EFFECTS OF WATER ADDITION ON BIOTIC AND ABIOTIC COMPONENTS OF A DRY BOREAL FOREST IN THE YUKON

by

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Abstract

To test the response of the dry Kluane boreal forest ecosystem (Yukon, Canada) to increased rainfall as predicted from climate change scenarios I irrigated three 1.5 ha forest stands from 1995-1999, to double baseline summer rainfall levels. I tested if various biotic and abiotic components of this ecosystem would react to the reduction of the summer water deficit relative to three control stands. I predicted that in response to irrigation: 1) growth (or biomass) in some species of plants would increase. 2) red-backed voles would in turn increase in numbers with greater plant-food availability because they are food-limited herbivores. 3) mushroom biomass would increase. 4) decomposition would increase, and hence 5) net nitrogen (ammonium, NH_4^+) mineralization by soil microbes (i.e. nitrogen availability for plant nutrition) would also increase, further improving plant growth (1).

Over the five years of irrigation, none of the selected species of plants nor the voles reacted to irrigation. Mushroom biomass increased 2.5-fold on irrigated stands. Litter decomposition increased log-linearly with the enhanced actual evapotranspiration (AET) following irrigation. Soil microbes immobilized NH_4^+ (rendering it unavailable to plants) as AET increased, while net NH_4^+ mineralization remained unchanged.

The lack of increase in net NH_4^+ mineralization was responsible for the lack of plant response to irrigation in this study because plants in the boreal forest, including those at Kluane, are nitrogen limited. In turn, this lack of change in net NH_4^+ mineralization can be attributed to the increase in microbial NH_4^+ immobilization. Several ecological conditions may lead to NH_4^+ immobilization by microbes, including the chemistry of the dead organic matter in the soil. Organic matter of high carbon-to-nitrogen (C/N) ratio (20 or 30/1) typically leads to net nitrogen immobilization. The C/N ratio was not monitored in this study, and more research is therefore needed to substantiate this hypothesis that Kluane soils have high C/N ratios; other studies have found high C/N ratios in boreal forest soils.

In the short-term, the detrital chain of this ecosystem would be stimulated by an increase in rainfall. No additional bottom-up effects are predicted to occur. Soil decomposers may therefore substantially enhance decomposition and CO_2 emissions of the ecosystem, without any concurrent increase in atmospheric CO_2 assimilation by plants. With climate change, the boreal forest ecosystem may become a net source of carbon to the atmosphere in the short-term, and hence exacerbate climate change through this positive feedback.

In the longer-term however, the C/N ratio of the dead organic matter in the soil may decrease, reducing microbial NH_4^+ immobilization and allowing net NH_4^+ mineralization to occur. This could eventually lead to greater primary production and more CO_2 assimilation by plants, hence counter-balancing the soil's positive feedback on climate change. The amplitude of this negative feedback through enhanced plant CO_2 assimilation and the time span before it occurs are not known. More experiments are therefore required to test whether the forest floor's C/N ratio would change in the longer term under increased precipitation and if net NH_4^+ mineralization and plant CO_2 uptake would later increase, leading to an enhancement of the carbon sink activity in this part of the boreal forest.

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Chapter I – Thesis introduction

1.1 – Boreal forests and rainfall

Boreal forests, which lie at high latitudes around the north pole, occupy 12 million km^2, or 8% of the worldwide continental surface (Lieth 1975). These forests are characterized by low primary productivity compared with other forest ecosystems because of cold temperatures and often excessive soil moisture (Elliott-Fisk 1988). Over the next 100 years, however, temperature and rainfall at the latitudes of those forests are projected to increase by 1.3-6.3°C and 5-20% because of climate change. These increases are the largest climatic changes anticipated for any latitudinal zone except tundra (Houghton et al. 2001).

Climate change may affect several biotic and abiotic components of these ecosystems, as well as the interactions between these components. Overall higher temperatures, precipitations, and CO_2 concentrations are of particular importance to boreal forest ecosystems, in addition to the projected increases in the frequency and severity of extreme weather events (Houghton et al. 2001). My study tested the effects of doubling summer rainfall on selected components of the Kluane boreal forest (southwestern Yukon, Canada).

Although soil moisture is generally not limited for plants in most boreal forests (Larsen 1980), the Kluane boreal forest is, on the contrary, dry because it lies in the rainshadow of the high St. Elias Mountains (Rowe 1972). Consequently, this forest is dominated by white spruce (*Picea glauca*) (Turkington et al. 1998), unlike most other North American boreal forests which are dominated by black spruce (*P. mariana*) (Elliott-Fisk 1988), which is entirely absent from the Kluane area (Douglas 1974). *Picea*

glauca usually dominates drier, more productive sites (Elliott-Fisk 1988), but the Kluane area is unusually unproductive compared to other boreal forests (Rowe 1972), probably due to low precipitation (306 mm per year over the period of 1944-1985, Canadian Meteorological Center 2002) and its resulting low soil moisture; I therefore expected a two-fold increase in summer rainfall to affect this ecosystem substantially.

The study area lies in the Shakwak Trench, an 8-14 km wide glacial valley, east of the high St. Elias Mountains, between the Kluane and Ruby Ranges. Although the study area lies in the zone of discontinuous permafrost (Krebs and Boonstra 2001), the soil at my sites we unfrozen. Because of the recent deglaciation (12 500 years ago, Krebs and Boonstra 2001), the main surficial deposits include glacial till, lacustrine deposits, alluvial gravels, sand dunes, and loess (Douglas 1974). Although loess is the typical basic mineral soil in the study area (Krebs and Boonstra 2001), the mineral horizon at my study sites was mostly sand. I also occasionally observed the thin (< 2 cm) white volcanic ash layer which is widespread (but sometimes completely absent) in the region, dating from 1400 years BP (Douglas 1974). The prevailing cold continental climate is particularly dry in this area because of the rainshadow of the St. Elias Mountains. During the 1958-2000 interval, the average yearly precipitation and temperature in Haines Junction (35 km south of my sites) were 335 mm and -2 °C, respectively (Tables 1 and 2). During the study period (1995-2000), rainfall and temperature however tended to be higher than those long-term averages.

The vegetation of the study area has been dominated by white spruce forests for the last 8 000 years (Lacourse and Gajewski 1998). The most extensive current community type in the area is the *Picea glauca-Salix glauca* community, those stands

being on average 130-160 years old (Douglas 1974). *Picea glauca* of the overstorey canopy on such stands has an average density of 283 stems/ha, with a mean DBH and height of 20 cm and 13m, respectively (Douglas 1974). The intermediate strata comprises 402 *P. glauca* stems/ha, of a mean DBH and height of 9 cm and 8 m, respectively (Douglas 1974). The sites I chose for my experiments were of that community type, the average spruce density (excluding trees smaller than 6 cm in DBH) was of 221 stems/ha, and their average DBH was of 13 cm. I did not measure the height of those trees nor their age. Dale et al. (2001) however found that according to their regression of DBH to age, a tree of 100 years of age should be of a DBH of 19.5 cm, suggesting that my sites may be less than 100 years old. I chose such sites because of their low tree density which allowed more efficient water distribution by the sprinklers, as water was not completely intercepted by tree trunks near the sprinklers. Densities of large spruce trees (DBH > 10 cm) on other research sites in the area ranged between 109 and 544 stems/ha, and between 685 to 985 stems/ha for small spruce trees (DBH < 10 cm) (Dale et al. 2001).

Like other areas of the boreal forest, the vegetation in Kluane is under the regime of forest fires, and partially burnt snags, stumps, and dead trees on the ground were found throughout my experimental sites. The most recent fire detected in the area dates from 1956 (Dale et al. 2001). Fire events in Kluane are usually stand-replacing, and although those fires vary in size, the majority are smaller than in other boreal forests (Dale et al. 2001). The larger fires are however responsible for most of the area burnt, as in other boreal forests of North America (Dale et al. 2001). Successive fires in Kluane tend to follow the same path, suggesting that from one occurrence to the other, they were

contained by the same topographic features of the landscape (Dale et al. 2001). 40% of the area is dominated by the post-fire regeneration of the spruce cohorts of 1870 and 1650, and another 27% of the area experienced no fire for the last 300 years (Dale et al. 2001). Dale et al. (2001) provide further details of the fire history of the area.

I review here some potential effects of enhanced rainfall (or irrigation) on selected components (or trophic levels) of this ecosystem. First, I focus on the above-ground components, namely *P. glauca* trees, as well as the shrub, herb, and moss layers, mushroom biomass, and finally herbivorous rodents and lagomorphs. Second, I focus on the (below-ground) detrital chain, namely litter decomposition and the resulting humus, and nitrogen mineralization and immobilization occurring in the humus layer. In relation to the last topic, I detail the importance of nitrogen limitation in boreal forest trees, shrub, herb, and moss layers. Finally, I point out the potential effects of enhanced rainfall on individual components of boreal forest ecosystems, and their possible feedbacks on climate.

Table 1: Monthly precipitation (mm) for summer months (May to August, inclusively) and total yearly precipitation (mm) in Haines Junction, averaged over the 1958-2000 interval, and each year from 1995-2000. Data from Environment Canada (2002).

	1958-2000 average	1995	1996	1997	1998	1999	2000
May	15	1	10	7	12	27	20
June	29	5	16	76	10	48	38
July	35	33	36	71	24	24	48
August	32	46	43	19	13	48	65
yearly	335	302	353	417	196	496	428

Table 2: Daily temperature (°C) for summer months (May to August, inclusively) and average yearly temperature (°C) in Haines Junction, averaged over the 1958-2000 interval, and each year from 1995-2000. Data from Environment Canada (2002).

	1958-2000 average	1995	1996	1997	1998	1999	2000
May	6	8	7	8	7	6	7
June	11	12	11	13	12	12	12
July	13	13	12	14	13	14	13
August	11	11	11	13	10	12	11
yearly	-2	-1	-3	0	-1	-1	0

1.2 - Above-ground effects

Plants

Sub optimal soil moisture (water deficit) often leads to reduced photosynthetic activity or plant growth. Consequently, irrigation may enhance plant growth in the Kluane forest. As a general rule, water deficits inhibit photosynthetic activity as well as total dry matter accumulation by plants (Boyer 1976). Photosynthesis is negatively affected by water deficits in several species of pines (*Pinus* spp.) across the world (Teskey et al. 1994). In the boreal forest biome, photosynthesis in *Pinus sylvestris* in Sweden decreased with the concurrent water deficit (Hellkvist et al. 1980), and was enhanced by irrigation (Bengtson 1980).

Reduced photosynthesis due to water deficits results in reduced growth in trees. Tree growth is negatively affected by soil water deficits in correlative studies in *Pinus taeda* and *Pinus echinata* in Arkansas (Basset 1964), as well as in Douglas fir (*Pseudotsuga menziesii*) in British Columbia (Giles et al. 1985). Adding support to those correlative studies, experimental irrigation enhances tree growth in several regions of the world, including boreal forests. Growth in *Picea abies* increased with irrigation in Denmark (Beier et al. 1995) and in Sweden (Nilsson and Wiklund 1992). Irrigation also enhanced growth of *Pinus sylvestris* in the Netherlands (de Visser and van Breemen 1995), as well as that of *Pinus radiata* (Raison et al. 1992, Connell et al. 1995) and of *Eucalyptus* spp. (Connell et al. 1995) in Australia.

Shrubs, herbaceous vegetation, and the moss layer may also be affected by additional rainfall, although those effects do not always occur. In one irrigation experiment on a *Pinus sylvestris* stand in Sweden, vegetation cover in both the understory

and the moss and lichen layers was enhanced (Persson 1981). A second experiment in *Pinus sylvestris* stands in Sweden generated only very small or undetectable effects on the ground vegetation (Aronsson and Elowson 1980). Herbaceous vegetation in Nevada is also affected by rainfall, where mass germination of winter annual plants depends on critical autumn rainfall amounts of at least 25 mm (Beatley 1969).

Irrigation in the Kluane boreal forest may therefore enhance growth in *Picea glauca*, but it is less clear whether the understory layer plants will respond or not. I therefore tested if irrigation enhanced growth or biomass of *Picea glauca* and several understory plant species.

Mushrooms

Mushroom production positively correlates with rainfall (Wilkins and Harris 1946, Montacchini and Caramiello 1968, Fogel 1976). Fungi participate in the dynamics of the boreal forest ecosystems in two ways, first as decomposers of dead organic matter, and second as food for mycophagous animals. Decomposition of dead organic matter in boreal forests is mostly accomplished by fungi (Frontier and Pichod-Viale 1990), and therefore decomposition may be particularly affected by an increase of rainfall in those forests. Also, the diet of the boreal red-backed vole (*Clethrionomys rutilus*) in Central Alaska comprised 6%, 2%, and 1% mushrooms during spring, summer, and fall, respectively (West 1982). Although the proportion of mushrooms in this rodent's diet was small in Alaska, and is not known for Kluane, mushrooms might stimulate a bottom-up increase in herbivore densities with irrigation. I therefore also tested whether mushroom biomass would increase with irrigation.

Small mammals

Bottom-up effects on herbivores triggered through year-to-year variations in rainfall have been documented in a number of species of small herbivorous rodents. In Denmark, densities of Bank voles (*Clethrionomys glareolus*) increased linearly with seed-masting of the European beech (*Fagus sylvatica*), which increased with the intensity of the June-July drought of the previous year (Jensen 1982). Spring densities of several species of small rodents in Nevada correlated positively with autumn rainfall amounts, through the enhancing effect of rainfall on plant germination (Beatley 1969, 1976). Similarly, spring densities of Pocket mice (*Perognathus parvus*) in Washington increased linearly with October-April precipitation, presumably through the effect of rainfall on plant productivity (Dunigan et al. 1980). In Sudan, peak reproduction in the desert jerboa (*Jaculus jaculus*) occurred during and after the rainy season, presumably through the appearance of rich food supplies (Ghobrial and Hodieb 1973).

Densities of some herbivores in the Kluane forest may similarly be susceptible to bottom-up trophic effects in relation to rainfall, if their plant food sources are rainfall-limited. In response to food-addition at Kluane, densities of snowshoe hares (*Lepus americanus*) increased 3-fold (Krebs et al. 1995), arctic ground squirrels (*Spermophilus paryii*) increased 3 to 8-fold (Hubbs and Boonstra 1997), and both deer mice (*Peromyscus maniculatus*) and boreal red-backed voles (*Clethrionomys rutilus*) increased 2 to 3-fold (Gilbert and Krebs 1981), respectively. Increased rainfall might also increase the densities of those herbivores in that area.

Because herbivorous red-backed voles are food limited (Gilbert and Krebs 1981, Schweiger and Boutin 1995) and plant growth may be water limited in the Kluane area, I

therefore also tested whether red-backed vole densities were subjected to a bottom-up increase through irrigation.

1.3 - Detrital chain effects

Litter decomposition and humus accumulation

Litter decomposition rate is largely under the influence of climate, litter chemical attributes (recalcitrance to decomposition), and the community composition of both the invertebrate detritivores and the soil microorganisms. Between-site (global-scale) differences in litter decomposition (e.g. Meentemeyer 1978, Aerts 1997), as well as temporal variations at a given site (e.g. Jansson and Berg 1985) generally correlate best with the actual evapotranspiration (hereafter AET) climatic parameter. Meentemeyer (1978) attributed the robustness of the AET model of decomposition to the fact that AET is an index of both soil thermal energy and moisture availability which affect decomposers.

Although AET is often the best climatic predictor of litter decomposition, other climatic predictors may perform better than AET. In 18 forest sites spread across Canada, litter decomposition was significantly correlated to mean annual AET, although the AET relationship was not as good a predictor as a multiple regression utilizing temperature and precipitation (Moore et al. 1999). Similarly, litter decomposition in Sweden was better correlated to a combination of temperature and soil water tension than to AET alone (Jansson and Berg 1985). Although those studies found temperature and moisture to be better predictors of decomposition than AET, they nonetheless support the general impact of temperature and rainfall on decomposition.

More important deviations from the AET model are that soil detritivores behave independently from AET (and override its effect on decomposition) in deserts and arid areas of New Mexico (Elkins et al. 1982). Clear-cutting of a hardwood forest in North Carolina negatively affected litter fragmentation by detritivorous arthropods, and hence litter accessibility to microbes. This relationship could not be accounted for by the AET model (Whitford et al. 1981). However, detritivorous arthropods are thought to be unimportant to litter decomposition in the boreal forest (Coûteaux et al. 1995) and should therefore not override the effect of AET on decomposition in those forests. The dry summers in the Kluane area result in a low AET regime and may therefore limit litter decomposition. Irrigation should therefore enhance litter decomposition at Kluane.

The effect of irrigation on the humus layer underlying the litter is, however, uncertain. Humus formation results from the decomposition of litter and should therefore be enhanced if litter decomposition is enhanced by irrigation. However, since humus formation and decomposition may both be enhanced by irrigation, the net effect of irrigation on humus will depend on the amplitudes of change in humus formation and decomposition.

The net effect of irrigation on humus may therefore be complex. I attempted to synthesize the results of 42 experimental studies, but all studies were published in Russian (37), Bulgarian (2), German (2), or Norwegian (2). The information in their English abstracts (in BIOSIS previews) suggests that humus amount decreased with irrigation in half (21) of these studies, due to decomposition (Karazhanov and Khaibullin 1988), run off (Panin and Tanasienko 1989), or increased mobility of organic substances (Panov et al. 1994). Humus content was unaffected by irrigation in 6 studies (e.g.

Kovaleva and Dergacheva 2001), and was increased in 11 studies (e.g. Akhtyrtsev and Lepilin 1979). Finally, humus thickness either increased or decreased with irrigation according to soil types or regions (4 studies): humus loss occurred in humus-rich soils, the opposite was found for soils containing little humus (e.g. Maksudov 1992).

I therefore tested if irrigation enhanced litter decomposition and reduced the amount of humus per m^2. I expected an increase in decomposition for three reasons. First, because saprophytic mushrooms may be water limited in the study area, second because litter decomposition correlates with AET (which should increase with irrigation), and third because the amount of humus decrease with irrigation more often than they increase.

Nitrogen

If changes in decomposition occur with increased rainfall, mineralization of dead organic matter by decomposers may in turn be affected by irrigation. N mineralization generally increases with soil moisture (Richards 1987), a conclusion supported by several correlative studies. For example, regional differences in temperature and moisture explained a small but significant portion of the differences in N mineralization across a broad range of forest areas of the United States (Scott and Binkley 1997). Similarly, finer textured soils (better water holding capacity) had significantly greater levels of N mineralization at 50 sites in deciduous forest sites of eastern North America, differing in soil conditions and canopy composition (Reich et al. 1997). In mixed forests of Ontario and New Hampshire, N mineralization was also correlated with soil moisture (Devito et al. 1999, Evans et al. 1998, respectively). Water added to Alaskan boreal forest soils

enhanced N mineralization at five sites differing in vegetation composition, including one dominated by *Picea glauca* (Binkley et al. 1994), the dominant tree species on my study sites.

