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ECOSYSTEMS

Impacts of Elevated Carbon Dioxide and Temperature on a Boreal Forest Ecosystem (CLIMEX Project)

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ABSTRACT

To evaluate the effects of climate change on boreal forest ecosystems, both atmospheric CO_2 (to 560 ppmv) and air temperature (by 3°–5°C above ambient) were increased at a forested headwater catchment in southern Norway. The entire catchment (860 m^2) is enclosed within a transparent greenhouse, and the upper 20% of the catchment area is partitioned such that it receives no climate treatment and serves as an untreated control. Both the control and treatment areas inside the greenhouse receive deacidified rain. Within 3 years, soil nitrogen (N) mineralization has increased and the growing season has been prolonged relative to the control area. This has helped to sustain an increase in plant growth relative to the control and has also promoted increased N export in stream water. Photosynthetic capacity and carbon–nitrogen ratio of new leaves of most plant species did not change. While the ecosystem now loses N, the long-term fate of soil N is a key uncertainty in predicting the future response of boreal ecosystems to climate change.

Key words: climate change; boreal forest; greenhouse; catchment; vegetation; soil; water; temperature; carbon dioxide.

INTRODUCTION

Rising atmospheric carbon dioxide (CO_2) concentrations and associated climate warming could strongly impact terrestrial ecosystems (Houghton and others 1995). Ecological effects are difficult to predict because (a) plant responses vary with species (Beerling and others 1996), (b) extrapolations from pot experiments are uncertain because of artificial conditions (Arp 1991) and lack of interactions with other organisms and ecosystem compartments, and (c) individual processes in the ecosystem biogeochemistry may oppose each other. Pools of carbon (C) and nitrogen (N) in boreal soils are large, and increases in global temperature are expected to be largest at high latitudes, so boreal ecosystems may be particularly sensitive to climate change (Shaver and others 1992; Steffen and others 1992; Pastor 1996). In situ whole-ecosystem experiments provide a powerful tool to evaluate ecosystem response and to test whole-ecosystem biogeochemical models (Carpenter and others 1995) and global dynamic vegetation models (Beerling and others 1997).

The CLIMEX (*clim*ate change *ex*periment) project is an international, multidisciplinary project designed to assess the potential impacts of increased

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CO_2 and temperature on forest ecosystems (Jenkins and others 1992; Dise and Jenkins 1995). CLIMEX is the world's only catchment-scale experiment to date in which both CO_2 and temperature are manipulated. CLIMEX began in 1992, using the former RAIN (Reverse Acidification in Norway) project catchments (Wright and others 1993) at Risdalsheia near Grimstad, Norway. From April 1994, CO_2 was increased to 560 ppmv and air temperature was increased by 3°–5°C above ambient at the KIM catchment contained within a 1200-m^2 transparent greenhouse. This level of CO_2 and temperature is in line with predictions from global circulation models (GCMs) for the middle of the next century at 60°N latitude (Houghton and others 1995; Sellers and others 1996). The ecosystem response to treatment has been followed through individual studies of leaf gas exchange, plant growth and nutrient content, litter decomposition, mineralization of soil N, soil water chemistry, soil water dynamics, and catchment output fluxes of water and chemicals. Here we present an overview of the integrated ecosystem response to 3 years of experimental treatment.

Site Description

The CLIMEX catchments (58°23′N, 8°19′E) are 300 m above sea level and are located at the southern limit of the boreal forest zone. The climate is maritime, with mean annual precipitation of 1400 mm, of which approximately 1200 mm comprises stream runoff. Mean annual temperature is approximately 5°C, with a strong seasonal variation; mean temperature is −3°C in January and 16°C in July. Vegetation comprises mainly a sparse cover of pine (*Pinus sylvestris*) and birch (*Betula pubescens*), with heather (*Calluna vulgaris*) and blueberry (*Vaccinium myrtillus* and *V. vitus ideaii*) as the dominant ground cover. Bedrock comprises biotite granite, and this is covered by thin (average depth, 10 cm) and patchy podsolic and peaty soils characterized by organic C content of 4%–20%, average pH of 4.0, and base saturation of less than 20% (Dise and Jenkins 1995). About 50% of the catchment is bare rock. Although most boreal forests have deeper soils and denser tree canopies, the CLIMEX site is typical of most boreal ecosystems in terms of climate, the dominance of evergreen coniferous trees, and the presence of acidic podsolic organic-rich soils.

