from the origin. Modified from Zoltai and Vitt (1995).

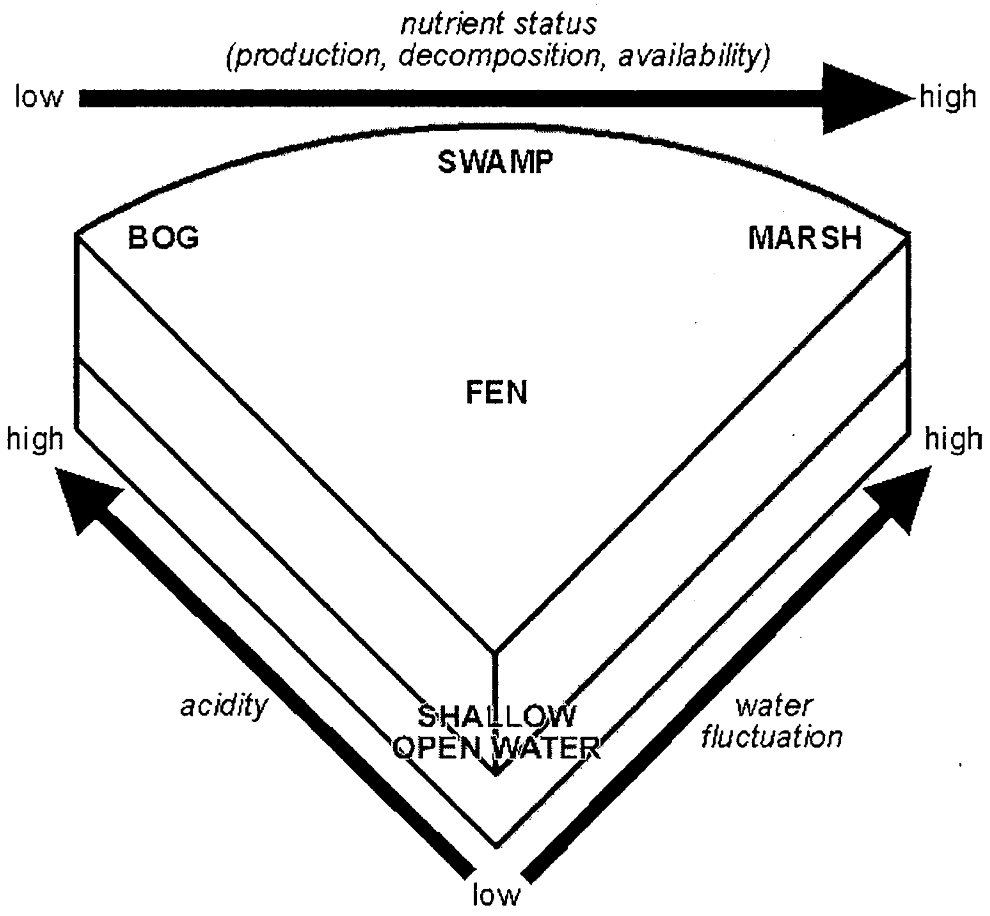