Others however have reported either the opposite effect, no effect, or more complex effects of irrigation on N mineralization. After several years of irrigation of stands of *Pinus radiata* and *Eucalyptus* spp. in Australia, N mineralization decreased relative to control conditions (Connell et al. 1995). Similarly, N mineralization in a *Pinus radiata* forest of Australia was greater during the first year of irrigation, but it was smaller during subsequent years (Raison et al. 1992). Irrigation decreased soil N in Russian southern chernozems (Mendeshev et al. 1985), but it is not clear (English abstract of Russian paper in BIOSIS previews) whether this was due to a decrease in mineralization, or to increases in microbial denitrification, or physical leaching. However, no change in total inorganic N occurred with irrigation of a *Picea abies* forest in Germany, because of opposite changes in NH_4^+ (which increased) and NO_3^- (Von Lutzow et al. 1992).

Another factor to consider is that gross N mineralization occurs simultaneously with gross microbial N immobilization, and it is the relative amplitudes of these opposing effects that dictates net N mineralization. Gross N immobilization by microbes may be influenced by soil moisture (Richards 1987), and may hence affect the response of net mineralization to enhanced rainfall. Over a seven-month period in a *Picea rubens* (red spruce) forest in Maine, microbial N was correlated to variations in soil moisture (Christ et al. 1997). In another study, microbial N increased with irrigation in a *Picea abies* forest in Germany (Von Lutzow et al. 1992). In Russian southern chernozem soils,

irrigation also enhanced growth of soil microorganisms, but soil inorganic N decreased concurrently (Mendeshev et al. 1985) and it is not clear (English abstract of Russian paper in BIOSIS previews) whether this inorganic N loss followed from microbial immobilization only, or if microbial denitrification and physical leaching were also involved.

In summary, the effect of enhanced rainfall on net N mineralization is uncertain but should be important for plants in the boreal forest because they often are N limited. I therefore tested whether irrigation affected net NH_4^+ mineralization and net NH_4^+ immobilization.

1.4 - Integrated effects

Nitrogen limitation

Primary production in forest ecosystems is usually nitrogen limited (Richards 1987), as has been shown for boreal forests both by fertilizer experiments and by correlational analyses. In the Alaskan boreal forest, plant productivity was higher on sites of faster nutrient turnover (Van Cleve et al. 1983). Reich et al. (1997) reported that above-ground primary production increased linearly with N mineralization in all 50 forest soils that they studied in the eastern deciduous biome.

Experimental manipulations of nutrient concentrations also support those correlative studies. In interior Alaska, growth of *Picea glauca* trees increased with fertilization, but this increase was significant for only three of the five years of study (Van Cleve and Zasada 1976). Fertilization during five years substantially enhanced growth of *Pinus sylvestris* in Sweden (Aronsson and Elowson 1980). The growth of the

dominant tree species *Picea glauca* in Kluane increased with NPK fertilization application over a period of 10 years (Turkington et al. 1998), as well as with N addition alone over a period of two years (Nams et al. 1993). In Denmark, however, five years of fertilization alone did not affect stem growth of *Picea abies* (Beier et al. 1995). In the Netherlands, intermediate nutrient additions over a period of three years stimulated *Pinus sylvestris* growth, although large amounts of nutrient addition initially enhanced, but later decreased, growth (de Visser and van Breemen 1995).

Irrigation in the Kluane boreal forest may therefore have two effects, tree growth may be enhanced simultaneously through reduction of the water deficit and enhanced nutrient availability.

Plants from the understory and ground layer may however react differently than trees to increased soil nutrients. The biomass of some understory species may increase as in trees, while that of other species may either be unaffected or depressed by enhanced soil nutrients. Over ten years, percent ground cover by some herbs and herbaceous plants such as *Festuca altaica*, *Epilobium angustifolium*, and *Mertensia paniculata*, as well as shrub species such as *Salix glauca* and *Betula glandulosa* in Kluane increased with NPK fertilization. Other species such as *Anemone parviflora* and *Arctostaphylos uva-ursi* decreased, and yet others (e.g. *Solidago multradiata*, *Achillea millefolium*) did not respond (Turkington et al. 1998). In Finnish boreal forest stands of *Pinus sylvestris* and *Picea abies*, fertilizer applications depressed the biomass of mosses while other species such as grasses increased, although the total ground vegetation biomass decreased (Makipaa 1994). Similarly, in Sweden, eight years of fertilization plus irrigation decreased moss and lichen cover, while shrubs decreased and were replaced by tall, fast-

growing herbs in a *Pinus sylvestris* stand (Kellner and Marshagen 1991). In another study of a *Pinus sylvestris* stand in Sweden, the total understory layer was enhanced during seven years of fertilization, although the moss and lichen layer decreased (Persson 1981). In a third study on *Pinus sylvestris* stands in Sweden, nutrient addition alone had little or no short-term effect on ground vegetation. In combination with irrigation however, fertilization enhanced ground vegetation during the first year of experiments, but invasive species eliminated the original species during the next four years (Aronsson and Elowson 1980).

The effect of irrigation on some species of understory plants in the Kluane boreal forest may therefore be stimulated (as in trees) through both the reduction of the water deficit and the potential enhancement of nutrient availability. Other plant species may however be suppressed by the enhanced competitive exclusion by the more dominant understory species in response to those higher nutrient levels. Finally, yet other understory plant species may be indifferent to both the reduced water deficit and the enhanced nutrient concentration.

Global carbon budget

A final important point concerning enhanced rainfall involves the carbon budget of boreal forest ecosystems. On the one hand, if photosynthesis in plants is enhanced by irrigation through the reduction of the water deficit and the potential increase in nutrient availability, CO_2 uptake by plants should increase with irrigation and the irrigated forest would become a greater CO_2 sink. On the other hand, if litter decomposition is enhanced by irrigation as predicted above, CO_2 emissions by decomposers respiring this litter

might increase and the irrigated forest would become a greater CO_2 source. Decomposer CO_2 production indeed increased with soil moisture in northwest England (Howard and Howard 1993). Similarly, small fluctuations in soil moisture and enhanced temperature stimulated tundra ecosystem CO_2 efflux through an increase in both plant and soil microbial respiration (Oechel et al. 2000). The amplitudes of the relative enhancements of CO_2 sinks and sources will hence determine the net effect of climate change on the carbon budget of boreal forest ecosystems, which may play a major role in the global carbon budget.

Seasonal fluctuations in boreal forest primary production accounted for 50% of the seasonal CO_2 fluctuations measured in the atmosphere over Alaska, or 30% of the more globally representative atmospheric CO_2 concentrations over Hawaii (D'Arrigo et al. 1987). Moreover, those circumpolar forests contain 1.8×10^{11} tonnes of organic carbon in their soils (Zinke et al. 1984), i.e. they are among the largest global soil C reservoirs. Climate change in boreal forests may alter the balance of increased primary production and enhanced decomposition, changing atmospheric CO_2 concentrations and their effects on global climate. Although I did not measure the effect of irrigation on carbon uptake and output in my study, simultaneous measurements of plants, decomposition, and nutrient dynamics may offer insights on the short-term effects of irrigation on the carbon budget of this ecosystem.

1.5 - Thesis overview

The aim of my research was to address in parallel some of the above-mentioned points through an artificial enhancement of summer rainfall by irrigating boreal forest stands in the Kluane boreal forest. From 1995-1999, I doubled summer rainfall on three replicate treatment grids, which I compared to three replicate control grids subjected to natural rainfall levels. 2X average rainfall was my target treatment level because the treatment should approximate the higher end of the natural spectrum of the area rather than mimicking a deluge. The average summer (May-August) rainfall 1958-2000 (1X rainfall) was 109 mm for the study area, while the minimum was 59 mm (1998) and the maximum (1997) was 173 mm (data from Environment Canada 2002, see Table 1).

In the next chapter (Chapter II), I tested if irrigation affected 1) growth or biomass of selected species of plants; 2) mushroom biomass; and 3) *C. rutilus* vole densities. In Chapter III, I tested if irrigation affected both short- and longer-term foliage litter decomposition of two dominant plant species of the study area (white spruce, *Picea glauca*, and gray willow, *Salix glauca*), and if in turn humus mass accumulation in the forest-floor was affected by irrigation. In Chapter IV, I tested if irrigation affected net nitrogen (ammonium, NH_4^+) mineralization and net microbial NH_4^+ immobilization. Finally, in Chapter V, I synthesize the effects of the experimental increase in rainfall on the overall dynamics of this ecosystem and make suggestions for improving our understanding of climate/boreal forest feedbacks.

Chapter II – Plants, mushrooms, and voles

2.1 - Abstract

The Kluane forest is unusual in that it is less productive than other boreal forests because it lies in a rainshadow zone. Densities of *Clethrionomys rutilus* voles are known to be food limited in Kluane, and those food sources (mostly plants) could be rainfall-limited. I therefore tested the hypothesis that rainfall indirectly controlled vole densities in Kluane. My predictions were that: 1) food for voles would increase with additional rainfall, and 2) food limited voles would in turn increase in numbers. Three sites in Kluane were irrigated during the growing season for five years, and these were compared to three paired control sites without irrigation. Irrigation increased rainfall 91% above normal on average. Neither understory plants, trees, invertebrates, nor the vole population reacted to irrigation. Only mushroom biomass increased. Hence, the above hypothesis must be rejected. The vegetation is not directly water limited at these sites, and nitrogen limitation probably prevailed. However, mushrooms increased with irrigation and in turn should have increased nitrogen mineralization. It is therefore unclear why plant production and vole numbers did not increase with mushroom biomass on the irrigated sites.

2.2 - Résumé

La productivité primaire de la forêt de Kluane est inférieure à celle des autres forêts boréales, en raison du microclimat xérique qui y règne. Les densités du campagnol *Clethrionomys rutilus* sont limitées par l'abondance de nourriture dans la région de Kluane, et ces sources de nourriture (principalement des plantes) pourrait y être limitées par la sécheresse. J'ai donc testé l'hypothèse qui était que l'abondance des pluies contrôle de manière indirecte les densités de campagnols dans la forêt de Kluane. Mes prédictions étaient que 1) l'ajout expérimental de pluie augmenterait la production de nourriture pour les campagnols et 2) la densité de campagnols en serait plus élevée. Durant cinq étés, j'ai irrigué trois sites expérimentaux dans la forêt de Kluane puis les ai comparés à trois sites témoins. Les sites irrigués ont reçu en moyenne 91% plus de pluie que les sites témoins. La biomasse de champignons a fortement augmenté suite à l'irrigation, mais aucune réponse ne fut détectée du côté des plantes herbacées, des arbres, des invertébrés, et des campagnols. L'hypothèse mentionnée ci-dessus doit donc être rejettée. La faible croissance végétale dans la région de Kluane n'est donc pas directement liée aux conditions xériques; C'est plutôt le manque d'azote dans le sol qui en serait probablement responsable. Cependant, l'accroissement de la biomasse de champignons aurait dû logiquement s'accompagner d'une plus grande minéralisation de l'azote, ce qui en revanche aurait stimulé les plantes. Il n'est donc pas clair pourquoi les plantes et les campagnols n'ont pas augmenté suite à la hausse de la biomasse de champignons sur les sites irrigués. [Traduit par P.C.]

2.3 - Introduction

In the Kluane boreal forest (Yukon Territory, Canada), populations of boreal red-backed voles (*Clethrionomys rutilus*) fluctuate in an irregular fashion. Vole densities are usually low, but unpredictable outbreaks occur (Krebs and Wingate 1985, Gilbert and Krebs 1991). Although the causes for these outbreaks are not clear, year-to-year variations in food abundance could be a determining factor on vole densities because both Gilbert and Krebs (1981) and Schweiger and Boutin (1995) obtained rapid population increases with food addition experiments. Plants, the food sources for voles (Banfield 1974), could in turn be rainfall-limited, because the region undergoes a water deficit during summer (Figure 1) because of the rainshadow of the St. Elias Mountains (Rowe 1972). Water deficits reduce photosynthetic activity (Boyer 1976, Hellkvist et al. 1980, Teskey et al. 1994) as well as plant growth (e.g. Basset 1964). Above-average rainfall in Kluane could reduce the summer water deficit, which would in turn enhance primary production and reduce food limitation in voles, ultimately leading to an outbreak.

Trophic levels other than plants might further fuel this bottom-up trophic linkage mediated by rainfall. Soil microbial activity such as litter decomposition rate (Meentemeyer 1978) and soil nitrogen mineralization (e.g. Binkley et al. 1994) increase with soil moisture. Above-average rainfall should increase decomposition rate and nitrogen availability, further enhancing plant production which is also nitrogen limited in the Kluane region (Turkington et al. 1998). At the same time, production of food sources other than plants might respond to increased rainfall and therefore, reduce food limitation in voles. For instance, mushroom production correlates with rainfall (Wilkins and Harris 1946, Montacchini and Caramiello 1968, Fogel 1976), and some insects proliferate as a

result of bottom-up trophic flows triggered by increased rainfall (Clark 1974). Further, survival rate, speed of development and number of eggs laid per female in many insects also correlate with relative humidity (Bursell 1964).

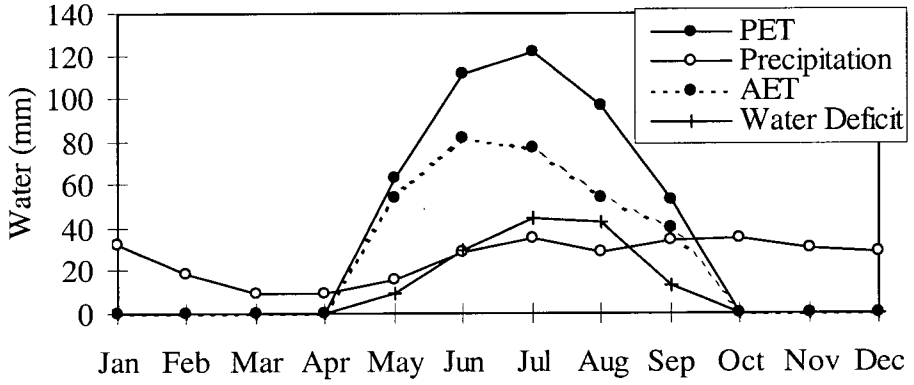

Figure 1: Average monthly water balance for Haines Junction, Yukon, showing a water deficit for each of the summer months. Climate Normals 1944-1985 from Canadian Meteorological Center (2002). Calculation methods from Thornthwaite and Mather (1957). Soil water retention assumed to be of 300 mm. PET: potential evapotranspiration; AET: actual evapotranspiration.

I tested the hypothesis that rainfall indirectly controls vole densities in the Kluane boreal forest through changes in plant production. My predictions were therefore that: 1) the biomass of plants and other food sources for voles would increase with increased precipitation, and: 2) food limited voles would in turn proliferate in response to this increase in food production. I experimentally tested these two predictions by irrigating three sites of boreal forest from 1995 to 1999, and concurrently comparing numbers of voles and their potential food sources such as mushrooms, understory vegetation, spruce

trees and forest-floor invertebrates between irrigated and nearby non-irrigated sites.

2.4 - Materials and methods

Study area and experimental sites

The study area was located in the boreal forest, near Kluane Lake (61° N, 138° W) in southwestern Yukon (Canada). Douglas (1974) classified the vegetation of the locality as a *Picea glauca-Shepherdia canadensis* (closed phase) community. The growing season lasts from mid-May to mid-August (Turkington et al. 1998). Summer rainfall (May to August inclusively) in the area is both low and variable: it ranged from 50 to 146 mm, averaging 110 mm, with a coefficient of variation (C.V.) of 31% (1944-1985 data for Haines Junction from Canadian Meteorological Center 2002).

Three replicate sites separated from each other by at least 3 km were chosen. On each site, one control ("C" grid) and one treatment grid ("T" grid) were separated by 50 to 100 m. While control grids were subjected to natural rainfall only, treatment grids were supplemented with irrigation. All grids were staked at 14-m intervals; grids at sites 1 and 2 were staked in a 10 by 10 fashion (1.6 ha each) and grids at site 3 were staked in a 13 by 7 fashion (1.4 ha each). Those six grids were used for the five years of experiments.

On treatment grids, an irrigation system was built with PVC pipe, on which 17 to 23 rotating sprinklers were installed at 30-m intervals. Sprinklers were 1.5 m above ground. Water was fed to the irrigation system with an 8 HP gas-powered pump that took water from a near-by pond. Each sprinkler delivered water over a 14 m radius area at a rate of *ca.* 35.8 l/min. During the five summers of irrigation, the three treatment

grids received between 23 and 186 mm of supplemental summer rainfall (average = 81 mm) compared to controls (Table 3). Control rainfall was increased by 16 to 380% (average = 91%) on the irrigated grids. The total amount of water received by the treatment grids during any experimental summer ranged between 82 and 214% (averaging 136%) of the maximal summer rainfall (146 mm) experienced in the region (1944-1985 data for Haines Junction from Canadian Meteorological Center 2002). Irrigation generally occurred on three occasions on each treatment grid each year, generally starting around June 15th and ending around August 7th. This irrigation period overlaps the last 2/3 of the growing season.

Sampling procedures

All samples (mushrooms, plants, or invertebrates) were taken from stations distributed in a checkerboard pattern on each grid. In 1995, sampling stations were located at grid stakes. However, on irrigated sites, sprinklers were not equally spaced from stakes, thus generating too much variability in water received at sampling stations. Therefore, from 1996 on, I positioned my sampling stations relative to sprinklers instead of stakes. For controls, sampling stations remained relative to stakes. There were 23 sprinklers on treatment grids 1 and 2, and 17 on the third. Hence, 23 stations were sampled on each of T_1, T_2, C_1 and C_2 ("C" grids being the corresponding control grids) and 17 stations were sampled on each of T_3 and C_3 from 1996 on, except when specified otherwise. The experimental units were grids. Similarly, if two quadrats were sampled per station, the sample was the average of the two quadrats, not the individual quadrats.

Table 3: Rainfall amounts (mm) between May 1 and August 31 in Haines Junction (near the experimental sites) during the five summers of experiments, as well as % increase (2 m from each sprinkler) on treatment grids compared to controls. Rainfall data from Environment Canada 2002.

Year	Controls (mm rain)	T_1 (% increase)	T_2 (% increase)	T_3 (% increase)
1995	110	47	56	51
1996*	110	47	67	67
1997	172	29	38	81
1998	49	198	143	380
1999	146	16	64	84

*: Rainfall data from May 1996 missing.

Mushroom biomass

To avoid destructive sampling of mushrooms, I first developed a predictive formula to calculate fresh biomass from their diameter. A small number (n = 62) of mature mushrooms collected in August 1995 (away from sampling stations) were used to determine this relationship. The cap diameter of each of those mushrooms was measured to the nearest 1 mm, while their weight was measured to the nearest 0.001 g. I did not distinguish species of mushrooms. Using this relationship, mushroom fresh biomass was determined once a year on quadrats on each grid, in August of 1995 to 1999.

In 1995, mushrooms were monitored using quadrats of 14 x 2m (n = 25 to 28 per grid), laid between adjacent grid stakes. Mushrooms were divided among three cap diameter size classes: 1) small (0-4 cm); 2) medium (4-8 cm); and 3) large (> 8 cm) and counted. Biomass in 1995 was calculated assuming an average diameter of 2, 6, and 8 cm for each class.