Experimental Design

The experimental design of CLIMEX was largely governed by the major objective of manipulating both atmospheric CO_2 concentrations and ambient air temperatures in whole undisturbed forests at the catchment scale. Due to logistical and financial restraints, this meant no replication of treatments and no separate temperature and CO_2 treatments. The experimental design thus does not enable separation of the effects of CO_2 or temperature alone. On the other hand, to date there is no other experiment that combines CO_2 and temperature manipulation at the catchment and whole-forest scale.

CLIMEX made use of the preexisting facilities of the RAIN project, which included three catchments that had been monitored since 1984, two of which were covered by transparent roofs without walls (Wright and others 1993). At the catchment scale, the effects of the CLIMEX treatments at KIM catchment are thus evaluated primarily by comparing 11 years of pretreatment with 3 years of treatment.

KIM catchment is 860-m^2 and is completely covered by a 1200-m^2 transparent roof (Wright and others 1993). Manipulation of the precipitation (termed *clean* precipitation) at KIM catchment began in June 1984 and has continued uninterrupted to date. Incoming precipitation is collected from the roof by gutters, led to storage tanks, filtered, passed through a mixed-bed ion-exchange resin, dosed with natural levels of sea salts (at about 1:8000 during summer and 1:5000 in winter), and automatically distributed back under the roof through a sprinkler system. During the winter, the sprinkling system is not operated and, from 1984 to 1993, snow was made with commercial snowmaking equipment using water from a nearby lake that was ion exchanged and with sea salts re-added. At all times, care was taken to avoid disturbance of the vegetation and soil within the catchment.

In the winter of 1993–94, the catchment was further modified for the CLIMEX project (Dise and Jenkins 1995). The KIM catchment was completely enclosed with airtight transparent walls (Figure 1). Snowmaking was then technically not feasible, and precipitation falling as snow outside was delivered as rain under the roof by the sprinkling system. The enclosure is divided by a transparent wall such that the uppermost 20% of the catchment (KIM-c) receives the clean rain treatment only, with no increase in CO_2 or temperature. The remaining 80% of the catchment (KIM-t) receives higher atmospheric CO_2 concentrations and ambient air temperatures, as well as clean rain. KIM-c serves as the control area for plant and soil studies, which are conducted on small replicated plots of about 4 m^2. Runoff from KIM-c flows into KIM-t.

Carbon dioxide is added to the air at six points inside the treatment section. The target concentration is 560 ppmv during the growing season, opera-