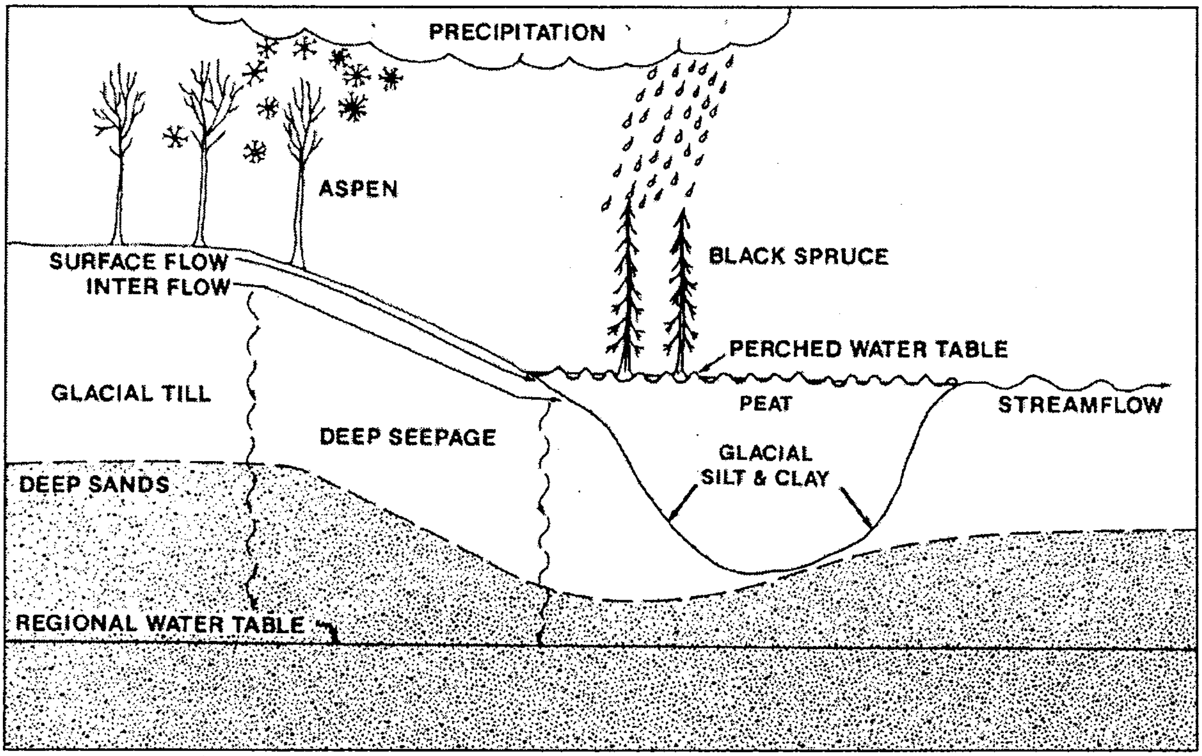
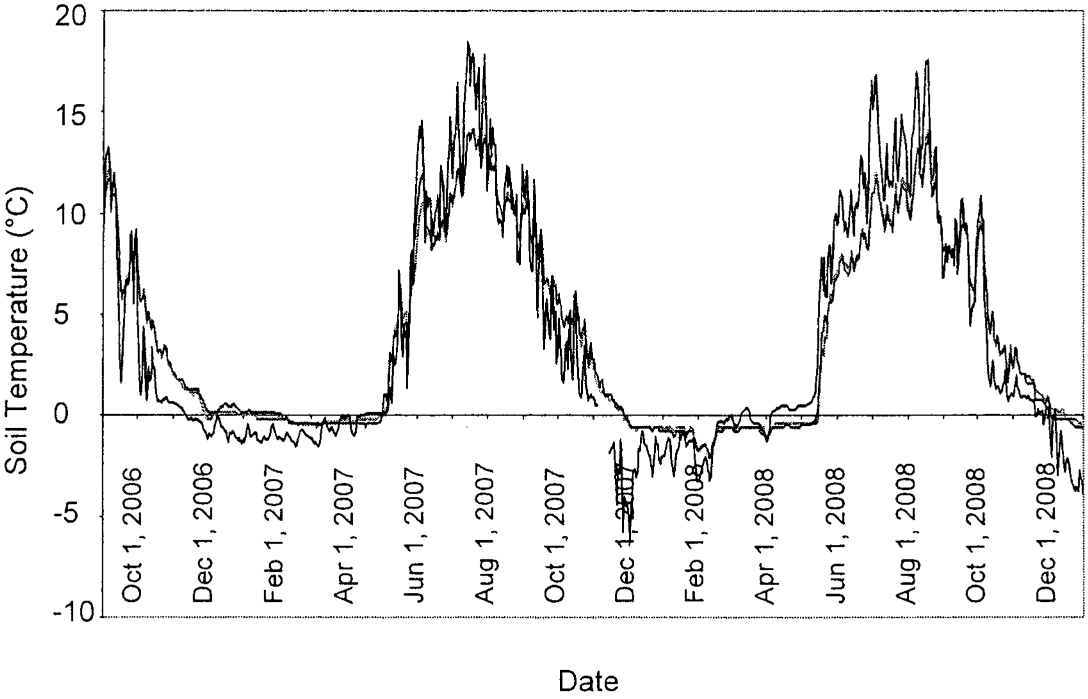