From 1996 to 1999, the yearly August mushroom surveys were done using 34 to 46 quadrats per grid. Two 10 x 2 m quadrats were laid on either sides of each sprinkler. The diameter of all mushrooms encountered in quadrats during those surveys was measured to the nearest 5 mm. Fresh biomass of mushrooms during those years was calculated from their individual cap size using the predictive formula developed in 1995.

Understory vegetation

In 1995 and 1996, above-ground biomass of the understory vegetation was measured on clip-plots once a year. In mid-August 1995, 30-34 clip-plots of 20 x 20 cm were used on each grid. Samples were air-dried for 4 months, and two species were weighed independently: *Arctostaphylos uva-ursi* and *Linnaea borealis*. The remaining species were weighed as one group. The clip-plots were larger in 1996 (30 x 30 cm) than in 1995, and were centered upon sprinklers (n = 17-23 per grid). Samples from August 1996 were oven-dried at 60 °C for 4 days, sorted, and weighed according to 8 species (or groups of species): grasses, *Arctostaphylos uva-ursi, Arctostaphylos rubra*, *Linnaea borealis*, *Equisetum* spp., *Epilobium* spp., *Achillea millefolium*, and remaining species as one group.

From 1997 to 1999, only three species were monitored at 17 to 23 stations

(sprinklers on treatments, and stakes for controls) per grid: *Festuca* sp., *Epilobium* sp., and *A. uva-ursi*. For the two former plants, total height of the four individuals closest to a station was measured as an index of growth. For *A. uva-ursi* (a perennial shrub), two branches per station were tagged at 10 mm from the terminal bud in June 1997, and the additional growth was measured each August until 1999.

Berry production in *A. uva-ursi* was also monitored. In July 1996, 15 permanent quadrats of 30 x 30 cm were installed on each grid, and all berries were removed from inside those quadrats, because they had been produced in 1994 or 1995. Each quadrat was installed as near as possible to a sprinkler (or stake for control grids), in as dense as possible a patch of *A. uva-ursi*. From 1996 to 1999, all fruits in each quadrat were harvested and counted at the end of August. An additional two to four quadrats per grid were installed in 1997.

Spruce

White spruce (*Picea glauca*) growth was estimated once a year during August of 1995-1998 through the "relative lateral branch growth ratio", or LBG (Krebs 1995 unpublished). The terminal growth of a lateral branch during a given year is compared to its terminal growth during a previous standard year. This comparison corrects for the inherent growth rate of that branch, because different trees and different branches within a tree have different growth rates. For example, if LBG 1995/LBG 1994 of a branch = 1.5, the growth in 1995 was 50% greater than that of the pre-irrigation year (1994). One branch in two to four trees per sprinkler (or stakes for control grids) were sampled, but trees less than 18 cm in circumference were excluded.

Invertebrates

Population indices for forest-floor invertebrates were obtained from pitfall traps in August 1995 and June 1996. For each trapping period, 16-25 pitfalls of 9 cm diameter and 12 cm depth were set for 17-34 days. The number of traps and the number of days of trapping was balanced for both the treatment and the control grids at each site. Pitfall traps were filled with a mixture of 3 cm of water, ethanol, and liquid soap. Invertebrates caught in traps were stored in 70% ethanol and identified later. Traps which were disturbed by animals or that dried during the trapping periods were not included in the analyses. Taxonomic groups monitored were: terrestrial snails (Mollusca; Gastropoda), centipedes (Chilopoda), spiders (Arachnida; Araneida), grasshoppers and allies (Insecta; Orthoptera), ground beetles (Insecta; Carabidae), carrion beetles (Insecta; Silphidae), and Hymenopteran and Lepidopteran caterpillars combined. Other invertebrates were ignored because they were too rare. The number of individuals of each group per pitfall per day was calculated. In 1995, the traps were installed 1 m from grid stakes, and in 1996 within 3 m of sprinklers (or stakes for control grids).

Voles

Voles were live-trapped, with 50 Longworth traps per grid set at every other grid stake in a checkerboard pattern for the entire duration of this experiment. Traps were prebaited (with apple bits and oats) for two days prior to each trapping session. Trapping sessions lasted for 2.5 days, except during 1999 when the trapping session lasted only one night. Trapping sessions occurred twice each year in 1995-1998, once in June and once in August in order to get seasonal population indices. In 1999, voles were trapped only

once in August. The minimum number of individuals known alive "MNA" (Krebs 1966) was used as the population index for each trapping session. Captured animals were individually identified to species, ear-tagged, weighed, and sex and reproductive condition determined before release. The reproductive condition of females was classified as: 1) recently mated (vagina opening perforated or not); 2) lactating; and 3) near parturition (wide gap between pubic symphyses). Obviously-pregnant females were also noted. The reproductive condition of males was classified as: 1) scrotal or 2) abdominal testes. The Animal Care Committee of The University of British Columbia approved the above procedures (protocol number: A97-0062).

Statistical analyses

When the data concerned multiple yearly surveys and did not depart from ANOVA assumptions, a 3-way ANOVA (year x site x treatment) mixed-model without replication was performed using grid averages. Year (number of levels according to number of yearly surveys) and treatment (two levels: irrigated or not) were fixed factors, while site (three levels) was random. If the data concerned a single yearly survey, a 2-way ANOVA (site x treatment) without replication was performed instead. If data severely departed from ANOVA assumptions and could not be corrected by log- or square root-transformations, a non-parametric Kruskal-Wallis one-way ANOVA with replication was performed. Since several species of plants and invertebrates were monitored simultaneously, Bonferroni corrections for multiple comparisons (according the number of groups analyzed for) were applied to determine the appropriate P-value threshold of acceptance and those are specified in the corresponding sections below.

Statistical analyses were done using SYSTAT for Windows (Wilkinson 1991).

2.5 - Results

Mushroom biomass

Fresh biomass of individual mushrooms was strongly correlated with cap area (r^2 = 0.93: Figure 2). The regression equation obtained from this relationship was used to calculate fresh biomass per quadrat. No data were collected in 1998 as mushrooms were nearly absent, and 1998 was therefore excluded from the statistical analysis. For all other years, average biomass per quadrat was on average 250% greater on treatment grids than on their respective controls (Figure 3 a). Biomass on all grids was greatest in 1997. The 3-way ANOVA (year x site x treatment) revealed that the treatment effect on mushroom biomass was statistically significant ($F_{1,2}$ = 63.0, P = 0.02). Neither the year effect nor the interaction term (year x treatment) were significant ($F_{3,6}$ = 3.2 P = 0.10, and $F_{3,6}$ = 2.5, P = 0.15, respectively).

Understory vegetation

Data on understory biomass from both 1995 and 1996 had to be analyzed with a non-parametric Kruskal-Wallis one-way ANOVA, since samples severely departed from ANOVA assumptions, even with log- or square root-transformations (Tables 4 and 5). Also, since the statistical analysis concerned several species in both years, the P-value acceptance level had to be corrected for multiple comparisons. In 1995, the acceptance level was of α = 0.05/4 = 0.013 (three species and total understory biomass), and α = 0.05/9 = 0.01 (eight species and total understory biomass) in 1996.

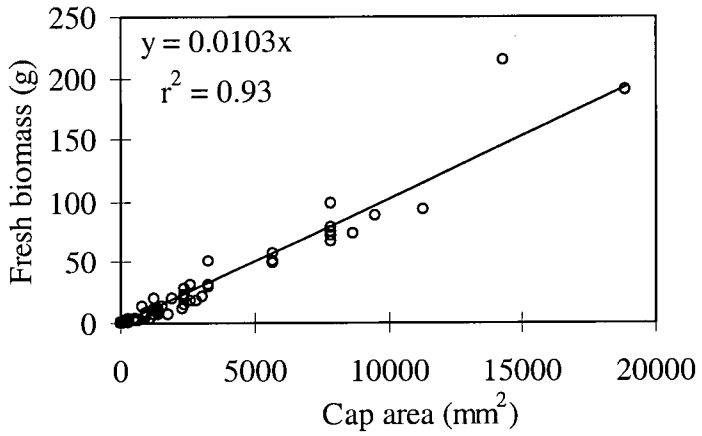

Figure 2: Linear relationship between individual mushroom fresh mass (g) and its respective cap area (mm^2) as calculated from 62 mushrooms collected in August 1995.

Irrigation had no significant effect on understory plant species or total understory biomass in both 1995 and 1996 at α levels of 0.013 and 0.01, respectively (Tables 4 and 5).

Both *Festuca* and *Epilobium* grew more in 1998 than in 1997 and 1999 (Figure 3 b, and c), and the year effect was significant for both species ($F_{2,4} = 8.5$, $P = 0.04$, and $F_{2,4} = 10.5$, $P = 0.03$ respectively). In *A. uva-ursi* (Figure 3 d), the data had to be log-transformed to meet ANOVA assumptions, and growth was not statistically different from year to year ($F_{2,4} = 2.3$, $P = 0.22$). The treatment and the year*treatment effects were not significant for either species.

For the purpose of the statistical analysis, the data on berry production in *A. uva-ursi* from 1995 was excluded because of the large error involved in dating the berries, since they were collected in early summer 1996 and could have been from 1994 or 1995. The data from 1996 to 1999 had to be log-transformed to conform to ANOVA

assumptions. Berry production was on average 150% higher on irrigated grids than on their respective controls (Figure 4 a), although this trend was not present in 1995 and 1997. Berry numbers were extremely low in 1997, while at their highest in 1998. Numbers were intermediate in 1996 and 1999. The 3-way ANOVA on the data from 1996-on revealed the presence of a year effect ($F_{3,6} = 10.7$, $P = 0.01$) but neither the treatment nor the year*treatment effects were significant ($F_{3,6} = 2.9$, $P = 0.13$ and $F_{1,2} = 8.5$, $P = 0.10$).

Spruce lateral branch growth

In general, spruce lateral branch growth from 1995-on was less than that of 1994 (Figure 4 b). The 3-way ANOVA showed the treatment effect to be not significant ($F_{1,2} = 0.7$, $P = 0.48$). However, as in the case with understory vegetation, the year effect was significant ($F_{3,6} = 7.83$, $P = 0.01$) and for spruce, so was the year*treatment effect ($F_{3,6} = 10.6$, $P = 0.01$).

Overall, plant measurements that spanned for at least 2 years and in which a year effect could be tested for in a 3-way ANOVA showed this effect to be significant, except for growth of *A. uva-ursi*. Neither the understory vegetation species that were monitored, nor spruce trees showed a significant treatment effect.

Invertebrate numbers

The 3-way ANOVA on invertebrates for 1995 and 1996 was performed on seven groups, hence the acceptance level was therefore $\alpha = 0.05/7 = 0.007$, as required by the Bonferroni correction. No significant effect of year, treatment, or year*treatment

interaction were found (Table 6).

Voles

Voles were absent at the beginning of the experiment in spring 1995 on all grids, and consistently increased until 1998 during both the spring and the fall (Figures 5 a and b, respectively). Voles were scarce again in August 1999. In both June (1995-1998) and August (1995-1999), there was neither a significant treatment effect ($F_{1,2} = 0.1$, $P = 0.76$ and $F_{1,2} = 0.1$, $P = 0.80$, respectively) nor a year*treatment effect ($F_{3,6} = 0.3$, $P = 0.82$ and $F_{4,8} = 0.3$, $P = 0.82$, respectively), but both showed a significant year effect ($F_{3,6} = 7.4$, $P = 0.01$ and $F_{4,8} = 10.4$, $P = 0.003$, respectively).

Table 4: Sample size per grid (n), average clip plot dry mass (g) per grid per group, within grid standard deviation, and non-parametric Kruskal-Wallis one-way ANOVA U and P-values. August 1995.

	C_1		T_1		C_2		T_2		C_3		T_3			
Group	n = 33		n = 33		n = 34		n = 33		n = 24		n = 26		U	P
	av.	S.D.	av.	S.D.	av.	S.D.	av.	S.D.	av.	S.D.	av.	S.D.		
A. uva-ursi	6.2	8.7	6.1	8.2	1.2	2.6	5.6	7.6	3.0	4.0	2.3	3.2	4.0	0.83
L. borealis	0.1	0.5	0	0	0.1	0.4	0.6	1.1	0.6	1.0	0.3	0.7	5.0	0.83
Others	1.2	1.1	1.1	1.2	1.3	1.9	0.9	0.9	1.2	1.1	1.1	1.5	9.0	0.05
Total	7.5	8.6	7.2	8.5	2.5	3.4	7.1	8.0	4.9	4.0	3.7	3.6	4.0	0.83

Table 5: Sample size per grid (n), average clip plot dry mass (g) per grid per group, within grid standard deviation, and non-parametric Kruskal-Wallis one-way ANOVA U and P-values. August 1996.

	C_1		T_1		C_2		T_2		C_3		T_3			
Group	n = 33		n = 33		n = 34		n = 33		n = 24		n = 26		U	P
	av.	S.D.	av.	S.D.	av.	S.D.	av.	S.D.	av.	S.D.	av.	S.D.		
A. uva-ursi	4.3	5.4	8.3	10.0	3.3	7.3	5.0	6.5	4.3	7.2	7.6	11.2	0.0	0.05
A. rubra	0.0	0.0	0.0	0.0	0.1	0.2	0.1	0.3	2.0.	2.3	0.6	1.5	4.5	1.00
Grass	1.4	1.2	1.3	1.3	1.0	0.9	1.5	1.3	0.4	0.4	0.7	0.9	3.0	0.51
Equisetum spp.	0.0	0.0	0.0	0.0	0.2	0.4	0.1	0.1	0.7	0.6	0.2	0.2	5.5	0.66
Epilobium latifolia	0.6	0.9	0.6	1.0	0.1	0.3	0.1	0.2	0.1	0.1	0.1	0.3	5.0	0.83
Achillea millefolium	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.2	4.5	1.00
Linnaea borealis	0.1	0.6	0.0	0.0	0.5	1.1	0.4	1.0	1.0	1.7	0.5	0.8	7.0	0.28
Others	0.2	0.3	0.2	0.3	0.4	0.9	0.2	0.2	0.6	0.5	0.4	0.5	5.0	0.83
Total	6.7	5.9	10.4	9.4	5.5	7.9	7.3	6.9	9.0	7.1	10.2	11.6	1.0	0.13

Table 6: Top: Average invertebrate number/trap/day for each grid (fall 1995 and spring 1996) using 16 to 25 pitfall traps, for 17-34 days. Bottom: 3-way ANOVA F and P-values for Y (year), T (treatment), and Y*T (interaction) effects.

Year	Grid	Snail	Spider	Centipede	Grasshopper	Carabidae	Silphidae	Lepidoptera
1995	C_1	0.026	0.249	0.020	0.091	0.043	0.018	0.067
	T_1	0.002	0.272	0.002	0.082	0.065	0.062	0.017
	C_2	0.003	0.468	0.008	0.127	0.066	0.014	0.083
	T_2	0.002	0.434	0.004	0.099	0.075	0.018	0.029
	C_3	0.048	0.496	0.012	0.058	0.029	0.031	0.044
	T_3	0.027	0.294	0.002	0.029	0.035	0.035	0.048
1996	C_1	0.000	0.315	0.006	0.002	0.161	0.000	0.027
	T_1	0.008	0.712	0.000	0.002	0.246	0.000	0.052
	C_2	0.008	1.214	0.013	0.035	0.168	0.000	0.201
	T_2	0.000	1.386	0.010	0.056	0.138	0.000	0.350
	C_3	0.058	0.767	0.004	0.004	0.094	0.000	0.125
	T_3	0.029	0.742	0.005	0.005	0.069	0.000	0.221
Y	$F_{1,2}$	0.0	7.0	0.2	23.0	10.2	17.3	3.2
	P	0.88	0.12	0.71	0.04	0.09	0.05	0.22
T	$F_{1,2}$	3.9	0.3	6.2	4.8	0.3	1.7	1.9
	P	0.19	0.62	0.13	0.16	0.65	0.32	0.30
Y*T	$F_{1,2}$	0.2	16.9	5.2	6.4	0.0	1.7	9.4
	P	0.71	0.05	0.15	0.13	0.95	0.32	0.09

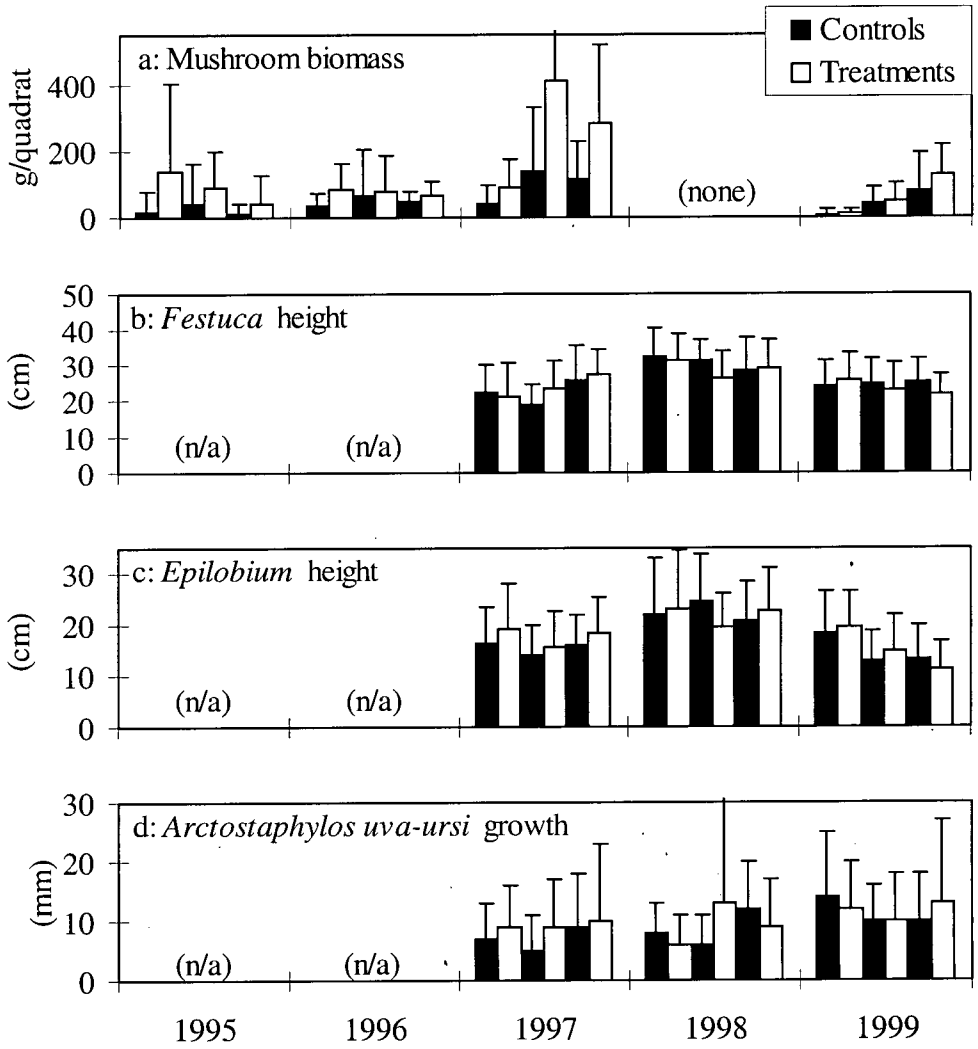

Figure 3: Time-series (grid averages) for a: mushroom fresh biomass (g/quadrat); b: *Festuca* height (cm); c: *Epilobium* height (cm); and d: *Arctostaphylos uva-ursi* growth (mm). Error bars: standard deviations around the means. Order of bars from left to right within any year is C_1, T_1, C_2, T_2, C_3, and T_3.