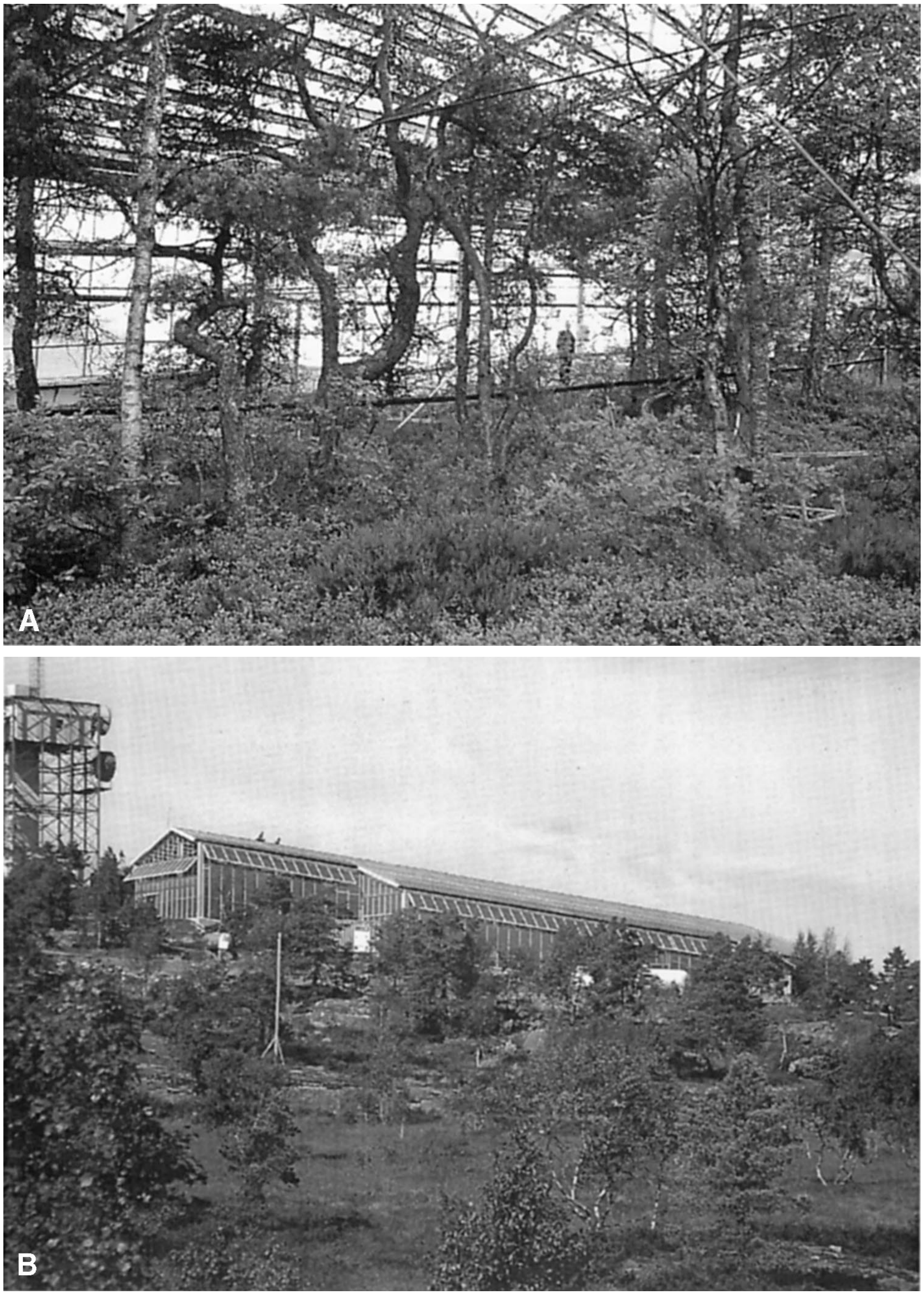


Figure 1. The greenhouse A covering an 860-m^2 natural headwater KIM catchment B at Risdalsheia, Norway.

tionally defined as 1 April–31 October (Figure 2). Difficulties with the dosing and control system during year 1 were remedied by year 2. Measurements are made every 15 min from air taken at six points and determined by infrared analyzer. Maximum dosing rate is 55 kg h^{-1} (1.3 tons day^{-1}). Carbon dioxide added is about 100 metric tons $year^{-1}$.

The air is warmed in KIM-t by a central electric heating system that operates at a maximum of 60°C and consists of three ranks of 6-cm-diameter steel pipes mounted on the inside of the surrounding walls. Air temperature is monitored continuously at six points in KIM-t and two points in KIM-c. The target is +5°C above KIM-c in January and +3°C in July, with linear interpolation in between (Figure 2).

Air is mixed by means of six large fans mounted in the roof of KIM-t and two in KIM-c. Each fan has a maximum circulation capacity of 1000 m^3 h^{-1}; fan

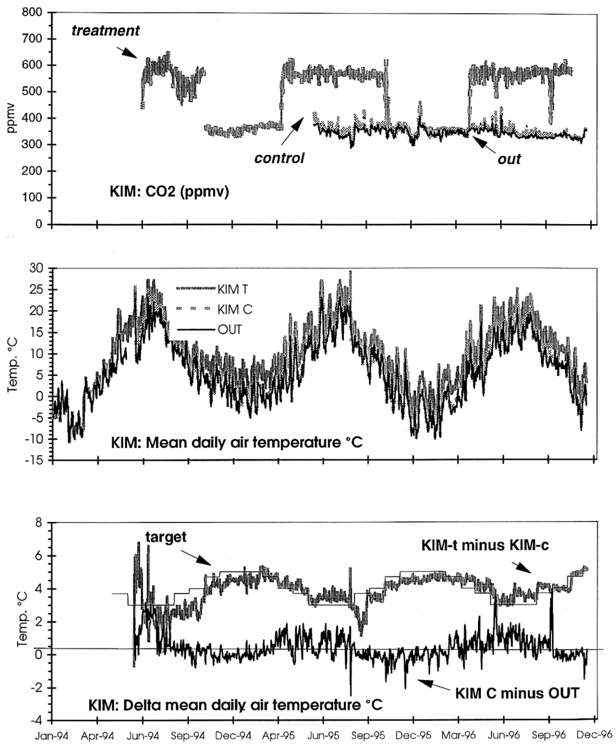


Figure 2. Mean daily CO_2 concentration (ppmv) and air temperature (°C) during the 3 years of CLIMEX treatment at KIM. KIM-t, KIM-c, and outside ambient levels are shown. Carbon dioxide measurements began in June 1994 in KIM-t and in June 1995 in KIM-c and outside.