Figure 3. Cross section of a wetland and surrounding landscape, showing water input routes.

From Verry and Timmons (1982). Used by permission from the Ecological Society of America.



Appendix B Soil temperature data



Appendix C

Runoff and flow weighted mean concentrations for four reference watersheds during 2004

Figure D-1: Runoff for four reference watersheds during 2004

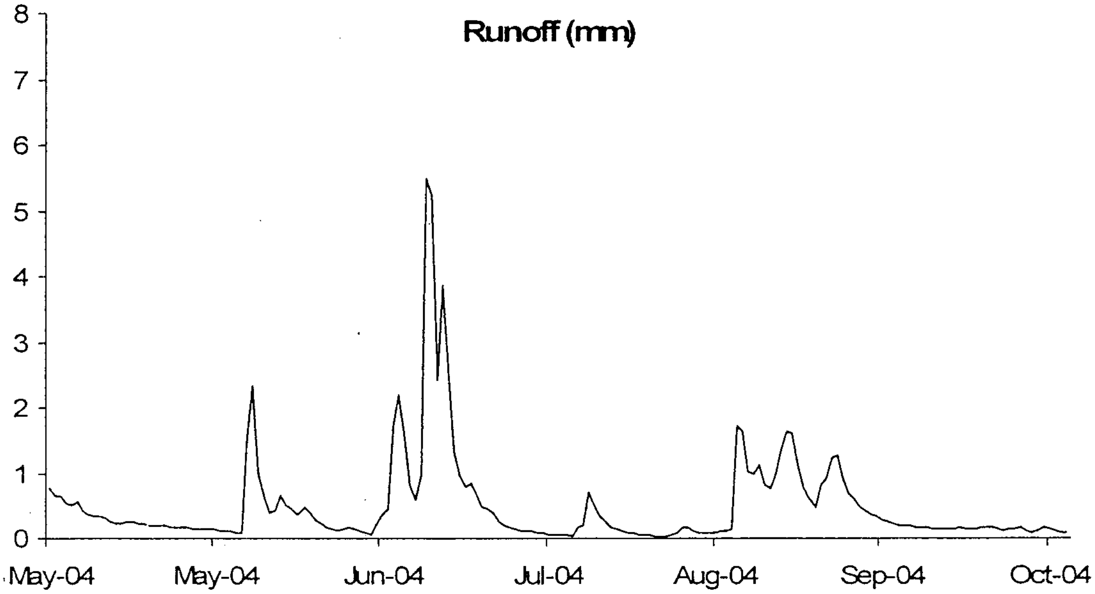
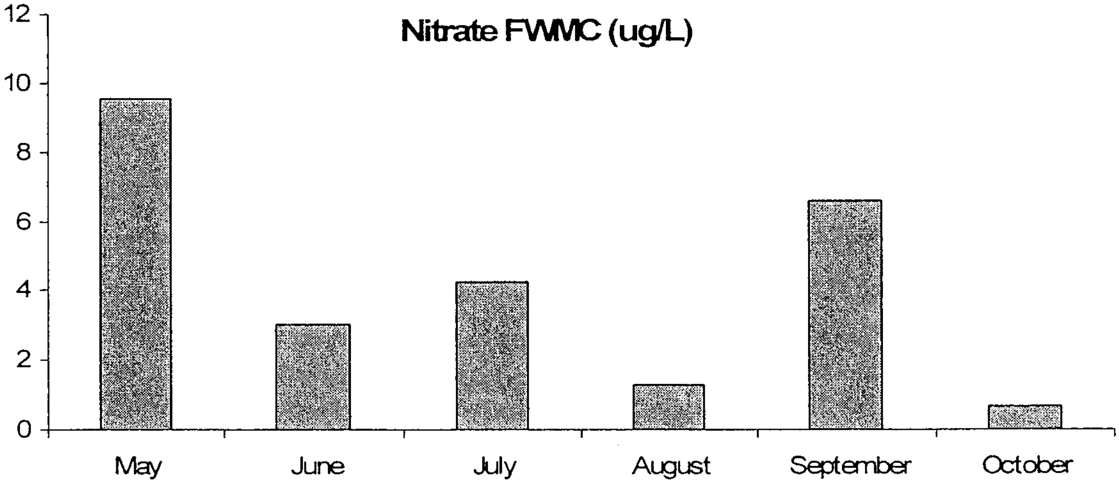


Figure D-2: Monthly flow weighted mean concentrations during 2004



Appendix D Dry weight of litterfall (g m^{-2})