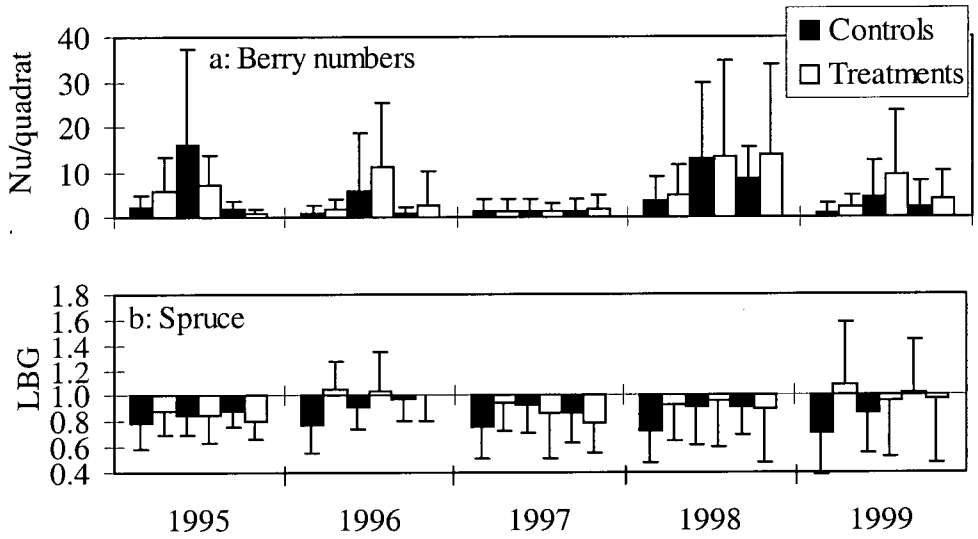

Figure 4: Time-series (grid averages) for a: *Arctostaphylos uva-ursi* berry numbers per quadrat, and b: Spruce LBG (relative to 1994). Error bars: standard deviations around the means. Order of bars from left to right within any year is C_1, T_1, C_2, T_2, C_3, and T_3.

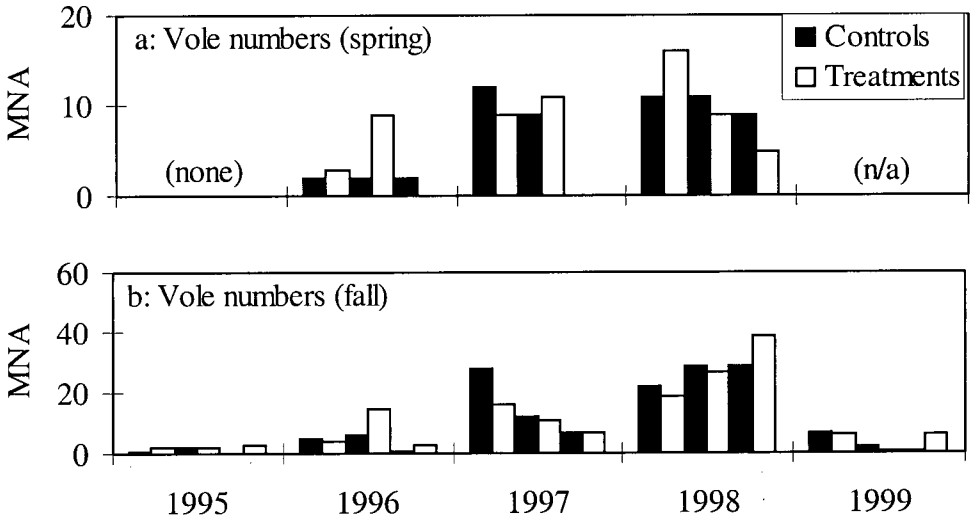

Figure 5: *Clethrionomys rutilus* minimum number alive (MNA) per grid per year, a: in the spring, and b: in the fall. Order of bars from left to right within any year and any time-series is C_1, T_1, C_2, T_2, C_3, and T_3.

2.6 - Discussion

The aim of this study was to test if rainfall indirectly controlled food limited vole densities through its effect on food availability. I therefore tested the predictions that: 1) the biomass of plants, mushrooms, and insects (food sources for voles) would increase with increased precipitation in the dry Kluane boreal forest, and: 2) food limited voles would proliferate in response to this increase in food production. Although voles varied in numbers from being absent to being in high densities during the course of this 5-year study, their numbers remained unaffected by irrigation across the nine trapping sessions, in both June and August. Because the watering levels on treatment grids ranged between 82 and 176% (averaging 112%) of the maximal summer rainfall experienced in that area between 1958 and 1999 (Environment Canada 2002), voles should have shown a response to irrigation if variation in rainfall levels affect their densities. Their lack of response therefore signifies that rainfall does not affect vole densities through a bottom-up trophic chain.

If rainfall does not affect vole densities, it is either because food sources for voles are not limited by summer rainfall, or that (even if their food is water limited) vole numbers are not food limited. The latter is unlikely, as both Gilbert and Krebs (1981) and Schweiger and Boutin (1995) generated population increases in this species with food addition in that area.

It is unlikely that the lack of vole response to irrigation followed from experimental discrepancies in population censuses, because both Schweiger and Boutin (1995) and Gilbert and Krebs (1981) obtained vole density increases with food addition on grids of comparable sizes (1.8 ha and 2.3 ha each, respectively) to mine (1.4 or 1.6 ha)

and using similar census methods.

Conversely, it is more likely that food sources for voles are not water limited in Kluane. In Central Alaska, *C. rutilus* feeds on lichens, mushrooms, mosses, dicot leaves, fruit and seeds, as well as arthropods (West 1982). Among the food categories which were monitored in my experiment, only mushrooms responded to irrigation. West (1982) found mushrooms in *C. rutilus*' s diet in Central Alaska, but only as a small fraction of their diet, i.e. 6%, 2%, and 1% during spring, summer, and fall, respectively. Fruit and seeds were eaten much more, representing 73%, 62%, and 92%, and arthropods constituted from less than 1% to 6% (West 1982). Although irrigation generated an average 2.5-fold (Figure 3 a) increase in mushroom fresh biomass and as high as 7.4-fold between C_1 and T_1 in 1995, this did not affect vole densities. Thus, voles were not "mushroom limited", and any food limitation had to be in relation to other food, likely fruit and seeds because those represent the staple of their diet. If fruit and seeds are the limiting food sources and they did not react to irrigation, it is not surprising that voles also showed no response. What is more surprising is that only mushrooms were shown to be water limited in the dry Kluane rainshadow zone, and not the plants. Water-deficits have been shown to substantially reduce growth in *Pinus taeda* and *P. echinata* (Basset 1964), so the reduction of the water deficit by irrigation was expected to increase plant growth. Therefore it appears that plants are either stress-tolerant or limited by other factors.

Grime (1977) considers plants of dry areas to be stress-tolerant, and hence, to have inherently slow growth rates. In his view, even when the stress in those species is relieved, they do not respond by growth. This seems unlikely for some of the plant

species found in Kluane, since nutrient additions in that area generated an increase in cover of *Festuca altaica*, *Mertensia paniculata* and *Achillea millefolium*, as well as an increased growth rate in white spruce, *Salix glauca* and *Betula glandulosa* (Turkington et al. 1998). Some plants in the Kluane area showed quick responses to nutrient stress-reduction, and are therefore not stress-tolerators, *sensu* Grime (1977). If plants in Kluane were water-stressed, their growth response would have been noticeable with irrigation. Alternatively, vegetation in the Kluane boreal forest may be nitrogen limited. Turkington et al. (1998) have obtained an immediate response to fertilizer addition at Kluane, and nitrogen limitation has been shown for the boreal forest in general (Zasada et al. 1977, Aronsson and Elowson 1980, Van Cleve and Alexander 1981, Bonan and Shugart 1989, Schulze et al. 1994). However, decomposition and nitrogen mineralization are known to depend on water availability (e.g. Meentemeyer 1978, Binkley et al. 1994). Decomposition in boreal forests is performed mostly by Fungi (Frontier and Pichod-Viale 1990), which also depend on soil humidity (Wilkins and Harris 1946). Mushrooms reacted strongly to irrigation and this suggests that nitrogen limitation in plants could have been alleviated by the treatment, assuming that mushroom biomass is indicative of the performance of decomposers and nitrogen mineralization. Thus, the idea that the lack of plant response to irrigation was due to nitrogen limitation and not water limitation seems discordant with the mushroom biomass response to irrigation. This inconsistency can be resolved by only one of the following three hypotheses (Figure 6): 1 a: plants in Kluane are not nitrogen limited, and therefore 1 b: water limited nitrogen mineralization by decomposers released unnecessary nitrogen with irrigation; 2: plants in Kluane are nitrogen limited, but decomposers are not water limited and therefore could not affect

nitrogen availability in response to irrigation; 3: plants in Kluane are nitrogen limited and decomposers are water limited, but in response to irrigation, decomposers immobilized nitrogen instead of mineralizing it. These hypotheses will be tested in the subsequent chapters.

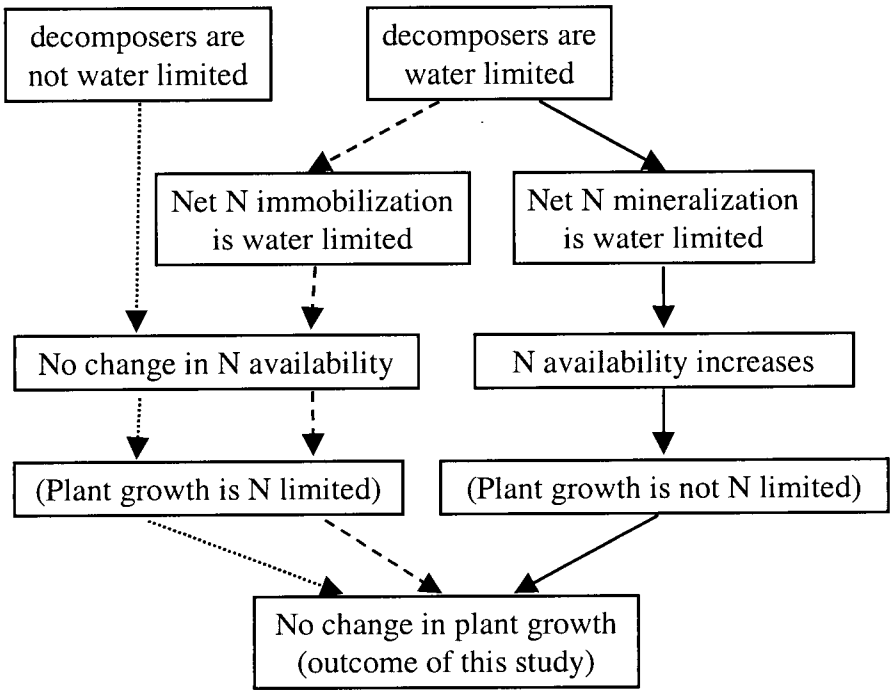

Figure 6: Alternative ecological processes proposed for the lack of plant response to irrigation in the Kluane boreal forest, and summary of predictions for the three hypotheses. ——: hypothesis 1; ····· : hypothesis 2; - - - - : hypothesis 3.

Despite lying in a rainshadow zone, the Kluane boreal forest vegetation is clearly not water limited. Nitrogen limitation is probably prevalent at Kluane, as is the case for boreal forests in general. However, mushroom biomass increased with irrigation in Kluane and in turn should have increased nitrogen mineralization. Hence irrigation should have reduced nitrogen limitation through its stimulation of decomposers. It is

therefore unclear why plant production and vole numbers did not correlate with mushroom biomass on the irrigated sites. Soil nutrient status must hold the key to this dilemma.

Chapter III – Litter decomposition and humus mass per m^2

3.1 - Abstract:

The effect of climate change on decomposition in boreal forests is important in predicting further climate change, due to the possibility of a positive feedback between climate change and ecosystems. From 1997 to 2001, I compared the decomposition of willow and spruce litter, as well as humus mass per m^2 of forest floor between three irrigated boreal forest stands of 1.5 ha each and three nearby control stands. I calculated actual evapotranspiration (AET) inclusive of irrigation for each stand and tested by ANCOVA the robustness of AET in predicting litter decay rates. Decomposition lasted 23-795 days, irrigation increased precipitation levels over controls by an average of 155%, and summer AET was greater on treatment grids than on controls. Decomposition in litter of both species was explained by log-cumulative AET ($P < 0.001$ both species; $r^2 = 0.90$ for willow and 0.91 for spruce). The irrigation effect added no additional significance ($P < 0.20$ both species) to the model, hence changes in cumulative AET due to irrigation were sufficient to predict litter decay. The increase in litter decomposition with irrigation suggests that humus input should have increased with irrigation. Five years of irrigation during the summer caused no change in humus mass per m^2, either under willows or under spruce trees (ANOVA, $p = 0.27$). I suspect that humus decay also accelerated with irrigation, and that this offset the additional humus input, but the experiment does not allow a test of this hypothesis. In another study of these same stands (Chapter II, above), plants did not react to irrigation. Hence decomposition (CO_2 release) seems more affected by climate change than plant growth (CO_2 absorption). This agrees with the hypothesis of a positive feedback between ecosystems and climate change.

3.2 - Introduction

Boreal and tundra ecosystems have recently received increasing interest owing to their role in the global carbon budget and concerns about climate change. Dead organic matter in those ecosystems decomposes slowly because temperature and moisture are sub optimal for microbes. Large amounts of plant material therefore accumulate in those soils, in contrast with other terrestrial ecosystems where better temperature and moisture tend to accelerate decomposition of plant remains and CO_2 efflux by microbes.

Because temperature and rainfall may increase at high latitudes with climate change and enhance decomposition rates (Coûteaux et al. 1995), carbon storage in these soils may decrease and exacerbate climate change. Boreal forests occupy 8 % (12 million km^2) of the Earth's terrestrial surface (Lieth 1975), and this substantiates the need to accurately forecast the response of decay rates to climate change in those forests.

Litter decay rates generally correlate best with the actual evapotranspiration (AET), a climatic variable that reflects soil temperature and moisture. AET accurately describes global differences in litter decomposition (e.g. Meentemeyer 1978, Aerts 1997), as well as temporal variations at a given site (e.g. Jansson and Berg 1985, but see Elkins et al. 1982, Moore et al. 1999). However, experimental manipulations of AET have not been used to test the response of within-site litter decay rates. It is therefore not certain to what extent global litter decay rates and AET are causally related. For example, Aerts (1997) showed that part of the relationship between decay rates and AET was indirect, due to a second correlation between litter chemistry (plant species) and AET.

Also, few manipulative experiments simulating climate change in boreal forests provide information on decay rates, and there are therefore few data to calibrate climate change models.

I irrigated three 1.5 ha stands in a dry boreal forest in southwestern Yukon (Canada). By comparing those stands to three nearby control stands of the same size, I tested if litter decomposition rates increased and if the humus mass per m^2 underlying the litter layer changed in response to this induced climate change. I also tested the robustness of AET as a predictor of litter decomposition under simulated climate change.

3.3 – Materials and methods

Study area and experimental sites

Six experimental grids were situated in the Kluane boreal forest in southwestern Yukon (Canada), *ca.* 35 km north of Haines Junction (61° N, 138° W). The area lies in the rainshadow of the Saint Elias Mountains (Rowe 1972). The canopy cover of the tree layer on the study sites is sparse, and is dominated by 17% white spruce (*Picea glauca*), followed by 3% trembling aspen (*Populus tremuloides*) and 1% gray willow (*Salix glauca*). The shrub layer is comprised of mostly gray willow (*Salix glauca*), bog birch (*Betula glandulosa*), and soapberry (*Shepherdia canadensis*). Bearberry (*Arctostaphylos uva-ursi*) accounted for most of the ground cover vegetation, generally followed by the grass *Festuca altaica* (Chapter II; Table 6).

I used the Thornthwaite and Mather (1957) water balance method, the weather data from Haines Junction (Environment Canada 2002), as well as the irrigation amounts on the irrigated grids to calculate daily AET for each grid. The daily weather record was

incomplete by 8%; I used the 1944-1985 monthly climate normals (Canadian Meteorological Center 2002) to obtain a conservative AET estimate for those days. I made the standard assumption that the soil water holding capacity of the root zone was 300 mm to facilitate comparison of my data to other studies (e.g. Meentemeyer 1978, Johansson et al. 1995, Aerts 1997). The study area receives an average of 110 mm of rain during the growing season. The average summer water deficit (May to August, inclusively) was 143 mm (Chapter II).

Of six grids, three were irrigated (treatments, T_1-T_3) and the other three were not (controls, C_1-C_3). One C and one T grid of *ca.* 1.5 ha each and spaced from one another by *ca.* 75 m were paired on three different sites, those sites being separated from one another by at least 3 km. Gas-powered pumps fed pond water to the sprinklers of the irrigation systems built with PVC pipe. Each of the 17-23 sprinklers per grid were spaced at regular intervals of 30 m, 1.5 m above the ground. Each sprinkler distributed water over a radius of 14 m. All grids were staked at regular intervals of 14 m for benchmarking samples. From 1995 to 1999, the T grids received an average of 81 mm more summer rainfall than the C grids. The litter bag experiments reported herein were however performed from 1997 through 2001. Irrigation from 1997 to 1999 increased precipitation by 155% on average (Figure 7), and no irrigation occurred after 1999. Irrigation varied between T grids because of technical difficulties. More details on the study area and on the experimental set up are found in Chapter II.

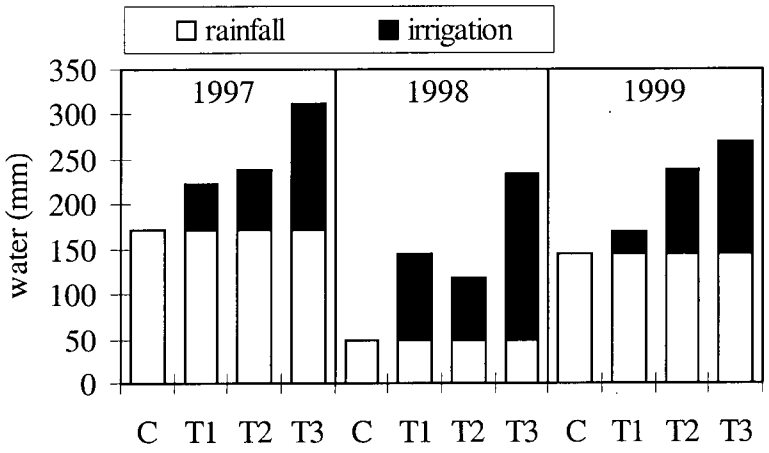

Figure 7: May to August (inclusive) rainfall (white bars) and irrigation (black bars) amounts (mm) for the C and T grids, for experimental years 1997-1999. Rainfall data from Haines Junction (Environment Canada 2002).