speed is adjusted continuously to maintain an even temperature within each section. Ventilation (cooling) is by means of windows mounted along the entire length of the four sides of the structure. The CO_2 and difference in temperature "climate" of KIM-t is continuously monitored and controlled automatically by a central computer that adjusts the CO_2 dosing, heating, ventilation, and fan speeds in real time to achieve the targets.

The roof structure modifies climatic and physical conditions. The most important differences are (a) a 45% reduction in light in the photosynthetically active region, (b) a significant decrease in mean wind speed, (c) exclusion of dew and hoarfrost, (d) change in intensity and duration of rainfall, and (e) the substitution of rain for snow. Thus, the comparison of KIM-t with KIM-c, and of pretreatment with treatment data from KIM-t, gives the best indication of changes caused by the CO_2 and temperature manipulation.

Measurements of soil and vegetation are carried out on five replicate plots and individual plants in the control area (KIM-c), the treatment area (KIM-t), and a nearby open reference catchment (METTE). To enable a comparison of pretreatment with posttreatment data, measurements were initiated 1 year prior to the start of treatment.

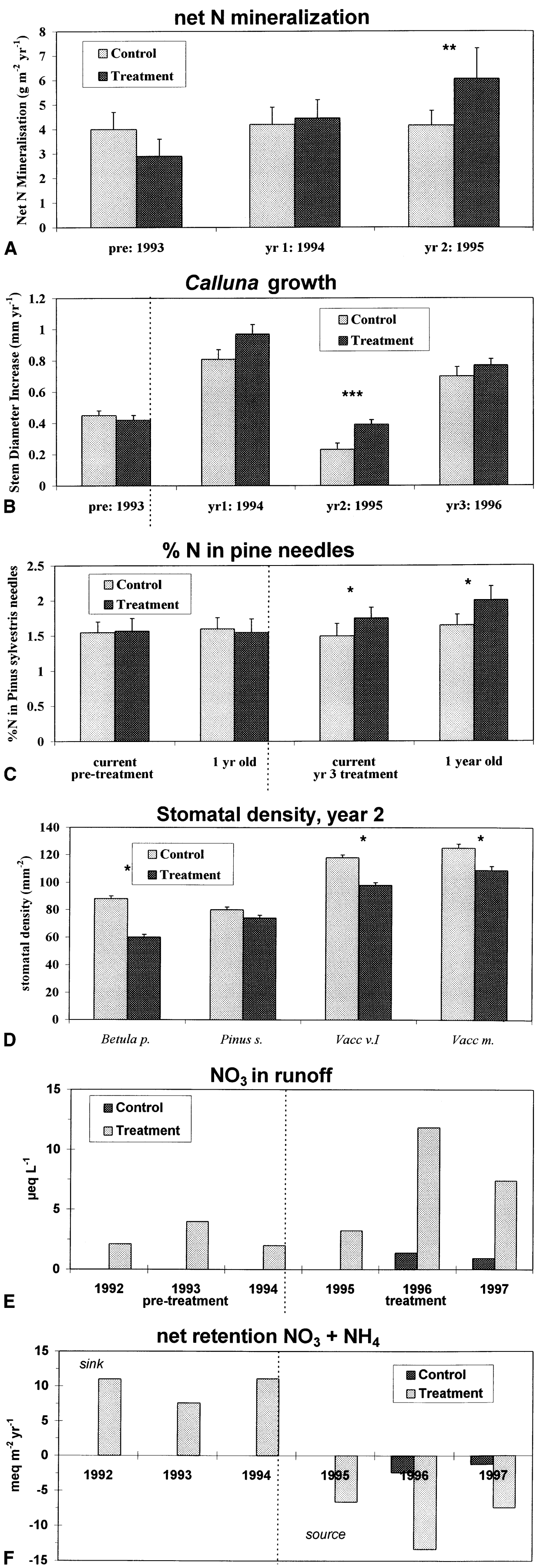
Soil N mineralization was measured at 10-cm depth intervals in 10-fold replicated incubation tubes (Raison and others 1987) under both dominant ground vegetation species during consecutive 3- to 4-month periods. Growth of *Calluna* and *Vaccinium* was estimated in replicated sets of five plots (4 m^2) from changes in diameter and length of differently aged stem sections (*Calluna* and *Vaccinium*) and the number of leaves of five marked shoots (*Vaccinium*) at four times in the growing season. Two 4-year-old shoots per plot were harvested to test for linear relationships between stem diameter and biomass, as well as for C and N analysis. All sampling and analytical procedures are fully described by Dise and Jenkins (1995).