Willow leaf litter bag method

In early June 1997, live gray willow leaves were collected from shrubs beside systematically distributed sprinklers on T grids, or beside grid stakes in similar positions on C grids (n = 15 per grid). This material was used for all willow leaf litter experiments. Leaves were oven-dried for four days at 60 °C and approximately 0.600 g dry weight was inserted in each litter bag. Each litter bag was placed on the forest floor at the base of the shrub that was the source of the leaf material. Litter bags (1 mm mesh size) measured 6 x 8 cm. They were in the field for 23-795 days (Table 7) and oven-dried for four days at 60 °C, after which the percent weight loss of the leaf material was obtained (to the closest 0.001 g).

Seven experiments on willow leaf weight loss were done between July 1997 and August 1999, and two additional experiments lasted for up to two years (2001) after the

end of the irrigation (1999). In experiment 1, all the litter bags were collected about one year after their installation on the forest floor (Table 7). In the other eight willow leaf experiments, multiple litter bags were placed under their shrub of origin at each station, and these were retrieved sequentially after different time intervals.

Reciprocal transplant

As part of experiment 1 (1997), I also tested whether irrigation during the years previous to the litter bag experiments (1995-1996) influenced the decomposability of the leaves collected on the T grids in 1997. Two replicate litter bags were made from each willow leaf sample, one was left to decompose under its shrub of origin (n = 15), the other at a similarly positioned station on its paired grid (n = 15). Hence during decomposition, leaves from shrubs on T grids were exposed to both C and T conditions, and leaves from shrubs on C grids were treated reciprocally. These data were first averaged by origin of leaves and the treatment to which they were exposed, and analyzed in a 3-way ANOVA, with treatment and origin of leaves as fixed factors, while site was random.

Spruce needle litter bags

In early June 1999, live needles were collected on white spruce trees at 14 systematically distributed stations on each grid, and this material was used to carry out experiments as in willow leaf experiments. Two bags per tree were set out at each station between June 15th and 23rd 1999, underneath the specific tree the needles came from. Of each pair of bags, one was retrieved between August 6th and 30th 1999 (Table 7), while

the other was collected one year later (August 2000).

Table 7: Average start date, end date, duration (days), and sample size per grid, for the willow leaf and spruce needle litter bag experiments, 1997 to 2001.

Species	Experiment number	Start date	End date	Duration (days)	n (per grid)
Willow	1	13-Jul-97	11-Jun-98	333	30
	2a	8-Jul-98	31-Jul-98	23	5
Willow	2b	8-Jul-98	24-Aug-98	47	5
	2c	8-Jul-98	20-May-99	317	5
	3a	11-Jun-98	20-May-99	344	5
Willow	3b	11-Jun-98	26-Aug-99	441	10
	4a	7-Jun-99	26-Aug-99	80	15
Willow	4b	7-Jun-99	10-Aug-00	430	15
	4c	7-Jun-99	10-Aug-01	795	5
	5a	19-Jun-99	28-Aug-99	69	14
Spruce	5b	19-Jun-99	11-Aug-00	418	14

Humus mass/m^2

The dry mass of humus per m^2 was measured during the fifth (and last) year of irrigation (1999). Samples were collected with a cylindrical corer of 6.7 cm in diameter by 30.0 cm deep, at five to 11 stations per grid. At each station, a core underneath a willow and one underneath a white spruce were taken, and the dry weights of those humus samples were transformed to kg/m^2.

Statistical analyses

All data from litter bags were averaged per grid for each experiment and litter type, and all statistical analyses were performed on those averages, using Statistica 6.0 (StatSoft Inc. 2001). Those averages were analyzed by ANCOVA for willow and spruce separately. Cumulative daily AET (inclusive of irrigation when applicable) for the duration of the experiments was the continuous effect, and treatment (C *versus* T grid) was the covariate. As the relationship between cumulative AET and cumulative % weight loss was curvilinear, the cumulative AET values were log-transformed.

A 3-way ANOVA (humus type x site x treatment) was performed on the average log-transformed humus mass/m^2 per grid, where humus type and treatment were fixed factors, while site was random. These data were log-transformed to homogenize the variances.

3.4 - Results

Willow leaf reciprocal transplant experiment

In experiment 1, neither the leaf origin, the treatment, nor the leaf origin*treatment effects were significant (3-way ANOVA $F_{1,2} = 0.00$, $P = 1.00$, $F_{1,2} = 0.57$, $P = 0.53$, and $F_{1,2} = 1.71$, $P = 0.32$, respectively). Accordingly, the data for all litter bags decomposing on a given grid were averaged, regardless of origin of leaves, and analyzed with the other eight willow leaf experiments.

Litter decomposition

For both willow leaves and spruce needles, cumulative % weight loss was highly correlated with log-cumulative AET ($r^2 = 0.90$, and $r^2 = 0.91$, respectively, Figure 8). For both species, the log-cumulative AET effect was highly significant ($F_{1,52} = 486$, $P < 0.001$, and $F_{1,10} = 102$, $P < 0.001$, for willow and spruce respectively). After the irrigation effect had been accounted for by AET, the treatment added no significance to either of those relationships ($F_{1,51} = 0.2$, $P = 0.68$, and $F_{1,9} = 2$, $P = 0.21$). Hence the higher AET on the T grids due to irrigation (Figure 9) was sufficient to predict the corresponding increase in % weight loss (Figure 8).

Humus mass/m^2

Humus mass per m^2 under willows averaged 26% less on T grids than on C grids (Figure 10), but between-site differences were much larger (up to 250%). No trend was found in humus under spruce trees. There was no significant humus type effect, no significant treatment effect, and no type*treatment interaction effect (3-way ANOVA $F_{1,2}$

= 12.0, P = 0.07, $F_{1,2}$ = 2.3, P = 0.27, $F_{1,2}$ = 1.2, P = 0.38, respectively).

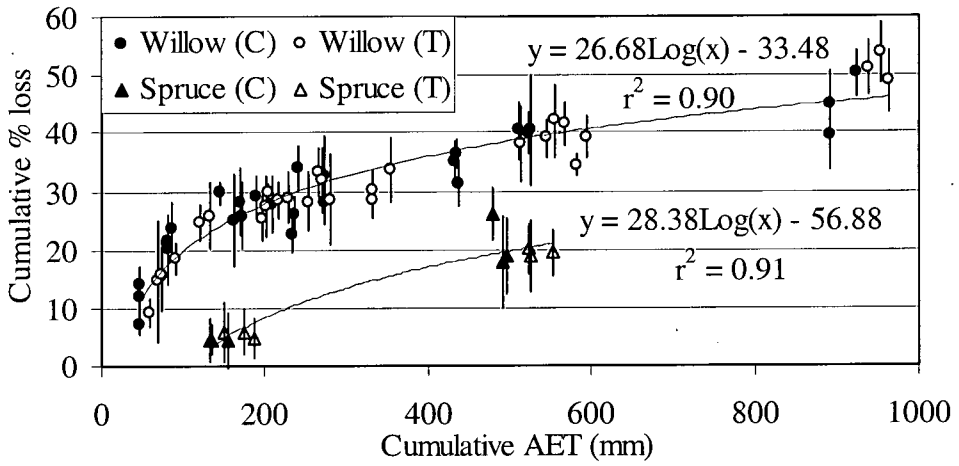

Figure 8: Willow leaf and spruce needle average cumulative % weight loss against average cumulative actual evapotranspiration (AET). AET calculated as in Thornthwaite and Mather (1957). Soil water holding capacity assumed to be 300 mm. Rainfall and temperature data from Haines Junction (Environment Canada 2002).

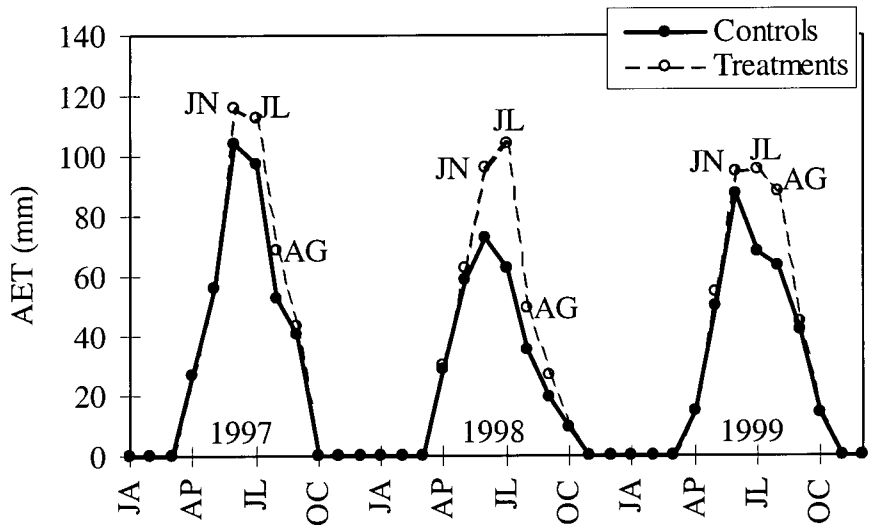

Figure 9: Monthly actual evapotranspiration (AET) for C and T grids, from January 1997 to December 1999. The averages of the three T grids are shown here for simplicity. AET calculated as in Thornthwaite and Mather (1957). Soil water holding capacity assumed to be 300 mm. Rainfall and temperature data from Haines Junction (Environment Canada 2002).

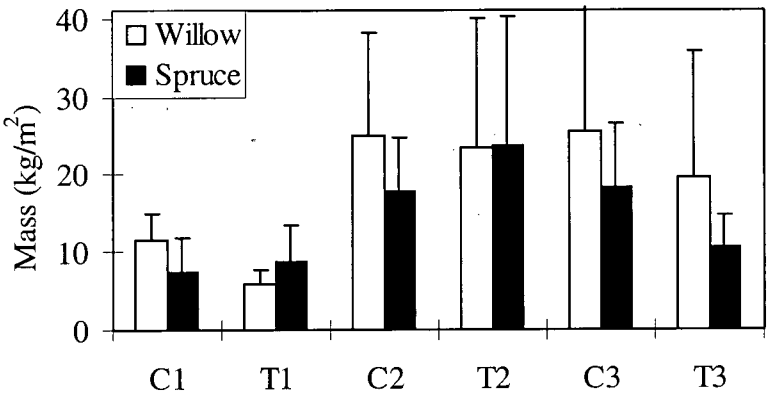

Figure 10: Willow and spruce humus average dry mass (kg/m^2) per grid in 1999. Error bars are standard deviations.

3.5 - Discussion

Litter decomposition

This study is a strong test of the robustness of the AET climatic variable as a predictor of litter decomposition. Because the Kluane boreal forest experiences a summer water deficit (Chapter II), irrigation translated into a direct and quantifiable manipulation of AET. My results indicate that AET, both between years (or time-spans) as well as between T and C grids, was an accurate and robust predictor of decomposition for both litter species. Although the importance of AET in driving decomposition has been supported by correlational studies (e.g. Meentemeyer 1978, Aerts 1997), my manipulative study supports the causality of this relationship. Hence, decomposer activity is related to AET not only at the macroscale/macroclimatic level (e.g. Meentemeyer 1978), but also at the local scale, which explains why the T and C grids close to one another had different decay rates.

If climate change models accurately project AET, and if litter decay in other ecosystems follows that in Kluane, short-term changes in litter decomposition rates could accurately be predicted because of the high r^2 values between decay and AET.

Humus

Humus mass/m^2 is the outcome of two opposed phenomena: 1) the addition of new mass through incompletely decomposed litter and dead roots; and 2) the mass loss of humus through decay or leaching of humus chemical components. Hence the acceleration of litter decay (above) should have added to the humus pool, but humus mass did not significantly increase. This unchanged humus mass could be explained by

the following mutually exclusive hypotheses: 1) this additional input was insignificant. Conversely, this input could have been significant, but it was cancelled by: 2) a reduction of root input, 3) an increase in translocation of humus matter to lower horizons, or 3) a faster rate of humus decay. Although I cannot eliminate the first three factors, my data on willow humus mass/m^2 is consistent with an increase in its decay rate with irrigation. However, spruce humus reacted differently from willow humus, which is consistent with spruce needles decomposing more slowly than willow leaves. More experiments over a longer time scale are needed to test the relative importance of those four factors on humus mass/m^2.

The global carbon budget

The correlation between litter decomposition and the experimentally increased AET indicates that decomposition in the Kluane forest fluctuates with varying rainfall and, by extension, so may CO_2 efflux by decomposers. With regards to global climate change, CO_2 efflux by decomposers may hence increase more than plant CO_2 absorption in the Kluane forest, because plants in that forest did not react to irrigation experiments (Chapter II). The combination of an enhanced CO_2 efflux by decomposers without more CO_2 uptake by plants in response to irrigation would signify a net reduction in ecosystem carbon storage. This agrees with the hypothesis of a positive feedback between climate change and ecosystem CO_2 efflux, at least in the Kluane forest. This feedback would be further exacerbated if the humus layer also decomposed faster and released more CO_2 in response to irrigation, but my data are uncertain here.

In any case, if litter in other boreal forests reacts similarly to that in the Kluane forest, the positive feedback may be substantial, because boreal forests are thought to be major sinks in the overall carbon budget (Coûteaux et al. 1995). Oechel et al. (2000), however, suggested that increased nutrient mineralization by soil microbes in a tundra ecosystem might occur in a time scale of decades rather than years, which would thereafter stimulate plant growth and CO_2 uptake. This would counter-balance the soil CO_2 efflux and therefore increase the carbon storage compared to the first few years of climate change (Oechel et al. 2000). My short-term study does not allow the testing of those hypotheses for the Kluane forest.

In brief, litter decay rates in the Kluane forest can be predicted by AET at small temporal and spatial scales. This relationship seems strongly causal due to its robustness to the artificial manipulation of AET in this study. Litter decay in the Kluane forest was accelerated by induced climate change through irrigation, which is consistent with the hypothesis of a positive feedback between climate change and ecosystems. The reaction of the humus horizon is also consistent with an increase in decay with irrigation, but further studies are required to eliminate other confounding factors regarding that horizon.

Chapter IV – Ammonium mineralization and immobilization

4.1 - Abstract

Ammonium (NH_4^+) is an important nitrogen source for plants in forests. Soil microbes may compete with plants for NH_4^+ (net immobilization) or may produce NH_4^+ for plant uptake (net mineralization), depending on climate and other factors. The climate of three boreal forest stands of 1.5 ha in northern Canada was modified by irrigation, which increased rainfall by an average of 145% during the summers of 1998-1999. Mineral and microbial NH_4^+ in the humus layer were monitored 30 hours after irrigation. Humus samples at three nearby non-irrigated sites were taken simultaneously to assess the effects of increased precipitation on the net mineralization/immobilization dynamics of NH_4^+. Longer-term effects were assessed in humus samples incubated inside sealed plastic bags in the field for an additional 30 days after irrigation. In the short-term, mineral NH_4^+-N was not affected by irrigation. However, microbial NH_4^+-N increased linearly with actual evapotranspiration (AET), which accounted for precipitation, irrigation (when applicable), and air temperature on each of the stands. Microbial NH_4^+ was best correlated to AET accumulated over three days before the sampling ($r^2 = 0.73$, $P < 0.001$). Mineral and microbial NH_4^+ after incubation were not statistically different from values at the beginning of incubation. Hence, irrigation enhanced net NH_4^+ immobilization. In the short-term, primary production of this ecosystem may not increase in a climate change scenario where rainfall increases, because primary production is nitrogen limited in this boreal forest. In the short-term, climate change may therefore cause a net decrease in carbon storage of this ecosystem.

4.2 - Introduction

The harsh climate in boreal forests hinders decomposition to a greater extent than photosynthesis. Hence, these forests tend to accumulate carbon, chiefly as plant biomass and as dead organic matter in the soil. The importance of boreal forests on the global carbon budget is therefore thought to be considerable (Anderson 1992). They occupy 12 million km^2, or 8 % of the continental surface (Lieth 1975), and their soils contain 178 Pg (1.78×10^{11} tonnes) of carbon (Zinke et al. 1984). Worldwide annual intake of CO_2 by boreal forests explains 50% of yearly variation in concentrations in the atmosphere over Alaska, or 30% of variation over Hawaii (D'Arrigo et al. 1987). Further, those high latitude forests are a net carbon sink of 4.8×10^8 tonnes of carbon per year (Ciesla 1995).

By 2100, temperature and precipitation in these forests are expected to increase by 1.3-6.3°C and 5-20%, respectively (Houghton et al. 2001). Warmer and wetter conditions may then affect the carbon budget of those forests through changes in decomposition and photosynthesis. Enhanced decomposition due to higher temperature and rainfall may generate larger CO_2 emissions, resulting in a positive feedback on climate change. Photosynthesis and CO_2 uptake by plants may be enhanced by both the more favourable climate and the larger CO_2 availability, resulting in a negative feedback on climate change.

Primary production in those ecosystems is limited by availability of nutrients, especially nitrogen (e.g. Zasada et al. 1977, Van Cleve and Alexander 1981, Van Cleve and Yarie 1986, Bonan and Shugart 1989, Nams et al. 1993, Schulze et al. 1994, Turkington et al. 1998). Therefore, the potential increase in plant CO_2 uptake may also depend on the effects of climate change on nitrogen (hereafter N) mineralization by

decomposers. Thus, decomposers may influence the carbon budget of boreal forests directly through their emissions of CO_2, and indirectly through their effects on plant nutrition.

Decomposers mineralize organic N to inorganic N (gross mineralization), and they assimilate a portion of this mineralized N (gross immobilization). It is the relative intensities of gross mineralization and gross immobilization that determine whether: 1) mineral N accumulates in the soil (net mineralization), or whether: 2) a net accumulation in microbes (net immobilization) occurs (Richards 1987). The rate of immobilization depends on the microbial community composition, the chemical attributes of the substrate, and climatic conditions (Richards 1987). The net feedback between ecosystems and climate may therefore depend on how climate change affects microbial requirements for N. It is therefore important to understand the effects of climate on N requirements and mineralization by soil microbes to forecast the net direction of boreal forest feedbacks on climate change.

I therefore irrigated three stands of *ca.* 1.5 ha each in a dry boreal forest in northern Canada, and tested if concentrations of both inorganic ammonium (hereafter NH_4^+) and microbial NH_4^+ were affected by enhanced summer precipitation compared to three nearby untreated control stands. I focused on NH_4^+-N because it usually is the most important inorganic form of N for plant nutrition in forests (Richards 1987).

4.3 – Materials and methods

Study area and experimental sites

The area lies in the rainshadow of the Saint Elias Mountains in southwestern Yukon (Canada). The three experimental sites are situated in the boreal forest *ca.* 35 km north of Haines Junction (61 N, 138 W). The tree canopy cover on those sites was low (21%, as measured with a spherical densiometer), out of which white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*), and gray willow (*Salix glauca*) represented 17, 3, and 1%, respectively. The growing season lasts from mid-May to mid-August (Turkington et al. 1998), and rainfall averages 110 mm from May 1st to August 31st in Haines Junction (Canadian Meteorological Center 2002). The water deficit from May 1st to August 31st averages 143 mm (Chapter II).