Results and Discussion

At KIM-t, annual mean net soil N mineralization at 0- to 10-cm depth increased significantly (t test, $P < 0.01$) under *Calluna* and *Vaccinium* from 3 and 4 g m^{-2}, respectively, before treatment to almost 6 g m^{-2} in 1996 (Figure 3A). There were no significant changes in KIM-c (Figure 3A) or in METTE. Increased N mineralization in KIM-t is most likely caused by elevated soil temperatures, which were 2.6°C (at 5-cm depth) higher in KIM-t than in KIM-c during 1996. No change in soil moisture regimen has been detected in either KIM-t or KIM-c. Similar changes in N mineralization occurred as a result of soil warming by electric cables at the adjacent EGIL catchment (Verburg and others forthcoming).

Growth of *Calluna* in KIM-t was greater than in KIM-c (Figure 3B). During year 3, the growth was less than in the other 2 years in part as a result of a strong infestation by the heather beetle (*Lochmaea suturalis*) in KIM-t. While *Lochmaea* was present in the surrounding area and in KIM-c, an outbreak (80% of the plants affected) occurred only in KIM-t. The *Lochmaea* outbreak may be linked with an increase in N content of the host plants (Brunsting and Heil 1985). However, the N content of *Calluna* in KIM-t in 1996 was lower than in previous years and not different from KIM-c. This suggests that the higher temperature in KIM-t may be the factor responsible for the greater survival of *Lochmaea*. These often unpredictable effects of climate change on natural ecosystems can have a significant impact and point to the need for whole-ecosystem experiments.

Vaccinium biomass also increased in both years, with greater stem-diameter growth and more leaves on first-year branches. Increased growth of dwarf



shrubs could be attributed in part to an extension of the growing season by about 3 weeks in KIM-t compared with KIM-c, as a result of the increased temperature.

In KIM-t, the carbon–nitrogen (C/N) ratio of young (green) and older stems of *Calluna* or *Vaccinium* shoots and of litter produced during the treatment period remained at pretreatment levels, while N content in pine needles (Figure 3C) and litter, as well as in birch leaves and litter, increased significantly. The constant or increasing N content of plants, in spite of elevated CO_2, probably reflects the increased N availability in the soil in KIM-t. In experiments with only increased CO_2, the N content of leaves and litter often decreases (O'Neill and Norby 1996).

Litterbag studies (mesh size, 1.5 mm; 10 replicates, retrieved half-yearly) with *Betula* and *Calluna* litter incubated in KIM-c, KIM-t, and METTE have so far revealed no change in decomposition rates of litter grown at high CO_2. In contrast, CO_2-only experiments indicate that litter with lower N content decomposes more slowly (Cotrufo and Ineson 1996; Coûteaux and others 1996).

Photosynthetic capacity of *Vaccinium*, *Betula*, and *Pinus*, as indicated by CO_2 assimilation curves, showed no marked changes after 3 years of exposure to elevated CO_2 and temperature (Beerling forthcoming). This is consistent with little or no change in C/N ratios of foliage. Leaf stomatal densities (density of stomatal pores per unit area of leaf surface) were reduced significantly in three of the four species studied (Figure 3D). Reduced stomatal densities of *Vaccinium* leaves were paralleled by significant reductions in stomatal index (number of stomata cells as a proportion of epidermal cells per unit leaf area). Stable C-isotope measurements,