At each of the three sites, two grids of *ca.* 1.5 ha separated by *ca.* 75 m were surveyed. The sites were at least 3 km apart. One of the two grids on each site was subjected to natural rainfall only (control, "C grid") while on the other (treatment, "T grid"), an irrigation system built with PVC pipe sprinkled supplemental water siphoned from a pond with a gas-powered pump. On each T grid, 17-23 sprinklers at 1.5 m above the ground were spaced at regular intervals of 30 m; each sprinkler distributed water to a radius of 14 m. Each grid was also staked at regular intervals of 14 m. Rainfall amounts from May 1st to August 31st in Haines Junction were 49 and 146 mm in 1998 and 1999, respectively (Environment Canada 2002). T grids received on average 167 and 224 mm of water (including rainfall and irrigation) which where 340 and 154% of rainfall amounts on C grids during 1998 and 1999, respectively. Irrigation events occurred on three occasions each summer. The first irrigation event generally occurred in mid-June,

the second in July, and the last during the first week of August. Further details on irrigation amounts for years 1995-1997 (which are not part of the present analyses) as well as on climate patterns of the area and irrigation system design can be found in Chapter II. NH_4^+ concentrations of the pond water used for irrigation in 1999 were 0.000 ppm, 0.032 ppm, and 0.000 ppm for T_1, T_2, and T_3 grids, respectively. Although no irrigation occurred in 2000, NH_4^+ concentrations of the pond water that year were measured for comparison, and were 0.000 ppm for all grids.

Sampling and chemical analyses

Humus was sampled at stations spread in a spatially systematic manner on each grid. Each sampling station was within a few meters from a sprinkler (or stake in a comparable position on C grids). Samples were collected three times during the growing season, 30 hours after irrigation events ended to allow microbial populations to stabilize after the irrigation "disturbance". Humus and fermentation layers were treated indiscriminately. In 1998, only one sample per station was collected, under a willow shrub. In 1999 and 2000, two samples were collected, one under a willow shrub and one under a spruce tree. All humus samples were sieved independently (5 mm mesh) and homogenized. Sample sizes were balanced between C grids and their respective T grids, and samples were taken simultaneously on paired T and C grids. For pre-incubation NH_4^+-N, sample sizes were 5-11 per grid for each of willow and spruce humus in 1999-2000, and 7-22 per grid in 1998 for willow humus (Table 8). Willow humus samples were taken under willows which were not immediately under a spruce tree (and vice-versa for spruce humus). This procedure avoided mixed humus types, although it was not

possible to obtain humus that was assuredly completely pure. However, most of the litter and fermentation material above the humus was mostly composed of the target species.

Post-incubation NH_4^+-N measurements were done only in 1998 (willow) and 1999 (both willow and spruce). Sample sizes were generally 5-13 per grid, but no post-incubation microbial NH_4^+-N measurements were taken on C_3 and T_3 grids in 1998.

Post-incubation mineral NO_3^--N was also monitored simultaneously to NH_4^+-N in four of the willow humus samples per grid in 1998. Pre-incubation NO_3^--N was measured only in four willow humus samples per grid, on C_1 and T_1 grids only, on July 16th 1998. Analyses of NO_3^--N were fewer than those on NH_4^+-N because the latter is usually more important in the N budget of forests than the former (Richards 1987).

The fumigation direct-extraction method (Brookes et al. 1985) was used to determine the concentrations of microbial NH_4^+ in the humus samples. Within one hour after collection, each homogenized sample was divided into four subsamples, two of 10 g, and two of 30 g (all fresh weights). The first 10 g subsample was used to determine pre-incubation KCl 2M extractable mineral NH_4^+, the second 10 g subsample for determining pre-incubation KCl 2M extractable microbial NH_4^+ after 24 hours exposure to chloroform fumigation. The first 30 g subsample was oven-dried to determine humus fresh-to dry weight ratio.

The second 30 g subsample was inserted in a 20 micron thick polyethylene bag (Eno 1960), and buried at its sampling station for approximately 30 days. After the incubation, it was retrieved, sieved, homogenized, and divided in three subsamples of 10 g each. The first 10 g was used to determine post-incubation mineral NH_4^+, the second for post-incubation microbial NH_4^+, and the last for determining fresh weight-to dry

weight ratio.

For all extractions, each subsample was mixed thoroughly in 60 ml KCl 2M, and the solution was filtered from the humus four hours later and frozen. Later, NH_4^+ (and NO_3^-, when applicable) were estimated using a Lachat Autoanalyzer. Fumigations lasted for 24 hours inside a vacuum desiccator containing wet paper towels (Jenkinson 1988) and 50 ml of alcohol-free chloroform which was brought to a boil by reducing the pressure, i.e. by evacuating air from the vacuum desiccator.

Table 8: Average pre-incubation sampling dates, sample sizes for mineral and microbial pre- and post-incubation NH_4^+-N measurements and time span of incubation.

Humus type	Year	Average sampling date	Pre-incubation n/grid	Post-incubation n/grid	Time span of incubation (days)
Willow	1998	Jul 14th	7-22	5-13	32-49
	1999	Jul 25th	8-11	4-9	18-35
	2000	Aug 27th	5-6	n/a	n/a
Spruce	1999	Jul 25th	8-11	5-9	18-36
	2000	Aug 27th	5-6	n/a	n/a

Data transformations and analyses

Data were treated separately for willow and spruce humus. Pre- and post-incubation data were analyzed independently. Mineral and microbial NH_4^+ were analyzed as NH_4^+-N (in μg N per g of humus dry weight) and as NH_4^+-N (mg N) per m^2 of forest floor. For each humus type and year and each of pre- or post-incubation and for both NH_4^+-N/g and NH_4^+-N/m^2, the data were averaged per grid because the experimental units were individual grids (not sampling stations within a grid).

The NH_4^+-N/m^2 of forest floor data were obtained by multiplying the NH_4^+-N/g of humus by the dry mass of humus per unit area. Humus mass per m^2 was estimated in 1999 using a cylindrical corer of 6.7 cm in diameter by 30 cm deep, at five to 11 stations per grid (Chapter III). One core was taken under a willow and one under a white spruce, and the dry weights of humus were transformed to kg per m^2. When no data on the humus amount were taken at a NH_4^+ - N station, the average humus amount for each grid was used for the transformation to mg of NH_4^+ - N /m^2. The NH_4^+ - N /m^2 data were log-transformed to homogenize the variances.

Statistical analyses

Pre-incubation NH_4^+-N was first analyzed by forward stepwise multiple regression for effects of humus moisture (%w/w), actual evapotranspiration (AET), and air temperature. AET is a climatically derived index of both soil moisture availability and temperature. It expresses water evaporated and used for plant transpiration which are under the control of air temperature. Daily precipitation and air temperature (Environment Canada 2002) from Haines Junction (*ca.* 35 km south of the study sites)

were used to calculate daily AET for each grid according to the Thornthwaite and Mather (1957) water balance method. Irrigation amounts were added to baseline precipitation for the T grids. More details are found in Chapter III.

AET and temperature values analyzed were those during the day of sampling, during the day before sampling, and accumulated (AET) or averaged (temperature) over the last 2, 3, 5, 10, 15, 20, 25, and 30 days, inclusive of the day of sampling. The longer time spans took into account the potential effects of recent weather conditions on baseline NH_4^+. In the most significant relationship found in the multiple regression analysis, year, site, and treatment effects were further tested by ANCOVA. Because analyses were done on two pre-incubation NH_4^+ measurements (mineral and microbial) expressed as per g of humus and per m^2 of forest-floor in two types of humus (willow and spruce), α was Bonferroni-adjusted to $0.05/(2 \times 2 \times 2) = 0.0063$. A final multiple regression followed by an ANCOVA were performed to test for differences in the reactions of willow and spruce humus to AET.

In willow humus samples, changes in NH_4^+ and in moisture between pre-and post-incubation were tested in a 4-way mixed-model ANOVA where year (1998 versus 1999), treatment (control versus irrigation), and collection time (pre- versus post-incubation) were fixed factors, while site (1, 2, or 3) was random. The spruce humus analyses were identical except for the exclusion of the year factor because spruce humus incubation occurred only in 1999.

4.4 - Results

Pre-incubation NH_4^+

During 1998-1999, cumulative 5-day AET on T-grids averaged 44% higher than controls (Figure 11a, circles and squares). AET accumulated over 3 days during 1998-1999 was 100% higher on T grids than on controls (Figure 12a). However, in 2000 when no irrigation occurred, cumulative AET values between T grids and their respective controls did not differ (Figure 11a, triangles).

For both willow and spruce humus (Figures 11a and 12a), mineral NH_4^+/g showed no trend according to T or C grids, and was not significantly correlated with any of the 21 parameters tested.

However, microbial NH_4^+-N/g was positively correlated with cumulative AET in both willow and spruce humus (Figures 11b and 12b, respectively). The most significant AET parameter for willow humus was the last 5 days before sampling ($F_{1,16} = 24.5$, $P < 0.001$), while in spruce humus it was that accumulated over the last 3 days ($F_{1,10} = 100.3$, $P < 0.001$). Neither the site nor the treatment had additional effects in either species. The year effect could not be tested because the ranges of AET in 1998 did not overlap with those of the other two years (Figures 11a and b).

Although a trend existed between humus moisture and microbial NH_4^+-N/g for willow in 1998 and 1999 (Figure 13b) and spruce in 1999 (Figure 14b), 2000 (circled data, Figures 13b and 14b) did not follow that pattern. Air temperature during sampling in 2000 was 3-9 °C lower than in previous years (Figures 15b and 16b, for willow and spruce respectively). Mineral NH_4^+-N/g in either humus type was not related to either humus moisture (Figures 13a and 14a) or air temperature (Figures 15a and 16a).

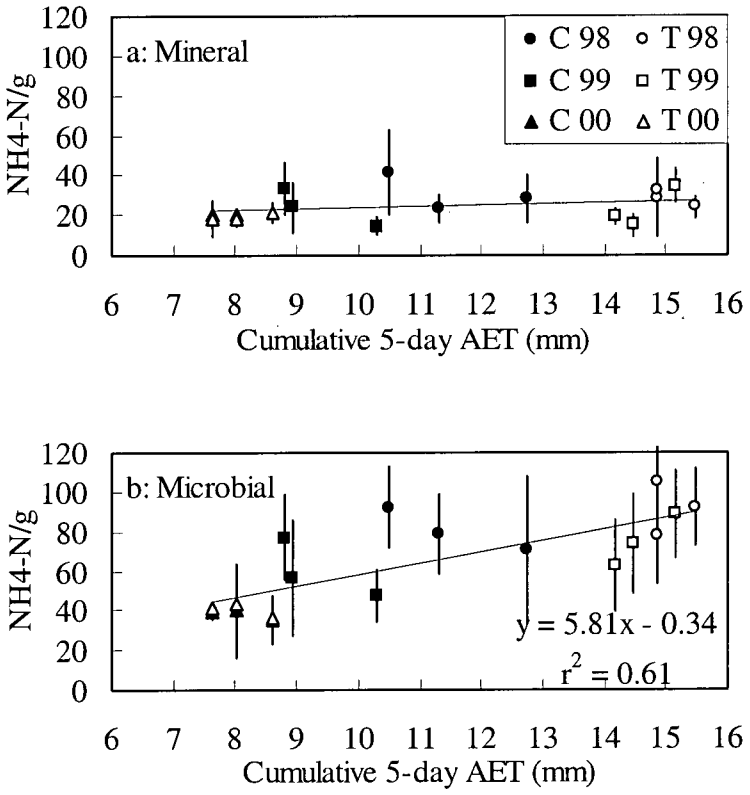

Figure 11: Pre-incubation average (± SD) mineral (a) and microbial (b) NH_4^+-N (μg/g) per grid, against cumulative 5-day AET in willow humus, 1998-2000.

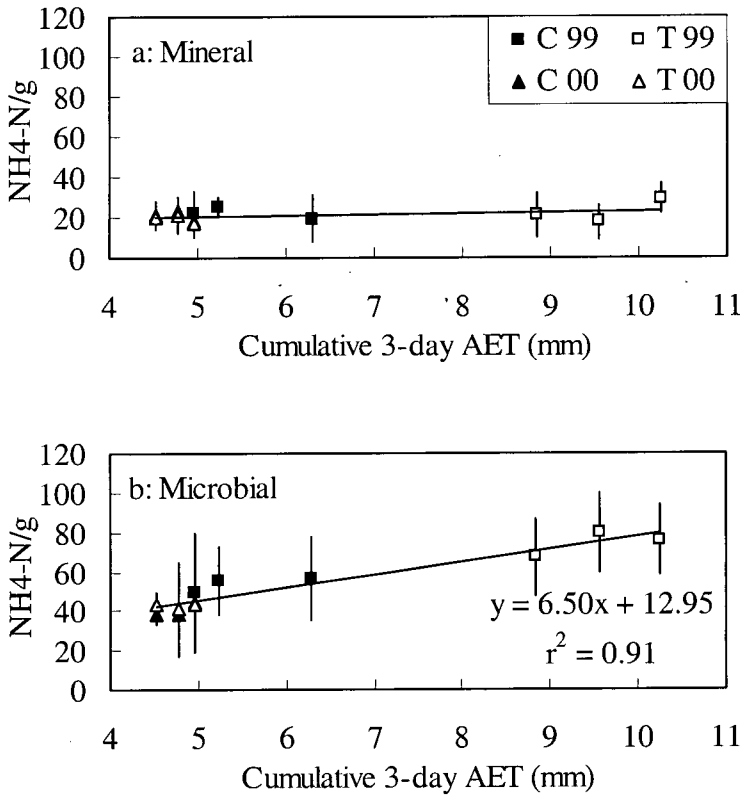

Figure 12: Pre-incubation average (± SD) mineral (a) and microbial (b) NH_4^+-N (μg/g) per grid, against cumulative 3-day AET in spruce humus, 1998-2000.

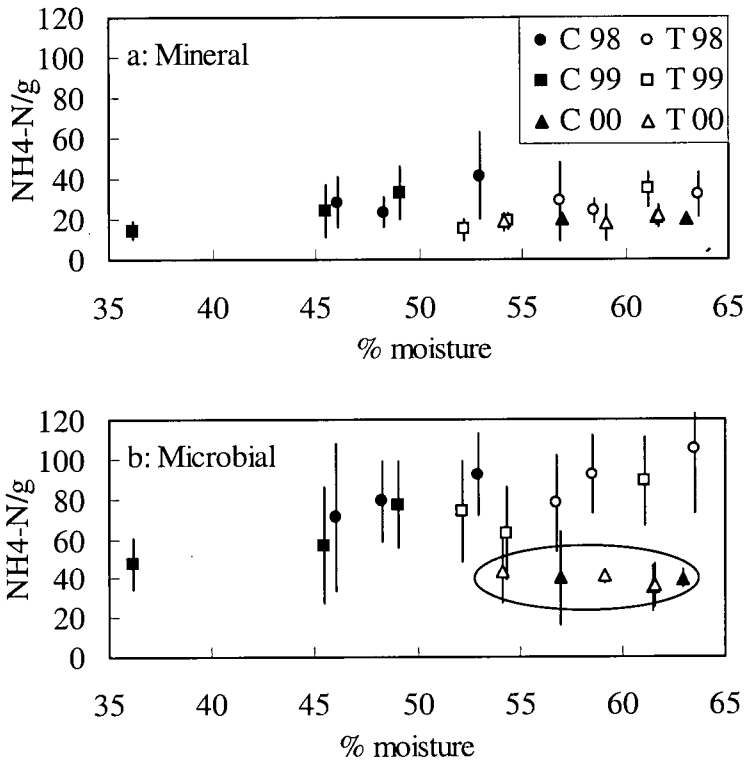

Figure 13: Pre-incubation average (± SD) mineral (a) and microbial (b) NH_4^+-N (μg/g) per grid, against willow humus moisture (%w/w), 1998-2000. Note: Microbial NH_4^+ increases with % moisture during 1998-1999, but not during 2000 (inside ellipse) when temperature was low (see ellipse in Figure 15b).

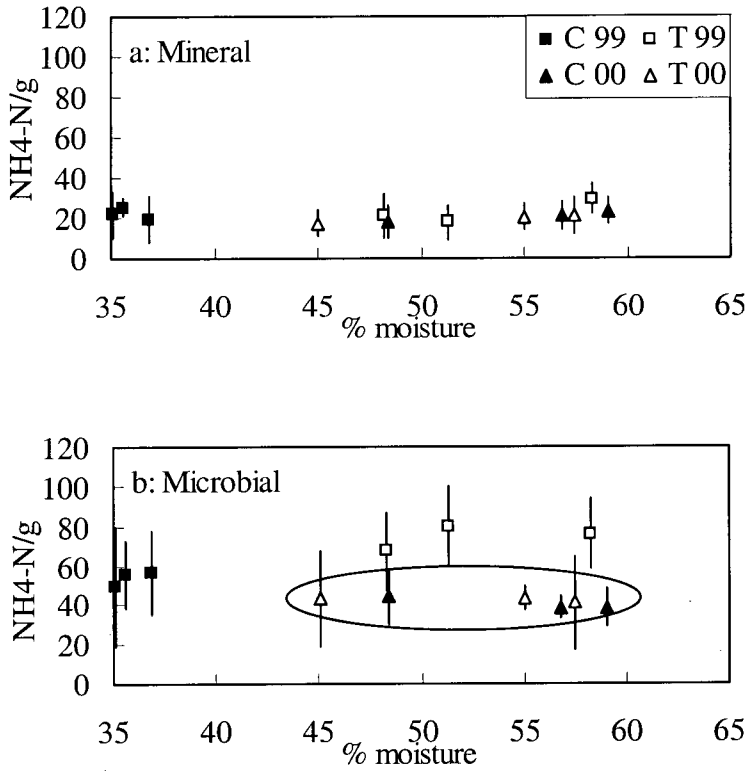

Figure 14: Pre-incubation average (± SD) mineral (a) and microbial (b) NH_4^+-N (μg/g) per grid, against spruce humus moisture (%w/w), 1998-2000. Note: Microbial NH_4^+ increases with % moisture during 1998-1999, but not during 2000 (inside ellipse) when temperature was low (see ellipse in Figure 15b).