Figure 3. Effects of elevated CO_2 and temperature on the biology and biogeochemistry of the manipulated ecosystem (KIM-t) relative to the control (KIM-c) and pretreatment relative to treatment years. Shaded columns represent pretreatment or control (KIM-c) data, and black columns the treatment (KIM-t) data. Error bars represent standard errors; significant differences between adjacent bars are indicated as * ($P < 0.05$), ** ($P < 0.01$), or *** ($P < 0.001$); A net soil N mineralization under *Calluna*; B growth of *Calluna* as mass fraction (%) of initial standing biomass in each growing season; C N content in current and 1-year-old needles of *Pinus sylvestris*; D stomatal density of leaves of dominant tree species and two species of *Vaccinium*; E volume-weighted mean concentrations of nitrate in runoff collected weekly; F ecosystem net retention (deposition minus runoff) of inorganic N. *Betula p.*, *Betula pubescens*; *Vacc. v. i.*, *Vaccinium vitus ideai; Vacc. m.*, *Vaccinium myrtillus.*

made after accounting for the isotopic composition of the source CO_2 (Beerling 1997), indicated that all four major tree and shrub species had higher leaf water use efficiency (WUE, amount of C fixed per unit time/amount of water lost per unit time) in KIM-t relative to KIM-c, after 3 years of treatment (Beerling forthcoming). Randomized intervention analysis made on the periodic instantaneous leaf gas exchange measurement between 1993 and 1996 indicated that this response was brought about through increased photosynthetic rates in *Pinus* and by decreased leaf stomatal conductance to water vapor in *Betula* and *Vaccinium* (Beerling forthcoming). Because the low rainfall intensity inside the greenhouse promotes maximum interception loss, direct extrapolation to the hydrological response of natural systems is problematic.

Concentrations of NO_3 and NH_4 in runoff at KIM-t increased relative to pretreatment levels despite lower N deposition due to exclusion of most dry deposition by the glasshouse (Figure 3E). Concentrations were higher from KIM-t relative to KIM-c (Wright 1998). The flux of inorganic N in runoff increased from 0.06 g m^{-2} $year^{-1}$ in the 3 years prior to treatment to 0.13 g m^{-2} $year^{-1}$ in the 3 years of treatment. The flux of organic N was about 0.3 m^{-2} $year^{-1}$ and did not change significantly. A similar increase in flux and concentrations of inorganic N also occurred at the soil-warming experiment at EGIL catchment (Lükewille and Wright 1997). The increased loss of inorganic N in runoff represents only about 10% of the estimated increase in net mineralization of N in the soil. As denitrification is probably negligible, the remaining 90% of the increased N supply must go to increased growth and biomass of vegetation and immobilization in the soil.

Increased growth cannot exceed the product of the mean N content of the annual biomass increment (about 1%) and the increased N availability (equals increased net N mineralization minus increased leaching losses). In this case, this amounts to about 100 g dry matter per g N * 2.5 g N per m^2 $year^{-1}$ = 250 g dry weight (DW) per m^2 $year^{-1}$. This is consistent with the fact that, 2 years after the start of the treatment, understory biomass (which makes up roughly half of the biomass in these ecosystems) was about 125 g DW per m^2 greater in KIM-t than in KIM-c. These values are per square meter of soil cover. About 50% of the catchment is bare rock.

These results may have been influenced by reduced light in the greenhouse structure (McKane and others 1997). Light is reduced by 45% in KIM-c and KIM-t compared with outside ambient conditions. The Nitrogen Isotope and Carbon Cycling in Coniferous Ecosystems (NICCCE) model (Van Dam and van Breemen 1995) has been calibrated for steady-state conditions at KIM-c and reproduces the essential features of the response in KIM-t (increases in soil N availability, plant biomass, and leaf N content, and net losses of N from the ecosystem) under reduced light. For full-light conditions, the NICCCE predicts a greater increase in biomass. Regardless of light level, however, the model predicts that N is transferred from the soil to the vegetation, as observed experimentally.

CONCLUSIONS

The results suggest that in a boreal forested ecosystem subjected to conditions of combined increased CO_2 and temperature, (a) mineralization rates of soil organic matter increase, leading to (b) increased N availability in soils and increased inorganic N in runoff. Increased N availability helps to sustain increased plant growth. In addition, plant water-use efficiency is significantly increased. There is no evidence of change in decomposability of newly formed plant litter. Over the longer term, increased availability of N may lead to a shift in plant species adapted to higher soil N levels. The fraction of the extra mineralized N that ends up in runoff is small, but comprises a doubling in nitrate concentrations. If nitrate in runoff were to increase due to climatic change, this might exacerbate acidification of surface waters (Wright and Schindler 1996) and cause nutrient imbalance and other undesirable effects in coastal marine waters (Fleischer and Hamrin 1988; Fisher and Oppenheimer 1991).

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