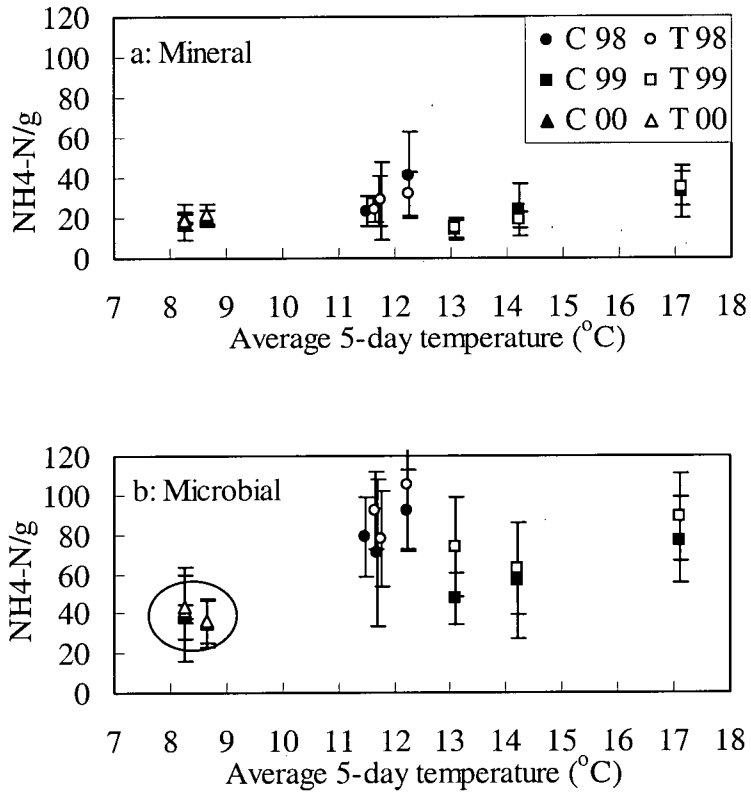

Figure 15: Pre-incubation average (± SD) mineral (a) and microbial (b) NH_4^+-N (μg/g) on each grid, against average 5-day temperature in willow humus, 1998-2000. Note: Temperature during microbial NH_4^+ measurement in 2000 (inside ellipse) was lower than in 1998-1999.

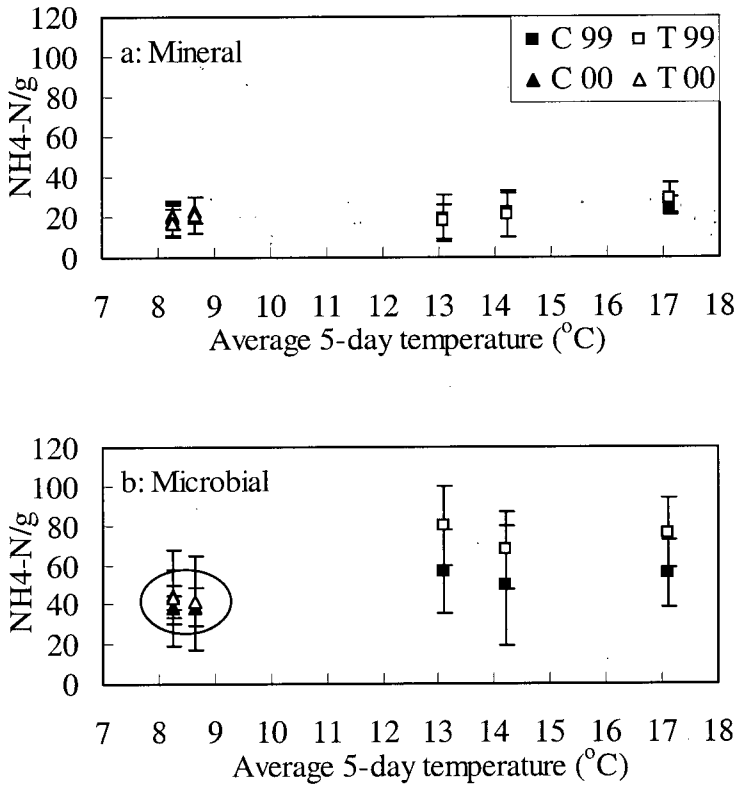

Figure 16: Pre-incubation average (± SD) mineral (a) and microbial (b) NH_4^+-N (μg/g) on each grid, against average 5-day temperature in spruce humus, 1998-2000. Note: Temperature during microbial NH_{4+} measurement in 2000 (inside ellipse) was lower than in 1998-1999.

The combined willow and spruce microbial NH_4^+/g were best correlated to cumulative 3-day AET (Figure 12, $F_{1,22} = 59$, $P < 0.001$). Humus type, treatment, and site effects were not significant ($F_{1,21} = 0.02$, $P = 0.88$, $F_{1,21} = 1.5$, $P = 0.24$, and $F_{2,20} = 0.3$, $P = 0.71$, respectively). The year effect could not be tested for the same reason as in the previous ANCOVA.

The pre-incubation mineral and microbial NH_4^+-N expressed per m^2 of forest floor (Table 9) were correlated to none of the 21 variables.

Table 9: Pre-incubation mineral and microbial NH_4^+-N (mg per m^2 of forest-floor) in the humus layer under willow shrubs and spruce trees, 1998-2000.

		Willow log NH_4^+-N (mg/m^2)				Spruce log NH_4^+-N (mg/m^2)			
Year	Grid	mineral		microbial		mineral		microbial	
		average	S.D.	average	S.D.	average	S.D.	average	S.D.
1998	C_1	2.4	0.2	2.9	0.1	n/a	n/a	n/a	n/a
1998	T_1	2.1	0.1	2.7	0.1	n/a	n/a	n/a	n/a
1998	C_2	2.7	0.3	2.6	1.7	n/a	n/a	n/a	n/a
1998	T_2	2.7	0.4	3.2	0.3	n/a	n/a	n/a	n/a
1998	C_3	2.8	0.2	3.3	0.2	n/a	n/a	n/a	n/a
1998	T_3	2.7	0.3	3.2	0.4	n/a	n/a	n/a	n/a
1999	C_1	2.2	0.3	2.7	0.2	2.1	0.4	2.6	0.2
1999	T_1	1.9	0.2	2.6	0.2	2.1	0.3	2.8	0.2
1999	C_2	2.7	0.3	2.9	0.8	2.5	0.3	2.9	0.4
1999	T_2	2.6	0.3	3.1	0.4	2.6	0.3	3.1	0.4
1999	C_3	2.9	0.2	3.2	0.1	2.6	0.2	3.0	0.2
1999	T_3	2.8	0.3	3.2	0.3	2.5	0.2	2.9	0.2
2000	C_1	2.3	0.2	2.6	0.3	2.0	0.4	2.4	0.3
2000	T_1	2.0	0.1	2.4	0.1	2.1	0.4	2.5	0.5
2000	C_2	2.7	0.2	3.0	0.2	2.6	0.2	2.9	0.2
2000	T_2	2.4	0.7	3.0	0.3	2.7	0.5	3.0	0.4
2000	C_3	2.6	0.1	2.9	0.2	2.6	0.2	2.8	0.2
2000	T_3	2.7	0.2	2.9	0.3	2.3	0.2	2.5	0.3

Post-incubation NH_4^+

There was no significant difference between pre- and post-incubation mineral and microbial NH_4^+-N, or humus moisture, for either willow or spruce humus (results not shown).

NO_3^-

Pre-incubation mineral NO_3^--N/g in willow humus in 1998 was over one order of magnitude smaller (1.29 and 1.22 μg/g humus, for C_1 and T_1, respectively) than NH_4^+-N/g (23.3 and 24.0 μg/g humus, for C_1 and T_1, respectively), and contributed to only about 5% of the total mineral N. Post-incubation NO_3^--N/g remained at similarly low concentrations (Figure 18), but was positively and significantly correlated with humus moisture ($F_{1,4} = 15.9$, $P = 0.02$).

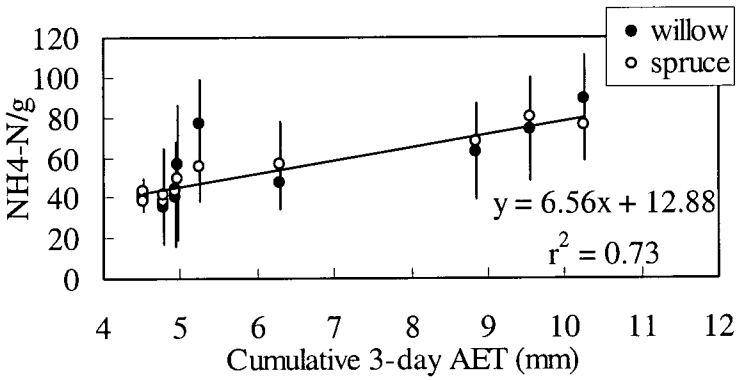

Figure 17: Pre-incubation average (± SD) microbial NH_4^+-N (μg/g) per grid, against cumulative 3-day AET for both willow and spruce, 1999-2000 (excluding willow data from 1998).

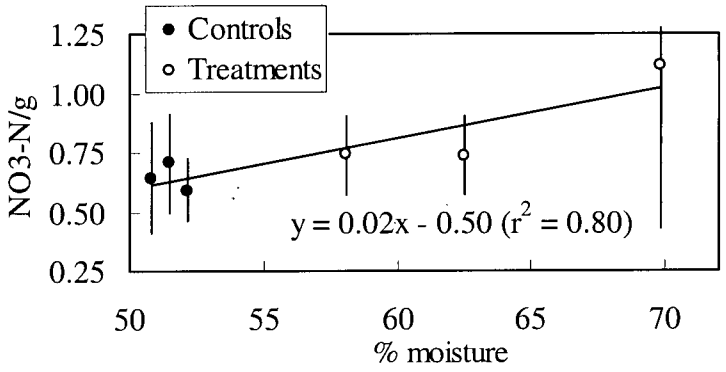

Figure 18: Post-incubation average (± SD) mineral NO_3^--N (μg/g) in willow humus against humus moisture (% w/w), 1998.

4.5 - Discussion

Pre-incubation microbial NH_4^+ (except in late August 2000) was strongly related to humus moisture, which was constant during the 30 day post-incubation experiments, likely because the incubating humus was inserted in plastic bags impermeable to moisture. The stability in humus moisture during the incubation time may therefore have caused the concurrent stability in microbial NH_4^+ between pre- and post-incubation times. Microbial NH_4^+ may already have been in equilibrium with humus moisture at the onset of the plastic bag incubations.

Similarly to microbial NH_4^+, mineral NH_4^+ was not different before (pre-incubation) and after (post-incubation) 30 days of incubation. Unlike microbial NH_4^+, however, mineral NH_4^+ was constant regardless of grid, year, date, temperature, moisture, AET, or irrigation. Sieving soil samples prior to incubation (as I did in my post-incubation experiments) can bias N mineralization compared to intact soil cores (e.g. Raison et al. 1987). Hence incubations of intact cores might be necessary to obtain unbiased post-incubation results. Because of this uncertainty concerning the validity of

my post-incubation results, and because of the lack of change between pre- and post-incubation for both mineral and microbial NH_4^+, I therefore focus on the pre-incubation results and disregard those from my post-incubation experiments.

Inorganic NO_3^--N contributed little (*ca.* 5%) to the mineral N pool, as is usually the case in forest ecosystems (Richards 1987). Therefore the correlation between NO_3^--N and humus moisture after 30 days of incubation contributes little N to plants at those study sites compared to NH_4^+-N. Hence I will disregard NO_3^--N in the remainder of this discussion.

NH_4^+ was monitored in humus under both gray willows, a dominant species of the shrub layer, and white spruce trees, the dominant tree canopy species in the area (Turkington et al. 1998). Hence the results should represent the major fraction of the humus in the study area. Concentrations of both mineral and microbial NH_4^+ were similar between willow and spruce humus, and humus type had no significant effect on the relationship between microbial NH_4^+ and AET. Thus my results can be generalized across humus types.

My results reveal the relative contributions of different potential limiting factors on microbial immobilization and mineralization in the Kluane boreal forest. First, microbial NH_4^+ was clearly limited by both temperature and moisture when all sampling periods were taken into account, because immobilization increased with AET. The closer correlation of microbial NH_4^+ to AET than to either temperature or humus moisture is explained on the basis that AET accounted for simultaneous variations in both components.

Second, the linearity of this relationship implies that chemical energy (mostly carbon) availability for microbes remained sufficient throughout the range of AET occurring in my experiments. If carbon were limiting, N immobilization by microbes would have reached a plateau instead of linearly increasing at the higher AET values, and N immobilization at the higher AET levels would have been lower than I observed. In turn, the amount of N in the humus would have been in excess of microbial demand, and hence net NH_4^+ mineralization should have increased, contrary to what I observed.

Third, synthesis of microbial cytoplasm during the warmer part of the summer in Kluane is mostly water limited, and little affected by temperature. Irrigation during the summer yielded both the highest AET and N immobilization levels. Under unmanipulated dry and warmer summer conditions, microbial cytoplasm synthesis and NH_4^+ immobilization are therefore low relative to energy availability. The importance of summer water limitation on soil microbes in Kluane is substantiated by the stimulating effects of irrigation on both litter decomposition (Chapter III) and mushroom biomass (Chapter II). Conversely, at the end of August 2000, the low temperature was the main limitation on N immobilization. The timing of the sampling and the concurrent changes in the relative contributions of moisture and temperature limitation are why AET explained both mid- and late-summer immobilization better than either moisture or temperature alone.

The lack of increase in net NH_4^+ mineralization after irrigation was unexpected, because N mineralization by microbes is often affected by water availability (Richards 1987). Previous studies have demonstrated that N mineralization is water limited (or correlated with soil moisture) in different forest types, including: boreal forests in Alaska

(Binkley et al. 1994), mixed forests in both Ontario (Devito et al. 1999) and New Hampshire (Evans et al. 1998), and in deciduous forests in eastern North America (Reich et al. 1997). Similarly, over a broad scale of litter chemistry and climates, temperature and moisture explained a small but significant portion of the differences in N mineralization (Scott and Binkley, 1997).

On the other hand, N mineralization has failed to respond to irrigation in other studies. N mineralization increased with irrigation in a *Pinus radiata* stand in Australia only during the first year, but decreased the following years relative to unmanipulated conditions (Raison et al. 1992). Raison et al. (1992) suggested that reduced N mineralization occurred because microbes depleted mineralizable soil organic N. Several years of irrigation also caused a decrease in N mineralization in stands of *Pinus radiata* and *Eucalyptus* spp. in Australia (Connell et al. 1995). I do not known if an initial increase in N mineralization occurred during the first year of irrigation in my study (1995), because I did not monitor N mineralization until 1998. Raison et al. (1992), however, found that *Pinus radiata* growth increased with this initial increase in mineralization. *Picea glauca* at my sites did not show a growth response the first year of irrigation (Chapter II), it is therefore unlikely that mineralization increased during 1995, because spruce growth is N limited in my study area (Nams et al. 1993, Turkington et al. 1998). Von Lutzow et al. (1992) reported that microbial N and mineral NH_4^+ increased with irrigation in a *Picea abies* forest in Germany. However, this increase was offset by a decrease in mineral NO_3^-, hence resulting in no change in total mineral N.

Net N mineralization is often negatively affected by high humus C/N ratios (Fernandez et al. 2000, Prescott et al. 2000, Seneviratne 2000), and it is possible that a high C/N ratio in my humus samples prevented net NH_4^+ mineralization from increasing with irrigation. Net N mineralization follows from N in excess of the concurrent microbial immobilization (Richards 1987). In turn, microbial immobilization depends on the availability of chemical energy (largely carbon) in the humus, soil temperature, and moisture (Richards 1987). Microbial immobilization is mediated by those three parameters interactively: if carbon availability exceeds the carbon demand by microbes, N demand by microbes will be high. If carbon availability is low compared to the carbon demand, N demand will be lower. On the other hand, if carbon availability is high but climate restrains microbial metabolic activity, N demand will remain low (Richards 1987).

I therefore propose that the N immobilization and mineralization processes can be synthesized by the following hierarchical model (Figure 19): Microbial N demand or "potential immobilization" (point 4) is dictated by carbon availability (point 3) relative to microbial carbon demand (point 2), the latter of which is dictated by AET (point 1). In turn, the amount of N in the humus (point 5) relative to microbial N demand (point 4) dictates how much N is in excess and hence how much net N mineralization will occur (point 6).

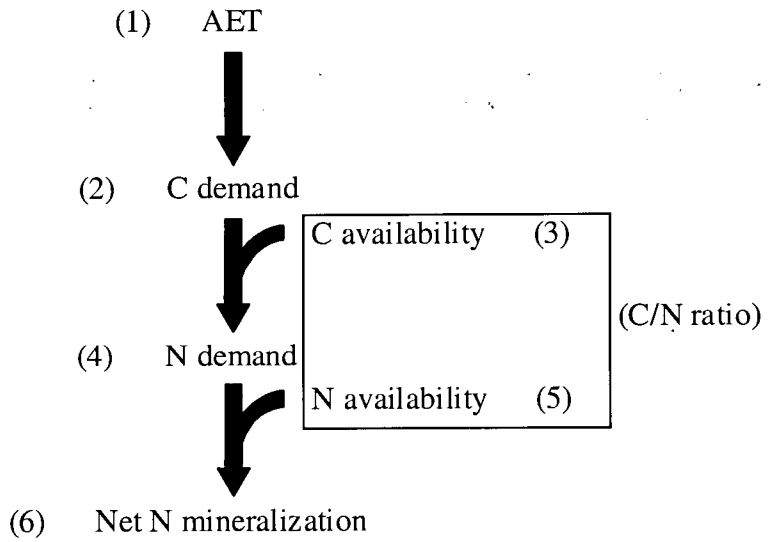

Figure 19: Proposed hierarchical model of factors limiting net N mineralization by soil microbes in the Kluane forest.

In agricultural systems, energy limitation in microbes usually does not occur when the C/N ratio of the substrate is above 20-30 (Richards 1987). A similar critical C/N ratio of 20-30 was documented for boreal forest sites in Alaska (Van Cleve et al. 1983), which is in the range for net N immobilization. I do not know the C/N ratio of the humus layer at my study sites (which are also dominated by white spruce), but the increase in net N immobilization and the lack of increase in mineralization suggest a similarly high C/N ratio.

The linear relationship between microbial NH_4^+ and AET cannot however be sustained indefinitely as AET increases, because energy for microbes is not inexhaustible. The energy supply must become limiting at some higher AET value, in turn causing NH_4^+ demand (and immobilization) to plateau (or even decrease) and hence potentially allowing net NH_4^+ mineralization to occur. Moreover, as the decomposition

of organic matter progresses, carbon is lost through microbial respiration (Richards 1987), and hence C/N ratios decrease (e.g. Vesterdal 1999). C/N ratios at my sites might also eventually decrease with larger amounts of irrigation and decomposition over a longer time span, and in turn lead to carbon limitation and enhanced net NH_4^+ mineralization. It is, however, not known how long this would take and over what AET values this would occur. Five years of irrigation (1995-1999) doubled rainfall amounts (Chapter II) but failed to trigger carbon limitation in microbes and a net increase in NH_4^+ mineralization.

My results first suggest that the seasonal and annual variation in microbial NH_4^+ immobilization in soils in the Kluane forest vary linearly with AET. However, further studies are required to verify whether this relationship applies to soils where the C/N ratio and the AET regimes differ from those in the Kluane forest. My results allow a further prediction: increased AET resulting from climate change at Kluane would stimulate in the short-term microbial NH_4^+ immobilization according to the above linear relationship, without any effect on NH_4^+ mineralization. Primary production is most often N limited in boreal forests, including Kluane (Nams et al. 1993, Turkington et al. 1998). Plants did not respond to irrigation (Chapter II), which is congruent with both the lack of enhanced NH_4^+ mineralization described above and with the importance of N limitation on plant growth at my study sites. This therefore suggests that the short-term response of this ecosystem to climate change may be an enhancement of soil CO_2 efflux associated with the enhancement of microbial activity. This conclusion is also supported by irrigation enhancing litter decomposition (Chapter III).

These reactions however, could be transient, not permanent. For example, Oechel et al. (2000) reported that although the first three decades of climate change in Alaskan tundra generated net CO_2 efflux through enhanced decomposition, this trend dampened after a fourth decade. This increased CO_2 sink activity was suspected to occur in response to an eventual increase in net N mineralization. I suggest that the results of Oechel et al. (2000) may occur when labile carbon sources are exhausted by decomposers, causing energy limitation, decreased N demand, and increased net N mineralization. How net N mineralization would respond at my sites in the long term requires further research. The spatial generality of my results, and the importance of the C/N ratio in mediating these effects also require further work.

Chapter V - Conclusion

5.1 - Kluane boreal forest community dynamics

In each of the chapters, I predicted and tested the reactions of different subsets of biotic and abiotic components of three dry, unproductive boreal forest stands to a doubling of summer rainfall over five years. In Chapter I, I reviewed effects of enhanced summer precipitation on biotic and abiotic forest ecosystem components. In Chapter II, I showed that in the Kluane boreal forest, neither plants, insects, nor voles responded to irrigation, but that mushroom biomass substantially increased. In Chapter III, foliage litter decomposition increased with the higher actual evaporation (AET) incurred through irrigation. Finally in Chapter IV, net microbial immobilization of nitrogen also increased with the higher AET incurred through irrigation, but concurrent net nitrogen mineralization remained unchanged. Here, I discuss the implications of those findings with respect to *i*) community dynamics of the Kluane boreal forest, and *ii*) global climate change.

Although vegetation biomass or growth often increases with a reduction of the water deficit (Chapters I and II), none of the plant species monitored responded to irrigation (Chapter II). The abundance of herbaceous vegetation (measured by % cover) in the Kluane area was also relatively invariant from 1990-1999 (Turkington et al. 2002), although baseline summer rainfall ranged from 52-177 mm during 1993-1999 (climate data for 1990-1992 unavailable) (Environment Canada 2002). Water availability therefore does not influence plant production in Kluane. Because the July average daily temperature varied from 12-14 ^{o}C during this period (Environment Canada 2002), the

above lack of change in plant cover (Turkington et al. 2002) also suggests that plant production in Kluane is not temperature limited during summer.

Conversely, experimental N addition in the Kluane forest generated rapid increases in biomass of several herbaceous, shrub, and tree species (Nams et al. 1993). Similarly, NPK addition in Kluane enhanced herbaceous vegetation total percent cover (John and Turkington 1995), and leaf length, number, and stem numbers in some species (John and Turkington 1997), as well as twig growth in shrubs and trees (Turkington et al. 1998). Hence nutrient mineralization and availability (especially N) limits plant production in Kluane.

However, net N mineralization did not respond to irrigation (Chapter IV), and by extension, should not respond to natural variations in rainfall amounts. Further, I also showed (Chapter IV) that net N mineralization was unaffected by differences in temperature or by differences in temperature and soil moisture (AET). Thus if net N mineralization limits plant production in Kluane but N mineralization does not respond to summer irrigation, rainfall, or temperature, plants therefore cannot react to these factors either.

In turn, the lack of increase in N mineralization with irrigation is a consequence of the response by soil microbes (decomposers). Either decomposers did not react to irrigation, or decomposers reacted by immobilizing N to a greater extent than they mineralized it – these hypotheses being mutually exclusive. My results reject the former and support the latter hypothesis. First, decomposition increased in the litter layer in response to the higher AET ensuing from irrigation (Chapter II). Second, decomposer activity in the humus layer under willow shrubs may have been also enhanced, as humus

mass under willows was reduced by irrigation (see Chapter III). Third, mushroom biomass increased by up to 700% with irrigation (Chapter II). Finally, N immobilization by soil microbes increased with the higher AET on the treatment grids as a result of irrigation (Chapter IV). Thus the unchanging plant production following the unchanging net N mineralization was due to an increase in net N immobilization by microbes in response to irrigation. Although gross N mineralization was presumably higher with irrigation because decomposition was greater, the supplemental N mineralized was taken up and immobilized by microbes.

Enhanced net N immobilization by microbes occurs under conditions of high chemical energy (carbon) availability for microbes relative to low N availability (i.e. high C/N ratio), if other factors such as temperature and moisture are not limiting. A C/N of greater than 20-30 (critical threshold) is typically necessary for such net N immobilization to occur (Richards 1987). The C/N ratio in boreal forest soils is typically in this range (e.g. 28, Van Cleve et al. 1983), and therefore the potential for immobilization is high if microbes are not limited by other factors. Although I did not monitor the C/N ratio of my humus samples, it was likely high, and was probably responsible for the enhanced net N immobilization. Therefore a high C/N ratio may have been responsible for the unchanging plant production in response to irrigation.

I expect that the C/N ratio of litter falling to the forest floor in Kluane is similar from year-to-year, as it is largely governed by plant species composition, which was stable (for herbaceous vegetation) from 1990-1999 (Turkington et al. 2002). If the C/N ratio is high, unchanging, and limits net N mineralization, net N mineralization should also be unchanging from year-to-year. Net mineralization in 1998, 1999, and 2000 was

indeed unchanging (Chapter IV). This therefore suggests that the vegetation, the C/N ratio, and net N mineralization, as well as the relationships between one-another, are inextricably linked and maybe unalterable.

If vole densities are limited by plant production, they should not vary from year-to-year as plant production seemingly does not change. Vole densities however decreased from approximately 30 per grid (20/ha) in 1998 to less than 10 per grid (6.7/ha) in 1999 (Chapter II), and hence fluctuations in vole numbers cannot be explained by plant production. Either plant (food) availability *per se* does not limit vole densities, or plant availability is not related to plant production. Rather than being controlled by food production, food-availability for voles could be controlled by direct exploitation competition with other, more dominant herbivores, such as snowshoe hares (*Lepus americanus*).

However, in a study in the Kluane forest spanning over 20 years, vole density peaks occurred independently from hare densities, although they did not occur during the hare peaks (Boutin et al. 1995), suggesting that voles are little affected by exploitation competition with hares except at hare peaks. Contrary to those observations, a vole peak however occurred in 1998 (Chapter II) simultaneously to the hare peak (Krebs unpublished), further rejecting the importance of exploitation competition with hares. Boonstra et al. (2001) reported no correlation between vole and hare densities over 23 years of censuses. Finally, hare exclusion experiments affected neither vole densities (Boonstra et al. 2001) nor the herbaceous vegetation (Turkington et al. 2002).

Apparent competition between voles and hares through shared predators such as coyotes (*Canis latrans*) could cause fluctuations in vole densities (Gilbert et al. 1986).

Vole densities in the Kluane forest were high in 1992, while hares were declining and their predators were still abundant, invalidating the apparent competition hypothesis (Boutin et al. 1995). Similarly, vole densities peaked in 1998 (Chapter II), simultaneously to the hare peak (2.78/ha), when predators such as coyotes and lynx (*Lynx canadensis*) were also at peak densities (Krebs unpublished).

Alternatively, snowshoe hares could affect soil nutrient availability for plants through their fecal pellets, and in turn this fertilization effect could affect food-availability for voles, especially berry crops (Boonstra et al. 2001). Hare densities in the Kluane forest ranged from 0.13 to 2.78 individuals/ha from 1990-1999, representing a 21-fold density increase from low to peak densities (Krebs unpublished). Pellet production by hares in the Kluane area averages 579 per hare per day (Hodges 1999), and pellet deposition/day/ha was therefore 75 at the hare low versus 1610 at the peak. However, the capacity of pellets to fertilize plants differentially according to hare densities depends on the C/N ratio of those pellets. Hare fecal pellets consist of digested plants (from which carbon has been used) which could therefore have a lower C/N ratio than that of undigested foliage litter. If the C/N ratio of pellets was below the critical 20-30 threshold, they could indeed enhance net N mineralization, plant growth, and vole densities.

Similar to the pellet fertilization hypothesis, 21-fold fluctuations in hare densities from 1990-1999 may have caused 21-fold fluctuations of urea input to the soil by hares. Larger amounts of urea input during hare peaks and hydrolyzed to NH_4^+ by soil microbes could also have enhanced N availability for plants.

However, the hypothesis of fluctuating N availability and hence plant production through fluctuating pellet or urea input over this 21-fold change in hare densities is not supported by the findings by Turkington et al. (2002). They found that herbaceous plant cover during the same interval was relatively constant. Fluctuations in hare densities and the concurrent deposition of pellets and urea had therefore seemingly no detectable effect on plant production as measured by % cover (Turkington et al. 2002). Boonstra et al. (2001) however suggested that berry production, which could influence vole densities, may be influenced by hare fertilization. Berry production was not specifically monitored by Turkington et al. (2002), and abundance of berries is not represented by measures of percent cover.

The hypotheses that hare pellet or urea input to the forest floor affect berry crops could be tested in small-scale experiments (< 10 x 10 m). I would first determine if hare pellets have a C/N ratio lower than 20-30 and have the potential to enhance net N mineralization. Secondly, pellet or urea input to the forest floor could be manipulated (e.g. 0, 50, 100% of maximum) to assess their effects on net N mineralization and berry production.

Boonstra et al. (2001) suggested that stochastic weather events favorable to high berry crops or high mushroom biomass may generate secondary vole peaks in addition to those occurring because of high fertilization following hare peaks. Table 10 below summarizes some trends in berry numbers, mushroom biomass, and vole densities from Chapter II.

Table 10: Summary trends in *Arctostaphylos uva-ursi* berry numbers, mushroom biomass, vole spring and fall minimum number known alive (MNA), for control grids, 1995-1999.

Parameter	1995	1996	1997	1998	1999
Berry numbers	medium	medium	low	high	medium
Mushroom biomass	low	medium	high	none	medium
Vole spring MNA	none	low	medium	high	n/a
Vole fall MNA	low	low	medium	high	low

In 1997 berry production was low, while the next year's vole densities were high. Reciprocally, in 1998 berry numbers were high but the next year's vole densities were low. Berry production in *A. uva-ursi* therefore does not seem to drive vole densities. I could not reject the hypothesis that other berry species may have caused fluctuating vole densities.

In contrast, low vole numbers often roughly coincided with low mushroom biomass on the control grids during the previous year. For example, 1995 and 1998 had low mushroom production, and in 1996 and in 1999, voles were low. In 1996, mushrooms were of medium abundance, and voles too were in medium abundance the next year (1997). Mushroom abundance was high in 1997 and voles numbers were high in 1998. However, two problems arise here: First, mushroom biomass was overall 250% higher on irrigated grids compared to controls (Chapter II). Why then did vole densities not increase with irrigation if vole densities are affected by mushroom biomass? Second, why were vole densities higher in 1999 following the year where mushrooms were absent

(1998) comparatively to 1996 which followed a year of better (although low) mushroom production? I did not differentiate species of mushrooms in this study, and it is possible that the biomass of nutritionally important mushroom species for voles was independent of the total mushroom biomass. Perhaps irrigation enhanced the biomass of mushroom species unimportant for voles.

Hence, according to my results, neither rainfall, plant growth, berry production, nor mushroom production can satisfactorily explain vole density fluctuations. Similarly, neither exploitation competition nor apparent competition with hares through shared predators convincingly explains variation in vole densities.

My results, however, reveal that net N mineralization and plant production in the Kluane area are unrelated to either rainfall, temperature, or AET. On the other hand, both decomposition and net N immobilization are strongly linked to AET. Soil microbes in Kluane therefore react very readily to variations in AET by enhancing decomposition and N immobilization. As a result, they prevent net N mineralization and plant production from responding to AET.

5.2 - Global climate change

My irrigation experiments not only clarified some effects of climate conditions on the community dynamics of the Kluane boreal forest, but provide further experimental evidence on how boreal forests may react to climate change. I have shown in Chapter II that plants did not respond to five years of irrigation simulating a doubling of summer precipitation. I have shown in Chapter III that litter decomposition increased with irrigation, and that humus under willows also seemingly decomposed faster. Finally in

Chapter IV, I demonstrated that net N mineralization did not react to irrigation, but that N immobilization by soil microbes increased with irrigation.

It is not known to what extent other boreal forests would react similarly to the Kluane forest to variations in summer precipitation. If a substantial portion of the 12 million km^2 (Lieth 1975) worldwide boreal forests reacts similarly to the Kluane boreal forest, my results support the notion that a positive feedback will occur between climate change and boreal forest ecosystems (*sensu* Houghton et al. 2001). In response to climate change, soil decomposition in boreal forests may increase more than plant photosynthesis, and therefore reduce the carbon (hereafter C) storage capacity of this ecosystem. This would result in enhanced atmospheric CO_2 concentrations. Such a reaction could strongly exacerbate climate change, especially since boreal forest soils contain 1.78×10^{11} tonnes of organic C (Zinke et al. 1984), which is among the largest global soil C reservoirs.

The response of microbes to irrigation is also consistent with the hypothesis of a positive feedback between climate change and boreal forest C dynamics. My experiments lasted for only five summers, and therefore cannot be extrapolated to the longer-term reactions of the boreal forest biome to climate change. In the Alaskan tundra, ecosystem total carbon storage progressively decreased during the first few decades of climate change, and increased during the later decades, although it remained lower than that prior to climate change conditions (Oechel et al. 2000).

Temperature manipulations would also be informative regarding the effects of climate change on the Kluane forest ecosystem. However, baseline year-to-year temperature fluctuated during my experiments (1993-1999 July average temperature 12-

14 °C, Environment Canada 2002), without causing changes in net N mineralization (and N availability for plants). This suggests that increased summer temperature in the Kluane forest may not affect plant growth or biomass greatly, and that my conclusions are robust to temperature variations. Decomposition and N immobilization were strongly correlated to AET (which expresses both temperature and moisture availability) and therefore those relationships also may be robust to increased summer temperature, although this too needs further evaluation.

Accurate measures of the effects of climate change on the carbon storage capacity of this ecosystem, and more particularly of its soils, requires further research. This would allow the positive feedback between climate change and boreal forest C dynamics to be measured, and would provide empirical estimates with which to parameterize climate change projections.

5.3 - Further improvements

Some of experiments above could have been performed differently to further improve the accuracy of some of my findings regarding the effects of rainfall on this ecosystem, more specifically with regards to the soil, the mushrooms, and the spruce trees.

Because of the high heat capacity of water, the addition of water through irrigation may also have had the undesirable effect of reducing soil temperature as compared to the soil of the control grids. The irrigated soil could take longer to warm up during warm days compared to the controls, and the increase in AET occurring on the irrigated sites could mean a greater soil heat loss to the atmosphere. To what measure the

reactions (or absence of reactions) in decomposition, NH_4^+ mineralization and immobilization, and plant growth were affected by this potential reduction of soil temperature is not known. It would have been desirable to monitor daily soil temperatures on all grids for the entire duration of this study in order to test whether the irrigation treatment had an effect on soil temperature, and whether this had further effects on decomposition, NH_4^+, and plants.

The Thornthwaite and Mather (1957) water balance and AET computation method used here was based on average daily air temperature, precipitation (and irrigation), and an assumed soil water holding capacity of 300 mm. That method has many advantages, including its relative computation simplicity, its being based on simple and readily available meteorological data, and its concept based on the soil water budget, inclusive of water gains (precipitation), losses (runoff and AET), and their impact on soil water reserves. There are however a few disadvantages to this computation method. Air temperature, although strongly affecting soil temperature, may not be completely representative of soil temperature. The amplitude of fluctuations in air temperature is notoriously greater than that of soil temperature, and soil temperature is typically lower than air temperature during the growing season. Although the correlations between both litter decomposition and microbial NH_4^+ immobilization and AET were highly significant and of high r^2 (0.90, and 0.65, respectively), *in situ* measurements of soil temperature and moisture might have further improved those fits. Similarly, water budget computations in relation to decomposition in forest ecosystems is usually based on the assumption that the water holding capacity of the root zone is of 300 mm (e.g. Meentemeyer 1978, Aerts 1997), and I also followed that standard assumption. Neither the depth of the root zone

nor its water holding capacity were determined in this study, and it is therefore not known how the *in situ* soil water holding capacity compares to 300 mm. If it differs substantially from 300 mm, the accuracy of my AET calculations would substantially improve from using the *in situ* water holding capacity. I however tested the effect of assuming a soil water holding capacity of 300 mm by recalculating AET accordingly to soil water holding capacities of 100, 150, or 250 mm. Soil water holding capacity had little effect on the overall patterns of AET, except that using lower values of soil water holding capacity generated slightly lower AET values. Because cumulative AET increases with cumulative time, I also tested how litter weight loss was correlated with time. Decomposition was significantly correlated with time in both willow leaves and spruce needles, but in willow leaves, the correlation between weight loss and AET was several orders of magnitudes more significant than that with time, revealing that AET was a better predictor of decomposition than time. In spruce needles, the correlations between weight loss with either time or AET were similarly significant, because only two sampling periods (sampling times) occurred in those litterbag experiments, hence making it harder to differentiate time from AET effects. In this case, a longer study including a greater number of sampling times, and several times each year, would have been beneficial.

A last issue regarding the soil regards the nitrogen budget. The understanding of the effects of irrigation on the Kluane forests' whole N budget would benefit from monitoring in greater depth the dynamics of NH_4^+, NO_3^-, NO_2^-, and N_2 (denitrification). Although NH_4^+ is thought to be the most significant N source for forest plants while other N sources such as NO_3^- are though to usually play little role in such ecosystems, analyses

using nitrogen tracers and stable isotopes in the soil, the microbes, and the plants would better ascertain our understanding of N dynamics in this forest.

Mushroom biomass in this study should have been monitored on a species-specific basis. This would have allowed to better discriminate the irrigation effects on saprophytic mushroom, who obtain organic carbon by decomposing dead organic matter in the soil, and non-saprophytic mushroom species who obtain photosynthates from live plants, which could be relevant to the carbon budget of this forest. Mushroom species-identification is often difficult, and it would have been extremely difficult to identify all species and determine their biomass species-specifically. As only the total mushroom biomass was determined, I do not know whether mushroom species used carbon from dead organic matter in the soil, or photosynthates from live plants. This represents a problem in accurately determining the effect of irrigation on the carbon budget of this forest.

Similarly, the herb layer biomass or height measurements, and spruce tree twig growth herein may not completely accurately represent total plant biomass, plant CO_2 uptake, and plant photosynthesis, which would be relevant to the understanding of the effects of rainfall on the carbon budget of this forest. Total plant biomass measurements, inclusive of root mass for all species inclusive of spruce trees would yield more robust estimates of plant reactions (or lack of) to increased rainfall. Other methods that could yield more information on those potential reactions include estimating the effect of increased rainfall on leaf area index, on a species-specific basis. Spruce-tree reaction to irrigation could also be more robustly determined using growth increments in tree trunk cores. Similarly, this study would have gained robustness by determining the effect of

rainfall on photosynthesis itself, by monitoring CO_2 intake using tracers, and it could be tested whether or not the irrigation water was used by trees by measuring stomatal conductance, stem water saturation or turgor (daily cycle of stem diameter change), or needle water potential. The effect of irrigation on litterfall mass and on litterfall chemistry would also further provide valuable information regarding the effects of increased rainfall on the carbon budget of this ecosystem.

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